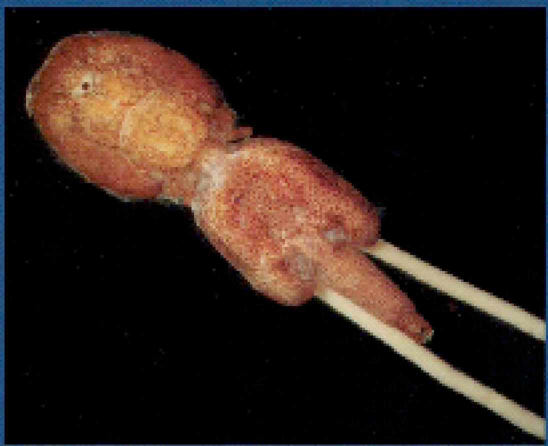
MARINE PARASITOLOGY



EDITOR

KLAUS ROHDE

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 clavavicular 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.

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 Cambrium. 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 interstine, 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,

Table 5.5 Parasitic gastropods (modified after Warén 1983, Rosenberg 1993)

Family	Parasitic species	Size (mm)	Hosts	Type of parasitism
Eulimidae	1500	2–140	Echinoderms	Ecto-, gall-, endo-
Pyramidellidae	>500	2–25	Molluscs, Annelids	Ecto-, suction
Ovulidae	400	5–80	Coelenterates	Ecto-
Epitoniidae	200	2–60	Coelenterates	Ecto-
Triviidae	100	3–20	Ascidians	Brood-
Architectonicidae	30	3–50	Coelenterates	Ecto-
Colubrariidae	30	15–70	Fish	Ecto-, suction
Velutinidae	30	5–25	Ascidians	Brood-
Cypraeidae	<20	8–150	Sponges	Ecto-
Cancellariidae	>150	5–40	Fish	Ecto-, suction
Marginellidae	>300	2–90	Fish	Ecto-, suction

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 1987).

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 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 Coralliophilidae 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 *Coralliophila* 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 Perrine 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).

Echineulima (Fig. 5.37B) parasitises the echinoid families Diadematidae and Echinometridae. They are protandric hemaphrodites. 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

