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Cestoda

Introduction to Cestodes (Class Cestoda)

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Phylum Platyhelminthes

Class Cestoda

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Chapter 16

Introduction to Cestodes (Class Cestoda)

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Introduction

Cestodes, also called tapeworms, are **acoelomate**, meaning that they do not have a body cavity lined with tissue derived from the embryonic **mesoderm**, and their bilateral symmetry, well-organized reproductive, osmoregulatory, nervous, and reproductive organs, place these animals in the monophyletic phylum Platyhelminthes. The name Cestoidea was established for these animals by Rudolphi (1809), although many current treatments refer to the class Cestoda, which is used here. Relatives of the class Cestoda include the digenetic trematodes, the Turbellaria, and the sister taxon to the cestodes, the Monogenea.

Cestodes have long excited in humans a sense of bewilderment, fascination, and sometimes even fear, because they seem to appear spontaneously within a host and, when present, they are occasionally pathogenic in various ways. People's interest in them may also be due to the fact that they are ubiquitous. Nearly every species of vertebrate examined by biologists has been shown to host 1 or more species of cestodes. Since there are about 68,000 known species of vertebrates, and only around 4,800 species of cestodes yet been described, it follows that an immense number of cestode species is yet to be discovered.

In addition to Rudolphi, the pioneering works of Karl von Siebold, Friedrich Küchenmeister, Rudolf Leuckart, Maximilian Braun, Constantin Janicki, Friedrich Zschokke, Gerald D. Schmidt, Robert Dollfus, Marietta Voge, Alekseĭ Andreevich Spasskii, Lidija Petrovna Spasskya, Masashi Ohbayashi, and others laid the foundation for the study of tapeworms, or **cestodology**. A vast literature on this group has accumulated through the years; even so, much remains unknown, and work to discover the diversity of cestodes is urgent. Due to varied pressures, such as anthropogenic deforestation, desertification, and general overharvesting and obliteration of nature—just as is true for species considered to be charismatic megafauna—more species of cestodes may be lost due to extinction than science is able to discover each year.

Morphology of Tapeworms

Although considerable variation of morphological characteristics occurs among different orders of cestodes, there are underlying **synapomorphies** that unite the various orders into the class Cestoda. The following generalized description is supplemented within the text of this book, especially where specialization has modified the basic pattern. Tapeworms usually consist of a chain of segments called **proglottids**, each of which contains 1 or more sets of reproductive organs although some species are **monozoic**. The proglottids are continuously produced near the anterior end of the animal by a process of **asexual budding** also called **strobilization**. Each bud moves toward the posterior end as a new one takes its place, and during the process, the budding segment or proglottid becomes sexually mature. This means that the segment has the full complement of male and female sex organs but does not yet have eggs (see Figures 1 and 2A). The **gravid** (meaning, full of eggs; see Figures 2B and 2C) or senile **terminal segments** either shed their eggs directly into the intestine (**anapolytic**) and then they eventually detach, or they may detach while still full of eggs (**apolytic**) and either disintegrate in the intestine leaving the eggs or the segments to exit the host digestive system in the feces. Sometimes the segments exit the body and begin to crawl away from the pile of feces. The entire body of a cestode consisting of repeating segments is called the **strobila** (see Figure 3A), and a segmented strobila is said to be

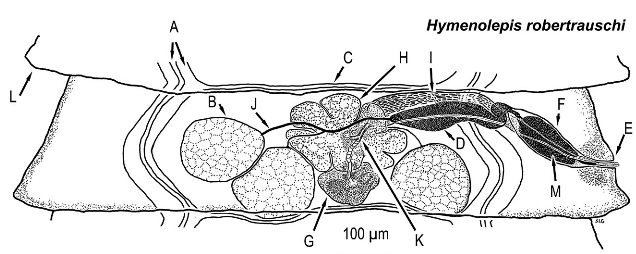

Figure 1. Mature proglottid (segment) of *Hymenolepis robertrauschi* from a grasshopper mouse (*Onychomys* sp.) collected in New Mexico, United States. A) Osmoregulatory canals, small canal is dorsal; wider canal is ventral; B) testis, here 3 are visible and are a characteristic of species of the genus *Hymenolepis*; C) lateral osmoregulatory canal passing ventrally across segment; D) external seminal vesicle; E) cirrus; F) cirrus sac, also called cirrus pouch; G) vitelline gland; H) ovary: I) seminal receptacle, J) vas efferens; K) ootype; L) vellum of segment. Source: S. L. Gardner, HWML. License: CC BY.

