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Gyrocotylidea

Gyrocotylidea (Order): The Most Primitive Group of Tapeworms

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Phylum Platyhelminthes

Class Cestoda

Subclass Cestodaria

Order Gyrocotylidea

doi:10.32873/unl.dc.ciap032
2024. *In* S. L. Gardner and S. A. Gardner, eds. Concepts in Animal Parasitology. Zea Books, Lincoln, Nebraska, United States.

Chapter 32

Gyrocotylidea (Order): The Most Primitive Group of Tapeworms

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Background

Gyrocotylidea is an order of parasitic flatworms comprising about 10 known species belonging to 2 genera, *Gyrocotyle* and *Gyrocotyloides* (although there has been much confusion about species identities; see, for example, Bristow, 1992). They are about 2–10 cm in length and are exclusively found in the spiral valve (spiral intestine) of Holocephali, a group of marine chondrichthyan fishes called chimaeras or ratfishes, which live in both the deep sea and cold surface marine waters. Like all tapeworms, species of Gyrocotylidea lack an intestinal tract in all developmental stages, have a neodermis with regularly shaped microtriches which are small villi-like protrusions on the external part of the tegument that probably serves to increase the absorptive surface area of the animal (see Poddubnaya et al., 2006), and a reticulate excretory system. Like the Amphilinidea, individuals have 10 posterior hooks (present only in the larvae), and a single set of reproductive organs but no proglottids (no segmentation) characteristic of almost all eucestodes (which are the genuine, or the true, tapeworms). Together with the Eucestoda and Amphilinidea, they form 1 monophyletic group (derived from a common ancestor), the Cestoda (tapeworms) (Ehlers, 1985; see also Littlewood et al., 1999; Xylander, 2001). Recent molecular studies have confirmed morphological indications of the monophyly of the Neodermata and the sister group relationship of the Gyrocotylidea to all other Cestoda (Park et al., 2007; Waeschenbach et al., 2012; Egger et al., 2015; Littlewood et al., 2015; Waeschenbach and Littlewood, 2017; list of morphological characters in Xylander, 2001).

Interestingly, these animals are not of any economic importance but have baffled biologists because of some unique morphological and biological features (Simmons, 1974). For a brief overview of the group see Rohde (2007) and Kuchta and colleagues (2017), and for a more detailed account, see Xylander (2001; 2006a).

Structure of the Adult

The outer surface layer of adult gyrocotylideans is a **neodermis**, that is, a syncytial non-ciliated body covering which replaces the ciliated epidermis of the larva after start of their life as parasites (Xylander, 2001). Larvae and adults lack an intestine. The **attachment organ** is located at the posterior end; in species of the genus *Gyrocotyle* (Figures 1–3) it increases in size and shape from a primitive cup-like structure in earliest intestinal stages to a ruffled structure, the so-called **rosette** (Halvorsen and Williams, 1968). With this structure the worms attach to the intestinal microvilli of their hosts. In the genus *Gyrocotyloides*, the **holdfast** is cup-like and located on a **caudal stalk**. A so-called **funnel** in the posterior part of the body opens dorsally through a pore; its function is unknown (it possibly contributes to attachment). The protonephridial system of the adult consists of **flame bulbs** (also called **flame cells**) and a **network of capillaries and ducts** which have ciliated tufts for transporting the excretory fluid and potentially nutrients (Xylander, 1992a). The paired **excretory pores** open not far from the anterior end.

Figure 1. *Gyrocotyle urna*, rosette left. Source: W. E. R. Xylander.

