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Aspidogastrea

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Phylum Platyhelminthes

Class Trematoda

Subclass Aspidogastrea

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Chapter 33

Aspidogastrea (Subclass)

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Introduction

Trematodes (also sometimes called flukes) are one of the largest groups of platyhelminths (parasitic worms) with thousands of species. They comprise the Digenea and **Aspidogastrea**. Many species of digeneans have great economic or medical importance. The Aspidogastrea (= Aspidobothria, Aspidobothrea), in contrast, are a very small group of trematodes with around 60 species, none of them of economic importance. But they are of great interest because of their unique structure, their simple life cycles (which may well be the most primitive or ancestral one among the trematodes; Rohde, 1971a), and the extraordinarily complex sensory/nervous systems found in some species. Extensive lists of references of the group have been compiled by Rohde (1999; available at http://tolweb.org/Aspidogastrea/20399 and Alves et al., 2015).

Main Characteristics

The larvae always have a posterior **sucker**, and an anterior **pseudosucker**, or **false sucker**, may also be present, which is not separated from the surrounding tissue by a genuine connective tissue sheath (Figure 1).

Adults do not have a posterior or ventral sucker, but a ventral **adhesive disc** consisting of transverse grooves (**rugae**) and a single row of well-separated small **suckers** (**suckerlets**) or 3 to 4 rows of **alveoli** (**suckerlets**) on a ventral disc (see Figures 2–4).

Hosts include vertebrates and molluscs. In the molluscan host, there is no multiplication of larval stages, that is, a single egg produces a single adult.

All species of Aspidogastrea are hermaphroditic, that is, the adults possess male as well as female reproductive systems. This is demonstrated in the example below, in the

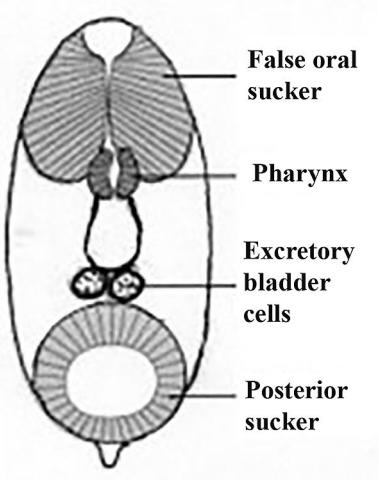

Figure 1. Larva of *Lobatostoma manteri*. Note the **false anterior sucker**, the **pharynx**, the **blind ending cecum**, and the 2 **excretory bladder cells**. The posterior end is drawn out into a short appendage of unknown function. Source: K. Rohde. License: CC BY-NC-SA 4.0.

Figure 2. Ventral view of *Rugogaster hydrolagi*, an aspidogastrean from the rectal glands of the elephant shark *Hydrolagus* in Tasmania, Australia. Note the row of **transverse grooves** (**rugae**). Source: K. Rohde. License: CC BY-NC-SA 4.0.

Figure 3. Part of the aspidogastrean *Multicalyx* sp, from the intestine of a shark. Note the single row of **alveoli** (**suckerlets**) separated by **transverse septa**. Source: K. Rohde. License: CC BY-NC-SA 4.0.

Figure 4. Scanning electron micrograph of the aspidogastrean *Lobatostoma manteri* from the intestine of the teleost fish *Trachinotus blochi*, ventral view. Note the **anterior head** and the **adhesive disc** consisting of 4 rows of **alveoli**. Source: K. Rohde. License: CC BY-NC-SA 4.0.

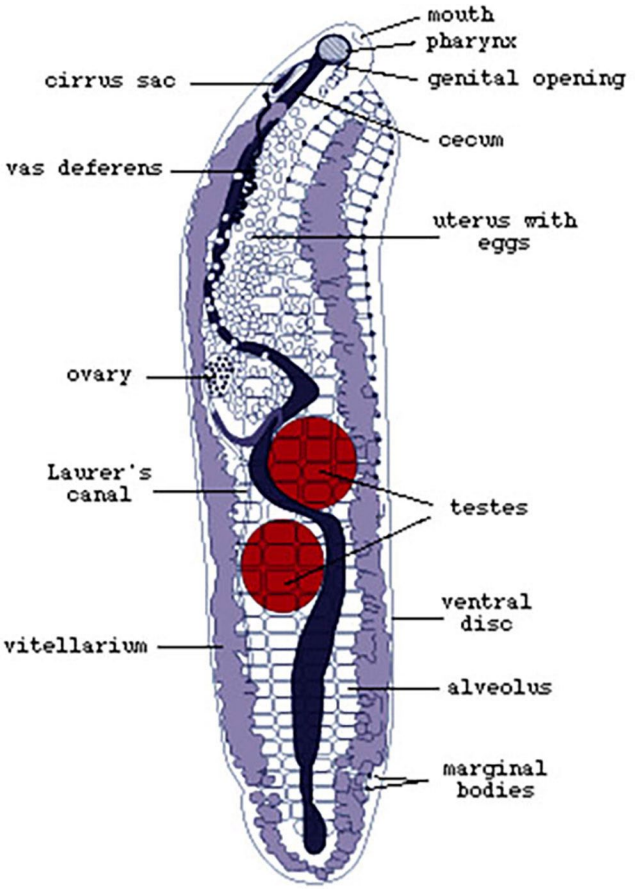

Figure 5. Adult *Multicotyle purvisi*. Note the single and blind ending **cecum** (**intestine**), the **ventral** (**adhesive**) **disc** consisting of 4 rows of **alveoli**, the **male genital system** consisting of 2 large **testes** opening into the **vas deferens** (**sperm duct**) and the **terminal cirrus pouch** (**copulatory organ**), as well as the **female genital system** with a single **ovary** and **vitellarium** (**yolk gland**). The common (to both the male and female systems) **genital opening** is located at the anterior end. The **marginal bodies** are located between the outer rows of **alveoli** and have a glandular function. **Laurer's canal** extends from the female reproductive system to the dorsal surface where it opens to the outside. Source: K. Rohde. License: CC BY-NC-SA 4.0.

image of *Multicotyle purvisi*, an aspidogastrean found in the stomach and intestine of freshwater turtles in Southeast Asia. It reaches a length of about 10 mm and contains both a fully mature male reproductive system as well as a fully mature and gravid female reproductive system (Figure 5).

Unique features of the Aspidogastrea include a septate **oviduct** (that is, the oviduct carrying the egg cells from the ovary has a number of concentric constrictions), and **marginal bodies**, which were long considered to be sensory in nature but are in fact secretory organs (Rohde, 1971d; Rohde and Watson, 1989b) (Figures 6 and 7).

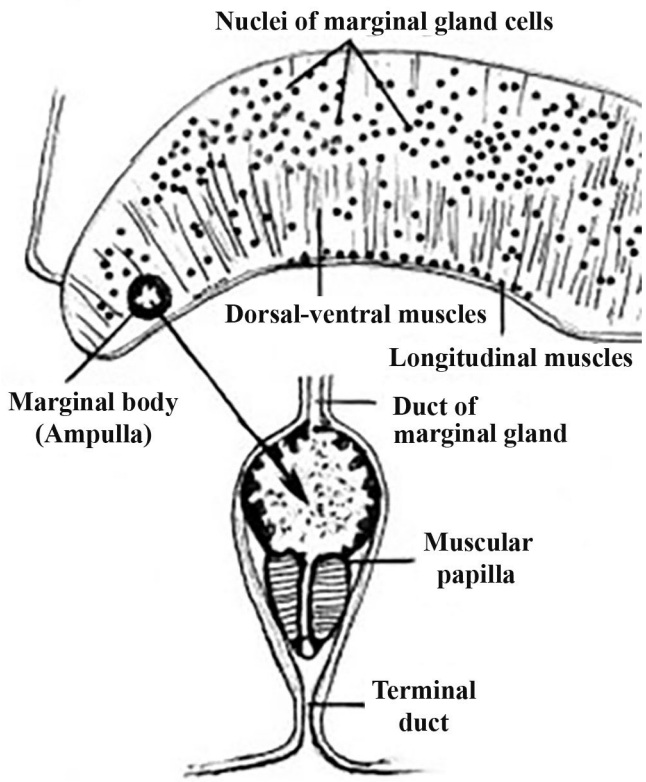

Figure 6. Cross section through the lateral part of the **adhesive disc** of *Lobatostoma manteri* showing the **nuclei** and the **terminal ampulla**, **papilla**, and **terminal duct** of a **marginal gland**. Source: K. Rohde. License: CC BY-NC-SA 4.0.

