Chapter 20 - Class Cestoidea: Form, Function and Classification

General

Cestodes differ from trematodes by the complete absence of an alimentary canal: no mouth, no gut, no anus. Thus, all nutrients are acquired through a specialized tegument. All cestoidea are endoparasitic, with sexually mature worms living in the alimentary tract and associated ducts of all classes of vertebrates. The larvae infect both vertebrates and invertebrates. The life cycle require one or two intermediate hosts, in each of which the tapeworm undergoes a specific phase of development.

Form and Function

The body of the typical cestode consists of 3 distinct regions: scolex, neck, and strobila.

Scolex

The scolex (pl. scolices), located at the anterior end, is the attachment portion, the morphology and dimensions of which are key features in identification of these worms. To facilitate attachment to the host’s intestinal wall, tapeworms utilize several types of structures on their scolices, the most common of which are suckers. In some groups, the holdfast function of the scolex is lost early in life, and the anterior end of the strobila becomes distorted into a pseudoscolex to function as a holdfast. Muscles in the scolex make possible the holdfast action of this organ.

The scolices of tapeworms are typically categorized as either acetabulate or bothriate, depending on the type of sucker present. An acetabulate scolex is characterized by the presence of 4 muscular cups sunk into the equatorial surface of the scolex. In addition to muscular cups, there may be accessory holdfast structures, such as hooks to help anchor the scolex to the host’s intestinal wall. In this case, the scolex is called an armed scolex.

These hooks are usually grouped at the apical end of the scolex on a protrusible rostellum.

A bothriate scolex is characterized by the presence of 2, or rarely 4 to 6, longitudinally arranged, shallow depressions called bothria (sing. bothrium).

Various types of glandular secretions are associated with the scolex of many tapeworms; they are proteolytic, adhesive, and/or stimulatory, depending on the species.
Neck

The neck is an unsegmented, poorly differentiated region immediately posterior to the scolex.
It contains stem cells that are apparently responsible for giving rise to new strobila
(= a series of proglottids)

Strobila

Strobila of cestodes is unique among the Metazoa.
As new proglottids are formed from the neck region, they push the older ones progressively posteriad, creating a chain of proglottids - the strobila.
The strobila consists of a linear series of “segments” called proglottids that contain sets of reproductive organs of both sexes.
The asexual process of forming segments is termed strobilation.
As each proglottid is shifted posteriad, its sexual reproductive system matures progressively.
This progressive maturity of the reproductive systems permits a loose subdivision of the strobila into regions of immature, mature, and gravid proglottids.
The reproductive organs in immature proglottids are visible but nonfunctional, while those of mature proglottids are fully functional.
At the posterior end of strobila are the gravid (egg-filled) proglottids.
Often the reproductive organs in gravid proglottids have atrophied.

In some groups the gravid proglottids detach from the other proglottids and are released with the host’s feces - apolysis.
The eggshells of these species are not resistant (e.g., to the digestive enzymes from the host).

In anapolytic species, eggs are released through a uterine or genital pore directly into the host’s intestine and, subsequently, also are discharged to the exterior in feces.
Most anapolytic tapeworms produce protective, tanned eggshells.

Tegument

The tegument of tapeworms is a syncytial epithelium.
The surface of the tapeworm tegument bears specialized microvilli known as microthrices (singl. microthrix) that project from the outer, limiting membrane of the tegument.
Each microthrix includes an electron dense, apical tip separated from the more basal region by a multilaminar plane.
These tips, applied to the host’s intestinal epithelium, not only provide resistance to the peristaltic movement of the intestine, but with each movement of the worm, agitate intestinal fluids in the immediate microhabitat, thus increasing accessibility of nutrient materials as well as flushing away waste products.
Covering the entire surface of the tegument is a layer of carbohydrate containing macromolecules - the **glycocalyx** - that serve several important purposes:

- protecting the parasite from host digestive enzymes
- enhancing nutrient absorption
- maintaining the parasite’s surface membrane

As in digeneans, the tegumental syncytium consists of 2 cytoplasmic regions, **distal** and **proximal**

The distal cytoplasm is replete with mitochondria, usually aligned in a broad, basal band, as well as several types of vesicles and scattered membranes

