

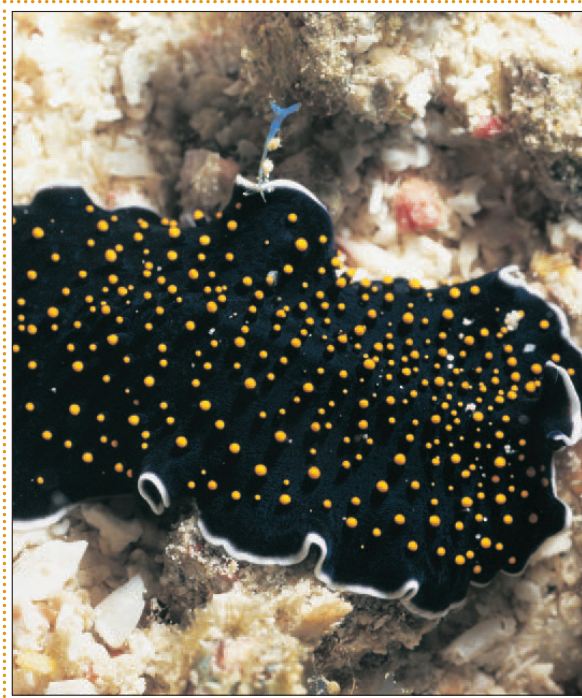


8

chapter eight

Acoelomate Bilateral Animals

Flatworms, Ribbon Worms, and Jaw Worms



Thysanozoon nigropapillosum, a marine turbellarian (order Polycladida).

Getting Ahead

For animals that spend their lives sitting and waiting, as do most members of the two radiate phyla we considered in the preceding chapter, radial symmetry is ideal. One side of the animal is just as important as any other for snaring prey coming from any direction. But if an animal is active in seeking food, shelter, home sites, and reproductive mates, it requires a different set of strategies and a new body organization. Active, directed movement requires an elongated body form with head (anterior) and tail (posterior) ends. In addition, one side of the body faces up (dorsal) and the other side, specialized for locomotion, faces down (ventral). What results is a bilaterally symmetrical animal in which the body could be divided along only one plane of symmetry to yield two halves that are mirror images of each other. Furthermore, because it is better to determine where one is going than where one has been, sense organs and centers for nervous control have come to be located at the anterior end. This process is called cephalization. Thus cephalization and primary bilateral symmetry evolved together.

The three acoelomate phyla considered in this chapter are not much more complex in organization than radiates except in symmetry. The evolutionary consequence of that difference alone was enormous, however, for bilaterality is the type of symmetry assumed by all more complex animals.

The term “worm” has been applied loosely to elongated, bilateral invertebrate animals without appendages. At one time zoologists considered worms (Vermes) a group in their own right. Such a group included a highly diverse assortment of forms. This unnatural assemblage has been reclassified into various phyla. By tradition, however, zoologists still refer to the various groups of these animals as flatworms, ribbon worms, roundworms, segmented worms, and the like. In this chapter we will consider Platyhelminthes (Gr. *platys*, flat, + *helmins*, worm), or flatworms, Nemertea (Gr. *Nemertes*, one of the nereids, unerring one), or ribbon worms, and Gnathostomulida (Gr. *gnathos*, jaw + *stoma*, mouth + *Lulus*, diminutive), or jaw worms. Platyhelminthes is by far the most widely prevalent and abundant of the three phyla, and some flatworms are very important pathogens of humans and domestic animals.

Phylum Platyhelminthes

Platyhelminthes were derived from an ancestor that probably had many cnidarian-like characteristics, including a gelatinous mesoglea. Nonetheless, replacement of gelatinous mesoglea with a cellular, mesodermal **parenchyma** laid the basis for a more complex organization. Parenchyma is a form of tissue containing more cells and fibers than mesoglea of cnidarians.

Flatworms range in size from a millimeter or less to some tapeworms that are many meters in length. Their typically flattened bodies may be slender, broadly leaflike, or long and ribbonlike.

Ecological Relationships

Flatworms include both free-living and parasitic forms, but free-living members are found exclusively in class Turbellaria. A few turbellarians are symbiotic (commensals or parasites), but the majority are adapted as bottom dwellers in marine or fresh water or live in moist places on land. Many, especially larger species, are found on undersides of stones and other hard objects in freshwater streams or in littoral zones of the ocean.

Relatively few members of class Turbellaria live in fresh water. Planarians (figure 8.2) and some others frequent streams and spring pools; others prefer flowing water of mountain streams. Some species occur in moderately hot springs. Terrestrial turbellarians are found in fairly moist places under stones and logs (figure 8.3).

All members of classes Monogenea and Trematoda (flukes) and class Cestoda (tapeworms) are parasitic. Most Monogenea are ectoparasites, but all the trematodes and cestodes are endoparasitic. Many species have indirect life cycles with more than one host; the first host is often an inverte-

position in animal kingdom

1. Platyhelminthes, or flatworms, Nemertea, or ribbon worms, and Gnathostomulida, or jaw worms, are the simplest animals to have **primary bilateral symmetry**.
2. These phyla have only one internal space, a digestive cavity, with the region between the ectoderm and endoderm filled with mesoderm in the form of muscle fibers and mesenchyme (parenchyma). Since they lack a coelom or a pseudocoelom, they are termed **acoelomate animals** (figure 8.1), and because they have three well-defined germ layers, they are termed **triploblastic**.
3. Acoelomates show more specialization and division of labor among their organs than do radiate animals because having mesoderm makes more elaborate organs possible. Thus acoelomates are said to have reached the **organ-system level of organization**.
4. They belong to the protostome division of the Bilateria and have spiral cleavage, and at least platyhelminths and nemerteans have mosaic (determinate) cleavage.

biological contributions

1. Acoelomates developed the basic **bilateral** plan of organization that has been widely exploited in the animal kingdom.
2. **Mesoderm** developed into a well-defined embryonic germ layer (**triploblastic**), making available a great source of tissues, organs, and systems.
3. Along with bilateral symmetry, **cephalization** was established. There is some centralization of the nervous system evident in the **ladder type of system** found in flatworms.
4. Along with the subepidermal musculature, there is also a mesenchymal system of muscle fibers.
5. They are the simplest animals with an **excretory system**.
6. Nemerteans are the simplest animals to have a **circulatory system** with blood and a **one-way alimentary canal**. Although not stressed by zoologists, the rhynchocoel cavity in ribbon worms is technically a true coelom, but because it is merely a part of the proboscis mechanism, it probably is not homologous to the coelom of eucoelomate animals.
7. Unique and specialized structures occur in all three phyla. The parasitic habit of many flatworms has led to many specialized adaptations, such as organs of adhesion.

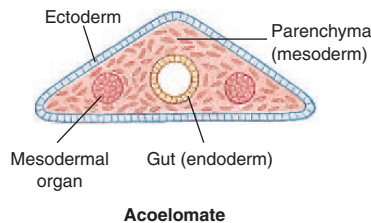


figure 8.1
Acoelomate body plan.



figure 8.3
Terrestrial turbellarian (order Tricladida) from the Amazon Basin, Peru.

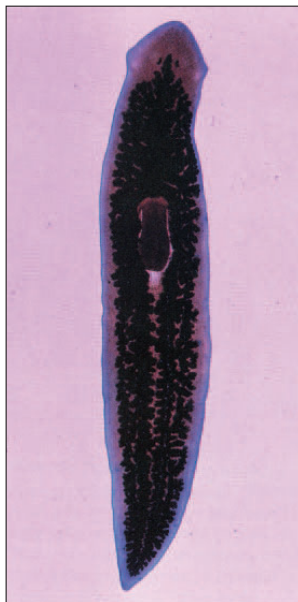


figure 8.2
Stained planarian.

brate, and the final host is usually a vertebrate. Humans serve as hosts for a number of species. Certain larval stages may be free-living.

