

# Platyhelminthes

Klaus Rohde, *University of New England, Armidale, New South Wales, Australia*

The Platyhelminthes are a group of nonsegmented invertebrates that occur worldwide in a wide range of habitats; more than half of the species are parasitic.

## Introduction

The Platyhelminthes or 'flatworms' are a phylum of invertebrates lacking true segments or appendages. The largely free-living 'turbellarians' inhabit freshwater and marine and, to a lesser extent, terrestrial habitats. The parasitic neodermatans comprise the flukes (trematodes), monogeneans and tapeworms (cestodes) and include species of great medical and economic importance. Only a small fraction of the species has been described. Platyhelminthes have been the subject of many phylogenetic studies because of their supposed position near the root of all bilaterian invertebrates.

## Basic Design

The Platyhelminthes are acoelomate, i.e. they lack a body cavity, and triploblastic, i.e. they have an ectoderm, mesoderm and endoderm. Cleavage is irregular or spiral (quartet spiral cleavage in the Polycladida, dual spiral or bilateral cleavage in the Acoela). The digestive system lacks an anus. Typically, the nervous system consists of longitudinal connectives and transverse commissures with a well-developed anterior commissure acting as a brain. Excretion/osmoregulation is by protonephridia which consist of terminal flame bulbs, capillaries and ducts opening to the outside via single or multiple excretory pores. The surface layer is a cellular or syncytial epidermis or, in the major parasitic groups, a syncytial surface tegument (neodermis) connected to deeper lying perikarya by cytoplasmic processes. The interior is filled by a parenchyma traversed by muscle fibres; a vascular system is absent except in some trematodes. Except for a few species which have secondarily acquired separate sexes, flatworms are hermaphroditic. Most Platyhelminthes range from less than a millimetre in length to a few millimetres, but some cestodes reach a length of several metres.

## Diversity

The Platyhelminthes consist of a large number of taxa (Figure 1), each with a number of shared acquired

