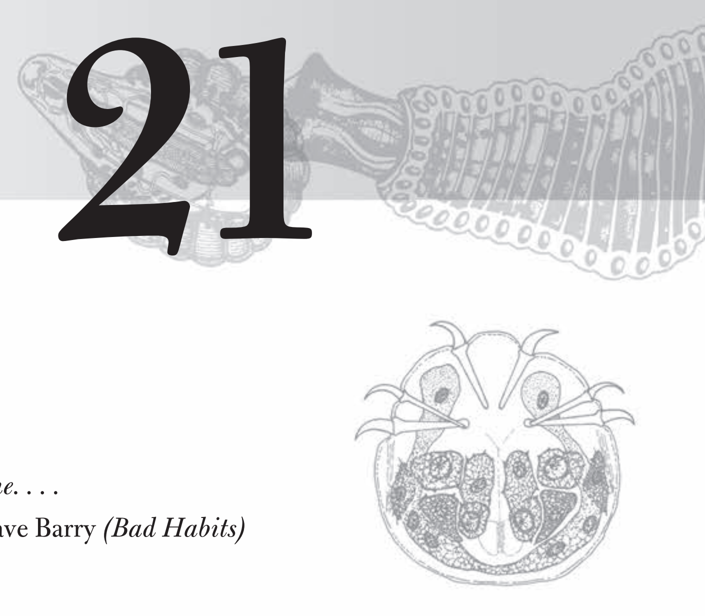

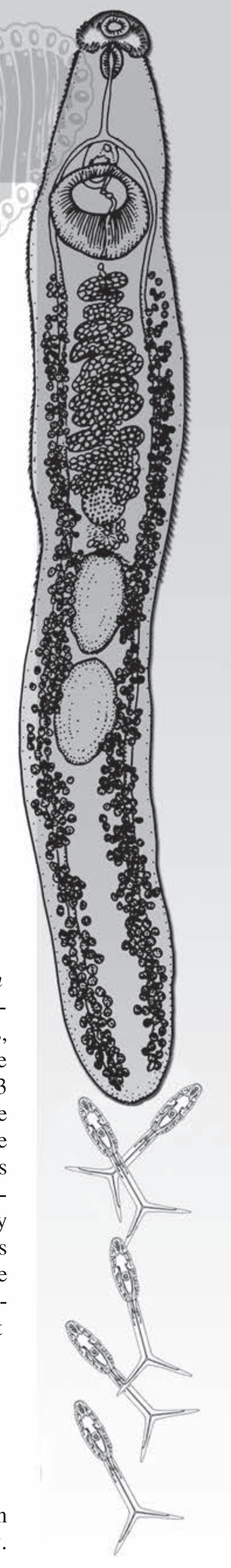

Chapter 21

Tapeworms

. . . we should all brush up on tapeworms from time to time. . . .

—Dave Barry *(Bad Habits)*

Although most species of cestodes are parasites of wild animals, a few infect humans or domestic animals and so are of particular interest. All tapeworms that parasitize humans belong to orders Diphyllobothriidea and Cyclophyllidea.

Many tapeworms cause no medical or economic problem. Still, they are interesting in their own right and deserve at least an introduction. Their diversity of morphology is astonishing, and study of their many varieties of life cycles is a science in itself. Many opportunities are available for research on these worms. For example, many cestodes exist for which not a single life cycle is known. Following discussions of Diphyllobothriidea and Cyclophyllidea and brief descriptions of several other orders, we give some very brief accounts of the sister group of subcohort Eucestoda, Amphilinidea, and of Gyrocotylidea, the sister group of cohort Cestoidea.

ORDER DIPHYLLOBOTHRIIDEA

A diphyllobothriidean cestode typically has a scolex with two longitudinal bothria. The bothria may be deep or shallow and smooth or fimbriated, and in some cases they are fused along all or part of their length, forming longitudinal tubes. Proteinaceous hooks accompany the bothria in some species. Genital pores may be lateral or medial, depending on the species. The vitellaria are always follicular and scattered throughout the segment. Testes are numerous. Generally life cycles of diphyllobothriideans involve crustacean first intermediate hosts and fish second intermediate hosts.

Some species are fairly small, but the largest tapeworms known are in Diphyllobothriidea. For example, *Hexagonoporus physeteris* from sperm whales measures more than 30 meters long. In addition, each segment has 4 to 14 complete sets of genitalia. One worm has up to 45,000 segments. The reproductive capacity of such an animal is staggering.

FAMILY DIPHYLLOBOTHRIIDAE

Diphyllobothrium Species

Species of *Diphyllobothrium* are difficult to distinguish from one another morphologically, and they typically exhibit little host specificity.[2] Usually called *broad fish tapeworms,* they have commonly been designated *D. latum* and have been reported from many canines, felines, mustelids, pinnipeds, bears, and humans. Many of these records, however, are misidentifications. Humans seem to be quite suitable as hosts for *Diphyllobothrium* spp., with at least 13 distinct species having been reported. The most prevalent are *D. dendriticum* and *D. latum*.[2] An estimated 9 million people are infected worldwide.[48] *Diphyllobothrium dendriticum* is most common and occurs throughout the Northern Hemisphere. Less widespread is *D. latum,* with major endemicity in Scandinavia, the Baltic states, and western Russia. It has been introduced in other parts of the world, including the Great Lakes area of the United States. There are numerous reports of *Diphyllobothrium* sp. from the West Coast of North America but species involved are not clear.[88] Although more recently reported for the first time from Argentina,[84] *Diphyllobothrium* spp. apparently parasitized native South Americans well before the "discovery" of the New World by Columbus.[51]

- **Morphology.** Adult *D. latum* (Fig. 21.1) may attain a length of 10 m and shed up to a million eggs a day. *Diphyllobothrium dendriticum* attains a length of 1 m. These species are anapolytic and characteristically release long chains of spent segments, usually the first indication that the infected person has a secret guest.

  Their scolex (Fig. 21.2) is finger shaped and has dorsal and ventral bothria. Proglottids (Fig. 21.3; see also Fig. 20.17) usually are wider than long. There are numerous testes and vitelline follicles scattered throughout each

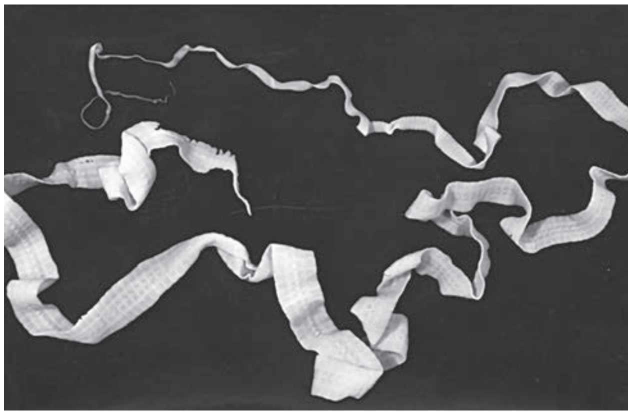

Figure 21.1 ***Diphyllobothrium latum*.**
The scolex is at the tip of the threadlike end at upper left.
Courtesy of Warren Buss.

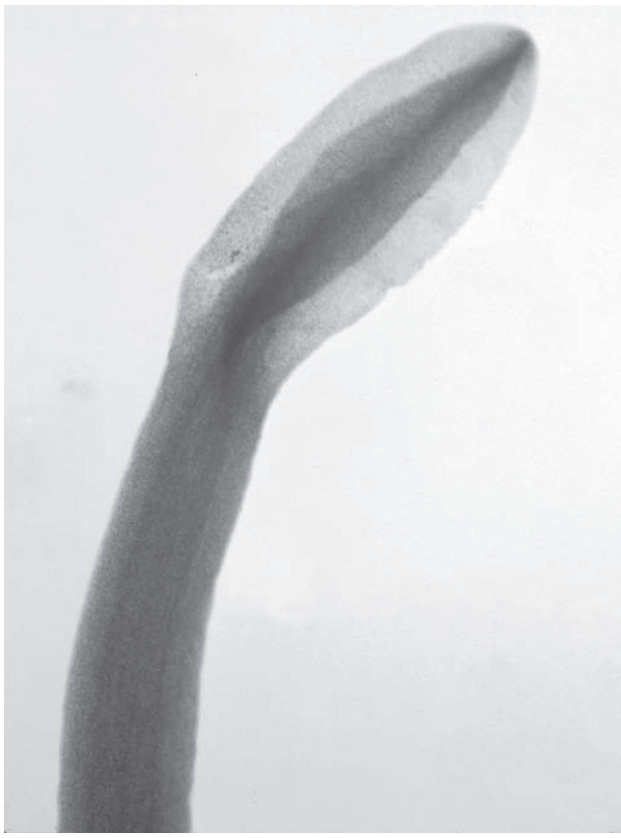

Figure 21.2 **Scolex of *Diphyllobothrium* sp.**
It is about 1 mm long.

Figure 21.3 **Gravid proglottids of *Diphyllobothrium* sp.**
Note the characteristic rosette-shaped uterus.
Courtesy of Larry Jensen.

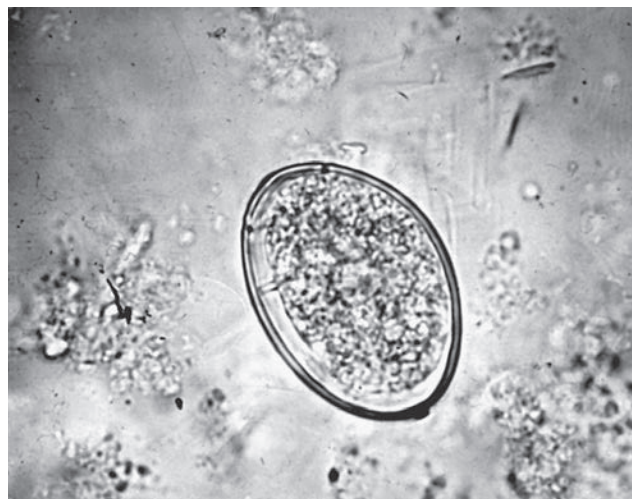

Figure 21.4 **Egg of *Diphyllobothrium* sp. in a human stool.**
Note the operculum at the upper end and the small knob at the opposite end. It is 40 μm to 60 μm long.
Courtesy of David Oetinger.

proglottid, except for a narrow zone in the center. Male and female genital pores open midventrally. The bilobed ovary is near the rear of the segment. The uterus consists of short loops and extends from the ovary to a midventral uterine pore.

- **Biology.** The ovoid eggs measure about 60 μm by 40 μm and have a lidlike operculum at one end and a small knob on the other (Fig. 21.4). When released through the uterine pore, the shelled embryo is at an early stage of development, and it must reach water for development to continue (Fig. 21.5). Completion of development to coracidium takes from eight days to several weeks, depending on the temperature. Emerging through the operculum, the ciliated coracidium swims randomly about, where it may attract the attention of predaceous copepods such as species of *Diaptomus* and related genera. Soon after being eaten, the coracidium loses its ciliated epithelium and immediately begins to attack the midgut wall with its six tiny hooks. Once through the intestine and into the crustacean's hemocoel, it becomes parasitic, absorbing nourishment from the surrounding hemolymph. Infection with

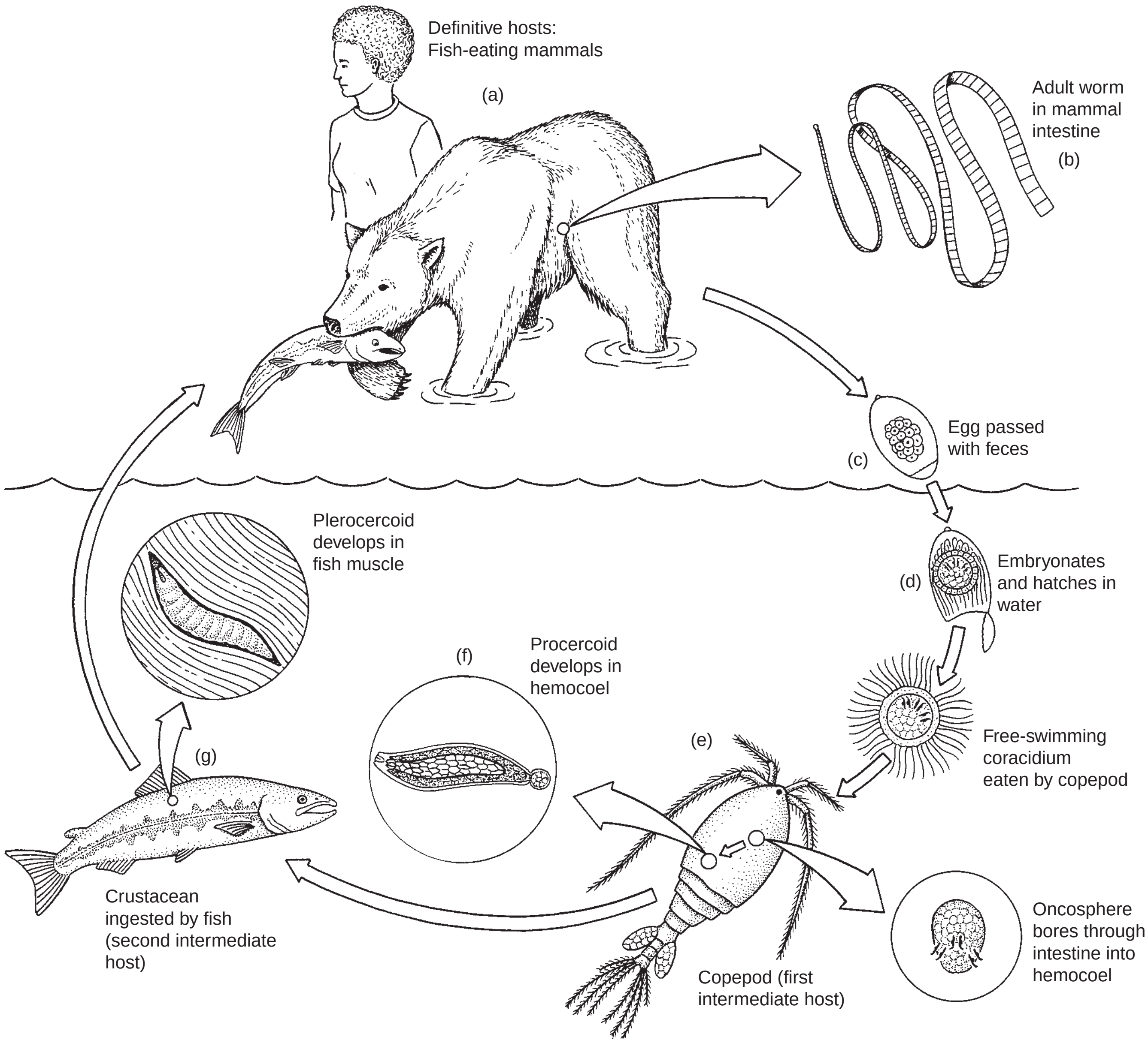

Figure 21.5 **Life cycle of *Diphyllobothrium latum*.**
(*a*) Definitive hosts are any of a number of fish-eating mammals. (*b*) Adult worm is in mammal small intestine. (*c*) Shelled embryo passes in feces at an early stage of development. (*d*) Embryogenesis continues in water, and free-swimming coracidium hatches. (*e*) Coracidium eaten by copepod, and oncosphere penetrates intestine into hemocoel. (*f*) Procercoid develops in hemocoel. (*g*) Copepod eaten by fish, where procercoid penetrates into muscle and develops into pleroceroid.
Drawing by William Ober and Claire Garrison.