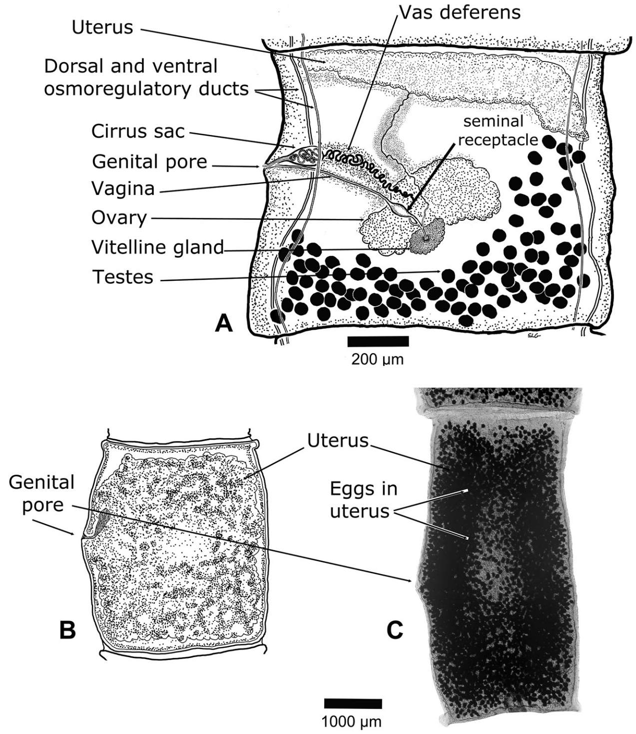

Figure 2. General structure of a craspedote tapeworm of the genus *Mathevotaenia* showing mature and gravid segments, also called proglottids. A) A fully mature proglottid showing male and female sex organs showing the longitudinal excretory ducts, testes, genital pore, cirrus sac, vitelline gland, lobed ovary, and seminal receptacle. The vasa efferentia (tubules that run from each testis to the vas deferens) are not shown; B) the gravid proglottid with eggs in the early stages of development; C) the terminal and fully gravid proglottid showing eggs filling the uterus. This species was collected in 1984 and described in 2023. Source: Adapted from Gardner and Grappone, 2023. License: CC BY.

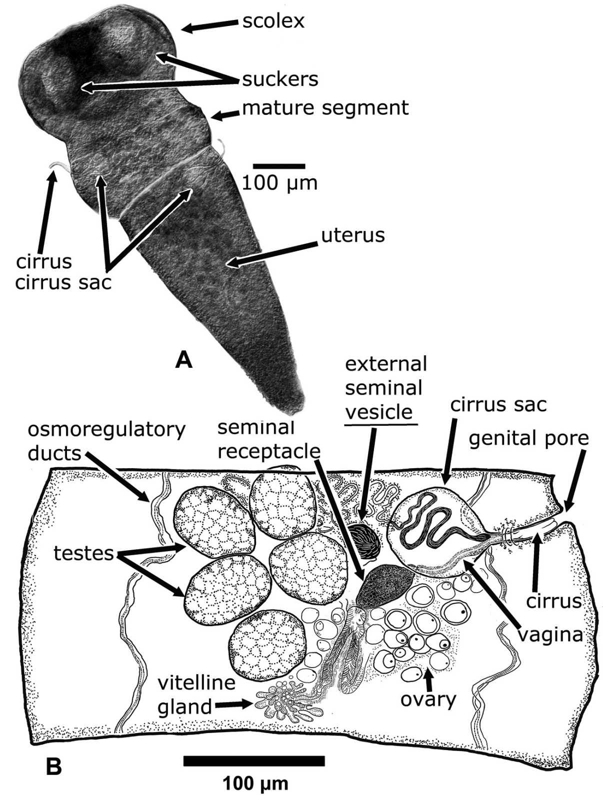

Figure 3. *Pritchardia boliviensis*. Known individuals of this species represent examples of a very small tapeworm, which as an adult has only a scolex and 3 discernible segments: One pre-mature segment, 1 mature segment, and 1 gravid segment. A) Photomicrograph of a whole animal; B) drawing of a mature segment of this same species with structures labeled. These cestodes are common in the small intestines of the small marsupials in the Andean foothills of South America but are very difficult to discover as they must be obtained from recently-collected mammals. Source: Adapted from Gardner et al., 2013. License: CC BY.