Form and Function

Tegument, Muscles

Most turbellarians have a cellular, ciliated epidermis. Freshwater planarians, such as *Dugesia*, belong to order Tricladida and are used extensively in introductory laboratory courses. Their ciliated epidermis rests on a basement membrane. It contains rod-shaped **rhabdites**, which swell and form a protective mucous sheath around the body when discharged with water.

characteristics of phylum platyhelminthes

1. Three germ layers (**triploblastic**)
2. **Bilateral symmetry**; definite polarity of anterior and posterior ends
3. **Body flattened dorsoventrally** in most; oral and genital apertures mostly on ventral surface
4. Epidermis may be cellular or syncytial (ciliated in some); **rhabdites** in epidermis of most Turbellaria; epidermis a syncytial **tegument** in Monogenea, Trematoda, Cestoda, and some Turbellaria
5. Muscular system of mesodermal origin, in the form of a sheath of circular, longitudinal, and oblique layers beneath the epidermis or tegument
6. No internal body space (acoelomate) other than digestive tube; spaces between organs filled with parenchyma
7. Digestive system incomplete (gastrovascular type); absent in some
8. Nervous system consisting of a **pair of anterior ganglia** with **longitudinal nerve cords** connected by transverse nerves and located in the parenchyma in most forms; similar to cnidarians in primitive forms
9. Simple sense organs; eyespots in some
10. Excretory system of two lateral canals with branches bearing **flame cells (protonephridia)**; lacking in some forms
11. Respiratory, circulatory, and skeletal systems lacking; lymph channels with free cells in some trematodes
12. Most forms monoecious; reproductive system complex, usually with well-developed gonads, ducts, and accessory organs; internal fertilization; life cycle simple in free-swimming forms and those with single hosts; complicated life cycle often involving several hosts in many internal parasites
13. Class Turbellaria mostly free-living; classes Monogenea, Trematoda, and Cestoda entirely parasitic

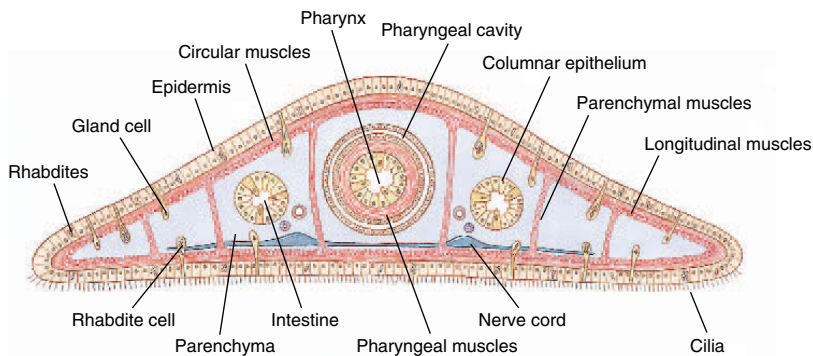


figure 8.4
Cross section of planarian through pharyngeal region, showing relationships of body structures.

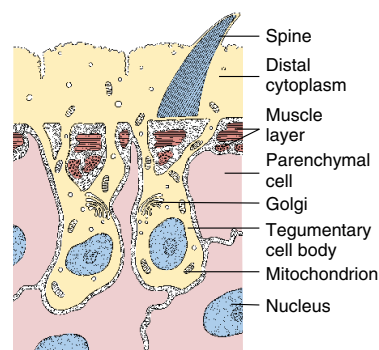


figure 8.6
Tegument of a trematode *Fasciola hepatica*.

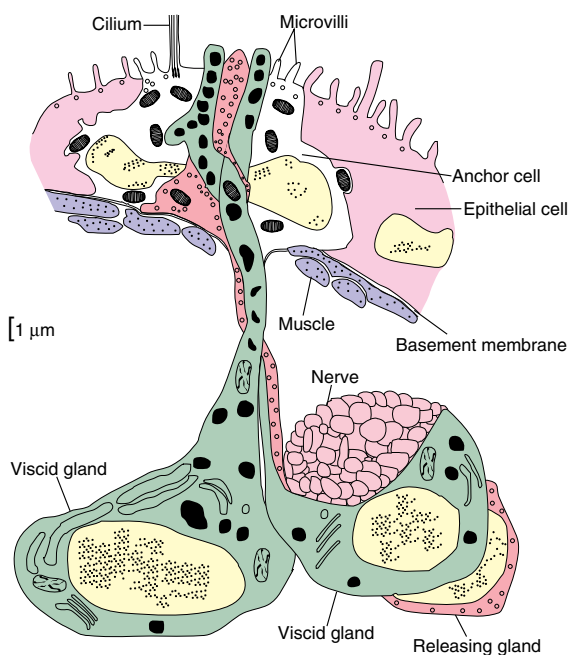


figure 8.5
Reconstruction of dual-gland adhesive organ of a turbellarian *Haplopharynx* sp. There are two viscid glands and one releasing gland, which lie beneath the body wall. The anchor cell lies within the epidermis, and one of the viscid glands and the releasing gland are in contact with a nerve.

Single-cell mucous glands open on the surface of the epidermis (figure 8.4). Most orders of turbellarians have **dual-gland** adhesive organs in the epidermis. These organs consist of three cell types: viscid and releasing gland cells and anchor cells (figure 8.5). Secretions of the viscid gland cells apparently fasten microvilli of the anchor cells to the substrate, and secre-

tions of the releasing gland cells provide a quick, chemical detaching mechanism.

In the body wall below the basement membrane of flatworms are layers of **muscle fibers** that run circularly, longitudinally, and diagonally. A meshwork of **parenchyma** cells, developed from mesoderm, fills the spaces between muscles and visceral organs. Parenchyma cells in some, perhaps all, flatworms are not a separate cell type but are noncontractile portions of muscle cells.

A few turbellarians have a **syncytial** epidermis (nuclei are not separated from each other by intervening cell membranes), and at least one species has a syncytial “insunk” epidermis, in which cell bodies (containing the nuclei) are located beneath the basement membrane and communicate with the distal cytoplasm by means of cytoplasmic channels. “Insunk” is a misnomer because the distal cytoplasm arises by fusion of extensions from the cell bodies.

The body covering of adults of all members of Trematoda, Monogenea, and Cestoda conforms to the plan just described. Furthermore, they lack cilia. Rather than “epidermis,” their body covering is designated by a more noncommittal term, **tegument** (figure 8.6). This distinctive tegumental plan is the basis for uniting trematodes, monogeneans, and cestodes in a taxon known as **Neodermata**. It is a peculiar epidermal arrangement and may be related to adaptations for parasitism in ways that are still unclear.

Nutrition and Digestion

The digestive system includes a mouth, pharynx, and intestine. In turbellarians the muscular **pharynx** opens posteriorly just inside the mouth, through which it can extend (figure 8.7). The mouth is usually at the anterior end in flukes, and the pharynx is not protrusible. The intestine may be simple or branched.

Intestinal secretions contain proteolytic enzymes for some **extracellular digestion**. Food is sucked into the intestine, where cells of the gastrodermis often phagocytize it and complete digestion (**intracellular**). Undigested food is

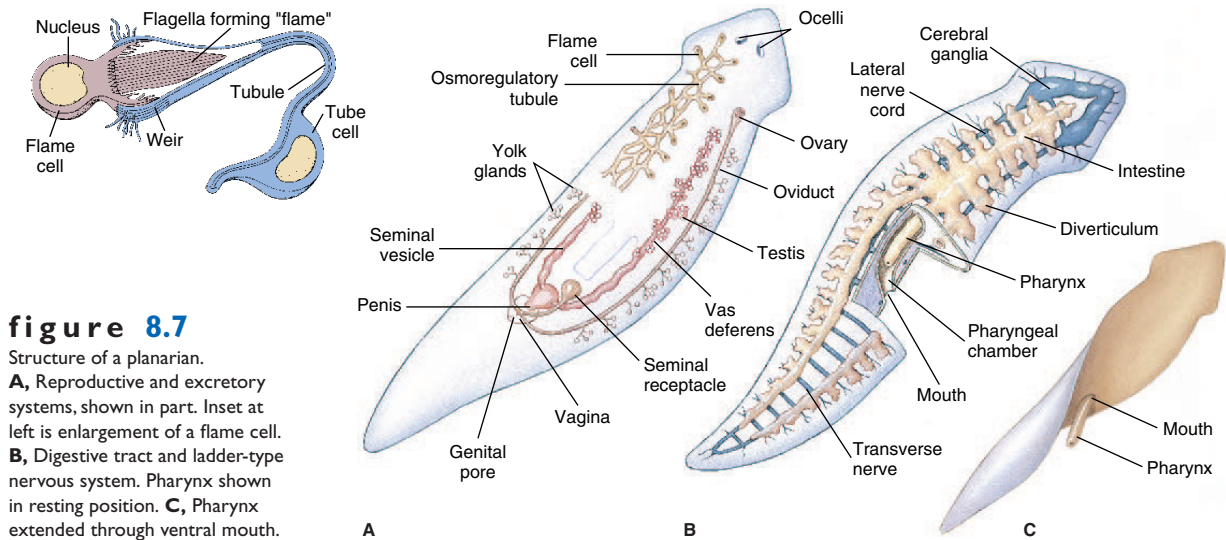


figure 8.7

Structure of a planarian.

A, Reproductive and excretory systems, shown in part. Inset at left is enlargement of a flame cell. **B**, Digestive tract and ladder-type nervous system. Pharynx shown in resting position. **C**, Pharynx extended through ventral mouth.

egested through the pharynx. The entire digestive system is lacking in tapeworms. They must absorb all of their nutrients as small molecules (predigested by the host) directly through their tegument.