Diphyllobothrium spp. impairs motility of copepods, thus rendering them more vulnerable to predation.[78]

In about three weeks the worm increases its length to around 500 μm, becoming an elongated, undifferentiated mass of parenchyma with a cercomer at the posterior end. It is now a procercoid (Fig. 21.6), incapable of further development until it is eaten by a suitable second intermediate host—any of several species of freshwater fishes, especially pike and related fishes, or any of the salmon family. The cercomer may be lost while still in the copepod or soon after the procercoid enters a fish. Large, predaceous fish eat comparatively few microcrustaceans but can still become infected by eating smaller fish containing plerocercoids, which then migrate into the new host. The larger fish is thus a paratenic host.

When a fish eats an infected copepod, the procercoid is released and bores its way through the intestinal wall and into the body muscles. Here it absorbs nutrients and grows rapidly into a plerocercoid. Mature plerocercoids vary in length from a few millimeters to several centimeters. They are still mainly undifferentiated, but there may be evidence of shallow bothria at the anterior end. Usually plerocercoids are found unencysted and coiled up in the musculature, although they may be encysted in the

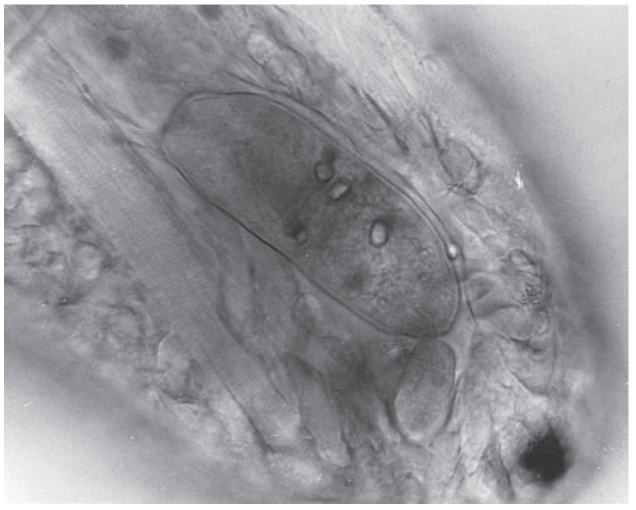

Figure 21.6 **Procercoid in the hemocoel of a copepod.** Note the anterior pit, the posterior cercomer, and the internal calcareous granules.

Courtesy of Justus F. Mueller.

Figure 21.7 **Two plerocercoids in the flesh of a perch.**

From R. Vik, in Marcial-Rojas (Ed.), *Pathology of protozoal and helminthic diseases, with clinical correlation,* © 1971. (Baltimore, MD: Williams & Wilkins).

viscera. They are easily seen as white masses in uncooked fish (Fig. 21.7), but when the flesh is cooked, worms are seldom noticed. They are also killed and thus rendered noninfective.

Plerocercoids of other diphyllobothriideans, as well as those of proteocephalatans and trypanorhynchans, are also found in fish and are often mistaken for those of *Diphyllobothrium*. When a plerocercoid is ingested by a suitable definitive host, it survives the digestive fate of its late host and begins a close relationship with a new one. The worms grow rapidly and may begin egg production in 7 to 14 days. Little of this initial growth may be attributed to the production of new proglottids but is caused by growth in primordia already in the plerocercoid. As much as 70% of the strobila may mature on the same day.[7]

- **Pathogenesis.** Many cases of diphyllobothriasis are apparently asymptomatic or have poorly defined symptoms associated with other tapeworms, such as vague abdominal discomfort, diarrhea, nausea, and weakness. However, the worm can cause a serious megaloblastic anemia in a small number of cases, virtually all in Finnish people. It was thought originally that toxic products of the worm produced the anemia, but we now know that the large amount of vitamin B_{12} absorbed by the cestode, in conjunction with some degree of impairment of the patient's normal absorptive mechanism for vitamin B_{12}, is responsible for the disease. Nyberg[74] reported that an average of 44% of a single oral dose of vitamin B_{12} labeled with cobalt 60 was absorbed by *D. latum* in otherwise healthy patients, but in patients with tapeworm pernicious anemia 80% to 100% of the dose was absorbed by the cestode. The clinical symptoms of tapeworm pernicious anemia are similar in many respects to "classical" pernicious anemia (caused by a failure in intestinal absorption of vitamin B_{12}), except that expulsion of the worm generally brings a rapid remission of anemia. For reasons that remain unclear, possibly due to improved nutritional level, tapeworm pernicious anemia has not been reported for several decades.[90]

- **Diagnosis and Treatment.** Demonstration of the characteristic eggs or proglottids passed with a stool gives positive diagnosis. In the past a variety of drugs was used against *Diphyllobothrium* spp. and other tapeworms; aspidium oleoresin (extract of male fern), mepacrine, dichlorophen, and even extracts of fresh pumpkin seeds (*Cucurbita* spp.) have anticestodal properties.[25] However, the drugs of choice are now niclosamide (Yomesan) and praziquantel.[89] The mode of action of niclosamide seems to be an inhibition of an inorganic phosphate—ATP exchange reaction associated with the worm's anaerobic electron transport system. We described the action of praziquantel on p. 230.

- **Epidemiology.** Obviously, persons become infected when they eat raw or undercooked fish. Hence, infection rates are highest in countries where raw fish is eaten as a matter of course. Communities that dispose of sewage by draining it into lakes or rivers without proper treatment create an opportunity for a massive buildup of *D. latum* or *D. dendriticum* in local fish. These fish may be harvested for local consumption or shipped thousands of miles by refrigerated freight to distant markets. An unsuspecting customer may thus gain infection in a restaurant or at home by tasting such dishes as gefilte fish during preparation. The higher prevalence of *Diphyllobothrium* in women is probably due to the higher prevalence of women among the ranks of cooks. The fad in the United States of eating raw salmon as sushimi has led to infections.[88]

Other Diphyllobothriideans Found in Humans

Several other species of *Diphyllobothrium* have been reported from humans in different parts of the world. These include *D. cordatum, D. pacificum, D. cameroni, D. hians,* and *D. lanceolatum,* parasites of pinnipeds, and *D. ursi* of bears. At least some infections of humans on the West Coast of North America and Hawaii apparently are due to *D. dendriticum,*[5] but some are likely to be from one or more species from pinnipeds with a marine life cycle. *Diphyllobothrium nihonkaeiense* is the dominant species in Japan, although other species occur there.[3, 65]

Digramma brauni and *Ligula intestinalis* have also been reported from humans, but such occurrences must be rare. *Diplogonoporus grandis (D. balaenopterae)* has been reported numerous times from humans in Japan.[2] A parasite of whales, its plerocercoid occurs in marine fish, the mainstay of the Japanese protein diet.

Sparganosis

With the exception of forms with scolex armature, species of plerocercoids found in humans are impossible to distinguish by examining their morphology. When procercoids of some species are ingested accidentally, usually when a person swallows an infected copepod in drinking water, they can migrate from the gut and develop into plerocercoids, sometimes reaching a length of 35 cm. This infection is called *sparganosis* and may have severe pathological consequences. Cases have been reported from most countries of the world but are most common in eastern Asia. Yamane, Okada, and Takihara[103] reported a living sparganum that had infected a woman's breast for at least 30 years.

Another means of infection is by ingestion of insufficiently cooked amphibians, reptiles, birds, or even mammals such as pigs.[24] Plerocercoids present in these animals may then infect a person indulging in such delicacies. Many Chinese are infected in this way because of their tradition of eating raw snake to cure a panoply of ills.[54]

A third method of infection results from the east Asian treatment of skin ulcers, inflamed vagina, or inflamed eye (Fig. 21.8) by poulticing the area with a split frog or flesh of a vertebrate that may be infected with spargana. The active worm then crawls into the orbit, vagina, or ulcer and establishes itself. Most cases of sparganosis in eastern Asia are probably caused by *Diphyllobothrium erinacei,* a parasite of carnivores.

In North America most spargana are probably *Diphyllobothrium mansonoides,* a parasite of cats.[71] It usually does not proliferate, except by occasionally breaking transversely, and may live up to 10 years in a human.[95] The current public awareness of the symptoms of cancer has led to an increase in reported cases of sparganosis in this country. Subdermal lumps are no longer ignored by an average person, and more than one physician has been shocked to find a gleaming, white worm in a lanced nodule. Wild vertebrates are commonly infected with spargana (Fig. 21.9).

Rarely a sparganum will be proliferative, splitting longitudinally and budding profusely. Such cases are very serious, since many thousands of worms can result, with the infected organs becoming honeycombed.[69]

Figure 21.8 **Right eye of patient with sparganosis.** Note the protruding mass in the upper conjunctiva.

From L. T. Wang and J. H. Cross, "Human sparganosis on Taiwan. A report of two cases," in *J. Formosan Med. Assoc*. 73:173–177. Copyright © 1974.

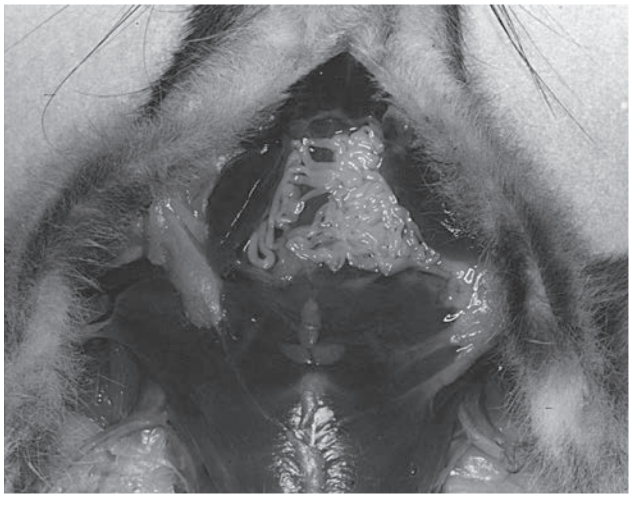

Figure 21.9 **Spargana in subcutaneous connective tissues of a wild rat in Taiwan.**

Courtesy of Robert E. Kuntz.

Treatment of sparganosis is usually by surgery, but supplementary treatment with praziquantel may be advisable.[88]

ORDER CARYOPHYLLIDEA

Caryophyllideans are intestinal parasites of freshwater fishes, except for a few that mature in the coelom of freshwater oligochaete annelids.[59, 62] All are monozoic, showing no trace of internal proglottisation or external segmentation (Fig. 21.10). The scolex is never armed. Usually it is quite simple, bearing shallow depressions (loculi), or it is frilled or entirely smooth. Some species seem to lack a scolex altogether. The anterior end of the worm is very motile, however, and functions well as a holdfast. Some species induce a pocket in the wall of the host's intestine in which one or more worms remain.

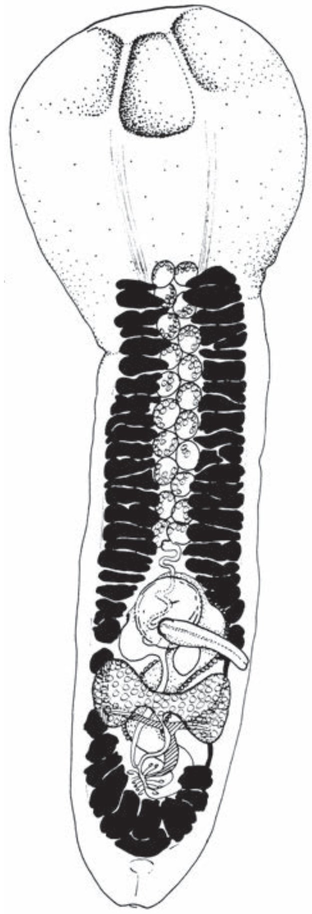

Figure 21.10 ***Penarchigetes oklensis,* a typical caryophyllidean cestode, from a spotted sucker.**

From J. S. Mackiewicz, "*Penarchigetes oklensis* gen. et sp. n. and *Biacetabulum carpiodi* sp. n. (Cestoidea: Caryophyllaeidae) from catostomid fish in North America," in *Proc. Helm. Soc. Wash.* 37:110–118, 1969.

Each worm has a single set of male and female reproductive organs. In most the ovary is near the posterior end. Testes fill the median field of the body, and vitelline follicles are mainly lateral. Male and female genital pores open near each other on the midventral surface.

Catfishes, true minnows (Cyprinidae), and suckers are the most common hosts of Caryophyllidea. *Glaridacris* spp., predominantly *G. catostomi,* are found abundantly in suckers (*Catostomus* spp.) in North America.[59] Intermediate hosts are aquatic annelids. After an oligochaete eats an egg, the oncosphere hatches and penetrates the intestine into the coelom. There it grows into a procercoid with a prominent cercomer, similar to that of *Diphyllobothrium* spp. When eaten by a fish, the procercoid loses its cercomer and grows directly into an adult.

It has been suggested that segmented adults once existed but became extinct with their hosts, probably aquatic reptiles. However, this did not happen before plerocercoids developed neotenically in fish second intermediate hosts. If this hypothesis is true, extant caryophyllaeid species actually are neotenic plerocercoids. Support is lent to this idea by the existence of several species of *Archigetes* that become sexually mature while in annelids. Reproductive adults retain their cercomer and infect no additional host, although they can live for some time if eaten by a fish. *Archigetes* spp., then, appear to be neotenic procercoids. However, this hypothesis is not supported by molecular evidence, which suggests that the monozoic condition is plesiomorphic.[64]

ORDER SPATHEBOTHRIIDEA

These are peculiar parasites of marine and freshwater teleost fishes. Their most striking characteristic is a complete absence of segmentation, with possession of a typically linear series of internal proglottids. The scolex always lacks armature. It may be totally undifferentiated, as in *Spathebothrium simplex;* it may be a shallow funnel-shaped organ, as in *Cyathocephalus truncatus;* or it may consist of one or two powerful cuplike organs (see Fig. 20.5*j*). Genital pores are ventral, testes are in two lateral bands, the ovary is dendritic, and vitellaria are follicular and lateral or scattered. The uterus is rosettelike and opens ventrally, usually near the vaginal pore.

No life cycles are known. Although these worms are of no known economic importance, they remain an interesting zoological group that should be studied further. *Bothrimonus,* a common genus in North America, has been investigated more fully;[19] *B. sturionis* parasitizes a wide variety of marine and freshwater fish, from sturgeons to salmonids to flounders.

ORDER CYCLOPHYLLIDEA

Cyclophyllidea and Proteocephalata both have scolices with four acetabula. In these orders, parenchyma is divided into highly distinct medullary and relatively extensive cortical regions defined by the longitudinal musculature. Brooks and McLennan[17] combined these two orders into the Proteocephaliformes, but we are retaining the traditional separation for the present.

The most obvious morphological feature that characterizes Cyclophyllidea is a single compact, postovarian vitelline gland (see Fig. 20.18). A rostellum, which usually bears an armature of hooks, is commonly present. Genital pores are lateral in all except family Mesocestoididae, in which they are midventral. The number of testes varies from one to several hundred, depending on the species. Most species are rather small, although some are giants of more than 10 m in length. Most tapeworms of birds and mammals belong to this order.