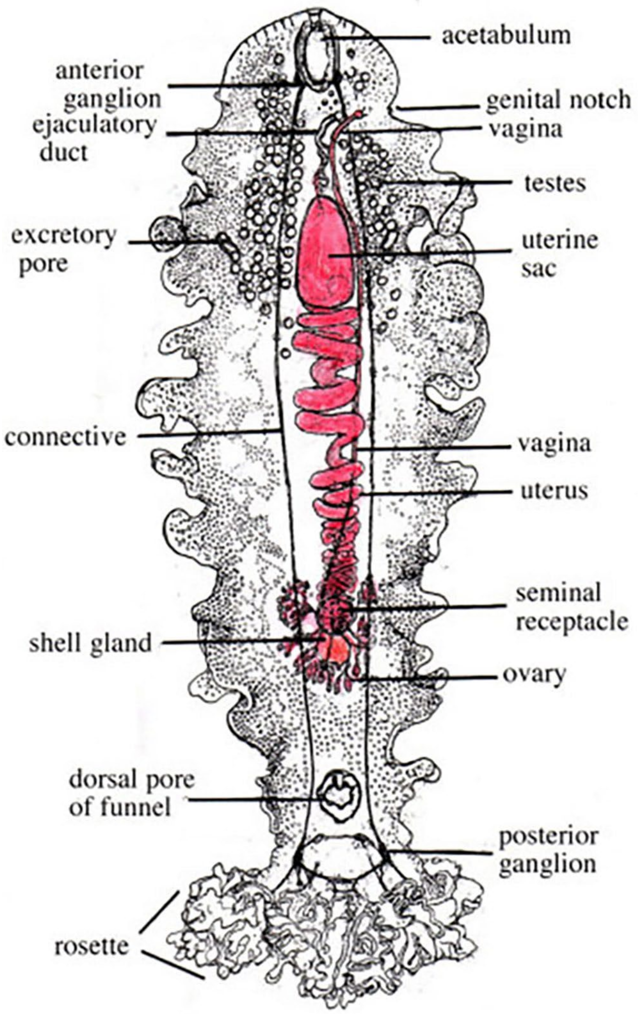

Figure 2. Adult *Gyrocotyle fimbriata*, dorsal view. Female reproductive system except vitellaria drawn red. Source: Adapted from Lynch (1945), Cheng (1986), and other sources. License: CC BY-NC-SA 4.0.

Figure 3. Scanning electron micrograph of the rosette of *Gyrocotyle* sp., probably *G. rugosa*, from the holocephalan *Callorhinchus milii* in Tasmania, Australia. Source: K. Rohde. License: CC BY-NC-SA 4.0.

Gyrocotylids are hermaphroditic. Follicular **testes** are located in the anterior part of the body and connect to **sperm ducts** (**vasa efferentia**) which unite to form 1 large sperm duct (**vas deferens**) whose terminal part is muscular forming an **ejaculatory duct**. It opens near the anterior end. The female reproductive system consists of a **germarium** (**ovary**) and a **vitellarium**. The ovary is located in the posterior part of the body and is composed of many **follicles**. The **oviduct**, into which the egg cells are discharged, leads to the **ootype** surrounded by the **Mehlis' gland**, into which or near which the **yolk ducts** and **vagina** open, as well. A very high number of **vitelline** (**yolk**) **follicles** are scattered throughout the body from the anterior to the posterior end (most are located laterally). The compound **eggs** (consisting of a single fertilized egg cell and many yolk cells surrounded by a shell originating from glands in the ootype, the Mehlis' gland and material discharged from the **vitellocytes**) are formed in the ootype. Fertilized eggs are stored for weeks in a large **uterine sac** and then are set free via a **uterine pore** near the anterior end. The vagina terminates at that point.

The main parts of the **nervous system** consist of an anteriorly located **brain** (or **cephalic ganglia**), large lateral **nerve cords** (and many **smaller nerves**) and large posterior **nerve ring** in the vicinity of the rosette. More than 10 different **sensory cells** have been found in mature *Gyrocotyle* specimens (Xylander, 1992b; Xylander and Poddubnaya, unpublished data).

Gyrocotylids, like all tapeworms, lack an intestine. Food must be absorbed by the neodermis. The neodermis is completely covered by regularly shaped typical tapeworm **microtriches** (Figure 4); these microtriches may be responsible for nutrient uptake, or may instead be involved in protection against the digestive enzymes of the host (Xylander, 2001).

For some recent ultrastructural studies see Poddubnaya and colleagues (2006; 2009; 2015), and Levron and colleagues (2016).

Structure of the Larva

The lycophora larva (decacanth) is about 0.2 mm-long and is completely surrounded by a syncytial ciliated **epidermis**

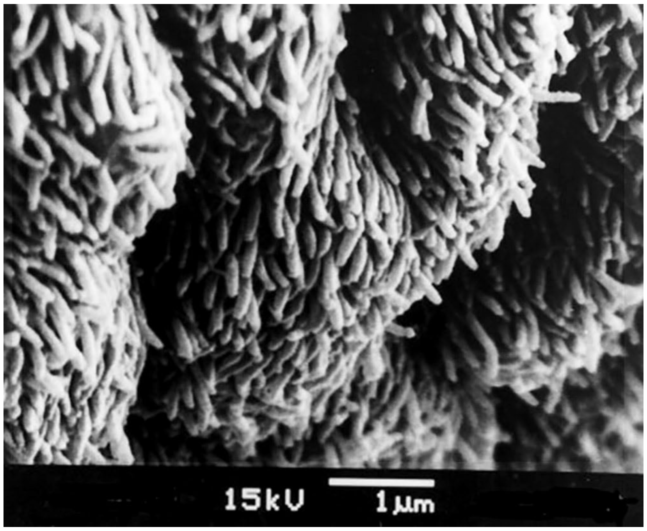

Figure 4. Scanning electron micrograph of the neodermis of *Gyrocotyle* sp., probably *G. rugosa,* from the holocephalan *Callorhinchus milii* in Tasmania, Australia. Note the numerous microvilli. Source: K. Rohde. License: CC BY-NC-SA 4.0.