## Introductory article

### Article Contents

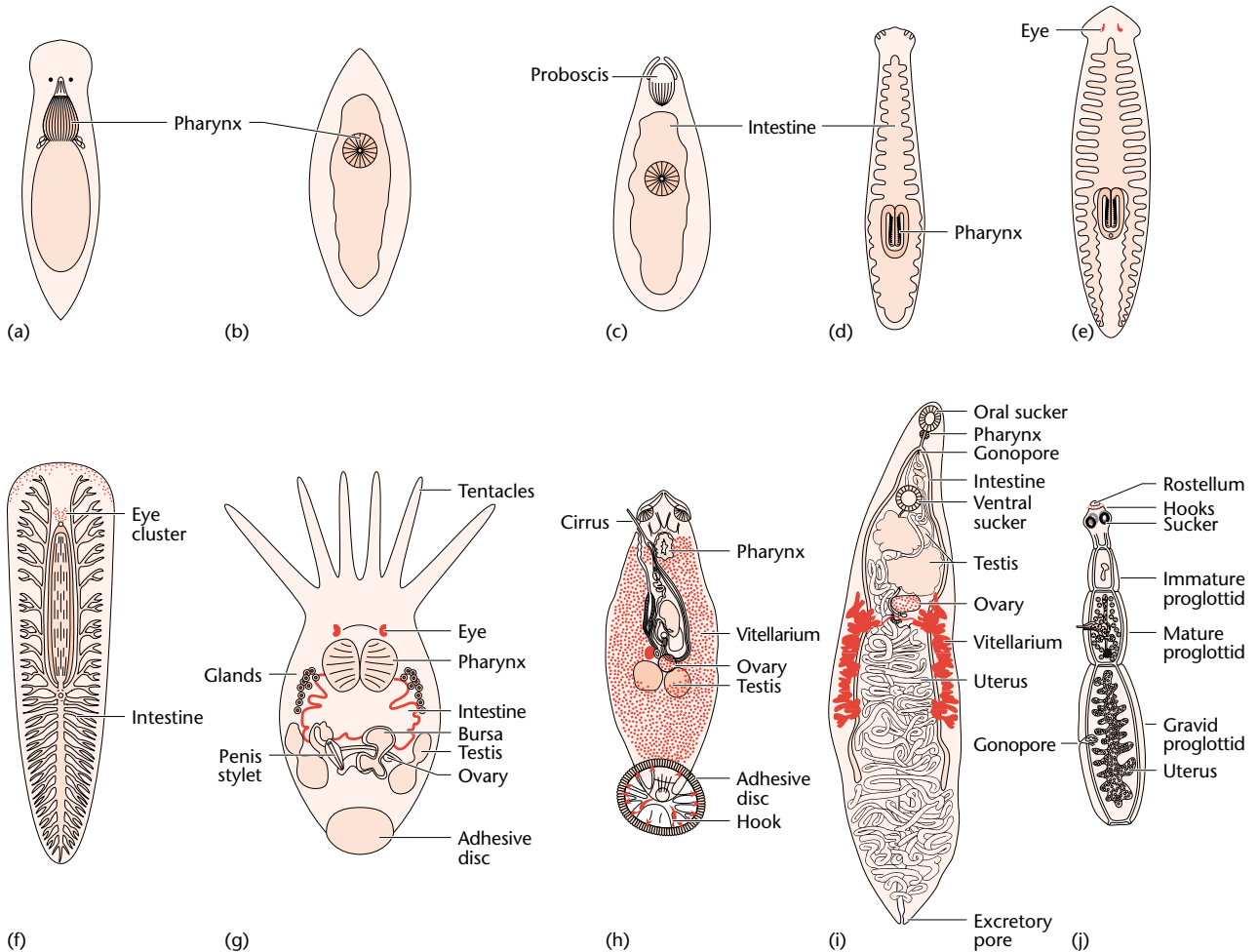
- Introduction
- Basic Design
- Diversity
- Habitats and Abundance
- Habits and Life Histories
- Fossil History
- Phylogeny

characters (synapomorphies) distinguishing them from other taxa. Although there is no agreement that they are monophyletic, the largely free-living groups are, in the following, referred to as turbellarians. There is consensus that the large taxa of parasitic flatworms (Trematoda, Monogenea, Cestoda) form one monophylum, the Neodermata.

Acoela (predominantly free-living, marine), which may not be monophyletic with the other Platyhelminthes (see Phylogeny, below), differ from all other flatworms (with some exceptions in which the intestine has been secondarily lost) in the lack of an intestine lined by an epithelium; they have a system of interdigitating digestive cells or a digestive syncytium instead. They lack protonephridia. The epidermal locomotory cilia have a complex system of ciliary rootlets and some peripheral microtubular doublets in the ciliary tips terminate abruptly. Cleavage is of the spiral-duet type. The statocyst consists of three cells. Nemertodermatida (free-living and symbiotic, marine) resemble the Acoela (with which they are often combined in the taxon Acoelomorpha) in some of these characters, but differ from them in the presence of a statocyst with two statoliths, and in the structure of sperm.

Catenulida (small, free-living, freshwater and marine) have unpaired protonephridia and the flame bulbs possess two cilia. All the other platyhelminths have paired protonephridia and multiciliary flame bulbs; they also have lamellated rhabdites (secretory granules with concentric layers of proteins), assumed to be secondarily lost in the Neodermata and some other taxa. They are therefore referred to as the Rhabditophora. Brief characterizations of the various taxa of Rhabditophora are given in the following.