Family Taeniidae

The largest cyclophyllideans are in family Taeniidae, as are the most medically important tapeworms of humans. A remarkable morphological similarity occurs among species in the family; striking exceptions are *Echinococcus* spp., which are much smaller than cestodes of other taeniid genera. An armed rostellum is present on most species and when present is not retractable. Testes are numerous, and the ovary is a bilobed mass near the posterior margin of the

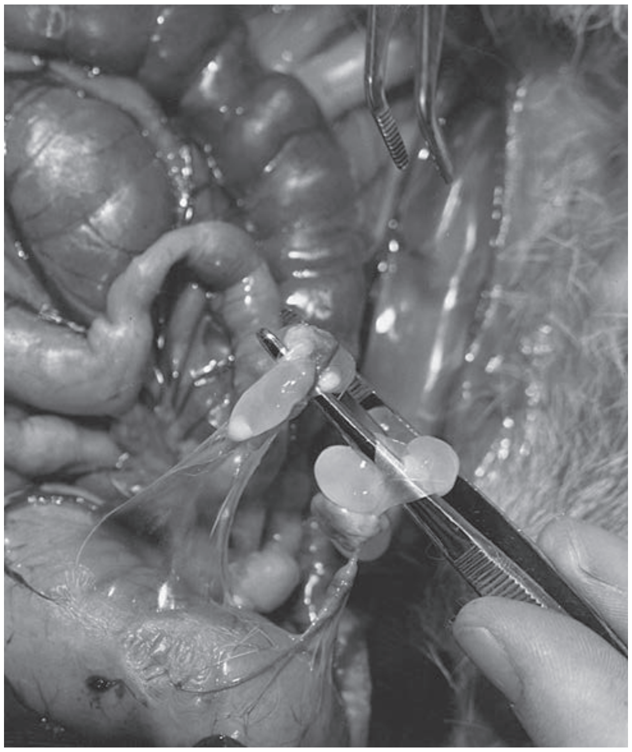

Figure 21.11 **Cysticerci of *Taenia pisiformis* in the mesenteries of a rabbit.**
Courtesy of John Mackiewicz.

proglottid. Metacestodes are various types of **bladderworms** (Fig. 21.11), and mammals serve as their intermediate hosts.

Taenia saginata. Among Taeniidae, *Taenia saginata* is by far the most common in humans, occurring in nearly all countries where beef is eaten. The beef tapeworm, as it is usually known, lacks a rostellum or any scolex armature (Fig. 21.12). Individuals of this exceptionally large species may attain a length of over 20 m, but 3 m to 5 m is much more common. Even the smaller specimens may consist of as many as 2000 segments.

In earlier editions of this text, we considered the unarmed scolex of this species sufficient reason to consign it to a separate genus, *Taeniarhynchus*.[91] However, nucleotide-sequence data support placement of *T. saginata* with other, well-recognized species of *Taenia*.[75] Subsequent cladistic studies with both morphological and molecular data clearly show that retention of *Taeniarhynchus* would render genus *Taenia* paraphyletic.[39, 47, 73, 80]

- **Morphology.** The scolex, with its four powerful suckers, is followed by a long, slender neck. Mature segments are slightly wider than long, whereas gravid ones are much longer than wide. Usually it is a gravid segment passed in the feces that is first noticed and taken to a physician for diagnosis. Because eggs of this species cannot be differentiated from those of *Taenia solium,* the next most common taeniid of humans, accurate diagnosis depends on other criteria. Of course, if an entire worm is passed, the unarmed scolex leads to an unmistakable diagnosis.

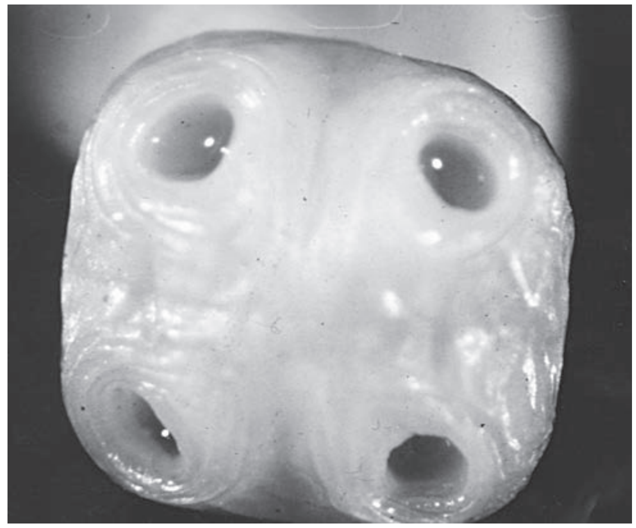

Figure 21.12 **En face view of the scolex of *Taenia saginata*.**
Note the absence of a rostellum or armature.
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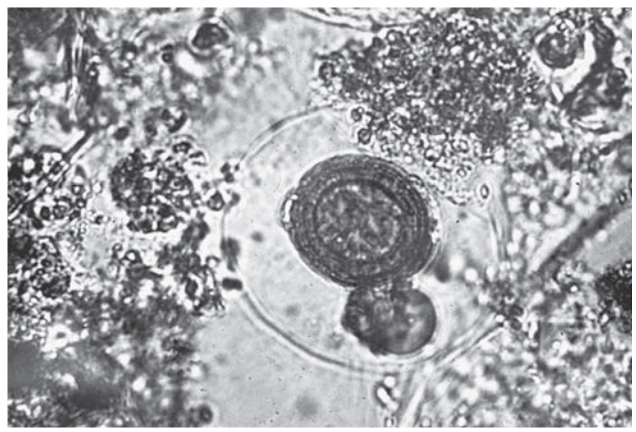


Figure 21.13 ***Taenia* sp. egg in human feces.**
The thin outer membrane is often lost at this stage.
Courtesy of David Oetinger.

The spherical eggs are characteristic of Taeniidae (Fig. 21.13). A thin, hyaline, outer membrane is usually lost by the time the egg is voided with the feces. The embryophore is very thick and riddled with numerous tiny pores, giving it a striated appearance in optical section. Unfortunately, the egg sizes of several taeniids in humans overlap, making diagnosis of species impossible on this character alone.

- **Biology.** When gravid, segments detach and either pass out with feces or migrate out of the anus. Each segment behaves like an individual worm, crawling actively about, as if searching for something. Segments are easily mistaken for trematodes or even nematodes at this stage. As a segment begins to dry up, a rupture occurs along the midventral body wall, allowing eggs to escape. Larvae are fully developed and infective to their intermediate host at this time; they remain viable for many weeks. Cattle are the usual intermediate hosts, although cysticerci have also been reported from llamas, goats, sheep, giraffes, and even reindeer (perhaps incorrectly).

When eaten by a suitable intermediate host, eggs hatch in the duodenum under the influence of gastric and intestinal secretions. Hexacanths quickly penetrate the mucosa and enter intestinal venules, to be carried throughout the body. Typically they leave a capillary between muscle cells and enter a muscle fiber, developing into infective cysticerci in about two months. These metacestodes are white, pearly, and up to 10 mm in diameter and contain a single, invaginated scolex. Humans are probably unsuitable intermediate hosts, and the few records of *Taenia saginata* cysticerci in humans are most likely misidentifications. Before the beef cysticercus was known to be a juvenile form of *T. saginata,* it was placed in a separate genus under the name of *Cysticercus bovis*. The disease produced in cattle is thus known as *cysticercosis bovis,* and flesh riddled with the juveniles is called *measly beef.*

A person who eats infected beef, cooked insufficiently to kill the juveniles, becomes infected. The invaginated scolex and neck of cysticerci evaginate in response to bile salts. The bladder is digested by the host or absorbed by the scolex, and budding of proglottids begins. Within 2 to 12 weeks the worm begins shedding gravid proglottids.

- **Pathogenesis.** Disease characteristics of *T. saginata* infection are similar to those of infection by any large tapeworm, except that the avitaminosis B_{12} found in association with *D. latum* is unknown. Most people infected with *T. saginata* are asymptomatic or have mild to moderate symptoms of dizziness, abdominal pain, diarrhea, headache, localized sensitivity to touch, and nausea. Delirium is rare but does occur. Intestinal obstruction with need for surgical intervention sometimes occurs. Hunger pains, universally accepted by lay people as a symptom of tapeworm infection, are not common, and loss of appetite is frequent. Worms release antigens, which sometimes result in allergic reactions. In addition, it is difficult to estimate the psychological effects on an infected person of observing continued migration of proglottids out of the anus.

- **Diagnosis and Treatment.** Identification of taeniid eggs according to species is impossible. Therefore, accurate diagnosis depends on examination of a scolex or perhaps a gravid segment. The latter is characterized by 15 to 20 branches on each side (contrasted with 7 to 13 in *T. solium*). Because these branches tend to fuse in deteriorating segments, freshly passed specimens must be obtained for reliable results; furthermore, several investigators have reported overlapping numbers.[86] A test for worm antigens passed in the feces (coproantigens) using a variant of the ELISA has been described, and an improved polymerase chain reaction-restriction fragment length polymorphism assay suitable for field samples is available.[4, 86]

  Numerous taeniicides have been used in the past. Today niclosamide and praziquantel are the drugs of choice.

- **Epidemiology.** Human infection is highest in areas of the world where beef is a major food and sanitation is deficient. Thus, in several developing nations of Africa and South America, for instance, ample opportunity exists for cattle to eat tapeworm eggs and for people to eat infected flesh. Many people are content to eat a chunk of meat that is cooked in a campfire, charred on the outside and raw on the inside.

  Local custom may have profound effects on infection rates. Hence, in India there may be a high rate of infection among Moslems, whereas Hindus, who do not eat beef, are unaffected. In the United States, federal meat inspection laws and a high degree of sanitation combine to keep the incidence of infection low. However, not all cattle slaughtered in the United States are federally inspected, and standard inspection procedures fail to detect one-fourth of infected cattle.[28] One wonders if backyard cookery and the popularity of rare steaks and undercooked hamburgers might not contribute to prevalence of taeniiasis, although well-publicized cases of bacterial *(Escherichia coli)* contamination of ground beef may have the reverse effect.

  Despite a high level of sanitation in any country, it still is possible for cattle to be exposed to eggs of this parasite. One infected person who defecates in a pasture or cattle-feeding area can quickly infect an entire herd. The use of human feces as fertilizer can have the same effect. Shelled larvae can remain viable in liquid manure for 71 days, in untreated sewage for 16 days, and on grass for 159 days.[51] Cattle are coprophagous and often will eat human dung, wherever they find it. In India, where cattle roam at will, it is common for a cow to follow a person into the woods, in anticipation of obtaining a fecal meal.[22]

  Prevention of human infection is easy; when meat is cooked until it is no longer pink in the center, it is safe to eat, since cysticerci are killed at 56° C. Furthermore, meat is also rendered safe by freezing at −5° C for at least a week.

Taenia asiatica. A taeniid very similar morphologically to *Taenia saginata* has been distinguished in Southeast Asia and China.[32] Many authors referred to this form as "Asian *Taenia*" because of uncertainty that it was a separate species, but *T. asiatica* can be distinguished from other *Taenia* species on biological, morphological, and molecular bases.[33] A striking biological difference from *T. saginata* is that cysticerci of *T. asiatica* develop in pigs, primarily in liver and other viscera and not in muscles. (Many rural Asians relish raw pig viscera.) Cysticerci of *T. asiatica* may have small hooklets on their scolex. *Taenia asiatica* is genetically and immunologically much closer to *T. saginata* than to other species of taeniids.[38, 79] They are sister species and only distantly related to *T. solium*.[47]

Taenia solium. The most dangerous adult tapeworm of humans is the pork tapeworm, *Taenia solium,* because humans can also serve as intermediate hosts; that is, infection with eggs results in development of cysticerci **(cysticercosis)** in humans. Thus, a person can become infected through contamination of food or fingers with eggs. Likewise, it is possible to infect others in the same household by the same means, often with grave results.

- **Morphology.** The scolex of an adult (Fig. 21.14) bears a typical, nonretractable taeniid rostellum armed with two

Figure 21.14 **Scolex of *Taenia solium*.**
Note the large rostellum with two circles of hooks.
Courtesy of David Oetinger.

circles of 22 to 32 hooks measuring 130 μm to 180 μm long. Whereas the scolex of *Taenia saginata* is cuboidal and up to 2 mm in diameter, that of *T. solium* is spheroid and only half as large. There are reports of strobilas as long as 10 m, but 2 to 3 m is much more common. Mature segments are wider than long and are nearly identical to those of *T. saginata,* differing in number of testes (150 to 200 in *T. solium,* 300 to 400 in *T. saginata*). Gravid segments are longer than wide and have the typical taeniid uterus, a medial stem with 7 to 13 lateral branches.

- **Biology.** The life cycle of *T. solium* (Fig. 21.15) is in most regards like that of *T. saginata,* except that its normal intermediate hosts are pigs instead of cattle. Gravid proglottids passed in feces are laden with eggs infective to swine. When eaten, oncospheres develop into cysticerci *(Cysticercus cellulosae)* in muscles and other organs. Blowflies can carry eggs from infected feces to uninfected meat, which is readily eaten by pigs,[55] and pigs feed on human feces where it is available.[37] Infection of black bears in California with *T. solium* cysticerci has been confirmed.[99]

  A person easily becomes infected when eating a bladderworm along with insufficiently cooked pork. Dogs and cats also can serve as intermediate hosts and so can serve as a source of infection for people where those animals are eaten.[90] Evaginating by the same process as in *T. saginata,* the worm attaches to the mucosa of the small intestine and matures in 5 to 12 weeks. Specimens of *T. solium* can live for as long as 25 years. Pathogenesis caused by adult worms is similar to that in taeniiasis saginata.

- **Cysticercosis.** Unlike those of most other species of *Taenia,* cysticerci of *T. solium* develop readily in humans. Infection occurs when shelled larvae pass through the stomach and hatch in the intestine. People who are infected by adult worms may contaminate their households or food with eggs they or others accidentally eat. Possibly, a gravid proglottid may migrate from the lower intestine to the stomach or duodenum, or it may be carried there by reverse peristalsis. Subsequent release and hatching of many eggs at the same time results in a massive infection by cysticerci.

  Virtually every organ and tissue of the body may harbor cysticerci. Most commonly they are found in the subcutaneous connective tissues. The second most common site is the eye, followed by the brain (Fig. 21.16), muscles, heart, liver, lungs, and coelom. A fibrous capsule of host origin surrounds the metacestode, except when it develops in the chambers of the eye. The effect of any cysticercus on its host depends on where it is located. In skeletal muscle, skin, or liver, little noticeable pathogenesis usually results, except in massive infection. Ocular cysticercosis may cause irreparable damage to the retina, iris, or choroid. A developing cysticercus in the retina may be mistaken for a malignant tumor, resulting in the unnecessary surgical removal of the eye. Removal of the cysticercus by fairly simple surgery is usually successful.

  Cysticerci occur rarely in the spinal cord but commonly in the brain.[13] Symptoms of infection are vague and rarely diagnosed except at autopsy. Pressure necrosis may cause severe central nervous system malfunction, blindness, paralysis, disequilibrium, obstructive hydrocephalus, or disorientation. Perhaps the most common symptom is epilepsy of sudden onset. When this occurs in an adult with no family or childhood history of epilepsy, cysticercosis should be suspected. Praziquantel is the drug of choice for neurocysticercosis, but it is not used against cysticerci in the brain ventricles or the eye.[37] Praziquantel can also be used against porcine cysticercosis, thus avoiding the need for condemnation of the carcass.[99]

  Cysticerci apparently evade a host's defenses by down-modulating its immune response,[44, 50] but when a cysticercus dies, it elicits a rather severe inflammatory response. Many of them may be rapidly fatal to the host, particularly if the worms are located in the brain. This was observed frequently in former British soldiers; a high proportion of those who served in India became infected. Other types of cellular reaction also occur, usually resulting in eventual calcification of the parasite (Fig. 21.17). If this occurs in the eye, there is little chance of corrective surgery.

