Chapter 5

Minor groups and fossils

This chapter consists of many sections dealing with a great variety of taxa. Some taxa contain few parasites that have been little studied, others contain parasites with well-known and fascinating adaptations to a parasitic way of life. The approach chosen by different authors reflects this diversity: some sections out of necessity contain brief descriptions of morphological characters, others go into great detail in discussing behavioural adaptations, complex life cycles or epidemiological patterns.

Parasitism is a very ancient way of life, but few parasite fossils are known because most parasites are small and soft-bodied and do not easily fossilise. Most evidence is indirect, based on galls, cysts and drill holes interpreted as resulting from parasite activity. Nevertheless, some parasites have fossilised, including larval pentastomids and crustaceans. The section on fossil parasites in this Chapter covers the literature up to 2003.

By far most parasitic species belong to a few phyla, such as various protistans, Myxozoa, Crustacea, Platyhelminthes and Nematoda. However, in addition, some small phyla consist entirely of parasites, and many phyla contain at least some parasite species. Such groups are discussed in this Chapter. Small groups consisting entirely of parasites at least during part of their life cycle are the Mesozoa, Myzostomida, Nematomorpha, Pycnogonida (possibly with a few non-parasitic species), and Pentastomida. Of these, the mesozoaans, myzostomids and pycnogonids are entirely marine, whereas the nematomorphs and pentastomids are predominantly terrestrial/freshwater parasites, only a few being found in the marine environment. Groups including at least some parasitic species are the sponges, cnidarians, ctenophores, polychaetes, leeches, nemerteans, rotifers (and Seison, long thought to be a rotifer), mites and ticks, insects, tardigrades, molluscs, echiurans, echinoderms and vertebrates. A fascinating phylum described only recently is the Cycliophora. Cycliophorans are probably ectocommensals rather than genuine parasites, living on the lip of lobsters. Like many genuine parasites restricted to specific hosts and microhabitats, they have an extremely complicated life cycle that ensures production of a huge number of offspring, necessary to guarantee infection of the very narrow microhabitat on one particular host species.

Many of the minor groups discussed in this Chapter, because of the few species involved and low prevalences and intensities of infection, are neither ecologically nor economically important. However, some include species of some significance. Parasitic sponges damage cultured oysters, and may be the most destructive organisms responsible for bioerosion of coral reefs. The parasitic hydrozoan Polypodium is the only intracellular metazoan parasite, it has a negative impact on caviar and the reproductive capacity of sturgeon. Some polychaetes are important pests in mollusc cultures, and marine leeches may be vectors of blood protistans transmitted to fish. Nemerteans may be important parasites (or perhaps predators) feeding on the eggs of
crabs, which makes them useful for controlling crab pests; and although there is no evidence that mites inflict damage on their invertebrate hosts, mites and ticks may cause severe damage including death to birds, either directly or, in the case of ticks, by transmitting disease agents. Larval pycnogonids may destroy bryozoan and hydrozoan colonies partly or entirely. Chewing lice may transmit parasites to seals, and it seems likely that fleas may be important in causing nesting mortality in marine birds.

Other groups are of great biological interest because of their unique and often mysterious adaptations. Thus, mesozoans have unique morphology and their life cycles are largely unknown; the best known of the few parasitic marine tardigrades has two types of males, including one of dwarf size. Transmission of the only marine pentastomid has not been clarified; parasitic molluscs have an extraordinary reduction in morphological complexity, some resembling worms rather than molluscs. Echiurans have extreme sexual dimorphism: the dwarf male parasitising the much larger female. The reader may be surprised to find that quite a few fish are genuine parasites. Parasitic fish are often ignored in discussions of parasitism, but they have ingenious adaptations to their way of life, which makes the section dealing with them so fascinating.

**Fossil parasites**

Greg W Rouse

**Introduction**

The broad range of Metazoa was clearly established by the Cambrian period, more than 500 million years ago. Given the present-day assortment of parasites across this assemblage, it is reasonable to assume a great diversity of parasites, similar to that of today, has been present for hundreds of millions of years. While this inference may be justifiable, and is well supported by the fossil record of Metazoa, direct fossil evidence of parasitism is poor and is likely to remain so. Most contemporary parasites are soft-bodied and they are furthermore associated with soft tissues that are unlikely to fossilise (Conway Morris 1990), and this is likely to have been the situation for most parasites. Therefore, the best chance of detecting parasitism via the fossil record is through indirect evidence such as cysts, galls or drill holes left on the host’s skeleton or shell. Thus, there is a bias, with a few taxonomic groups (e.g. echinoderms) preserving parasite activity better than others. There are only a few exceptional cases of marine parasites where there has been direct fossilisation. The paucity of data on fossil parasites means that few studies have dealt with evolution of parasites and parasite–host interactions, and the ecological impact of parasitism on fossil communities. However, Gahn and Baumiller (2003) and Littlewood and Donovan (2003) point to new developments in these areas.

**Indirect fossil evidence**

Although there may be little direct evidence of parasites, the existence of those that had hosts with hard skeletons can often be inferred. This may be in the responses of the host’s skeleton and there is clear evidence of such parasitism on groups such as bivalves, crustaceans and echinoderms. Many papers concerning traces of fossil parasite activities are rather speculative, however, particularly when concerning the parasite’s identity. A thorough and critical review of the existing literature is needed.

Bivalves are often the intermediate host for digeneans and cestodes, and the metacercariae of the former and metacestodes of the latter have been implicated in causing pearl formation. Littlewood and Donovan (2003) surveyed current bivalve diversity and the incidence of pearl formation and contemporary digenean parasitism. Their study suggests that the occurrence of fossil pearls back to the Triassic period may reflect a long history of parasitism on bivalves by Digenea, even though there is little direct evidence for this. Drill holes in the valves of bivalves
Minor groups and fossils

and brachiopods have been documented from at least the Permian period and while many of these represent predation, it is possible that some are parasitic (Kowalewski et al. 2000). Some fossilised crabs from the Jurassic period have swellings evident in the branchial region that have been inferred to represent parasitism by epicarid isopods (Radwanski 1972). Feminisation of fossil xanthid crabs from the Miocene epoch has been found by Feldmann (1998) who argued that this represents parasitic castration by rhizocephalan barnacles. Feminised crabs dating even further back, to the Cretaceous period, indicate that rhizocephalans may have evolved during the Mesozoic era (Feldmann 1998). Ascothoracican barnacle parasitism on fossil echinoid echinoderms from the Cretaceous period has been inferred from characteristic elongate boreholes in the test of the host (see Baumiller and Gahn 2002).

Indirect evidence of parasitism has in general been well studied in fossil echinoderms, particularly crinoids dating back to the Ordovician period. Various kinds of galls have been described on the arms and stalks of Palaeozoic crinoids and many of these would appear to have been caused by Myzostomida (Fig. 5.1A). Other galls dating through the Palaeozoic appear to have been caused by now extinct organisms called Phosphannulus (Hyolothelminthes). The galls had a tube that penetrated into the crinoid stem (Welch 1976), suggesting the parasite directly consumed the crinoid. Organisms such as ophiuroid echinoderms have also been found on the fossilised remains of crinoids (Hess et al. 1999). These date back to the Devonian period and similar suspension-feeding ophiuroids use crinoids as perches for feeding today (see pp. 248–250).

**Direct fossil evidence**

Platyceratidae, an extinct group of gastropods, were associated with crinoids, as well as the now-extinct blastoids and cystoids, throughout the Ordovician and Triassic periods. The snails are
generally found around the anal area of the echinoderms (Fig. 5.1B) and this has been used to argue that the group was coprophagous. Others have suggested that the snails were suspension feeders, while others have argued that the snails were drilling parasites on the echinoderms (Gahn and Baumiller 2003). Gahn and Baumiller (2003) argue that the parasitic interpretation is correct and show that crinoids infested with the platyceratids were significantly smaller than those that were not. Fossilised siphonostome copepods have been found in the gills chambers of Cretaceous fish (see Conway Morris 1981), but the most remarkable recent fossil discovery that concerns parasites is that of larval Penstastomida fossils. Contemporary Penstomida are endoparasitic and feed on blood or other fluids in the respiratory tract of tetrapods ranging across amphibians, turtles, crocodiles, birds and mammals (see pp. 235–240). There are no known pentastomids living in marine organisms and no fossils of the adults are known. This makes the finding of fossilised pentastomid larvae dating back to the Ordovician and upper Cambrian periods, initially by Andres (1989) and further documented by Walossek and colleagues (e.g. Walossek and Müller 1994) absolutely stunning. Several different species of pentastomids have been described from the larvae, preserved three-dimensionally via secondary phosphatisation of the cuticle (‘Orsten’ preservation). They show extraordinary details (Fig. 5.1C) and two basic kinds have been recognised, 'hammer-headed' and 'round-headed' larvae. These details have allowed important reinterpretations of recent pentastomid anatomy. Obviously, the hosts of these ancient larvae are unknown, but Walossek and Müller (1994) postulate that they may have still been chordates since the fossil record of this group does extend back that far. They also suggest that the pentastomids were originally ectoparasitic forms.

Important references
There have been some reviews on fossil parasites including those of Conway Morris (1981, 1990) and Littlewood and Donovan (2003), the latter from a helminthological perspective. Baumiller and Gahn (2002) provide the most recent tabulation of the occurrence of parasitism in the fossil record. Boucot (1990) edited an extensive book on organismal interactions and the fossil record.

Porifera (sponges)
John NA Hooper

Introduction
The Porifera (sponges) is a large group of presumed monophyletic aquatic invertebrates at the base of the Metazoa, with about 15,000 species worldwide, predominantly marine, living from the abyssal zone to ephemeral aquatic habitats. They are united by the unique possession of choanocytes (flagellated or collar cells that actively beat to produce a water current), lining simple or complex chambers, and connected to the external water column by a system of inhalant and exhalant canals with external pores, together forming a highly efficient aquiferous system that maintains basic metabolism and contributes significantly to reef filtration. They lack a tissue grade of construction but have a highly mobile population of cells capable of totipotency, and possess siliceous or calcitic spicules in many (but not all) species. Sponges have free-swimming or creeping sexual larvae, so far with no known pelagic phase (thus potentially limiting their ability to disperse over long ranges, unlike e.g. corals), although most groups have considerable means of asexual propagation, and all have extensive regenerative powers that appear to be vital for sustaining local populations. There are three distinct classes (Hexactinellida, Demospongiae and Calcarea), with the extinct class Archaeocyatha having suspected affinities with Demospongiae. An overview of the phylum, including a revision of nearly 700 genera, has been undertaken (Hooper and Van Soest 2002).
Parasitic sponges
Sponges have long been known as a host to a plethora of prokaryote and eukaryote commensals (e.g. Carter 1871, Humes 1996), including other sponges (e.g. Annandale 1915) – hence the term ‘sponge hotels’ (Wilkinson 1984) – and in some cases these may greatly exceed the native sponge cell biomass (e.g. Price et al. 1984, Wilkinson 1992). These commensal relationships span the continuum from obligatory symbionts to parasites (e.g. Uriz et al. 1992). It is less well known, however, that some sponges themselves are obligatory parasites on other life forms, for part of their life history at least. These predominantly consist of the excavating (or ‘boring’ or bioeroding) sponges belonging to the Hadromerida demosponge families Clionaidae, Alectoni-dae and Spirastrellidae – although a parasitism has been independently acquired in other sponge groups too, such as the poecilosclerid Paracornulum and Zyzzya, and the haplosclerid Aka – but together consisting of only relatively few species (perhaps several hundreds). These parasitic sponges excavate chambers in calcium carbonate substrata, contributing significantly to reef carbonate recycling, but also damaging living tissue and sometimes killing the host (e.g. Wesche et al. 1997, Schönberg and Wilkinson 2001). They have been responsible for extensive damage to commercial shellfish (e.g. Rosique et al. 1996), other molluscan hosts (e.g. Lauckner 1983), hard corals and octocorals (e.g. Schönberg and Wilkinson 2001, Rützler 2002b), and they have reportedly caused extensive damage to community structure and physical stability of shallow reefs (Rützler 2002a).

Effects of sponges on hosts
The most visibly destructive cases of bioeroding sponge infections can be seen in edible oyster cultures infected with clionaid species (Fig. 5.2A), producing ‘spice bread disease’ (Thomas 1981), with reported infection rates of up to 50% in some commercial oyster leases (Wesche et al. 1997). Their ability to infect both living and dead calcitic substrates, their reported tolerance to low salinities (20 parts NaCl per thousand, ppt – g of solute per kg of sea water) and ability to survive when the host is exposed to the air (Hartman 1958), their ability to infect several species of host (Thomas 1981), and the common practice of translocating young oyster spat between commercial oyster beds has produced nearly cosmopolitan distributions for some species (e.g. Pione vastifica). At larger spatial scales excavating sponges seem the most destructive internal

Figure 5.2  Sponges parasitic in mollusc and coral hosts. A. Radiograph of an oyster shell (Saccostrea glomerata) infected with Pione vastifica. B. Parasitic sponge (Alectona millari) in an excavated coralline chamber, showing spined acanthoxea megasclere spicules (centre) and pits on the chamber wall. Scale bar = 100 µm. Figure 5.2A is reprinted from Aquaculture, Volume 157, Wesche, Adlard and Hooper, ‘The first incidence of clionid sponges (Porifera) from the Sydney rock oyster Saccostrea commercialis’ (Iredale and Roughley 1933), pp. 173–180, Copyright (1997), with permission from the authors and Elsevier. Figure 5.2B is reproduced from Rützler (2002b), with permission from the author and Kluwer Academic/Plenum Publishers.
bioeroding organisms of coral reefs both in terms of effects (i.e. weakening coral platforms, production of dead coral rubble) and rates of destruction (up to 15 kg/m² per year), and much of the damage caused to corals during storms has been attributed to weakening of basal structures by bioerosion (Wilkinson 1983). Moreover, there is evidence of a significant increase in the prevalence of bioeroding sponges over the past 20 years within the Caribbean, which has been attributed to increased seawater temperatures (either from local or global mechanisms) and probably other biotic, climatic and anthropogenic sources of stress on coral reefs (Rützler 2002a). Although clionaid sponges have the ability to invade living coral tissue and to survive direct contact with coral polyps (Schönberg and Wilkinson 2001), their ecological success may be largely due to their ability to undermine and erode the coral skeletal base, thus avoiding contact with the coral polyp defensive mucus and nematocysts (Rützler 2002a).

Adaptations to a parasitic existence

The families Clionaidae (Cliona, Cliothosa, Pione, Thoosa and Volzia) and Alectonidae (Alectona, Delectona, Dotona, Neamphius and Spiroxya) are capable of bioeroding in the alpha, beta and gamma growth stages (Fig. 5.3), while Spirastrellidae (Diplastrella, Spirastrella) lacks an adult endolithic habit and excavates only in the alpha stage (Rützler 2002b). In clionaid sponges excavation is a two-step cellular process, via special etching cells in the sponge larvae (and/or in mature sponges) in contact with the calcitic substrate (Rützler and Rieger 1973). The pseudopodial processes of these cells produce a carbonic anhydrase-regulated acid phosphatase secretion at the periphery of the filopodial sheet, and together with the action of a lysosomal enzyme system which dissolves organic matter, limestone chips are created and physically liberated into the sea water via the sponge exhalant canal (Pomponi 1979). Etching initially produces a cavity, then a series of connected chambers, some extending up to 80 mm through the substratum, depending on the porosity of the host (MacGeachy 1977), and eventually consuming the entire calcitic substratum (in the case of corals at least). As the sponge grows it fills the excavated chambers with its cells and siliceous spicules (megascleres and microscleres) (Fig. 5.2B), and maintains contact with the external water column by growing papillae bearing inhalant (ostia) and exhalant pores (oscula). Three growth stages are defined for excavating sponges: in the alpha stage sponges are predominantly confined within the excavated chambers with only the papillae protruding outside the host (Figs 5.2B, 5.3A). There are differentiated inhalant and exhalant papillae to minimise incoming water contamination, the former with numerous ostia and the latter with only a single terminal osculum. In the beta stage the papillae fuse to form a continuous sponge crust covering the external surface of the host (Fig. 5.3B), and in the gamma stage sponges become massive (often burrowing inside the calcitic substratum) (Fig. 5.3C), with

Figure 5.3  Growth stages of parasitic sponges. A. Alpha stage, Cliona sp. #2670 boring on dead coral substrate, orange alive (arrow indicates an individual pit). B. Beta stage, Cliona orientalis overgrowing a faviid coral, olive green alive. C. Gamma stage, massive Cliona montiformis on top of a coral head, yellow alive (arrow indicates pore sieve plate on the apex of the sponge). All photos JNA Hooper.
the exhalant papilla (or fistule) sometimes also developing a special pore sieve at its end to pre-
vent smothering from surrounding sediments. Gamma stage growth forms are known only for
a few of the excavating sponges, and are thought to occur as the sponge becomes massive with
age, or after the original substrate has been completely outgrown and the sponge becomes free
living (Rützler 2002b).

Estimating the effects of parasitic sponges
During the processes of parasitism etching pits and scars are left inside the host, with the geom-
etry of scarring differing according to the species of sponge, and these are thus a useful diagno-
sic tool for both Recent and fossil faunas (Calcinai et al. 2003). Similarly, the extent of sponge
bioeroding activity in time and space can be measured by the abundance of etched limestone
chips in surrounding sediments, with one estimate indicating that 20% to 40% of all silt on
patch reefs in Belize are excavated chips (Halley et al. 1977), and some of which are subsequently
lithified to form consolidated reef rock (Wilkinson 1983). Clearly, therefore, parasitic sponges –
although not widely recognised as such – have contributed significantly to modern day coral reef
structure and composition (and have existed at least since the Mesozoic as evidenced from
endolithic scar patterns in the fossil coral record; Perry and Bertling 2000), as well as continuing
to be a major pest of commercial molluscan fisheries.

Important references
Important references on the effects of boring sponges on coral reefs are by MacGeachy (1977),
economically important molluscan beds and coral reefs in Indian seas. The chapter by Lauckner
(1983) on diseases of molluscs contains a section on sponges. Rosique et al. (1996) evaluated the
influence of the sponge *Cliothosa hancocki* on the European flat oyster bed, *Ostrea edulis*. The
fine structure of *Cliona lampa* penetrating calcareous substrata was described by Rützler and
Rieger (1973), and the ultrastructure and cytochemistry of the etching area of boring sponges by
Pomponi (1979).

Cnidaria and Ctenophora (cnidarians and comb jellies)
Ferdinando Boero and Jean Bouillon

Introduction
Cnidaria and Ctenophora (see Grassé and Doumenc, 1987, 1993 for a detailed account) are
known both as benthic organisms (polyps of the Cnidaria) and as gelatinous plankton (medusae
of Cnidaria, and Ctenophora). The parasitic forms are usually neglected, with the exception of
the hydrozoan *Polypodium hydriiforme*, parasite of sturgeon eggs, one of the few metazoan intra-
cellular parasites. Within the two phyla, the Hydrozoa show the greatest diversity in parasitic life.
Many species are epibiotic and not parasitic, using the surface of other organisms as a settling
substrate. Two forms of association are here considered as parasitic:

1. at least part of the guest body is embedded in the host tissues
2. the guest lives inside the host (e.g. in the flagellate chambers of sponges, the mantle cavity
   of mollusc bivalves or the atrial cavity of tunicates).

A third but rare case is that of predators that feed only on parts of their prey, without killing
it. Since most hosts have almost no economic importance, the impact of these associations is
unstudied and, in most cases, it is not clear if they cause any harm. Relatively few species have
been directly observed while feeding on their hosts. In some cases, the host might receive some
compensation from the guest (e.g. encrusting bryozoans inhabited by hydroids whose hydrorhizae grow under the host skeleton have an increased competitive ability). Such cases might suggest a long history of coexistence, beginning as mutualism and ending as parasitism (Piraino et al. 1992).

In almost all species, host infection presumably occurs via the planula stage. The asexual reproduction so common in cnidarian polyps is a way of increasing the number of zooids deriving from a single zygote and resembles a common life history pattern of many parasites: larval amplification by asexual reproduction. Due to the paucity of records, the geographic distribution of these associations seems to be scattered. Proper observation on potential hosts at any marine location might reveal the presence of parasitic Cnidaria, especially Hydrozoa.

**Parasitic Cnidaria**
The parasitic relationships of Cnidaria are described by considering selected examples of each parasitised phylum. A list of known species with similar habits is also given.

- **Sponges.** Many polyps live embedded in sponges (26 Hydrozoa and two Scyphozoa), projecting distally from their surface. Some species live in the flagellated chambers. Penetration of tissues by the guests should cause some harm to the hosts and, thus, the association can be considered as parasitic, although Uriz et al. (1992) suggested that the sponge profits from the association by receiving physical support from the guests, thus saving energy in producing a skeleton of its own. The polyps may use the currents produced by the sponge to obtain food, and receive protection by being partially embedded in its body. Species: Dipurena halterata, D. simulans, D. strangulata, Sarsia bella, Bicorona elegans, Sphaerocoryne agassizi, S. bedoti, Heterocoryne caribbensis (Fig. 5.4B), Cladonema sp., Hybocodon cryptus, H. prolifer, H. unicus, Zyzzyzus calderi, Z. floridanus, Z. robustus, Z. spongicolus, Z. warreni (Fig. 5.4C), Ectopleura exxonia, Tubularia ceratogyne, Bibrachium euplicellae, Cytaeis spongicola, C. abyssicola, C. nuda, Gastroblasta sp., Nausithoe punctata, N. racemosa.

- **Cnidaria.** The polyps of 12 hydrozoans live embedded in the bodies of colonial Hydrozoa, Alcyionacea, Pennatulacea, Gorgonacea and Scleractinia. They use the host for support, but might also feed on its tissues. Species: Hebella dispolians (Fig. 5.4D), Hebella furax, Pteroclava kremphf, Ralpharia cocinea, R. gorgoniae, R. magnifica, R. neira, R. parasitica, R. sanctisebastiani, Hydrichthella epigorgia (Fig. 5.4E), Pitlocodium repens, Zanclea gilii (Fig. 5.4F).

The larval stages of several Narcomedusae (seven species, but probably many more) are parasitic in the gastric pouches or the manubrium of other medusae, using their food. Once grown, they leave their hosts and live freely. Tentaculate Actinaria larvae are parasitic in the gastrovascular system of medusae, using food particles of their host by means of siphonoglyph currents. Species: Cunina becki, C. octonaria, C. peregrina (Fig. 5.4G), C. proboscidea, Peganta clara, P. rubiginosa, P. triloba, Peachia spp., Halcampa spp.

- **Ctenophora.** Young Edwardsia (Actiniaria, Anthozoa) are parasites of the ctenophore Mnemiopsis leidyi.

- **Annelida.** The Narcomedusa (Hydrozoa) Canina globosa parasitises the coelomic cavities of the pelagic polychaete Tomopteris.

- **Mollusca.** Cnidaria living on gastropod shells containing living molluscs or hermit crabs are either simple epibionts or even mutualists. Polyps of three hydrozoan species live on the shells of pteropods, feeding on their epithelium and on their embryos (i.e. they are real parasites). Species: Kinetocodium danae (Fig. 5.4H), Perigonella sulphurea, Pandea conica.
Polyps of five hydrozoan species live in the mantle cavity of bivalve molluscs, attached to the tissues of the mantle cavity by stolonal sucker-like structures or by hydrorhizae penetrating into the host tissues. They use food collected by the ciliary movements of the bivalve gills and the labial palps but their exact parasitic relationships are not known. Some have been observed feeding on the larvae of other parasites of their hosts. Species: Eugymnanthea inquilina (Fig. 5.4I), E. japonica, Eutima commensalis, ?E. ostrearum, E. sapinhoa.

- **Crustacea.** Some Crustacea Decapoda use Cnidaria as defence, actively putting them on their bodies; only two species of Hydrozoa live on the exoskeleton of crustacean hosts: Rosalinda incrustans (Fig. 5.4J) on decapods, Hydrichthys sarcotretis on parasitic copepods.

- **Bryozoa.** Hydrorhizae of the hydrozoan guest grow in spaces among bryozoan zooids and are covered by host skeleton. Polyps project from holes in the host skeleton. The host receives protection by the nematocysts of the guest which, in turn, receives protection by the calcareous skeleton of the bryozoan and takes advantage of the currents created by the lophophore. One species feeds on the lophophore arms of the bryozoan and this habit might be common in other species as well. Species: Zanclea sessilis, Z. protecta, Z. bomala, Z. divergens, Z. giancarloi, Z. retractilis, Z. polymorpha, Z. hirohitoi, Z. exposita, Zancella bryozoophila, Z. diabolica, Z. glomboxis, Halocoryne epizoica (Figs 5.4K, 5.4L), H. frasca, H. pirainoid, Octotiara russelli (Fig. 5.4M), Cytaeis schneideri, Hydranthea margarica.

- **Urochordata.** The Hydrozoa Bythotiara parasitica (Fig. 5.5) and B. hunstmanni live in the prebranchial cavities of ascidians.
• **Chordata.** Seven Hydrozoa live on the body surface of fish, with a hydrorhiza forming a naked encrusting plate that can erode the host tissues with haustorium-like structures, the tentacle-less polyps bend over and feed by applying their open mouth to the injured parts, sucking in blood and tissues. Species: *Hydrichthys mirus* (Fig. 5.6), *H. boycei*, *H. cyclothonis*, *H. monocanthi*, *H. pacifica* and, *H. pietschi*, *Larsonia pterophylia*.

*Polypodium hydriforme* (Fig. 5.7), the single representative of the hydrozoan subclass Polypodiozoa, is one of the few known metazoans adapted to intracellular parasitism. It

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**Figure 5.7** *Polypodium hydriforme.* After Raikova (1973). A. General cycle: 1, reversed stolon prolifer; 2, stolon prolifer living in infected Acipenserid egg; 3, stolon prolifer in water; 4, fragment of stolon; 5, polyp with 12 tentacles; 6, polyp with 24 tentacles; 7, polyp with six tentacles; 8, female polyp; 9, male polyp; 10, binucleate cell parasite of an Acipenserid oocyte; 11, encapsulated morula; 12, planula; 13, budding planula; 14, stolon prolifer without tentacles; 15, reversed stolon prolifer with internal tentacles. B. Diagram of formation of the medusae. a, sexual medusa; b, gonad with binucleated cells; c, binucleated cells; d–g, binucleated cells in a fish oocyte; h, segmentation of embryo; i, morula stage; j, planula stage; 3, ovary of *Acipenser*, large eggs are parasitised, small ones are not. 4. A–C, reversed buds with internal tentacles on a stolon prolifer (St.); D, stolon prolifer with external tentacles; E, medusae liberated from an infected fish egg.
has a unique life cycle, with a succession of a free-living stage and an intracellular parasitic stage in some Acipenseridae and Polyodontidae fish eggs. The species decreases the quality of caviar and the reproductive potential of the host.

**Parasitic Ctenophora**

*Gastrodes parasiticum* is an internal parasite in the tunic of *Salpa fusiformis*. Some authors believe that it is the juvenile cydippoid larva of *Lampea pancerina* that, as adult, is usually attached to the body of salps with its pharynx.

*Haeckelia rubra* eats the tentacles of the narcomedusa *Aegina citrea*, and retains the prey’s unfired cnidocysts for its own defence (cleptocnidae).