Macrostomida (free-living, marine and freshwater) have nonciliated sperm and a special glandular organ. Haplopharyngida (free-living, marine) have a cranial proboscis-like invagination of the surface layers. Polycladida (mainly free-living and marine) have an intestine with many radiating branches; some species are large (a few centimetres across) and very colourful. Lecithoepitheliata (free-living, freshwater, terrestrial and marine) have a special type of ovary and characteristic flame bulbs. Prolecithophora (mainly or entirely free-living, freshwater and



**Figure 1** Examples of major platyhelminth taxa. (a) Dalyelliida. (b) Typhloplanida. (c) Kalyptorhynchia. (d) Proseriata. (e) Tricladida. (f) Polycladida. (g) Temnocephalida. (h) Monogenea. (i) Trematoda. (j) Cestoda. Redrawn and modified from various sources.

marine) have special types of flame bulbs and nonciliated sperm. Proseriata (mainly free-living, marine and freshwater) have follicular yolk glands arranged along the vitelline duct. Tricladida ('planarians', freshwater, terrestrial and marine) have a characteristic intestine consisting of one anterior and two posterior branches. Typhloplanida (marine, freshwater and terrestrial) have a characteristic anterior end, but lack a permanent sheathed proboscis, whereas the Kalyptorhynchia (mainly marine) have a sheathed proboscis. Dalyelliida (marine, freshwater, parasitic) have a well-developed pharynx of a special type, and the Temnocephalida (ectocommensal), which are closely related to them, typically have anterior tentacles and a posterior sucker. Fecampiida (endoparasitic) lack an intestine and have ciliated larvae. Possibly closely related to the Fecampiida are some species of doubtful taxonomic position.

The Neodermata include the major groups of parasitic Platyhelminthes, i.e. the Monogenea, Trematoda and Cestoda. Characteristics are as follows: all adult neodermatans are endo- or ectoparasites usually of vertebrates; the larval ciliated epidermis is, in the adult, replaced by a syncytial tegument connected to underlying perikarya by branching cytoplasmic processes; epidermal cilia of the larva have a single, anteriorly directed ciliary rootlet; sensory receptors have characteristic electron-dense collars; flame bulbs of protonephridia are formed by two interdigitating cells; during spermiogenesis, flagella are incorporated in the sperm body beginning at the base of the flagella. Among the Neodermata, the Monogenea consist of two groups, the Monopisthocotylea and Polyopisthocotylea. Both have posterior attachment organs bearing hooks, but the latter also have attachment clamps. Recent studies using DNA sequences have cast some doubt on

whether these two groups are monophyletic. The Trematoda include the Aspidogastrea, characterized by a ventral adhesive organ subdivided into alveoli or other sucker-like structures, and the Digenea, which typically have one anterior and one more posteriorly located sucker. Cestoda include the Gyrocotylidea (infecting the intestine of chondrichthyan fishes) and Amphilinidea (infecting the body cavity of turtles and teleosts) which lack proglottids ('segments'), and the Eucestoda which have proglottids. All cestodes lack a digestive tract.

## Habitats and Abundance

Few Platyhelminthes are found on land (e.g. land planarians), but freshwater and in particular marine habitats have been colonized by a wide variety of species. Platyhelminthes are a dominant group in the meiofauna, i.e. many species are found in the spaces between sand grains of beaches and the sublittoral. Platyhelminthes also represent one of the major groups of parasites infecting humans and animals. Most of these parasites belong to the Neodermata (Trematoda, Monogenea and Cestoda), but some species of turbellarians are parasites of various invertebrates and a few vertebrates. Almost all adult trematodes (flukes) are endoparasites of vertebrates, infecting the digestive tract, liver and other organs, whereas most monogeneans are ectoparasitic on the gills and skin of fishes, although some infect the body cavity of sharks, the urinary bladder, mouth cavity and conjunctival sac of turtles, and the urinary bladder and gills of amphibians. Adult cestodes (tapeworms) parasitize the digestive tract and sometimes the body cavity of vertebrates.