Glycogen granules are also present in this region of some species

The vesicles arise in the nucleated, proximal cytoplasm, or **cyton**, sunk deep in the parenchyma

The cyton region contains Golgi complexes, mitochondria, rough ER, and other organelles involved in protein synthesis and packaging

Underlying the distal cytoplasm are 2 layers of muscles, collectively known as the **tegumental musculature**

**Parenchyma**

The space enclosed by the tegument is filled with a spongy tissue known as **parenchyma**

In live tapeworms, fluid fills the spaces between the parenchyma cells

Parenchyma cells are the primary sites for synthesis and storage of glycogen

**Calcareaous Corpuscles**

Large numbers of concretions known as **calcareaous corpuscles** occur in the parenchyma of numerous cestodes

These spherical bodies, which are most noticeable in larval forms, consist of organic and inorganic components

The organic portion consists of DNA, RNA, proteins, glycogen, mucopolysaccharides, and alkaline phosphatase

The inorganic portion consists of calcium, magnesium, phosphorous, and traces of metals

It has been suggested that they may have any of the following functions:

- buffers against anaerobically produced acids
- serve as reservoirs for inorganic ions required during development
- act as enzyme activators
- be a form of excretory product of metabolism
**Nervous System**

The “brain” located in the scolex, is a rectangular or circular nervous tissue varying in complexity from a simple ganglion to a combination of several ganglia and commissures. It gives rise to short anterior and posterior nerves that richly support various portions of the scolex with more fibers and receive sensory fibers from rostellum, suckers, and tegument.

Several pairs of longitudinal nerve cords extend posteriorly from this “brain” along the length of the strobila, lateral to the osmoregulatory canals. The cords are connected in each proglottid by cross connectives, producing a ladder-like appearance.

Small motor nerves emanating from the cords and cross-connectives innervate the reproductive organs and musculature, while small sensory nerves supplying the tegument merge with the cords and connectives.

Certain organs of both the scolex and the proglottids, such as parts of the reproductive system and suckers, are more extensively innervated than other regions of the body.

**Osmoregulatory System**

The cestode osmoregulatory-excretory system is essentially the same as the flame cell system for other platyhelminthes.

In most cases, it serves to maintain within the worm an optimal hydrostatic pressure for extensory movements of the strobila and scolex. However, some tapeworms (e.g. *H. diminuta*) are actually conformers in that they cannot regulate internal osmotic pressure. Thus, in these species, the system is strictly excretory.

The osmoregulatory-excretory system consists of 2 components: the collecting canals and the flame cells.

Four laterally aligned **collecting canals** (2 dorsal and 2 ventral) extend the entire length of the strobila.

All 4 canals lie just inside the medullary margin of the parenchyma, and a single transverse canal connects the ventral canals at the posterior end of each proglottid. The ventral canals carry fluid away from the scolex, the dorsal canals toward it.

In some tapeworms, the 4 longitudinal canals are linked within the scolex by either a network of canals or a single ring of vesicles. In others, the dorsal and ventral canals on each side are linked by a simple connection in the region of the scolex, with no apparent exchange between the 2 sides.
In the terminal proglottid of young worms, there is an excretory vesicle into which the ventral canals empty. However, in older tapeworms that have sloughed the original posterior most proglottid, the posterior ends of the ventral canals open independently to the exterior.

Flame cells are associated with the ventral canals. Fluid connected by the flame cells passes through secondary tubules into the main canals. Analysis of fluid within the osmoregulatory system of certain species has revealed that its consists primarily of glucose, soluble proteins, lactic acid, urea, and ammonia.

Reproductive Systems

Tapeworms are, for the most part, monoecious; each proglottid usually has one complete set of both male and female reproductive organs. Most cestodes are protandrous; on rare occasion the female system is known to develop first - protogyny.

For the most part, the reproductive systems of cestodes resemble those of trematodes except:

- for the cul-de-sac uterus in some forms
- the presence of a separate vaginal canal
- and often a laterally situated genital pore

Male System

The male reproductive system consists of one to many testes. Emanating from each testis is a single vas efferens. The efferentia unite to form a common vas deferens, which is usually coiled.