**Important references**


**Mesozoa Orthonectida (orthonectids)**

Hidetaka Furuya

**Introduction**

Orthonectids (Phylum Orthonectida) belong to a small group of mesozoans with about 20 described species. Orthonectids have been reported from temperate and cold waters of coastal regions of the English Channel, the Dover Strait, the Strait of Kattegat, the Barents Sea, the White Sea, the North-western Pacific Ocean (Japan), and the North-eastern Pacific Ocean, United States of America (USA). One family, the Rhopaluridae, contains all four genera: *Rhopalura*, *Intosha*, *Ciliocincta*, and *Stoecharthrum* (Kozloff 1992).

**Morphology and diversity**

The genera, *Rhopalura*, *Intosha* and *Ciliocincta* are dioecious and sexually dimorphic. The genus *Stoecharthrum* is characterised by hermaphroditism. Adults range in length from 0.05 mm to 0.8 mm. The body of the adult consists of a jacket of ciliated and unciliated epidermal cells arranged in rings around an internal axial mass (Fig. 5.8). The pattern of ciliation is characteristic of the genus. In *Rhopalura* some rings of epidermal cells are completely ciliated, whereas others lack cilia. In *Intosha* the ciliated rings are mostly covered with cilia. In *Ciliocincta* and *Stoecharthrum* the cilia are restricted to the anterior or posterior margins, or both, of certain rings. Contractile muscle cells differentiate to pack the gonad with longitudinal, circular and oblique orientations. The oocytes in females of *Intosha*, *Ciliocincta* and *Stoecharthrum* form a single row of cells within the axial mass. In *Rhopalura* the oocytes are packed into the central mass (Fig. 5.8).

Orthonectids live in tissues of a wide variety of marine invertebrate phyla, Platyhelminthes, Nemertea, Annelida, Mollusca, Echinodermata, Bryozoa and Urochordata. In *Rhopalura* all species are associated with the gonads of brittle stars, various bivalves and gastropods. The remaining genera, *Intosha*, *Ciliocincta* and *Stoecharthrum*, are found in the parenchyma or tissues of the body wall, rather than the gonads.
Life cycles

The life cycle of orthonectids is complex (Fig. 5.9). In *Rhopalura ophiocoma* the infection takes place through a genital bursa or the gut of the host *Amphipholis squamata* (Kozloff 1969, 1971). The infective germinal cell penetrates the epithelium and enters a contractile cell, in which embryos develop from the germinal cell. This structure is called plasmodium; however, it belongs not to the orthonectid, but to the host contractile cell (Kozloff 1994). Thus, the plasmodium consists of modified host tissues. The germinal cells give rise to morula or berry-like clusters that form sexual individuals in the plasmodium (Metschnikoff 1881). Adults escape through the genital slits of the host. In *R. ophiocoma* males are smaller than females. During mating males make brief contact with females when sperm are released. Fertilisation is inside the female bodies. In this species maturation of the egg is not completed until after entrance of the sperm (Caullery and Lavallée 1908). Embryos are formed around 22 hours after the first cleavage of eggs. When the embryos are fully developed, the female ruptures and dies, releasing ciliated dispersal larvae *in vitro*.

The method of infection is unknown. In *R. ophiocoma*, Caullery and Mesnil (1901) considered that larvae enter the genital slits of the ophiuroid host. Mature larvae have not been studied
in detail but appear to differ morphologically between species (Caullery and Lavallée 1908, 1912, Atkins 1933). Differences in larval form are possibly related to host differences (Furuya 2001). In contrast, host species of dicyemids are specific to benthic cephalopods. Larvae of dicyemids demonstrate less interspecific variation than larvae of orthonectids.

Effects on hosts and ecological importance
Heavy infections have some effects on hosts. In *R. ophiocomae* young plasmodia are located in ophiuroid hosts in the ventral part of the disk, the interradial spaces, and near the gonads and genital ducts. As embryos grow in size the plasmodia enlarge, eventually destroying the host gonad and even invading the host coelom. Ophiuroids infested with older plasmodia of *Rhopalura ophiocomae* are easily recognised. The ventral surface is grayish instead of orange. They are more flaccid than normal because they are sterile and the genital pouches are not distended.
with embryos (Kozloff 1969). *Ciliocincta sabellariae* infects the muscle tissue of the dorsal body wall and cirri of the polychaete *Sabellaria cementarium*. Heavily infested individuals can be recognised by the presence of grayish patches on the dorsal surface (Kozloff 1971).

Except for a brief free-living phase during which mating and the incubation of developing embryos take place, the entire life cycle is confined to the gonads and other organs and tissues of their invertebrate hosts. The incidence of infection ranges from about 1% to 15% but typically is less than 5%. Infections are often highly localised and in some study sites may be restricted to areas of only a few hundred square metres (Caullery and Mesnil 1901). The ecological importance of orthonectids is likely to be small because of the few species and the low prevalence.

**Important references**
The group was reviewed by Kozloff (1990, 1992). A key to the genera was given by Kozloff (1992). The morphology, life cycles and early development were studied by Giard (1880), Caullery and coworkers (1901, 1908, 1912), Julin (1882) and Metschnikoff (1881).

**Mesozoa Dicyemida (dicyemids)**
Hidetaka Furuya

**Introduction**
Dicyemid mesozoans (Phylum Dicyemida) are the commonest and most characteristic parasites of benthic cephalopod molluscs. About 120 species have been reported in at least 50 species of benthic cephalopods distributed in many geographical localities: Sea of Okhotsk, Japan Sea, Western and Eastern North Pacific Ocean, New Zealand, North Indian Ocean, Mediterranean, Western North and Eastern Atlantic Ocean, Gulf of Mexico and the Antarctic Ocean.

**Morphology and diversity**
Species of dicyemids range in length from 0.1 mm to 5 mm. Dicyemids have neither body cavities nor differentiated organs. Their bodies consist of a central cylindrical cell called the axial cell and a single layer of 8 to 30 ciliated external cells called the peripheral cells (Fig. 5.10). The phylum Dicyemida includes three families, Conocyemidae, Dicyemidae and Kantharellae. The number of peripheral cells is species specific and constant in the families Conocyemidae and Dicyemidae. The family Kantharellidae contains only one species that is characterised by variable number of peripheral cells. At the anterior region of dicyemids, 2 to 10 peripheral cells form the calotte. Genera are characterised by the number and orientation of cells in each tier of the calotte (Hochberg 1990). The calotte shape varies, depending on the species, and might be an adaptation for attachment to the various regions of host renal tissues (Fig. 5.11). The family Conocyemidae is characterised by an irregular shape of the adult form and includes two genera, *Conocyema* and *Microcyema*. The head of *Conocyema polymorpha* looks like a balloon (Fig. 5.12A). In *Microcyema vespa*, peripheral cells are fused into a syncytium (Fig. 5.12B).

Dicyemids generally are found in benthic cephalopods, namely octopuses and cuttlefishes. But a few species of dicyemids were reported from squids, *Sepioteuthis lessoniana* (Nouvel 1947) and *Loligo* sp. (Kalavati and Narasimhamurti 1980). Such cases have been considered to be exceptional. Recently, two undescribed dicyemid species have been found in two species of squid, *S. lessoniana* and *Todarodes pacificus* (Furuya and Tsuneki 2003). Host species of dicyemids might not be necessarily restricted to the benthic cephalopods. Dicyemids are found primarily in the fluid-filled renal sacs or kidneys. In decapod cephalopods, squids, sepiolids and teuthoids they have been found also in the reno-pancreatic coelom and occasionally in the pericardium (Hochberg 1990).
Life cycles
The life cycle of dicyemids consists of two phases with different body organisation (Fig. 5.10): (1) the vermiform stages, in which the dicyemid exists as a vermiform embryo formed asexually from an agamete, and as a final form, the nematogen or rhombogen, and (2) the infusoriform embryo which develops from a fertilised egg produced around the hermaphroditic gonad called the infusorigen. The infusorigen itself is formed from an agamete. Two posterior diapolars are somewhat specialised as uropolars. The development of infusorigens, gametogenesis around the infusorigen and development of two types of embryo all proceed within the axial cell cytoplasm. Abbreviations: A, apical cell; AG, agamete; AN, axial cell nucleus; AX, axial cell; C, calotte; DP, diapolar cell; DV, developing vermiform embryo; MP, metapolar cell; PP, propolar cell; UP, uropolar cell. After Furuya and Tsuneki (2003).

Figure 5.10  Life cycle of dicyemids. The process involved in the infection of a new cephalopod and the development into the adult are not known. In vermiforms (nematogen, rhombogen, vermiform embryo), a large cylindrical axial cell is surrounded by peripheral cells. Four to 10 anterior peripheral cells (propolars and metapolars) form a calotte. The other peripheral cells are diapolars. Two posterior diapolars are somewhat specialised as uropolars. The development of infusorigens, gametogenesis around the infusorigen and development of two types of embryo all proceed within the axial cell cytoplasm. Abbreviations: A, apical cell; AG, agamete; AN, axial cell nucleus; AX, axial cell; C, calotte; DP, diapolar cell; DV, developing vermiform embryo; MP, metapolar cell; PP, propolar cell; UP, uropolar cell. After Furuya and Tsuneki (2003).
infusoriform embryos escape from the host into the sea to search for a new host. However, it remains to be understood how infusoriform larvae develop into vermiform stages in the new host.

In dicyemids, the population may develop from a small number of individuals (one or few) at the initiation of the infection of the renal sac because success of infecting new hosts is apparently low. Dicyemids are occasionally found in only one of the two renal sacs in a host octopus. Two different dicyemid species are occasionally detected, one each in the right and left renal sacs of the same host individual. These cases suggest that only a few propagules may infect an individual host. Subsequently asexual multiplication leads to a large population in the renal sac. In such conditions, cross-fertilisation is of little advantage and self-fertilisation via a hermaphroditic gonad has developed.

Infusoriform larvae actively swim close to the bottom for only a few days in vitro (McConnaughey 1951), an adaptation to the close proximity of cephalopod host individuals. At the anterior region of the embryo, there is a pair of unique cells called the apical cells (Fig. 5.10). Each contains a refringent body composed of a hydrated magnesium salt of inositol hexaphosphate (Lapan and Morowitz 1975). Its high specific gravity imparts a negative buoyancy to the dispersal larvae. This suggests the role of refringent bodies is to help the larvae to remain near the sea bottom where larvae can encounter another host. Dicyemids eventually enter the kidney and apparently do not move once attached. A very short larval stage in the plankton also is
typical in colonial benthic animals. The analogy between colonial animal and dicyemids can be attributed to their sedentary life styles (Furuya et al. 2003a).

**Effects on hosts and ecological importance**

The renal sac of cephalopods is a unique environment providing living space for the dicyemids. The fluid-filled renal coelom provides an ideal habitat for the establishment and maintenance of dicyemids (Hochberg 1982). More than one species of dicyemids are usually found in each cephalopod species or individual. Most species of dicyemids are host specific (Furuya 1999). Generally, dicyemids occur at high prevalences (Furuya et al. 2003b). Dicyemids are usually found to be infecting renal organs heavily, but damages have never been observed. Lapan (1975) suggested that dicyemids facilitate host excretion of ammonia, contributing to acidification of the urine. In addition to the contraction of renal appendages, ciliary activity of dicyemids makes urine flow constant and, as the result, it assists in removal of urine. Thus, dicyemids are in a symbiotic, rather than a parasitic, relationship with cephalopods.

There is an interesting relationship between the calotte configuration and the co-occurrence pattern in hosts. The calotte shapes are distinctly different when dicyemid species co-occur (Furuya et al. 2003b). Four basic types of calotte shapes are recognised. A conical calotte (Fig. 5.12F) is by far the most typical configuration. Dicyemids with a discoidal calotte (Figs 5.12C, D) frequently are found together with species having cone-shaped calottes. Cap-shaped calottes (Fig. 5.12E) appear to be intermediate in shape between the conical and discoidal type, and tend to occur in the cephalopods when more than two species of dicyemids are present. Dicyemids with irregularly shaped bodies and calottes (Figs 5.12A, B) occur when more than three species coexist. When more than two dicyemid species were present in a single host

![Figure 5.12](image-url)

**Figure 5.12** Diversity of dicyemid species. A. *Conocyema polymorpha*. B. *Microcyema vespa*. C. *Dicyemennea trichocephalum* (anterior part). D. *Dicymodeca anthinocephalum* (anterior part). E. *Pseudicyema nakaoi*. F. *Dicyema acuticephalum*. 
individual, calotte shapes were dissimilar as a rule. It is a common phenomenon that calotte shapes in dicyemid species from different host species more closely resemble each other than those of dicyemids observed within the same host species. Species of dicyemids that possess similar calotte shapes are very rarely found together in a single host individual, and in all such cases one species is dominant. In these cases, the species best adapted to the habitat possibly becomes a dominant species. In a host individual, interspecific competition between dicyemids may result when they have similar calotte shapes, and therefore, these dicyemids tend to infect different host individuals.

Species of dicyemids with different calotte shapes, for example, *D. misakiense* (conical) and *D. japonicum* (discaloid) inhabit different regions of the renal organs (Fig. 5.11). In general, dicyemids with conical calottes insert the anterior region of the body into crypts or folds in the renal appendages. In contrast, dicyemids with cap-shaped or disc-shaped calottes attach to the broad, flat or gently rounded surfaces of the renal appendages. Interspecific competition is most likely avoided by the habitat segregation in dicyemids that possess different calotte shapes.

### Important references

The group was reviewed by Nouvel (1947, 1948), McConnaughey (1951), Lapan and Morowitz (1975), Hochberg (1990), and Furuya and Tsuneki (2003). A key to the families Conocyemidae and Dicyemidae was given by Hochberg (1990). The family Kantharellidae was discussed by Czaker (1994). A review of the development of two types of larvae and hermaphroditic gonad is by Furuya et al. (1996).

### Myzostomida (myzostomids)

**Greg W Rouse**

### Introduction

Myzostomida is a small taxon comprising around 150 described nominal species. There is debate on the overall position of the group, with authors variously favouring a position among polychaetes (Rouse and Pleijel 2001) or outside annelids and closer to platyhelminths (Eeckhaut *et al.* 2000) or rotifers (Zrzavy *et al.* 2001). Myzostomida are all parasitic on echinoderms, mainly crinoids, but also a few asteroids and ophiuroids. There are also records of them from sponges and from inside antipatharian corals (Grygier 2000).

### Diversity and geographical distribution

Most myzostomes are mobile, reaching up to 1 cm in length, and roam over the host stealing food from it (e.g. *Myzostoma, Hypomyzostoma*), but others are sessile near a convenient 'feeding' site or even in the host's mouth. Some induce the host to form hard galls or soft cysts (Fig. 5.13A–D) around them (e.g. *Notopharyngoides, Endomyzostoma*), while others are endoparasitic (Fig. 5.13E), reaching 3 cm or more in length and live in the gut lumen, coelom or gonads of their host (e.g. *Mesomyzostoma*). There is a wide range of body forms in Myzostomida, with flattened oval or disc-like forms being predominant. However, many are elongate (Fig. 5.14E, F), ridged, or have extensions of the body that allow them, for example, to resemble the pinnules of their crinoid hosts (Fig. 5.14B, C). Mobile, free-living Myzostomida show a wonderful diversity of colour patterns that generally matches those of their hosts. Gall-forming and internal parasitic forms (Fig. 5.13) tend to be pale and unpigmented. Most Myzostomida are placed within *Myzostoma* (Fig. 5.14A–D) and are external parasites. The diversity of sessile and internal parasitic forms is much lower.
Myzostomida have been recorded from most marine areas, wherever their hosts are found, down to depths of more than 2000 m. Not surprisingly, myzostome diversity is highest where crinoid diversity is greatest, namely coral reef environments, and more than 100 described species are known from the Indo-Pacific (see Grygier 1990, 2000). Myzostome diversity is low in colder waters, with, for instance, only a few known from the well-studied European waters. Interestingly none have been recorded from the eastern tropical and south-eastern Pacific (Grygier 2000). The most comprehensive regional reviews on the occurrence of Myzostomida have been for the Indo-Pacific and around Australia by Grygier (1990, 2000). Some groups have relatively few records. *Protomyzostomum*, living in ophiuroid basket stars, have been found only in temperate (Japan) or cold seas (Arctic and Antarctic), as have those ectoparasitic (on asteroids) taxa in *Asteromyzostomum* (Arctic and Antarctic). *Asteriomyzostomum*, another taxon containing endoparasites (of asteroids), has taxa described from the Mediterranean and from off California. *Mesomyzostoma* (Fig. 5.13E) contains two endoparasitic taxa (of crinoids) described from Indonesia and Japan (Grygier 2000). Presumably, further investigation of asteroids, crinoids and ophiuroids will yield many more Myzostomida, particularly endoparasites. Host-
specificity of Myzostomida varies considerably. Some will only infest a single kind of crinoid, but others live on three or four different crinoid taxa. In addition, some crinoid taxa may be hosts to several different myzostomes (Grygier 1990, 2000).

**Morphology**

The head of myzostomes is not a distinct structure, there are no eyes and the buccal opening is a ventral or terminal structure. The body is segmented and in most myzostomes there are five pairs of appendages (Fig. 5.14D, F), arguably similar to the parapodia of polychaetes, each bearing an emergent hook-shaped chaeta and an internal ‘acicula’. In internal parasitic forms such as *Mesomyzostoma* the appendages are limited to the emergent chaetae only (Fig. 5.13E). The lateral margin of many myzostomes has cirri, usually 10 pairs, though they maybe absent or far more numerous than this. The ventral body surface generally has four pairs of ‘lateral organs’ that may be eversible and are probably sensory. They generally alternate with the parapodia.

*Myzostoma*, *Hypomyzostoma* and *Notopharyngoides* have a protrusable proboscis that Rouse and Fauchald (1997) regarded as homologous with the muscular axial proboscis found in some polychaetes. The everted tip of the proboscis is the mouth and this may be fringed with 4 to 30 papillae. In all others the proboscis, if present, is of a different organisation and represents the posterior region of the buccal cavity that is everted through the mouth. In some taxa, such as
internal parasites like *Mesomyzostoma* a proboscis is absent (Fig. 5.13E). Behind the pharynx in most myzostomes is a large ‘stomach’ with several pairs of diverticula that branch extensively. From the stomach there is a straight intestine leading to the terminal anus. No circulatory system has been described for any Myzostomida and the stomach diverticula are thought to transport nutrients and wastes from around the body (Grygier 2000). Five pairs of protonephridia have been described in *Myzostoma cirriferum* by Pietsch and Westheide (1987). The pairs of nephridia lie anterior to each pair of parapodia. A pair of ciliated ducts that usually connect the uterus to the intestine have commonly been referred to as metanephridia. They are thought to serve an excretory function in removing waste gametes but may not actually represent metanephridia (Grygier 2000). Apart from the lateral organs and some sensory patches of cilia scattered over the body, no other sensory organs have been reported in Myzostomida.

**Reproduction and life cycles**

Myzostomida are usually protandric hermaphrodites and pass through a functional male stage to be simultaneous hermaphrodites at maturity (Grygier 2000). The male system is paired with diffuse testes lying ventral to the gut. Seminal vesicles are connected to the testes via vasa deferentia and exit on each side of the body next to the third parapodia. A pair of protrusible penises is present in taxa such as *Myzostoma* and *Notopharyngoides*, but are absent in the endoparasitic forms. Spermatogenesis is unusual and sperm develop in vacuoles inside spermocytes. Spermatophores are placed on the surface of recipient worms and the spermocytes pass into the body of the worm before migrating to the uterus (Grygier 2000) The female system has one or two ovaries dorsal to the gut that lead into uterine diverticula that fuse into a median uterus that exits, via an oviduct, near the anus. A pair of ciliated ducts (referred to above as possible metanephridia) also lead from the diverticula to the intestine.

Fertilisation is internal and probably occurs in the uterus. Larval development has been described for several *Myzostoma* taxa (see Eeckhaut *et al.* 2003) and it would appear that all fertilised eggs are spawned into the surrounding water, though Grygier (2000) reports brooding in some *Endomyzostoma*. The fertilised eggs of *Myzostoma* are very small (50 µm in diameter or less) and give rise to a planktonic, non-feeding trophophore larva (Fig. 5.13D) that is ready to settle on a host after five to eight days. Larvae develop two bunches of very long chaetae, similar to those seen in the larvae of some polychaetes. After settling, the larvae pass through further development in a cyst before becoming free living. Reproduction in endoparasitic and permanent cyst-dwellers has yet to be documented.

The only study on population dynamics of Myzostomida has been on *Myzostoma cirriferum*, living on the crinoid *Antedon bifida* from Europe (Eeckhaut and Jangoux 1997). They showed that juveniles live encysted for two months after settling and then live freely for four to five months. Population density increases through the spring and reaches an average maximum of around 70 per host.

**Effects on hosts and ecological importance**

Most Myzostomida associated with crinoids (*Contramyzostoma, Endomyzostoma, Hypomyzostoma, Myzostoma, Notopharyngoides* and *Pulvinomyzostomum*) would appear to feed by taking food from their host’s ambulacral grooves, or from the oesophagus or gut before it is digested. The exceptions are the endoparasitic *Mesomyzostoma*, which presumably eats its crinoid host’s gonad tissue and *Mycomyzostoma* that lives in cysts on the stalk of its sea lily host and so has no possibility of stealing food. *Asteromyzostomum* taxa living in the ambulacral grooves of asteroids insert their mouth through the skin of their host. *Asteriomyzostomum* and *Protomyzostomum* presumably live off their asteroids or ophiuroid host’s internal tissues. No studies have been done on any possible detrimental effect of myzostomes, but the high densities of up to 3200
**Minor groups and fossils**

*Myzostoma cirriferum* per host (Woodham 1992) would presumably have some effect on the crinoid’s food-gathering ability. High infestation of the endoparasitic *Mesomyzostoma* can also occur (up to 10 or more per host, GW Rouse pers. obs.) and these may have the potential to castrate their host.

**Important references**

The most important publications on the taxonomy of myzostomes are by Graff who described more than half the known species (e.g. Graff 1877, 1884, 1887). Recent reviews on myzostomes include a comprehensive account by Grygier (2000) and a briefer one in Rouse and Pleijel (2001). Eeckhaut and colleagues have published excellent papers on the larval development, phylogenetic placement and taxonomy of myzostomes (Eeckhaut 1998, Eeckhaut et al. 1998, Eeckhaut et al. 2000, Eeckhaut et al. 2003).

**Polychaeta (bristle worms)**

**Greg W Rouse**

**Introduction**

Polychaetes comprise many of the annelids and occur in most marine habitats from the intertidal to the deepest sediments. Some polychaetes dominate hydrothermal vent communities, while others comprise a major component of the interstitial fauna. Most polychaetes are cryptic, living under rocks or burying themselves in sediment. Some dig continuously through the sediment, while others make permanent burrows or tubes that they secrete or construct from gathered materials. Although most polychaetes are free living, it is not surprising that parasitism in the group has evolved several times. There are estimated to be around 9000 valid species (Rouse and Pleijel 2001), although there are many more to be described.

**Morphology and diversity**

The best known parasitic Annelida, the leeches (Hirudinea, Clitellata) are blood-feeders on animals (including humans). However, following the broad definition of parasitism used in this volume, namely that the parasite depends on the host and derives some benefit from it, there are many polychaete groups that can be characterised as parasitic. Parasitism among the polychaetes has evolved often and occurs in a great variety of forms. Most parasitic polychaetes are placed in the clade Aciculata, which comprises more than half of described polychaetes and contains two major groups, Eunicida and Phyllodocida. Parasitic Eunicida include a few Dorvilleidae, all Histriobdellidae and many Oenonidae. Phyllodocida has a wide range of parasitic forms including *Ichthyotomus*, Nautiliniellidae, *Antonbrunnia*, Syllidae and many scaleworms (Polynoidae). *Spinther* is another parasitic genus in Aciculata, but its affinities are uncertain. Outside the Aciculata, the incidence of parasitism is more sporadic, with the exception of Spionidae, though a few Sabellidae are found in association with molluscs.

While most Dorvilleidae are free living, some *Ophryotrocha* and all *Iphitime* are parasites on decapods, where they graze with their jaws on material drawn into, or growing in, the branchial chamber. They are best known from European waters. *Iphitime* and *Ophryotrocha* were placed in Iphitimidae until analysis by Eibye-Jacobsen and Kristensen (1994) established that they are dorvilleids. Histriobdellidae (Figs 5.15A, B) are also only found in association with crustaceans. *Histriobdella homari* occurs on North Atlantic marine lobsters such as *Homarus gammarus* and grazes on bacteria and blue-green algae on the gills and branchial chamber (Jennings and Gelder 1976). *Stratiodrilus* live on the gills of freshwater crustaceans in Australia (Fig. 5.15B), Madagascar and South America. An exceptional form, *Stratiodrilus cirolanae* (Fig. 5.15A), is marine and...
found on the pleopods of the intertidal isopod *Cirolana venusticauda* in South Africa. Many Oenonidae live at least part of their lives in the coelomic cavity of other polychaetes (Fig. 5.16F) or bivalves. *Notocirrus* parasitises other polychaetes with infection intensities of up to 50; it ranges in size from a few to hundreds of segments. The group is found worldwide.

Within Phyllodocida, Nautiliellidae represents a recent discovery from deep-sea hydrothermal vents and cold seeps, where they are parasites of bivalves. Adults of Nautiliellidae reach a length of 10 cm and have hundreds of segments. Several species may inhabit the same host (Fig. 5.15C). Nautiliellidae have been found off southern Japan, California, western Mexico and the western North Atlantic. *Antonbruunia viridis* was described by Hartman and Boss (1965) from lucinid bivalves from Madagascar. All were collected on a single occasion and have not been reported since. Most hosts contained one female (up to 14 mm long) and one dwarf male, about half the size. *Ichthyotomus sanguinarius* was recorded once; it reaches 10 mm in length with about 90 segments and has separate sexes. Eisig (1906) showed that it pierces the host’s skin with its jaws to suck blood. Syllid parasites have been mainly reported from sponge hosts, the best known are *Haplosyllis spongicola* (thousands of worms can occur on a single sponge) and *Myrianida prolifer* (Fig. 5.16A–D), a parasite of hydroids. *Calamyzas amphictenicolae* and *Asetocalamyzas laonicola* are also thought to be syllids, found in European waters and the White Sea, respectively; they parasitise polychaetes, penetrating the body wall or gills with their pharynx. *Asetocalamyzas laonicola*, which lives on a spionid polychaete, may actually be a

**Figure 5.15** Parasitic polychaetes. A. Arrows indicate *Stratiodrilus cirolanae* (Histriobdellidae) on pleopod of host isopod *Cirolana venusticauda*. B. Male of *Stratiodrilus tasmaniae*. The head has appendages and jaws similar to other Eunicida. C. Deep-sea vesicomyid clam containing three specimens (arrows) of an undescribed nautiliellid. D. Sediment tubes of an undescribed *Polydorella* (Spionidae) visible on the surface of a sponge in South Australia. A, B, and D by G Rouse; C courtesy of J Dreyer.
Many Polynoidae (scaleworms) are commensal, predominantly with echinoderms or burrowing animals such as other polychaetes and decapods. Some appear to be parasitic, especially those found on crinoid echinoderms. *Spinther* is a small group, all species are parasites on sponges.

