PLATYHELMINTHES, NEMERTEA, AND "ASCHELMINTHES"

A. Schmidt-Rhaesa
University of Bielefeld, Germany

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Summary

This chapter provides information on several basal bilaterian groups: flatworms, nemerteans, Gnathifera, and Nemathelminthes. These include species-rich taxa such as Nematoda and Platyhelminthes, and as taxa with few or even only one species, such as Micrognathozoa (*Limnognathia maerski*) and Cycliophora (*Symbion pandora*). All Acanthocephala and subgroups of Platyhelminthes and Nematoda, are parasites that often exhibit complex life cycles. Most of the taxa described are marine, but some have also invaded freshwater or the terrestrial environment. "Aschelminthes" are not a natural group, instead, two taxa have been recognized that were earlier summarized under this name. Gnathifera include taxa with a conspicuous jaw apparatus such as Gnathostomulida, Micrognathozoa, and Rotifera. Although they do not possess a jaw apparatus, Acanthocephala also belong to Gnathifera due to their epidermal structure.

For Cycliophora, phylogenetic relationships are not clearly resolved, but they may also belong to Gnathifera. Nemathelminthes contains taxa with a cuticle which, with the exception of Gastrotricha, is subject to molting. Besides Gastrotricha, Nematoda, Nematomorpha, Priapulida, Kinorhyncha and Loricifera belong to Nemathelminthes.

1. Introduction

The three groups described in this chapter, flatworms, ribbon worms, and "aschelminthes" constitute the basal groups within one of the two major branches of bilaterian animals which is called Protostomia or Gastroneuralia. "Aschelminthes" are set into quotation marks because it has become clear that they are not a natural group but consist of two clades called Gnathifera and Nemathelminthes (common names are not available). Nemathelminthes presumably form the basal branch within Protostomia/Gastroneuralia. Their sister group, Spiralia, includes Platyhelminthes, Gnathifera, and Nemertini, and other, higher spiralian taxa, such as Mollusca (see *Mollusca),* Annelida, Echiurida, Pogonophora (see *Annelida),* Arthropoda (see *Arthropods Other than Insects*), Kamptozoa, Sipunculida, Onychophora, and Tardigrada (see *Other Invertebrate Taxa*).

	taxon	approximate species number	habitat
	Platyhelminthes	13 000	marine, freshwater, terrestrial, parasitic
	Nemertea	900	marine, freshwater, terrestrial
Gnathifera	Gnathostomulida	100	marine
	Micrognathozoa (*Limnognathia*)	1	marine
	Rotifera	2000	marine, freshwater
	Acanthocephala	1100	parasitic
	Cycliophora (*Symbion*)	1	marine
Nemathelminthes	Gastrotricha	450	marine, freshwater
	Nematoda	20 000	marine, freshwater, terrestrial, parasitic
	Nematomorpha	300	marine, freshwater
	Priapulida	18	marine
	Kinorhyncha	150	marine
	Loricifera	80	marine

Table 1. Summary of species numbers and habitats

2. General Morphology

The body wall of several of the taxa described in this chapter is composed of a ciliated epidermis and underlying sheets of muscles, usually an outer circular and an inner

longitudinal layer. The primary function of the epidermal cilia is locomotion. The structure of the epidermis is quite variable. In Nemathelminthes the epidermal cells secrete extracellular material to the outside, which is called a cuticle and covers the whole body. Locomotory cilia are then reduced, with the exception of Gastrotricha. Most Gnathifera have a structure analogous to the cuticle, but inside the epidermis (internal layer). Further special derivatives, such as the neodermis in parasitic platyhelminthes, are described below.

With the development of a cuticle or an internal layer, the muscular sheets may dissolve more or less into separated muscle strands. In other taxa, additional layers may be present, such as diagonal muscles. In most of the taxa, all internal organs are in close proximity and no body cavities are present (acoelomate condition). If body cavities are present, such as in Rotifera, Acanthocephala, large nematodes, nematomorphs, and priapulids, they are always primary body cavities. The only exceptions are nemerteans, which have an epithelially lined rhynchocoel (a secondary body cavity or coelom).