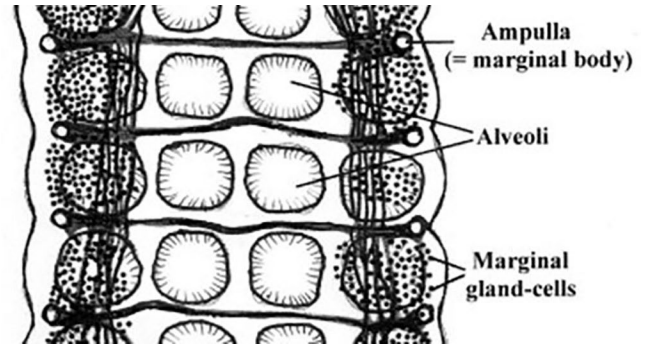

Figure 7. Ventral view of part of the ventral disc of *Lobatostoma manteri* showing the marginal glands and bodies connected by longitudinal and transverse ducts. Source: K. Rohde. License: CC BY-NC-SA 4.0.

Juvenile and Adult Sensory Receptors

Two species of Aspidogastrea in particular, *Multicotyle purvisi* from Malaysian turtles and *Lobatostoma manteri* from Australian marine fish, were examined using light microscopy, as well as scanning electron microscopy. It is important to understand that juveniles of Aspidogastrea from the intermediate host that are infective to the final host differ little from adults; either stage will therefore give identical results. Rohde (1966; 1968a) drew attention to the great variety of **sensory receptors** and their great numbers in *M. purvisi* based on examination of serial sections impregnated with silver under a light microscope. Subsequently, numerous studies, also using scanning electron microscopy (SEM) and transmission electron microscopy (TEM), confirmed this not only for *Multicotyle*, but for *Lobatostoma*, as well.

Location and Number of Surface Receptors

Scanning electron microscopy only shows **surface receptors** (Figure 8). Rohde (1973) counted the surface receptors on scanning electron micrographs of 1 specimen of *Lobatostoma manteri* supplemented by counts of another specimen impregnated with silver, and reported the numbers as follows (see Table 1).

Receptors close to the surface form only a small proportion of receptors, therefore, the total number is far greater. Considering this, Rohde (1989) estimated that a fully grown worm of this species (4 mm-long, unpressed, or unflattened) has a total of 20,000–40,000 receptors, which appears to be extraordinary for a worm of such a small size.

Interior Structures

Transmission electron microscopy is not restricted to the surface but can be used to examine interior structures, as well. Comparison of serial ultrathin sections has shown that juvenile and adult *Lobatostoma manteri* have at least 8 and possibly up to 14 types of **receptors** (Rohde, 1989; Rohde and Watson, 1989a). The receptors are distinguished by the presence or absence of a **cilium**. The length of the receptors is

Table 1. Surface receptors on *Lobatostoma manteri*.

Location	Number
In each anterior marginal alveolus	35
In each marginal alveolus in the middle of the body (among all 60 marginal alveoli, 2,700; and in all 29 median alveoli, 870) (total of 3,570)	50
In a marginal row of papillae just dorsal to the alveoli	780
On the dorsal part of the body	1,200
Along the ventral margins of the ventral head lobes	1,600
On the anterior side of the median dorsal head lobe	140
On the anterior side of the ventral head lobes	300
On the anterior sides of the lateral dorsal head lobes	300
On the posterior side of the dorsal head lobes	200
On the posterior side of the ventral head lobe	150
On the neck	200
Overall total	**8,475**

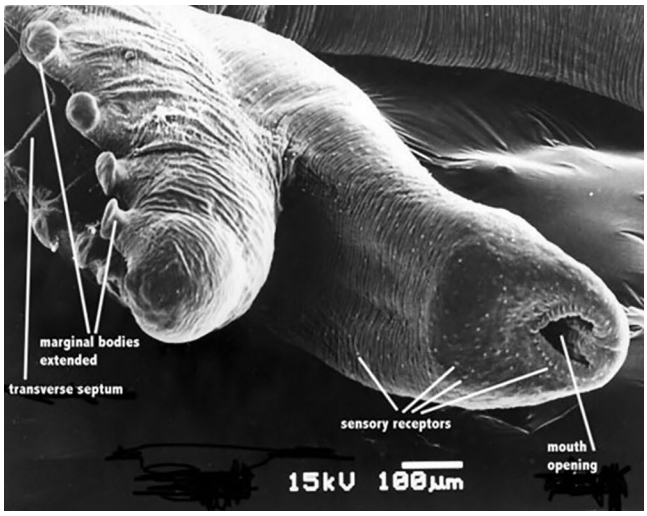

Figure 8. Scanning electron micrograph of anterior end of *Multicalyx elegans*. Source: K. Rohde. License: CC BY-NC-SA 4.0.

determined by the absence or presence of ciliary **rootlets** and their shape, by the number of axonemal **microtubules** in the **axoneme** of the cilium, and whether they are part of a complex organ or not. Juvenile and adult *Multicotyle* have 7 and possibly up to 9 types of receptors. A few major types of receptors that are found in *L. manteri* are illustrated in the following images by single sections (although for distinguishing different receptor types, in all cases serial sections were used). All receptors represent differentiated endings of **dendrites** (that is, **nerve fibers**), usually with ciliary structures within them. For example, the receptor illustrated in Figure 9 has a short cilium at the end of the dendrite, which is embedded in the worm's surface layer (also called its **tegument**). Typically, cilia have a 9 + 2 structure of the **axoneme**, that is, each contains 9 pairs (doublets) of microtubules in the periphery and 2 single microtubules in the center, but there may be deviations from this pattern. Figure 10 shows a receptor without a free cilium, in which the rootlet is widened to form a large disc. The receptor in Figure 11 has a branched ciliary rootlet.

Electron microscopic studies of *Multicotyle purvisi* (Rohde, 1990) have shown the following receptor types, in many respects similar to those of *Lobatostoma*, but differing in some aspects:

1) Disc-like receptor with many dense collars and a modified ciliary rootlet forming a disc;
2) Non-ciliate receptor with a long rootlet;
3) Non-ciliate receptor with a branching rootlet and a dense mass of irregularly arranged microtubules;
4) Non-ciliate receptor with a rootlet fanning out from a basal body, cross-striated in the upper region and with electron-dense structures in the lower part;

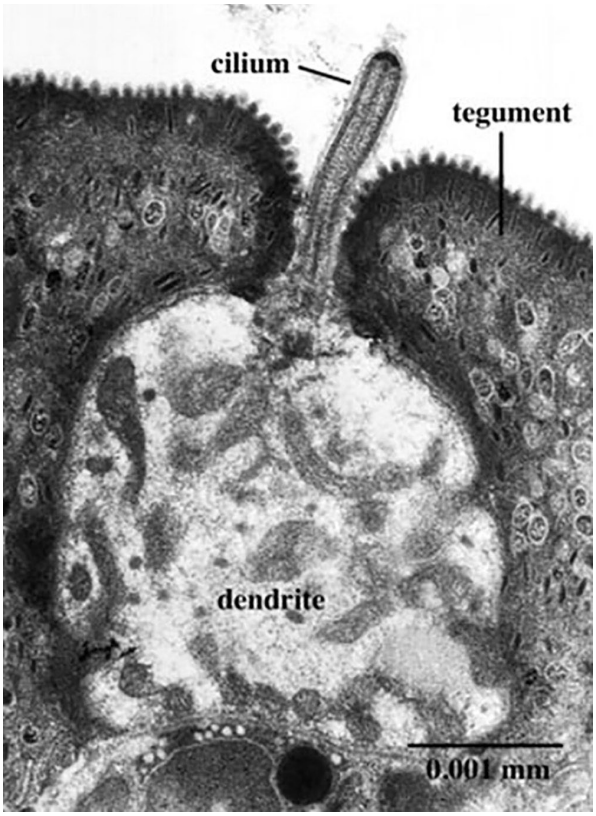

Figure 9. Ciliated surface receptor of *Lobatostoma manteri*. A single cilium arises from the terminal dendritic swelling. Source: K. Rohde. License: CC BY-NC-SA 4.0.