Excretion and Osmoregulation

Except in some turbellarians, the osmoregulatory system consists of canals with tubules that end in **flame cells (protonephridia)** (figure 8.7A). Each flame cell surrounds a small space into which a tuft of flagella projects. In some turbellarians and in the other classes of flatworms, the protonephridia form a **weir** (Old English *wer*; a fence placed in a stream to catch fish). In a weir the rim of the cup formed by the flame cell bears fingerlike projections that interdigitate with similar projections of a tubule cell. The beat of the flagella (resembling a flickering flame) provides a negative pressure to draw fluid through the weir into the space (lumen) enclosed by the tubule cell. The lumen continues into collecting ducts that finally open to the outside by pores. The wall of the duct beyond the flame cell commonly bears folds or microvilli that probably function in reabsorption of certain ions or molecules. It is likely that this system is osmoregulatory in most forms; it is reduced or absent in marine turbellarians, which do not have to expel excess water.

Metabolic wastes are largely removed by diffusion through the body wall.

Nervous System

The most primitive flatworm nervous system, found in some turbellarians, is a **subepidermal nerve plexus** resembling the nerve net of the cnidarians. Other flatworms have, in addi-

tion to a nerve plexus, one to five pairs of **longitudinal nerve cords** lying under the muscle layer (figure 8.7B). Connecting nerves form a “ladder-type” pattern. Their brain is a mass of ganglion cells arising anteriorly from the nerve cords. Except in simpler turbellarians, which have a diffuse system, the neurons are organized into sensory, motor, and association types—an important advance in evolution of nervous systems.

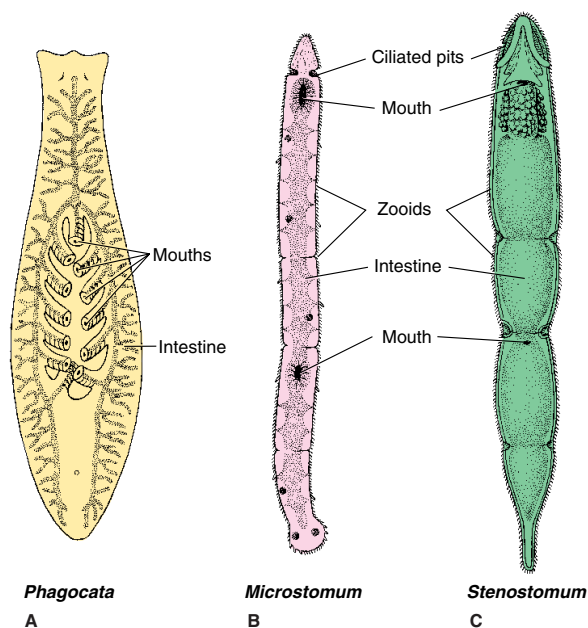
Sense Organs

Active locomotion in flatworms has favored not only cephalization in the nervous system but also advancements in development of sense organs. **Ocelli**, or light-sensitive eyespots, are common in turbellarians (figure 8.7A), monogeneans, and larval trematodes.

Tactile cells and chemoreceptive cells are abundant over the body, and in planarians they form definitive organs on the **auricles** (the earlike lobes on the sides of the head). Some also have **statocysts** for equilibrium and **rheoreceptors** for sensing water current direction.

Reproduction

Many flatworms reproduce both asexually and sexually. Many freshwater turbellarians can reproduce by fission, merely constricting behind the pharynx and separating into two animals, each of which regenerates the missing parts. In some forms such as *Stenostomum* and *Microstomum*, individuals do not separate at once but remain attached, forming chains of zooids (figure 8.8B and C). Flukes reproduce asexually in their snail intermediate host (p.145), and some tapeworms, such as *Echinococcus*, can bud off thousands of juveniles in their intermediate host.

**figure 8.8**

Some small freshwater turbellarians. **A**, *Phagocata* has numerous mouths and pharynges. **B** and **C**, Incomplete fission results for a time in a series of attached zooids.

Most flatworms are monoecious (hermaphroditic) but practice cross-fertilization. In some turbellarians yolk for nutrition of the developing embryo is contained within the egg cell itself (**endolecithal**), just as it is normally in other phyla of animals. Possession of endolecithal eggs is considered ancestral for flatworms. Other turbellarians plus all trematodes, monogeneans, and cestodes share a derived condition in which female gametes contain little or no yolk, and yolk is contributed by cells released from separate organs (**yolk glands**). Usually a number of yolk cells surrounds the zygote within an eggshell (**ectolecithal**). Ectolecithal turbellarians therefore appear to form a clade with Trematoda, Monogenea, and Cestoda to the exclusion of endolecithal turbellarians.

In some freshwater planarians egg capsules are attached by little stalks to undersides of stones or plants, and embryos emerge as juveniles that resemble miniature adults. In other flatworms, an embryo becomes a larva, which may be ciliated or not, according to the group.

Class Turbellaria

Turbellarians are mostly free-living worms that range in length from 5 mm or less to 50 cm. They are typically creeping forms that combine muscular with ciliary movements to achieve locomotion. Their mouth is on the ventral side. Unlike trematodes and cestodes, they have simple life cycles.

Very small planaria swim by means of their cilia. Others move by gliding, head slightly raised, over a slime track secreted by the marginal adhesive glands. Beating of epidermal cilia in the slime track moves the animal forward, while rhythmical muscular waves can be seen passing backward from the head. Large polyclads and terrestrial turbellarians crawl by muscular undulations, much in the manner of a snail.

As traditionally recognized, turbellarians form a paraphyletic group. Several synapomorphies, such as “insunk” epidermis and ectolecithal development, show that some turbellarians are phylogenetically closer to Trematoda, Monogenea, and Cestoda than they are to other turbellarians. Ectolecithal turbellarians therefore appear to form a clade with trematodes, monogeneans, and cestodes to the exclusion of endolecithal turbellarians. Endolecithal turbellarians also are paraphyletic; presence of a dual-gland adhesive system in some endolecithal turbellarians indicates a clade with ectolecithal flatworms to the exclusion of other endolecithal turbellarian lineages. Turbellaria therefore describes an artificial group, and the term is used here only because it is prevalent in zoological literature.

Characteristics used to distinguish orders of turbellarians are form of the gut (present or absent; simple or branched; pattern of branching) and pharynx (simple; folded; bulbous). Except for order Polycladida (Gr. *poly*, many, + *klados*, branch), turbellarians with endolecithal eggs have a simple gut or no gut and a simple pharynx. In a few turbellarians there is no recognizable pharynx. Polyclads have a folded pharynx and a gut with many branches. Polyclads include many marine forms of moderate to large size (3 to more than 40 mm) (p. 139), and a highly branched intestine is correlated with larger size in turbellarians. Members of order Tricladida (Gr. *treis*, three, + *klados*, branch), which are ectolecithal and include freshwater planaria, have a three-branched intestine.

Members of order Acoela (Gr. *a*, without, + *koilos*, hollow) have been regarded as having changed least from the ancestral form. In fact, molecular evidence suggests that acoels should not be placed in phylum Platyhelminthes and that they represent the earliest divergent Bilateria (p. 152). In body form they are small and have a mouth but no gastrovascular cavity or excretory system. Food is merely passed through the mouth into temporary spaces that are surrounded by mesenchyme, where gastrodermal phagocytic cells digest food intracellularly.

Class Trematoda

Trematodes are all parasitic flukes, and as adults they are almost all found as endoparasites of vertebrates. They are chiefly leaflike in form and are structurally similar in many respects to more complex Turbellaria. A major difference is found in the tegument (described earlier, figure 8.6).