The body consists of up to 50 segments and may reach several centimetres in length. They are parasitic dwarf males and is the topic of further research (AB Tzetlin, pers. comm. July 2004.)

Figure 5.16  Parasitic polychaetes. A–D. Life cycle summary of *Myrianida prolifera* (Reproduced with permission from Fischer A., Reproductive and developmental phenomena in annelids: a source of explanatory research problems, *Hydrobiologia* 402: 1–20; copyright (1999) Albrecht Fischer). A. Adult specimen on host hydroid. This will bud off free-swimming epitokes. B. Male epitoke with large eyes and palps to detect females. C. Female epitoke. D. After mating the female broods the embryos on her ventral surface until they swim away as trochophore larvae to find a host hydroid. E. Dorsal view of *Spinther alaskensis* taken from a sponge. Reproduced with permission from Hartman O, The polychaetous annelids of Alaska, *Pacific Science* 2: 3–58; published by the University of Hawai’i Press 1948. F. Lateral view of a syllid, *Haplosyllis spongicola*, that parasitises sponges. In this case the syllid itself is host to two specimens of the oenonid *Labrorastatus luteus*. The arrow near the head of the host points to the emerging head of one parasite. The other arrow points to the stippled outline of another *L. luteus* lying in the coelom of the host. Modified from Ubelacker (1978) *Journal of Parasitology*, 64: 151–154, with permission of the *Journal of Parasitology*. G. The bodies and palps *Polydorella smurovi* (Spionidae) are visible on the surface of a sponge. Reproduced with permission from Tzetlin AB and Britayev TA, A new species of the Spionidae (Polychaeta) with asexual reproduction associated with sponges. *Zoologica Scripta* 14: 177–181; published by Blackwell Publishing 1985.
flattened and rounded to oval in outline (Fig. 5.16E), and occur on the surfaces of sponges from shallow to moderate depths, with bright colouration that may be cryptic.

Outside Aciculata, parasites are much less diverse. The ‘polydorid’ group of Spionidae is well known for boring into the shells of molluscs and is found worldwide. Other spionids, Polydorella, are found only on sponges (Tzetlin and Britayev 1985) and are easily recognised by their sediment tubes on the surface sponges (Figs 5.15D, 5.16G). Terebrasabella heterouncinata is a recently described sabellid that forms burrows in the shells of molluscs and is a pest of abalone (Fitzhugh and Rouse 1999). Caobangia is another genus of sabellids, recorded from rivers in Asia, where they infest freshwater snail shells (Jones 1974).

Reproduction and life cycles
Reproductive mechanisms of most parasitic polychaetes are unknown. One phenomenon that is common among Aciculata is epitoky, and this also occurs in some parasitic forms. It is illustrated in the life cycle of the syllid Myrianida prolifer (formerly Autolytus), which is parasitic on hydroids (Fig. 5.16A). In M. prolifer, the sexes are separate and each individual buds off epitokes from the posterior end (Fig. 5.16B, C). These are filled with either eggs or sperm and swim to near the surface where they meet other epitokes. The females retain the eggs, after they are fertilised by the male epitoke (which dies), until they develop into trochophore larvae (Fig. 5.16D) before dying themselves. Meanwhile ‘stock’ animals remain on the hydroid and bud off further epitokes. Spionids show a range of reproductive mechanisms, but most are brooders of larvae within the parental tube, including parasitic forms such as Polydora species. Polydorella species, all parasites on the surface of sponges, are unusual in showing asexual reproduction and this allows them to reach high densities on their host. Histriobdellidae are known to have separate sexes and lay embryos attached to the base of the gill filament, the directly developing young then hatching out onto the host (GW Rouse, pers. obs.). In the simultaneous hermaphrodite sabellids Caobangia and Terebrasabella heterouncinata the larvae are also brooded on the tube of the parent and have a brief dispersal phase (Fitzhugh and Rouse 1999).

Effects on hosts and ecological importance
Whereas Aciculata contains most parasitic forms, the most important economically are Spionidae, which can have an effect on commercial bivalve fisheries, such as oysters. Polydora spp. use acid secretions and chaetae to create a burrow in the shell, and sediment is carried in from outside to create an inner tube. When the burrow reaches the inner shell layers, the mollusc reacts by secreting more shell material. This can result in damaging ‘mud blisters’. Sometimes the mud blisters may be so numerous that they lead to the host’s death (Martin and Britayev 1998).

Important references
Symbiotic polychaetes have been comprehensively reviewed by Martin and Britayev (1998). Older reviews are by Paris (1955) and Clark (1956). For a general overview of polychaete diversity that places this review in context see Rouse and Pleijel (2001).

Hirudinea (leeches)
Fredric R Govedich, Bonnie A Bain and Ronald W Davies

Introduction
Leeches are a diverse group of animals with many species living in marine environments, including intertidal regions and the deep ocean, with other species living in lakes and rivers on every continent (except Antarctica), and in moist terrestrial environments of Australasia and Oceania.
They can be predators or temporary ectoparasites (sanguivory) and feed on a range of invertebrate and vertebrate prey (Sawyer 1986a,b, Davies and Govedich 2001, Govedich 2001, Kutschera and Wirtz 2001). This diversity makes them an interesting group of animals to study.

**Morphology and diversity**

The Annelid subclass Hirudinea includes the Acanthobdellida, which consists of only two species of salmonid ectoparasites in the genus *Acanthobdella*, and the Euhirudinea or ‘true’ leeches (Siddall and Burreson 1995, Davies and Govedich 2001, Govedich 2001, Kutschera and Wirtz 2001). Leeches (Euhirudinea) are divided into two major groups or orders: The Rhynchodbdellida (leeches with a protrusible proboscis and true vascular system) which include the marine and freshwater members of the Piscicolidae, Ozobranchidae and Glossiphoniidae, and the Arhynchobdellida (leeches with a non-protrusible muscular pharynx, either with or without jaws, and a haemocoelomic system) which consists of the freshwater and terrestrial members of the Hirudinidae, Haemadipsidae and Erpobdellidae (Sawyer 1986b, Siddall and Burreson 1995, Davies and Govedich 2001, Govedich 2001, Kutschera and Wirtz 2001).

Leeches have sensory structures including simple eyes and oculiform spots, papillae and sensilla that allow them to find prey or hosts and interact with their environment. Eyes are typically arranged on the dorsal surface of the ‘head’ and are found either along the margins or near the midline (Fig. 5.17). The eyes in some species are very close together or even fused into lobed composite eyes and the original number of eyes can only be determined by counting the lobes. Oculiform spots or eyespots can also be found along the margins of the body and on the

![Figure 5.17](image) Dorsal view showing the body outline and eye position in four families of leeches (Euhirudinea). A. Piscicolidae. B. Ozobranchidae. C. Hirudinidae. D. Glossiphoniidae. Figure labels: as, anterior sucker; ps, posterior sucker; e, eye; es, eyespot; t, trachelosome; u, urosome; g, gills.
posterior suckers of some piscicolids. Sensilla act either as mechanoreceptors or chemoreceptors and may be located on papillae and tubercles. Papillae are typically small protrusible sense organs and tubercles are large fleshy protrusions that consist of some dermal tissues and muscles. Both types can be arranged in rows or scattered on the dorsal and ventral surfaces of the animal (Sawyer 1986b, Davies and Govedich 2001, Govedich 2001).

Leeches lack chaetae (bristles) and have both an anterior or oral sucker which contains the mouth and a wider ventrally directed posterior or caudal sucker (Figs 5.17, 5.18). Suckers are often used to attach to substrates, prey, and hosts, and are used for locomotion by some aquatic and most terrestrial leech species. Crawling typically involves a looping motion consisting of body elongation and shortening and the alternation of attachment by the anterior and posterior suckers. In addition to crawling, leeches swim by using dorsoventral undulations of their flattened body. Many aquatic leeches are very good swimmers (particularly the erpobdellids and hirudinids), but only a few piscicolids and glossiphoniids are able to swim well (Sawyer 1986a,b, Davies and Govedich 2001, Govedich 2001, Kutschera and Wirtz 2001).

Bodies of most leeches are not externally divided into distinct regions. However, most species in the primarily marine family Piscicolidae (except for the genera Myzobdella and Piscicolaria) have a body that is divided into a narrow ‘neck’ or trachelosome and longer and wider ‘body’ or urosome (Fig. 5.17). Leech bodies consist of two preoral, non-metamereric segments called the prostomium and peristomium and 32 postoral somites (metameres) labeled I through XXXIV (Sawyer 1986a,b, Davies and Govedich 2001, Govedich 2001). Each of the postoral somites is externally subdivided into annuli with mid-body (complete) somites having the full number (2–16) of annuli. Within each somite, individual annuli are numbered based on the three primary annuli, a1, a2, and a3, counting from the anterior. The a2 (middle) or neural annulus contains the ventral nerve cord ganglion and is typically delineated externally by a transverse row of papillae or sensilla. Some species have fewer than three annuli due to the loss or fusion of the primary annuli (biannulate condition) and others have more than three annuli resulting from the repeated bisection of the primary annuli. These additional annuli give the more complex annulation patterns observed in many species and are labeled depending on the original annulus that was bisected. For example, if the a1 annulus is bisected, the anterior annulus becomes b1 and the second becomes b2. With further bisection, b1 becomes c1 and c2 and so on. The resulting numbering system can become complex with some annuli bisected and others remaining in the primary condition. For example, a five annulate leech may have the a1 and a3 annuli bisected, but still have the primary a2, giving the formula b1, b2, a2, b5, b6 for the somite (Moore 1900, Sawyer 1986a,b, Davies and Govedich 2001, Govedich 2001).

Leeches primarily respire through their epidermis; however, many piscicolids and ozo-branchids may also have paired pulsatile vesicles or in some species ‘gills’ on the neural (a2) annuli of the urosome. Pulsatile vesicles and gills aid in gas exchange and are connected to the circulatory system via special coelomic passages (Sawyer 1986a,b, Davies and Govedich 2001). The coelomic system of leeches is highly modified and reduced with intersegmental septa absent in adults (although remnants are found in some glossiphoniids). Piscicolids, ozobranchids and glossiphoniids have a coelom that has been modified to enclose the blood vascular system with a ventral lacuna surrounding the ventral nerve cord and blood vessel, and a dorsal lacuna surrounding the dorsal blood vessel. Dorsal, ventral, and lateral lacunae are connected via transverse communicating lacunae and many piscicolids have pulsatile vesicles that are modified coelomic chambers connected into the coelomic network via additional lacunae (Sawyer 1986a,b, Davies and Govedich 2001, Govedich 2001). Under hypoxic or low oxygen conditions, many species compensate behaviourally by using dorsoventral undulations of the body to move water across their epidermis. Most piscicolids and ozobranchids do not ventilate. Instead they use their gills or pulsatile vesicles to move oxygenated coelomic fluid through the body (Sawyer
Some species are also able to compensate for low oxygen levels metabolically and use alternative energy reserves including amino acids, lipids and glycogen, producing succinate and alanine rather than lactic acid as metabolic wastes (Reddy and Davies 1993, Davies and Govedich 2001).

The excretory system of leeches includes up to 17 pairs of modified metanephridia that are connected to small external pores located in somites VII to XXII with a reduced number in the gonad-containing somites and at the anterior end of the animal. In addition, some marine species have an extensive network of finely branched tubes connected to the nephridia, forming a modified plectonephridium. This network is located under the longitudinal muscle layer and may be an adaptation to life in the ocean as it is found only in marine or closely related freshwater species that may have reinvaded freshwater ecosystems. In all leeches, the metanephridia excrete nitrogenous wastes such as ammonia and maintain salt and water concentrations within the body (Sawyer 1986a,b, Davies and Govedich 2001). Specialised botryoidal (Arhynchobdellida) and chloragogen (Rhynchobdellida) tissues function in a manner similar to the liver and kidneys of other animals. These special tissues are located in coelomic chambers around the gut or in clusters between longitudinal muscle layers and are important in metabolic processes such as lipid metabolism, carbohydrate catabolism, oxidation and detoxification. They also function in the storage of lipids, phospholipids and pigments resulting from the breakdown of blood in sanguivorous species (Sawyer 1986a, Govedich 2001).

Leeches are typically simultaneous hermaphrodites, although some may have a brief protandrous stage, and all have internal fertilisation (Sawyer 1986a,b, Davies and Govedich 2001, Govedich 2001, Kutschera and Wirtz 2001). Typically both partners exchange gametes; however, this is not always the case. Glossiphoniids mate through hypodermic implantation of a spermatophore and some individuals (called ‘sneakers’) have been observed mating with individuals that were unable to implant a reciprocal spermatophore either because they were feeding or otherwise occupied. Though rare, self-fertilisation has also been observed in some glossiphoniids (FR Govedich unpublished data).

Gonopores are located (Fig. 5.18) near the midline on the ventral surface of somites XI and XII, respectively, and are visible in reproductively mature individuals. The male gonopore is anterior to the female gonopore with the two gonopores separated by a number of annuli that are often species-specific. The male gonopore is typically larger, more obvious and may be raised or surrounded by papillae. The female gonopore is posterior to the male gonopore and is smaller in size, sometimes making it difficult to locate (Sawyer 1986a,b, Davies and Govedich 2001, Govedich 2001).

Leeches do not have true testes or ovaries, instead they have paired testisacs and ovisacs. These thin-walled sacs are derived from coelomic sacs that are lined by a special germinal epithelial layer that produce either spermatozoa (testisacs) or ova (ovisacs). Spermatozoa and ova remain within the liquid-filled sacs where they develop and mature (Anderson 1973; Sawyer 1986a; Davies and Govedich 2001; Govedich 2001). Multiple pairs of testisacs (Fig. 5.18) are usually found in the somites posterior to XI and may be discrete spherical structures (Piscicolidae, Ozobranchidae, Glossiphonidae and Hirudinidae) or multifollicular columns (resembling bunches of grapes) located next to the crop on either side of the ventral nerve cord (Erpobdellidae) (Davies and Govedich 2001, Govedich 2001). The testisacs are connected to the vasa deferentia via a short vasa deferentia. The vasa deferentia run along each side of the body, and form large coiled epidymes or sperm vesicles at their anterior end. Ejaculatory ducts run from the epidymes through the atrial cornua and unite to form the male atrium that in some species may be modified into a protrusible penis. A single pair of ovisacs (Fig. 5.18) are usually found in the somites posterior to XII and may be small spherical organs or elongate tubes that can be straight, coiled or recurved back on themselves. The ovisacs are connected by a pair of short
oviducts that converge to form a common oviduct that leads either to a vagina or directly to the female gonopore (Sawyer 1986a, b, Davies and Govedich 2001, Govedich 2001).

The digestive system consists of a mouth (Fig. 5.18) that in some leeches is a small pore located in the center or anterior part of the oral sucker, and in others the sucker may be almost completely replaced by the mouth. Leeches with a small mouth pore (piscicolids, ozobranchids and glossiphoniids) typically have an eversible muscular proboscis (Fig. 5.18), and those with a large mouth which fills the oral sucker have a buccal cavity that may lack jaws (erpobdellids) or have two or three sets of jaws that resemble half circular saw blades (hirudinids and haemadipsids) (Sawyer 1986a,b, Davies and Govedich 2001, Govedich 2001, Kutschera and Wirtz 2001).

The mouth leads to the pharynx that is connected to the salivary glands which produce chemicals used for the processing and breakdown of food. The saliva of predacious and sanguivorous (blood feeding) leeches typically serve different functions. The salivary glands of predacious leeches secrete digestive enzymes that break down the tissues and body fluids of their prey. Salivary glands in most sanguivorous leeches secrete compounds that are used for bloodsucking rather than digestion. Functions of these compounds include mucus to lubricate the mouth parts, a hyaluronidase or spreading factor to make the host’s skin more permeable, a histamine-like secretion used for vasodilation (blood vessel dilation), an anticoagulant that may prevent or break down blood clots, and possibly an anaesthetic-like compound, though this has yet to be verified (Sawyer 1986a,b, Davies and Govedich 2001, Govedich 2001).
The pharynx leads to a crop that is adapted for the storage of blood in sanguivorous leeches and food storage, digestion and absorption in many predacious leeches. The crop may be either acaecate or contain 1–11 pairs of lateral caeca (Fig. 5.18) but the number and arrangement of caeca is highly variable between genera. The crop is connected to the intestine (Fig. 5.18) where digestion and absorption of food and nutrients occurs in both predacious and sanguivorous leeches. Predacious leeches are able to digest their food within a few days, but sanguivorous ones take much longer (weeks or even months) due to their reliance on endosymbiotic bacteria that produce the enzymes needed to break down blood (Sawyer 1986a,b, Graf 1999, Davies and Govedich 2001, Govedich 2001). The anus usually opens dorsally just anterior to the posterior sucker in or near somite XXVII. The anus in a few species including Branchellion torpedinis, Actinobdella peduculata and Marsupiobdella africana is displaced further anteriorly (Sawyer 1986b, Davies and Govedich 2001, Govedich 2001).

**Life cycle**

Leeches are hermaphrodites with functional male and female reproductive systems and internal fertilisation. Once individuals reach maturity, typically three to four months after hatching under ideal conditions, individuals will mate and produce several cocoons (Fig. 5.18). In most leeches, including marine species, these cocoons are large fluid-filled chambers that contain the eggs and are provisioned with a nutrient fluid. This fluid supplies the eggs and developing young with all of the energy and nutrition they will require for growth and development. Following cocoon production, most leeches abandon their cocoons after they have been attached to vegetation, solid substrates or even future hosts (Sawyer 1986a,b, Kutschera and Wirtz 2001). In contrast glossiphoniids have extended parental care with eggs brooded in an external nest, on the ventral surface of the parent, or, in a few species, in a special brood pouch. Once glossiphoniid eggs hatch, the young are brooded and cared for by the parent (Sawyer 1986a,b, Kutschera and Wirtz 2001).

Adult marine leeches are often found attached within or near gill chambers or at fin bases of many fish, including salmon, grouper, sharks, skates and rays although a few leeches prefer to live on turtles and crocodiles. Most species must leave their host to reproduce and free-living adults are often found in estuaries where they mate and then produce their cocoons. The cocoons are abandoned and often the adults die soon after their production. Once the juveniles hatch they find their way to potential hosts where they begin feeding and growing. The hosts will often move out of estuaries after a time carrying the leeches with them (Sawyer 1986a,b).

**Economic and medical importance**

Freshwater and terrestrial leeches are recognised for their medicinal properties and have been used as a component of traditional medicines for many centuries. Leeches are used in the treatment of a variety of circulatory diseases and for reconstructive plastic surgery (Sawyer 1986a,b, Govedich 2001, Kutschera and Wirtz 2001). The saliva of leeches is also economically important with spreading factors such as hyaluronidase, and anticoagulants such as hirudin, hementin, hemenerin and destabilase synthesised and sold as medications for the treatment of blood-clotting disorders and other forms of heart disease (Sawyer 1986a,b, Govedich 2001, Kutschera and Wirtz 2001). Salivary compounds (including anticoagulants and vasodilators) of marine species have not been extensively studied and there may be many new medicinal compounds yet to be discovered.

Marine leeches have been known to reduce the value of fish catches, particularly when they have reached high densities on economically important fish species (Cruz-Lacierda et al. 2000). The economic value of these losses is not known due to inadequate records and a lack of reporting (FR Govedich pers. obs).
Effects on hosts and ecological importance
Leeches are distributed worldwide and can be found living in marine, estuarine, moist terrestrial and freshwater ecosystems. Leeches can be an integral component of benthic and occasionally pelagic communities with some species feeding on invertebrates, and others, including many piscicolid, glossiphoniid, hirudinid and haemadipsid species acting as temporary ectoparasites (sanguivory) on fish, amphibians, reptiles (turtles and crocodiles), birds and mammals. Sanguivorous species are typically not host-specific and will feed on a range of available hosts (Sawyer 1986a,b, Davies and Govedich 2001, Govedich 2001, Kutschera and Wirtz 2001).

Sanguivorous leeches typically do not permanently harm their hosts and act only as temporary ectoparasites, leaving their host following a blood meal. This is not always the case with some marine leeches spending most of their life on a host, leaving only to reproduce and lay cocoons. Typically leeches are only a minor irritant; however, there have been cases where hosts have become infested with a large number of individuals causing them stress and in extreme cases, death (Cruz-Lacierda et al. 2000). Also leeches can serve as intermediate hosts of haematozoa, particularly trypanosomes, and can act as vectors for the infection of fish (Sawyer 1986a, b, Negm-Eldin 1997).

Important references

Cycliophora (wheel wearers)
Iben Heiner and Reinhardt Møbjerg Kristensen

Introduction
The marine phylum Cycliophora was described by Funch and Kristensen (1995), the third phylum described in the 20th century. It consists presently of a single species Symbion pandora, two other species are under description. All occur in the Northern hemisphere. Symbion pandora is a microscopical animal found on the mouthparts (setae) of the lobster Nephrops norvegicus (Figs 5.19, 5.20A and B), the two other species are from the lobsters Homarus gammarus and H. americanus (Figs 5.20C and D). The Cape lobster H. capensis from the southern hemisphere has not been found in recent years and has not yet been examined. Other decapods from the Southern hemisphere seem to lack cycliophorans (RM Kristensen, pers. obs).

Cycliophora have a very complicated reproduction, involving asexual and sexual reproduction. The sessile and feeding forms of Cycliophora are epibionts (i.e. they live on another living organism, a lobster). Cyciophorans filter the water for bacteria and algae (Funch and Kristensen 1997), and therefore are commensals rather than parasites. However, they face the same problem as do parasites (i.e. they have to locate a specific host and a very small microhabitat on it), a problem they have solved in an ingenious way, having adopted a complicated life cycle that leads to the production of a great number of offspring. In addition to the feeding sessile stage, there are three non-feeding larval stages, the Pandora larva (asesexual larva), the Chordoid larva (dispersal stage) and the Prometheus larva (primary male), and two mature sexual stages, the dwarf males and the females.

The phylogenetic position of Cycliophora has been much debated since their discovery (Kristensen 2002b). The general opinion of morphologists is that they are a sister group to either
Entoprocta or to the clade Entoprocta/Ectoprocta (Funch 1996, Funch and Kristensen 1995, 1997). However, the first molecular analysis using 18S rRNA of Cycliophora showed a sister group relationship with Rotifera and Acanthocephala (Winnepennincks et al. 1998), and investigations of the phylogenetic position of Micrognathozoa using four molecular loci (Giribet et al. 2004) suggest a relationship of Cycliophora with Micrognathozoa and Syndermata (Rotifera and Acanthocephala).

Morphology and life cycle

Cycliophorans are bilateral-symmetric and have a well-differentiated cuticle. The sessile and feeding stage of *Symbion pandora* is about 0.33 mm long. The body of the animal consists of a ciliated buccal funnel, an ovoid trunk with a U-shaped digestive system, and a short stalk with an adhesive disc that attaches the animal to its host. The U-shaped digestive system ends in an anus located near the buccal funnel and the upper part of the trunk (Fig. 5.19).

In the asexual reproductive cycle the sessile animal grows by producing a single internal bud with a new buccal funnel and intestine, which later replaces the old feeding structures. The old intestine is reabsorbed and the old buccal funnel is cast off. This form of growth, inner budding, is repeated several times in each animal (Kristensen 2002a).

At some point, when the sessile animal is large enough, it produces a mobile Pandora larva inside a brooding chamber, together with the formation of an internal bud. This larva is produced asexually and while in the brooding chamber the larva already develops a new 'head' (buccal funnel), which is later used in the feeding stage (Kristensen and Funch 2002, fig. 11.2).
The Pandora larva leaves the maternal animal when the old buccal funnel is cast off. Consequently, the maternal individual can successively produce more larvae and thereby produce many offspring (Funch and Kristensen 1999). The larva moves around somewhat before settling close to the maternal individual with its head down: the new buccal funnel being formed at the rear end (Fig. 5.20D). The Pandora larva is now sessile and grows in the same way as described for the mother animal. It can then produce its own Pandora larva and thereby the asexual cycle can continue and produce more sessile feeding animals.

The sexual reproductive cycle (Kristensen 2002a) begins at the end of the lobster’s moulting cycle. The cycle starts with the sessile animal developing a Prometheus larva or a female in the same way as the Pandora larva (Obst and Funch 2003). The female resembles a Pandora larva, which has become sexually mature (neoteny) containing a large oocyte (Funch and Kristensen 1997, 1999). The Prometheus larva leaves the brooding chamber and settles on a sessile feeding individual, which starts producing a female inside its brooding chamber. The Prometheus larva develops one to several dwarf males by internal budding (Obst and Funch 2003). These dwarf

**Figure 5.20** Scanning electron micrographs of cycliophorans. A. *Symbion pandora* from Kaldbak Fjord, Faroe Islands, collected from a Norway lobster. The colony consists of young feeding stage individuals. B. Sessile feeding stage individual of *S. pandora* with attached Prometheus larva. The lobster was the same as in Fig. 5.20A. C. An undescribed species of *Symbion* from an American lobster (Maine, USA). The colony consists of old feeding stage individuals with several attached Prometheus larvae. D. A newly settled Pandora larva of *Symbion* from an American lobster (Maine, USA).
males consist mainly of a large brain, a cuticular penis and a cluster of spermatozoa. Fertilisation of the female is internal: the penis from one of the dwarf males penetrates the chamber of the sessile individual, where the female is located.

The fertilised female escapes the sessile feeding animal and may settle on the same seta as the maternal individual or further away on the palp of the mouth limb. The female also settles head down by secreting a kind of cement from numerous glands on the head forming an adhesive disc. The fertilised egg develops into a new type of larva, the Chordoid larva, eating the female, which becomes cyst-like. The Chordoid larva hatches from the cyst of the female. The larva has well-developed locomotory cilia, which it uses to swim away, dispersing to a new host. It settles on a new host, a lobster, and metamorphoses into a sessile feeding individual.

Important references
Funch, and Kristensen (1995) established the new phylum, Funch and Kristensen (1997, 1999), Kristensen (2002a,b), and Kristensen and Funch (2002) reviewed the knowledge of the group. Investigations on the phylogenetic position of the Cycliophora are by Winnepenninckx et al. (1998) and Giribet et al. (2004). Obst and Funch (2003) described the dwarf male of *Symbion pandora*. Funch (1996) showed that the chordoid larva of *Symbion pandora* is a modified trochophore.

Nemertea (ribbon worms)
Kirsten Jensen and Patricia S Sadeghian

Introduction
Ribbon worms are characterised by a ciliated epidermis and an eversible proboscis. The phylum contains more than 1100 species and about 250 genera (Gibson 1995, Thollesson and Norenburg 2003). Most species are found in benthic and pelagic marine habitats, a few species in freshwater or on land. Traditionally, the Nemertea have been divided into four subclasses: Palaeonemertea, Heteronemertea, Hoplonemertea and the Bdellonemertea. Based on molecular sequence data, Thollesson and Norenburg (2003) showed the monogeneric Bdellonemertea to be hoplonemerteans and the palaeonemerteans to be paraphyletic. To date, at least 40 species have been reported to live in symbiotic relationships with other organisms. Most of these symbiotic nemertean species are hoplonemerteans; only two records exist of symbiotic heteronemerteans. In all cases the associations are with marine invertebrates. Reports of up to ten additional undescribed symbiotic species exist in the literature (see e.g. Wickham and Kuris 1985, Sadeghian and Kuris 2001). The true nature of the symbiotic association in many cases is unknown. In early descriptions, most symbiotic nemertean taxa were considered to be true parasites (Coe 1902, Humes 1942), but most are now considered to be commensals, parasites or specialised egg predators (Berg and Gibson 1996).