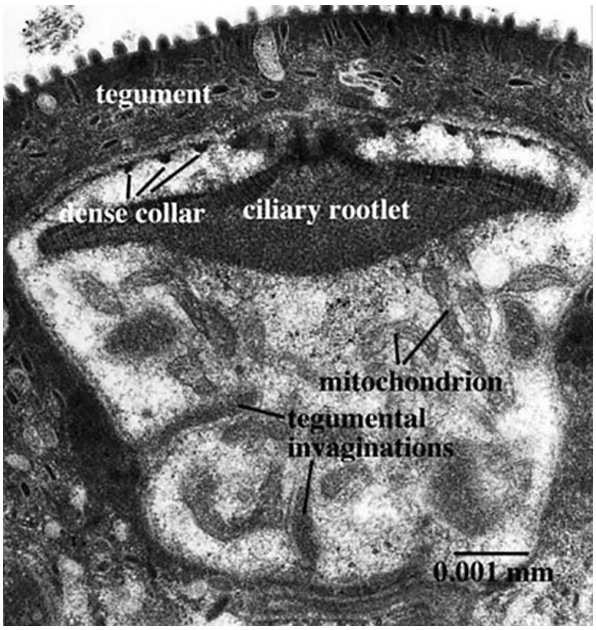

Figure 10. The receptor of *Lobatostoma manteri* without a free cilium, but with an expanded ciliary rootlet. Also note the sections through the dense collars around the upper part of the dendrite. Source: K. Rohde. License: CC BY-NC-SA 4.0.

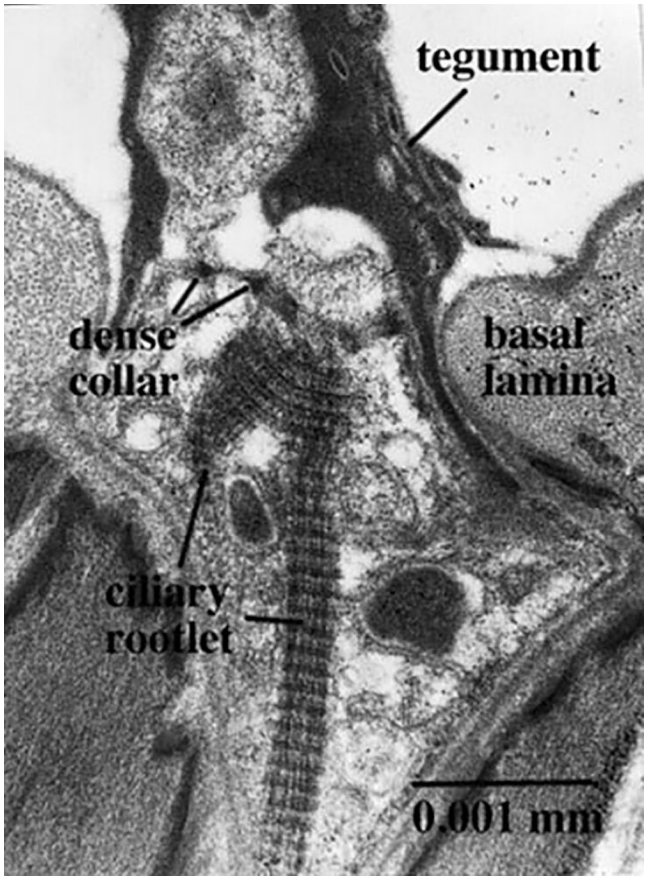

Figure 11. Non-ciliate receptor of *Lobatostoma manteri* located in a deep pit, with branching ciliary rootlet. Source: K. Rohde. License: CC BY-NC-SA 4.0.

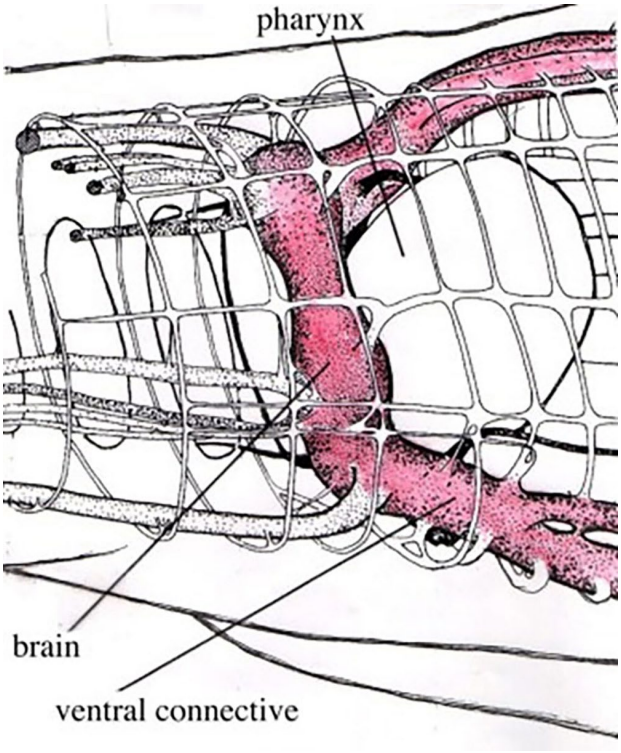

Figure 12. **Nervous system** of *Multicotyle purvisi* in the anterior part of the body. Some nerves on the right-hand side of the worm have been cut in order to show the arrangement of the nerves in cross section. Note the 2 rings of commissures, and the very large brain (**cerebral commissure**) and **main ventral connective** (pink). Source: K. Rohde. License: CC BY-NC-SA 4.0.

5) Uniciliate receptor with a thick layer of cytoplasm around the axoneme;
6) Receptor with a short cilium, at the base of a deeply invaginated tegument;
7) Receptor with a short cilium terminating in an electron-denser apical cap;
8) Uniciliate receptor with a long cilium.

In addition, there may be a small non-ciliate receptor with a long ciliary rootlet at the base of the thick dorsal tegument, and uniciliate receptors differing from the uniciliate receptor with a long cilium in the number of dense collars and the length of the cilium and ciliary rootlet.

Juvenile and Adult Nervous System

The **nervous system** of larval and adult *Multicotyle purvisi* has been reconstructed in detail using serial sections impregnated with silver and supplemented by sections stained with various other stains, among them some specific for neurosecretion (Rohde, 1968b; 1971c; review in Rohde, 1972). In most Platyhelminthes, the nervous system consists of **longitudinal nerves** (**connectives**) connected by **transverse nerves** (**commissures**). The dorsal part of one of the most anterior commissures is often particularly well-developed, forming the **cerebral commissure**, or **brain**. In *Multicotyle*, the number of anterior connectives is much greater than in any species of the many turbellarians that have been examined, and there are 2 rings of commissures, 1 close to the tegument, the other deeper in the tissue. The dorsal part of an interior commissure just anterior to the **pharynx** is very large, forming the brain (Figure 12). More posteriorly, the nerves form a typical system of connectives and commissures (with 1 pair of dorsal, 1 pair of lateral and 1 pair of ventral connectives), as well as a complex pattern innervating the **ventral** (**adhesive**) **disc** (Figure 13).

Interestingly, a dense network of nerve fibers (**nerve plexus**) innervates the **intestine** (Figure 14), and the **connective tissue septum** separates the dorsal part of the body from the ventral disc. Transmission electron-microscopy of the nerves of *Multicotyle purvisi* revealed the presence of a nerve sheath around parts of a posterior connective (Rohde, 1970), a structure not known from other flatworms.

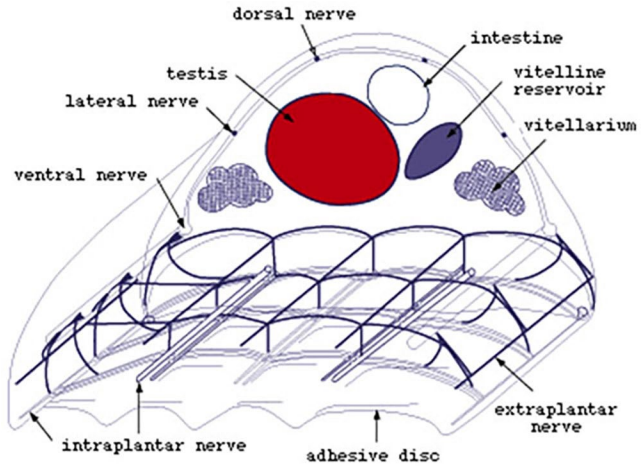

Figure 13. **Nervous system** of *Multicotyle purvisi* in the middle part of the body, showing a typical arrangement of connectives and commissures in the dorsal part of the body, and an intricate pattern of nerves innervating the **ventral** (**adhesive**) **disc**. Source: K. Rohde. License: CC BY-NC-SA 4.0.