polyzoic. In some groups of cestodes, the body consists of a single segment, and is then said to be **monozoic**. If each proglottid or segment overlaps and is wider at the posterior part than the anterior part of the following segment, the whole strobila is said to be **craspedote**, if not, it is called **acraspedote**. Often, between the holdfast organ, called the **scolex** (Figures 3A, 4A, 6A, and 7B), and the first segments of the strobila there is a smooth, relatively undifferentiated zone called the **neck**. This may be long or short, or absent altogether. The neck, or in its absence the posterior part of the scolex, contains **germinal cells** that have the potential for budding of the segments, a process called **strobilization**. The compact germinal cells visible in the nascent proglottids are called the **anlagen**.

There is usually a scolex at the anterior end that is the principal means of attachment or locomotion of these animals. Depending on the group, the scolex may have suckers, grooves, hooks, spines, glandular areas, or combinations of these. In some instances, the scolex is quite simple, lacking any of these specializations, or it may be absent altogether. In a few species it is normal for the scolex to be lost and replaced in function by a distortion of the anterior end of the strobila; this called a **pseudoscolex**. A few species are capable of penetrating into the gut wall of the host where the scolex, and sometimes a considerable length of strobila, are encapsulated by host immune reactions, while the remainder of the strobila dangles into the lumen of the gut.

Following are descriptions of the organ systems of cestodes. Since the taxonomy of cestodes is based primarily upon the anatomy of the reproductive organ systems, an understanding of these systems, particularly, is essential to have a clear understanding of these interesting animals.

Organ Systems

Nervous system

The nervous system appears to be a modified ladder-type, with a **longitudinal cord** near each lateral margin and **transverse commissures** in each segment. The 2 lateral cords are united in the scolex in a complex arrangement of ganglia and commissures. The nervous system is rarely used as a **taxonomic character**, although the lateral cords are convenient points of reference for the location of other structures. There are abundant characters of the nervous system of these animals that can be used for morphological descriptive and comparative purposes, but few authors use these characters for this purpose.

Osmoregulatory system

As in other groups of worms in the phylum Platyhelminthes, the organ of osmoregulation is the **protonephridium**, or **flame cell**. These unicellular glands remove excess fluid from the **parenchyma tissues** and discharge this fluid from the body by a series of **collecting tubules**. The largest of these tubules are called the **osmoregulatory** or **excretory canals** (Figures 2A and 3B) and are typically of two pairs, one ventrolateral and the other (usually smaller) dorsolateral on each side. These canals may be independent throughout the strobila or may **ramify** and **anastomose** in each proglottid. Commonly, a transverse canal near the posterior margin of each segment unites the ventral canals while the dorsal canals remain simple. The dorsal and ventral canals join in the scolex, usually in association with complex branching, sometimes associated closely with the posterior part of the **apical organ** or the **rostellar pouch** (Figures 4A and 4C) depending on the species. Posteriad, the 2 pairs of canals unite into an **excretory bladder** with a single pore. In polyzoic species this bladder is lost with the detachment of the **terminal proglottid**, and thereafter the canals empty independently at the end of the strobila. In a few instances the major canals also empty through short, lateral ducts. The major function of the osmoregulatory system seems to be water balance, but some excretion of metabolic wastes also probably occurs. The dorsal canals carry fluid anteriad toward the scolex and the ventral canals carry fluid posteriad. Occasionally, the dorsal canals are absent. The arrangement of major canals is of taxonomic importance.

