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DIGENEA, PLAGIORCHIIDA

XIPHIDIATA

Lecithodendriidae Lühe, 1901 (Family)

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Phylum Platyhelminthes

Class Trematoda

Subclass Digenea

Order Plagiorchiida

Family Lecithodendriidae

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Chapter 45

Lecithodendriidae Lühe, 1901 (Family)

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Introduction

The Lecithodendriidae Lühe, 1901 is a family of cosmopolitan digeneans in the suborder Xiphidiata. Adult lecithodendriids inhabit the intestinal tract of insectivorous bats (and occasionally birds). They are of mostly minor consequence in human and veterinary health but have been more important for parasite ecology. They use an aquatic snail as first intermediate host, an insect as second intermediate host, and the bat as definitive host. Humans and other mammals can become infected when ingesting infected insects. For veterinary science, the Lecithodendriidae have been found to be reservoirs for the causative agent of Potomac horse fever. They are important for studies of parasite ecology because they comprise a substantial component of the infracommunities of bats. Several species of Lecithodendriidae are often found in chiropteran infracommunities providing communities of several closely related members. Studies of those communities have contributed to better understanding of the assembly, structure, and dynamics of parasite communities.

Identifying Lecithodendriidae

Adults of the Lecithodendriidae (Figure 1) are typically less than 1 mm in length, possess an acetabulum, oral sucker, pharynx, and short cecae. They are monoecious with a single ovary, restricted follicular vitellaria (found in fore-, mid-, or hindbody), and a uterus containing tanned eggs most of which are found in the hindbody. From the ovary the uterus expands into a seminal receptacle and the Laurer's canal empties on the dorsal surface. The uterus empties into the genital atrium near the acetabulum (most often anterior). The male reproductive system comprises 2 testes, with vasa efferentia that meet to form the vas deferens. The vas deferens expands into a seminal vesicle which then narrows and is surrounded by the pars prostatica (Figure 2). The seminal vesicle is contained in a thin membranous sac (pseudocirrus sac) in

members of the subfamily Lecithodendriinae; however, it lies free in the parenchyma of members of the subfamily Ophiosacculinae (genera *Ophiosacculus* and *Castroia*—Figure 1D and 1G). A true cirrus (eversible terminal male reproductive tract—vas deferens) is lacking and, therefore, a cirrus sac is lacking; however, the pseudocirrus sac is likely homologous with the cirrus sac of other digeneans. The male and female systems empty into a common genital atrium before exiting the body. The genital atrium of lecithodendriids is most commonly a modest expansion that receives contents from the vas deferens and the metraterm and exits through the genital pore (Figure 2A). However, variations exist in the terminal genitalia among many genera. For example, in *Glyptoporus* (Figure 1A) and *Caprimulgorchis* (Figure 2D) the genital atrium is protrusible and may resemble a cirrus. In other species the atrium is not eversible but is expanded and armed as in *Acanthatrium* (Figure 1E, Figure 2C) or contains a papilla as in *Papillatrium* (Figure 2B). Typically, the excretory bladder is V-shaped and the flame cell pattern is $2((2 + 2 + 2) + (2 + 2 + 2))$.

Systematics and Taxonomy

The Lecithodendriidae belongs to the superfamily Microphalloidea. The morphological characteristics that hold the Microphalloidea together are few and the best evidence for their relationship is molecular (Olson et al., 2003; Tkach et al., 2003; Bray, 2008). The application of molecular systematics to the Microphalloidea and Lecithodendriidae began in 2000 (Tkach et al., 2000) and continues to help clarify the relationships among the families. Those relationships as well as the content of the families are regularly being revised and undoubtedly will continue to be so for the foreseeable future. Further, more needs to be known of the life cycles and larval characteristics of the lecithodendriids both for possible systematic importance and for understanding the evolution of the group. The microphaloid families for which at least 1 life cycle is known are the Zoogonidae, Pleurogenidae, Prosthogonimidae, Leyogonimidae, Collyriclidae, Phaneropsolidae, and Microphallidae. The families of the Microphalloidea for which no life cycles are known are the Faustulidae, Anenterotrematidae, Eumegacetidae, Exoditdendriidae, and Stomylotrematidae.