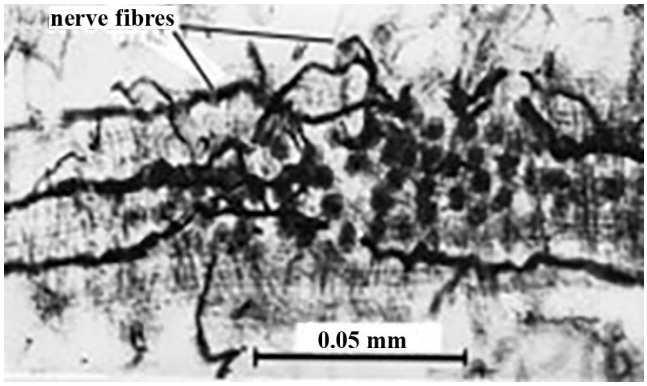

Figure 14. **Nerve plexus** around the intestine of *Multicotyle purvisi*. Section impregnated with silver as seen under the light microscope. Source: K. Rohde. License: CC BY-NC-SA 4.0.

Larval Sensory Receptors and Nervous System

Information about the sensory receptors of the larvae of *Multicotyle purvisi* and *Lobatostoma manteri* has been published in several papers (Rohde and Watson, 1990a; 1990b; 1990c; 1991; 1992a; reviews in Rohde, 1994; 1999). In *M. purvisi*, 13 receptor types were found altogether. *Multicotyle purvisi* has a paired eye and a paired receptor complex dorsal to the mouth cavity, each complex consisting of 2 dendrites. One of the dendrites forms a large liquid filled cavity with at least 10 short cilia lacking ciliary rootlets but possessing basal bodies and lamellate extensions of the ciliary membrane. The other of the dendrites penetrates the anterior wall of the cavity formed by the first dendrite and possesses a single cilium, star-shaped in cross section. Each **eye** (**ocellus**) consists of 1 **pigment cell** and 2 **receptor cells** with **rhabdomeres** (the light-sensitive dendritic endings) (Figure 15).

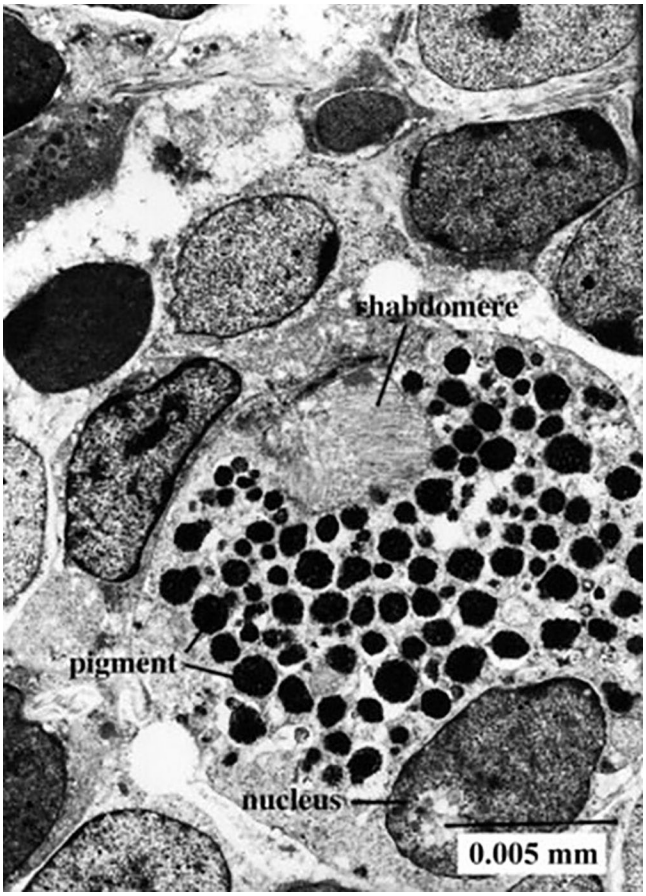

Figure 15. Transmission electron micrograph of ocellus (eye) of larval *Multicotyle purvisi*. Note the pigment cell with pigment granules, nucleus of pigment cell, and rhabdomere (light-sensitive dendritic endings). Source: K. Rohde. License: CC BY-NC-SA 4.0.

The larva of *Lobatostoma manteri* has only about 9 types of receptors. In *L. manteri*, eyes are lacking and anterior receptor complexes are not found, either. The difference between the 2 larvae can be explained by the way infect the intermediate host. *Lobastoma manteri* does not hatch, it is ingested by a snail. *Multicotyle purvisi* hatches, swims in water, is attracted to the surface layer by light stimuli, and is then inhaled by a snail host.

The nervous system of larval *Multicotyle* was reconstructed using serial sections impregnated with silver. It shows the basic pattern also found in the adult, with nerves innervating the pharynx, intestine, and posterior sucker, and a large number of anterior connectives (Rohde, 1971c).

Life Cycles

The life cycles of several species have been worked out. Based on the knowledge available to date, 2 kinds of life

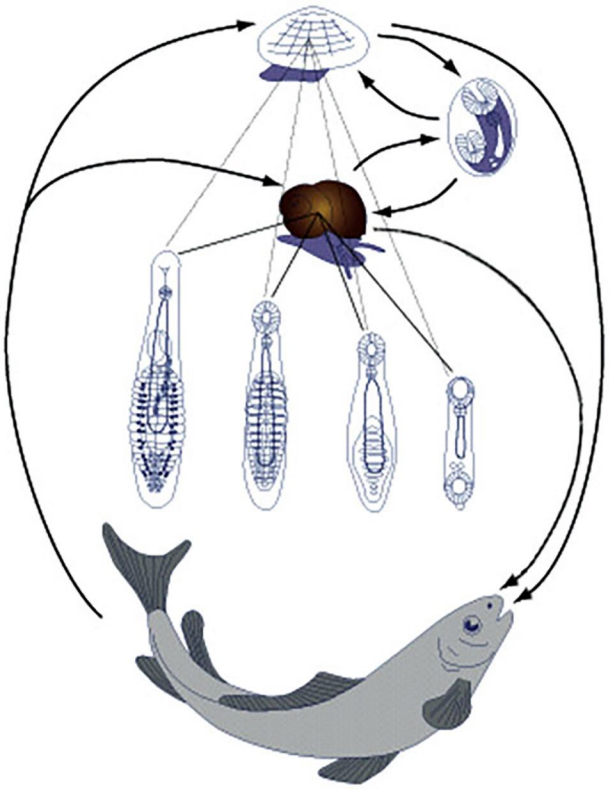

Figure 16. Life cycle of *Aspidogaster conchicola*. Only molluscs (freshwater bivalves or snails) are necessary for the completion of the life cycle. Adult worms produce eggs in which a non-ciliated larva with an anterior and posterior sucker develops. There are conflicting reports on how molluscs become infected: Either by eggs containing larvae or by hatched larvae. The life cycle can be completed without involvement of a vertebrate host, but if a fish eats an infected mollusc, adults can produce eggs in it. Source: K. Rohde. License: CC BY-NC-SA 4.0.

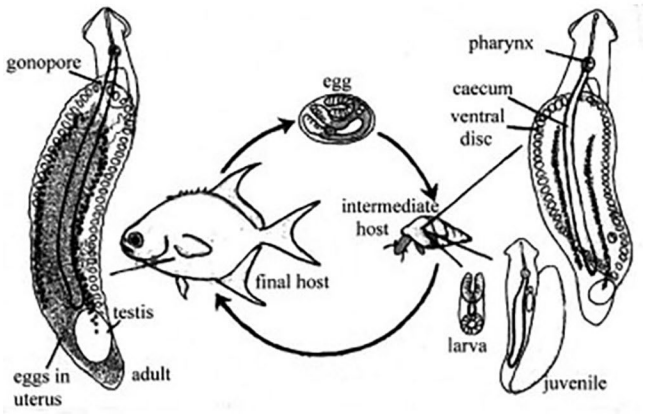

Figure 17. The life cycle of *Lobatostoma manteri*. Adults live in the small intestine of the marine teleost fish *Trachinotus blochi* (family Carangidae). They possess fully mature male and female reproductive systems with 1 large posterior testis, and a uterus filled with eggs which are shed through the gonopore at the anterior end. Eggs are deposited with the feces of the fish on the sea floor, where they are eaten by snails such as *Cerithium* (*Clypeomorus*) *moniliferum*. In the snail, the posterior sucker of the larva develops to the adhesive disk, and reproductive organs develop to (almost) the final state, without, however, maturing and producing sperm and eggs. Adapted from Rohde, 2001. License: CC BY-NC-SA 4.0.

cycles can be distinguished. In one type, the entire life cycle can be completed in molluscs, although vertebrates may act as facultative hosts (not obligate hosts). In the other, both a mollusc and a vertebrate are required for completion of the life cycle. An example of the first kind is *Aspidogaster conchicola*, whose life cycle has been studied by many authors beginning in the 19th century (references in Rohde, 1972; 1999) (Figure 16). Another example is *Cotylaspis insignis,* sexually mature specimens of which were found in molluscs and turtles (references in Rohde, 1972). The species has found considerable attention in the last decade (for example, see Rosen et al. 2016a; 2016b; 2016c; 2017).