Hoplonemertea
Within the Hoplonemertea, most symbiotic species belong to the families Malacobdellidae, Carcinonemertidae, Tetrastemmatidae and Emplectonematidae (see Thollesson and Norenburg 2003). However, the familial affiliations of several taxa are unclear.

*Malacobdellidae*
The Malacobdellidae contains a single genus, *Malacobdella*, with six valid species (Gibson 1995, Ivanov et al. 2002) (Table 5.1). Species of *Malacobdella* are generally considered to be endocommensals, although Sundet and Jobling (1985) argue for a parasitic life style. They inhabit the mantle cavity of bivalves predominantly of the subclass Heterodonta, but also Protobranchia
and Pteriomorphia. Five species have been reported from a single host species, whereas the type species, *Malacobdella grossa*, has been reported from at least 27 species of bivalves (in 20 genera, 13 families, 3 orders, 2 subclasses). The family has a global distribution occurring in the Eastern and Western Atlantic, and the Eastern Pacific Ocean, north of 30˚N and south of 30˚S latitude.

Malacobdellans possess a short, ventral, flattened, leech-like body. Their anterior end is notched and the posterior end bears a single, ventral, large muscular sucker. They possess a pharynx with pharyngeal papillae. The proboscis is unarmed with the stylet armature lacking. Malacobdellans are dioecious (Gibson 1968). Species of *Malacobdella* filter feed through a ciliary feeding mechanism with pharyngeal papillae trapping the food (Gibson and Jennings 1969). They ingest microscopic organisms (e.g. small algae, bacteria, protozoans) and possibly larger organisms (e.g. small copepods, nauplii) (Gibson and Jennings 1969). Typically only one adult worm is present per host clam (Gibson 1982), and, at least for *M. grossa*, a longevity of up to 20 years has been suggested (Sundet and Jobling 1985).

**Carcinonemertidae**

Carcinonemertids are symbiotic on decapod crustaceans. Historically, four genera (*Carcinonemertes*, *Ovicides*, *Alicynus*, *Pseudocarcinonemertes*) have been considered to belong to this family. However, Uhazy et al. (1985) and Campbell et al. (1989) have suggested that *Pseudocarcinonemertes* does not belong in this family, and the taxonomic position of *Alaxinus* remains uncertain. Species in the genera *Carcinonemertes* and *Ovicides* are considered ectocommensal specialised egg predators of decapod crustaceans. Adult worms are primarily found on the eggs of ovigerous females, whereas, depending on the species, juveniles can be found on the exoskeleton and gills of non-ovigerous females or the exoskeleton and gills of male crabs (Shields and Kuris 1990, Kuris 1993).

Twelve species of *Carcinonemertes* are recognised (Sadeghian 2003) (Table 5.1). Of these, seven (i.e. *C. australiensis*, *C. coei*, *C. errans*, *C. humesi*, *C. pinnotheridophila*, *C. sp. A* and *C. wickhami*) have each been reported from a single host species, and one, *C. regicides*, occurs on two host species, a lithodid and a majid crab; *C. mitsukurii* has been reported from five species of brachyuran crabs (in 3 genera, 2 families); *C. carcinophila imminuta* (awaiting elevation to species level) from 17 species of brachyuran crabs (in 11 genera, 5 families); *C. epialti* from 11 species of brachyuran crabs (in 6 genera, 5 families); *C. carcinophila*, the type species, from 17 species of brachyuran crabs (in 11 genera, 6 families) and from one species of anomuran crab. At least six undescribed species have been reported (Wickham and Kuris 1985, Sadeghian and Kuris 2001), including reports from new host families, Hippidae (see Subramonian 1970 in Wickham and Kuris 1985) and Atelecyclididae (see Wickham and Kuris 1985). *Ovicides* is monotypic, with *O. juliae* found on the brachyuran crabs *Chorodiella nigra* and *C. xishaensis* (Xanthidae).

Carcinonemertids are dioecious, rarely hermaphroditic, and are capable of parthenogenesis (Roe 1986, Shields et al. 1989). They feed on the eggs of their host by piercing the egg coat with their stylet and subsequently ingesting yolk. Life cycles of carcinonemertids range from simple (e.g. male and female worms of *C. regicides* occur only on the egg mass of ovigerous female crabs throughout the year) (Fig. 5.21), to complex (e.g. mature male and female worms of *C. epialti* live on the egg mass of ovigerous female crabs, while juvenile worms (Fig. 5.22) ensheath on the exoskeleton of juvenile and non-ovigerous females and on juvenile and adult male crabs) (see Shields and Kuris 1990, Kuris 1993). In all cases, however, male and female worms require a reproductive female crab for nutrition, maturation and reproduction.

**Tetrastemmatidae**

Four genera of tetrastemmatids have been reported to live in association with other invertebrates: *Tetrastemma*, *Asteronemertes*, and the two monotypic genera *Amphinemertes* and
Table 5.1  Symbiotic monostiliferan Hoplonemertea (Nemertea)

<table>
<thead>
<tr>
<th>Nemertean taxon</th>
<th>Host taxon</th>
</tr>
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<tbody>
<tr>
<td><strong>Monostilifera</strong></td>
<td></td>
</tr>
<tr>
<td>Malacobdellidae</td>
<td></td>
</tr>
<tr>
<td><em>Malacobella</em> (endocommensal or parasite) (see e.g. Gibson 1968, Gibson &amp; Jennings 1969, Sundet &amp; Jobling 1985)</td>
<td></td>
</tr>
<tr>
<td><em>M. arrokeana</em></td>
<td>Bivalvia: Heterodonta: Hiatellidae</td>
</tr>
<tr>
<td><em>M. grossa</em></td>
<td>Bivalvia: Heterodonta &amp; Pteromorphia</td>
</tr>
<tr>
<td><em>M. japonica</em></td>
<td>Bivalvia: Heterodonta: Mactridae</td>
</tr>
<tr>
<td><em>M. macomae</em></td>
<td>Bivalvia: Heterodonta: Tellinidae</td>
</tr>
<tr>
<td><em>M. minuta</em></td>
<td>Bivalvia: Protobranchia: Yoldiidae</td>
</tr>
<tr>
<td><em>M. siliquae</em></td>
<td>Bivalvia: Heterodonta: Pharidae</td>
</tr>
<tr>
<td><strong>Carcinonemertidae</strong></td>
<td></td>
</tr>
<tr>
<td><em>Carcinonemertes</em> (ectocommensal/egg predator) (see e.g. Kuris 1993)</td>
<td></td>
</tr>
<tr>
<td><em>C. australiensis</em></td>
<td>Decapoda: Palinura: Palinuridae</td>
</tr>
<tr>
<td><em>C. carcinophila</em></td>
<td>Decapoda: Brachyura &amp; Anomura</td>
</tr>
<tr>
<td><em>C. coei</em></td>
<td>Decapoda: Brachyura: Portunidae</td>
</tr>
<tr>
<td><em>C. epialti</em></td>
<td>Decapoda: Brachyura</td>
</tr>
<tr>
<td><em>C. errans</em></td>
<td>Decapoda: Brachyura: Cancridae</td>
</tr>
<tr>
<td><em>C. humesi</em></td>
<td>Decapoda: Brachyura: Majidae</td>
</tr>
<tr>
<td><em>C. carcinophila imminuta</em></td>
<td>Decapoda: Brachyura</td>
</tr>
<tr>
<td><em>C. mitsukuri</em></td>
<td>Decapoda: Brachyura</td>
</tr>
<tr>
<td><em>C. pinnotheridophila</em></td>
<td>Decapoda: Brachyura: Pinnotheridae</td>
</tr>
<tr>
<td><em>C. regicides</em></td>
<td>Decapoda: Brachyura &amp; Anomura</td>
</tr>
<tr>
<td><em>C. wickhami</em></td>
<td>Decapoda: Brachyura: Leucosiidae</td>
</tr>
<tr>
<td><strong>Ovicides</strong> (ectocommensal/egg predator) (see e.g. Sadeghian 2003)</td>
<td></td>
</tr>
<tr>
<td><em>O. juliae</em></td>
<td>Decapoda: Brachyura: Xanthidae</td>
</tr>
<tr>
<td><strong>Tetrastemmatidae</strong></td>
<td></td>
</tr>
<tr>
<td><em>Amphinemertes</em> (commensal/parasite ?) (see Roe 1988, Gibson 1995)</td>
<td></td>
</tr>
<tr>
<td><em>A. caeca</em></td>
<td>Urochordata: Ascidiae</td>
</tr>
<tr>
<td><em>Asteronemertes</em> (commensal) (see e.g. Gibson 1995)</td>
<td></td>
</tr>
<tr>
<td><em>A. commensalis</em></td>
<td>Echinodermata: Asteroidea: Solasteridae</td>
</tr>
<tr>
<td><em>A. gibsoni</em></td>
<td>Echinodermata: Asteroidea: Solasteridae</td>
</tr>
<tr>
<td><strong>Pseudocarcinonemertes</strong> (ectocommensal/egg predator) (see e.g. Kuris 1993)</td>
<td></td>
</tr>
<tr>
<td><em>P. homari</em></td>
<td>Decapoda: Stenopodidea: Nephropidae</td>
</tr>
<tr>
<td><strong>Tetrastremma</strong> (symbionts) (see e.g. Gibson 1995)</td>
<td></td>
</tr>
<tr>
<td><em>T. flavidum</em></td>
<td>Urochordata: Ascidiae</td>
</tr>
<tr>
<td><em>T. fozensis</em></td>
<td>Bivalvia: Heterodonta: Semelidae</td>
</tr>
<tr>
<td><em>T. kefersteinii</em></td>
<td>Urochordata: Ascidiae</td>
</tr>
<tr>
<td><em>T. marionis</em></td>
<td>Urochordata: Ascidiae</td>
</tr>
<tr>
<td><em>T. suhmi</em></td>
<td>Crustacea: Brachyura: Grapsidae</td>
</tr>
<tr>
<td><em>T. vittigerum</em></td>
<td>Urochordata: Ascidiae</td>
</tr>
</tbody>
</table>
Pseudocarcinonemertes. The genus *Tetrastemma* is comprised of 107 species (Gibson 1995), six of which have been reported to live in association with another invertebrate (symbionts in Table 5.1): *Tetrastemma flavidum*, *T. kefersteinii*, *T. marionis* and *T. vittigerum* live in the branchial or mantle cavity of tunicates (Roe 1988); *T. fozensis* lives in the mantle cavity of the bivalve *Scrobicularia plana*; and *T. suhmi* occurs on the abdomen of the grapsid crab *Planesminutus* in the Sargasso Sea (Gibson 1995). The two species of *Asteronemertes* have been reported from the ambulacral grooves of seastars, that is *A. commensalus*, from *Crossogaster papposus* from the Sea of Okhotsk, and *A. gibsoni* from *Solaster pacificus* from the Pacific coast of Russia (Gibson 1995).
Amphinemertes lives in association with tunicates dredged from Kodiak Island, Alaska (Gibson 1995). Like Carcinonemertes, Pseudocarcinonemertes is an ectocommensal egg predator. It is exclusively found on the eggs and gills of the American lobster Homarus americanus (Nephropidae), on the Atlantic coast of Canada (Fleming and Gibson 1981). The life cycle of P. homari is similar to that of carcinonemertids.

Emplectonematidae
Two genera in this family are considered to be symbionts. The monotypic genus Coenemertes has been reported ‘gliding among the thoracic legs … , near the branchial chamber’ (Corrêa 1966, p. 366) of the Ghost shrimp Callianassa sp. Of the six or seven valid species of Nemertopsis, two species have been reported from the mantle cavity, rarely the outer surfaces, of barnacles from the Banda Sea, Hong Kong and Japan (Gibson 1995). Roe (1988) suggested that N. quadripunctatus might be a true commensal or parasite. Two additional species have been reported in loose association with another invertebrate (Dichonemertes hartmanae associated with burrows of mud shrimp and Emplectonema kandai on tunicates).

Genera of uncertain familial status
Five species in four genera are considered to live in association with other invertebrates: species in the monotypic genera Alaxinus and Cryptonemertes, both species of Gononemertes and one of the 19 species of Oerstedia. The familial placement of these genera is currently unclear.

Alaxinus oclairi is an ectocommensal egg predator on the eggs of the anomuran crab Paralithodes camtschatica (Lithodidae). Cryptonemertes actinophila occurs as a potential commensal
beneath the pedal disk of five different species of sea anemones (in three genera, three families) (Gibson 1986). Both species of Gononemertes are endocommensals within ascidians. Specifically, G. australiensis has been reported from the liver or anus, in the atrium under the pharynx, or among liver and gonad tissue (Gibson 1974). Each species has been reported from two host species, in two different families of ascidians (Table 5.1). Finally, one of 19 species of Oerstadia recognised by Gibson (1995) is found ‘with ascidians’ (p. 524).

Heteronemertea

Only two heteronemertean worms have been documented in association with other invertebrates (Table 5.2). Nemertoscolex parasiticus was reported from the coelomic fluid of the echiuran Echiurus echiurus collected on the west coast of Sweden (Berg and Gibson 1996). It may be a true endoparasite. Uchidana parasita was described from the mantle cavity, but also from ‘the spaces between the shell and mantle’ (p. 135) of the bivalve Mactra sulcataria from the Mie Prefecture in Japan (Iwata 1967). Uchidana parasita may be a true ectoparasite, since the species appears to ingest host gill tissue (Iwata 1967).

Economic importance

Nemertean egg predators (i.e. species of Carcinonemertes, Ovicides, Alaxinus and Pseudocarci
nonemertes) have the potential for great ecological or economic impact on their host populations. Egg mortality arising from these infections have been documented from several host populations including the Dungeness crab, Cancer magister, and the Tanner crab, Chionoecetes bairdi (see e.g. Kuris and Wickham 1987), the Yellow shore crab, Hemigrapsus oregonensis (see e.g. Shields and Kuris 1988), the American lobster, Homarus americanus (see e.g. Fleming and Gibson 1981) and the Red king crab, Paralithodes camtschatica (see e.g. Kuris et al. 1991). Widespread outbreaks of C. errans and C. regicides occurred in the 1970s and 1980s resulting in significant damage to both the Dungeness and Red king crab fisheries (Wickham 1980, Kuris et al. 1991). Due to the massive presence of these egg predators (mean intensities up to 1000 worms per pleopod), many crab hosts were effectively castrated, losing all of their eggs (Kuris et al. 1991). Kuris (1993) suggested significant egg loss on a population level due to egg predation and/or increased grooming behaviour of hosts as a result of infection. At least for C. regicides, outbreaks were associated with hydrographic features that contributed to the retention of the infectious larvae in the system (Kuris et al. 1991).

Important references

Rotifera and Seison (rotifers)
Wilko H. Ahlrichs

Introduction
Most rotifers occur in freshwater, and fewer than 5% of the about 2000 species are marine. Very few are parasitic. The genus Seison was formerly included in the Rotifera. However, recent ultrastructural studies have shown that it should not be included in that group (Ahlrichs 1995).

Rotifera
Morphology and diversity
Females are about 100 µm to 200 µm long, males of most species are not known. Those that are known are generally much smaller than females and usually lack a digestive system and some other organs. The body of the female is elongated and consists of three regions: head including the rotatory organ, body or trunk, and foot (Fig. 5.23). Each region shows characteristic folds, the so-called pseudosegments. These folds function like joints, but genuine segmentation is not present.

Life cycle
In Bdelloidea no males are present at all. Parthenogenesis is common in rotifers; females produce diploid amictic (‘without mixing’) eggs by mitosis that develop into diploid females. During unfavourable periods, females may produce haploid mictic eggs that if not fertilised, develop into males. If these mictic eggs are fertilised, they become resistant eggs that can remain dormant.

A parasitic life has been suggested for Zelinkiella synaptae, Albertia crystallina, Albertia naidis, Proales paguri, and Proales gonothyraeae.

Zelinkiella synaptae (Bdelloidea) (150–200 µm long) has a rotatory organ that has two separate trochoal discs. It is viviparous and lives on the body surface (tentacles) mainly of the sea cucumbers Synapta digitata and S.inhaerens (Holothuria, Echinodermata) but is also found on Amphithritae (Annelida). It is not known if Z. synaptae harms its hosts, it may be commensal (Remane 1929b).

Albertia naidis (Monogononta) (Syn. A. intrusor; A. soyeri) (94–340 µm long) is oviparous and cosmopolitan, and parasitic in freshwater oligochaetes. Levander (1894) found this species in Stylaria lacustris in brackish water in the far eastern Baltic Sea. It has also been found in Nais elinguis from brackish water but has not been reported from saltwater habitats (Remane 1929b, De Smed 1996).

Figure 5.23  Proales paguri, female, dorsal view. Redrawn and modified after Thane-Fenchel (1966).
**Albertia crystallina** (220 µm long) lives attached to the intestinal epithelium of brackish or marine *Paranais littoralis* (Oligochaeta, Annelida) in the Baltic Sea (?). It has not been found again since its first description in 1851. The description is insufficient (Remane 1929b, De Smed 1996).

*Proales paguri* (Monogononta) (199–213 µm long) (Fig. 5.23) lives on the gills of the hermit crab, *Eupagurus bernhardus*, and apparently feeds on the gill epithelium of its host (i.e. it is a genuine parasite) (Thane-Fenchel 1968, De Smed 1996).

*Proales gonothyraeae*, (250–300 µm long), has an almost ventral rotatory organ. It lives within the theca of the hydroid polyp, *Laomedea loveni*. *Proales gonothyraeae* may be ectoparasitic, but whether it harms the host is unclear (Remane 1929a, De Smed 1996).

**Seison**

**Morphology and diversity**

The taxon *Seison* consists of two dioecious species, *Seison nebaliae* (2000 µm long) and *S. annulatus* (1100 µm long). Both species have a head, a long and narrow telescopic neck, a ventrally bent trunk, and a foot with several pseudosegments and ending in an adhesion disc (Fig. 5.24). They live on the surface of leptostracan crustaceans (e.g. *Nebalia bipes*). It seems that only older hosts with a carapax larger than 6 mm are chosen. *Seison nebaliae* lives on the entire surface of the crustaceans, whereas *S. annulatus* seems to prefer the gills of the thoracopods below the carapax. Ultrastructural findings indicate that *S. annulatus* feeds on haemolymph of the host, whereas *S. nebaliae* feeds on bacteria (Ahlrichs 1995).

**Life cycle**

Males and females are of equal size. Parthenogenetic reproduction, common in rotifers, is absent. The eggs are glued to the body surface of the host (Koste 1975, Ahlrichs 1995, 2003).

**Important references**

Ahlrichs’ (1995) electron microscopic studies suggest that *Seison* is not a rotifer. Koste (1975) described *Seison annulatus* in some detail. Remane (1929a) described *Proales gonothyraeae*, a parasitic rotifer on hydroid polyps. Comprehensive accounts of rotifers are by Remane (1929b) and De Smet (1996).
Introduction
The Nematomorpha have a superficial resemblance to nematodes. They are parasites of arthropods which complete their development within hosts but emerge from these for reproduction. About 300 species have been described. Most (taxon Gordiida) reproduce in freshwater and parasitise terrestrial hosts, but the genus *Nectonema* with five species is marine.

Morphology and diversity
Species of *Nectonema* show sexual dimorphism. Females are generally larger than males and have a round posterior end, whereas the posterior end of males is tapering and curved at an angle of 90° towards the ventral side (Figs 5.25, 5.26). The smallest body length reported is 10 mm (male of *N. melanocephalum*), the maximum length is 960 mm (female of *N. munidae*). Average lengths are 100 mm to 150 mm for males and around 400 mm for females. Males are almost transparent and generally much more mobile than females, while females are opaquely white in colour. Some species have darker pigments in some body regions. Characteristic for *Nectonema* is a ventral and a dorsal row of cuticular bristles (Figs 5.25, 5.26, 5.28, 5.29). On close view, it consists of two parallel rows. The function is likely to support a pelagic lifestyle, therefore they are named natatory bristles. The body is covered with a cuticle which is moulted once.

Figure 5.25  General organisation of a male *Nectonema agile*. The posterior end is bent 90° in relation to the remaining body. Note natatory bristles along the body. After Fewkes (1883).

Figure 5.26  Male posterior end of *Nectonema agile*. After Beattie (1987).
during the parasitic phase. Internally, the reproductive system is dominant and adult worms are almost completely filled with gametes. The head region is separated from the remaining body by a solid muscular septum. Within the head is a cavity which includes up to four giant cells with unknown function. Ultrastructural studies have shown a connection to the nervous system and the cells might be sensory in function (Schmidt-Rhaesa 1996a). Nutrients are consumed during the parasitic phase through the integument and probably additionally through the intestinal system (Skaling and MacKinnon 1988). In adults, the intestine is non-functional and ends blindly.

Five species and some unidentified specimens have been reported from several locations. The most abundant species is *Nectonema agile*. It was described and reported several times from the northwest Atlantic, mainly from the region around the marine station of Woods Hole (Massachusetts, USA) and from the Bay of Fundy, New Brunswick, Canada. Additionally, specimens

![Figure 5.27 Larva of *Nectonema munidae*. After Huus (1932).](image)

Figure 5.27 Larva of *Nectonema munidae*. After Huus (1932).

![Figure 5.28 Anterior end from a specimen of *Nectonema agile* from the Mediterranean Sea, close to Naples. From museum specimen, Museum für Naturkunde, Berlin, accession no. 5284).](image)

Figure 5.28 Anterior end from a specimen of *Nectonema agile* from the Mediterranean Sea, close to Naples. From museum specimen, Museum für Naturkunde, Berlin, accession no. 5284).
Minor groups and fossils

from the northeast Atlantic (near Bretagne, France, and in the Mediterranean Sea) and the Black Sea are also assigned to *N. agile*. Regionally restricted, but collected several times is *N. munidae* from a few fjords near Bergen, Norway. Three species have been found only once: *N. melanocephalum* from near the Indonesian islands (Nierstrasz 1907), *N. svensksundi* from Svalbard (Bock 1913) and *N. zealancorta* from the South Island of New Zealand (Poinar and Brockerhoff 2001). Additional undetermined records come from Western Greenland (Nouvel and Nouvel 1938), Northern Norway (Bakke 1975) and Japan (Oku et al. 1993).

Species resemble each other in general but differ in size, pigmentation and the presence or absence of septum and giant cells. Because septum and giant cells appear late in the development of *N. munidae* (see Schmidt-Rhaesa 1996a), their partial or complete lack in species such as *N. svensksundi* and *N. melanocephalum* might be due to immature specimens.

Life cycles

Life cycles are incompletely known. *Nectonema* specimens are most often found in the body cavity of their host as late, worm-like juveniles. Rarely have they been caught in the sea where they were found close to the surface. In two cases, specimens were kept in the laboratory and some details on reproduction and early larval development were observed (Huus 1932 and a Masters thesis by Beattie 1987, some details from this thesis can be found in Schmidt-Rhaesa 1999). Sperm transfer is direct, the male inserts its complete posterior end into the female genital opening. From eggs hatch microscopic larvae with two rings containing six spines each and two central hooks (Fig. 5.27). This roughly resembles the larvae of freshwater Gordiida which have three rings of hooks and three central stylets. These structures are used for host infection which can also be assumed for the larva of *Nectonema*. Whereas in Gordiida, a paratenic host is often present, there is no such evidence in *Nectonema* and the final host may be infected directly. Life cycle is most mysterious in *N. munidae* because reproduction takes place close to the water surface, but hosts (mostly *Munida* species) live benthic in the more than 700 m deep fjords. Probably larval, planktonic stages of the crustaceans are already infected by larvae of *N. munidae*.

All hosts of *Nectonema* species are decapod crustaceans. A summary has been given by Poinar and Brockerhoff (2001). A variety of decapods are parasitised, ranging from shrimp-like forms to galatheid crabs, hermit crabs and brachyuran crabs. Rates of parasitisation seem to be generally low. For *N. munidae*, a prevalence of less than 10% has been reported, in *N. agile* it ranges from 0.5% to 50% (summary in Arvy 1963), and in *N. zealancorta* 12.7% of the
investigated crabs are parasitised (Poinar and Brockerhoff 2001). Parasitisation is periodic and varies throughout the year (Poinar and Brockerhoff 2001). Usually one single specimen of *N. zealandica* was found per crab, but multiple parasitations (up to four specimens) also occur (Poinar and Brockerhoff 2001).

**Important references**

There are only about 40 publications dealing with *Nectonema*. Early morphological investigations are by Bürger (1891), Ward (1892), Nierstrasz (1907), Bock (1913) and Feyel (1936). Ultrastructural details have been reported by Bresciani (1975, 1991), Skaling and MacKinnon (1988) and Schmidt-Rhaesa (1996a,b, 1997, 1998). Summaries of hosts and data on parasitisation rates can be found in Arvy (1963), Nielsen (1969), Leslie et al. (1981), Brattey et al. (1985) and Poinar and Brockerhoff (2001).

**Acari (mites and ticks)**

Jacek Dabert

**Introduction**

Mites and ticks (subclass Acari) are members of the class Arachnida (Evans 1992). Forty thousand species have been described, but there may be more than one million (Walter and Proctor 1999). Therefore, mites may be among the most species-rich groups of animals, after insects and possibly nematodes. The main and most important evolutionary novelty of Acari – an extreme body miniaturisation – allows them to exploit many niches that most other arthropods cannot use. The group is primarily terrestrial, but many mites live in fresh or salt water.

All ticks are blood-sucking parasites of vertebrates, attacking mammals, birds, reptiles and occasionally amphibians. In contrast, mites utilise many food resources as predators, phytophages, fungivores, saprophages, ectoparasites and, more rarely, endoparasites of invertebrate and vertebrate hosts, including many marine animals.

**Systematics and morphology**

It is not certain that the two main lineages of the class Acari, superorders Actinotrichida (Acariformes) and Anactinotrichida (Opilioacariformes + Parasitiformes) are monophyletic. Parasitic mites of marine animals belong to both lineages (i.e. to the four orders: Astigmata and Prostigmata) (Acariformes), and Ixodida and Mesostigmata (Parasitiformes). Members of the clade of mites called ‘ticks’ (Ixodida, Metastigmata) are much larger than other mites (to over 1 cm), and because of their leathery, stretchy integument may reach 3 cm when engorged (Evans 1992). The movable gnathosoma is adapted for blood sucking and has characteristic anteriorly projecting saw-like hypostome and chelicerae with outwardly directed teeth modified for cutting skin. A complex chemosensory apparatus, Haller’s organ, is situated dorsally on the tarsus of the first leg pair. These sense organs together with various mechanoreceptors and olfactory setae on the palps enable ticks to locate hosts and attach to them.