The distal portion of the vas deferens are modified as a muscular cirrus, usually enclosed within a cirrus sac. In some species, the cirrus is equipped with spines that hold the organ in place during copulation. The cirrus everts through the male genital pore, which in turn, opens into the common genital atrium. In most species there is an enlarged area of the vas deferens, the seminal vesicle, for the storage of sperm. When located within the cirrus sac, it is designated an internal seminal vesicle. Located outside the sac, it is termed an external seminal vesicle. Some species possess both.
Female System

Ova are produced in a single, sometimes bi-lobed ovary. Following fertilization in the proximal portion of the oviduct, the resulting zygote passes into a region of the oviduct, the ootype, equipped with structures involved in eggshell formation similar to those of digeneans. A Mehlis’ gland surrounds the ootype and secretes into it material essential to the formation of the egg shell.

A single common vitelline duct enters the oviduct in the vicinity of the ootype. Vitelline duct is formed by the union of many primary vitelline ducts arising from vitelline glands, which vary in size and location according to species. With few exceptions, secretions from the vitelline glands contain shell precursors as well as provide nourishment for developing larva.

The vagina, a tubular organ that joins the oviduct at the level of Mehlis’ gland, carries sperm from the genital atrium to the oviduct, and fertilization occurs in the region where the vagina and oviduct join. Sperm is stored in an enlargement of the vagina known as the seminal receptacle. The oviduct continues as the uterus, which in some tapeworms (e.g. Pseudophyllidea) opens to the outside of the proglottid through a uterine pore. Eggs are expelled through this opening. In other species (e.g. Cyclophyllidea) the uterus is a blind sac in which developing eggs accumulate.

The uterus becomes distended with eggs, filling the medullary region of the proglottid. And this gravid proglottid later becomes detached from the strobila and is discharged from the host.

The Egg

The oncosphere (larvae within the egg), containing 3 pair of hooks, is encased in an inner envelope that in turn is surrounded by another membranous structure, the embryophore. A cellular zone known as the outer envelope lies between the embryophore and the shell (capsule), usually the outer most covering of the egg.

Tapeworm eggs exhibit certain variations on this basic theme and can be classified into 4 types: 1) Pseudophyllidean, 2) Dipylidium, 3) Taenioid and 4) Stilesian.

1. The Pseudophyllidean egg (e.g. Diphyllobothrium) is similar in many respects to the egg of digeneans. The fully developed egg has a thick, quinone-tanned shell, usually with a lid-like operculum at one end. Numerous vitelline cells are associated with the zygote, providing stored food for subsequent development.
The zygote develops into an oncosphere, which is covered by a ciliated embryophore that enables it to swim upon hatching. This form of organism is called a **coracidium** (pl. coracidia). 

2. The **Dipylidean** egg (e.g. *Dipylidium* and *Hymenolepis*) possesses a thin shell, a thin nonciliated embryophore, and a relatively thick outer envelope. 

3. In the **taenioid** egg (e.g. *Taenia* and *Echinococcus*) the shell and outer envelope are lacking, and the thick, nonciliated embryophore constitutes the outermost covering. 

4. The **Stilesia** type, is formed by species with no distinct vitellaria. The cellular cover is laid down by the uterine wall. 

**Life Cycle Patterns**

**Pseudophyllidean Pattern**

In this order, eggs containing coracidia leave the host with the feces to water. The coracidium escapes from the eggshell through the operculum and swims for a brief time by means of its ciliated embryophore.

Survival of the organism depends on the coracidium being ingested by the first intermediate host - an aquatic arthropod - within which the embryo sheds its ciliated embryophore and metamorphoses into a globular procercoid in the hemocoel.

During this development, the oncosphere hooks are retained, albeit nonfunctionally, in a tail-like structure called the cercomer.

When the first intermediate host is ingested by a second intermediate host, usually a fish, the procercoid migrates via the peritoneal cavity to various parts of the body, primarily the musculature, where it grows and develops into a solid, vermiform plerocercoid that shows the beginning of strobilation and a self-formed adult scolex.