An example of the second kind of life cycle is *Lobatostoma manteri* from the small intestine of the marine teleost fish *Trachinotus blochi* (Rohde, 1973) (Figure 17).

At Heron Island on the Great Barrier Reef north of Australia, only juvenile *Trachinotus* (a few cm-long) were found to be infected. They crush very thick-shelled snails with their well-developed pharyngeal plates (Figure 18). When first infected, larvae hatch in the stomach of the snails but move into the digestive gland where they develop (Figure 18).

Like *Lobatostoma manteri*, *Multicotyle purvisi* (Figure 5) also needs a mollusc and vertebrate host for the completion of its life cycle. However, infection of the mollusc is not by an egg that is ingested, but by a larva that hatches in freshwater and then swims for hours by means of its 10 ciliary tufts with support by a flotation mechanism, a thick sheath of microfila (Figure 19). Larvae are inhaled by snails and migrate into the kidneys where they grow to the stage infective to turtles (Rohde, 1971b).

It is possible that other species of aspidogastreans have more complex life cycles. Thus, larvae of *Stichocotyle nephropis*, were found encapsulated in the intestinal wall of lobsters, while adult *S. nephropis* infect elasmobranchs. Immature *Multicalyx* have been recorded from the intestines of teleost fish, while adult *Multicalyx* infect holocephalans (class Chrondrichthyes: subclass Holocephali—that is, ratfish and ghost sharks) and elasmobranchs (class Chondrichthyes: subclass Elasmobranchii—that is, sharks, skates, and rays). This suggests that, in addition to the intermediate and final hosts, a further host acting as a transport host (that is, a host containing immature stages which do not develop in it), may be involved.

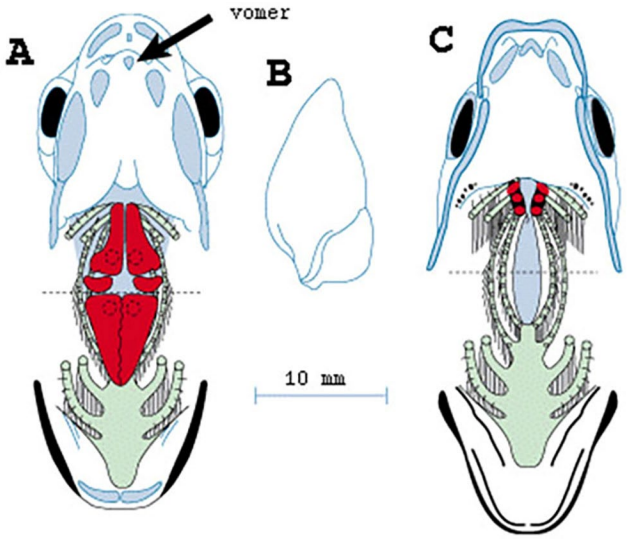

Figure 18. The head of juvenile *Trachinotus blochi* (A) opened along the dotted line. Snails (B) are crushed between the pharyngeal plates (red) which are moved by strongly developed muscles responsible for the peculiarly shaped head of the fish species (snub-nosed dart). The pointed vomer (arrow) prevents the snail from slipping out of the mouth. On the right a close relative of *Trachinotus blochi* of about the same size (C): Note the ostensibly normal pharyngeal plates. This fish species cannot become infected because it cannot crush the snails. Source: K. Rohde. License: CC BY-NC-SA 4.0.

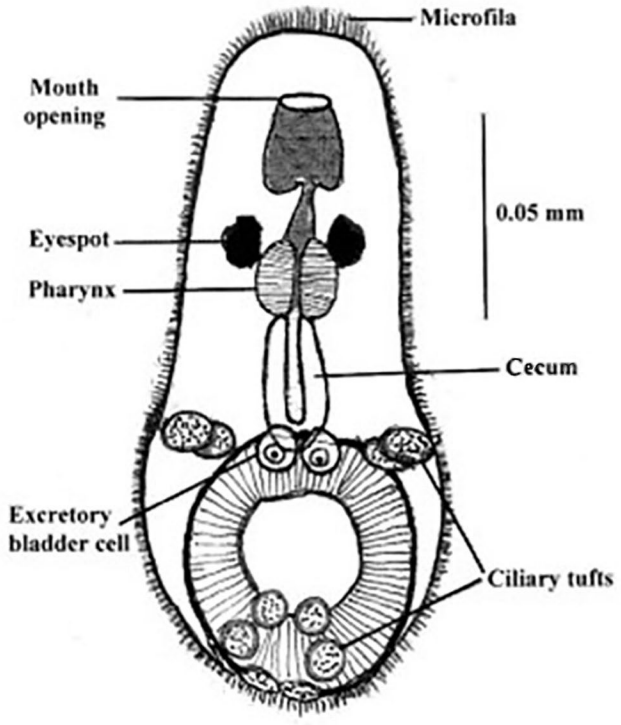

Figure 19. Larva of *Multicotyle purvisi*. Note the anterior mouth not surrounded by an anterior sucker, followed by the pharynx and cecum. As in the larva of *Lobatostoma manteri* (see Figure 1), there are a posterior sucker and 2 excretory bladder cells. In addition, the surface is covered by a thick sheath of microfila which appear to help in flotation. Altogether 10 ciliary tufts enable the larva to actively swim, and a pair of eyespots (ocelli) facilitate reaction to light. Source: K. Rohde. License: CC BY-NC-SA 4.0.

In all species of Aspidogastrea that have been studied, the posterior sucker of the larva is transformed into an adhesive disc. In *Rugogaster*, for example, the rugae are formed by the posterior wall of the sucker (Rohde and Watson, 1992b). In species of *Lobatostoma* and *Multicotyle*, among others, alveoli are formed within the sucker. Detailed studies of *Stichocotyle* have not been made.

Taxonomy and Phylogeny

About 60 species of aspidogastreans in 13 genera have been described. There has been some controversy about the relationships of the various genera of aspidogastreans, but according to the prevailing view, 4 families are distinguished, as follows (Rohde, 2002; see Figure 20):

1) **Rugogastridae** (2 ceca, single row of transverse rugae) comprising a single genus *Rugogaster* with 2 species from the rectal glands of holocephalan fishes;
2) **Stichocotylidae** (1 cecum, single row of well separated suckerlets) with a single species, *Stichocotyle nephropis*, from the intestine of elasmobranchs;
3) **Multicalycidae** (1 cecum, single ventral row of alveoli separated by transverse septa) with a single genus *Multicalyx* from the intestine of holocephalan fishes and elasmobranchs;
4) **Aspidogastridae** (1 cecum, ventral disc with 3 or 4 rows of alveoli) with 9 genera in 3 subfamilies from molluscs, turtles, and teleost fishes (however, note that new work shows that this family to be polyphyletic; see Sokolov et al., 2019).
    4a) Subfamily **Rohdellinae** (terminal part of male and female reproductive ducts united to form a hermaphroditic duct) with a single species *Rohdella siamensis* from freshwater teleosts;
    4b) Subfamily **Cotylaspidinae** (3 rows of alveoli) with 3 genera, *Cotylogaster*, *Cotylaspis*, and *Lissemysia* which differ in the number of testes (1 or 2) and the absence or presence of a cirrus pouch;
    4c) Subfamily **Aspidogastrinae** (4 rows of alveoli) with 6 genera, *Multicotyle*,

Lobatostoma, *Aspidogaster*, *Lophotaspis*, *Sychnocotyle*, and *Neosychnocotyle*, which differ in the number of testes (1 or 2), the absence or presence of a cirrus pouch, and the absence or presence of head lobes and/or papillae on the ventral disc.