Mites of the Mesostigmata (=Gamasida) are a large and diverse group adapted to many habitats and life strategies, including ectoparasitism and endoparasitism. They range in size from 0.2 cm to almost 2.5 cm. Modifications for parasitism concern mainly the chelicerae, in particular the degree of development of the fixed digit, dentation of both digits, and the relative lengths of the first and second segments (Evans 1992). Body modifications may also be pronounced (e.g. body elongation in some Halarachnidae parasitising pinnipeds) but many parasitic forms have a body plan similar to the predatory ones (e.g. haematophagous dermanyssids or macronyssids of birds).
Prostigmata (=Actinedida) is the most enigmatic taxon and needs fundamental revision (Evans 1992). It is the most heterogeneous mite order, comprising very diverse forms that use many habitats and food resources. About 70% of the Prostigmata are parasites or parasitoids of various animals including other mites (Kethley 1982). The biggest prostigmatid mites are water and velvet mites, which may be 0.5 cm to more than 1 cm long, but most are smaller than 1 mm. The body of parasitic forms may be greatly modified (e.g. in worm-like Demodecidae in hair follicles, or cigar-like Syringophilidae in feather quills). The chelicerae may be dentate-chelate but often, especially in parasitic forms, they are modified to long stilettos. Legs, especially in parasitic forms, may be greatly modified and one or more pairs may even be lost.

Most taxa within the Astigmata (=Acaridida) are associated with vertebrate and invertebrate animals and relatively few are exclusively free living. However, the most characteristic feature of astigmatid mites is the phoretic, highly modified deuteronymph (hypopus) that occurs in many free-living groups and is lost in more derived parasitic forms. The body size range is generally about 0.5 mm to 1 mm long. Astigmata are usually soft-bodied but the hypopi and many commensals and parasites (e.g. most pterolichoid and analgoid feather mites) are covered by strongly sclerotised shields. The primarily ovate body of free-living species may be strongly modified in parasitic ones. The most bizarre body shapes are displayed by feather mites (Fig. 5.30A–D) with, for example, hypertrophied particular body parts and/or legs, variously shaped opisthosomal lobes, leaf-like setae or fancily sculptured cuticular shields; males of some species are asymmetric. Chelicerae are generally not modified, chelate-dentate with exception of Histiostomatoidea in which chelicerae are modified to filter-feeding structures. In some parasites chelicerae and/or palpi may be hypertrophied. The pretarsi in most parasitic and commensal forms are modified into a membranous ambulacrum. Legs of parasitic forms may be variously modified (e.g. to clasp organs, Myocoptidae) or to hypertrophied legs with various apophyses in males of many feather mites.

Diversity of parasitic Acari of marine animals

Most parasitic Acari are associated with terrestrial or freshwater hosts. Examples of parasitic acarids of marine animals are briefly discussed below.

Parasites of invertebrates

Almost all parasitic mites of marine invertebrates belong to the prostigmatid family Halacaridae (Bartsch 1987) and are associated with hosts of several phyla. Spongihalacarus longiscutus, a halacarid mite with completely reduced palps, is a probable parasite of the sponge Haliclona cymaeformis (Otto 2000). Members of the genus Bradyague live on colonial sublittoral and bathyal hydrozoans (Cnidaria) and have hind legs adapted for grasping the stolons (Bartsch 1989). However, hypotheses about parasitic lifestyles of these mites (Walter and Proctor 1999) are not fully supported by recent investigations (I Bartsch, pers. comm. 24 Feb. 2004). Parhalixodectes travei is probably a sublittoral ectoparasite on Cerebratulus hepaticus (Nemertini) (Walter and Proctor 1999). Halixodes chitonis (Halixodinae) is a parasite of gills and mantle cavity of chitons (Mollusca) in New Zealand (Walter and Proctor 1999). Another mollusc, Mytilus (Bivalvia), is a host to two mite genera: the halacarid Copidognathus and astigmatid Hyadesia (Cáceres-Martínez et al. 2000). Halacarids are relatively common parasites of decapods (Crustacea). Two Copidognathus species are parasitic in the gill chambers of the slipper lobster Parribacus antarcticus and on the egg packets of the spider crab Maja squinado (Walter and Proctor 1999). The gill chambers of a marine decapod (Peltarrium spinulosum) are infested by Veladeacarus gasoni. Enterohalacarus minutilpalpis (Enterohalacarinae), a mite with remarkably reduced palps, has been recorded as an internal parasite in digestive tracts of deep-sea urchins Plesioderma indicum (Echinoidea) in the Pacific (Bartsch 1987).
Parasites of vertebrates

Marine mammals, birds and reptiles are hosts of several unrelated mite groups: Halarachnidae and Rhinonyssidae (Mesostigmata); Ixodidae and Argasidae (Ixodida); Demodecidae, Syringlyophilidae, Trombiculidae and Cloacaridae (Prostigmata); Hypoderatidae and numerous families of feather mites (Astigmata). Records of mite infestation in fishes concern exclusively freshwater ones (Walter and Proctor 1999, Halliday and Collins 2002). Mites of hosts that spend at least part of their life in the open ocean or sea are discussed below.

Reptilia. Marine iguanas *Amblyrhynchus cristatus* (Iguanidae) are infected by hard ticks *Amblyomma* (Ixodidae) and soft ticks *Ornithodoros* (Argasidae) (Wikelski 1999). Trombiculid mites of the genus *Vatacarus* live in their nasal fossae, tracheal passages and lungs (Wikelski 1999). *Vatacarus* undergoes remarkable neosomy (cuticular growth within a stage) and feeds only as a larva (Krantz 1978, Walter and Proctor 1999). Another member of this genus (*V. ipoides*) is found in the same locations in sea snakes (Krantz 1978). Sea snakes are also hosts of other trombiculids (*Eutrombicula poppi*) (Krantz 1978). *Chelonacarus elongatus* (Cloacaridae) is found in the cloacal tissue of the sea turtle *Chelonia mydas* from the Atlantic coast (Pence and Scott 1998).

Aves. Terrestrial and aquatic birds are hosts of many acarids (Proctor and Owens 2000). Ticks belong to the most abundant and harmful ectoparasites. *Ixodes uriae* (Ixodidae) is the most common parasite of many sea birds in the northern and southern circumpolar regions and has one of the widest distributions of any tick species (McCoy and Tirard 2002). In the northeast Atlantic it infects dense colonies of cliff-nesting sea birds, (e.g. the common guillemot, *Uria aalge*, and the black-legged kittiwake, *Rissa tridactyla*) (Danchin 1992, Barton et al. 1995). It commonly infests also many penguin species (Sphenisciformes), especially chicks. *Haemaphysalis leporispalustris* is another hard tick infesting marine birds (Laridae) (Hyland et al. 2000). Soft ticks of the genus *Ornithodoros* (Argasidae) are largely restricted to the Western Hemisphere and some are truly cosmopolitan, parasitising many birds, including marine species (Keirans et al. 1980, Wikelski 1999). Rhinonyssidae (Mesostigmata) are other blood-sucking ectoparasites that inhabit the nares of many birds, including marine ones (*Larinyssus* on gulls, *Rhinonyssus* on marine ducks) (Butenko 1975, Butenko and Staniukovich 2001).

Bird plumage, skin and subcutaneous tissue are infested by numerous mite parasites of the orders Astigmata and Prostigmata. The deuteronymphs of Hypoderatidae live under the skin of many terrestrial birds and are also found in marine birds (many Procellariiformes and Charadriiformes) (OConnor 1985, Pence and Hoberg 1991, Pence and Cole 1995). The prostigmatid Syringlyophilidae inhabit feather quills of many bird taxa and feed on soft tissue fluids by piercing the quill wall with long chelicerae (Kethley 1971). Marine birds are parasitised by the genera *Creagonycha, Philoxanthornea* (on Lari), *Syringonomus* (on Procellariiformes) and *Stibarakris* (Pelecaniformes). The prostigmatid, *Eutrombicula orlovensis*, is known from gulls (Kudryashova 1998).

Two astigmatid superfamilies, Analgoidea and Pterolichoidea, are the most diverse mite groups inhabiting plumage and skin of all avian orders, excluding penguins (Gaud and Atyeo 1996). Feather vanes of large contour feathers are inhabited by analgoid Alloptidae, Avenzoariidae, Psoroptoidae and pterolichoid Freyanidae, Kramerellidae, Piloxenidae (on Gaviiformes, Procellariiformes, Pelecaniformes, Charadriiformes, Podicipediformes and Anseriformes). In down feather live mites of the analgoid family Xolalgidae (on Procellariiformes, Pelecaniformes, Charadriiformes, Podicipediformes and Anseriformes). Feather quill are parasitised by three families: analgoid Apionacaridae, Dermogliphidae and pterolichoid Syringobiidae (on Charadriiformes and Pelecaniformes). Skin parasites belong to the analgoid families Dermatiodae and Epidermoptidae (on Procellariiformes, Charadriiformes, Pelecaniformes and Anseriformes). Some mites of the family Laminosioptidae (Fainocoptinae) that are sometimes
included into the Analgoidea are parasites of the follicles of developing feathers in Podicipediformes. Nasal parasites of the pyroglyphoid family Turbinoptidae are known from Charadriiformes (Fain 1977).

**Mammalia.** Endoparasitic mites of pinnipeds (seals, walruses and sea lions) and sea otters belong to the mesostigmatic Halarachnidae (lung mites), and include the viviparous genera *Halarachne* and *Orthohalarachne* (Kenyon et al. 1965, Konishi and Shimazaki 1998). Halarachnids commonly occur on the surface of mucous membranes of the nasal passages, trachea, bronchi, and lungs and feed on the blood and mucosal tissue (Kim 1985). These marine mammals are infected by two species of minute (0.1 mm) mites of the genus *Demodex* (*D. zalophi* and *D. phocidi*, Demodecidae) (Dailey and Nutting 1980, Desch et al. 2003). *Demodex* mites are observed in hair follicles and sebaceous glands around the face, over the genitalia, flippers and ventral body.

**Life cycles**

The primary number of stages in the life cycle of Acari is seven: egg, prelarva, larva, protonymph, deuteronymph, tritonymph and adult (Evans 1992). This full scheme is shortened by omitting particular stages in most recent Acari (Walter and Proctor 1999). Selected examples of life cycles of main parasitic mite groups from marine animals are briefly discussed below.

Hard ticks have only three active stages: larva, nymph (probably protonymph) and adult; in soft ticks there are two to eight nymphal molts (Hoogstraal 1973). Most ixodid ticks have different hosts for each stage, but some species are one-host or two-host parasites (Oliver 1989). The single-host tick *Ixodes uriae* shows a highly seasonal pattern of feeding which coincides with the main breeding period of its sea bird hosts taking its blood meal during the few months in which the sea birds return to land to breed (Barton et al. 1995). The tick cycle lasts for at least three years. Each developmental stage (with exception of adult males) takes one blood meal during the bird’s breeding season. The duration of the blood meal is at least six days for each tick stage (Murray and Vestjens 1967, Barton et al. 1995). Ticks are on the hosts only during the blood meal, spending most of their lives in a limited area surrounding the sea bird’s nests on the ground, mainly under stones (Frenot et al. 2001).

Mesostigmatans have reduced ontogeny to a larva, two nymphs and adults by suppression of the tritonymph. In parasitic Halarachnidae the larva is an active, feeding and dispersing stage. Short-lived proto- and deuteronymph are non-feeding stages. Adults are feeding stages, sometimes with highly modified worm-like body (*Orthohalarachne attenuata*). The suppression of nymphal stages is also a common phenomenon in other mites (e.g. Halacaridae). The larva after a short immobile period molts into various numbers of nymphal stages. All three nymphs are present only in one freshwater species, in most other species the tritonymph is suppressed or only protonymph is retained as in marine species.

Adult Hypoderatidae are nidicolous (living in a nest) and free-living forms. Females are ooviviparous. The larvae moult in the nest into protonymphs. The next stage is the small, heteromorphic deuteronymph (hypopus) that penetrate actively through the skin of the nestlings. In gannets, *Sula*, the hypopus greatly grow and live to five years waiting for the host maturity (Fain and Clark 1994). Because of hormone activity of hosts the tissular hypopi are rejected into the nest where they molt to the tritonymph or directly to the adult.

The complete life cycle of feather mites takes place on the body of bird hosts. As in all Psoroptidia the deuteronymph is absent. The gravid female is most often the dispersal stage. Generally the transfer is vertical from adult birds to fledglings; exceptionally horizontal by means of parasitic insects (Epidermoptidae). Eggs are stuck to the bases of feather barbs or in the feather quills; ooviviparity sometimes occurs (e.g. in some Syringobiidae). The life cycle
may be synchronised with those of the hosts (Mironov and Malyshev 2002); however, no data on marine birds exist.

**Effects on hosts**

There is no evidence of detrimental effects of parasitic halacarid mites on marine invertebrates. However, there are some data indicating that some Acari harm their marine bird and mammal hosts, both directly and as vectors of diseases. Mites and ticks do not invariably cause severe disease, but environmental conditions may sometimes be suitable for heavy infestations resulting in debilitation and death of affected animals (Kerry et al. 2000).

Ticks may cause damage by their consumption of blood (anaemia) and dermatological illnesses caused by mechanical injuries and toxins injected (dermatosis and paralysis) (Sonenshine 1991, Roberts and Janovy 1996). But much more dangerous are pathogens transmitted by ticks. Ticks transmit more infectious agents than any other blood-feeding arthropods (e.g. Lyme disease, relapsing fever, tick fever, and boutonneuse fever) (Nuttall 1984). Lyme disease spirochetes, *Borrelia burgdorferi*, have been found in both sea birds nesting on sub-Antarctic islands and their tick *Ixodes uriae* (Gauthier-Clerc et al. 1999, Gylfe et al. 1999). Also viruses are carried by ticks and can infect the birds on which ticks feed. Antibodies to flaviviruses have been found in several sub-Antarctic penguin species, although associated disease has not been observed (Morgan et al. 1985).

Gauthier-Clerc et al. (1998) reported that the high infestation of king penguins by *Ixodes uriae* may induce some deaths, and several dozen birds were observed in poor condition. The blood loss on a dead hyperinfested adult was estimated at 100 mL to 300 mL, which corresponds to more than 10% of its total blood volume. Penguins with ticks had lower success in rearing chicks than uninfested parents. Tick infestation leads to large featherless areas in king penguins, which could increase heat loss and affect diving efficiency (Mangin et al. 2003).

The effect of halacarid infection on pinnipeds or sea otters depends on the intensity of infection. These mites cause copious amounts of mucus in the upper respiratory tract and nose, nasal discharge, dyspnea, and coughing. Severe infections may lead to an impairment of respiration followed by lesions in the lungs. Intensive infection predisposes the host to more serious diseases, or even kills the host. Transmission from animal to humans with subsequent ocular discharge has been reported in one case (Dahme and Popp 1963, Dunlap et al. 1976, Fay and Furman 1982, Raga 1992).

Follicle mites (Demodecidae) are generally considered harmless. However *Demodex zalophi* from sea lions has been implicated in the development of alopecia and thickening of the skin over host genitalia, flippers and belly. Sea otters have also been observed to have *Demodex* mites but no serious dermatologic conditions have been observed. They cause only a mild follicular ectasia and minimal associated folliculitis (Moeller 1997).

Examples of detrimental parasitism among astigmatid feather mites of marine birds are rare. Some of them are undoubtedly detrimental causing skin lesions (Epidermoptidae) or destroying the feathers by chewing out the medulla (some Syringobiidae). However, other feather mites are paraphages constantly removing preen oil from the feathers and perhaps forcing birds into energetically costly supplementary production of this substance. There are experimental data supporting the hypothesis that feather mites negatively affect the fitness of hosts (J Dabert, unpubl. data). Another astigmatid group, Hypoderatidae, comprises ‘real’ parasites; their deutero-nymphs live under the skin destroying the subcutaneous tissue.

As a final note, crested auklets, *Aethia cristatella*, nest in dense colonies that smell like tangines from a long distance. A provocative hypothesis is that the birds may produce this unique scent, among other things, to repel ectoparasites (H Douglas, Institute of Marine Science, University of Alaska pers. comm.).
Important references

Pycnogonida (pycnogonids)
David Staples

Introduction
Over 1200 species belonging to about 80 genera are recognised worldwide. Records of endoparasitic or ectoparasitic relationships are so common that probably a parasitic stage is obligatory in the life cycle of all species. Associations are often with colonial animals such as hydroids, bryozoans and corals, colonies of which are made up of individual intercommunicating hydranths, zooids and polyps. Observations of pycnogonids feeding on these groups could simply be interpreted as predation, but because feeding does not necessarily lead to the demise of the colony they are regarded here as parasitic. Movement of pycnogonids is typically sluggish and tentative; consequently recorded associations are commonly with sessile or slow-moving animals such as sea anemones, bryozoans, hydroids, algae and sponges.

Morphology and diversity
The relationship of pycnogonids to other groups of arthropods has been a contentious issue resulting in varying classifications of the group. The rank of subphylum is common in the literature; however, current thinking based primarily on morphological characters places them as a class of the subphylum Cheliceriformes. Possession of multiple gonopores, a well-developed proboscis, ovigers (specialised grooming and egg-bearing appendages) and a much reduced abdomen, highlight the distinctiveness of the group, tempting some authors to go so far as to treat the taxon Pycnogonida as an infraphylum or phylum. Current researchers using DNA sequencing to establish relationships between arthropods are also divided on the standing of the group. It is anticipated that the growing body of molecular work will ultimately provide a greater understanding of these unresolved issues.

Only two diverse families lack records of a parasitic stage but both are difficult to observe in situ; the Colossendeidae primarily because it inhabits great depth and the Rynchothoracidae because of its tiny size and interstitial life style. The remaining eight families are the Nymphoniidae, Ammotheidae, Callipallenidae, Pallenopsidae, Phoxichilidiidae, Endeidae, Pycnogonidae and Austrodecidae. All families are accommodated in the only extant order, the Pantopoda.

The adult body consists of an anterior proboscis with a mouth at its tip, a trunk, usually consisting of four (but seven species with five and two with six) segments that support the four, five or six pairs of walking legs and a reduced one-segmented abdomen with terminal anus. Each body segment has a pair of lateral processes with which the legs articulate. The anterior-most segment (cephalon) supports several additional appendages and bears a dorsal ocular tubercle. A reduced one-segmented abdomen is attached to the posterior-most segment. Classification is primarily dependent on the presence, absence or degree of development of the appendages attached to the cephalon. These are the chelifores, originating above the proboscis, the palps, carried either side of the proboscis, and the ventrally situated ovigers posterior to the proboscis.
Life cycles

With few exceptions the sexes are distinct and separate. The externally fertilised eggs are passed from the female and gathered by the male onto the ovigers where they are cemented individually into balls or bracelets or embedded into a gelatinous ribbon-like mass wrapped around both ovigers. In some species, ovigers are entirely absent in which case the eggs are cemented directly onto the ventral surface of the trunk of the male.

The larval form is called the protonymphon in which stage a parasitic phase is most common (Fig. 5.31A). The extraordinary numbers of transitional forms that separate adult pycnogonids are not apparent in the protonymphon, which makes it difficult to identify specimens to species level. Larval development is variable but typically they hatch from the egg with an ovoid body bearing an anterior proboscis and functional chelifores (present in all protonymphon) and two pair of 'larval legs'. Spinous or tendril-like processes that possibly provide additional means of attachment and entanglement around a host often accompany these larval legs. In some cases a long thread, presumably serving a similar function, is also

Figure 5.31  A. Protonymphon Ammomothea australiensis removed from adult male. Blanket Bay, Vic., Australia. B. Unidentified protonymphon with two pair of adult legs developed, grasping stolon of hydroid Plumularia australis. Penguin I., WA. C. Juvenile Ascarhynchus? inside gall on gorgonia Chrysogorgia papillosa. After Stock (1953). D. Unidentified protonymphon encapsulated in hydrotheca of hydroid Obelia bidentata from Papua New Guinea. E. Larva of Tanystylum sp. attached to the hydranth of hydroid Pennaria wilsoni. F. Unidentified protonymphon attached to the mantle fold of nudibranch Jorunna sp. (ventral view) from Bass Strait, SA.
secreted from a gland at the base of each chelifore. Walking legs are added sequentially with subsequent moults.

The chelae function as the primary attachment to the host, each bearing one fixed and one moveable finger. The fingers are gaping, pointed and pincer-like, capable of penetrating the host tissue. In some instances the chelae serve the sole purpose of grasping the host during the early life stages after which they are shed or atrophy to non-functional knobs with the last larval moult.

The protonymphon leaves the male at differing stages of development, in some cases shortly after emerging from the egg to invade cnidarians, especially hydroids (Fig. 5.31B). In other instances the protonymphon develop to a more advanced stage before commencing a free-living existence on the same host substrate as the adult, usually a hydroid or bryozoan. Species associated with sand, some living interstitially, may deposit protonymphon among the grains, which could account for their parasitic association with soft-bodied invertebrates found in these environments such as opisthobranchs, holothurians and bivalve molluscs. The diversity of hosts and infrequency of repeated observations suggests that many of these associations are a consequence of a chance encounter. In other instances a greater degree of host specificity is demonstrated.

Cnidarians are particularly well represented in parasitic associations within diverse pycnogonid families; the Pycnogonidae, Endeidae, Phoxichilidiidae, Nymphonidae, Ammotheidae, Pallenopsidae and Callipallenidae. Three families are recorded living parasitically with anemones. *Pycnogonum* has a particular relationship with several anemone species; the adults feeding ectoparasitically on the outside wall of the host and the juveniles endoparasitically in the gastrovascular cavity. The Ammotheid *Ammothella biunguiculata* (Dohrn 1881) has also been recorded in the gastrovascular cavity of an anemone; in one instance 67 juveniles infested a single host (Miyazaki 2002).

In their natural environment, individuals appear able to feed without obvious ill-effect on the anemone, survival possibly being dependent on the pycnogonid moving on in search of a new host. Stock (1953) figured gall-like swellings on the gorgonian *Chrysogorgia papillosa* (Fig. 5.31C). Each gall was slightly larger than a retracted polyp and contained a tightly folded pycnogonid. There are numerous records of associations between pycnogonids and scleractinian corals. Child (1988) recorded six pycnogonid families being associated with a single species of coral. Similarly five pycnogonid families have been recorded in association with zoanthids.

The most frequently reported endoparasitic association in pycnogonid literature is between larval pycnogonids and hydroids, where pycnogonids are either encapsulated in gall-like vesicles or attached to a hydranth of the host (Staples and Watson 1987) (Figs 5.31D, E). Researchers noted pyriform sacs for some time before it was realised that a solitary larva was tucked inside an aborted hydrotheca or gonotheca. Most records of larval encystment are in athecate hydroids and involve larvae predominantly of the family Phoxichilidiidae. These larvae have also been observed living free in the gastric cavity of Tubularian hydroids without any apparent ill effects on the host (Loman 1907). The Nymphonidae also have a strong association with hydroids, adults and juveniles being frequently recorded feeding ectoparasitically on the same hydroid colony.

One of the most puzzling associations is that of larval pycnogonids and hydroid medusae. As many as 30 individuals of the larva stages of *Ammothella alaskensis* have been found attached to Anthomedusae dredged from a muddy sea floor. The larvae were on the wall of the manubrium under the exumbrella with their proboscides piercing the soft tissue of the host (Okuda 1940). Other records indicated similar infestation of medusae belonging to several hydroid genera but it is still unknown how the protonymphon become attached or if this association eventually leads to the demise of the medusae. Arango (2001) recorded a species of *Endeis* feeding in large numbers on the Hydrozoan (hydrocoral) *Millepora exaesa*. The only endoparasitic record with a
Predation on bryozoans by pycnogonids is well documented. Adult and juvenile pycnogonids feed by consuming the contents of individual zooids either by crushing the zooid before feeding or by sucking out the contents directly through the frontal pore. Such an association has been observed in southern Australian waters where species of *Pseudopallene* have an obligate association with catenicellid bryozoans, namely, *Orthoscuticellid spp.* Wyer and King (1973) record the use of palps by *Achelia echinata* to prevent closure of the operculum on the frontal pore of bryozoan zooids allowing insertion of the proboscis to suck out the contents. An encystment stage has not been recorded in bryozoans.

Juvenile pycnogonids of the Ammotheid genus *Nymphonella* have been reported living parasitically in several species of infaunal and epifaunal bivalve molluscs in Japanese waters. From one to 21 young and adults of *Achelia chelata* were also found infesting the mussel *Mytilus californianus*, partly destroying the tissue, in some instances to the point of atrophy (Benson and Chivers 1960).

Opisthobranchs are a diverse group of molluscs that include the bubble shells, the sea hares and the nudibranchs, all of which have a documented parasitic association with pycnogonids. Young pycnogonids are most often found attached to the foot and mantle of the host by means of their chelifores and with their proboscides piercing the host tissue (Fig. 5.31F). Forty young stages of *Ammothea* were recorded as ectoparasites on the nudibranch *Arminia variolosa* (Ohshima 1933).

In a collection of ophiuroids from the Seychelle Islands, three species of the genus *Ophiocoma* were found infested with 1 to 29 specimens of *Anoplodactylus ophiurophilus*. All three species of ophiuroid feed by mucus entrapment of particles suggesting that the presence of pycnogonids on the ventral side of the arms, near the mouth and along the ambulacra placed them in the best position to encounter the mucus-impregnated food being transported towards the mouth of the host. Fewer pycnogonids were, however, observed with podia firmly grasped in their chelae, possibly feeding on the soft tissue of the host (Sloan 1979).

In the few ectoparasitic associations with asteroids, all specimens have been taken from the oral surface and ambulacral grooves.

There are also few recorded associations with sea urchins. In one case 19 juvenile specimens of *Pycnosomia strongylocentroti* fixed by their chelae were found among the spines of *Strongylocentrotus* sp. (Losina-Losinsky 1933). This could suggest a parasitic association involving the protruding soft parts of the echinoid such as the podia.

Ohshima (1927) gives an account of up to 30 individuals of *Ammothela hilgendorfi* attached to the holothurian *Holothuria lubrica*. Parasitic associations involving both errant and sedentary polychaetes have been recorded. Juveniles of what were thought to be *Ammothella spinifera* have been found as apparent ectoparasites on the polychaete *Sabella melanostigma*. Several juveniles living inside the Sabellid tube were attached by their chelifores, depressions in the body wall of the Sabellid suggesting that they were feeding on the host tissue (Salazar-Vallejo and Stock 1987).

**Effects on hosts and ecological importance**

It is difficult to assess the importance of pycnogonids in marine food chains. They are active predators of hydroids and bryozoans and there is no doubt that when present in large numbers their impact on individual colonies can be significant. Entire colonies of the hydroid *Halocordyle wilsoni* can be stripped completely by a species of *Tanystylum* found in southern Australian waters and significant portions of bryozoan colonies are destroyed as a consequence of
predation by *Pseudopallene* spp. Ryland (1976) is of the opinion that pycnogonids are the most important consumers of bryozoans.

**Important references**
For comprehensive reviews of the group, readers are referred to Arnaud and Bamber (1987) and Cadien (1997).

**Insecta (insects)**
Kirsten Jensen and Ricardo L. Palma

**Introduction**
The Insecta is the most diverse group of metazoan animals on land, possibly including over one million species (most of them not yet described). Few free-living species have invaded marine habitats, but many are parasitic on marine mammals and birds, often causing considerable harm to their hosts. Only five of the over 12 000 species of caddisflies are marine, and only one of these is known to be a larval parasite of starfish.