According to Bray and Gibson (Museum of Natural History, London, personal communication), approximately 20 000 species of Trematoda, 10 000 species of Monogenea and 10 000 species of Cestoda have been described to date. However, every year many additional species are described and it is, therefore, certain, that only a small fraction of all Neodermata is known. It is also certain that only some of the numerous turbellarian species have been described. The total number of turbellarians may be about 15 000, but this may well be a severe underestimate. The total number of platyhelminth species may be well above 100 000.

## Habits and Life Histories

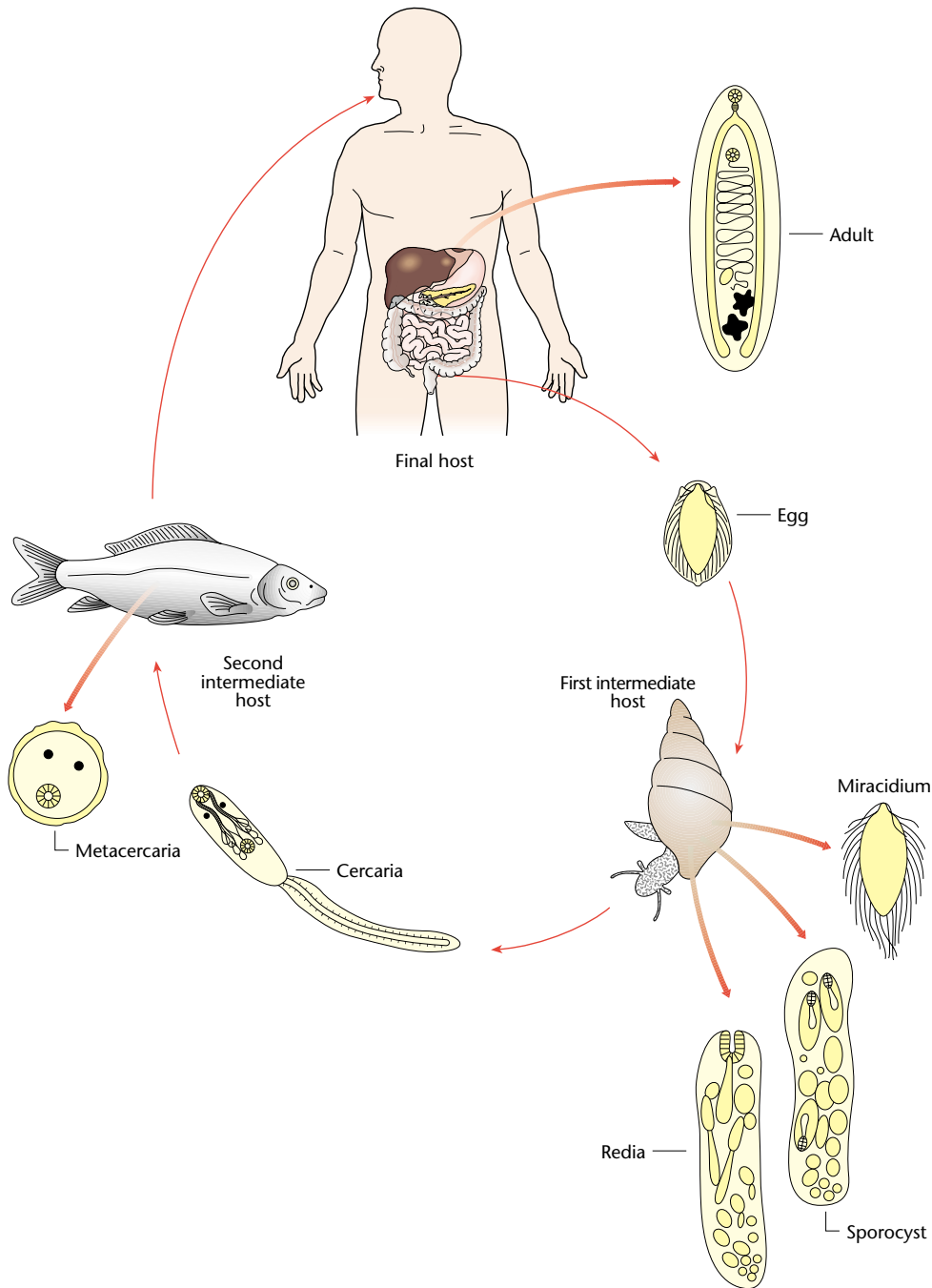
Some Platyhelminthes feed on detritus and bacteria, others are predatory (e.g. many Dalyelliida, Tricladida), commensal (e.g. Temnocephalida), or parasitic (Neodermata, some Dalyelliida) (see Diversity, above).