Other structural adaptations for parasitism are apparent: various penetration glands or glands to produce cyst material; organs for adhesion such as suckers and hooks; and increased reproductive capacity. Otherwise, trematodes share several characteristics with turbellarians, such as a well-developed alimen-

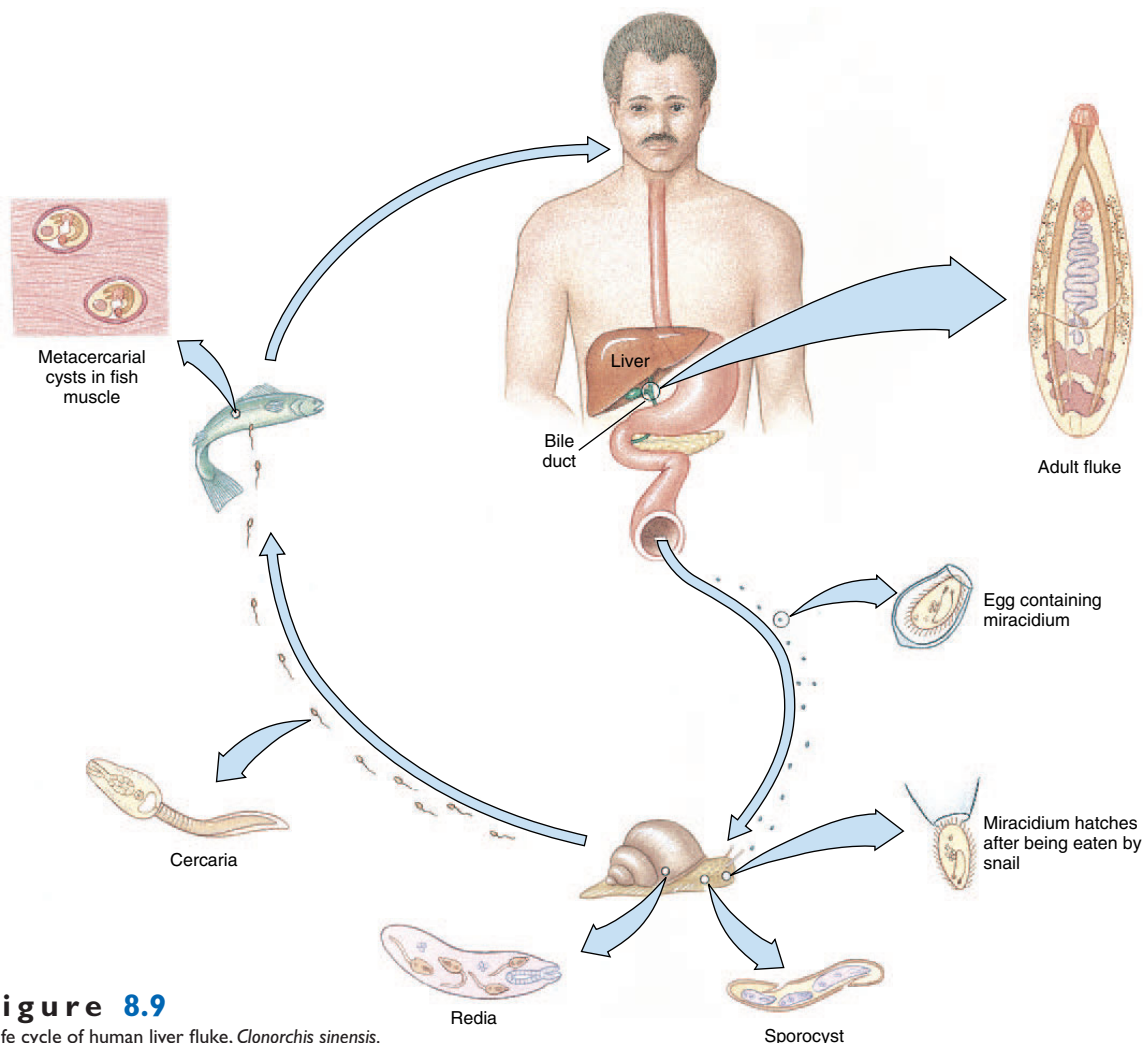


figure 8.9

Life cycle of human liver fluke, *Clonorchis sinensis*.

tary canal (but with the mouth at the anterior, or cephalic, end) and similar reproductive, excretory, and nervous systems, as well as a musculature and parenchyma that differ only slightly from those of turbellarians. Sense organs are poorly developed.

Of the three subclasses of Trematoda, two are small and poorly known groups, but Digenea (Gr. *dis*, double, + *genos*, descent) is a large group with many species of medical and economic importance.

Subclass Digenea

With rare exceptions, digenetic trematodes have a complex life cycle, the first (**intermediate**) host being a mollusc and the final (**definitive**) host being a vertebrate. In some species a second, and sometimes even a third, intermediate host intervenes. The group has many species, and they can inhabit diverse sites

in their hosts: all parts of the digestive tract, respiratory tract, circulatory system, urinary tract, and reproductive tract.

Among the world's most amazing phenomena are digenetic life cycles. Although cycles of different species vary widely in detail, a typical example would include an adult, egg (shelled embryo), miracidium, sporocyst, redia, cercaria, and metacercaria stages (figure 8.9). The shelled embryo or larva usually passes from the definitive host in excreta and must reach water to develop further. There, it hatches to a free-swimming, ciliated larva, the **miracidium**. The miracidium penetrates the tissues of a snail, where it transforms into a **sporocyst**. Sporocysts reproduce asexually to yield either more sporocysts or a number of **rediae**. Rediae, in turn, reproduce asexually to produce more rediae or to produce **cercariae**. In this way a single zygote can give rise to an enormous number of progeny. Cercariae emerge from the snail

table 8.1 Examples of Flukes Infecting Humans

Common and scientific names	Means of infection; distribution and prevalence in humans
Blood flukes (<i>Schistosoma</i> spp.); three widely prevalent species, others reported <i>S. mansoni</i> <i>S. haematobium</i> <i>S. japonicum</i>	Cercariae in water penetrate skin; 200 million people infected with one or more species Africa, South and Central America Africa Eastern Asia
Chinese liver flukes (<i>Clonorchis sinensis</i>)	Eating metacercariae in raw fish; about 30 million cases in Eastern Asia
Lung flukes (<i>Paragonimus</i> spp.), seven species, most prevalent is <i>P. westermani</i>	Eating metacercariae in raw freshwater crabs, crayfish; Asia and Oceania, sub-Saharan Africa, South and Central America; several million cases in Asia
Intestinal fluke (<i>Fasciolopsis buski</i>)	Eating metacercariae on aquatic vegetation; 10 million cases in Eastern Asia
Sheep liver fluke (<i>Fasciola hepatica</i>)	Eating metacercariae on aquatic vegetation; widely prevalent in sheep and cattle, occasional in humans

and penetrate a second intermediate host or encyst on vegetation or other objects to become **metacercariae**, which are juvenile flukes. Adults grow from the metacercaria when that stage is eaten by a definitive host.

Some of the most serious parasites of humans and domestic animals belong to the Digenea (table 8.1).

Clonorchis (Gr. *clon*, branch, + *orchis*, testis) (figure 8.9) is the most important liver fluke of humans and is common in many regions of the Orient, especially in China, southern Asia, and Japan. Cats, dogs, and pigs are also often infected. Adult flukes live in the bile passages, and shelled miracidia are passed in feces. If ingested by certain freshwater snails, sporocyst and redia stages develop, and free-swimming cercariae emerge. Cercariae that manage to find a suitable fish encyst in the skin or muscles as metacercariae. When the fish is eaten raw, the juveniles migrate up the bile duct to mature and may survive there for 15 to 30 years. The effect of the flukes on humans depends mainly on extent of infection. A heavy infection may cause a pronounced cirrhosis of the liver and death.

Schistosomiasis, an infection with blood flukes of genus *Schistosoma* (Gr. *schistos*, divided, + *soma*, body) (figure 8.10), ranks as one of the major infectious diseases in the world, with 200 million people infected. The disease is widely prevalent over much of Africa and parts of South America, West Indies, Middle East, and Far East. It is spread when shelled miracidia shed in human feces and urine get into water containing host snails (figure 8.10B). Cercariae that contact human skin penetrate through the skin to enter blood vessels, which they follow to certain favorite regions depending on the type of fluke. *Schistosoma mansoni* lives in venules draining the large intestine; *S. japonicum* localizes more in venules draining the small intestine; and *S. haematobium* lives in venules draining the urinary bladder. In each case many eggs released by female worms do not find their way out of the body but lodge in the liver or other organs. There they are sources of chronic inflammation. The inch-long adults may live

for years in a human host, and their eggs cause such disturbances as severe dysentery, anemia, liver enlargement, bladder inflammation, and brain damage.

Cercariae of several genera whose normal hosts are birds often enter the skin of human bathers in their search for a suitable bird host, causing a skin irritation known as “swimmer’s itch” (figure 8.11). In this case humans are a dead end in the fluke’s life cycle because the fluke cannot develop further in humans.

Class Monogenea

Monogenetic flukes traditionally have been placed as an order of Trematoda, but they are sufficiently different to deserve a separate class. Cladistic analysis places them closer to Cestoda. Monogeneans are mostly external parasites that clamp onto the gills and external surfaces of fish using a hooked attachment organ called an **opisthaptor** (figure 8.12). A few are found in urinary bladders of frogs and turtles, and one has been reported from the eye of a hippopotamus. Although widespread and common, monogeneans seem to cause little damage to their hosts under natural conditions. However, like numerous other fish pathogens, they become a serious threat when their hosts are crowded together, as in fish farming.