In Platyhelminthes, the intestinal system is sack-like and has only one opening that acts at the same time as mouth and anus. All other taxa have developed a "through-gut" with an anterior mouth and an anus. The anterior region of the intestine is often very rich in musculature and is then called a pharynx. In most Nemathelminthes, this pharynx has a triradiate lumen, which opens up effectively by the contraction of the radial pharyngeal muscles. This pharynx is an effective sucking device. In many platyhelminthes, the pharynx can be everted and participate in prey ingestion. Gnathifera have, with the exception of Acanthocephala, complex jaws in the pharyngeal region.

The basal condition of the nervous system (as present in cnidarians) is a simple nerve net, a plexus. This plexus is still present in most of the taxa described. However, there are, additionally, certain concentrations of nerve fibers, such as longitudinal nerve cords and cerebral ganglia (brain). In Nemathelminthes, to the exclusion of Gastrotricha and Nematomorpha, the cerebral ganglia are modified into a circumpharyngeal nerve ring.

If excretory organs are present, they are almost always so-called protonephridia. Protonephridia function in the solid tissue of acoelomate organisms. Through the action of one or more cilia, liquid is filtered from intercellular spaces through an extracellular membrane into a duct. Water and substances such as salts are resorbed, while a concentrated solution is excreted through a pore in the body wall. Nematodes possess special excretory systems. With the exception of nemerteans (see *Nemertea (Nemertini), the Ribbon Worms*), no circulatory organs are present. None of these animals has clearly defined respiratory organs (except, probably, the caudal appendages in priapulids).

Sexes can either be separate or hermaphroditic, and the reproductive system is extremely variable. Reproduction is therefore described separately in each taxon. Development is mostly direct, although larval types can be developed in some taxa.

There can be no doubt that the primary habitat for metazoans is the marine environment. Some groups invaded fresh water and are distributed in both aquatic habitats. Only a few of the taxa treated in this chapter occur in the terrestrial environment. Platyhelminthes, nematodes, and acanthocephalans have successfully adapted to

parasitism. This environment is extremely rich in nutrients, but strategies must be developed to cope with defensive reactions of the host, and with the fact that hosts eventually die and are therefore only transient environments. Therefore, a number of morphological adaptations as well as complex life cycles have evolved. This often includes the production of enormous quantities of gametes, and therefore an increased size compared with free-living taxa of the same group.

3. Platyhelminthes, the Flatworms

The Platyhelminthes comprise about 13 000 free-living and parasitic species. The name flatworm is derived from well-known representatives such as the flukes or the tapeworms, although basal flatworms are round in cross section. The parasitic forms have received, due to their medical importance, the major interest. All platyhelminthes have a compact body organization without body cavities. Their alimentary system is sac-shaped and an anus is absent. In tapeworms, the intestine is entirely reduced and nutrients are absorbed through the integument. The epidermis is rich in glands; one conspicuous type is rhabdites, which are present in the subtaxon Rhabditophora. Another characteristic of Rhabditophora is the duo-gland adhesive system, which comprises two glands, one containing glue and the other a substance that dissolves this glue. This system is extremely efficient in the interstitial habitat, that is, between grains of sand in the marine environment where the danger of being washed away by wave action is high.

Almost all flatworms are hermaphrodites with considerably variable and elaborated reproductive organs. In basal groups, yolk is accumulated in the oocytes themselves, but in higher derived flatworms (Neoophora), several yolk cells are enclosed with one oocyte by a membrane to form compound eggs. Development is usually direct; only in the large polyclads and in the parasitic forms did larval stages develop.

In earlier classifications, three subgroups of platyhelminths were recognized: Turbellaria (free-living forms), Trematoda (flukes), and Cestoda (tapeworms). Turbellaria is not a natural group. Instead, some subgroups are closer related to parasitic forms. The above mentioned taxa, Rhabditophora and Neoophora, each include several free-living forms plus all parasitic forms, and represent major steps in flatworm evolution: the development of special epidermal glands and, later, of an advanced reproductive system. The evolution of flatworms started in the marine environment or in sediment. From there, several groups invaded freshwater and, in some cases (terricolous Tricladida), even became terrestrial. At some point, flatworms developed adaptations for a parasitic life and became successful at it.
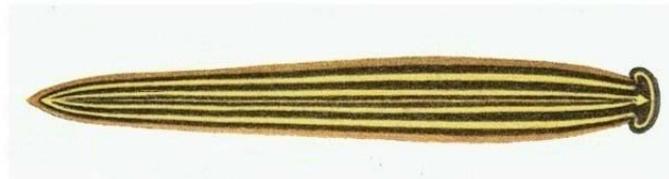