  Cysticerci occur in three distinct morphological types, of which the most common is the ordinary "cellulose" cysticercus, with an invaginated scolex and a fluid-filled bladder about 0.5 cm to 1.5 cm in diameter. The "intermediate" form (with a scolex) and the "racemose" (with no evident scolex) are much larger and more dangerous.

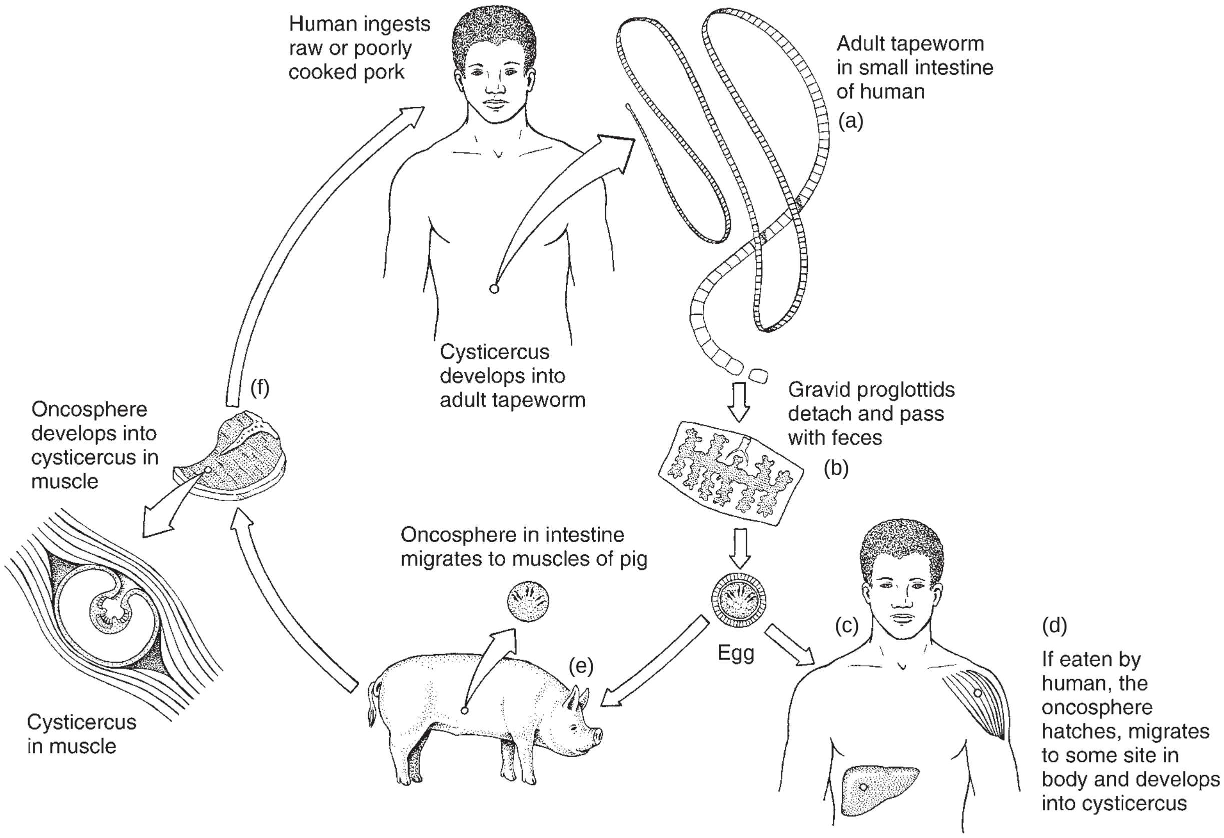


Figure 21.15 **Life cycle of *Taenia solium*.**

(*a*) Adult tapeworm in the small intestine of a human. (*b*) Gravid proglottids detach from the strobila and migrate out of the anus or pass with feces. (*c*) Shelled oncosphere. (*d*) If eaten by a human, the oncosphere hatches, migrates to some site in the body, and develops into a cysticercus. (*e*) Cysticerci will also develop if the eggs are eaten by a pig. (*f*) The life cycle is completed when a person eats pork containing live cysticerci.

Drawing by William Ober and Claire Garrison.

Figure 21.16 **Human brain containing numerous cysticerci of *Taenia solium*.**

From A. Flisser, "Neurocysticercosis in Mexico," in *Parasitol. Today* 4:131–137. Copyright © 1988.

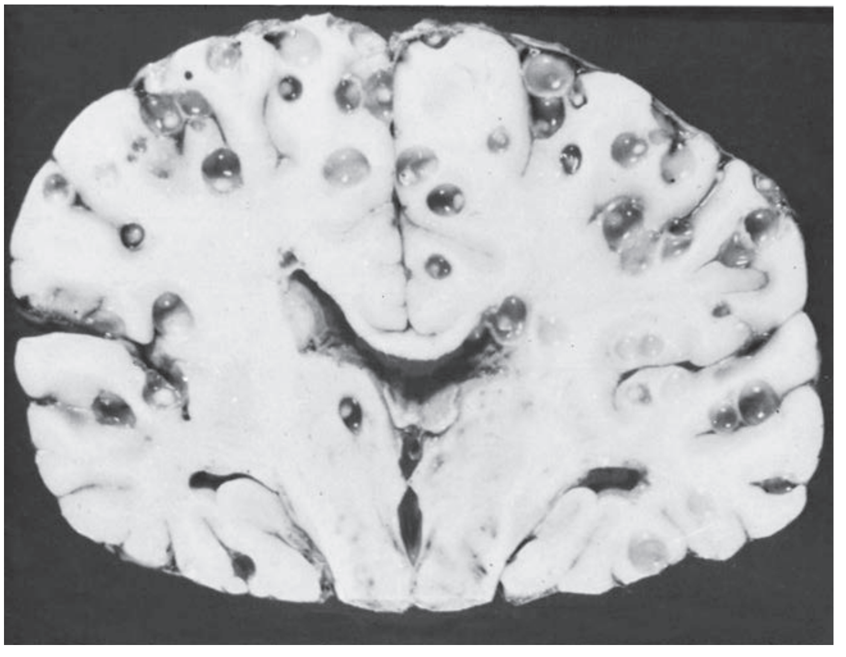


Figure 21.17 ***Cysticercus cellulosae.***
Partially calcified cyst *(arrow)* found in a routine X-ray examination of a human leg.
From R. L. Roudabush and G. A. Ide, "*Cysticercus cellulosae* on X-ray," in *J. Parasitol*. 61:512. Copyright © 1975.

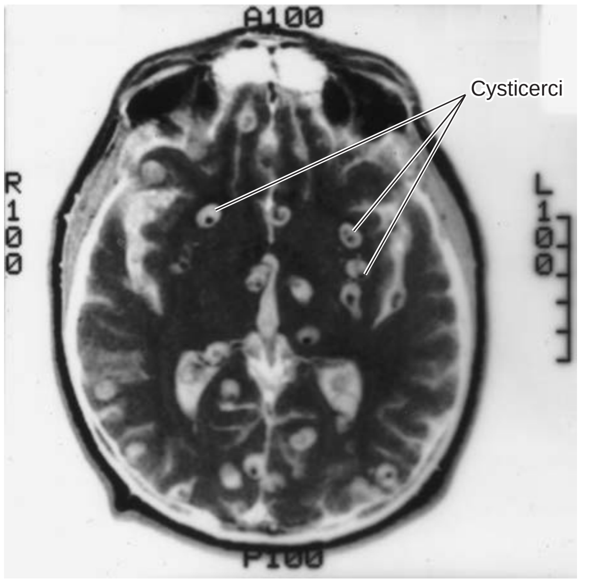


Figure 21.18 **Neurocysticercosis.**
Computerized axial tomography scan (CAT scan) of a patient with multiple *T. solium* cysticerci in the brain.
Courtesy Herman Zaiman.

They can measure up to 20 cm and contain 60 ml of fluid. Up to 13% of patients may have all three types in the brain.[81]

Prevention of cysticercosis depends on early detection and elimination of the adult tapeworm and a high level of personal hygiene. Fecal contamination of food and water must be avoided and the use of untreated sewage on vegetable gardens eschewed. The majority of cases apparently originate from such sources, including contamination by infected food handlers.[31] ELISA-based tests for *T. solium* antigens in feces have been described that are more sensitive than microscopical diagnosis.[4]

Although neurocysticercosis has been considered uncommon, improved brain imaging (through computerized axial tomography and magnetic resonance imaging Fig. 21.18) has demonstrated a higher frequency in the United States than once thought.[20] Of 138 cases reported from Los Angeles County, California, from 1988 to 1990, most were in immigrants from Mexico,[94] where cysticercosis is a major public health problem;[36] however, 9 were travel-associated cases, and 10 were infections acquired in the United States.

A very sensitive and specific, enzyme-linked immunoelectrotransfer blot (EITB) test for serum antibodies has been described.[69, 100] It can detect 98% of parasitologically proven cases with two or more cysts and 60% to 80% of patients with only one lesion. The EITB showed that 1.3% of the people in an Orthodox Jewish community in New York were infected, apparently having become so by domestic employees who were immigrants from countries endemic for *T. solium*.[66]

Cysticercosis due to *T. solium* is highly endemic in Mexico, Central and much of South America, much of sub-Saharan Africa, India, China, and other parts of eastern Asia.[24] Some observers believe that it was deliberately introduced into Irian Jaya by Indonesians as a biological weapon against certain primitive peoples that opposed annexation.[49] This worm remains one of the most serious parasitic diseases in Irian Jaya, Papua Indonesia, and Papua New Guinea.[8, 92]

Other Taeniids of Medical Importance

Taenia multiceps, T. glomeratus, T. brauni, and *T. serialis* are all characterized by a coenurus type of bladderworm (Fig. 21.19). This juvenile type is similar to an ordinary cysticercus but has many rather than one scolex. Such coenuri occasionally occur in humans, particularly in the brain, eye, muscles, or subcutaneous connective tissue, where they often grow to be longer than 40 mm. The resulting pathogenesis is similar to that of cysticercosis. Adults are parasites of carnivores, particularly dogs, with herbivorous mammals serving as intermediate hosts. Accidental infection of humans occurs when eggs are ingested. Coenuriasis of sheep, caused by *T. multiceps,* causes a characteristic vertigo called *gid,* or *staggers*.

Echinococcus granulosus. Genus *Echinococcus* contains the smallest tapeworms in Taeniidae. However, their juveniles often form huge cysts and are capable of infecting

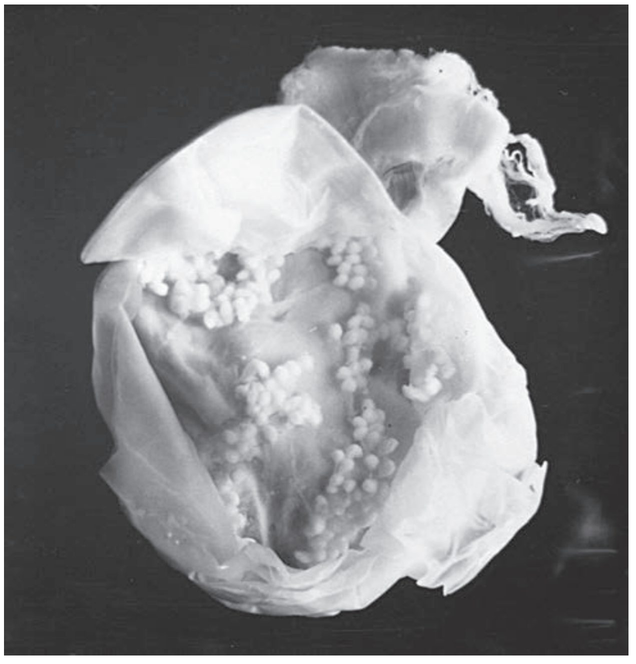


Figure 21.19 Coenurus metacestode of *Taenia serialis*. This metacestode is from the muscle of a rabbit that has been opened to show the numerous scolices arising from the germinal epithelium. The cyst is about 4 in. wide.

Courtesy of James Jensen.

humans, resulting in a very serious disease in many parts of the world.

Echinococcus granulosus causes **cystic echinococcosis.** It uses carnivores, particularly dogs and other canines, as definitive hosts (Fig. 21.20). Many mammals may serve as intermediate hosts, but herbivorous species are most likely to become infected by eating eggs on contaminated herbage.

Adults (Fig. 21.21) live in the small intestine of their definitive host. They measure 3 mm to 6 mm long when mature and consist of a typically taeniid scolex, a short neck, and usually only three proglottids. The nonretractable rostellum bears a double crown of 28 to 50 (usually 30 to 36) hooks. The anteriormost segment is immature; the middle one is usually mature; and the terminal one is gravid. The gravid uterus is an irregular longitudinal sac. The eggs cannot be differentiated from those of other taeniids. Ripe segments detach and develop a rupture in their wall, releasing the eggs, which are fully capable of infecting an intermediate host.

Hatching and migration of oncospheres are the same as previously described for *Taenia saginata,* except that liver and lungs are the most frequent sites of development. By a very slow process of growth, an oncosphere metamorphoses into a type of bladderworm called a **unilocular hydatid** (Fig. 21.22). In about five months the hydatid develops a thick outer, laminated, noncellular layer and an inner, thin, nucleated germinal layer. The inner layer eventually produces brood capsules, within which develop protoscolices (Fig. 21.23) that are infective to definitive hosts. Brood capsules are small cysts, containing 10 to 30 protoscolices, which usually are attached to the germinal layer by a slender stalk; they may break free and float within the hydatid fluid. Similarly, individual scolices may break free from the germinal layer of the capsule (Fig. 21.24). Rarely germinal cells penetrate the laminated layer and form daughter capsules. When a carnivore eats the hydatid, the cyst wall is digested away, freeing the protoscolices, which evaginate and attach among the villi of the small intestine. A small percentage of hydatids lack protoscolices and are sterile, being unable to infect a definitive host. The worm matures in about 56 days and may live for 5 to 20 months.

- **Epidemiology**. The life cycle of *Echinococcus granulosus* in wild animals may involve a wolf-moose, wolf-reindeer, dingo-wallaby, lion-warthog, or other carnivore-herbivore relationship, which is known as **sylvatic echinococcosis.** Humans are seldom involved as accidental intermediate hosts in these cases. However, ample opportunities exist for human infection in situations in which domestic herbivores are raised in association with dogs. For example, hydatid disease is a very serious problem in sheep-raising areas of Australia, New Zealand, North and South America, Europe, Asia, and Africa. Similarly, goats, camels, reindeer, and pigs, together with dogs, maintain the cycle in various parts of the world. Dogs are infected when they feed on the offal of butchered animals, and herbivores are infected when they eat herbage contaminated with dog dung. Humans are infected with hydatids when they accidentally ingest *Echinococcus* spp. eggs, usually as a result of fondling dogs.