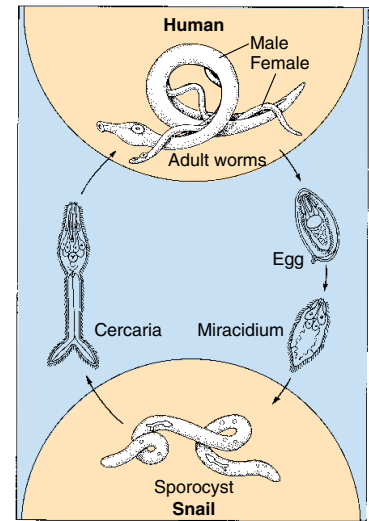
Life cycles of monogeneans are simple, with a single host, as suggested by the name of the group, which means “single descent.” The egg hatches a ciliated larva that attaches to a host or swims around awhile before attachment.

Class Cestoda

Cestoda, or tapeworms, differ in many respects from the preceding classes: they usually have long flat bodies composed of many reproductive units, or **proglottids** (figure 8.13), and they completely lack a digestive system. As in Monogenea and Trematoda,



A



B

figure 8.10

A, Adult male and female *Schistosoma japonicum* in copulation. Blood flukes differ from most other flukes in being dioecious. Males are broader and heavier and have a large, ventral gynecophoric canal, posterior to the ventral sucker. The gynecophoric canal embraces the long, slender female (darkly stained individual) during insemination and oviposition. **B**, Life cycle of *Schistosoma* spp.

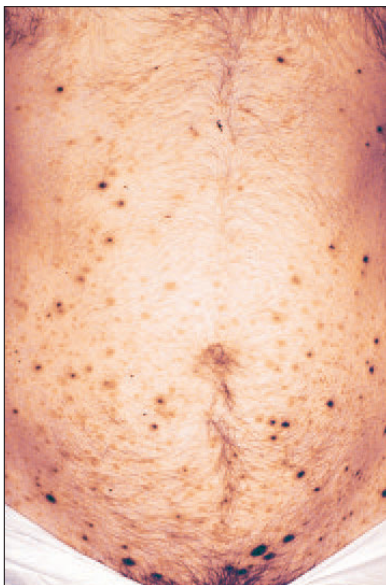


figure 8.11

Human abdomen, showing schistosome dermatitis caused by penetration of schistosome cercariae that are unable to complete development in humans. Sensitization to allergenic substances released by cercariae results in rash and itching.

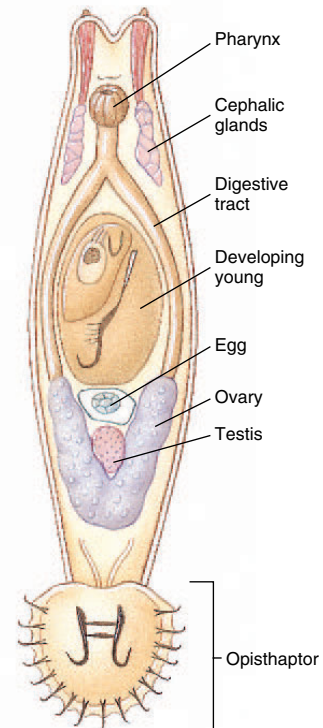


figure 8.12

Gyrodactylus sp. (class Monogenea), ventral view.

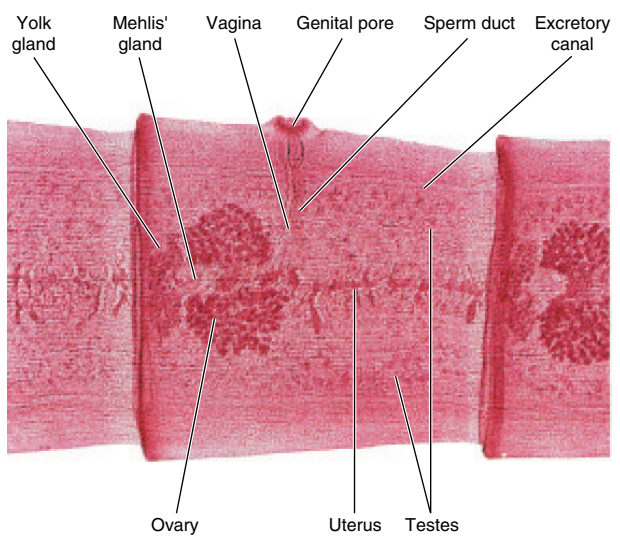


figure 8.13
Mature proglottid of *Taenia pisiformis*, a dog tapeworm. Portions of two other proglottids also shown.

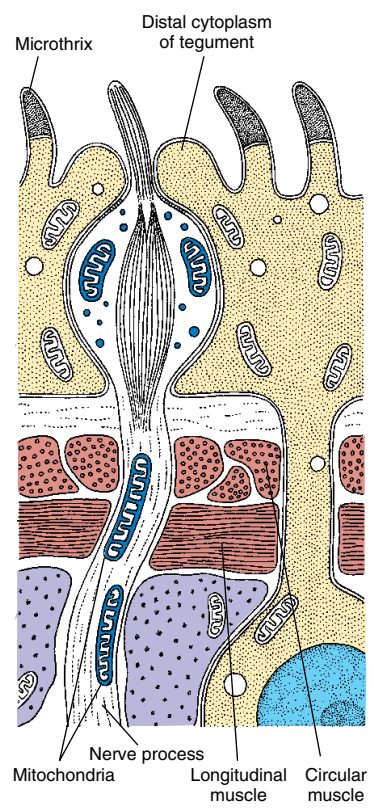


figure 8.14
Schematic drawing of a longitudinal section through a sensory ending in the tegument of *Echinococcus granulosus*.

there are no external, motile cilia in adults, and the tegument is of a distal cytoplasm with sunken cell bodies beneath the superficial layer of muscle (see figure 8.6). In contrast to monogeneans and trematodes, however, their entire surface is covered with minute projections that are similar in certain respects to microvilli of the vertebrate small intestine (figure 8.14). These **microtriches** (sing. **microthrix**) greatly amplify the surface area of the tegument, which is a vital adaptation for a tapeworm, since it must absorb all its nutrients across the tegument.

Tapeworms are nearly all monoecious. They have well-developed muscles, and their excretory system and nervous system are somewhat similar to those of other flatworms. They have no special sense organs but do have sensory endings in the tegument that are modified cilia (figure 8.14). One of their most specialized structures is a **scolex**, or holdfast, which is the organ of attachment. It is usually provided with suckers or suckerlike organs and often with hooks or spiny tentacles (figure 8.15).

With rare exceptions, all cestodes require at least two hosts, and adults are parasitic in the digestive tract of vertebrates. Often one of the intermediate hosts is an invertebrate.

The main body of a cestode is a chain of proglottids called a **strobila** (figure 8.15). Typically, there is a **germinative zone** just behind the scolex where new proglottids form. As new proglottids differentiate in front of it, each individual unit moves posteriorly in the strobila, and its gonads mature. A proglottid usually is fertilized by another proglottid in the

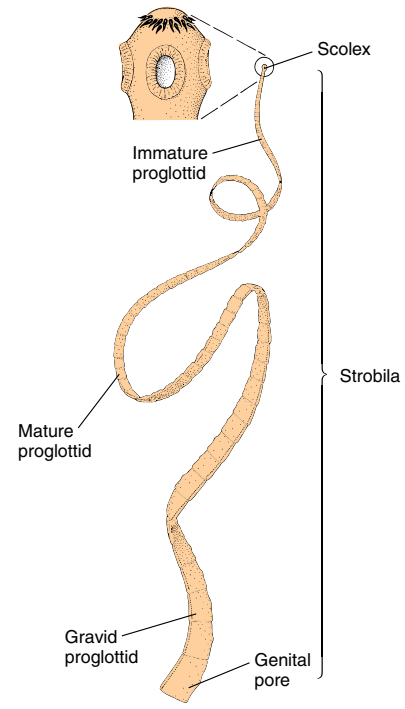


figure 8.15
A tapeworm, showing strobila and scolex. The scolex is the organ of attachment.

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table 8.2 Common Cestodes of Humans

Common and scientific names	Means of infection; prevalence in humans
Beef tapeworm (<i>Taenia saginata</i>)	Eating rare beef; most common of large tapeworms in humans
Pork tapeworm (<i>Taenia solium</i>)	Eating rare pork; less common than <i>T. saginata</i>
Fish tapeworm (<i>Diphyllobothrium latum</i>)	Eating rare or poorly cooked fish; fairly common in Great Lakes region of United States, and other areas of world where raw fish is eaten
Dog tapeworm (<i>Dipylidium caninum</i>)	Unhygienic habits of children (juveniles in flea and louse); moderate frequency
Dwarf tapeworm (<i>Hymenolepis nana</i>)	Juveniles in flour beetles; common
Unilocular hydatid (<i>Echinococcus granulosus</i>)	Cysts of juveniles in humans; infection by contact with dogs; common wherever humans are in close relationship with dogs and ruminants
Multilocular hydatid (<i>Echinococcus multilocularis</i>)	Cysts of juveniles in humans; infection by contact with foxes; less common than unilocular hydatid

same or a different strobila. Shelled embryos form in the uterus of the proglottid, and they are either expelled through a uterine pore, or the entire proglottid detaches from the worm as it reaches the posterior end.