An interesting character found only among the Microphalloidea is the virgula organ of the cercaria (Figure 3). The virgula is a mucin reservoir contained in the oral sucker of most members. Lotz and Font (2008) included the Lecithodendriidae among a group of digeneans the members of which possess a virgula in the cercaria. At the time they suggested that the virgula might form a synapomorphy for that group of digeneans. However, based on the phylogeny proposed by

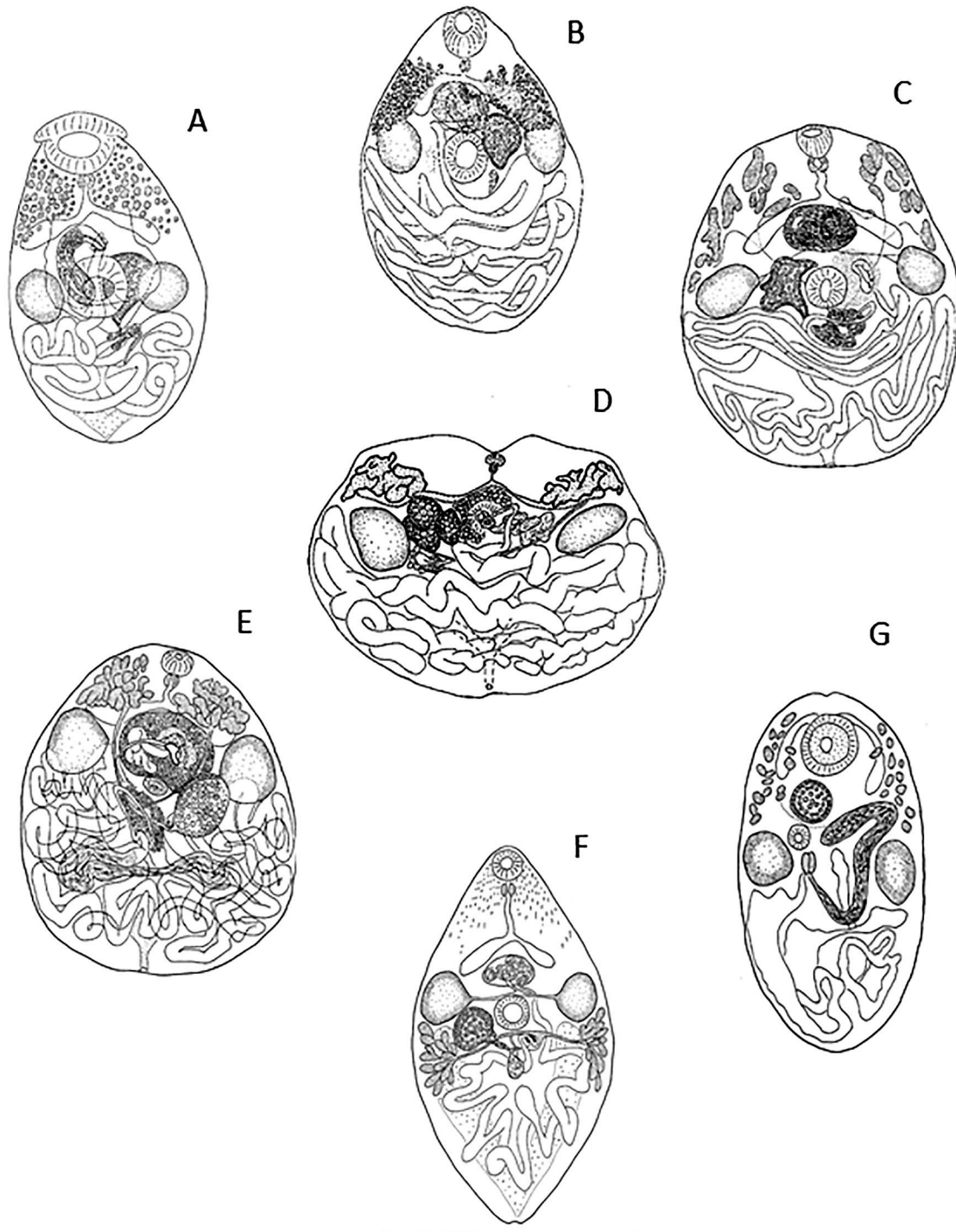


Figure 1. A) *Glyptoporus noctophilus*. B) *Paralecithodendrium swansoni* Macy, 1936. C) *Ochoterenatrema labda*. D) *Castroia silvai* Travassos, 1928. E) *Acanthatrium nycteridis* Faust, 1919. F) *Lecithodendrium linstowi*, Dollfus, 1931. G) *Ophiosacculus mehelyi* (Modlinger, 1930) Macy, 1935. Source: Lotz and Font, 2007. License: CC BY-NC-SA 4.0.