  The species *E. granulosus* is composed of a number of genetically differing strains.[56, 104] Strain differences include morphology, development, metabolism, and intermediate host specificity, and are revealed by DNA hybridization and restriction site analysis. Worms of one strain are adapted to one species of intermediate host—for example, cattle, horses, sheep, or pigs—and they do not develop well in other species. The strains have considerable epidemiological significance for humans: Horse and pig strains in Europe probably do not infect humans, but sheep and cattle strains do. Molecular evidence suggests that several strains of *E. granulosus* may represent distinct species and that *E. granulosus* is paraphyletic.[16, 58]

  Local traditions may contribute to massive infections. Some tribes of Kenya, for instance, are said to relish dog intestine roasted on a stick over a campfire. Because cleaning of the intestine may involve nothing more than squeezing out its contents, and cooking may entail nothing more than external scorching, these people probably have the highest rate of infection with hydatids in the world.[71] A further complication lies in the lack of burial of the dead by the Turkana people of Kenya. When the corpses are eaten by carnivores, humans become true intermediate hosts of *E. granulosus*.[61]

  A different set of circumstances leads to infection in tanners in Lebanon, where dog feces are used as an ingredient of a solution for tanning leather. Scats picked off the street are added to the vats, and any eggs present may contaminate their handler.[91]

  Sheepherders in the United States and elsewhere risk infection by living closely with their dogs. Surveys of cattle, hogs, and sheep in abattoirs reveal that *E. granulosus* occurs throughout most of the United States, with greatest concentrations in the deep South and far West. Recent outbreaks have been diagnosed in California and Utah.

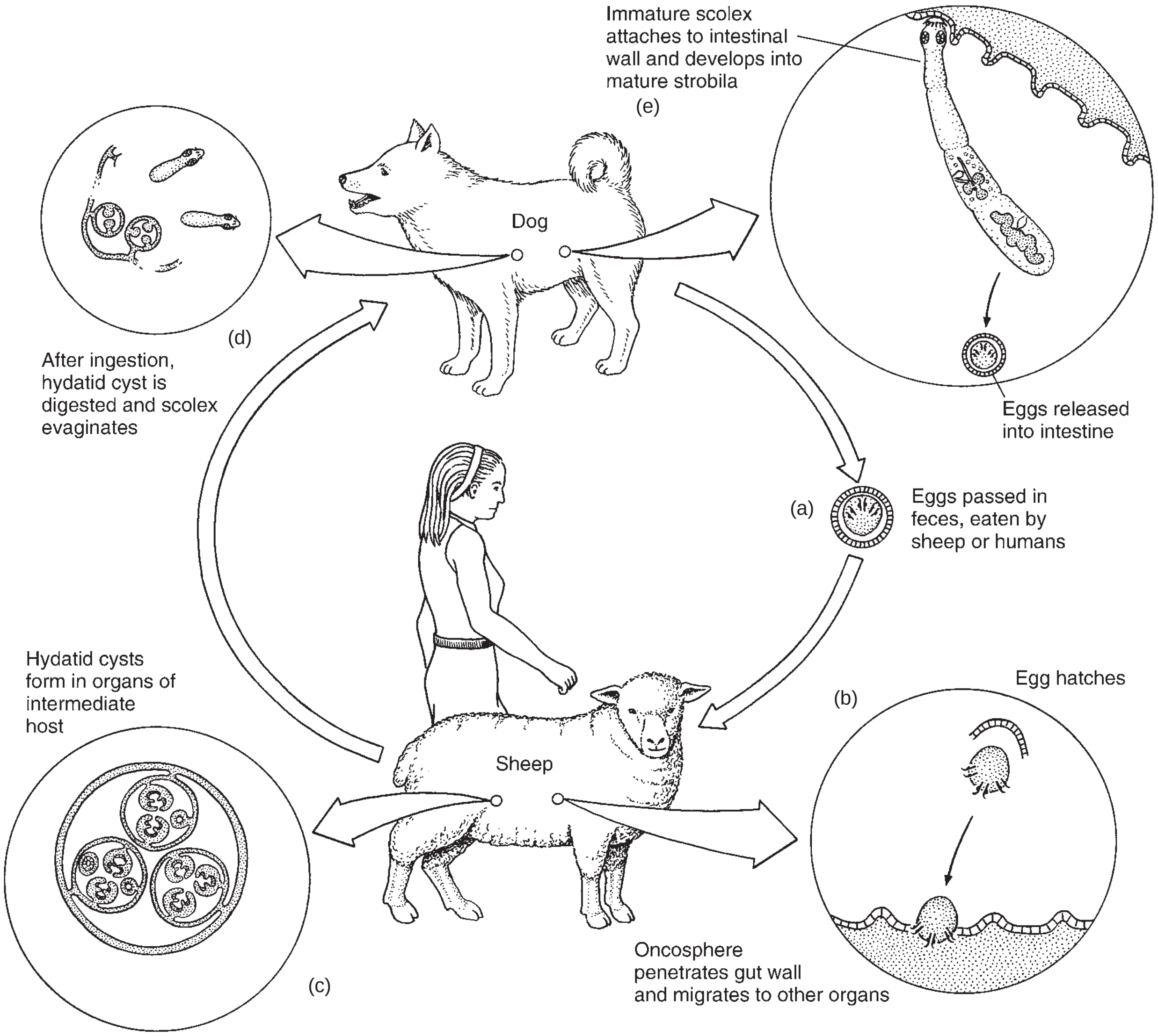


Figure 21.20 **Life cycle of *Echinococcus granulosus*.**
(*a*) Shelled oncosphere is passed in feces and eaten by hooved animals or humans. (*b*) Oncosphere penetrates gut wall and is carried to liver and other sites by circulation. (*c*) Hydatid cysts form in organs of intermediate host. (*d*) After ingestion by canid, hydatid cyst is digested and scolex evaginates. (*e*) Scolex attaches to intestinal wall and develops into strobila.
Drawing by William Ober and Claire Garrison.

Nevertheless, 98% of hydatid infections diagnosed in the United States are imported, the most frequent contributor of cases being Italy.[17]

This disease can be eliminated from an endemic area only by interrupting the life cycle by denying access of dogs to offal, by destroying stray dogs, and by a general education program.[39, 65]

- **Pathogenesis.** Effects of a hydatid may not become apparent for many years after infection because of its usual slow growth. Up to 20 years may elapse between infection and overt pathogenesis. If infection occurs early in life, the parasite may be almost as old as its host.[12]

Cases have been reported in which liver, lungs, and brain simultaneously bore hydatids,[103] and cysts may occur in almost any organ.[68] Thus, the type and extent of pathological conditions depend on the location of the cyst in the host. As the size of a hydatid increases, it crowds adjacent host tissues and interferes with their normal functions (Fig. 21.25). The results may be very serious. If the parasite is lodged in the nervous system, clinical effects may be manifested relatively early in the infection before much growth occurs. When bone marrow is affected, the growth of the hydatid is restricted by lack of space. Chronic internal pressure caused by the parasite usually causes necrosis of the bone, which becomes thin and fragile; characteristically, the first sign of such an infection is a spontaneous fracture of an arm or leg. When a hydatid grows in an unrestricted location, it may become enormous, containing more than 15 quarts of fluid and millions of protoscolices. Even if it does not occlude a vital organ, it can still cause sudden death if it ruptures.

Figure 21.21 Adult *Echinococcus granulosus* from the intestine of a dog.
Adults are only 3 mm to 8 mm long.
Courtesy of Ann Arbor Biological Center.

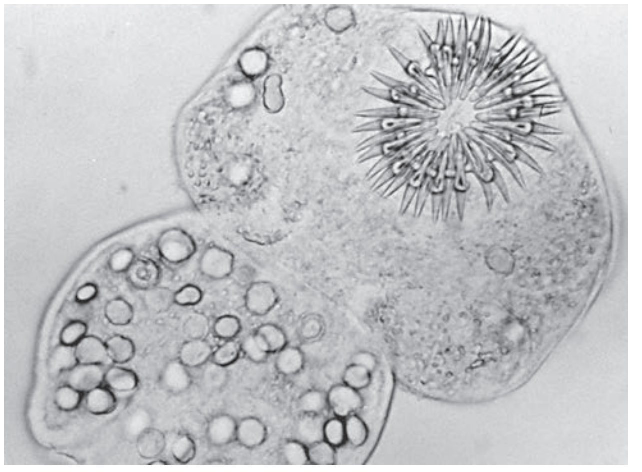


Figure 21.23 Protoscolex of *Echinococcus granulosus*, removed from a hydatid cyst.
Courtesy of Sharon File.

Figure 21.22 Several unilocular hydatids in the lung of a sheep.
Each hydatid contains many protoscolices.
Courtesy of James Jensen.

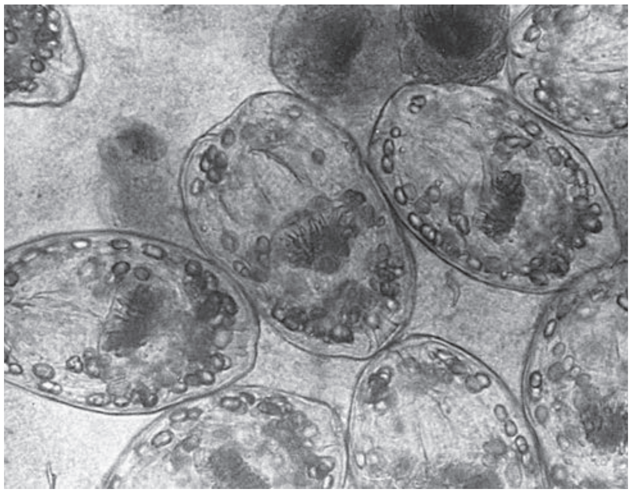


Figure 21.24 Unattached protoscolices of *Echinococcus granulosus* from a hydatid cyst.
Courtesy of Robert E. Kuntz.

The host is sensitized to *Echinococcus* antigens during its long-standing infection, and sudden release of massive amounts in the hydatid fluid induces an adverse host reaction called *anaphylactic shock*. Unconsciousness and death are nearly instantaneous in such instances.

- **Diagnosis and Treatment.** When hydatids are found, it is often during X-radiography, ultrasonography, or CAT scans. Several immunodiagnostic techniques are available, but these are generally less sensitive than imagery.[10]

  Surgery remains the only routine method of treatment and then only when the hydatid is located in an unrestricted location; for treatment of an inoperable hydatid, albendazole is recommended.[68] The typical surgical procedure involves incising the surrounding adventitia until the capsule is encountered and aspirating the hydatid fluid with a large syringe. Considerable delicacy is required at this point, since fluid spilled into a body cavity can quickly cause fatal anaphylactic shock. After aspiration of the cyst contents, 10% formalin is injected into the hydatid to kill the germinal layer. This fluid is withdrawn after five minutes, and the entire cyst is then excised. A high rate of surgical success is obtained on ocular hydatidosis.

Echinococcus multilocularis. *Echinococcus multilocularis* causes **alveolar echinococcosis**. It is primarily boreal in its distribution, being widespread in Eurasia (central Europe, most of Russia, northern and western China, and Tibet, with southernmost records from Kashmir); Hokkaido Island in Japan; and two cases diagnosed from North Africa. In North America its range extends from the tundra zone in Alaska and northwest Canada through the provinces of Alberta, Saskatchewan, and Manitoba in Canada and in the United States from western Montana east to Ohio and south to Missouri. Adults are mainly parasites of foxes, but dogs, cats, and coyotes may also serve as definitive hosts. Several

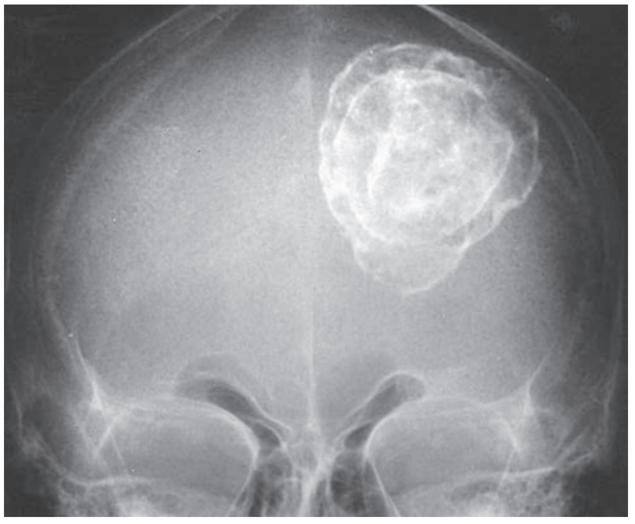


Figure 21.25 **Partially calcified hydatid cyst in the brain.**
AFIP neg. no. 68-2740.

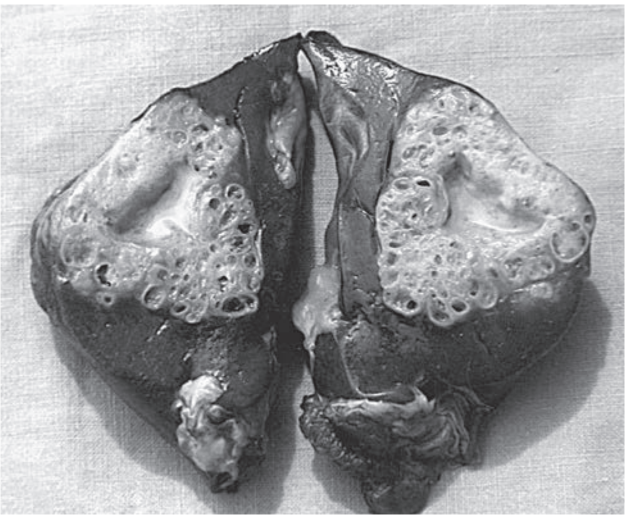


Figure 21.26 **Alveolar metacestode in the liver of a rhesus monkey infected experimentally 15 months earlier.** The central cavity is a result of necrosis.
Courtesy of Robert Rausch.

species of small rodents such as voles, lemmings, and mice are intermediate hosts.

- **Morphology.** Adults are very similar to those of *E. granulosus,* differing from them in the following characteristics: (1) *E. granulosus* is 3 mm to 6 mm long, whereas *E. multilocularis* is only 1.2 mm to 3.7 mm long; (2) genital pores of *E. granulosus* are about equatorial, but they are preequatorial in *E. multilocularis;* and (3) *E. granulosus* has 45 to 65 testes with a few located anterior to the cirrus pouch, but *E. multilocularis* has 15 to 30 testes, all located posterior to the cirrus pouch.

- **Biology.** Metacestodes (Fig. 21.26) differ in several respects from those of *E. granulosus*. Instead of developing a thick, laminated layer and growing into large, single cysts, this parasite has a thin outer wall that grows and infiltrates processes into surrounding host tissues like a cancer. Following transformation of the oncosphere, extensions of germinal tissue invade surrounding hepatic tissue of the host, followed by formation of small chambers, each surrounded by a thin layer of laminated tissue lined by germinal tissue, from which a brood capsule arises. In rodents, each chamber contains a few protoscolices. In humans and other unnatural hosts the pockets typically lack protoscolices. In natural intermediate hosts the cyst is more regular. In humans, pieces of the cyst sometimes break off and metastasize to other parts of the body.[40] Because of its type of construction, this metacestode form is called an **alveolar** or **multilocular hydatid.**

  Human infection with alveolar echinococcosis is unusual, although more intensive investigation in recent years has shown a much higher prevalence than previously realized. Humans do not seem to be very good hosts because protoscolices may not develop in humans, but the germinal membrane is still viable.[82] Dogs that catch and eat wild rodents seem to be the main source of infection for humans.[31] Studies conducted in Alaska showed that human infection was highly correlated with a close human-dog association, and trapping or skinning foxes was not associated with greater infection risk.[31] There is some evidence that there are strains that differ in virulence.[55] Some human infections seem to disappear spontaneously, while others seem to march inexorably toward death. Such differences may be explained by differing immune responses.[41]

- **Diagnosis and Treatment.** Diagnosis of an alveolar echinococcosis is difficult, particularly because the protoscolices may not be found. Even at necropsy cysts may be mistaken for malignant tumors. As a result of the difficulties of liver surgery, excision is usually practical only when the hydatid is localized near the tip of a lobe of the liver; infections of the hilar area are inoperable. The infiltrative nature of the cyst and its slow rate of growth may advance the disease to an inoperable state before its presence is detected. Praziquantel, the drug that is so effective for most flatworm parasites, may actually enhance growth of alveolar hydatids.[62] Albendazole may be effective in some patients; encouraging results have been obtained in mice treated with albendazole-loaded nanoparticles.[84]

  Alveolar echinococcosis can be prevented only by avoiding dogs and their feces in endemic regions, by carefully washing all strawberries, cranberries, and the like that may be contaminated by dung, and by regularly worming dogs that may be liable to infection.