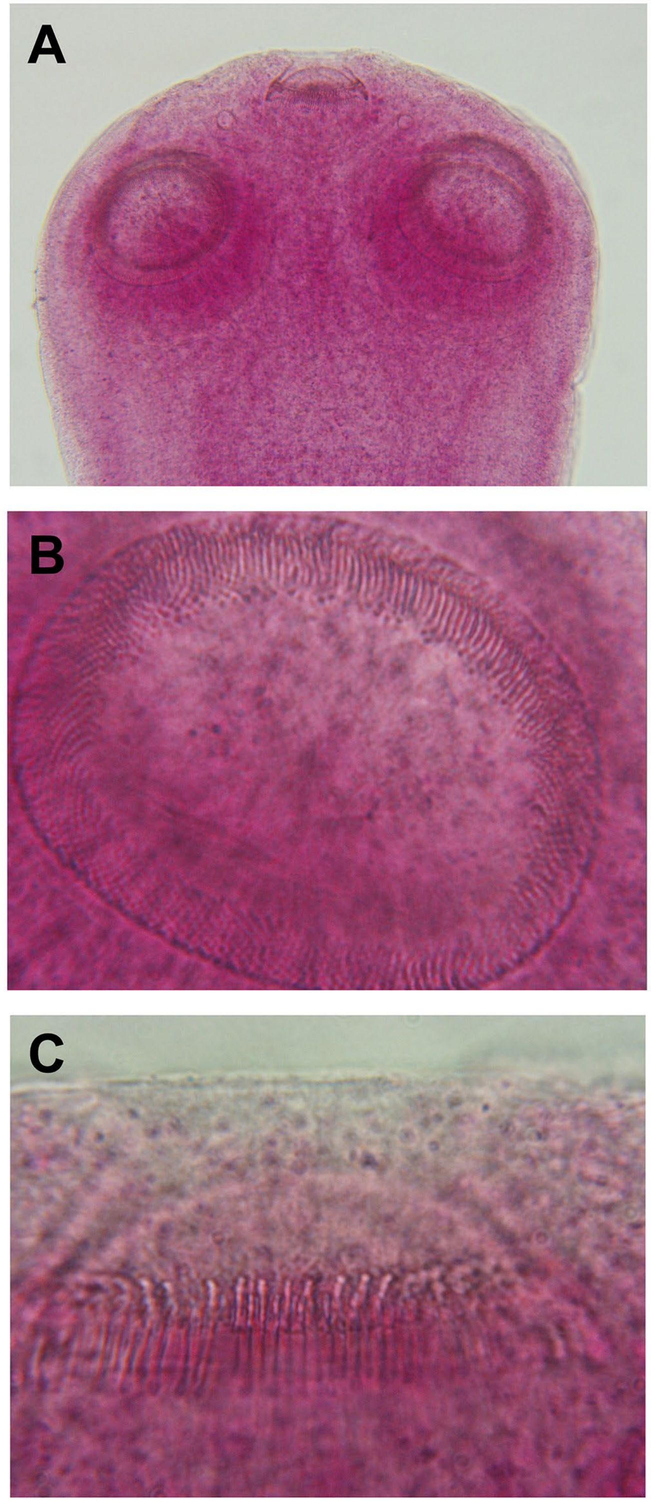

Figure 4. A) A species of *Raillietina* with hooks visible on the retracted rostellum and small hooklets visible on the suckers; B) a highly magnified view of one of the suckers showing the small hooks arranged around the margins of the sucker; C) a closer look at the hooks arranged around the rostellum of the scolex; they alternate long and short and are about 20 µm-long and 2 µm in maximum width. Source: S. L. Gardner, HWML, 2023. License: CC BY.

Muscular system

Most cestodes possess well-defined, longitudinal bundles of muscle fibers along with scattered dorsoventral groups of muscles. The scolex is well supplied with muscles and nerve fibers, making it extraordinarily motile. In the strobila, the

Figure 5. Larva of *Hymenolepis diminuta* (Rudolphi, 1819) grown from an experimentally infected *Tenebrio molitor* Linnaeus 1758. The scolex can be seen inverted in the enter of the larva. Stained in Semichon's acetic carmine and counterstained with fast green, mounted on a microscope slide in Canada balsam. Source: S. L. Gardner, HWML. License: CC BY.