Most free-living Platyhelminthes, the turbellarians, have a direct development from egg to adult, not involving larval stages. The Polycladida have lobed ciliated larvae, the so-called Müller's larvae.

Among the Neodermata, Monogenea lack intermediate hosts, i.e. they have a direct life cycle. Eggs sink to the bottom, larvae (usually ciliated) hatch and infect other fish hosts. Hatching may be induced by host-specific or host-nonspecific urea, and/or there may be a circadian rhythm, i.e. larvae hatch at a particular time which is particularly favourable for finding a host. Among the polystome monogeneans infecting turtles and amphibians, there are species that have remarkable life cycles. Thus, *Polystoma integerrimum* matures when its frog host enters water for reproduction. Worms produce eggs from which larvae hatch and infect the gills of tadpoles. When young tadpoles are infected, juvenile worms mature fast and produce eggs starting a new cycle. When older tadpoles are infected, worms do not mature. They migrate, at night and very fast, over the ventral body surface of metamorphosing tadpoles into their urinary bladder where they mature.

Aspidogastrea use molluscs (bivalves and snails) and vertebrates (elasmobranch and teleost fishes and turtles) as hosts. The former act as intermediate hosts and sometimes as definitive hosts as well. Vertebrates are definitive (final) hosts.

The digenean trematodes have remarkably complex life cycles which are always indirect, that is, involve at least one intermediate in addition to the definitive, vertebrate host. Intermediate hosts are almost always molluscs, but annelids are used in a few cases. The Chinese liver fluke, *Opisthorchis (Clonorchis) sinensis*, is an example of a species using two intermediate hosts (Figure 2). Adult worms infect the liver of fish-eating mammals including humans. Eggs are produced which pass out in the faeces. Hatching of larvae (miracidia) occurs in freshwater. The larvae swim around until they encounter a suitable snail host into which they penetrate, shedding their cilia. The larva now grows into a sporocyst, a sac-like structure lacking a digestive system, in which numerous rediae develop. Rediae have a pharynx and short intestine and give rise to many tailed larvae, the cercariae. Cercariae escape from the snail, swim around in freshwater until they encounter a fish into which they penetrate, shedding the tail. Worms now encapsulate, forming the metacercariae. When fish are eaten by a mammal, the capsule wall is digested and the worm develops to the adult stage in the liver. The sheep liver fluke, *Fasciola hepatica*, has a life cycle similar to that of the Chinese liver fluke. However, the metacercaria is found not in a second intermediate host but on vegetation which is eaten by sheep and cattle. The bisexual blood flukes of humans (schistosomiasis, bilharzia) and animals lack a redial stage and metacercaria. Miracidia infect snails in which mother and daughter sporocysts develop. The latter give rise to cercariae with a forked tail (furcocercariae) which escape from the snail and



**Figure 2** Life cycle of the Chinese liver fluke.

penetrate through the skin into the final host. They enter the blood system, reach the liver and finally the small blood vessels around the intestine or urinary bladder where eggs are laid. Eggs escape into the lumen of the intestine or bladder and leave the host in the faeces or urine. Some trematodes are known to induce behaviour changes in the

intermediate host which increases their chances reaching the final host. Thus, *Levinseni* uses land snails as intermediate hosts. During the day, sporocysts containing cercariae infective to birds extend into the snail's tentacles. The attention of birds is attracted by rhythmical pulsations of the sporocysts which are conspicuously banded. Birds

bite off the tentacles and become infected. Also, infected snails tend to expose themselves to birds at the tip of vegetation.