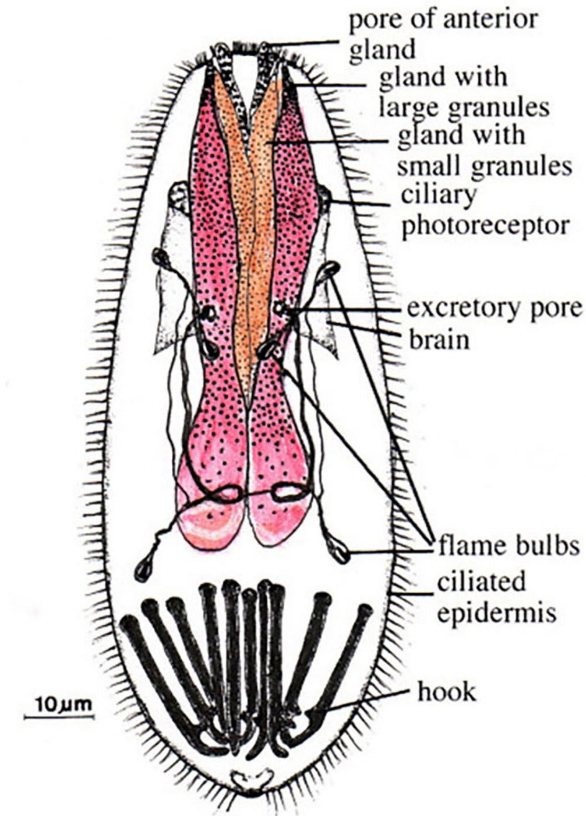

Figure 5. Lycophora larva of *Gyrocotyle urna*. Adapted from Xylander (1997c; 1990; 1991; 2001; 2006b) and Rohde (1994). License: CC BY-NC-SA 4.0.

(Xylander, 1987a). There are 4 pairs of **gland cells**, each pair with a different secretion extending from the posterior half of the body to the anterior body tip where they open (Xylander, 1990). Lycophores have a well-developed **brain**, at least 7 different ciliary **sensory receptors** (the majority at the anterior end) as well as a paired **photoreceptor** located at the anteriolateral margins of the brain (Figure 5, Xylander 1984; 1987b). Such a well elaborated nervous system is lacking in the larvae of more derived tapeworms (such as an oncosphere or coracidium). At the posterior end they bear 10 **hooks** resembling the hooks of oncomiracidia (Xylander, 1991). The **protonephridial** (excretory/osmoregulatory) system consists of 3 pairs of **terminal cells** connected to **capillaries**, which unite in 2 **ducts** terminating in **excretory pores** at the transition between the anteriormost to the middle-third of the body (Xylander, 1987c).

Life Cycle

The complete life cycle of all species of the Gyrocotylidea is still unknown. However, Xylander (1989; 2006a) has argued for a 2-host life cycle in Gyrocotylidea based on: 1) Even the earliest stages of *Gyrocotyle* found in the spiral valve show an anterior pit which develops in other tapeworms within the first (crustacean) intermediate host; and 2) infection of hosts is correlated with feeding. Young holocephali restricted to yolks are not infected, whereas young host specimens which have already preyed on invertebrates (mainly smaller crustaceans) very often are infected; so, it is highly probable that gyrocotylids do not infect a fish directly but that a (crustacean) intermediate host is involved in the life cycle.

The lycophora larva hatches from the egg after a maturing period of more than 30 days. In vitro, lycophores swim for about 24 hours before dying.

Host individuals are usually (but not always) infected by only one gyrocotylid species, but each holocephalan host species can harbor 2 species (though in *Chimaera monstrosa*, each can harbor 3 species), usually attached to different sites along their spiral valve. One of each species pair belongs to the *urna group*, and the other to the *confuse group*. The former has many marginal body undulations and very elaborate folds of the rosette, whereas the latter has a smaller rosette with fewer folds, a more elongate body, and less elaborate body undulations.

Unique to this group are the post-larvae which may be present in the parenchyma of larger gyrocotylids of the same species (see, for example, Halvorsen and Williams, 1968). They seem to disintegrate after a while; the biological function of this phenomenon is unclear. It may be an intraspecific regulation procedure to reduce the number of gyrocotylids per host; so, young hosts may harbor many, larger ones, but seldom more than 2 parasites.

Ecological and Economic Importance

As for pathogenic effects on hosts, inflammation of the epithelium of the spiral valve has been observed, but this observation is mostly restricted to heavily infected individuals. Due to the small number of species occurring in a host group (chimaeras) restricted to specific habitats and of low economic relevance, the group is unlikely to have any economic importance, and further, probably negligible ecological importance.

Acknowledgement

The authors wish to thank Tim Littlewood for information on latter developments in the phylogeny of parasitic platyhelminths including the gyrocotylids.

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