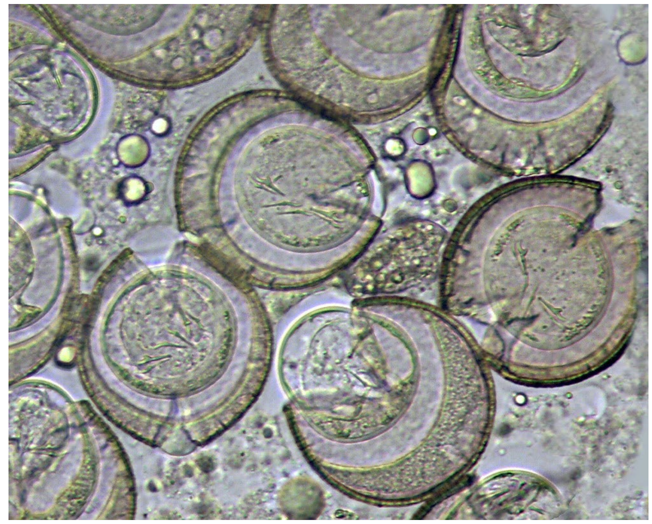

Figure 6. Eggs of *Hymenolepis weldensis* Gardner and Schmidt, 1988 from a Sandhills pocket gopher (*Geomys lutescens* Merriam 1890) from near Cedar Point Biological Station, near Ogallala, Nebraska, United States. The eggs were imaged after they were removed from the gravid uterus of a living tapeworm. The eggshells cracked under pressure of the coverslip while on the microscope slide. The larvae, or **embryophores**, can be seen pushing out of the eggs. In this stage, the embryos are motile and the hooks can be seen thrusting and trying to penetrate the intermediate host, which is probably a beetle of the family Tenebrionidae, although the life cycle is still unknown for this species. Source: Adapted from Gardner and Schmidt, 1988. License: CC BY-NC-SA 4.0.

longitudinal muscle bundles often are arranged in a definite layer within the parenchyma, dividing it into a well-defined cortex and medulla. The arrangement of these muscles is of taxonomic importance but is not much used for this purpose.

Reproductive systems

Almost all known cestodes are **monoecious**, or **hermaphroditic**, with the exception of a few species from birds and stingrays, which are **dioecious** or **gonochoristic**. Most commonly, each proglottid, or segment, contains 1 complete set each of male and female reproductive organs, although a few species have 2 complete sets in each segment, and some have many. A few rare species in birds have 1 female and 2 male sets in each proglottid. After its origin in the neck, and as the segment moves toward the rear of the strobila, as described above (Figures 1, 2, and 3), the reproductive organs mature and **embryonated** eggs are formed. Most commonly, the male organs mature first and produce sperm, which are stored until maturation of the ovary. Early maturation of the testes is called **protandry** or **androgyny** and is used as a taxonomic character. In fewer species the ovaries mature first which gives rise to a condition known as **protogyny** or **gynandry**. This is also used as a taxonomic character.

Male reproductive system.

Depending on the species, the male reproductive system (Figures 1, 2, and 3) may have as few as 1 up to many hundreds of **testes**, each of which has a fine **vas efferens** that transmits sperm toward the **genital pore**. If there are numerous testes, these vasa efferentia unite into a common **vas deferens** which enables transfer of sperm toward the genital pore. The vas deferens may be a simple dilation, or it may expand into a spheroid, often pear-shaped, or piriform external seminal vesicle or it may be highly convoluted, with the convolutions functioning in sperm storage. Eventually, the vas deferens leads into a **cirrus pouch** or **cirrus sac**, which is a muscular sheath containing the terminal portion of the male system. Depending on the species of cestode, inside the cirrus pouch, the vas deferens may form a convoluted ejaculatory duct or form an expanded internal seminal vesicle. Distally, the duct is modified into a muscular cirrus,