**Phthiraptera**
Phthiraptera (lice) are wingless, dorso-ventrally flattened, ectoparasitic insects with single host life cycles, completing their life cycle in or on the feathers, hair or skin of vertebrates. They are hemimetabolous and their developmental stages consist of the egg, three nymphal stages and adult. Four suborders are recognised in the order (Barker et al. 2003), three of which are known to parasitise marine vertebrates: the Amblycera (Fig. 5.32A) and Ischnocera (Fig. 5.32B), both known as chewing lice, and the Anoplura (Fig. 5.32C), known as sucking lice. Amblycera and Ischnocera are ectoparasites of birds and mammals. The Anoplura exclusively parasitise mammals.

**Chewing lice of marine birds (Amblycera and Ischnocera)**
Over 4460 valid species of amblycerans and ischnocerans are recognised (Price et al. 2003), 88% parasitising birds, and the rest mammals. In marine ecosystems, amblycerans and ischnocerans are restricted to birds. This section is focused on amblyceran and ischnoceran lice that are associated with bird families that consist entirely or largely of marine species (e.g. Diomedeidae and Laridae, respectively).

Amblycera and Ischnocera possess mandibulate chewing mouthparts and a head that is as wide as or wider than the prothorax. Two characters used to distinguish between these groups are the presence or absence of maxillary palps and form of the antennae. Amblycerans possess maxillary papillae and have four-segmented antennae concealed in lateral grooves. Ischnocerans lack maxillary papillae and possess filiform antennae that are fully visible (Johnson and Clayton 2003). Amblycerans feed mainly on feathers, host skin products and blood, as well as on eggs and moulting nymphs of conspecifics or lice of other species. In contrast, most ischnocerans feed on feathers and dead skin (see Murray 1976, Johnson and Clayton 2003). In general, amblycerans are less site-specific than are ischnocerans (see Marshall 1981), but some degree of site specificity is exhibited by most taxa. For example, *Saemundssonia* species parasite the heads of their hosts (see Marshall 1981), *Naubutes* primarily the wing feathers (see Palma and Pilgrim 2002), and adults of *Piagetiella* the throat pouch (see Marshall 1981). The major mode of transmission of these lice between hosts is via direct contact of individual birds (Johnson and Clayton 2003).
Lice of marine birds, in general, do not possess adaptations to cope with the marine environment since they essentially lead a terrestrial life style, including lice parasitising penguins, which live in a pocket of air among the water repellent feathers, without contact with the marine environment.

Sucking lice of marine mammals (Anoplura)
Over 532 species of anoplurans in 15 families are known (Durden and Musser 1994). Echinophthiriidae is the only anopluran family reported from marine mammals. Anoplurans possess a head that is narrower than the prothorax, and piercing–sucking mouthparts. They feed on host blood by inserting their mouthparts directly into the host blood vessels.

Lice of hair seals (Phocidae) live exposed to the marine environment among sparse, scale-like hair on regions of the body used in heat dissipation (e.g. flippers, tail, genital and anal orifices), and thus are required to spend prolonged periods of time submersed (see Marshall 1981). These lice require adaptations to cold-water temperatures, and submersion. Lice of fur seals (Otaridae) either parasitise the pelage and therefore live in the air space created by the fur, not exposed to the marine environment, or, like lice of hair seals, live on the exposed/naked areas of the body (e.g. fins, nostrils and eyelids). Adaptations include unusually well-developed musculature and valves of the atria of the thoracic and abdominal spiracles, presumably to prevent water from entering during prolonged dives (Marshall 1981). In addition, modified scale-like setae on the abdomen are thought to trap air to allow for gaseous diffusion through the cuticle when submersed (see Murray 1976, Mehlhorn et al. 2002).

Host associations and specificity
Eight genera of Amblycera have been reported from marine bird families (Table 5.3), but five of them also include species parasitic on non-marine birds: species of Colpocephalum and...
Austromenopon parasitise birds in 11 and four avian orders, respectively; species of Actornithophilus parasitise birds in 11 families of Charadriiformes, but only three of them are exclusively marine; and Eidmanniella and Piagetiella include a few species parasitic on freshwater species of cormorants and pelicans. Therefore, only three amblyceran genera are restricted to exclusively marine bird families: Ancistrona and Longimenopon with species parasitic on petrels, and Fregatiella unique to the frigatebirds.

Based on the index of host specificity as defined by Caira et al. (2003) and the data from (Price et al. 2003), specificity index values were calculated for 22 species of amblycerans in five genera (i.e. genera parasitising bird groups in which all or most of the species are marine). Five of the six species of Longimenopon are oioxenous (only found in one species of host), and one species is euryxenous (parasitising hosts in more than one family). All nine species of Piagetiella are either oioxenous or mesostenoxenous (restricted to a number of species in one genus). Four of the five species of Eidmanniella are mesostenoxenous, and one species is metastenoxenous (parasitising hosts in one family, but more than one genus). The single species of Fregatiella is mesostenoxenous. Ancistrona vagelli is euryxenous.

Ischnoceran lice of marine birds are more diverse than amblycerans. Eighteen genera have been reported from marine birds (Table 5.3). Fifteen of these are restricted to exclusively marine birds, whereas most species of Quadraceps and Saemundssonia, but only a few species of Pectinopygus, are found also on non-marine birds. Specificity of these lice at the generic level is pronounced. Eleven of the 16 genera are each unique to a single bird family. These are: Austrogoniodes and Nesiotinus on penguins (although see Mey et al. 2002), Bedfordiella, Pseudonirmus, Naubates and Trabeulus on petrels, Episbates and Harrisoniella on albatrosses, Haffneria on skuas and jaegers, Pelmatocerandra on diving petrels and Philoceanus on storm petrels. Five genera (Pectinopygus, Docophoroides, Paraclisis, Halipeurus and Perineus) are each reported from two or more families within one order.

Host specificity index values (sensu Caira et al. 2003) based on data from Price et al. (2003) and Banks and Palma (2003) were calculated for 140 species of ischnocerans in 16 genera which parasitise only marine birds. By this analysis, 66 species are oioxenous, 59 are mesostenoxenous, 14 are metastenoxenous and one is euryxenous.

Because of their narrow specificity (89% of the 162 ambllyceran and ischnoceran species analysed parasitise one or more species within a single genus), lice of marine birds have been used in cophylogenetic studies, mainly comparing louse and host phylogenies using a variety of methods (Paterson et al. 2000, Paterson and Banks 2001, Banks and Paterson 2004, Page et al. 2004). Evidence of cospeciation is not consistently unequivocal.

Marine mammals serving as hosts for sucking lice are pinnipeds, belonging to the carnivore families Odobenidae (walruses), Otariidae (eared seals, fur seals and sea lions) and Phocidae (true, earless or hair seals). The sucking louse family Echinophthiriidae consists of five genera, four of which (Antarctophthirus, Echinophthirus, Lepidophthirus and Proechinophthirus) are restricted to pinnipeds. While Antarctophthirus parasitises all three pinniped families, Echinophthirus and Lepidophthirus parasitise only phocids, and Proechinophthirus is restricted to otariids (Durden and Musser 1994). A total of 11 species of sucking lice have been reported from 21 of the 33 species of pinnipeds. Seven of the 11 species are oioxenous (also Kim 1985). Among the species that parasitise more than one species of host, none parasitise hosts from more than one family (i.e. are mesostenoxenous or metastenoxenous).

**Effects on hosts**

Studies on the effect of chewing lice on marine birds are few (see Johnson and Clayton 2003) and little is known overall.
Direct and indirect effects on the health of their marine mammal hosts by anopluran lice have been suggested. During times of decreased food availability, high burdens of the louse *Echinophthirius horridus* on harbour seals, *Phoca vitulina*, may ultimately contribute to a reduction in the survival of young seals (Thompson et al. 1998). In addition, *E. horridus* is the intermediate host of the seal heartworm, *Dipetalonema spirocauda*. Infection by this nematode impairs the host’s blood circulation (Geraci and Lounsbury 2002).

### Siphonaptera

Siphonaptera (fleas) are wingless, bilaterally flattened, ectoparasitic insects on warm-blooded vertebrates. Fleas are holometabolous and their developmental stages consist of the egg, usually three larval stages, pupa and adult. With two exceptions, the adult is the only parasitic stage. Adult fleas possess piercing–sucking mouth parts and feed exclusively on host blood. When the adults reproduce and oviposit on the host, the eggs are not attached and drop off, commonly into the nest of their hosts or the surroundings. Consequently, development from egg to pupae occurs away from the host, with the larvae feeding on debris, including the faeces of the adult fleas.

The order Siphonaptera consists of almost 2000 species (not including subspecies) in 15 families (Lewis 1998), most of which parasitise mammals; however, some species are found
parasitising birds. There are no records of fleas from marine mammals. According to Lewis (1998), 106 species of fleas in 16 genera parasitise birds. At least 30 species of fleas in 10 genera (i.e. Actenopsylla, Ceratophyllus, Dasypsyllus, Glaciopsyllus, Listronius, Megabothris, Miotenopsylla, Notiopsylla, Parapsyllus and Xenopsylla) belonging to four families (Ceratophyllidae, Pulicipidae, Pygiopsyllidae and Rhopalopsyllidae), parasitise marine birds as their primary host (Johnson 1957, Smit 1979, Hoberg and Wéhle 1982, Traub et al. 1983, Smit 1984, Holland 1985). A marine bird is considered the primary host if the bird shows the highest prevalence of infection with this flea as compared to other non-marine birds, and if the flea breeds in the marine bird’s nest. One species of flea with a most unusual life history is Glaciopsyllus antarcticus (Ceratophyllidae), a species parasitising two petrel species breeding in Antarctica. This species is one of only two flea species in which the larvae are also parasitic on the host, feeding on blood, and pupating on the host, instead of in the nest (Bell et al. 1988).

While there are few studies in which the effects of fleas on marine bird populations have been measured (see e.g. Merino et al. 1999), effects similar to those of ticks and mites (i.e. nestling mortality and nest abandonment) can be speculated with high intensities of infestation (Merino et al. 1999).

Trichoptera
Though poorly known, one species of caddisfly is intriguing because of its apparent parasitic association with starfish. While all of the about 12 000 caddisfly species (order Trichoptera) develop in freshwater, only the five species in the family Chathamiidae are known to have marine larvae. One of these five species (Philanisus plebeius) is unique among caddisflies in that females may oviposit individual, small clusters or strings of eggs in the coelomic cavity of starfish of the genus Patiriella (Asteroidae, Asterinidae), where they hatch. The larvae subsequently leave the starfish and become free living in the intertidal zone. Philanisus plebeius occurs in coastal south-eastern Australia and New Zealand. Anderson et al. (1976) reported caddisfly eggs from the starfish Patiriella exigua in Australia, while Winterbourn and Anderson (1980) reported them from Patiriella regularis in New Zealand. Eggs of Philanisus plebeius are not surrounded by a protective gelatinous or cement-like matrix common among other trichopterans (Anderson and Lawson-Kerr 1977). Unfortunately, oviposition and escape of larvae from the starfish have not been observed in nature.

Important references

Tardigrada (water bears)
Reinhardt Møbjerg Kristensen and Jesper Guldberg Hansen

Introduction
The phylum Tardigrada (water bears) consists of microscopic, multicellular coelomates with four pairs of segmented legs. Tardigrades belong to the Panarthropoda group, together with fossil lobopodians, onychophorans (velvet worms) and arthropods (Nielsen 2001). Recent
molecular studies support the tardigrade–arthropod relationship (Giribet et al. 1996, Garey et al. 1999). With an adult size of 0.08 mm to 1.2 mm (most marine species are only 0.1 mm to 0.3 mm) they are among the smallest Metazoa. The herbivorous tardigrades move with a slow, bear-like gait, hence their common name ‘water bears’, whereas the carnivorous tardigrades are some of the fastest moving animals in the world (relative to their size). About 930 species have been described worldwide today, but taxonomists expect that at least 10 000 species exist. About 770 species are semiterrestrial and the rest (160 species) are true marine species. Tardigrades are found from highest elevations in the Himalayas to deep trenches in the deep sea, and from hot springs to the ice cathedrals inside the ice cap of Greenland. However, they are all aquatic animals in the active state, whether from the dry desert or tropical rainforest. Only three extant ectoparasitic tardigrades have been described; however, a recently recorded fossil from Siberian limestone (mid Cambrian, approximate 520 million years ago) indicates that parasitism in heterotardigrades may have developed very early (Maas and Waloszek 2001). The claws and the whole body configuration are similar to the extant tardigrade *Tetrakentron synaptae* living on holothurians (Kristensen 1980). True heterotardigrades and eutardigrades are found in Cretaceous amber from North America (Cooper 1964, Bertolani and Grimaldi 2000) (i.e. the modern lineages of heterotardigrades and eutardigrades have existed for at least 90 million years).

**Morphology**

The body is bilaterally symmetrical with five distinct body segments including a cephalic segment and four trunk segments each bearing a pair of segmented legs. The terrestrial and limnic forms have reduced the segmentation in their stumpy legs with two to four claws, while marine forms may have telescopically segmental legs with up to 13 claws or four to six toes with complex claws. Other marine tardigrades have rod-shaped adhesive discs or round suction discs also inserted on the foot via toes.

The digestive system consists of three major parts: the foregut (ectodermal origin), the midgut (mesodermal origin) and the hindgut (ectodermal origin). The foregut is a very complex feeding structure and consists of a mouth cavity, buccal tube, pharyngeal apparatus with placoids and oesophagus all lined with cuticle. Furthermore, associated with the buccal tube is a stylet apparatus, which in the plesiomorphic condition consists of a calcium carbonate-encrusted stylets and stylet supports. The stylets and the stylet supports may be strongly reduced mouth limbs (mandibles and maxillae).

The nervous system is distinctly metameric consisting of the three-lobed brain, the subpharyngeal ganglion and the four ventral trunk ganglia. Characteristic for all tardigrades is the paired commissure going from the protocerebrum to the first ventral trunk ganglion. Both heterotardigrades and eutardigrades may have eyespots, usually located inside the protocerebrum. The sensory structures found on the head, trunk and legs seems to be homologous to that of single arthropod sensillae. Tardigrades lack respiratory organs or gas exchange structures. Gaseous exchange takes place trough the epidermal cells and the complex cuticle.

**Diversity and life styles**

Hermaphrodism has been reported to occur in representatives of most families of eutardigrades; however, only one marine heterotardigrade species is hermaphroditic, all others are dioecious.
Males are unknown in many species of the heterotardigrade genus *Echiniscus*. Sexes are not always easily distinguished externally but males can be smaller, and in heterotardigrades the chemoreceptors (clavae) can be longer. Internal fertilisation by copulation is present in nearly all marine species, preceded by complex courtship behaviour. Eggs are round or oval and possess a smooth or ornamented shell. Ornamented eggs are generally laid free and are found in many eutardigrade genera and in the heterotardigrade genus *Oreella*. All other known heterotardigrades lay smooth eggs either free or in the exuvium.

The life span of tardigrades varies according to temperature; arctic species can live more than one year, temperate–tropic species only a few months. As a reaction to desiccation or low temperature the life cycle can be lengthened by cryptobiosis, a state without any metabolism. In this state the tardigrade can survive many years.

Most heterotardigrades are herbivorous, feeding by piercing plants cells with the two stylets, and sucking the contents by the strong muscular pharyngeal apparatus with armature (placoids). Almost all true carnivorous species are terrestrial eutardigrades. Bacterivorous tardigrades are perhaps more common than we know today, and many small soil tardigrades feed on bacteria. Symbiotic bacteria in the head are found in many arthrotardigrades of the subfamily Florarctinae.

**Parasitism in the tardigrades**

Tardigrades are found in association with several other invertebrates, for example *Actinarctus doryphorus* with the echinoderm *Echinocyamus pusillus* (see Schultz 1935, Grell 1937) and *Echiniscoides sigismundi* in *Mytilus edulis* (see Green 1950) or on *Semibalanus balanoides* (see Kristensen and Hallas 1980). However, in all these cases the tardigrades have been found later to be free living, interstitial or living on algae. True ectoparasitism on animals is only found in three marine species:

1. *Tetrakentron synaptae* (subfamily Styraconyxinae, Arthrotardigrada) is an obligate ectoparasite on the holothurian *Leptosynapta galliennei*
2. *Pleocola limnoriae* (subfamily Styraconyxinae, Arthrotardigrada) is a facultative ectoparasite on the pleotelson and pleopods of the isopod *Linnornia lignorum*
3. *Echiniscoides hoepneri* (family Echiniscoidea, Echiniscoidea) is an obligate ectoparasite on the cirriped *Semibalanus balanoides*.

*Pleocola limnoriae* was only collected once on *Linnornia lignorum* at Roscoff, France (Cantacuzène 1951). Only one to two tardigrades were found on the isopod, and about 3% of the isopods were infected. There is no sign of adaptation to parasitism in the morphology of the tardigrade. It has never been found again, in spite of thorough studies. LW Pollock has claimed that he has observed the species free living in the interstitial environment, but his observation could be on a closely related species.

The tidal tardigrade *Echiniscoides hoepneri* was only found on the cirriped *Semibalanus balanoides* at three localities in Greenland. It lives together with its sister species *Echiniscoides sigismundi* (see Kristensen and Hallas 1980); however, whereas *E. sigismundi* sucks out green algae on the barnacle, *E. hoepneri* sucks out the embryos in the brood chamber of its host. The species was only found on the basal membrane, when the barnacle was released from the substrate. The species is adapted to ectoparasitism. The stylets are extremely long compared with the stylets of other species of free-living *Echiniscoides*. Furthermore, the stylets grow longer after each moult, while the length of the stylets in other species of *Echiniscoides* usually stop growing after the last instar of juveniles (Kristensen and Hallas 1980, Fig. 49). Elsewhere, the morphology of *E. hoepneri* does not show adaptation to parasitism; however, the species has lost the ability to anhydrobiosis, a physiological character exhibited by the sister species *E. sigismundi*. 
The ectoparasite *Tetrakentron synaptae* on the holothurian *Leptosynapta galliennei* has been well investigated since its discovery in Roscoff, France (Cuénot 1892). The species has never been collected outside Brittany and it has not been found on other holothurians (Marcus 1929, van der Land 1975, Kristensen 1980). Cuénot (1932) recorded only one to three specimens on each host’s tentacles; however, more than 100 may be present on the trunk of the host. The incidence of infection may be as high as 25% to 50% in the Bay of Roscoff depending of how old the host is. The tardigrade is strongly adapted to parasitism and was for the first time observed to suck out epidermal cells of the holothurian in the investigation of Kristensen (1980, Fig 7a). New data of the morphology and life cycle of this aberrant tardigrade are included in the following paragraph. *Tetrakentron synaptae* specimens were investigated in a period from 1974 to 2004. Adults were found on the sea cucumber from April to October, juveniles only in June and July. The sediment of the slimy tube of the sea cucumber was investigated. Two species of the tardigrade genus *Batillipes* were found, but not one specimen of *Tetrakentron synaptae*, indicating that this species really is closely associated with its host.

The species, *Tetrakentron synaptae*, is closely associated with the sea cucumber *Leptosynapta galliennei*. It does not occur on *L. inhaerens*, which was also investigated for the tardigrade at Roscoff, Brittany. *Tetrakentron synaptae* adheres strongly to the sea cucumber; however, the tardigrades can be detached by freshwater treatment of the host. The tardigrades survive freshwater, and especially the large females (182–238 µm) will survive for several days (Fig. 5.33A). In the laboratory the female lays free eggs in clusters (4–8), thereafter the female moults. Hence, the eggs are not deposited in the exuvium as seen in some other heterotardigrades. One week after the eggs are laid, embryos are observed inside the eggs (Fig. 5.33B). The exuvium of the female was investigated, and the very complex seminal receptacles were observed for the first time. Later the two cuticular receptacles were also found in the adult female (rs, Fig. 5.33A). The female is strongly dorsoventrally flattened and has an enlarged epicuticle without pillars. The lack of pillars makes the outer epicuticle very loose, and this part of the cuticle breaks off often (arrows, Fig. 5.34). The anus is located almost dorsally and the gonopore caudally. Two different types of males were collected. One type of male (127–198 µm) is less modified than the female (Fig. 5.33D) and is more slender. This male is strongly mobile and virile and was seen moving around on the sea cucumber. Mating was not observed; however, females had many spermatozoans in the seminal receptacles. The secondary clavae (chemoreceptors) are dome-shaped (sc, Fig. 5.33D) and larger than in a sessile female. This type of male actively locates the female on the sea cucumber. The other type of male is a dwarf male (75–83 µm). It is as dorsoventrally flattened as the female (Fig. 5.33E), and this type was always observed close to the females. The dwarf male was observed only when the population of tardigrades was large (more than 200 animals on one sea cucumber). Both type of males have mature spermatozoa in the testis (te, Fig. 5.33D, E). The egg measured 45 µm, and the smallest juvenile (probably the first instar), 55 µm in length. However, this juvenile had already four sets of claws (Fig. 5.33C), unique for an arthrotardigrade, whose first instar larva usually has two sets of claws at hatching.

Adaptation to parasitism is also observed in the enlarged claws and stylet glands, and the reduction in all sensory structures except for the cirrus E (cE) and secondary clava. Furthermore all stages have four sets of three-pointed claws on each leg.

**Important references**

For comprehensive accounts of Tardigrada the reader is referred to the monographs by Marcus (1929), Cuénot (1932) and Ramazzotti and Maucci (1983). Important papers on the best known species, the parasitic marine tardigrade *Tetrakentron synapta*, are by Van der Land (1975) and Kristensen (1980).
Figure 5.33 Life cycle studies of the arthrotardigrade *Tetrakentron synaptae*. A. Ventral view of an adult female. B. Lateral view of embryo inside the free-laid egg. C. Ventral view of juvenile (female?). D. Ventral view of mobile male. E. Dorsal view of nearly sessile dwarf male. Abbreviations: an, anus; cE, cirrus E; cg, enlarged claw gland; ec, external cirrus; go, gonopore; ic, internal cirrus; lc, lateral cirrus; le1–le4, leg anlage; mc, median cirrus; mg, midgut; oo, oocyte; pc, primary clava; ph, pharyngeal bulb; sg, enlarged stylet gland; te, testis.
Pentastomida (tongue worms)
Wolfgang Böckeler

Introduction
The pentastomids (tongue worms) include about 120 species. It is still uncertain whether they are a separate phylum closely related to the arthropods (Storch and Boeckeler 1979, Böckeler 1984a, Storch 1993) or whether they should be included within the branchiuran Crustacea (Wingstrand 1972, Abele 1989, Storch and Jamieson 1992, Zrzavi 2001).

Pentastomids have two pairs of hooks (Fig. 5.35) at the distal end of more or less pronounced appendages. The two orders of pentastomids (Storch 1993) can be distinguished by the position of the hooks. In the approximately 40 species of Cephalobaenida, they lie behind each other, whereas in the Porocephalida they are aligned in one row besides the mouth opening. In addition to the genera *Cephalobaena* and *Raillietiella*, the ‘lower’ Cephalobaenida also contain the marine *Reighardia*. All other genera are included within the Porocephalida.

The free-living ancestors of pentastomids were microscopic (several hundred micrometres) with seven to eight metameres, and can be traced back to the Cambrium (about 500 million years ago, mya). They were discovered as part of the marine fauna among the upper Cambrian ‘Orsten’ fossils of Sweden (Waloszek and Möller 1994, Waloszek et al. 1994). They are thought to have adapted to parasitism by enlarging their body size (especially of females) and adapting their digestive apparatus to blood meals (Böckeler 1984a).

Ontogenetic studies on *Reighardia sternae* show clearly that the expansion of body size was due to a sac-like enlargement of the last original segment caudal to the genital pore (Böckeler 1984a).

Morphology and diversity
Pentastomids are obligate parasites at all stages of their life cycle. The definitive hosts of Pentastomida are usually reptiles, about 70% of which are snakes. Intermediate hosts are found among invertebrates and vertebrates of all classes, except birds. Within the intermediate host, larvae
become encapsulated and develop to the 5th larval stage by moulting. Species of the genus *Lin-\textguatula* have mammals as final and intermediate hosts.

All recent species are vermiform; they are bloodsuckers (respiratory system and air sacs of sea birds and reptiles) or feed on mucus and sloughed cells (nasopharyngeal cavity of mammals) and attain maturity in the respiratory tract of their final hosts. The length of the females ranges from 20 mm to 160 mm and thus they belong to the largest endoparasites within the arthropods. Males reach a size between 10 mm and 20 mm. Ten different types of glands have been described from *Raillietiella* sp. (Stender-Seidel et al. 2000). Penetration by histolytic processes, evasion of the host’s immune response (Riley et al. 1979, Riley 1992), pheromones, migration within the body cavity of the host and antimicrobial avoidance in the lungs of the host require high specialisations of the glandular system. Their migration over a long distance in the final hosts also demands a surprising number of different kinds of sensilla (Storch and Böckeler 1979). However, a vascular system and respiratory organs are lacking. Special cells, the ionocytes may have replaced an excretory system. Strong sexual dimorphism is known for all species. The species *Reighardia sternae* parasitising sea birds differs in its morphology from that of other species: the exocuticle exhibits tubercular structures, the intestine ends blindly and the eggs develop synchronously in the uterus.

**The genus Reighardia**

Although the genus *Reighardia* occurs and is transmitted within the marine environment, it is not a typical marine parasite since it only infects marine birds. *Reighardia sternae* has been recovered from 17 species of sea birds worldwide (Laridae; Sterndidae; Alcidae). Dyck (1975) has described a second species, *R. lonvnia*, from *Uria aalge*. Transmission is direct and no intermediate hosts (e.g. fish or invertebrates) are involved.

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**Figure 5.35** Anterior end of a female of *Reighardia sternae*. Scale bar = 0.5 mm.
The biology of Reighardia sternae

Incidence of infection

The occurrence of *R. sternae*, which to date has only been reported in sea birds, makes it the only pentastomid species occurring in a marine environment (beside *R. lomvia*). *Reighardia sternae* is euryxenous (i.e. a parasite with a wide host range), since it has been isolated from 17 different species of sea birds worldwide (Laridae; Sternidae; Alcidae).

Collections of seagulls, mainly *Larus argentatus*, from British coasts (Halton Deans, Calverly Bridge, Scarborough and at other locations on the east coast of Yorkshire) and from German coasts (Helgoland, Cuxhaven, Lübeck and Kiel) followed by laboratory experiments (Banaja et al. 1975, Böckeler 1984b, Riley 1972, Vauk-Hentzelt 1984, von Haffner and Rack 1965) strengthen the opinion that *R. sternae* is homoxenous (i.e. occurs only) in sea birds. The questions of the time and mode of transmission and the quest for a facultative intermediate host are fascinating and, until now, have only been solved indirectly.

Investigations of seagulls from Helgoland, Cuxhaven, Lübeck and Kiel have elucidated the epidemiological situation of *R. sternae* (Böckeler 1984b, Vauk-Hentzelt 1984) on German coasts and on the east coast of Yorkshire (Riley 1972). The investigations were based on 2270 *Larus argentatus* collected to clarify extensive and intensive infections by *R. sternae*.

Studies by different authors at different places (Table 5.4) show remarkably similar results: the lowest incidence of *R. sternae* is observed in adults. All authors have reported no findings in nestlings. Similar outcomes have been obtained in *L. marinus* (Böckeler and Vauk-Hentzelt 1979) and *L. ridibundus* (Riley 1972, Böckeler 1984b).