Whereas the Aspidogastridae have an adhesive disc bearing 3 or 4 rows of alveoli and use teleosts or turtles as hosts, all the other families share the characters (synapomorphies) rugae or a single row of deep suckers/alveoli, as well as the use of elasmobranchs or holocephalans as hosts. Gibson and Chinabut (1984) distinguished 2 orders: 1) **Aspidogastrida** with the single family Aspidogastridae, and 2) **Stichocotylida** with the other families. Since DNA studies on the relationship of the families with each other have not been made, the following diagram illustrates the likely relationship of the aspidogastrean families with each other based on morphology and hosts.

The sister group of the Aspidogastrea is the very large group Digenea, with thousands of species and many families (for example, see Park et al., 2007). The ancestor of the Digenea split from the ancestor of the Aspidogastrea early in evolutionary history of the flatworms, probably more than 400 Ma (= million years ago; Littlewood et al., 1999a). Comparative studies using 18S rDNA (Littlewood et al., 1999b), 28S rDNA (Litvaitis and Rohde, 1999b), as well as extensive electron microscopic studies (for example, Ehlers, 1985; Littlewood et al., 1999b) have demonstrated that all the major groups of parasitic Platyhelminthes, the Trematoda, Eucestoda, Gyrocotylidea, and Amphilinidea, as well as the Polyopisthocotylea and Monopisthocotylea—have 1 common ancestor, that is, from 1 monophylum, the Neodermata (for example, see Ehlers, 1985; Rohde, 1997). This hypothesis was also confirmed by later DNA studies (for example, see Egger et al., 2015). Note, however, that the Polyopisthocotylea and Monopisthocotylea are commonly put in the Monogenea which is not a monophyletic group (for example, see Littlewood, 2006).

Infection Process and Localization in the Host

As discussed above, the 2 species of Aspidogastrea examined in detail possess some intriguing differences both in morphology and life cycles. The larva of *Multicotyle purvisi* has a larger variety of sensory receptors than that of *Lobatostoma manteri*, including a pair of eyes and an anterior paired receptor complex which are absent in the latter species. It also has 10 ciliary tufts and a coat of microfila, that is, very thin processes of the tegument. The larva of *L. manteri,* on the other hand, has a well-developed pseudosucker absent in the former species.

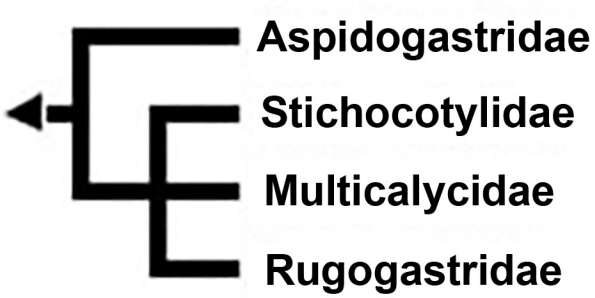

Figure 20. The likely relationship of the aspidogastrean families with each other based on morphology and hosts. Source: K. Rohde. License: CC BY.

Adults of *Multicotyle purvisi* reach a length of at least 10 mm (unpressed, or unflattened). Adults of *Lobatostoma manteri* reach a length of about 7 mm (pressed) and 4 mm (unpressed, or unflattened). The former species has a uterus coiled up in the anterior part of the body, with relatively few eggs. The latter species has a uterus filling most of the body, with a large number of eggs. The juvenile and adult of both species have a large number of marginal organs (terminal parts of glands) between the marginal alveoli of the adhesive disc. In the following sections, these differences will be explained by distinctions in the life cycles of the species.

***Multicotyle purvisi*: Infection Process and Localization in the Intermediate Host**

Rohde (1971b) described the infection process of *Multicotyle purvisi* from the stomach and occasionally the anterior part of the duodenum of several species of Malayan turtles, with freshwater snails as intermediate hosts, as follows:

Eggs containing embryos at the 1–3 cell stage are laid. Larvae develop in the egg after it has escaped in the feces of turtles into freshwater. In experiments at temperatures of 27–29 ºC, first hatching occurred 25 days after egg laying, at 21–28 ºC first hatching occurred after 35–40 days, at 19–22 ºC after 103 days. Environmental temperatures in Malaysia are 21–32 ºC (in the shade in the lowlands). At higher temperatures the hatching process takes only a few minutes. Hatching in cultures under normal diurnal fluctuations of light and temperatures occurs, with few exceptions, in the early hours of the morning. In cultures kept in the dark beyond the normal time of hatching, hatching occurred only after illumination. However, when cultures were kept in the dark over days, hatching occurred also without a light stimulus.

Immediately after hatching, larvae swim usually with an extended anterior end, rotating around their longitudinal axis, either along the bottom or straight upwards to the surface, but also irregularly in all directions in the water. They often

remain attached to the surface, slowly rotating, or sink slowly to the bottom with the posterior end directed downwards, or faster with the anterior end directed downwards. Larvae can also float in the middle of the water column rotating slowly around their longitudinal axis, carried sidewards by water currents. They sometimes remain at the bottom, appearing to touch and feel the substratum.

Larvae are positively phototrophic and survive at 26–30 ºC for 5 to over 33 hours. They reach the host less by their own movements, but rather by water currents produced by snails, which carry them into the inhalant opening.

Localization of larvae in the snails was determined in 3 specimens of the snail *Pila scutata*. At 50 and 69 days, respectively, after infection, a larva was found in the anterior kidney chamber; 108 days after infection, a larva was found in the posterior kidney chamber of the snail. Experiments showed that turtles become infected by ingesting infected snails.

The smallest specimens of *Multicoyle* found in a large number of naturally infected turtles had 17 and 18 transverse rows of alveoli, respectively. It therefore seems that specimens must be of a certain minimum size before they become infective. Fully grown up and mature specimens have 50 transverse rows of alveoli.

Functional Morphology

These features of the life cycle suggest that the larval eyes are responsible for phototaxis which keeps them in the water column where they can encounter snails, but they may also contribute to hatching in the morning.

The paired anterior sensory complex may have the function of a balancing organ, as suggested by the ciliary structure extending into interior liquid filled cavities.

The coat of microfila increases the surface area without increasing the weight, suggesting that it makes floating in the water column more effective.

Ciliary tufts are necessary for swimming, which leads the larvae not directly to the snails, but into the water column where snails may inhale them. This kind of infection behavior is possible only because the habitat of these freshwater snails is relatively undisturbed, that is, eggs and larvae after hatching do not run a great risk of being swept away into a less favorable site by adverse currents.

The numerous sensory receptors may enable the parasite to keep damage to the very delicate tissues of the host, in particular their kidneys, on which it depends for survival, at a minimum. But they may also contribute to finding the snails' habitat and to mate-finding.

The uterus of the adult can be kept relatively short, because larvae in the eggs develop only after leaving the worm.

***Lobatostoma manteri*: Infection Process and Localization in the Intermediate Host**

Rohde (1973; 1975) described the infection process of *Lobatostoma manteri* as follows: Eggs are laid which contain already fully developed larvae. Snails become infected by eating eggs containing larvae. In experiments, larvae hatched in the stomach of snails (*Planaxis sulcatus* and *Cerithium moniliferum*) and migrated immediately along the ducts of the digestive gland into the digestive follicles.

Host Tissue Reactions

Larvae of *Lobatostoma* feed on secretions and probably epithelial cells of the follicles of the digestive gland of snails. The posterior sucker and developing ventral disc are used for adhesion to the epithelium, and they contribute to its erosion. In heavy experimental infections, 47–49 and 65–66 days after infection, only small parts of the epithelium are still secretory, and the larvae live in large, fused cavities. Juveniles are usually found in a cavity formed by an enlargement of the main duct and 1 (or maybe more?) side duct of the digestive gland near the stomach in *Cerithium moniliferum*, or in the stomach and main ducts of the digestive gland of *Peristernia australiensis*. They may creep from the ducts into the stomach and back into the ducts. Fish become infected by eating snails.

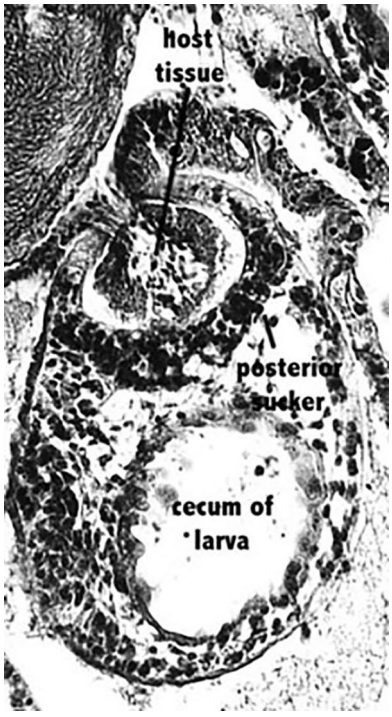

Figure 21. Young larva of *Lobatostoma manteri* (47–49 days old) feeding on the digestive gland of an experimentally infected *Cerithium moniliferum*. Note the posterior sucker around some host tissue. Source: K. Rohde. License: CC BY-NC-SA 4.0.