***Echinococcus vogeli* and *E. oligarthrus*.** *Echinococcus vogeli* causes polycystic echinococcosis in humans in tropical America and is responsible for significant morbidity and mortality in several countries, while infections with *E. oligarthrus* are apparently quite rare.[81] Normal definitive hosts of *E. vogeli* are bush dogs, *Speothus venaticus,* while those of *E. oligarthrus* are several species of wild cats. The most important sources of infection for humans are domestic dogs and possibly domestic cats. Cysts of these species are relatively large, fluid-filled vesicles with numerous protoscolices. Their natural intermediate hosts are pacas and agoutis (rodents).[25]

Family Hymenolepididae

The huge family Hymenolepididae consists of numerous genera with species in birds and mammals. Only two species, *Hymenolepis nana* and *H. diminuta,* can infect humans. The family offers considerable taxonomic difficulties because of the large number of species and the immense and far-flung literature that has accumulated. However, the family's morphology is relatively simple compared with, for example, Pseudophyllidea, and most species are small, transparent, and easy to study.

The most characteristic morphological feature of the group is the small number of testes: usually one to four. The combination of few testes, usually unilateral genital pores, and a large external seminal vesicle permits easy recognition of the family. All except *H. nana* require arthropod intermediate hosts.

Hymenolepis nana. Commonly called the *dwarf tapeworm, Hymenolepis nana* (Fig. 21.27), also known as *Vampirolepis nana,* is a cosmopolitan species that is one of the most common cestodes of humans in the world, especially among children. Rates of infection run from 1% in the southern United States to 9% in Argentina and to 97.3% in Moscow.[51]

- **Morphology.** As its name implies (Gr. *nanos* = dwarf), this is a small species, seldom exceeding 40 mm long and 1 mm wide. The scolex bears a retractable rostellum armed with a single circle of 20 to 30 hooks. The neck is long and slender, and the segments are wider than long. Genital pores are unilateral, and each mature segment contains three testes. After apolysis gravid segments disintegrate, releasing eggs, which measure 30 μm to 47 μm in diameter. The oncosphere (Fig. 21.28) is covered with a thin, hyaline, outer membrane and an inner, thick membrane with polar thickenings that bear several filaments. The heavy embryophores that give taeniid eggs their characteristic striated appearance are lacking in this and the other families of tapeworms infecting humans.

- **Biology.** The life cycle of *H. nana* is unique among tapeworms in that an intermediate host is optional (see Fig. 21.27). When eaten by a person or a rodent, eggs hatch in the duodenum, releasing oncospheres, which penetrate the mucosa and come to lie in lymph channels of the villi. Here each develops into a cysticercoid (Fig. 21.29). In five to six days cysticercoids emerge into the lumen of the small intestine, where they attach and mature.

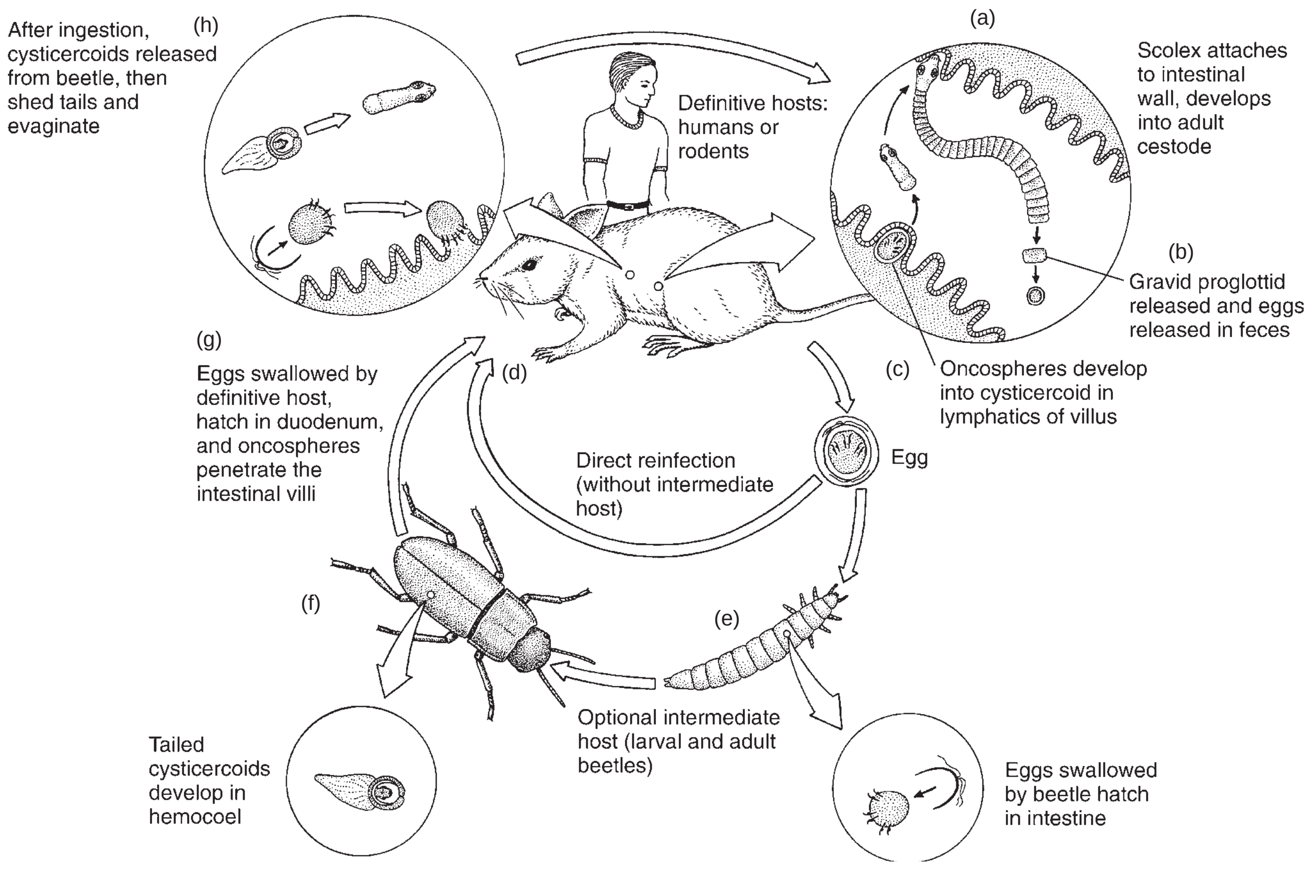


Figure 21.27 **Life cycle of *Hymenolepis nana,* the dwarf tapeworm.**
(*a*) Adult attached to intestinal wall releases gravid proglottids (*b*) and shelled oncospheres in feces (*c*). (*d*) Direct reinfection when definitive host swallows shelled oncosphere. (*e*) Larval and adult beetles are optional intermediate hosts. (*f*) Cysticercoids develop in hemocoel of beetle. (*g*) When shelled oncospheres are ingested by definitive host, they hatch in the duodenum and penetrate the intestinal villi. (*h*) Ingested cysticercoids shed tails and evaginate, and scolices attach to intestinal wall.
Drawing by William Ober and Claire Garrison.

Figure 21.28 **Egg of *Hymenolepis nana*.**
Note the polar filaments on the inner membrane and the well developed oncosphere. Its size is 30 μm to 47 μm.
Courtesy of Jay Georgi.

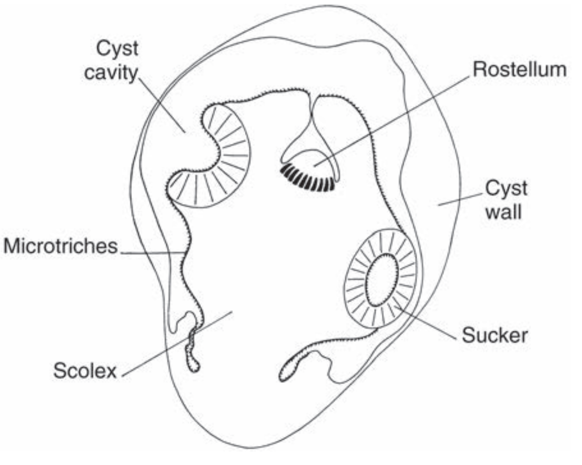


Figure 21.29 ***Hymenolepis nana*.**
Diagrammatic representation of a longitudinal section through a cysticercoid from a mouse villus.
From J. Caley, "A comparative study of two alternative larval forms of *Hymenolepis nana,* the dwarf tapeworm, with special reference to the process of encystment," in *Z. Parasitenkd*. 47:218–228, 1975. Copyright © 1975 Springer-Verlag, New York. Reprinted by permission.

This direct life cycle is doubtless a recent modification of the ancestral two-host cycle, found in other species of hymenolepidids, because cysticercoids of *H. nana* can still develop normally within larval fleas and beetles (Fig. 21.30). One reason for the facultative nature of the life cycle is that *H. nana* cysticercoids can develop at higher temperatures than can those of other hymenolepidids. Direct contaminative infection by eggs is probably the most common route in human cases, but accidental ingestion of an infected grain beetle or flea cannot be ruled out.

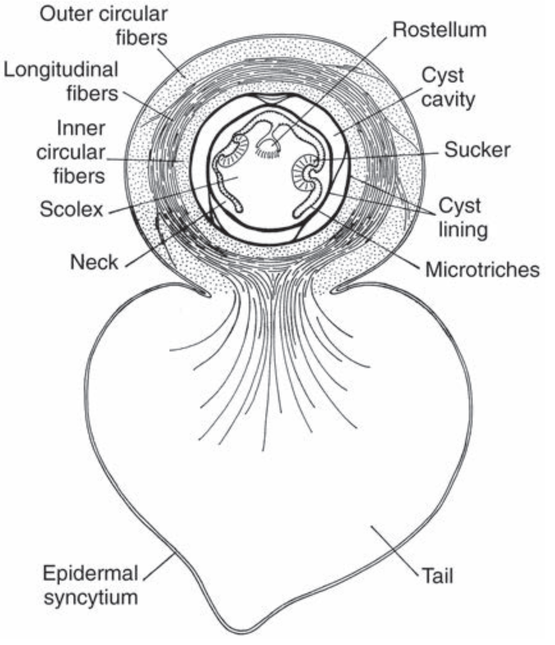


Figure 21.30 **Diagrammatic representation of a longitudinal section through a cysticercoid of *Hymenolepis nana* from the insect host.**
From J. Caley, "A comparative study of two alternative larval forms of *Hymenolepis nana,* the dwarf tapeworm, with special reference to the process of encystment," in *Z. Parasitenkd*. 47:218–228, 1975. Copyright © 1975 Springer-Verlag, New York. Reprinted by permission.

Besides humans, domestic mice and rats also serve as suitable hosts for *H. nana*.[35] Some authors contend that two subspecies exist: *H. nana nana* in humans and *H. nana fraterna* in murine rodents. Differences do seem to exist in the physiological host-parasite relationships of these two subspecies, because higher rates of infection result from eggs obtained from the same host species than from the other.[76] This is probably an example of allopatric speciation in action.

Pathological results of infection by *H. nana* are rare and usually occur only in massive infections. Heavy infections can occur through autoinfection,[45] and the symptoms are similar to those already described for *Taenia saginata* infection. Praziquantel acts very rapidly against *H. nana* and *H. diminuta*.[5, 13] In vitro the drug produces vacuolization and disruption of the tegument in the neck of the worms but not in more posterior portions of the strobila.

Hymenolepis diminuta. *Hymenolepis diminuta* is a cosmopolitan worm that is primarily a parasite of rats (*Rattus* spp.), but human infections are not uncommon. It is a much larger species than *H. nana* (up to 90 cm) and differs from *H. nana* in lacking hooks on the rostellum. Typical of the genus, it has unilateral genital pores and three testes per proglottid. Eggs (Fig. 21.31) are easily differentiated from those of *H. nana,* since they are larger and have no polar filaments. It has been demonstrated experimentally that more than 90 species of arthropods can serve as suitable intermediate hosts. Stored-grain beetles (*Tribolium* spp.) are probably

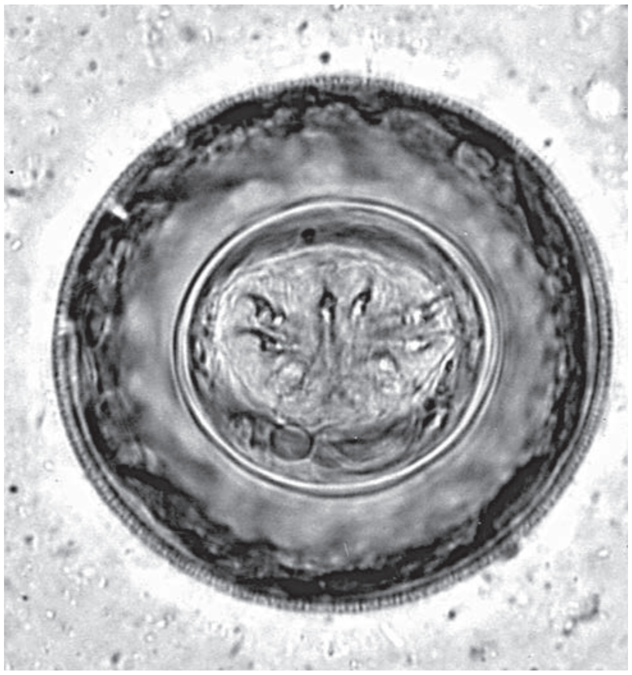


Figure 21.31 **Egg of *Hymenolepis diminuta*.**
It is 40 μm to 50 μm wide.
Courtesy of Jay Georgi.

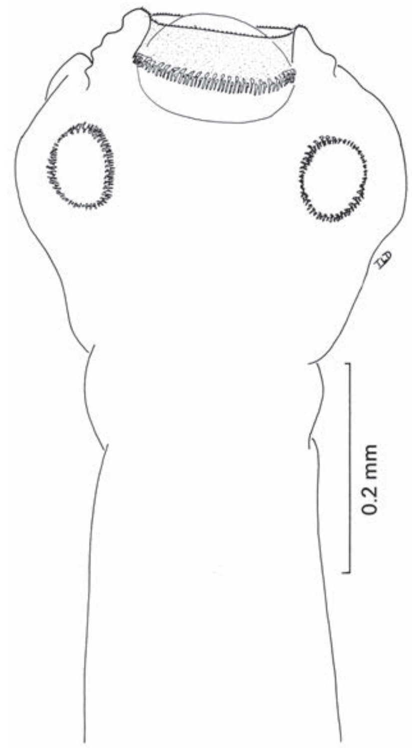


Figure 21.32 **Scolex of *Raillietina*.**
The suckers are weak and have a double circle of spines, and the massive rostellum has many hammer-shaped hooks.
Drawing by Thomas Deardorff.

most commonly involved in infections of both rats and humans. A household shared with rats is also likely to have its cereal foods infested with beetles. Treatment is as recommended for *H. nana*.