About 4000 species of tapeworms are known to parasitologists. Almost all vertebrate species are infected. Normally, adult tapeworms do little harm to their hosts. Table 8.2 lists the most common tapeworms in humans.

In the beef tapeworm, *Taenia saginata* (Gr. *tainia*, band, ribbon), shelled larvae shed from the human host are ingested by cattle (figure 8.16). The six-hooked larvae (oncospheres) hatch, burrow into blood or lymph vessels, and migrate to skeletal muscle where they encyst to become “bladder worms” (**cysticerci**). Each of these juveniles devel-

ops an invaginated scolex and remains quiescent until the uncooked muscle is eaten by humans. In the new host the scolex evaginates, attaches to the intestine, and matures in 2 or 3 weeks; then ripe proglottids may be expelled daily for many years. Humans become infected by eating raw or rare infested (“measly”) beef. Adult worms may attain a length of 7 m or more, folded back and forth in the host intestine.

The pork tapeworm, *Taenia solium*, uses humans as definitive hosts and pigs as intermediate hosts. Humans can also serve as intermediate hosts by ingesting shelled larvae from contaminated hands or food or, in persons harboring an adult worm, by regurgitating segments into the stomach. Cysticerci may encyst in the central nervous system, where great damage may result (figure 8.17).

classification of phylum platyhelminthes

Class Turbellaria (tur´bel-lar´e-a) (L. *turbellae* [pl.], stir, bustle, + *-aria*, like or connected with). **Turbellarians**.

Usually free-living forms with soft flattened bodies; covered with ciliated epidermis containing secreting cells and rod-like bodies (rhabdites); mouth usually on ventral surface sometimes near center of body; no body cavity except intercellular spaces in parenchyma; mostly hermaphroditic; some have asexual fission. A paraphyletic taxon. Examples: *Dugesia* (planaria), *Microstomum*, *Planocera*.

Class Trematoda (trem´a-to´da) (Gr. *trēma*, a hole, + *eidōs*, form). **Digenetic flukes**. Body covered with a syncytial tegument without cilia; leaflike or cylindrical in shape; usually with oral and ventral suckers, no hooks; alimentary canal usually with two main branches; mostly monoecious; life cycle complex, with first host a mollusc, final host usually a vertebrate; parasitic in all classes of vertebrates. Examples: *Fasciola*, *Clonorchis*, *Schistosoma*.

Class Monogenea (mon´o-gen´e-a) (Gr. *mono*, single, + *genos*, descent). **Monogenetic flukes**. Body covered with a syncytial tegument without cilia; body usually leaflike to cylindrical in shape; posterior attachment organ with hooks, suckers, or clamps, usually in combination; monoecious; life cycle simple, with single host and usually with free-swimming, ciliated larva; all parasitic, mostly on skin or gills of fish. Examples: *Dactylogyrus*, *Polystoma*, *Gyrodactylus*.

Class Cestoda (ses-to´da) (Gr. *kestos*, girdle, + *eidōs*, form). **Tapeworms**. Body covered with nonciliated, syncytial tegument; general form of body tapelike; scolex with suckers or hooks, sometimes both, for attachment; body usually divided into series of proglottids; no digestive organs; usually monoecious; parasitic in digestive tract of all classes of vertebrates; life cycle complex, with two or more hosts; first host may be vertebrate or invertebrate. Examples: *Diphyllobothrium*, *Hymenolepis*, *Taenia*.

figure 8.16

Life cycle of beef tapeworm, *Taenia saginata*. Ripe proglottids break off in the human intestine, leave the body in feces, crawl out of the feces onto grass, and are ingested by cattle. Eggs hatch in the cow's intestine, freeing oncospheres, which penetrate into muscles and encyst, developing into "bladder worms." A human eats infected rare beef, and cysticercus is freed in intestine where it attaches to the intestinal wall, forms a strobila, and matures.

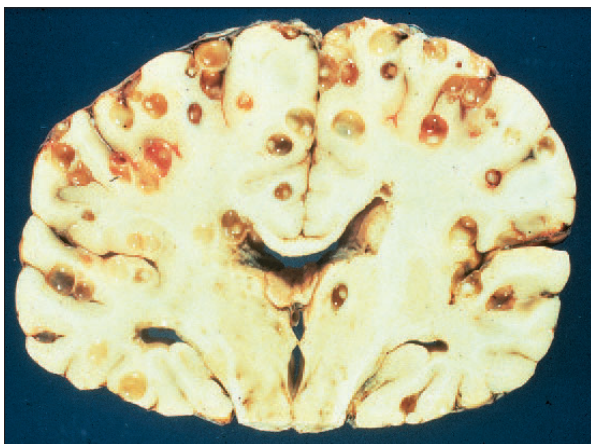
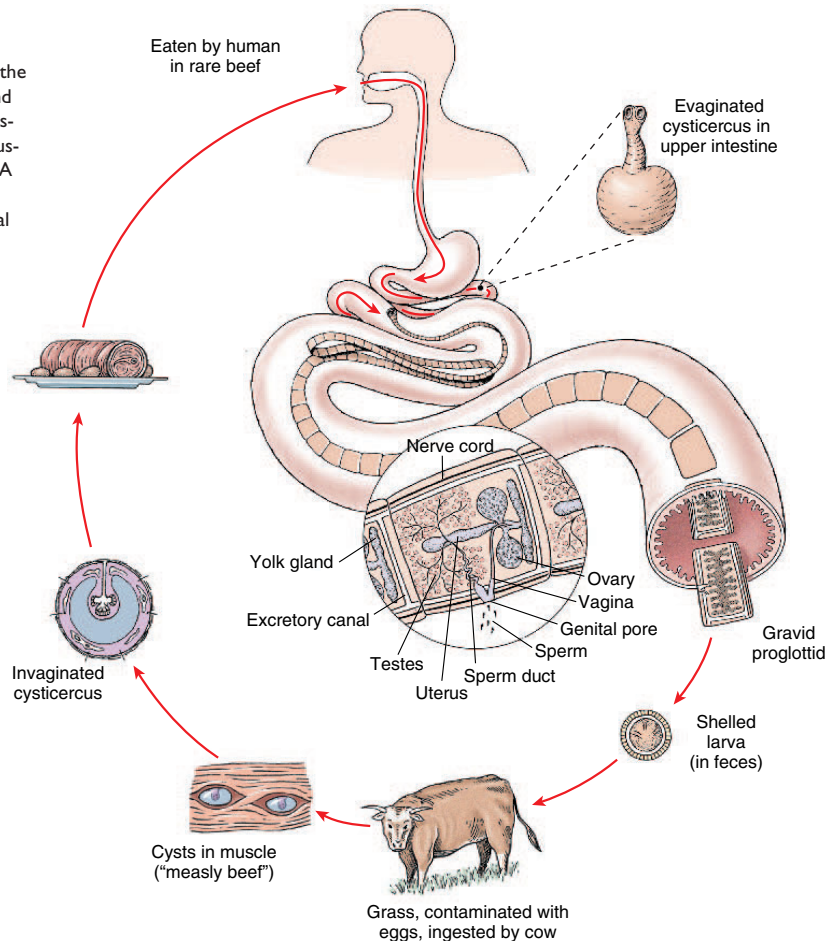


figure 8.17

Section through the brain of a person who died of cerebral cysticercosis, an infection with cysticerci of *Taenia solium*.

Phylum Nemertea (Rhynchocoela)

Nemerteans are often called ribbon worms. Their name (Gr. *Nemertes*, one of the nereids, unerring one) refers to the unerring aim of the proboscis, a long muscular tube (figures 8.18 and 8.19) that can be thrust out swiftly to grasp the prey. The phylum is also called Rhynchocoela (Gr. *rhynchos*, beak, + *koilos*, hollow), which also refers to the proboscis. They are thread-shaped or ribbon-shaped worms; nearly all are marine. Some live in secreted gelatinous tubes. There are about 650 species in the group.

Nemertean worms are usually less than 20 cm long, although a few are several meters in length (figure 8.20). Some are brightly colored, although most are dull or pallid.