Among the cestodes, *Taenia saginata* infects the intestine of humans. Gravid proglottids ('segments') containing large numbers of eggs are shed in the stool and eaten by the intermediate host, cattle. Larvae with three pairs of hooks, the so-called hexacanth or oncosphere larvae, hatch in the small intestine, penetrate through the wall of the intestine and reach the striated muscles, where they turn into the bladderworm or cysticercus. The bladderworm is a liquid-filled sphere containing a single tapeworm head. Humans become infected by eating raw or undercooked beef. The wall of the bladderworm is digested and the tapeworm head attaches itself to the intestinal wall, growing up to the mature tapeworm. The broad fish tapeworm, *Diphyllobothrium latum*, uses two intermediate hosts. Adult worms infect the intestine of fish-eating mammals including humans. Eggs are shed, a ciliated larva (coracidium) hatches in fresh or brackish water and is swallowed by copepods where it develops to the proceroid. When copepods are ingested by fish, the proceroid becomes a plerocercoid. Mammals become infected by eating infected fish.

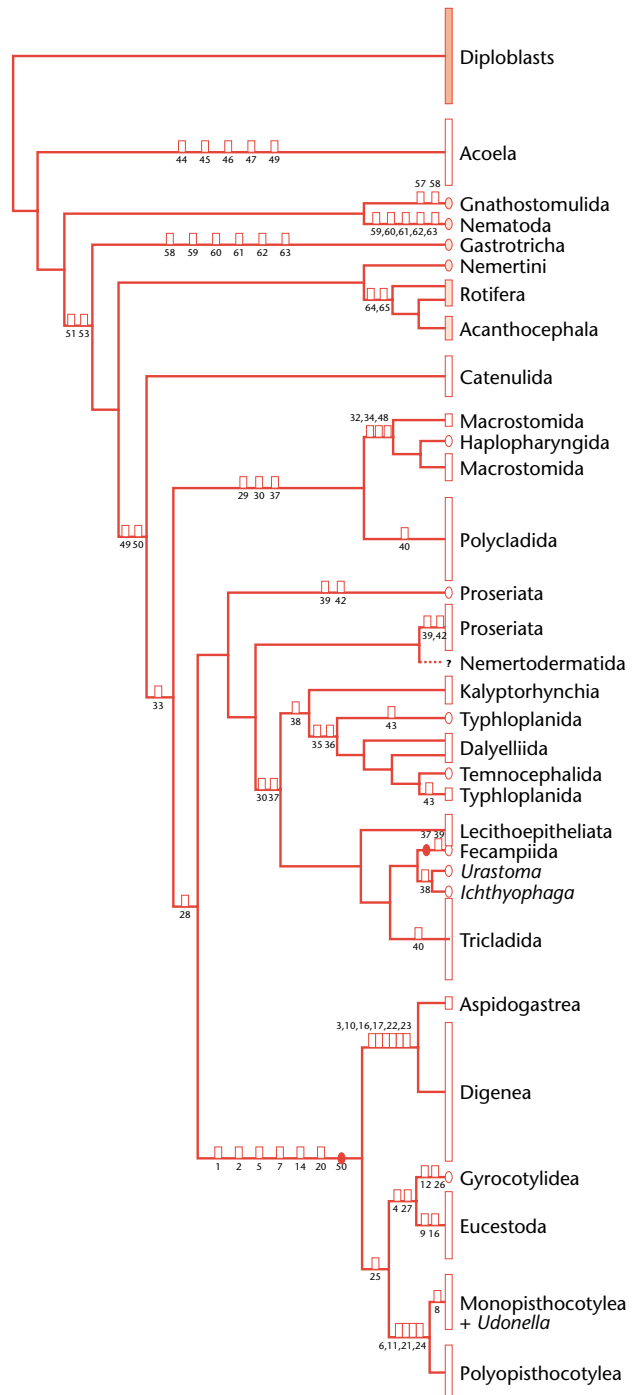
## Fossil History

Schistosome eggs have been recovered from ancient Egyptian mummies, but older fossils that can with certainty be identified as Platyhelminthes are not known.