The ease with which this parasite is maintained in laboratory rats and beetles makes it an ideal model for many types of experimental studies; its physiology, metabolism, development, genetics, and nutrient uptake have been more thoroughly examined than those of any other tapeworm.[6] Research on *H. diminuta* has contributed enormously to our concepts of the world of tapeworms, including our understanding of how they survive, reproduce, and develop and of their adaptations for parasitism.

Family Davaineidae

Raillietina Species

The following species of *Raillietina* have been reported from humans: *R. siriraji, R. asiatica, R. garrisoni, R. celebensis,* and *R. demarariensis*. All normally parasitize domestic rats and possibly represent no more than two actual species. The genus is easily recognized by its large rostellum with hundreds of tiny, hammer-shaped hooks and by its spiny suckers (Fig. 21.32). Life cycles of these species are unknown, but they probably use insects as intermediate hosts; their epidemiology is probably similar to that of *H. diminuta*.

Raillietina cesticillus is one of the most common poultry cestodes in North America, and a wide variety of grain, dung, and ground beetles serve as intermediate hosts. The genus is very large, with species in many birds and mammals. The closely related genus *Davainea* is nearly identical to *Raillietina,* except that its strobila is very short, consisting of only a few proglottids. *Davainea* spp. are found in galliform birds and use terrestrial molluscs as intermediate hosts. Other genera infect a wide variety of hosts, from passeriform birds to scaly anteaters.

Family Dilepididae

Dipylidium caninum. A cosmopolitan, common parasite of domestic dogs and cats, *Dipylidium caninum* often occurs in children.[67] It is easily recognized because each segment has two sets of male and female reproductive systems and a genital pore on each side (Fig. 21.33). The scolex has a retractable, rather pointed rostellum with several circles of rose thorn-shaped hooks. Its uterus disappears early in its development and is replaced by hyaline, noncellular egg capsules, each containing 8 to 15 eggs. Gravid proglottids detach and either wander out of the anus or are passed with feces. They are very active at this stage and are the approximate size and shape of cucumber seeds. As detached segments begin to desiccate, egg capsules are released.

Fleas are the usual intermediate hosts, although chewing lice have also been implicated. Unlike adults, larval fleas have simple, chewing mouthparts and feed on organic matter, which may include *D. caninum* egg capsules. The resulting cysticercoids survive their host's metamorphosis into the parasitic adult stage, when fleas may be nipped or licked out of the fur of a dog or cat, thereby completing the life cycle. This, by the way, is an example of hyperparasitism, since the flea is itself a parasite.

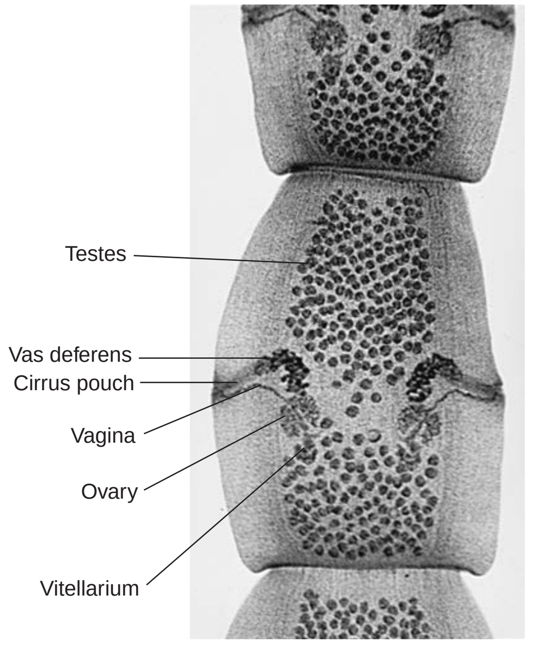


Figure 21.33 Mature segment of *Dipylidium caninum*, the "double-pored tapeworm" of dogs and cats.
The two vitelline glands are directly behind the larger ovaries. The smaller spheres are testes.
Courtesy of Ann Arbor Biological Center.

Nearly every reported case of infection of humans has involved a child. Adult humans may be more resistant, or else children may have increased chances of accidentally swallowing a flea. The symptoms and treatment are the same as for *Hymenolepis nana*.

The only feature separating this family from Hymenolepididae is a larger number of testes, usually more than 12. This family, too, consists of hundreds of species that parasitize birds and mammals. Taxonomic difficulties also attend this family.

Family Anoplocephalidae

Moniezia Species

The numerous species of *Moniezia* use hoofed animals as definitive hosts. The most frequently encountered species in domestic animals are *M. expansa* and *M. benedeni* in sheep, cattle, and goats. These are large tapeworms, up to 6 m, and their proglottids are much wider than long. They have two sets of reproductive organs in each proglottid, and their scolex is unarmed. They have curious interproglottidal glands that open along the junctions between proglottids; the function of the glands is unknown.[93] Eggs of *M. benedeni* are rather square in shape, and those of *M. expansa* are more triangular. Oncospheres of both are borne within an oddly shaped pyriform apparatus, an embryophore with long hookor hornlike extensions.

Moniezia expansa was the first anoplocephalid for which a life cycle was discovered. Parasitologists had been mystified for many years as to how herbivorous animals could be infected with tapeworms, and small arthropods that might be ingested along with herbage were diligently investigated as potential intermediate hosts. Finally in 1937 Horace Stunkard announced that the intermediate host of *M. expansa* was a minute, free-living mite in the family Oribatidae.[95]

Ba and coworkers[9] sorted *M. expansa* and *M. benedeni* from France and Senegal, Africa, on the basis of patterns of their interproglottidal glands and then performed isoenzyme analysis on them. They found that French worms were very similar genetically to some African worms, and these were identified as *M. expansa*. They came from sheep and goats but not from cattle. Other African worms, putatively assigned to either *M. expansa* or *M. benedeni,* seemed to represent at least four distinct species. Thus, species diversity of *Moniezia* spp. in domesticated ruminants may be greater than previously believed.

Bertiella studeri. Normally a parasite of Old World primates, *Bertiella studeri* has been reported many times from humans, especially in southern Asia, the East Indies, and the Philippines. The scolex is unarmed, and proglottids are much wider than they are long, with the ovary located between the middle of the segment and the cirrus pouch. The egg is characteristic: 45 μm to 50 μm in diameter, with a bicornuate pyriform apparatus on the inner shell.

Ripe segments are shed in chains of about a dozen at a time. Intermediate hosts are various species of oribatid mites. Accidental ingestion of mites infected with cysticercoids completes the life cycle within primates. No disease has been ascribed to infection by *B. studeri*. Treatment is as for *Hymenolepis nana*.

Bertiella mucronata is similar to *B. studeri* and also has been reported from humans.[75] It appears to be a parasite of New World monkeys, and children may become infected when living with a pet monkey and the ubiquitous oribatid mite. Distinguishing this species from *B. studeri* normally requires a specialist.

Inermicapsifer madagascariensis. *Inermicapsifer madagascariensis* is normally parasitic in African rodents, but it has been reported repeatedly in humans in several parts of the world, including South America and Cuba. Baer[11] concluded that humans are the only definitive host outside Africa.

The scolex is unarmed. The strobila is up to 42 cm long. Mature proglottids are somewhat wider than long. The uterus becomes replaced by egg capsules in ripe segments, each capsule containing 6 to 10 eggs, which do not possess a pyriform apparatus.

The life cycle of this parasite is unknown but undoubtedly involves an arthropod intermediate host. Clinical pathological conditions have not been studied, and treatment is similar to that described for other species.

Family Mesocestoididae

Mesocestoides Species

Unidentified specimens of the genus *Mesocestoides,* whose definitive hosts are normally various birds and mammals, have occasionally been reported from humans in Denmark, Africa, the United States, Japan, and Korea.[48] The ventromedial location of the genital pores is clearly diagnostic of the genus (Fig. 21.34). The complete life cycle is not known for

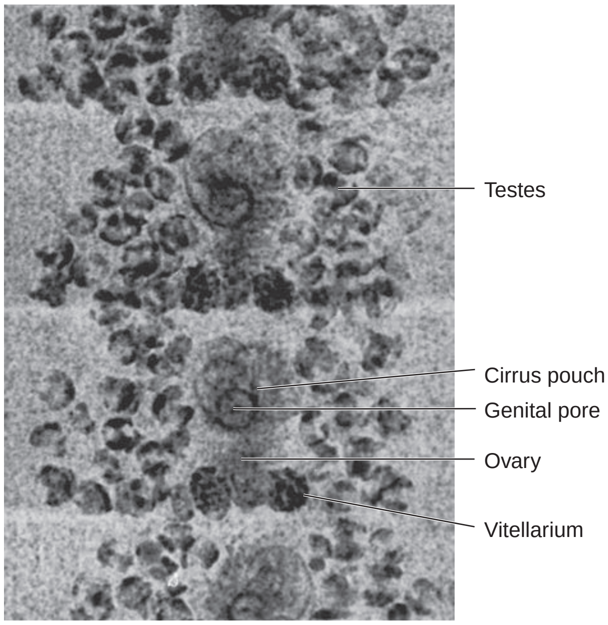


Figure 21.34 ***Mesocestoides* sp., a cyclophyllidean cestode with a midventral genital pore and a bilobed vitellarium.**
Courtesy of Larry Shults.

Figure 21.35 **Tetrathyridial metacestodes of *Mesocestoides* sp. in the mesenteries of a baboon, *Papio cyanocephalus*.**
Courtesy of Robert E. Kuntz.

any species in this difficult family, but many have a rodent or reptile intermediate host, in which a cysticercoid type of larva known as a *tetrathyridium* (Fig. 21.35) develops. Neither mammals nor reptiles can be infected directly by eggs, so a first host must be involved. As yet, such a host has not been identified (Fig. 21.36). Pathological conditions and treatment of humans have not been studied.

Mesocestoides sp. is very curious in that it may undergo asexual multiplication in the definitive host (see Fig. 21.36)—not by budding, as in coenuri and hydatids, but by longitudinal fission of the scolex! An inwardly directed protuberance of the tegument between the suckers, the "apical massif," has morphocytogenetic power.[44] Although we know that this one isolate of *Mesocestoides* reproduces in this astonishing way (and the isolate has been widely propagated and used as an experimental model), the phenomenon may not be typical of the genus.[23] Etges contended that developmental differences made it unlikely that the proliferative tetrathyridium could be *M. corti,* and he thus described it as a new species, *M. vogae*.[34]

The scolex of *Mesocestoides* has four simple suckers and no rostellum. Each proglottid has a single set of male and female reproductive systems; the genital pores are median and ventral. Otherwise, their morphology is typically cyclophyllidean, with a paruterine organ replacing the uterus in most species.

Mesocestoides spp. are widespread in carnivores throughout most of the world. Some specialists consider members of this family a distinct order of tapeworms.

Family Dioecocestidae

The only dioecious tapeworms are found in this family, except for species in the genus *Dioecotaenia,* which form a family of tetraphyllideans in rays. All dioecocestids are parasites of shorebirds, grebes, or herons. Some species are completely dioecious, whereas others are only regionally so. There are wide variations in scolex types, although all have four suckers. In some species, such as *Shipleya inermis* in dowitchers, both sexes have secondary sex organs of the opposite sex. Hence, the male has a uterus and the female a cirrus and cirrus pouch, but each has only an ovary or testes.[90]

ORDER PROTEOCEPHALATA

Proteocephalatans are all parasites of freshwater fishes, amphibians, or reptiles. Scolices (see Fig. 20.5*d*) are much like those occurring in cyclophyllideans, bearing four simple suckers and occasionally armature or a rostellum. Proglottids, however, are much more like those of Tetraphyllidea. Genital pores are lateral. The ovary is posterior, and numerous testes fill most of the region anterior to it. Vitellaria are follicular and are restricted to lateral margins of the proglottid.

We know complete life cycles for several species. All involve a cyclopoid crustacean intermediate host, in which the worm develops into a procercoid (the plerocercoid I, according to some authors; see p. XXX). This metacestode has a well-developed scolex and a cercomer at the posterior end. In some species the procercoid is directly infective to a definitive host; in others it burrows into the viscera for a time before reemerging and maturing in the lumen of the gut. Paratenic hosts are common in proteocephalid life cycles. The boring action of the plerocercoid (as it is now called, since it loses the cercomer as it penetrates the intestinal wall; it is also known as plerocercoid II) may be highly pathogenic to its host. For example, *Proteocephalus ambloplitis* in bass in North America sometimes castrates its fish host.

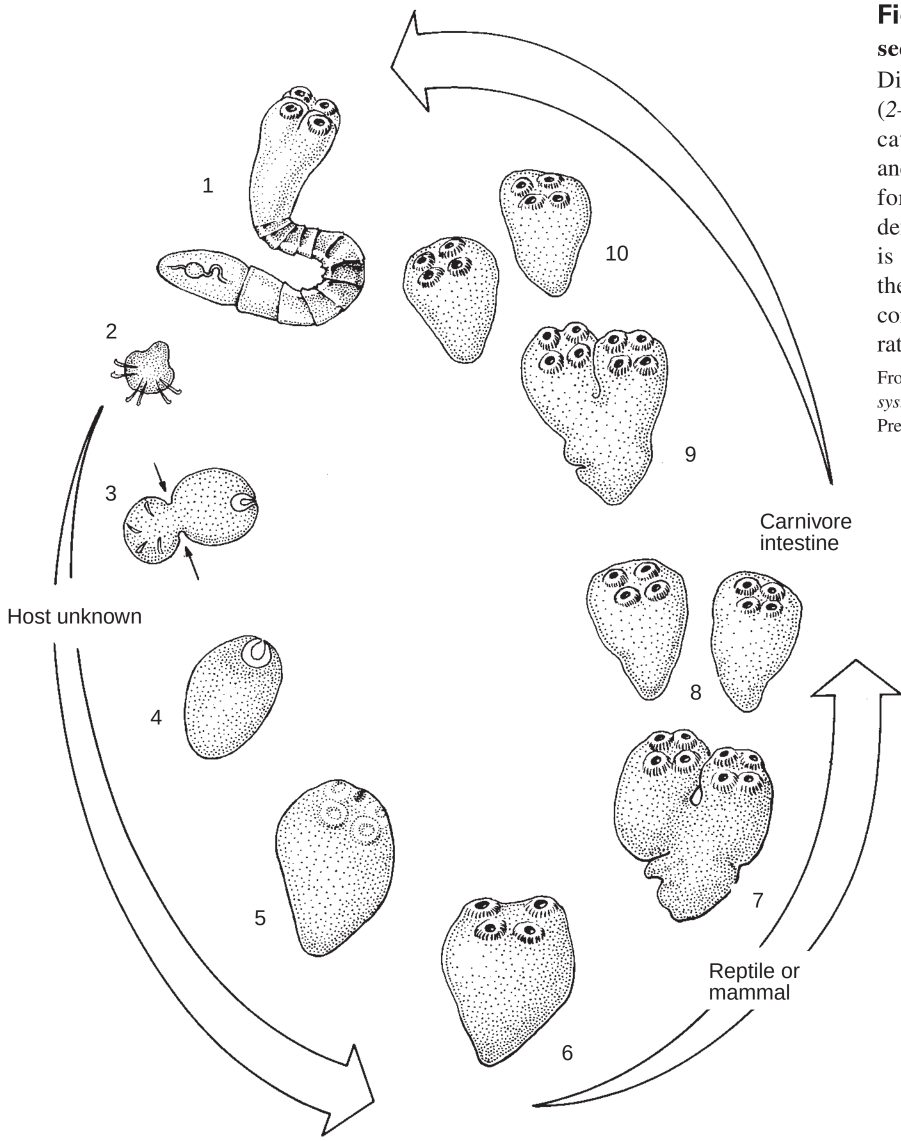


Figure 21.36 **Developmental sequence of *Mesocestoides vogae*.**
Diagram illustrates developmental stages (*2–5*), tetrathyridium and asexual multiplication in second intermediate host (*6–8*), and asexual multiplication with subsequent formation of adult worms in intestine of definitive host (*9–10*). Not illustrated here is the potential reinvasion of tissues from the intestinal lumen of the carnivore with continuing asexual multiplication of the tetrathyridial stage.