Olson and colleagues (2003) it appears that the virgula has either arisen more than once, has been lost in various clades, or a combination of the two. At least 2 species of Lecithodendriidae (*Paralecithodendrium chilostomum* and *Lecithodendrium linstowi*) (Kudlai et al., 2015; Enabulele et al., 2018) have

been shown by molecular matching to lack a virgula in the cercaria. Further, Enabulele and colleagues (2018) found the first intermediate host to be a pulmonate rather than a prosobranch snail (the most common for microphalloids generally). Among the families of Microphalloidea whose life cycles are

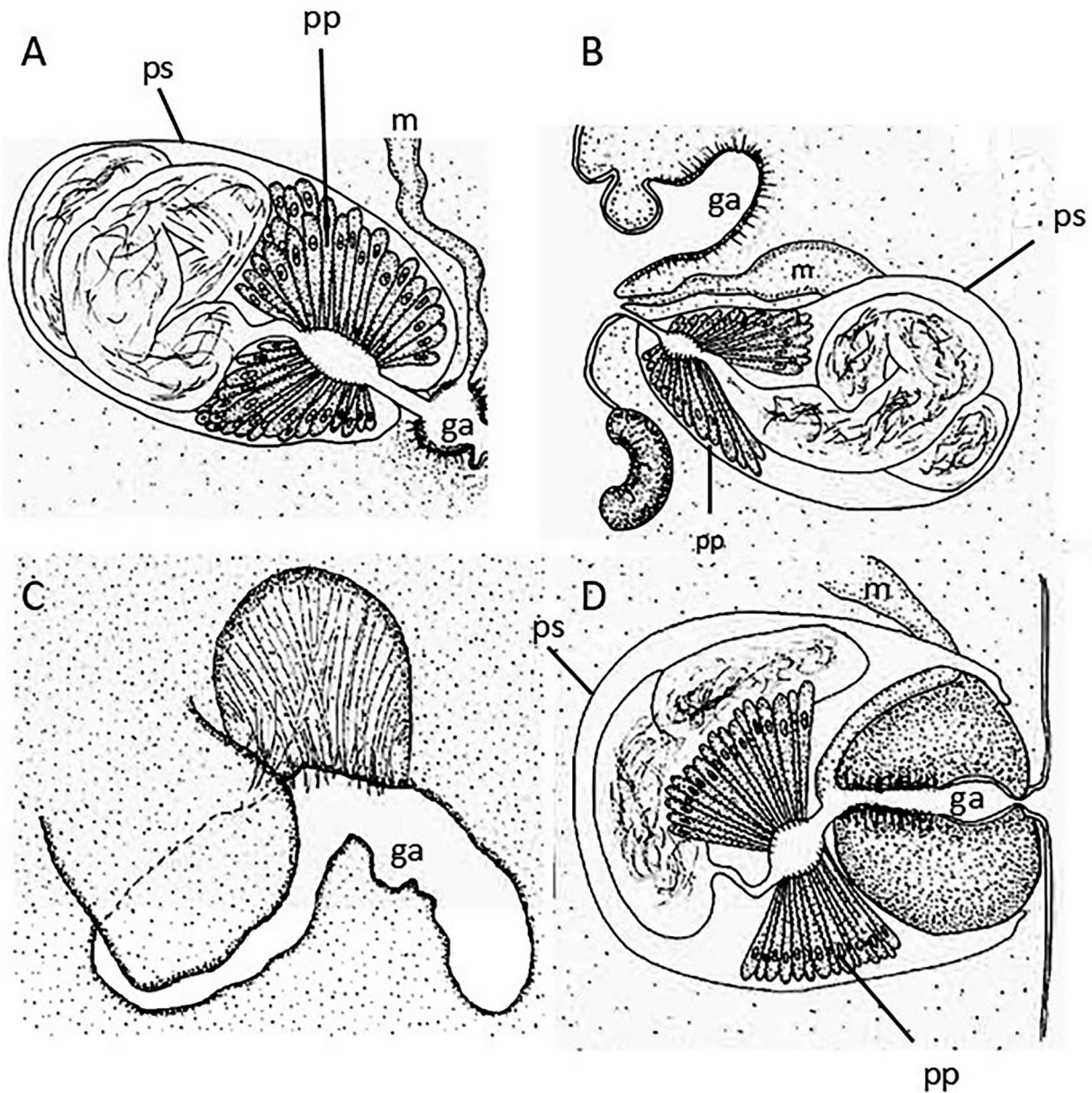


Figure 2. A) *Paralecithodendrium ovimagosum* (Bhalero, 1926); B) *Papillatrium parvouterus* (Bhalero, 1926); C) *Acanthatrium eptesici* Alicata, 1932; D) *Caprimulgorchis molenkampi* (Lie Kian Joe, 1951). A, B, and D are sagittal sections. C is a ventral view of terminal genitalia of whole mount. Ps: Pseudocirrus sac; m: Metratrem; sv: Seminal receptacle; ga: Genital atrium (hermaphroditic duct if narrowed); pp: Pars prostatica. Sources: A, B, D) Lotz and Palmieri, 1985; C) Lotz and Font, 1983. License: CC BY-NC-SA 4.0.

known, the virgula is absent in the Zoogonidae, Microphallidae, and Prosthogonimidae but present in the Lecithodendriidae, Phaneropsolidae, Collyriclidae, and Pleurogenidae.

Life Cycles

Members of the Lecithodendriidae have a typical digenean 3-host life cycle. Operculated eggs are passed from the definitive chiropteran host. Life cycle studies have not reported whether those eggs contain miracidia at release. Therefore, embryonation of eggs must be determined from examination of

eggs from adults. However, it is very difficult to observe the development of the miracidium in the eggs of lecithodendriids because the eggs are small and numerous. The only explicit mention in the literature of egg embryonation in adults was made by Etges (1960) noting that eggs were unembryonated in adult *Acanthatrium anaplocami*. On the other hand, a number of authors have reported intrauterine embryonated eggs in allied families. Hall (1959) reported them in *Mosesia chordileisia* (a putative phaneropsolid). For pleurogenids they have been reported by Vaucher (1968) in *Paraleyogonimus baeri*,