## Phylogeny

The generally accepted view is that Platyhelminthes are close to the root of the bilateral invertebrates. However, evidence from 18S rDNA, and hox genes, as well as the occurrence of quartet spiral cleavage in some Platyhelminthes as well as the annelids, suggests that the Platyhelminthes (possibly excluding the Acoela) may be of coelomate origin, i.e. they may be animals that have secondarily lost the coelom and anus. This suggestion is supported by the presence of a remarkably complex nervous and sensory system, and of a pulsating vascular system with cellular inclusions in some Platyhelminthes.

A considerable effort has been made to study the interrelationships of the various platyhelminth taxa with each other, using data from life histories, development, light and electron microscopy, and DNA sequences. Phylogenetic trees based on molecular biology and morphology do not agree in all aspects, but there is now consensus that all the major groups of parasitic Platyhelminthes (including the Trematoda, Monogenea and Cestoda) form one clade (monophylum), i.e. that they have one common ancestor. It is also likely that the Acoela are not monophyletic with the other Platyhelminthes. A



**Figure 3** Phylogenetic tree of the Platyhelminthes using 'total evidence' (morphology, whole sequences of 18S rDNA). The numbers refer to morphological characters. From Littlewood *et al.* (1999a) with permission of Academic Press.

phylogenetic tree based on 'total evidence' (using DNA as well as morphological/developmental data) is illustrated in **Figure 3**.

## Further Reading

- Balavoine G (1998) Are Platyhelminthes coelomates without a coelom? An argument based on the evolution of *Hox* genes. *American Zoologist* **38**: 843–858.
- Caira JN and Littlewood DTJ (in press) *Diversity of Platyhelminthes*. In: Levine S (ed.) *Encyclopedia of Biodiversity*. Boston, MA: Academic Press.
- Cannon LRG (1986) *Turbellaria of the World. A Guide to Families and Genera*. Queensland, Australia: Qld. Museum, South Brisbane.
- Ehlers U (1985) *Das phylogenetische System der Plathelminthes*. Stuttgart, Germany: Gustav Fischer Verlag.
- Harrison FW and Bogitsh BJ (eds) (1991) *Microscopic Anatomy of Invertebrates*, vol. 3: *Platyhelminthes and Nemertinea*. New York: Wiley-Liss.
- Littlewood DTJ, Rohde K and Clough KA (1999a) The interrelationships of all major groups of Platyhelminthes – phylogenetic evidence from morphology and molecules. *Biological Journal of the Linnean Society* **66**: 75–114.
- Littlewood DTJ, Rohde K, Bray RA and Herniou EA (1999b) Phylogeny of the Platyhelminthes and the evolution of parasitism. *Biological Journal of the Linnean Society* **68**: 257–287.
- Rohde K (1994) The minor groups of parasitic Platyhelminthes. *Advances in Parasitology* **33**: 145–234.
- Rohde K (ed.) (1997) Origins of parasitism in the Platyhelminthes. *International Journal for Parasitology* **27**: 677–746.
- Ruiz-Trillo I, Riutort M, Littlewood DTJ, Herniou EA and Baguña J (1999) Acoel flatworms: earliest extant bilaterian metazoans, not members of Platyhelminthes. *Science* **283**: 1919–1923.
- Schmidt GD and Roberts LS (1999) *Foundations of Parasitology*, 6th edn. Santiago, CA: McGraw-Hill.