With few exceptions, the general body plan of nemerteans is similar to that of turbellarians. Like the latter, their epidermis is ciliated and has many gland cells. Another striking similarity is the presence of flame cells in the excretory system. Rhabdites occur in several nemerteans. In marine forms



figure 8.18
Ribbon worm *Amphiporus bimaculatus* (phylum Nemertea) is 6 to 10 cm long, but other species range up to several meters. The proboscis of this specimen is partially extended at the top; the head is marked by two brown spots.



figure 8.20
Baseodiscus is a genus of nemerteans whose members typically measure several meters in length. This *B. mexicanus* from the Galápagos Islands was over 10 m long.

there is a ciliated larva that has some resemblance to trochophore larvae found in annelids and molluscs. Other flatworm characteristics are the presence of bilateral symmetry and a mesoderm and the lack of coelom. All in all, present evidence seems to indicate that nemerteans share a close common ancestor with Platyhelminthes. Nevertheless, they differ from flatworms in several important aspects.

Form and Function

Many nemerteans are difficult to examine because they are so long and fragile. *Amphiporus* (Gr. *amphi*, on both sides, + *poros*, pore), one of the smaller genera that ranges from 2 to 10 cm in length, is fairly typical of nemertean structure (see figure 8.19). Its body wall consists of ciliated epidermis and layers of circular and longitudinal muscles. Locomotion consists largely of gliding over a slime track, although larger species move by muscular contractions.

The mouth is anterior and ventral, and the **digestive tract is complete**, extending the full length of the body and ending at an anus. Development of an anus marks a significant advancement over the gastrovascular systems of flatworms and radiates. Regurgitation of wastes is no longer necessary; ingestion and egestion can occur simultaneously. Cilia move food through the intestine. Digestion is largely extracellular.

Nemerteans are carnivorous, feeding primarily on annelids and other small invertebrates. They seize their prey with a **proboscis** that lies in an interior cavity of its own, the **rhynchocoel**, above the digestive tract (but not connected with it). The proboscis itself is a long, blind muscular tube that opens at the anterior end at a proboscis pore above the mouth. (In a few nemerteans the esophagus opens through the proboscis pore rather than through a separate mouth.) Muscular pressure on fluid in the rhynchocoel causes the long tubular proboscis to be everted rapidly through the proboscis pore. Eversion of the proboscis exposes a sharp barb, called a stylet (absent in some nemerteans). The sticky, slime-covered proboscis coils around the prey and stabs it

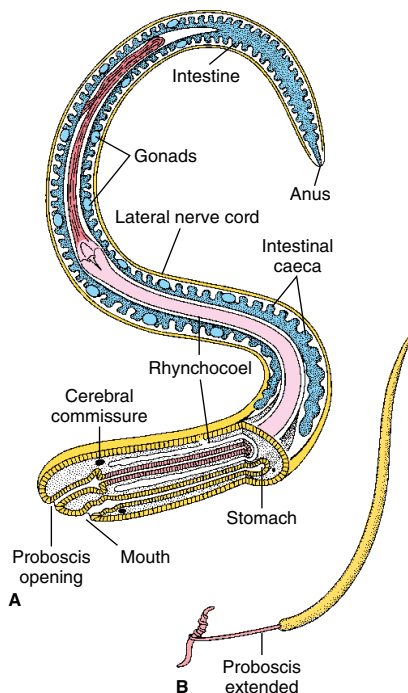


figure 8.19
A, Internal structure of female ribbon worm (diagrammatic). Dorsal view to show proboscis. **B**, *Amphiporus* with proboscis extended to catch prey.

repeatedly with the stylet, while pouring a toxic secretion on the prey. Then, retracting its proboscis, a nemertean draws the prey near its mouth, through which the esophagus is thrust to engulf the prey.

Unlike other acoelomates, nemerteans have a true circulatory system, and an irregular flow is maintained by the contractile walls of the vessels. Many flame-bulb protonephridia are closely associated with the circulatory system, so that their function appears to be truly excretory (for disposal of metabolic wastes), in contrast to their apparently osmoregulatory role in Platyhelminthes.

Nemerteans have a pair of nerve ganglia, and one or more pairs of longitudinal nerve cords are connected by transverse nerves.

Some species reproduce asexually by fragmentation and regeneration. In contrast to flatworms, most nemerteans are dioecious.

Phylum Gnathostomulida

The first species of Gnathostomulida (*nath`o`sto-myū`lid-a*) (*Gr. gnatho*, jaw, + *stoma*, mouth, + *L.-ulus*, diminutive) was observed in 1928 in the Baltic, but its description was not published until 1956. Since then these animals have been found in many parts of the world, including the Atlantic coast of the United States, and over 80 species in 18 genera have been described.

Gnathostomulids are delicate wormlike animals 0.5 to 1 mm long (figure 8.21). They live in interstitial spaces of very fine sandy coastal sediments and silt and can endure conditions of very low oxygen.

Lacking a pseudocoel, a circulatory system, and an anus, gnathostomulids show some similarities to turbellarians and were at first included in that group. However, their parenchyma is poorly developed, and their pharynx is reminiscent of the rotifer mastax (p. 158). Their pharynx is armed with a pair of lateral jaws used to scrape fungi and bacteria off the substratum. Although the epidermis is ciliated, each epidermal cell has but one cilium, which is a condition not found in other bilateral animals except in some gastrotrichs (p. 159).

Phylogeny and Adaptive Radiation

Phylogeny

There can be little doubt that bilaterally symmetrical flatworms were derived from a radial ancestor, perhaps one very similar to the planula larva of cnidarians. Some investigators believe that this **planuloid ancestor** may have given rise to one branch of descendants that were sessile or free floating and radial, which became the Cnidaria, and another that acquired a creeping habit and bilateral symmetry. Bilateral symmetry is a selective advantage for creeping or swimming animals because sensory structures are concentrated anteri-

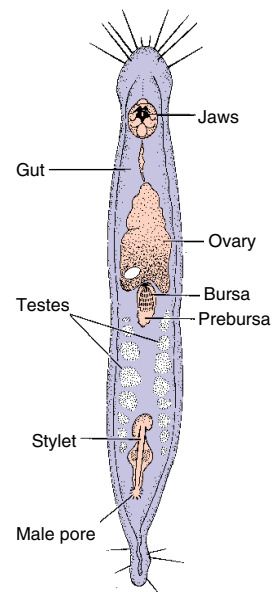


figure 8.21

Gnathostomula jeneri (phylum Gnathostomulida) is a tiny member of the interstitial fauna between grains of sand or mud. Species in this family are among the most commonly encountered jaw worms, found in shallow water and down to depths of several hundred meters.

orly (cephalization), which is the end that first encounters environmental stimuli.

A recent report¹ cites sequence data from small-subunit rDNA, embryonic cleavage patterns and mesodermal origins, and nervous system structure as evidence that acoels are not, in fact, members of the phylum Platyhelminthes. These investigators conclude that acoels are the sister group to all other Bilateria. If this arrangement is sound, then Platyhelminthes as currently constituted is polyphyletic. Other scientists, however, interpreting sequence data from large-subunit ribosomal DNA, concluded that another order of Turbellaria (not Acoela) was basal for Platyhelminthes.² Neither report disputed paraphyly of Turbellaria.

Relationships of Nemertea and Gnathostomulida are not clear, but they apparently belong in the Lophotrochozoa (see p. 81). Ultrastructural similarities of gnathostomulid jaws and trophi of rotifers (p. 157) suggest that these two phyla are sister groups.

Although Turbellaria is clearly paraphyletic, we are retaining the taxon for the present because presentation based on thorough cladistic analysis would require introduction of many more taxa and characteristics that are beyond the scope of this book and not yet common in zoological literature. For example,

¹Ruiz-Trillo et al. 1999. *Science* **283**:1919–1923.

²Livaitis and Rohde. 1999. *Invert. Biol.* **118**:42–56.