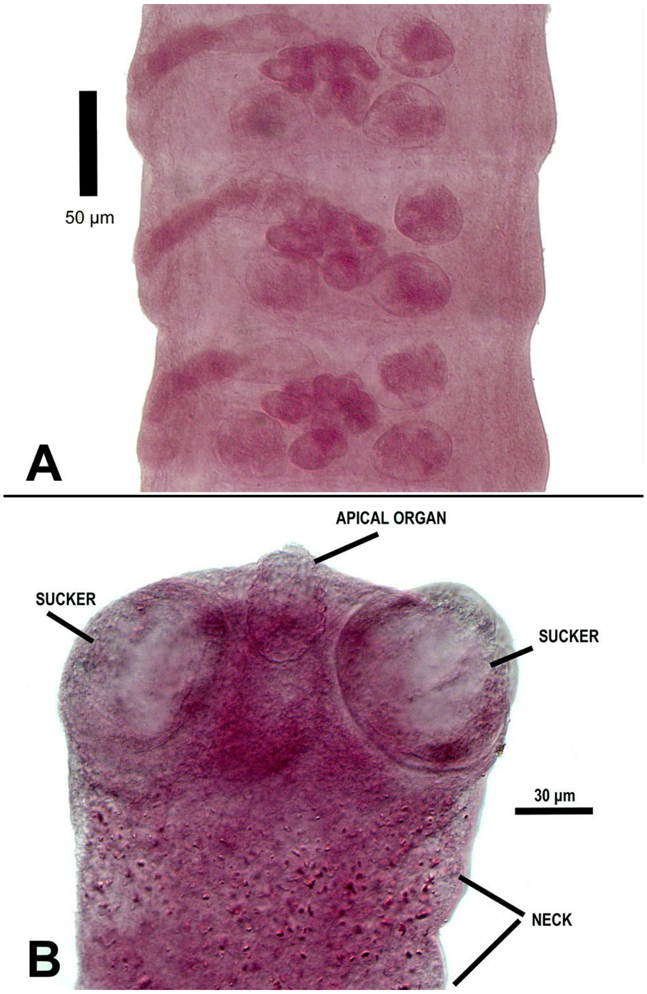

Figure 7. A) Example of a cyclophyllidean cestode in the family Hymenolepididae (*Hymenolepis tualatinensis* Gardner, 1985); B) scolex of the same specimen. Source: S. L. Gardner, HWML. License: CC BY.

the male copulatory organ. The cirrus may be spinous or not and may vary considerably in size, including length and diameter, among species. The cirrus can **invaginate** into the cirrus pouch and **evaginate** through the **cirrus pore**. Often, the male and female genital pores open into a common depressed chamber called the **genital atrium**. This atrium may be simple, or armed with a variety of spines, stylets, or hooks and may be glandular or possess accessory pockets. Also, depending on the species, the cirrus pore or the **atrial pore** may open on the margin or somewhere on a flat surface of the proglottid.

Female reproductive system.

The female reproductive system consists of a single **ovary** which may be large or small, compact or diffuse, and may be located almost anywhere within the proglottid, depending on the species. Associated with the ovary are **vitelline cells**, or **vitellaria**, which contribute to eggshell formation and nutrition for the developing embryo. These may be in a single compact vitellarium called the **vitelline gland** or scattered as follicles in various patterns. After an ovum matures in the ovary it leaves the ovary through a single **oviduct** that may have a controlling sphincter, the **ovicapt**. Fertilization of the ovum usually occurs in the proximal oviduct. Cells from the vitelline glands pass through a common vitelline duct, sometimes equipped with a small vitelline reservoir, and join with the fertilized ovum that is now called a **zygote**. Together they pass into a zone of the oviduct surrounded by unicellular glands called **Mehlis' glands**. The lumen of this zone is known as the **ootype**. The Mehlis' glands secrete a very thin membrane around the zygote and associated vitelline cells. Eggshell formation is then completed from within by the vitelline cells. Leaving the ootype, the developing egg passes into the **uterus** where embryonation is completed and a larval cestode comes into being.

The form of the uterus varies considerably among groups and may consist of a simple or convoluted tube, a reticular, lobated or simple sac, or may be replaced by other structures. In some groups the uterus disappears and the eggs, either singly or in groups, are enclosed within hyaline egg capsules imbedded within the parenchyma. In other groups one or more fibro-muscular structures, the **paruterine organs**, form within and attached to the uterus. In this case the eggs pass from the uterus into the paruterine organs, which assume the function of a uterus. The uterus then usually disintegrates.

Eggs (Figure 6) are released from the worm through a preformed uterine pore in many groups. In others, the proglottid splits or fragments, thus releasing the eggs. In many apolytic species, the gravid proglottids detach from the strobila and are passed from the host, where they crawl about on feces or soil scattering eggs as they go. In most anapolytic species the eggs are first discharged, then the **senile segments** break off and are released from the strobila, either singly or in chains.