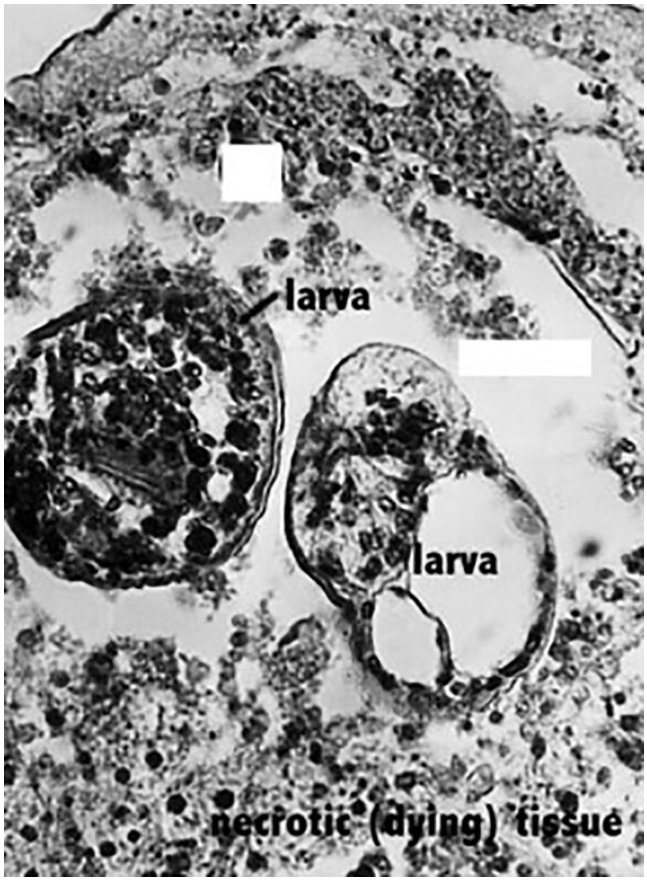

Figure 22. Two larvae (65–67 days old) of *Lobatostoma manteri* in the digestive gland of an experimentally-infected *Cerithium moniliferum*. Note the functional glandular tissue replaced by necrotic (dead and dying) cells. Source: K. Rohde. License: CC BY-NC-SA 4.0.

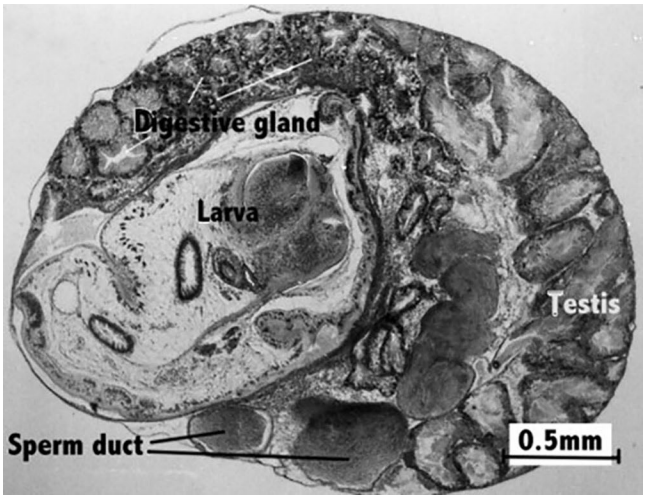

Figure 23. *Cerithium moniliferum* with one large juvenile *Lobatostoma manteri* ("larva") in the digestive gland. Source: K. Rohde. License: CC BY-NC-SA 4.0.

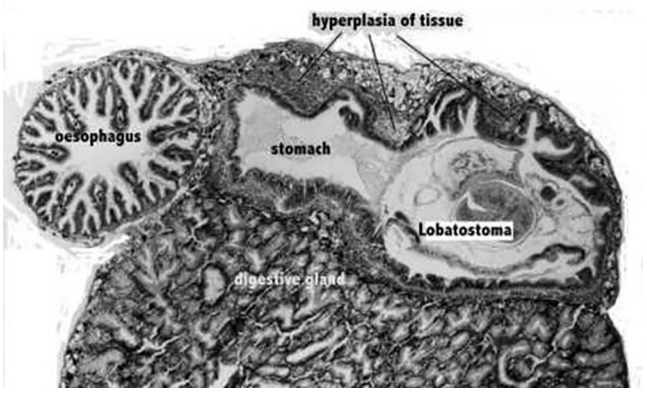

Figure 24. Large juvenile of *Lobatostoma manteri* in the stomach of naturally infected *Peristernia australiensis*. Note the enlarged subepithelial tissue (hyperplasia), that is, fibrosis (abnormally thick connective tissue) around parts of the stomach. Source: K. Rohde. License: CC BY-NC-SA 4.0.

Rohde and Sandland (1973) examined histological sections of *Cerithium moniliferum* and *Peristernia australiensis* infected with *Lobatostoma manteri*. In the former species (much smaller than the latter), a single parasite is usually present, coiled up in a cavity formed by the main digestive gland, and perhaps 1 or more side ducts of the digestive gland, causing metaplasia of the duct epithelium, hyperplasia of the inter-follicular connective tissue, an increase in the number of amoebocytes, and necrosis of some glandular follicles. The latter species may harbor up to 6 parasites in the stomach and in the large ducts of the digestive gland, with a thickening of the subepithelial connective tissue layer.

Some stages of pathogenesis caused by larval and growing *Lobatostoma* are illustrated in Figures 21–23. Note in particular that in the small snail species infected, *Cerithium moniliferum,* a single large juvenile worm is usually located in the digestive gland, in which only a few digestive follicles remain functional, whereas in the much larger *Peristernia australiensis* several large juveniles are often found in the stomach, with tissue reactions around it but most glandular follicles functional (Figures 24–26).

The illustrations show the considerable damage done to the hosts by the infection, although it should be pointed out that, during investigations, naturally infected snails never had as many parasites as experimentally infected ones. Reasons may be that snails in their natural habitat never encounter so many eggs, that heavily infected snails die, or that in natural infections later infections are suppressed by larvae or juveniles already present, either by predation of large on smaller larvae, or by tissue reactions induced by older parasites.

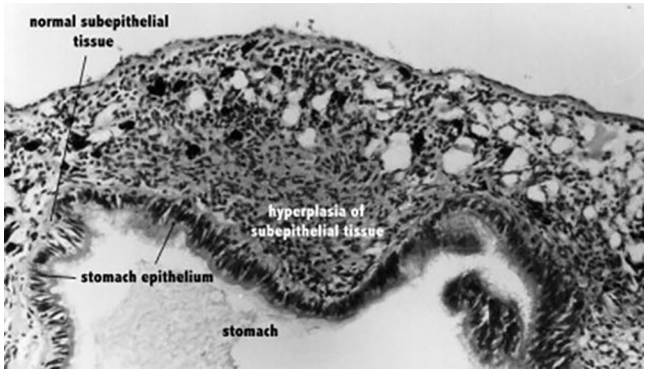

Figure 25. Another view of the *Lobatostoma manteri* specimen in the stomach of naturally infected *Peristernia australiensis* shown in Figure 24. Source: K. Rohde. License: CC BY-NC-SA 4.0.

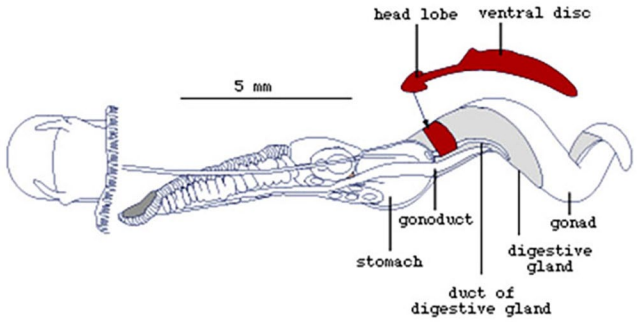

Figure 26. *Peristernia australiensis* infected with *Lobatostoma manteri.* This is an enlarged portion of Figure 25. Source: K. Rohde. License: CC BY-NC-SA 4.0.