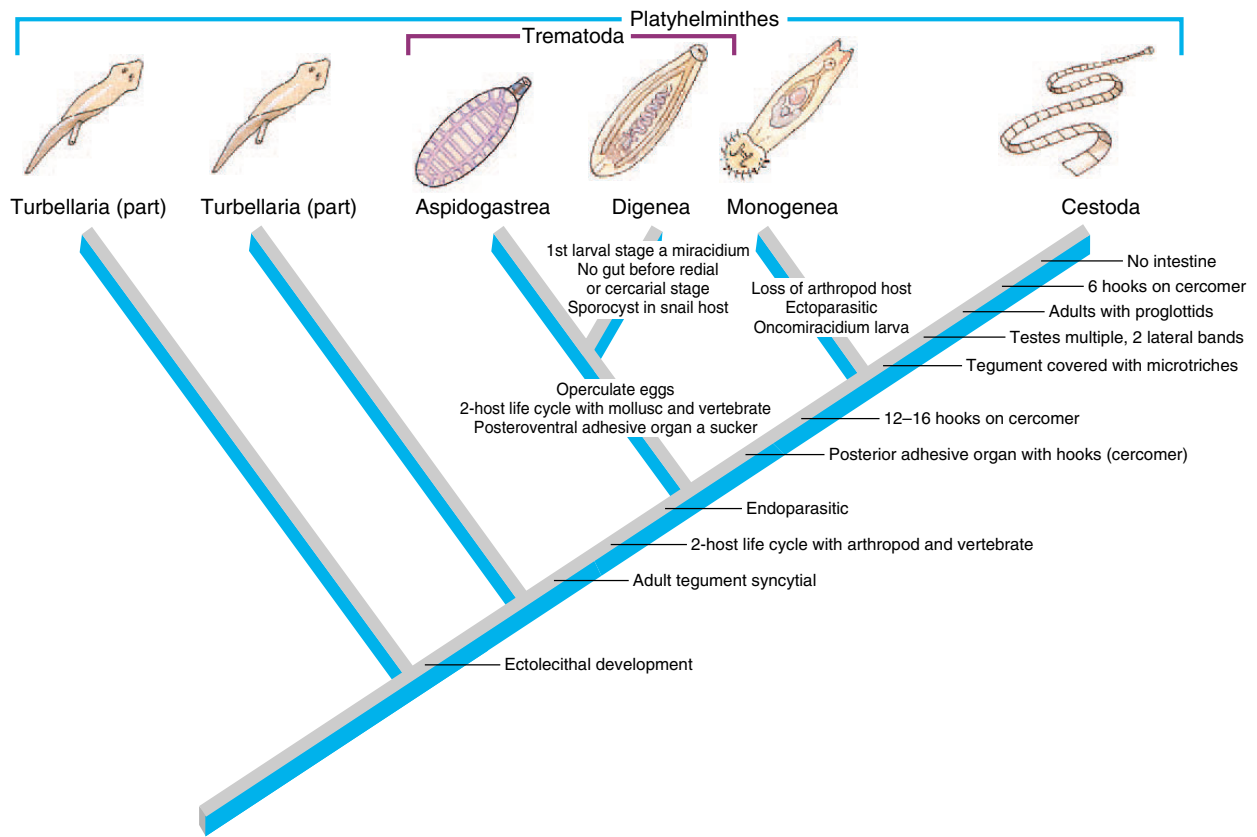


figure 8.22

Phylogenetic relationships among parasitic Platyhelminthes. The traditionally accepted class Turbellaria is paraphyletic. Some turbellarians have ectolecithal development and, together with Trematoda, Monogenea, and Cestoda, form a monophyletic clade and a sister group of endolecithal turbellarians. For the sake of simplicity, synapomorphies of those turbellarians and of Aspidogastrea, as well as many others given by Brooks (1989) are omitted. All of these organisms comprise a clade (called Cercomeria) with a posterior adhesive organ.

(Source: D. R. Brooks, "The Phylogeny of the Cercomeria (Platyhelminthes: Rhabdocoela) and General Evolutionary Principles," in *Journal of Parasitology*, **75**:606–616, 1989.)

ectolecithal turbellarians should be allied with trematodes, monogeneans, and cestodes in a sister group to endolecithal turbellarians. Some ectolecithal turbellarians share a number of other derived characters with trematodes and cestodes and have been placed by Brooks (1989) in a group designated Cercomeria (Gr. *kerkos*, tail, + *meros*, part) (figure 8.22). Several synapomorphies, including the unique architecture of the tegument, indicates that neodermatans (trematodes, monogeneans, and cestodes) form a monophyletic group, and monophyly of Neodermata is supported by sequence data. (See footnote ² on p. 152).²

Adaptive Radiation

The flatworm body plan, with its creeping adaptation, placed a selective advantage on bilateral symmetry and further development of cephalization, ventral and dorsal regions, and caudal

differentiation. Because of their body shape and metabolic requirements, early flatworms must have been well predisposed toward parasitism and gave rise to symbiotic descendants in Neodermata. These descendants radiated abundantly as parasites, and many flatworms became highly specialized for that mode of existence.

Ribbon worms have stressed the proboscis apparatus in their evolutionary diversity. Its use in capturing prey may have been secondarily evolved from its original function as a highly sensitive organ for exploring the environment. Although ribbon worms have evolved beyond flatworms in their complexity of organization, they have been dramatically less abundant as a group.

Likewise, jaw worms have not radiated nor become nearly as abundant or diverse as flatworms. However, they have exploited marine interstitial environments, particularly zones of very low oxygen concentration.

summary

Platyhelminthes, Nemertea, and Gnathostomulida are the simplest phyla that are bilaterally symmetrical, a condition of adaptive value for actively crawling or swimming animals. They have neither a coelom nor a pseudocoel and are thus acoelomate. They are triploblastic and at the organ-system level of organization.

The body surface of turbellarians is a cellular epithelium, at least in part ciliated, containing mucous cells and rod-shaped rhabdites that function together in locomotion. Members of all other classes of flatworms are covered by a nonciliated, syncytial tegument with a vesicular distal cytoplasm and cell bodies beneath superficial muscle layers. Digestion is extracellular and intracellular in most; cestodes must absorb predigested nutrients across their tegument because they have no digestive tract. Osmoregulation is by flame-cell protonephridia, and removal of metabolic wastes and respiration occur across the body wall. Except for some turbellarians, flatworms have a ladder-type nervous system with motor, sensory, and association neurons. Most flatworms are hermaphroditic, and asexual reproduction occurs in some groups.

Class Turbellaria is a paraphyletic group with mostly free-living and carnivorous members. Digenetic trematodes have mollusc intermediate hosts and almost always a vertebrate definitive host. The great amount of asexual reproduction that occurs in their intermediate host helps to increase the chance that some offspring will reach a definitive host. Aside from the tegument, digeneans share many basic structural characteristics with the Turbellaria. Digenea includes a number of important parasites of humans and domestic animals. Digenea contrast with Monogenea, which are important ectoparasites of fishes and have a direct life cycle (without intermediate hosts).

Cestodes (tapeworms) generally have a scolex at their anterior end, followed by a long chain of proglottids, each of which contains a complete set of reproductive organs of both sexes. Cestodes live as adults in the digestive tract of vertebrates. They have microvillus-like microtriches on their tegument, which increase its surface area for absorption. The shelled larvae are passed in the feces of their host, and the juveniles

develop in a vertebrate or invertebrate intermediate host.

Members of Nemertea have a complete digestive system with an anus and a true circulatory system. They are free-living, mostly marine, and they ensnare prey with their long, eversible proboscis.

Gnathostomulida are a curious phylum of little wormlike marine animals living among sand grains and silt. They have no anus, and they share certain characteristics with such widely diverse groups as turbellarians and rotifers.

Flatworms and cnidarians both probably evolved from a common ancestor (planuloid), some of whose descendants became sessile or free floating and radial (cnidarians), while others became creeping and bilateral (flatworms).

Sequence analysis of rDNA, as well as some developmental and morphological criteria, suggest that Aceola, heretofore considered an order of turbellarians, diverged from a common ancestor shared with other Bilateria and may be the sister group of all other bilateral phyla.

review questions

- Why is bilateral symmetry of adaptive value for actively motile animals?
- Match the terms in the right column with the classes in the left column:

___ Turbellaria	a. Endoparasitic
___ Monogenea	b. Free-living and commensal
___ Trematoda	c. Ectoparasitic
___ Cestoda	
- Give several major characteristics that distinguish Platyhelminthes.
- Distinguish two mechanisms by which flatworms supply yolk for their embryos. Which system is evolutionarily ancestral for flatworms and which one is derived?
- How do flatworms digest their food?
- Briefly describe the osmoregulatory system and the nervous system and sense organs of platyhelminths.
- Contrast asexual reproduction in Turbellaria and Trematoda.
- Contrast a typical life cycle of a monogenean with that of a digenetic trematode.
- Describe and contrast the tegument of turbellarians and the other classes of platyhelminths. Could this be evidence that the trematodes, monogeneans, and cestodes form a clade within the Platyhelminthes? Why?
- Answer the following questions with respect to both *Clonorchis* and *Schistosoma*: (a) How do humans become infected? (b) What is the general geographical distribution? (c) What are the main disease conditions produced?
- Define each of the following with reference to cestodes: scolex, microvilli, proglottids, strobila.
- Why is *Taenia solium* a more dangerous infection than *Taenia saginata*?
- Give three differences between nemerteans and platyhelminths.
- Where do gnathostomulids live?
- Explain how a planuloid ancestor could have given rise to both Cnidaria and Bilateria.
- What is an important character of Nemertea that might suggest that the phylum is closer to other bilateral protostomes than to Platyhelminthes? What are some characters of nemerteans suggesting that they be grouped with platyhelminths?
- Recent evidence suggests that acoels are not members of Platyhelminthes but constitute a sister group for all other Bilateria. If so, what is a consequence to phylogenetic integrity of Platyhelminthes if Acoela remains within that phylum? What evidence indicates that the traditional class Turbellaria is paraphyletic?

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