From M. Voge, in G. D. Schmidt (Ed.), *Problems in systemics of parasites*. Baltimore, MD: University Park Press, 1969.

ORDER TETRAPHYLLIDEA

Tetraphyllideans are notable for their astonishing variety of scolex forms (see Figs. 20.4*a* and 20.5*i*). Basically, there are four bothridia, which may be stalked or sessile, smooth or crenate, or subdivided into loculi or major units. Often there are accessory suckers (see Fig. 20.4*a*) and/or hooks (Fig. 21.37) or spines. An apical, stalked, suckerlike organ, the myzorhynchus, is present on some. A neck is present or absent. The strobila and proglottids are essentially identical to those of Lecanicephalidea and Trypanorhyncha, and, like members of those orders, adult tetraphyllideans are all parasites of the spiral intestine of elasmobranchs.

As far as is known, life cycles are also similar. No complete cycle has been discovered, but infective plerocercoids are common in molluscs, crustaceans, and fishes. Fishes undoubtedly are paratenic hosts, as may be some molluscs and crustaceans. In vitro cultivation of *Acanthobothrium* sp. plerocercoids in the presence of urea, a substance they encounter in their definitive host, causes the scolex to differentiate into the adult condition.[42]

ORDER TRYPANORHYNCHA

Scolices (see Fig. 20.5*f*) of trypanorhynchans are extraordinary organs. They usually are elongated with two or four shallow bothridia, which may be covered with minute microtriches. Four eversible tentacles (atrophied in *Aporhynchus norvegicum*) emerge from the apex of the scolex. The tentacles are armed with an astonishing array of hooks and spines (Fig. 21.38), shaped and arranged differently in each species. Interpretation of the hook arrangement is difficult but must be accomplished before species identification is possible. Each tentacle invaginates into an internal tentacle sheath, provided at its base with a muscular bulb. A retractor muscle originates at the base or front end of the bulb, courses through

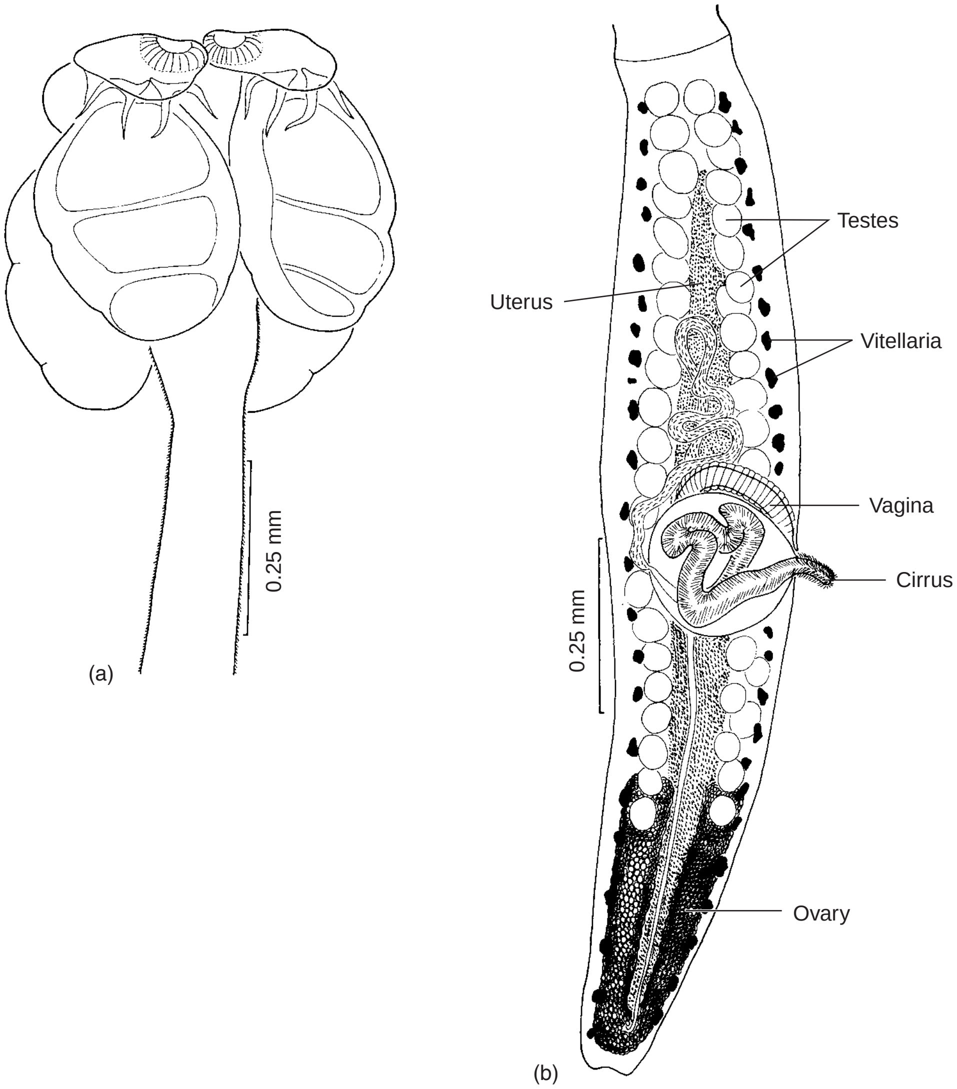


Figure 21.37 ***Acanthobothrium urolophi*, an armed tetraphyllidean.**
(*a*) Scolex; (*b*) mature proglottid.

From G. D. Schmidt, "*Acanthobothrium urolophi* sp. n., a tetraphyllidean cestode (Oncobothriidae) from an Australian stingaree," in *Proc. Helm. Soc. Wash*. 40:91–93.

the tentacle sheath, and inserts inside the tip of the tentacle. When the retractor muscle contracts, it invaginates the tentacle, detaching it from host tissues. When the bulb contracts, it hydraulically evaginates the tentacle, driving it deep into the host's intestinal wall. This process is very similar to that which manipulates the proboscis of an acanthocephalan (chapter 32).

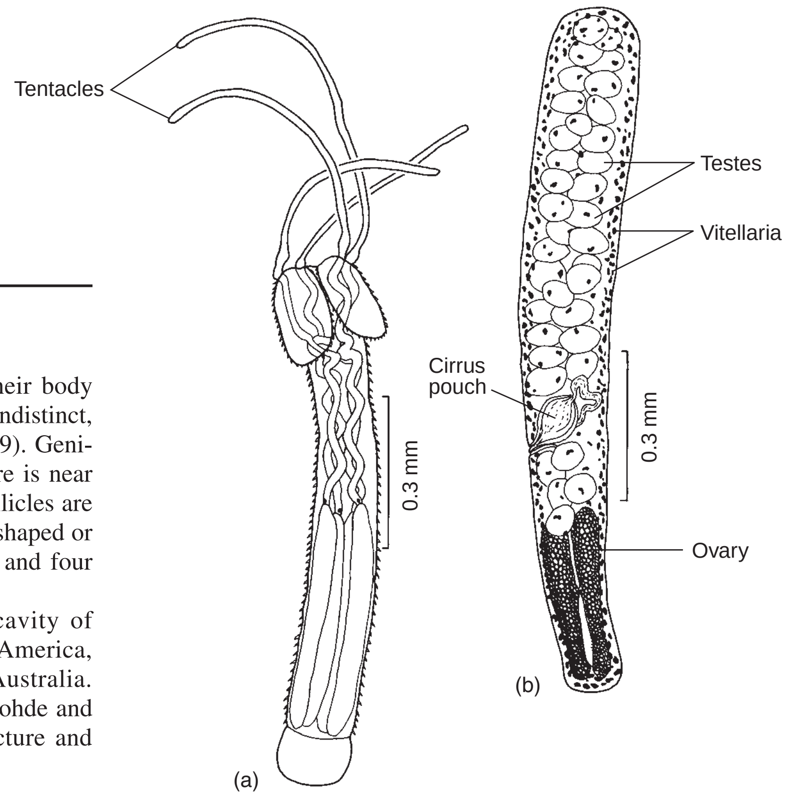
A neck is present or absent; the strobila varies from hyperapolytic to anapolytic. Proglottids of trypanorhynchans are morphologically very consistent with those of tetraphyllideans. The single ovary is basically bilobed and posterior. Vitellaria are follicular, cortical, and lateral or circummedullary. The uterus is a simple sac, usually in the anterior two-thirds of a gravid segment. Testes are few to many and medullary, and cirrus pouch and cirrus often are huge relative to the proglottid. All genital pores are lateral.

Adult trypanorhynchans are all parasites of the spiral intestine of sharks and rays. Infective metacestodes are common in marine molluscs,[19] crustaceans, and fishes. Sakanari and Moser[89] reported experimental infection of copepods with coracidia of *Lacistorhynchus tenuis* which developed into procercoids. These grew into plerocercoids after being eaten by mosquito fish, which produced immature adults after being fed to leopard sharks. This life cycle is similar to that of another trypanorhynchan, *Grillotia erinaceus,* but many other members of this order do not have operculated eggs that release ciliated coracidia.[37]

The plerocercoid, sometimes called a *plerocercus,* may or may not bear a posterior sac, or blastocyst, into which the scolex is inverted. Plerocerci may be so plentiful in the flesh of certain fish or shrimps as to make them unpalatable and thereby unsalable. This is one known economic importance of trypanorhynchans. They have never been reported from humans. However, they remain among the most enigmatic and challenging invertebrates for taxonomists. Dollfus published classical reviews,[28, 29] and Schmidt provided a key to families and genera.[90]

Figure 21.38 ***Eutetrarhynchus thalassius,* a typical trypanorhynch.**
(*a*) Scolex; (*b*) proglottid.

From K. J. Kovacs and G. D. Schmidt, "Two new species of cestode (Trypanorhyncha, Eutetrarhynchidae) from the yellow-spotted stingray, *Urolophus jamaicensis,*" in *Proc. Helm. Soc. Wash*. 47:10–14. Copyright © 1980. Reprinted with permission of the publisher.



SUBCOHORT AMPHILINIDEA

Amphilinidea is the sister group of Eucestoda. Their body is monozoic and dorsoventrally flattened, with an indistinct, proboscislike holdfast at the anterior end (Fig. 21.39). Genital pores are near the posterior end; the uterine pore is near the anterior end. The ovary is posterior, vitelline follicles are bilateral, and testes are preovarian. The uterus is *N*-shaped or looped. The oncosphere is provided with six large and four small hooks.

Amphilinideans are parasites of the body cavity of fishes and turtles in Asia, Japan, Europe, North America, Sri Lanka, Brazil, Africa, the East Indies, and Australia. They are of no medical or economic importance. Rohde and Georgi[86] presented an excellent study on the structure and life history of *Austramphilina elongata*.

COHORT GYROCOTYLIDEA

This is the sister group of Cestoidea. They are also monozoic, and their anterior end is provided with a small, inversible holdfast organ. The posterior end is a frilled, rosette-like organ, and the lateral margins may be frilled (*Gyrocotyle* spp., Fig. 21.40), or it is a long, simple cylinder, and the lateral margins are smooth *(Gyrocotyloides nybelini).* The ovary is posterior; the uterus has extensive
304 lateral loops, terminating in a midventral pore in the anterior half. Testes are anterior. Genital pores are near the anterior end. Whether or not the structures on their tegumental surface were indeed microtriches (p. XXX) has been controversial, but evidence appears strong that they are indeed microtriches.[78] Gyrocotylideans have a larva with 10 equal-sized hooks. They are parasites of the spiral intestine of Holocephali.

Gyrocotylidea have traditionally been placed with Amphilinidea in subclass Cestodaria of Class Cestoidea. Present opinion places them as the sister group of cohort Cestoidea in infraclass Cestodaria, and makes Cestodaria the sister group of infraclass Monogenea in subclass Cercomeromorphae.[16]

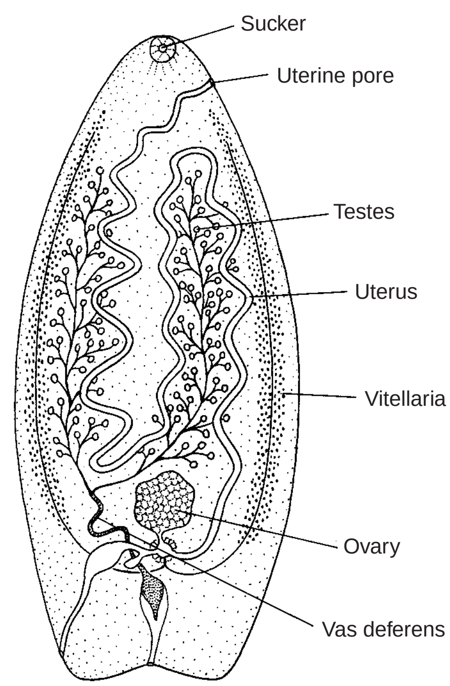


Figure 21.39 **The monozoic tapeworm *Amphilina foliacea*.**

Redrawn from R. A. Wardle and J. A. McLeod, *The Zoology of Tapeworms,* 1952, Hafner Publishing Co., New York, NY.

Learning Outcomes

By the time a student has finished studying this chapter, he or she should be able to:

1. Explain the differences among the various types of cestode larvae.

Figure 21.40 ***Gyrocotyle parvispinosa*** **from the ratfish *Hydrolagus colliei*.**
Courtesy of Warren Buss.

2. Explain the epidemiological significance of different kinds of cestode larvae, with emphasis on cysticerci and cysticercoids.
3. Describe the difference between a cysticercus and a cysticercoid.
4. Name a tapeworm with a cysticercus in its life cycle and one with a cysticercoid. What are implications for the epidemiology of each?
5. Understand and diagram the life cycle of *Diphyllobothrium latum, Dipylidium caninum, Taenia saginata, Taenia solium, Taenia asiatica, Echinococcus granulosus, Hymenolepis diminuta, H. nana, Bertiella studeri,* and *Bertiella mucronata,* including the source(s) of human infection for each.
6. Tell which of the aforementioned has been the most thoroughly studied tapeworm in laboratories. Why?
7. Which of the aforementioned is the most common cause of sparganosis in humans? Of cysticercosis?

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