The female genital pore, also called the vaginal pore, usually opens near the cirrus pore and often, but not always, this is in the **genital atrium** that is the termination of both the male and female reproductive tracts. The vagina may be armed distally with minute spines and may have 1 or more sphincters along its length. Near the proximal end, usually close to the ovary, there is usually a dilation called the seminal receptacle that stores sperm received in copulation. From the seminal receptacle a duct continues into the ootype.

There is a dichotomy in number of eggs produced among species, some of which have a reproductive potential that truly staggers the imagination. Within the family Taeniidae, individuals of most species of *Echinococcus* produce only a few hundred eggs per day versus individuals of most species of *Taenia* that can produce hundreds of thousands, up to millions, of eggs per day (Moore, 1981).

Acknowledgement

This section was modified from Schmidt (1986).

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17

Eucestoda

Introduction to Cyclophyllidea Beneden in Braun, 1900 (Order)

Scott L. Gardner

Phylum Platyhelminthes

Class Cestoda

Subclass Eucestoda

Order Cyclophyllidea

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Chapter 17

Introduction to Cyclophyllidea Beneden in Braun, 1900 (Order)

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Introduction

Cestodes in the order Cyclophyllidea are the most-commonly encountered cestodes in amphibians, reptiles, birds, and mammals. Interestingly, they are mostly absent from fishes, with just a single species known from bony, or teleost, fishes, such as the elephant fish in Africa. In terms of diversity of species, the Cyclophyllidea is the largest order of all the cestodes with more species in this group than all other orders combined. As with most cestodes, almost all cyclophyllidean cestodes use an intermediate host as a necessary first step in their life cycle. In some species, the intermediate stages serve as an amplification stage in which a single egg of a cestode that is eaten by an intermediate host may proliferate into millions of potential larvae that will each grow into an adult cestode if the correct species of definitive host eats the infected intermediate host. This is common in the family Taeniidae. The characters of this group of animals are what most people relate to when they think of cestodes.

A character that serves to place a cestode firmly in the cyclophyllidean group is the presence of a **scolex**, or anterior holdfast, that usually has 4 simple, rounded suckers, arranged symmetrically, usually with 2 arranged dorsally and 2 arranged ventrally. There is usually a **rostellum** on the apical part of the scolex and, if the rostellum is present, it may or may not be supplied with **hooks**. The state of having hooks, in cestode parlance, is termed armed. There may be a neck, or not.

The strobila, or the repeating segments that make up the cestode, may be variable, but it usually has distinct **metamerism**, meaning repeating duplicated segments or **proglottids**. Most have segments or proglottids that are hermaphroditic, meaning that they have both male and female gonads in one segment. Some species may have a **strobila** that is all male and another separate strobila that is all female, this phenotype is called gonochoristic, but these species are relatively rare and occur in just a few species of shorebirds. The **genital pores** are usually found on the lateral surface of the segment, but in species of Mesocestoididae, the genital pore is ventral and centrally located in the segment.

The second main character that places a given species of cestode in the order Cyclophyllidea is the single, compact **vitelline gland** that is usually situated posterior to the ovary in the segment. Depending on the species, the uterus can be variable and can be a simple tube, a reticulated mass, or a paruterine organ. There is no uterine pore in individuals within the Cyclophyllidea.

List of Families

Mostly following Schmidt (1986), families of Cyclophyllidea include: **Mesocestoididae** Perrier 1897, **Dioecocestidae** Southwell 1930, **Progynotaeniidae** Fuhrmann 1936, **Taeniidae** Ludwig 1886, **Amabiliidae** Ransom 1909, **Acoleidae** Fuhrmann 1906, **Davaineidae** Fuhrmann 1907, **Hymenolepididae** Perrier 1897, **Catenotaeniidae** Spasskii 1950, **Dilepididae** Railliet et Henry 1909, **Anoplocephalidae** Cholodkovsky 1902, **Nematotaeniidae** Lühe 1910, **Dipylidiidae** Stiles 1896, **Paruterinidae** Fuhrmann 1907, and **Metadilepididae** Spasskii 1959. The most recent summary of the families of cestodes in the Cyclophyllidea by Mariaux and colleagues (2017) also includes the **Gryporhynchidae** Spasskii & Spasskaya, 1973.

Due to its potential for zoonotic infections, species in the family Taeniidae Ludwig 1886 are the most commonly studied and species from 2 genera from this family are discussed in some detail in the following sections, including both *Taenia* and *Echinococcus*.

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