The plerocercoid is infective to the definitive host. When ingested, it attaches to the wall of the small intestine, where strobilation occurs.

**The Cyclophyllidean Pattern**

Adapted as it is to terrestrial hosts, the oncosphere (also called a **hexacanth** because it possesses 3 pairs of hooks) of this order lacks a ciliated embryophore and must remain passive until the egg is ingested by a vertebrate or invertebrate host.
In species that normally utilize an invertebrate host (e.g. an arthropod) the oncosphere upon hatching in the digestive tract, employs its hooks and its penetration glands to enter the hemocoel, where it metamorphoses into a cysticercoid. This form is solid-bodied and possesses a fully developed acetabulate scolex. It is surrounded by several layers of cystic tissue and has a prominent cercomer containing hooks. The cystic tissue and cercomer are digested away in the digestive tract of the definitive host, freeing the scolex and neck to begin strobilation.

In species that utilize vertebrate intermediate hosts, the oncosphere, after ingestion, penetrates the intestinal lining and enters a venule. It is carried by the blood to any of several areas of the body where it develops into a cysticercus with an acetabulate scolex invaginated into a fluid-filled vesicle or bladder. Thus, the common name bladderworm.

Two other forms that follow this developmental pattern are the coenurus and the hydatid cysts. In the former, the wall of the bladder develops several invaginated scolices. In the latter, secondary cysts are formed as invaginations on the walls. These second generation cysts are called brood capsules since they, in turn, give rise to scolices, each of which, when ingested by a suitable definitive host, can develop into an adult worm.

**Physiology**

The adaptive morphology of adult tapeworms and the environment in which they occur are probably the most significant factors influencing their physiology. Lacking a digestive tract, these worms must derive all nutrient molecules from the host or its microhabitat, and such molecules must cross the tegument. The methods by which nutrients cross the tegument include active transport, facilitated diffusion, and simple diffusion.

The most important nutrient molecule is glucose, which after polymerization within the parasite, is stored as glycogen usually in the parenchyma and interstitial fluid. The only other major, transported carbohydrate is galactose.

The environment in which tapeworms reside (the small intestine) is one of very low oxygen tension, necessitating anaerobic metabolism. Considering the intestinal environment, it is not surprising that most energy is derived by substrate phosphorylation via glycolysis. Some tapeworms possess a mammalian type electron transport system but its role in energy production is minor.
Metabolic rates differ in different parts of the strobila. The neck and immature proglottids have a much higher rate of metabolism than the mature and gravid proglottids, reflecting the high-energy requirements for new proglottid formation and organ development. Most of the energy requirement in mature proglottids is for egg production.

**Treatment**

In most instances, adult tapeworms have little visible effect upon their hosts except in heavy infections, which may result in anemia, weight loss, and various secondary manifestations. The treatment of choice for all tapeworms infecting the small intestine of humans is essentially the same and consists of oral administration of the drug niclosamide, which disrupts proglottids and interferes with the worm’s substrate phosphorylation processes, depriving it of required ATP. Praziquantel has also been used and has the same effect as niclosamide. In addition, this drug causes vacuolization of the tegument and rapid paralysis of the worm’s musculature. Two other drugs, quiniacrine HCl and aminocrine, have also proven effective in treating infections.

**Origin**

One evolutionary scheme proposes that they arose from a stock of aquatic, free-living, bottom-dwelling protonomonogeneans that, in turn, evolved from a rhabdocoel-like ancestor similar to the ancestral form suggested for digenetic trematodes. The immediate ancestors of modern tapeworms evolved adhesive organs that enabled them to become attached to, and subsequently ectoparasitic upon, bottom-dwelling vertebrates. Some representatives of this population migrated internally to the gut of these vertebrates and became endoparasitic.

To survive in that hostile environment, these organisms evolved protective modifications, such as a glycocalyx on the body surface and resistant quinone tanned eggshells. Such modifications enabled them to resist the actions of the host’s digestive enzymes.

They also underwent physiological adaptations that enabled them to survive in an environment with reduced oxygen tension. At least one branch of these monozoic animals evolved additional modifications, such as the loss of a gut, development of anterior attachment organs, and duplication of reproductive structures (leading to segmentation of the body).