Seasonal occurrence

The distribution of *R. sternae* in the host population is heterogeneous throughout the year. In October–November on German coasts, more seagulls than usual are found to be infected. Not only have recent infections by *Reighardia* larvae been found, but also seagulls with transmittable gravid females. A corresponding biometrical analysis has suggested that, in the autumn and winter, subspecies populations of *L. argentatus* move from the north Atlantic to the German coasts. This implies that infected seagulls migrate to the ‘warmer’ regions, since feeding resources in the north Atlantic become scarce. Another (lower) peak has been shown for March and April. Between May and September, the prevalence of *R. sternae* is very low, since the infected gulls return to their original biotope. In May–June, adult *L. argentatus* are feeding and raising their nestlings. As adults are rarely infected and nestlings never contain *R. sternae* (Table 5.4), transmission to the nestlings cannot take place during the spring or by feeding.

Intensity of infection

The results of different authors are both similar and remarkable: the intensity of *R. sternae* infections is strikingly low. Out of 185 gulls, 96 individuals were inhabited by only one or two
pentastomids; three or four *R. sternae* individuals were isolated from 40 gulls; five or six from 26; and seven to eight from 16, and nine or 10 from only seven gulls. A strong, intensive infection (more than 10 *R. sternae* specimens per seagull) appeared seldom (only in 23 cases of 208). Only twice were heavy infections (more than 50 parasites) observed. Similarly low infections have been observed in *Larus marinus, L. canus,* and *L. ridibundus* (Böckeler 1984b). Riley (1972) has reported an average of three *Reighardia* females per bird.

**Epidemiology and life cycle**

The results given above indicate a homoxenous, but euryxenous, life cycle for *R. sternae* (Fig. 5.36): intensive infections and egg production are relatively low. *Reighardia* embryos grow until the transmissible (5th) infective stage for final hosts inside the uterus of the female and not as in other pentastomids (*e.g.*, *Raillietiella* sp.) (Thomas 1995), encapsulated inside an intermediate host, where the 5th stage remains until an oral transmission to the final host takes place. Investigations on freshly shot and dissected seagulls, laboratory experiments and the study of the complete ontogenesis (Böckeler 1984b) strengthen the opinion of direct transmission in *R. sternae* (Banaja et al. 1975, 1976, Riley 1972, Böckeler 1984b). An intermediate host has not yet been detected, either naturally or experimentally. Some marine organisms (Amphipoda, Decapoda, and the flatfish *Pleuronecta platessa*) have been studied for their possible role as intermediate hosts for *R. sternae* (Vauk-Hentzelt and Schumann 1980), but without success.

Seagulls (*e.g.* *L. argentatus*) come into contact with the eggs or total gravid females of *R. sternae* containing the 5th stage larvae. Depending on abiotic factors (ground/temperature/humidity), the females or eggs stay alive for different time periods. Experiments (Vauk-Hentzelt 1984) show the longest survival of 84 hours for vomited eggs or females, when kept in original ocean water near Helgoland at a temperature of 10.7°C.

The expelling of pentastomids via the nasopharynx by infected final hosts is quite normal in *Linguatula* sp. and has been observed by the author in *Raillietiella* sp. (coughed out by the gecko *Hemidactylus* sp.) and in an unknown pentastomid by a snake regurgitating complete conglutinated egg masses and destroyed females.

**Possible paths of transmission**

On leaving the interclavicular air sac and migrating via the trachea, *R. sternae* females reach the buccal cavity. The parasite might be passed here directly or via the external environment to the next sea bird:

1. when, for example, seagulls hunt each other and strangle their prey containing *Reighardia* eggs or females, the parasite will be taken up with the prey by the superior gull, thereby facilitating direct transmission
2. because they irritate the tracheal and pharyngeal mucous membranes, the parasites cause the bird to cough and vomit complete pentastomids or aggregated egg masses into the environment
3. when spit balls are regurgitated, the complete pentastomids or aggregated egg masses will be passed into the environment
4. when *R. sternae* stays in the buccal cavity of the original host, the worms or eggs will be swallowed; since an autoreinfection has been reported, the beginning of a new life cycle in this way cannot be excluded – deposition of the eggs or parts of the female(s) by defaecation into the environment where they are ingested by a not yet immune host, is, however, likely.
Figure 5.36  *Reighardia sterna*, life cycle.
_Behaviour inside the host_

Within three days of ingestion, digestion causes the rupture of egg shells; the larvae hatch, penetrate the gut wall and remain outside the duodenum within the body cavity. There they feed on ruptured intestinal capillaries. They grow to about 10 mm. Sexual differentiation and mating take place within four weeks. Females become precociously mature. Copulation takes place when both sexes have a length of about 10 mm and the uterus of the female is not yet filled with eggs. Spermatozoa are stored in two seminal receptacles.

Males then migrate and can be found in all part of the gull’s interior where they die, whereas females start their migration by penetration into the abdominal air sac. Within the air sac system, they move via two thoracic air sacs (anterior, posterior) to the clavicular air sac, feeding on the capillaries of the air sac layer. This phase is characterised by an elongation of the slender body of the pentastomid to up to about 50 mm, and high activity of the ovary (oogenesis). The eggs are shed via the oviduct and along the seminal receptacle towards the uterus, only when the females arrive at the clavicular air sac, and start synchronous development. Females grow to their final size (65 mm) and store a total of about 6000 eggs. In about six weeks, the embryos reach the 5th larval stage with two pairs of limbs.

After a prepatent time of about six months, the second migration of the female leads from the clavicular air sac via the bifurcatio tracheae and trachea to the pharynx. There, the whole animal or part of it can be coughed out or swallowed. _Reighardia_ eggs, hundreds of which are embedded as a conglomerate in a sticky mucus (produced by the dorsal organ), or whole females are expelled into the environment orally or via faeces.

_Effects on hosts and ecological importance_

Pentastomids rarely have pathological effects on their hosts. _Reighardia sternae_ has a low incidence of infection. According to biometrical analysis (size, body weight and plumage), seagulls infected with _R. sternae_ are without anomalies. Repeated infections are reduced by the development of an immune response (Riley 1979, 1992, Böckeler 1984b). As known to date, pentastomids have no significant ecological importance.

_Important references_

A general account of the Pentastomida is by Storch (1993). Banaja _et al._ (1976), Riley (1972), Riley (1975), Banaja _et al._ (1976) and Böckeler (1984b) made important contributions to our understanding of the life cycle of _Reighardia sternae_.

The drawings of Jens Müller, Kiel (Germany) are gratefully acknowledged.

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**Mollusca (molluscs)**

**Felix Lorenz**

_**Introduction**_

With more than 50 000 living species, the Mollusca are the second largest phylum and among the most important components of marine ecosystems. The first molluscan fossils appear in the early Cambriam. The phylum comprises seven classes, the Aplacophora (worm snails, marine, 250 species), Polyplacophora (chitons, marine, 600 species), Monoplacophora (marine, 10 species), Bivalvia (mussels, marine and limnic, 7500 species), Scaphopoda (tusk shells, marine, 350 species), Gastropoda (snails, marine, limnic and terrestrial, >40 000 species) and Cephalopoda (octopuses and squids, marine, 600 species). Among the bivalves, certain larval stages parasitise the gills of freshwater fish, but only gastropods have become parasitic in and on marine animals.
Morphology of molluscs

Molluscs are bilateral Spiralia in which the pericard, gonocoel and nephrocoel are the only remnants of a reduced coelom. The body of molluscs is usually composed of four functional sections:

1. The **head** carries optical and sensory organs and the proboscis, a snout or tube containing the radula, the universal feeding-organ of the Mollusca – it is usually a tape-like structure covered with tiny calcareous teeth that enable the snail to rasp food particles off a hard substrate; on either side of the radula there are ‘jaws’ which may be modified or absent in some groups. The Bivalvia are lacking a head.

2. The **foot** is a muscular organ of locomotion. It is densely ciliate and rich in mucous glands. In many gastropods it has a horny or calcareous operculum.

3. The **visceral sac** contains stomach and intestine, digestive gland, gonads, heart and excretory organs.

4. The **mantle** carries respiratory organs as well as sensory organs (ctenidium). It forms an ectodermal skeleton, the shell, consisting of inorganic (calcium carbonate, aragonite) and organic (conchin) components. The shell may cover the visceral sac, protect the head and the mantle cavity housing the respiratory organs, or as in the Bivalvia and the Scaphopoda, the entire animal. The shell may consist of eight plates (Polyplacophora), two valves (Bivalvia) or is single. It characterises the classes and has taxonomical importance.

Morphology and development of gastropods

Only the Gastropoda have a significant number of parasitic forms in marine ecosystems, although some limnic Bivalvia have parasitic phases in their larval development: their glochidian larvae settle in the gills of various species of fish. There are no significant parasitic Bivalvia known from marine ecosystems.

Most gastropods are characterised by a torsion of the visceral sac and a subsequent coiling of the univalve shell, and a highly modifiable radula. These characteristics have probably led to the evolutionary success of the gastropods. The protective shell may be modified for several purposes: shelter, camouflage, brood-case, attachment platform, tool for opening bivalve shells, and the radula, used for rasping off food, may show great variability. In some groups (Toxoglossa) the radula is modified to poison-loaded barbs which are shot into the prey. In parasitic groups, it may be reduced or absent, whereas the jaws may be stiletto-like for penetration of host tissue.

Gastropods have a characteristic veliger larva with an operculum and ciliate sail-like protrusions on either side of a simple, coiled larval shell. Many families disperse with a planktonic veliger phase, others are intracapsular developers that may use sponges and other marine organisms as vehicles for their brood and hence for dispersal. This strategy might have lead to some forms of parasitism in the Gastropoda.

Parasitism in the gastropods

Marine gastropods can be ectoparasites or endoparasites of many slow moving or sessile marine invertebrates, with a variety of transitional stages (Table 5.5). In the following parts of this subsection, the origins and types of parasitism are discussed, as well as sexual dimorphism and hermaphroditism in some species, and finally, the transition from a commensal life to specialised parasitism.

The way to ectoparasitism

The transition from a free-living mollusc that feeds on debris, sponges and soft corals to a temporary ectoparasite of a particular host can be observed in closely related species. Among the cowries,
family Cypraeidae, *Cypraeovula algoensis* from the Atlantic coast of South Africa feeds on small sponges and soft corals. On the Indian Ocean side of the Cape, *Cypraeovula mikeharti* is adapted to parasitising black sponges *Tetrapocillon* sp. and *Guitarra* sp. into which it eats holes and chambers that serve as hiding places and for the deposition of egg clusters. Similar transitions are observed in other cypraeid genera which are ectoparasitic on large sponges. Some of these species may return to preying on various sponges in the absence of their preferential host sponges. This potential of becoming parasitic is found mainly in cowries adapted to areas with extreme conditions and high competition with closely related species. Species of *Zoila* eat deep cavities into sponges in which they hide and deposit their spawn. When torn off the ground, the sponge may serve as a vehicle for juveniles developing in capsules (Lorenz and Hubert 1993, Lorenz 2001).

**Obligatory ectoparasitism**

The large family of egg-cowries, *Ovulidae*, comprises obligatory ectoparasites on gorgonians, alcyonarians and antipatharians. The species have spindle-shaped to cup-shaped shells with a concave base that protects the foot of the snail which firmly attaches to the stem or the branches of the host. Most species have separate sexes. The mantle lobes usually cover the shell and have the same colour as the host. They often carry papillae which resemble the host’s polyps, camouflaging the parasite perfectly. Ovulids usually spend their whole lives on their host coelenterates, with differing degrees of host specificity. They feed on polyps or body fluids, but retain the capability of moving rather quickly about the host, sometimes causing obvious damage to the colony (Liltved and Gosliner 1983, Liltved 1989, Fretter and Graham 1997).

**Brood parasitism**

As a form of parental care, some species place their spawn into pockets eaten into the tissue of compound tunicates with the aid of an ovipositor (Fretter 1946). Adults of the family *Triviidae* live on or in close association with the tunicates, feeding on them and using them as hiding places. Some *Triviidae* have developed mantle patterns that camouflage them perfectly among their hosts (Liltved and Gosliner 1983, Liltved 1989, Fretter and Graham 1997).

**Parasitism or symbiosis?**

In the derived ovulid genus *Pedicularia*, a transition from a parasitic to a symbiotic life can be observed. The female stage of these protandric hemaphrodites becomes sessile and firmly

<table>
<thead>
<tr>
<th>Family</th>
<th>Parasitic species</th>
<th>Size (mm)</th>
<th>Hosts</th>
<th>Type of parasitism</th>
</tr>
</thead>
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<tr>
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<td>Echinoderms</td>
<td>Ecto-, gall-, endo-</td>
</tr>
<tr>
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<td>&gt;500</td>
<td>2–25</td>
<td>Molluscs,</td>
<td>Ecto-, suction</td>
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<td></td>
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<td></td>
<td>Annelids</td>
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<tr>
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<td>5–80</td>
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<td>2–60</td>
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<tr>
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<td>3–20</td>
<td>Ascidians</td>
<td>Brood-</td>
</tr>
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<td>Ecto-, suction</td>
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<td>30</td>
<td>5–25</td>
<td>Ascidians</td>
<td>Brood-</td>
</tr>
<tr>
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<td>8–150</td>
<td>Sponges</td>
<td>Ecto-</td>
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<td>Cancellariidae</td>
<td>&gt;150</td>
<td>5–40</td>
<td>Fish</td>
<td>Ecto-, suction</td>
</tr>
<tr>
<td>Marginellidae</td>
<td>&gt;300</td>
<td>2–90</td>
<td>Fish</td>
<td>Ecto-, suction</td>
</tr>
</tbody>
</table>
Minor groups and fossils

attaches the shell to stems of sylasterine corals. The proboscis is prolonged for feeding on the mucus that the sylasterine corals secrete (Liltved 1989).

The path between symbiosis and parasitism is narrow in many families of gastropods. Examples for this phenomenon are species of the large family Epitoniidae, the often bizarre-shelled Coralliophiliidae as well as the Architectonicidae. Young specimens of these families may crawl about freely, but at a certain size become attached to a host coelenterate. For example, many species of Epitonium and Coralliophila attach firmly to soft corals of the genus Palythoa and subsequently become overgrown (Robertson 1970, 1981). Some of them feed on the host’s tissue and hence are parasitic, others feed exclusively on the mucus that the coelenterates secrete. Colonies of discosomatid anemones were observed to grow denser and larger when inhabited by Corallioaphila which keeps the coelenterate colony clean of secretions (Lorenz 1996).

Temporary ectoparasitism
Those ectoparasitic species that feed by suction usually have reduced radulae and a prolonged proboscis, a suction pump is formed by the buccal mass. The jaws may be modified to stylets that aid in the penetration of host tissue. Temporary ectoparasitism by sucking body liquids or blood is found in many families of gastropods (e.g. Eulimidae and Pyramidellidae) (Vaney 1913, Fretter and Graham 1949, Fretter 1951, Morton 1979, Robertson and Mau-Lastrovicka 1979, Wise 1993). The hosts may be coelenterates, molluscs, annelids, echinoderms, but also fish. Certain species of the families Marginellidae, Cancellariidae and most Colubrariidae (Fig. 5.37A) are known to approach sleeping rays, parrot fish and others, and insert their extremely prolonged proboscis in body openings such as the mouth to reach thin, well-blooded tissues (e.g. of the gills) (O’Sullivan et al. 1987, Bouchet 1989, Johnson and Jazwinski 1995, Bouchet and Perrier 1996).

Sexual dimorphism, hermaphrodites
The large family Eulimidae represents all levels of parasitism, commonly on all classes of Echinodermata (Humphreys and Lützen 1972, Lützen 1972a,b, Warén and Crossland 1975 and Warén 1981, 1983). The members differ from other gastropods in a high degree of sexual dimorphism. The limpet-shaped Indo-Pacific Thyca cristallina is a famous ectoparasite living on the starfish Linckia laevigata. Subadult specimens crawl across the arms of their host, female adults attach firmly to the oral side of the arms, to the right of the ambulacral groove, facing the oral opening. Dwarfed males live in the mantle cavity of the females. Thyca burrows its proboscis deeply into the host tissue, feeding on body fluids (Elder 1979, Egloff et al. 1988).

Echinoeulima (Fig. 5.37B) parasitises the echinoid families Diadematidae and Echinometridae. They are protandric hermaphrodites. The presence of a female suppresses other males to become females. These parasitic snails attach themselves to the host’s test with a disk-like ‘snout’ (opening of the proboscis) that forms microvilli-like protuberances attaching it firmly to the host tissue. Through this ‘anchor’, the long proboscis reaches deep into the perivisceral cavity of the host (Lützen and Nielsen 1975).

Gall formation and the way to endoparasitism
The infection with some parasitic eulimids causes the formation of galls within which the parasitic snail is embedded. Sabinella inhabits the spines of sea urchins and forms galls in which female, male and egg capsules find shelter (Fig. 5.37C). The proboscis of the adults reaches into the host tissue through an opening at the base of the spine (Warén 1983).

Stilifer burrows deep into the tissue of its host asteroid, forming galls. The shell is entirely covered by a pseudopallium. Typical organs of a snail (e.g. tentacles) are absent in this genus as an adaptation to parasitic life. In the related genus Gasterosiphon (Fig. 5.37D) only a long canal leaves an opening from the internalised parasite through which the larvae can escape from the
Marine Parasitology

Endoparasitism is an exception in the Mollusca. Some genera of the large family Eulimidae have become mostly worm-like, highly modified endoparasitic snails lacking head, radula,
blood system, nervous system and most other organs (Diacolax, Entocolax, Entoconcha, Thyonicola and Enteroxenos), their host is usually a holothurian. The female of Diacolax (Fig. 5.37E) has a rostrum (probably a modified proboscis) deeply inserted in the body cavity of its holothurian host Cucumaria. Its intestine forms a blind sac at whose outer side a massive ovary releases its products into a large brood pouch for eggs and larvae formed by the pseudopallium. It covers the entire animal, at whose terminal end there is an opening ('sipho') to release the larvae (Voigt 1901, Koehler and Vaney 1903, Mandahl-Barth 1941, 1946, Tikasingh 1961, Lützen 1979, Warén 1983).

Entocolax (Fig. 5.37F), Entoconcha (Fig. 5.37G), Thyonicola and Enteroxenos (Fig. 5.37H) are genera with endoparasitic species in holothurians. They show gradual morphological transitions to highly derived endoparasites without sensory and locomotory organs, large ovaries, sexual dimorphism, occurrence of dwarf males to absorption of the male, very short larval periods outside their host, and finally, complete loss of intestines (Vaney 1913, Warén 1983).

A well-studied example is Enteroxenos, parasitic in aspidochirote holothurians. It has lost most of its organs, including its mouth and an alimentary canal. The larva enters the host through the oral opening, sheds its larval shell and the operculum and becomes a female, up to 14 cm long, a worm-like appendage to the host's viscera. It is covered by a peritoneum of the host, and has a ciliated tubule, a canal communicating with the host's oesophageal lumen on one side, opening into a central body cavity on the other side. An ovarian ridge protrudes into this cavity. The male enters the female through the ciliated tubule from the host's oesophagus, entering the female's body cavity, sheds the shell and operculum and attaches to the 'receptaculum masculinum', an epithelial protrusion of the female's body cavity at the terminal end of the tubule. The male grows to an irregular-shaped vesicle – basically the male becomes nothing but a testis. After oviposition, the female detaches from the host's viscera. Larvae and parasites are released during the holothurian's annual evisceration. The veligers are suspected to have a very short phase outside the host, which probably gets reinfected by swallowing larvae with the debris they feed on (Lützen 1979).

Effects on hosts
The effect of parasitism on the host, with few exceptions, is relatively low. Coelenterate colonies usually seem to suffer very little damage from gastropod parasitism (Robertson 1970). One exception is Ovula ovum (Ovulidae), an ectoparasite of the soft coral Sarcophyton. A single individual of this 5 cm to 8 cm long snail can destroy a 30 cm diameter colony of polyps within one day (F Lorenz, pers. obs.). Ectoparasitic and endoparasitic eulimids seem to have little effect on their hosts (Warén 1983). Infected holothurians do not show any effects of the parasite on their growth or fertility (Lützen 1979).

Important references
Echiura (spoon worms)
Kirsten Jensen

Introduction
The phylum Echiura (spoon worms) comprises slightly more than 150 species (Hessling and Westheide 2002). Echiurans are bilaterally symmetrical coelomate worms that are considered closely related to annelids (see Edmonds 2000, Hessling and Westheide 2002). In general, echiurans are marine. They are gonochoric and possess a free-swimming, planktotrophic (i.e. feeding) ciliated larva, known as a trochophore. Typically, adult echiurans have a body consisting of two parts, an anterior proboscis and a posterior trunk; and they possess a complete digestive system, with a mouth at the base of the proboscis, and an anus terminally on the trunk. The main organs of excretion are a pair of anal vesicles. In both females and males, metanephridia function as gonoducts, opening via pores on the ventral side of the trunk. Mature female or male gametes are released from the gonads into the coelom, filtered out of the coelomic fluid by the nephrostome and subsequently stored in the gonoduct.

Four families of echiurans (Echiuridae, Bonelliiidae, Urechidae and Ikedaidae) are recognised (Murina 1998, Brusca and Brusca 2003). Species in the family Bonelliiidae are unique within the phylum in that they exhibit pronounced sexual dimorphism. Female bonellids with everted proboscis can reach a length of over 1 m, whereas males rarely exceed a length of 3 mm (Baltzer 1931a). Murina (1998) recognised 70 bonellid species in 28 genera. Bonellids, however, are most unusual in that dwarf males live in a symbiotic ('parasitic') relationship with females. In general, the morphology of a female bonellid is like that of a typical echiuran, while the morphology of the dwarf male is rather atypical (Fig. 5.38). Males possess a ciliated epidermis, and lack a proboscis. They possess a rudimentary digestive system that lacks both mouth and anus. Instead of gonoducts, they possess a sperm sac consisting of three functional regions: the vas deferens, the sperm reservoir and the terminal funnel with its inlet canal (Schuchert and Rieger 1990). Individual mature male gametes are filtered out of the coelom into the sperm sac, and released via the vas deferens. In addition, whereas time to maturation for females is estimated to be at least two years, males reach sexual maturity within one to two weeks. Depending on the species, bonellid males have been reported from either the body wall, the gonoducts, the anterior regions of the digestive system or the coelomic cavity of the female (Dawydoff 1959). Most information on life cycles and sex determination in the bonellids has resulted from work on Bonellia viridis.

Sex determination and life cycle of Bonellia viridis
Sex determination in B. viridis is highly unusual, in that for most trochophore larvae sex is not determined at fertilisation (i.e. larvae are metagamic), but in response to an environmental factor: trochophores usually develop into females in the absence of adult females, but develop into males when they come into contact with adult females. The main factor inducing masculinisation is the green pigment bonellin produced by adult females (e.g. Baltzer 1931a,b). Bonellin is produced in the tegument of the proboscis, and to a lesser degree in the trunk (Jaccarini et al. 1983, Edmonds 2000). Jaccarini et al. (1983) demonstrated that in addition to metagamic larvae, a small percentage of larvae (about 17%) are syngamic (i.e. direction of sexual differentiation (female, male or intersex) is determined genetically at the time of fertilisation).

In the life cycle of B. viridis, fertilised eggs are released by the female during annual spawning periods (Baltzer 1931a). Eggs of B. viridis are 70–80 µm in diameter. Trophophore larvae of B. viridis are unusual among echiurans in that they are lecithotrophic (i.e. non-feeding), with large yolk supply (i.e. with a large yolk supply on which they feed), pigmented green and possess
eyespots (Dawydoff 1959) (Fig. 5.39). Trochophore larvae first settle on the proboscis of the adult female and attach using their anterior ciliary band, the prototroch. Development into the male body form occurs within about 100 hours of settlement. During this metamorphosis, the anterior end of the larvae is reduced in size, the green pigmentation and the eyespots are lost, the coelom develops, spermatogenesis initiates in the gonads and precursors to the sperm sac develop. At day four to eight post-settlement, males migrate towards the mouth of the female, settling in the pharynx and foregut. Up to 85 males have been found in the foregut of a single female (Baltzer 1931a). A subset of males subsequently migrates from the digestive system to the gonoduct. Males release their gametes directly into the gonoduct of the female. Consequently, whereas fertilisation in most echiurans is external, fertilisation in bonellids is internal.

Although the morphology of dwarf males has been intensively studied, details on the association between male and female bonellids are sparse (Baltzer 1931a). Dawydoff (1959), for example, referred to the association between male and female bonellids as parasitic, whereas Baltzer (1931a) suggested a more symbiotic relationship of the male with the female. Benefits for the
male include shelter and unchanging environmental conditions inside the female. It has been suggested that after settlement on females, the large yolk deposit of *Bonellia* larvae (Dawydoff 1959, Edmonds 2000) is slowly consumed (Jaccarini et al. 1983), and might not last the male over its seven to eight month life span (Baltzer 1931a). The male may be able to obtain nutrition from its location living in the foregut of the female where digestion in the females is initiated. In addition, the gonoducts are lined with secretory cells which have been suggested to produce substances of nutritive value to the male (Baltzer 1931a).

**Important references**

General accounts of the Echiurida are by Baltzer (1931a), Dawydoff (1959), Murina (1998), Edmonds (2000) and Brusca and Brusca (2003). Baltzer (1931b) described the development of *Bonellia viridis*. Hessling and Westheide (2002) conducted an immunohistochemical analysis of the nervous system in the development of *Bonellia viridis* and examined the question of whether echiurids are derived from a segmented ancestor. The ultrastructure of the dwarf male of *Bonellia viridis* was examined by Schuchert and Rieger (1990).

**Echinodermata (echinoderms)**

Greg W Rouse

**Introduction**

With around 7000 described extant species and a fossil record dating back more than 500 million years (Rowe and Gates 1995), it is somewhat surprising that echinoderms have very few incidences of parasitism, even in a broad sense. All extant echinoderms are marine, and most are relatively large. This large size, combined with their hard calcitic skeleton, may explain the scarcity of parasitic forms. Echinodermata contains five major clades, usually given the rank of class: Asteroidea (seastars), Ophiuroidea (brittlestars and basketstars), Echinoidea (sea urchins), Holothuroidea (sea cucumbers) and Crinoidea (featherstars). Concentricycloidea, a group containing only two described species and given class rank by Baker et al. (1986) is now regarded as
derived Asteroidea (Janies 2001). Of these groups, only Holothuroidea and Ophiuroidea contain taxa that can be regarded as parasitic.

**Parasitic echinoderms**

*Rynkatorpa pawsoni* (Synaptidae: Apodida) was referred to by Martin as the first ectocommensal sea cucumber (Martin 1969). Four specimens of this extraordinary holothurian were found, attached by their posterior ends to the host anglerfish *Giganactic macronema*. The fish had been trawled from between 1000 m and 2000 m depth off southern California and the four holothurians were found in a group on one side of the host. *Rynkatorpa pawsoni* (Fig. 5.40A) reaches around 7 mm in length and 2.5 mm in width. It lacks many typical holothurian features, including tube feet and a respiratory tree. It also appeared to lack skeletal elements such as anchors and plates, though these may have been destroyed in the treatment of the specimens (Martin 1969). It does have 12 digitiform retractable tentacles and typical echinoderm features such as a water vascular system. Martin (1969) found that, although the *R. pawsoni* were firmly attached to the host’s skin, there was no evidence of invasion. Benefit to the sea cucumbers from the association is unknown.