Functional Morphology

In view of the pathological findings, it seems reasonable to assume that one function of the variety and number of sensory receptors may be to limit damage done to the delicate host tissue by the parasites. However, they may also play a role in mate finding. Rohde (1973) discussed the adaptive value of the ventral disc: It could be an adaptation for locomotion in or on the soft tissues of the host (snails), perhaps facilitating adhesion of only small portions to a small area of the host's tissue and preventing damage to it. Observations of digeneans and *Multicotyle* and *Lobatostoma* showed that the ventral disc is not more effective for attachment to the vertebrate intestine than the suckers of digeneans, suggesting that it is indeed an adaptation to life in molluscs. It is also very rarely used for tight attachment to the surface of containers or snails. The secretion produced by the marginal glands on the discs has not been examined, but it may be digestive, contributing to the erosion of the digestive gland follicles of the snails, as seen in histological sections. The long uterus of *Lobatostoma* is necessary, because eggs leave the worm only after larvae infective to snails have developed in them. This is necessary because the habitat is rather violent, exposed to strong tidal currents, and may dry out at low tide, making rapid ingestion of eggs by snails essential.

Ecology: Infection Dynamics

At Heron Island, Australia, prevalence of infection of several snail species with various Digenea and *Lobatostoma* was monitored around the island over an extended period (Rohde, 1981). Only snails of the species *Cerithium moniliferum*, *Peristernia australiensis*, and *Planaxis sulcatus* were found to be infected with *Lobatostoma*. The aspidogastrean and 11 species of larval digeneans were found in *Cerithium moniliferum* (Rohde and Sandland, 1973). *Peristernia australiensis* did not harbor any digeneans. Except for a few exceptions, *Lobatostoma* was found only in a small part of Heron Island's Shark Bay (which has a flat bottom formed by beach rock), and on beach rock close to it, possibly carried there by snails that had acquired their infection in Shark Bay (Figure 27) (Rohde, 2013). Examination of beach rock in Shark Bay showed a large number of shell fragments on it, mainly of *Cerithium*.

Netting in Shark Bay yielded small snubnosed dart, *Trachinotus blochi*. Its name is derived from the strongly developed muscles in the forehead which move the large pharyngeal plates, an adaptation to crushing the very thick shell of snails. Dissection of these fish revealed *Lobatostoma* in the small intestine and shell fragments in the stomach. Other fish caught in Shark Bay without this structure were never found to be infected.

From January 1971 to April 1972, there was a strong decrease in the relative number of infected snails. During the period of high frequency of infection, *Cerithium* infected with Digenea contained *Lobatostoma* relatively more frequently than snails without Digenea. Snails with double infections disappeared first. Infection with *Lobatostoma* did not affect the relative number of egg-producing *Cerithium* during the period of high frequency of infection. *Lobatostoma* from fish with single infections produced eggs with the haploid number of 7 chromosomes and development did not proceed beyond the blastula stage (Rohde, 1973).

Populations and Communities in Equilibrium or Non-Equilibrium?

There has been much debate about how common equilibrium conditions, largely determined by competition, are in ecological populations and communities. An attempt has been made to interpret the findings on *Lobatostoma* using 2 ecological paradigms, referred to as the demographic and autecological paradigms by Walter and Hengeveld (2000; see also, Hengeveld and Walter, 1999; Walter, 2013).

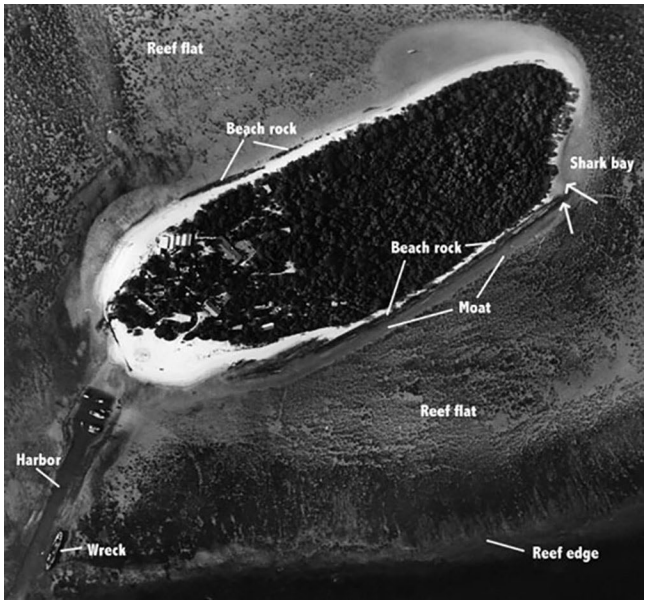

Figure 27. The distribution and infection of snails with *Lobatostoma manteri* at Heron Island at the southern end of the Great Barrier Reef in January–April 1971. Note: Beach rock around much of the island, the harbor and the moat (shallow channel) extending from the harbor area towards Shark Bay. At incoming tide, the moat fills first and fish swim from the reef edge into Shark Bay. The snails *Cerithium moniliferum*, *Planaxis sulcatus*, and *Peristernia australiensis* were infected with *Lobatostoma*, but infection was practically restricted to a small area of Shark Bay with a bottom of flat beach rock (arrows), although snails occurred all around the island on beach rock and rubble. A few *Lobatostoma* were also found a short distance from Shark Bay, possibly acquired in Shark Bay by snails which subsequently migrated along the beach rock. Source: K. Rohde, Vertikalphoto Royal Australian Air Force Number 2 Squadron. License: CC BY-NC-SA 4.0.

In the **demographic paradigm**, species are thought to be demographically similar but have different functions in communities. Intra- and interspecific competition have great importance, leading to co-evolution by optimization processes (that is, processes that bring about optimal adaptation to environmental conditions), to saturation of communities with species, and to equilibrium. Optimization is thought to be possible over short time spans because the abiotic environmental component is, on average, constant.

According to the **autecological paradigm**, species are dissimilar entities affected by abiotic and demographic factors. Optimization is impossible because of the greatly variable environment.

The demographic paradigm gives rise to the question: Why do so many species share the same resources? The autecological paradigm leads to the question: How did species arise and how do they survive in a variable and heterogeneous environment? It focuses on the unique nature of adaptations and on species with their spatial responses to environmental conditions. Walter and Hengeveld (2000) claim that the 2 paradigms are mutually exclusive.

Which of the 2 paradigms is better suited to explain the unique adaptations of the 2 aspidogastreans discussed, and the distribution of *Lobatostoma*? As pointed out above, the Aspidogastrea are a very ancient group, having diverged from the digenean trematodes more than 400 Ma. Its unique features (such as the adhesive disc, marginal glands, great variety and number of sensory receptors, and no multiplication of larvae in the intermediate host) also are likely to be very ancient. It is unlikely that they have evolved due to short-term adaptations to particular environments.

Possible competitors with the 2 aspidogastreans are larval Digenea in the snails. However, the distribution of *Lobatostoma* and Digenea at Heron Island clearly shows that prevalence of infection with Digenea is greatest in a small habitat which also has the heaviest infections with *Lobatostoma*, making it unlikely that interspecific competition plays any role in determining the distribution of *Lobatostoma* at Heron Island. Intraspecific competition, that is competition between individuals of *Lobatostoma* in the snails, may well occur, as suggested by the observation that the smallest of the 3 snail species infected, *Cerithium moniliferum*, very rarely contains more than 1 juvenile of *Lobatostoma*. More individuals simply cannot be accommodated. But it is difficult to see how this could have led to any of the adaptations and to the distribution of the species. Clearly, each species has features that are long-term adaptations to a particular kind of life cycle and habitat. In other words, only the autecological paradigm can explain them.

However, caution is necessary in accepting the statement that the 2 paradigms are mutually exclusive. Rohde (2005), in discussing the relative frequency of equilibrium (caused by competition) and non-equilibrium conditions in biological systems, stressed that groups with certain characteristics will tend to exist in equilibrium, others will tend to exist in non-equilibrium. Both conditions are possible and depend on the size of populations and individuals, and on the vagility of the species. If all these are small (as in the aspidogastreans), a tendency towards non-equilibrium results (Rohde, 2005).

Acknowledgment

The foregoing text is based on the author's online articles (further details therein):

https://krohde.wordpress.com/2011/12/31/the-aspidogastrea-a-parasitological-xk923bc3gp4-13/

https://krohde.wordpress.com/2011/12/31/the-aspidogastrea-a-parasitological-xk923bc3gp4-15/

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