Figure 1. The beautifully colored terrestrial flatworm Bipalium girardi (Tricladida) (from L. von Graff, *Atlas zur Monographie der Turbellarien*. II. Tricladida Terricola,

1899)

The two basal groups, Acoela and Catenulida, are regarded by some authors as not belonging to the flatworms, but having branched off earlier, probably at the basis of all bilaterian animals. Acoels are interesting in the respect that they lack a defined alimentary system but digest food by parenchyma cells. These cells are often organized as a syncytium. Several acoels have symbiotic algae in their parenchyma.

Flatworms have the potential for asexual reproduction, which is beautifully illustrated by the freshwater Catenulids that often form chains of individuals by a process called paratomy. In addition to the parasitic forms, the most well-known flatworms belong to the two groups Polycladida and Tricladida. Polyclads are large marine forms that are often beautifully colored and therefore known to divers.

Their name refers to a high number of intestinal diverticula that distribute nutrients throughout the body. As the only marine free-living forms, they have developed larval forms. Triclads include abundant and well-known representatives, such as the planarians or the terrestrial flatworm *Bipalium* in North America.

All parasitic flatworms are included in the taxon Neodermata. This name refers to the loss of the ciliated epidermis with the infection of a host and its replacement by a new epidermis, the neodermis. The most common parasitic flatworms are flukes and tapeworms. Flukes of the species-rich taxon Digenea (7200 species) have a complex life cycle, including free-living larval forms and parasitic larval and adult stages. Adults live in vertebrates and release eggs through the host's intestine into the water.

The larvae infect intermediate hosts, most often gastropods, in which an asexual increase in number is achieved. Further larval stages, the cercaria, leave the intermediate host and enter the final host.

Some deviations from this generalized cycle are possible, such as the adaptation to dry habitats by a reduction of aquatic larval stages in *Dicrocoelium dendriticum*. A famous example of Digenea is *Schistosoma mansoni*, which causes bilharzia in tropical Africa and South America.

It is one of the few flatworms with separate sexes. Adults live in human portal veins. The female lives permanently in a ventral fold of the male. Their eggs have spines with which they injure blood capillaries, especially those surrounding the intestine. Through these injuries they reach the intestine and finally leave the host with its feces.

A first larval stage, the miracidium, hatches and infects freshwater snails (*Biomphalaria*). In the snail, the number of larvae is multiplied through asexual reproduction. These stages are called sporocysts. Finally, the snails are left by a swimming larval stage called cercaria, which penetrates the skin of humans and develops to adult flukes.

Figure 2. A pair of *Schistosoma mansoni* with larger male and smaller female (photo courtesy of Rolf Mannesmann, Bielefeld, Germany)

Figure 3. Cercaria of *Schistosoma mansoni* (photo courtesy of Rolf Mannesmann, Bielefeld, Germany)

Tapeworms (Cestoda) are endoparasites with, usually, an intermediate and a final host. The body is divided into numerous segment-like parts called proglottids that include almost only the reproductive system. The posteriormost proglottids are full of fertilized