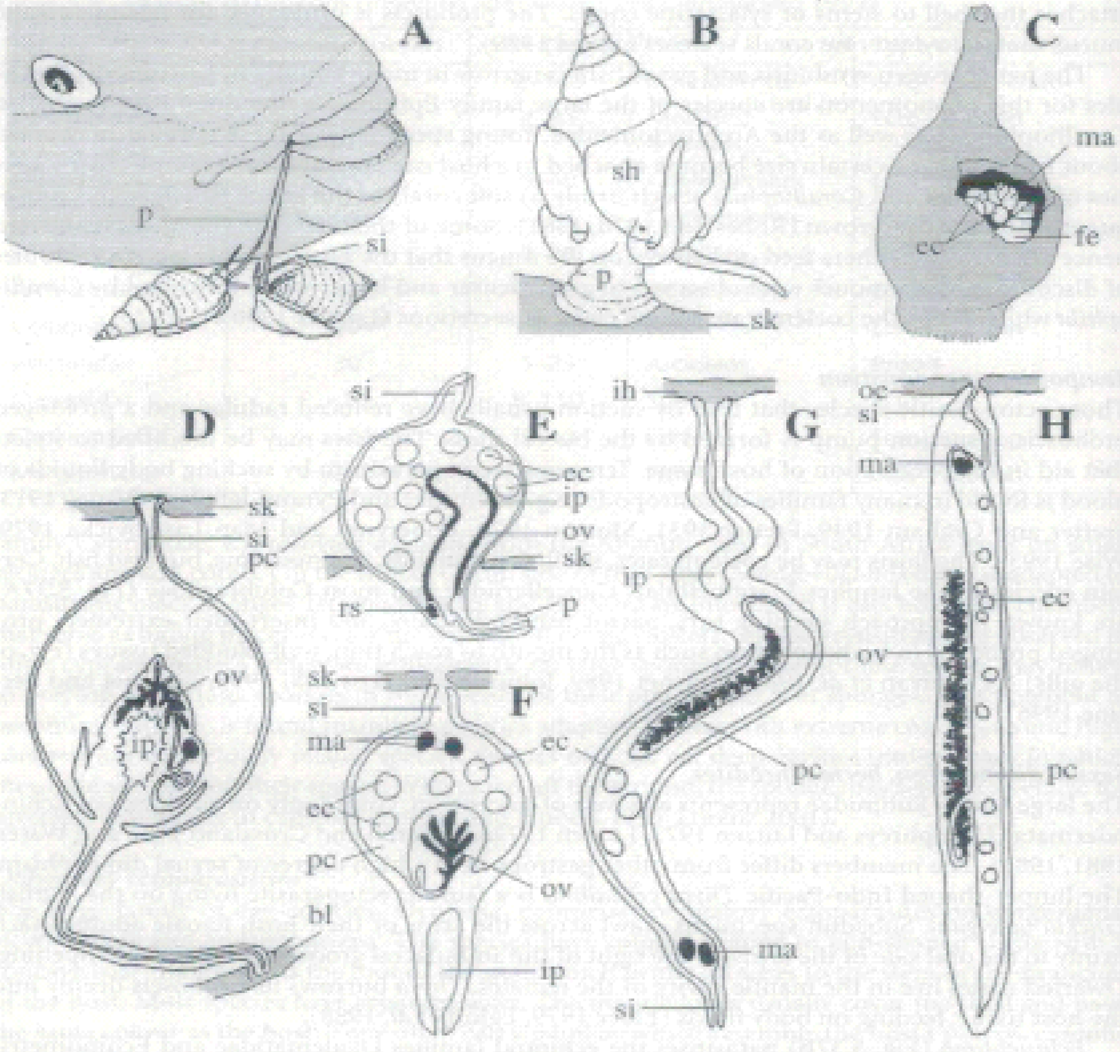


Figure 5.37 A. Temporary ectoparasitism. A parrot-fish, *Scarus sordidus*, parasitised by two *Colubraria obscura*. B. Ectoparasitism: *Echineulima* sp. parasitising an echinoid. C. Gall-formation: male and female *Sabinella* with egg capsules in a gall of a spine of *Eucidaris*. D.–H. Transition to endoparasitism. D. *Gasterosiphon* in a holothurian. E. Female *Diacolax* in host holothurian. F. *Entocolax*. G. *Entoconcha*. H. *Enteroxenos*. Abbreviations: bl, blood-lacuna of host; ec, egg capsule; fe, female; ih, intestine of host; ip, intestine of parasite; ma, male; oe, oesophagus of host; ov, ovary; p, proboscis; pc, pseudopallial chamber; rs, receptaculum seminis; sh, shell; si, sipho; sk, skin of host. A. After a photo by M. Strickland. B. and C. after Warén 1983. D.–H. After Warén (1983).

host holothurian. These genera demonstrate transitions to endoparasitism (Warén 1983, Fretter and Graham 1997).

Endoparasitism

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 ovarial ridge protrudes into this cavity. The male enters the female through the ciliated tubule from the host's oesophagus, enters 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

An early account of adaptations of gastropods to parasitism is by Vaney (1913). Humphreys and Lützen (1972), Lützen and Nielsen (1975), and Lützen (1972a, b, 1979) made important contributions to gastropods infecting echinoderms. Papers by Bouchet (1989), Johnson and Jazwinski (1995) and Bouchet and Perrine (1996) contain information on gastropods parasitising sleeping fishes. Robertson (1970) reviewed the predators and parasites of stony corals, with special reference to symbiotic prosobranch gastropods, and Robertson (1981) discussed two prosobranch gastropods symbiotic with Indo-Pacific zoanthids. A detailed study of the anatomy and functional morphology of the feeding structures of an ectoparasitic pyramidellid gastropod is by Wise (1993).

National Library of Australia Cataloguing-in-Publication entry

Marine parasitology.
Bibliography.
Includes index.
ISBN 0 643 09025 8.

1. Parasitism. 2. Marine animals – Parasites.
I. Rohde, Klaus, 1932– . II. CSIRO.

578.65

Published exclusively in Australia, New Zealand and the Americas, and non-exclusively in other territories of the world (excluding Europe, the Middle East, Asia and Africa), by:
CSIRO PUBLISHING
PO Box 1139 (150 Oxford St)
Collingwood VIC 3066
Australia

Tel: (03) 9662 7666 Int: +(613) 9662 7666
Fax: (03) 9662 7555 Int: +(613) 9662 7555
Email: publishing.sales@csiro.au
Website: www.publish.csiro.au

Published exclusively in Europe, the Middle East, Asia (including India, Japan, China, and South-East Asia) and Africa, and non-exclusively in other territories of the world (excluding Australia, New Zealand and the Americas) by CABI Publishing, a Division of CAB International, with the ISBN 1 84593 053 3.

CABI Publishing
Wallingford
Oxon OX10 8DE
United Kingdom

Tel: 01491 832 111 Int: +44 1491 832 111
Fax: 01491 829 292 Int: +44 1491 829 292
Email: publishing@cabi.org
Website: www.cabi-publishing.org

Front cover:
Background: A heavy infection by *Cyamus ovalis* on skin of the Northern right whale, *Eubalaena glacialis*, from East Iceland. Photo by Jørgen Lutzen.

Inset: A mature female salmon louse, *Lepeophtheirus salmonis*, with newly extruded, whitish egg strings. Photo by Øivind Øines.

Set in 10 pt Adobe Minion and Stone Sans
Cover and text design by James Kelly
Typeset by Desktop Concepts Pty Ltd, Melbourne
Printed in Australia by Ligare