Ophiuroids are commonly found using other organisms as substrates. Members of Euryalinida (snake-snakestars and basket-stars) are found perched on sponges and colonial cnidarians such as gorgonians, soft corals and black corals. Hyman (1955) provides a summary of known associations between ophiuroids and other animals and many snakestars seem to be using the ‘hosts’ in order to be higher in the water column in order to capture zooplankton. A few arms will be coiled around the host with other arms waving freely in the water column. Basketstars such as *Gorgoncephalus* are known to attach to soft corals while very young and once their arms have started to branch will move onto adults of their own species. Panikkar and Prasad (1955)
reported that several hundred specimens of the ophiuroid *Ophiocnemis marmorata* could be found on the scyphozoan *Rhopilema hispidum*. Marsh (1998) reported *Ophiocnemis marmorata*, which is well known as a benthic ophiuroid, ‘hitch-hiking’ on another jellyfish, *Cephea cephea*. It appears the ophiuroids settle on the oral arms of the jellyfish as larvae and stay there. Their food source is not known. Some comatulid crinoids (featherstars) also appear to have favoured ‘hosts’ on which to perch for favourable feeding. These are usually soft corals or gorgonians. One example is *Colobometra perspinosa* (Fig. 5.40B) that is usually found clinging, often in large numbers, to gorgonians.

A commonly seen association is that between ophiuroids using their close relatives crinoids, or even echinoids (sand dollars) as hosts. Numerous ophiuroids are known to be associated with comatulid crinoids and wrap their arms around the cirri and arm bases of their hosts (see Hyman 1955). Many would appear to be obligate associates of crinoids (e.g. *Ophiomaza*) and lie with their mouths close to the crinoids oral disc or ambulacral grooves of the arms. Presumably they steal food from the crinoid before it reaches its mouth (GW Rouse, pers. obs.). Other ophiuroids such as *Nanophiura lagani* and *Amphilycus androphorus* are intimately associated with echinoids and lie attached to the undersides of their hosts. The benefits they gain from this association are not known.

**Important references**

Hyman (1955) has reviewed echinoderm parasitism. Ophiuroids (Euryalinida) in New Zealand that are often found associated with other animals were recently reviewed by McKnight (2000). Martin (1969) described *Rynkatorpa pawsoni*, and Marsh (1998) discussed ‘hitch-hiking’ ophiuroids.

**Parasitic marine fishes**

David Woodland

**Introduction**

Apart from kleptoparasitic birds such as skuas and frigate birds (*Fregata* spp.) which harass other sea birds, causing them to regurgitate their prey of fish, squid or prawns, and the kelp gull, *Larus dominicanus*, which parasitises whales by feeding on their flesh, all other vertebrate marine parasites are fishes. Even among the fishes relatively few species are parasitic. One group, the pearlfishes, are endoparasites of sea cucumbers, but the rest, that is the lampreys, anglerfishes, cleanerfish mimics, fangblennies, scale feeders, cookiecutters and various browsers, are ectoparasites, especially of other fishes. Of the ectoparasites, some spend extended times attached to a single host; others strike, detach a piece of flesh, and depart. We will treat the ectoparasites first, beginning with the most primitive, the lampreys.

**Lampreys**

The lampreys, along with the hagfishes, are the only surviving representatives of that ancient group of jawless fishes, the *Agnatha*. Hagfishes are scavengers; but the adults of some lampreys, *Petromyzontiformes*, are parasitic: 15 of the 34 species in the northern hemisphere *Petromyzonta*, and three of the four species in the southern hemisphere *Mordaciidae* and *Geotriidae* (Gill *et al.* 2003). Of these 18 parasitic species, nine spend their adult life in the sea (Potter and Gill 2003). These sea lampreys occur off the coasts of countries bordering the North Atlantic and North Pacific, along the coast of northern Eurasia, in the western Mediterranean and the Caspian Sea, and off the coasts of South America, southern Australia and New Zealand (Hubbs and Potter 1971).
Lampreys spend much of their life as larvae; they live in burrows in soft bottoms of rivers and streams, feeding on detritus, diatoms and bacteria (Rogers et al. 1980, Potter et al. 1986). Depending on the species, larval life span varies between three and seven years, after which a radical metamorphosis occurs which includes the development of a suctorial disc (Fig. 5.41A). Following metamorphosis the adolescents migrate downstream to larger bodies of fresh water or to the sea. The anadromous species spend anywhere between a few months to a few years in the open sea (the exact duration is not known for some species) where they feed mainly on bony fishes. They then re-enter freshwater and cease to feed. Over the next several months their gonads ripen, they migrate to the headwaters of rivers and streams, spawn and die.

The shift from microphagy to parasitism requires radical changes in anatomy and physiology. These include the development of buccal glands whose secretion has both anticoagulant
and cytolytic properties (Baxter 1956) and the development of a tooth-bearing suctorial disc that serves for attachment to the body of the host. The disc is present even in non-parasitic species where it is used, as in all lampreys, for grasping the bottom and for moving stones when constructing the nest used for spawning). Attachment to a host depends on two things, the embedding of disc teeth into its integument and the creation of a negative pressure within the buccal funnel. A fringe of mucus-secreting fimbriae around the circumference of the disc assists in maintaining the suction pressure (Lethbridge and Potter 1979).

The dentition on the disc of the adult lamprey consists of many circumoral teeth. Their principal role is to lock the disc in place on the host, but in tissue feeders the supraoral tooth plate can be involved in the excision of tissue. The processes of gouging out or of abrading tissue are carried out largely by the backward and forward thrusting of ‘the piston’ that sits on the floor of the oral cavity. On the tip of the piston there are three horny plates (laminae) – one transversely placed, two longitudinally placed (Fig. 5.41A). As the piston moves forward these plates ride up and over its tip. In tissue feeders, the transverse lamina is large and toothed; it closes against the supraoral plate, gouging out tissue; the longitudinal laminae have opposed, serrated edges that snip off bits of teased tissue. In blood feeders, the laminae are small and finely serrated; they abrade the surface of the wound to ensure a continuous supply of blood (Potter and Hilliard 1987).

All nine anadromous species feed on bony fishes. Some feed exclusively on blood (Petromyzon marinus, Mordacia lapicida and M. mordax); others feed primarily on tissues (Geotria australis and Lampetra spp.) and these may even invade the internal organs leading to the death of the host. Many different species serve as hosts. In laboratory tests involving seven fish species some species were preferred over others, but none was immune from attack (Farmer and Beamish in Hardisty and Potter 1971, p. 148). In the field, attachment to a host is probably opportunistic. At least two species (Petromyzon marinus and Lampetra tridentata) attach to whales and porpoises (Pike 1951, van Utrecht 1959). As most P. marinus attachment sites on right whales, Eubalaena glacialis, occur on the highly vascularised flukes, it seems likely that attachment is for feeding rather than for ‘hitchhiking’ (Nichols and Hamilton 2004).

While most sources classify adult lampreys as parasitic, in some situations they act more like predators. Mortality is likely to be highest where the lamprey is a tissue feeder and the host small. Nevertheless, the frequency of healed scars (40%) on commercial catches of a small species like the smelt, Osmerus eperlanus, due to attacks by the tissue feeding Lampetra japonica (Nikol’skii 1956 in Hardisty and Potter 1971, p. 150) demonstrates that individuals often survive. Clearly, in many cases lampreys are indeed parasites.

Water flow for respiration in lamprey larvae is unidirectional, entering via the mouth and exiting via the gill openings. But when an adult lamprey is attached to a host this method of water circulation is not possible; instead, water flow is tidal, entering and leaving through all seven pairs of openings into the branchial chambers (Roberts 1950, Randall 1972). While jawless fishes have solved the problem of respiring while attached to a host, simultaneous host attachment and respiration is a far greater evolutionary obstacle for jawed fishes. Of the marine species, only the male ceratioid anglerfishes have risen to the challenge.

Ceratioidei
Apart from their larvae, which live in warm surface waters down to about 200 m, deepsea anglerfishes (with the exception of the genus Thaumatichthys which is benthic) are pelagic at a depth of 300 m to 2000 m (Pietsch 1999). This is one of the most impoverished zones in the sea; here communities depend on dead and decaying mesopelagic zooplankton and faecal material raining down from above to support their food web. Despite this, the number of bathypelagic fishes is remarkably large (Marshall 1979, p. 407). However, with its members dispersed in a
three dimensional world – unlike those of surface and bottom dwelling species – the distances between nearest neighbours of any single species is likely to be large. The ceratioids face two problems then: how to get enough to eat and how to locate a mate at spawning time.

Their solution to the first problem is extreme sexual dimorphism in size. Females grow to 30 cm to 100 cm; they are equipped with a luminescent lure at the end of a moveable rod (except Neoceratiidae) and a large gape to accommodate, hopefully, the largest prey they might attract (Fig. 5.41C). However, post larval males lack a lure, have very small mouths, and most free-living individuals attain a length of less than 3 cm during their lifetime (Pietsch 2005). Thus, by leaving food acquisition largely to the females, a population might increase its density almost twofold. Even so, there is still the problem of being able to locate a mate. Adolescent males have large, invovled olfactory organs; in females they are only small papillae. It is presumed females produce a pheromone that can be traced to its source by the olfactory sensitive males. Further, males have hooked denticles on their chin and usually on their snout that enable them to attach themselves to a female. In the caulophrynids, ceratiids, neoceratiids, linophrynids and the oneirodrid Leptacanthichthys gracilispinis – the so-called ‘parasitic’ species – attachment may be permanent and intimate. Typically, at any one time only one male is attached to a female although as many as eight have been recorded (Pietsch 1976, 2005). In most species, males become fused to the females by outgrowths from their lower jaw and snout, and female tissue may invade their buccal cavity; within the fused tissue there are thin-walled intercommunicating blood sinuses (Pietsch 1976). In some species the male is carried at the end of a papilla protruding from the female. In Neoceratias spinifer the dermis degenerates at the point of fusion; blood vascular plexuses are present in the adjacent connective tissues of the head of the male and the skin of the female (Munk 2000).

As attached ‘parasitic’ males are larger than conspecific unattached males, as much as 10 cm long in some species, they must obtain nourishment from the females to which they are attached (Pietsch 1976, 2005). But how this is achieved is not known (Munk 2000). It seems likely that there is an anastomosis of both male and female capillaries within the fused tissues (i.e. the union is ‘placental’) but the definitive histological study remains to be done (TW Pietsch, pers. comm.). In any event it seems chemical signals are passed between the male and female that synchronise their gonadal development. This is supported by the fact that in the Ceratiidae and Linophrynidae non-parasitised females and free-living males never have developed gonads. However, in the Caulophrynidae and in Leptacanthichthys gracilispinis developed ovaries have been found in both parasitised and non-parasitised females. In these taxa perhaps union is temporary if spawning occurs soon after the male attaches, with fusion occurring only if spawning is delayed (Pietsch 1976). Tissue fusion has been recorded in 22 species (Pietsch 2005). There are around 139 ‘non-parasitic’ species (i.e. the males attach to females but no fusion of tissue occurs) (Pietsch 2005).

Norman and Greenwood (1975) asserted that ‘true parasitism’ in fishes occurs only among the Ceratioidei. In the opinion of the present author this intraspecific relationship between the sexes is not truly a parasitic one but a mutually beneficial symbiotic one; the female diverts a small amount of her resources to the attached male in exchange for his services as a sperm donor.

Fusion of the male’s mouth to the female and the invasion of its buccal cavity by tissues obviously restrict the flow of water through the mouth to the gill chamber. In some cases lateral openings into the pharynx are retained which might permit at least some limited flow of oxygenated water through to the gills. However, in Neoceratias and some linophrynids the pharynx becomes completely obstructed (Pietsch 1976, pers. comm.). Nevertheless, the gills in attached males are well developed, which suggests ‘water might be pumped in and out through the opercular openings’ (Pietsch 1976). If so, both the lampreys and parasitic anglerfishes have solved
the problem of supplying oxygen-rich water to the gills by resorting to tidal ventilation. An alternative solution to this problem is to resort to ‘hit and run’ tactics. Several species have adopted this approach.

**Cleaner fish mimics**

A remarkable example of the ‘hit and run’ approach involves the blenny, *Aspidontus taeniatus*, which mimics the cleaner wrasses, *Labroides* spp., that remove ectoparasites from various species of tropical reef fishes. *Labroides dimidiatus* has the broadest distribution; both it and the mimic are widespread throughout the Indo-Pacific Region. Both species grow to the same size (11.5 cm), and are strikingly similar in superficial body form, in colours and colour pattern. The colouration of *L. dimidiatus* alters with age and there are also regional differences; individual mimics match these variations both by size and locality (Randall and Randall 1960, Springer and Smith-Vaniz 1972)! In some areas additional species of cleaner wrasse coexist with *L. dimidiatus*; their colouration may also be mimicked by some of the local populations of *A. taeniatus* (Russell et al. 1976).

There is also behavioural mimicry. Members of the wrasse family have a distinctive mode of swimming – stroking with their pectoral fins; blennies depend on their caudal fin for locomotion. When stalking a host, *A. taeniatus* paddles with its pectoral fins like a labrid, but reverts to the typical blenny manner of progression when retreating (Randall and Randall 1960). One obvious difference between cleaner and mimic is their dentition: the mimic has a pair of large fangs in the lower jaw; cleaner fishes are fangless. Individuals of *Labroides* operate at fixed locations on coral reefs, providing a parasite removal service to fishes that visit the sites. *Aspidontus taeniatus*, by deception, stalks its target slowly and then strikes rapidly, biting off a piece of fin or skin. Young, naïve fish are more vulnerable to attack than older fish which learn to distinguish mimics from cleaner fishes and drive them away (Randall and Randall 1960).

The relationship between cleaner fishes and the fishes they clean is not entirely benign; gut contents often include scales, mucus and epidermal and dermal tissues (Losey in Randall and Helfman 1972, Gorlick 1980). Fish will sometimes twitch while being cleaned and chase the wrasse away; such ‘displeasure’ is probably expressed when the cleaner has exhausted the supply of ectoparasites and turned to parasitic feeding. Besides the five species of Indo-Pacific cleaner wrasses in the genus *Labroides*, there are many species of fish that clean ectoparasites from other fishes, and some of them also engage in eating mucus, scales and skin from their hosts (e.g. the Caribbean broadstripe goby, *Gobiosoma prochilos*, and the Mediterranean cleaner wrasse, *Symphodus melanocercus*) (Arnal and Coté 2000, Arnal and Morand 2001) (see also pp. 264–278).

**Fangblennies (*Plagiotremus* spp.)**

Another group of ‘hit and run’ parasitic fishes are the fangblennies in the genus *Plagiotremus*, small tropical species from the Indian and Pacific Oceans. Like their relative, the cleaner fish mimic *Aspidontus taeniatus*, these solitary hunters employ various forms of deception that allow them to approach a potential fish host sufficiently closely to be able to dart in and detach a piece of its skin. Three species are mimics in both colouration and behaviour of three species of *Meiacanthus*, fangblennies that feed on zooplankton and small benthic organisms and thus are no threat to the fishes that are deceived by the resemblance of *Plagiotremus* to them (Springer and Smith-Vaniz 1972, Russell et al. 1976, Randall et al. 1997). Moreover, the fangs of *Meiacanthus*, unlike those of *Plagiotremus*, have associated venom glands which are used defensively (Springer and Smith-Vaniz 1972). Not only then are potential hosts duped into a false sense of security by the disguise, but the predatory species among them will be less likely to attempt to capture an individual which may prove to be equipped with venomous fangs. The resemblance of mimics
to models is highly coevolved in these relationships; geographical variations in colour are closely paralleled by the mimics.

Another species of *Plagiotremus*, *P. rhinorhynchos*, uses two different strategies to enable it to get close to a potential host. It has two colour forms. The common morph is striped blue, black and silver; like *Aspidontus taeniatus* it is a mimic of the cleaner wrasse *Labroides dimidiatus*. However, the less common orange morph has been observed swimming with a school of the plankton-feeding *Pseudanthias huchti* (=*Anthias mortoni*) from which it launched attacks against passing fish (Russell *et al*. 1976). A similar activity involving this morph and *Pseudanthias squamipinnis* has also been recorded (Randall *et al*. 1997). Apart from the orange colour, the blenny did not resemble the anthine fishes with which it was associating; apparently blending in with a school of innocuous plankton feeders is effective in improving its chances of launching a successful attack.

*Plagiotremus tapeinosoma* is another species in which the mimetic association is more flexible than in those species which are mimics of *Meiacanthus*. On the Great Barrier Reef individuals associate with schools of the labrid *Thalassoma amblycephalus*; but during summer when the species extends its range south into the temperate zone, individuals associate with the plesiopid, *Trachinops taeniatus*, in southeast Australia, while in northeast New Zealand they associate with a tripterygiid, *Fosterygion* sp. (Russell *et al*. 1976). All the species involved in these relationships are slender and similarly coloured with alternating light and dark stripes; and all the models are midwater swimmers that feed on plankton.

The general consensus is that all 10 species of *Plagiotremus* feed exclusively on mucus, skin and scales. The host species are many and varied, almost any largish fish suffices (e.g. scarids, siganids, acanthurids, labrids, serranids and carangids).

**Scale feeders**

There is a group of fishes that also detach skin and scales from other fishes but they use stealth rather than disguise to approach their target. Scale feeding is particularly common among juvenile arid catfishes. Szelistowski (1989) found scales in 60% of the stomachs of all seven species of arid taken on the Pacific coast of Costa Rica, with the highest individual count of 596 scales. Sample size was large enough for one species, *Ariopsis seemanni*, to demonstrate that scale feeding declined with increasing size. In aquaria, this fish fed upon the fins and scales of live and dead fish. Hoese (1966) observed juvenile sea catfish, *Ariopsis felis*, chasing and biting the sides of the mullet *Mugil cephalus* in a boat harbour in Texas. Scales from nine species of fishes were found in the stomachs of 50% of a sample of *A. felis*, although if the largest fish were excluded, the frequency of occurrence rose to 75%. In aquaria the catfish approached their hosts from behind, taking scales from the posterior parts of the body and fins. The same strategy is used by *Terapon jarbua*. By contrast, however, when a sample of this fish from an estuary was divided into those larger and those smaller than 10 cm long, with increasing size the proportion of fish with scales in their stomachs increased from 52% to 76% while the mean number of scales per fish quadrupled (Whitfield and Blaber 1978). Moreover, in aquaria *T. jarbua* only removed scales from live fish. Scale feeding also occurs in two genera of carangids. The juvenile stages of three species of queenfish, *Scomberoides*, and two species of leatherjacks, *Oligoplites*, have specialised dentitions used for prising scales from hosts such as mullets (*Mugilidae*) and anchovies (*Engraulidae*) (Major 1973, Smith-Vaniz and Staiger 1973, Sazima and Uieda 1980). As the fish grow from 50 mm to 150 mm in length, the outer row of spatulate teeth in the dentary is replaced by a row of conical ones and the parasitic habit is abandoned (Major 1973). Interestingly, juvenile *O. saurus* also act as cleaners for other fish.

In all the above species, although skin, scales and mucus form a significant part of their diet, various invertebrates supplement their food intake. However two triacanthodids, *Tydemania*
navigatoris and Macrorhamphosodes uradoi, appear to feed exclusively on scales and mucus (Tyler 1968, Mok 1978). These small demersal fishes live between depths of 50 m and 700 m. Nakae and Sasaki (2002) showed that M. uradoi removed scales from at least 14 species; it attacks from the rear, taking scales from the caudal fin and its base. The teeth of both species are thin, wide and chisel-like, the mouth is supraterminal and the lips large. As these characters are peculiar to these two species, they are probably the only lepidophagous triacanthodids.

Cookiecutters

Deep, crater wounds found on the sides of large pelagic fishes, whales and dolphins were once thought to be the result of secondary infection at old attachment sites of invertebrate parasites. But Jones (1971) linked them to attacks by sharks of the genus Isistius. These small sharks (50 cm) have suckorial lips, and very large lower teeth set in powerful jaws; in I. plutodus these lower teeth are proportionally larger than those of any other living shark (Fig. 5.41B). The lower teeth of Isistius spp. are broad, flat and sharp edged, the upper ones are small and acutely pointed. These sharks feed by locking onto their hosts with their suckorial lips and sawing out a plug of flesh with their lower teeth. In I. brasiliensis the plug is conical, while in I. plutodus it is cylindrical, and up to twice the length of the diameter of the mouth (Compagno 1984). Whatever the differences in feeding actions, the official name ‘cookiecutter’ is especially apt.

There are two, perhaps three, species of Isistius (Compagno 2000). We know little about two because they have limited distributions but they probably have a similar biology to I. brasiliensis which is found offshore in all tropical seas. It is sometimes caught at the surface at night but more often at depths between 85 m and 3500 m. This suggests the shark undertakes an extensive daily vertical migration in search of prey. The lower surface of its trunk is luminous; such counter-illumination is common in deepsea fishes where its proposed function is to obliterate the outline of the fish to avoid detection by both its predators and its prey. However, it has been suggested that in this case the light might be used to attract large predators that are then themselves attacked (Compagno 1984).

Cookiecutter wounds have been found on the sides of large pelagic fishes such as marlin, tuna and albacore, on the rarely seen giant megamouth shark, Megachasma, as well as on whales and dolphins. Size of host is of no consequence to a cookiecutter, they have even attempted to gouge chunks out of the rubber sonardomes of U.S. nuclear submarines (170 m long, 19 000 tonnes) (Compagno 1984, 2001)! Cookiecutters are, however, not exclusively parasitic, their diet also includes whole large squid, small gonostomatid fishes and benthic crustaceans (Strasburg 1963).

Coral reef and deep-sea browsers

Many coral reef fishes specialise in feeding on one of the most abundant resources around them – coral polyps. For example, 23 species of butterflyfishes (Chaetodontidae) feed exclusively on the polyps of hard or soft corals (Allen 1981, Tables 1–3). Individuals or pairs of species of Chaetodon either defend feeding territories or have extensive home ranges (Reese 1975). Typically, their feeding does not damage the coral skeleton. By limiting their feeding on any particular colony, the damaged polyps are able to regenerate (D. Woodland pers. obs., Randall 1974). Other reef species that appear to feed exclusively on coral polyps are the two species of filefish, Oxymonacanthus spp. (Myers 1991). Species of Labropsis feed primarily but not exclusively on polyps (Randall 1981). Then there are species that do damage the skeleton; for example, species of trigger, file and pufferfish bite the tips off branching species; none of these feed exclusively on coral (Hiatt and Strasburg 1960).

The diet of the family Chaetodontidae as a whole is extremely varied (Allen 1981). For example, several species feed on a range of invertebrates; but in the present context Chaetodon
capistratus is probably representative of species that feed mainly on coral polyps. Birkeland and Neudecker (1981) found these comprised 82.5% by volume of its diet. It also browsed on the tentacles of tube dwelling serpulid polychaetes (11.25%), again apparently without killing its hosts. By contrast, 68% of the diet of *C. aculeatus* was found to consist of the tentacles of serpulids, the remainder being mainly benthic crustaceans and fish eggs; it was also seen picking at sea urchins, presumably removing pedicellariae and tube feet (Birkeland and Neudecker 1981).

Interestingly, several polyp feeders are cleaner fishes as juveniles (e.g. *Labropsis* spp. and *Diproctacanthus xanththurus*) (Randall and Helfman 1972, Randall 1981, Myers 1991) suggesting the parasitic habit may be established early in life.

There are also deep-sea dwellers that nip pieces off epibenthic and burrowing invertebrates instead of ingesting them whole. For example, the cusk eel *Barathrites parri* feeds on the tentacles of holothurians and tube-dwelling polychaetes (Gartner *et al.* 1997). The large spiny eel *Notacanthus chemnitzii* has knife-like dentition that it uses to clip the tentacles from anemones, corals, bryozoans and hydrozoans (McDowell 1973). The smaller *N. bonaparte* feeds on sponges, bryozoans and ophiuroids (Coggan *et al.* 1998). There are probably many other deep-sea fishes with this habit so far unrecorded. Though fishes that feed in the way described are usually called ‘browsers’, they might equally well be classified as full or part-time parasites.

**Pearlfishes**

Considering their respiratory requirements, it is difficult to imagine how a fish might adapt to an endoparasitic mode of life; however, one group of fishes has achieved this by exploiting an unusual habitat – the coelom and respiratory trees of sea cucumbers (holothurians). The Cara-pidae or pearlfishes are slender, eel-like fishes, attaining 35 cm. About half of the 35 species are free living, but the others spend at least part of their day hiding inside sea squirts (ascidians), bivalve molluscs and seastars (asteroids) – especially the giant pin-cushion star, *Culcita*, and seacucumbers (Nielsen *et al.* 1999). While most of these are commensals, at least three and probably all five species of the genus *Encheliophis* (as restricted by Parmentier *et al.* 2000, Parmentier 2004) feed on the internal tissues of their holothurian hosts.

Holothurians make ideal hosts; they are large, elongate and their respiratory trees are inviting places for any delicate, slender, weak-swimming fish seeking somewhere to hide. The trees are a pair of much branching organs that extend throughout the coelomic cavity and open into a cloaca. The flushing of the trees is extremely efficient: the anal sphincter opens wide, the cloaca contracts rhythmically forcing oxygenated seawater into the branches of the tree. In the reverse process, the trees themselves contract, forcing water out of even the terminal vesicles (Hyman 1955). Moreover, the amplitude of contractions of the cloaca is sensitive to oxygen levels (Lutz 1930), so that the host will compensate when a carapid is in residence.

Adult carapids worm their way into holothurian hosts tail first, a manoeuvre facilitated by a tapering body and an absence of spines in the fins. Furthermore, almost all species lack pelvic fins, and two of the five species of *Encheliophis* also lack pectoral fins (Parmentier 2004). In addition, in species of *Encheliophis* the dentition is reduced and the upper jaw is immovably bound by skin to the head – features that one might expect where feeding on host tissue replaces active hunting for small crustaceans and annelid worms, as practised by their commensal relatives.

Dissected *Encheliophis* usually prove to have empty alimentary canals, but pieces of internal organs presumably from the host animal have been identified: respiratory tree (Murdy and Cowan 1980), testis (Smith 1964) and ‘gonads’ (Strasburg 1961, Trott and Trott 1972). How a fish penetrates the wall of the respiratory tree to ingest gonads without inconveniencing the host is not known. As the occupancy level of hosts is low it is possible that fish move from one host animal to another to minimise damage; however, in this context, it is worth noting that when irritated holothurians may void their internal organs and subsequently regenerate them.
However, feeding only on gonadal tissue is a form of ‘parasitic castration’, leaving the host alive but with impaired reproduction. Although, Smith (1964) recorded an individual of *E. gracilis* swimming outside its host, significantly, no free-living invertebrate has ever been recorded in the gut contents of any *Encheliophis*. But there may be another explanation for Smith’s observation. Usually only one specimen of *Encheliophis* is found in a host; where two have been found, the fish were sexually mature animals of the opposite sex (Trott and Trott 1972, Murdy and Cowan 1980). It seems that mature adults may go in search of a partner and be prepared to share a host at spawning time. This is just one of many unanswered questions about the biology of this fascinating group of endoparasitic fishes.

**Important references**