eggs. They are separated and released to the outside through the host's intestine. The worm is anchored in the host's intestinal wall by hooks and suckers on the anterior end, the scolex. The eggs are often ingested by the intermediate host, which, in turn, is eaten by the final host. Humans can become infected by, for example, the bovine tapeworm *Taenia saginata*, through eating raw beef containing encysted larvae. Adult *Taenia saginata* live in the intestine of several carnivorous hosts. The eggs leave the host with the feces and may be ingested by cows. Then a larva, the oncosphaera, hatches and penetrates the intestinal wall. It reaches the musculature through the circulatory system and encysts there. If this musculature is eaten by a carnivorous animal or human, *Taenia* excysts, anchors itself in the intestinal wall with its scolex, and the cycle is complete. Some tapeworms, such as *Echinococcus granulosus*, can be of considerable medical importance because they form large cysts with asexually reproducing larvae that are extremely difficult to remove and are potentially deadly to humans.
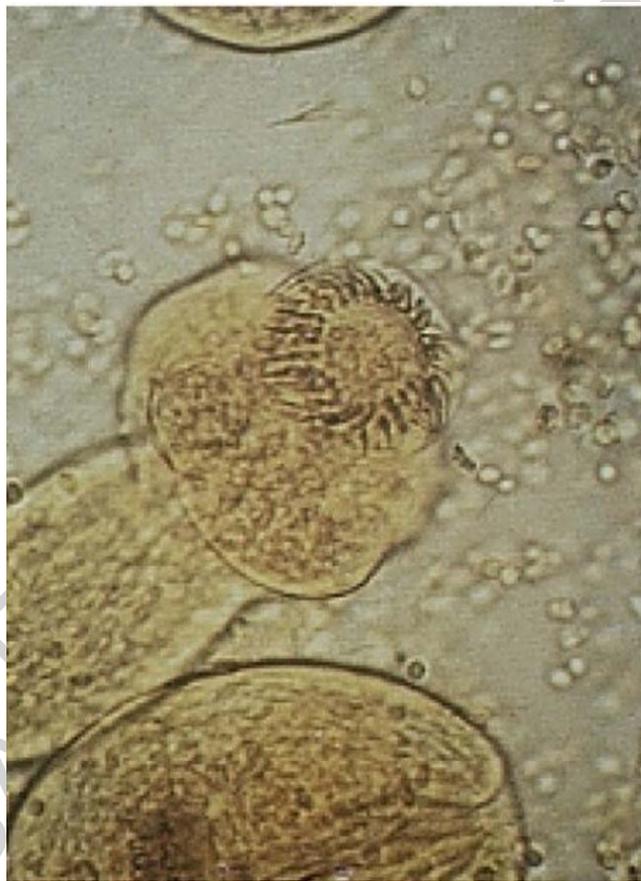
Figure 4. Infective stages of Echinococcus granulosus as a product of asexual reproduction in cysts (hydatids). Note the scolex with hooks with which the worm attaches itself to the intestinal wall (photo courtesy of Rolf Mannesmann, Bielefeld, Germany)

4. Nemertea (Nemertini), the Ribbon Worms

Nemerteans (Nemertea, Nemertini), or ribbon worms, include about 900 species of small to large (30 m) worms. The majority live in the benthos of the marine

environment; fewer species are pelagic, living in fresh water or on land. Nemerteans are predators that capture prey with the aid of an enormously long proboscis. This proboscis can be supplemented by one or more stylets, and may include poison glands to paralyze prey. The proboscis lies in an epithelially lined cavity, the rhynchocoel, and is everted by increased internal pressure. A retractor muscle retracts the proboscis into the rhynchocoel. A special feature of nemerteans is their circulatory system, because their blood vessels have, exclusively within invertebrates, an endothelium.

Nemerteans are, with few exceptions dioecious. Fertilization of gametes is usually external, but it may take place in mucous sheets and is then called a pseudocopulation. Few species are viviparous. Some nemerteans (Heteronemertini) have a larva, called pilidium larva. The adult worm develops within the larva from precursor structures called imaginal discs and finally emerges from the larval body. Other nemerteans do not have a larva and develop directly.

Within Nemerteans, two groups are distinguished. In Anopla the proboscis and mouth opening are separate, in Enopla, there is usually one opening. Anopla include the Paleonemertini and the Heteronemertini (with pilidium larva), to which the well-known genus *Lineus* belongs. Enopla include the Hoplonemertini**,** which have one or more stylets in the proboscis, and Bdellonemertini, to which the bivalve commensal *Malacobdella* belongs. Hoplonemertini are distributed over a diversity of habitats, including pelagic (e.g., *Nectonemertes*), fresh water (e.g., *Prostoma*), and terrestrial (e.g., *Geonemertes*) environment.

Figure 5. Tubulanus rhabdotus, a representative of Palaeonemertini (photo courtesy of Jon Norenburg, Washington, DC, US)

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Biographical Sketch

Andreas Schmidt-Rhaesa is Research Assistant in the Department of Zoomorphology and Systematics at the University of Bielefeld, Germany. He graduated from the University of Göttingen, Germany, and worked on a project at Duquesne University in Pittsburgh, Pennsylvania, and the University of South Florida in Tampa, Florida. His research interests include phylogenetic relationships of metazoans,

especially of Nemathelminhtes, and all aspects of the biology of Nematomorpha, primarily morphology, taxonomy, and life cycle research.