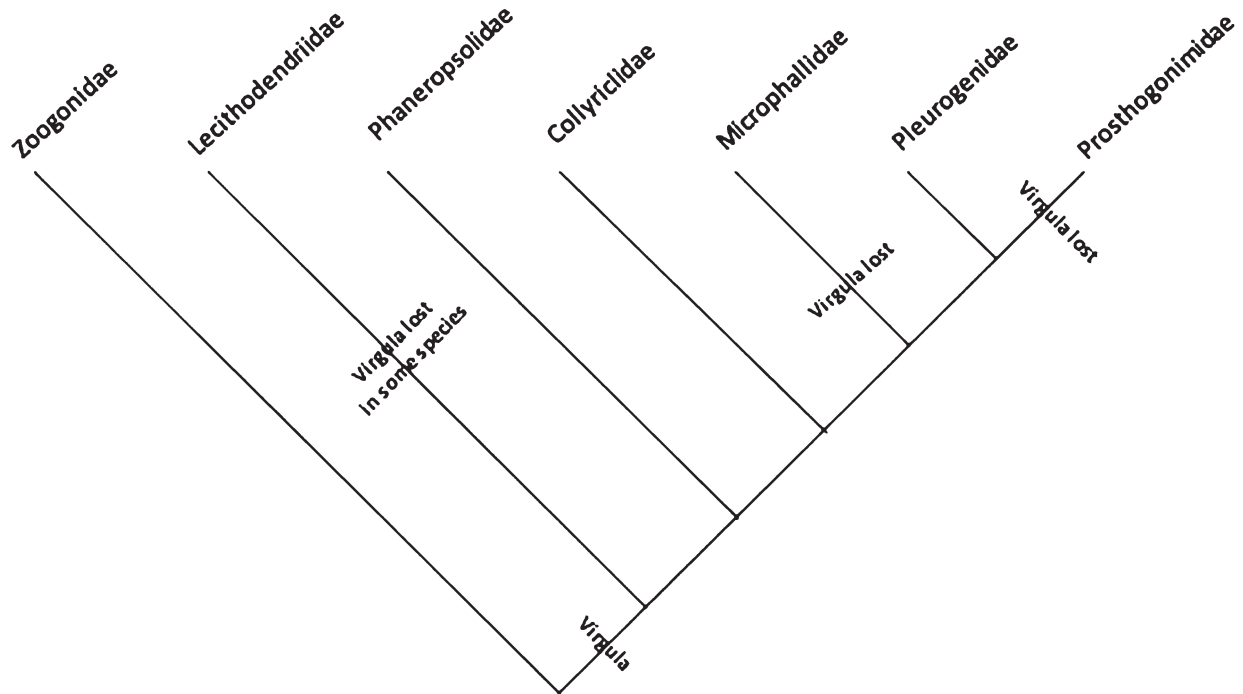


Figure 3. Distribution of virgulate cercariae among families of the Microphalloidea for which cercariae are known. Cladogram of the Microphalloidea. Sources: Adapted from Olson et al., 2013; Kanarek et al., 2014. License: CC BY-NC-SA 4.0.

Madhavi et al. (1987) in *Pleurogenoides orientalis*, Janardanan and Prasadani (1991) in *Pleurogenoides ovatus*, and Świdorski et al. (2014) in *Brandesia turgida*.

Studies of lecithodendriid life cycles have rarely addressed infection of snails from eggs or miracidia, therefore, it is rarely known whether an egg hatches a free-living miracidium which penetrates the snail or the egg is ingested before hatching. Although this information does not exist for the Lecithodendriidae, it does for a few allied families. In pleurogenids the eggs hatch only upon ingestion by the snail (Madhavi et al., 1987; Janardanan and Prasadani, 1991; Retnakumari et al., 1991). Further, the egg is ingested for reported life cycles of the Prosthogonimidae and Microphallidae. The first intermediate host of lecithodendriids is primarily a pro-sobranch snail, although pulmonates have been reported (Enabulele et al., 2018).

Within the first intermediate host the egg hatches and presumably the miracidium penetrates the intestinal wall and becomes a mother sporocyst. It is not known how many generations of daughter sporocysts are produced; however, snails typically harbor numerous daughter sporocysts, suggesting more than 1 generation of daughter sporocysts. Of significance, the sporocysts hold relatively few cercariae. Burns (1961) found 4–20 cercariae in the sporocysts of 5 virgulate digeneans. However, Etges (1960) reported sporocysts with up to 150 developing cercariae for *Acanthatrium anaplocami*.

Following intramolluscan development, cercariae leave the snail host, then seek out and penetrate the second intermediate host. The second intermediate host is the aquatic larva or naiad of an insect. For lecithodendriids second intermediate hosts have been reported from members of the insect orders Diptera, Trichoptera, and Plecoptera (see Brown, 1933; Etges, 1960; Burns, 1961; and El-Naffar et al., 1979). Second intermediate hosts for pleurogenids additionally include Megaloptera, Ephemeroptera, Odonata, Hemiptera, and Coleoptera. Subsequent to metamorphosis of the insect larva or naiad the adult infected host conveys the metacercaria to the definitive host.

The cercaria (Figure 3) is armed and the oral sucker of most members contains a unique mucin reservoir, the virgula. Investigations of the development and function of the virgula have been done most extensively by Kruidenier (1951). The virgula is embedded in the oral sucker ventral to the buccal cavity (Kruidenier, 1951). It is formed quickly in developing cercariae from swelling of the distal ends of pre-virgula mucoid glands during development of the cercariae in the sporocysts (Kruidenier, 1951). The virgula stores mucins that are released from those glands. According to Kruidenier (1951) the virgula contents are used both before and after penetration of the arthropod second intermediate host. However, most of the contents are used after penetration. Presumably the mucins released from the virgula aid in cercarial migration within the second intermediate host but appear not to

aid in penetration per se as the virgula does not diminish in size as the cercaria penetrates into the arthropod second intermediate host.

Burns (1961) noted that when a cercaria of *Acanthatrium oregonense* finds a suitable host it enters through thin portions of the cuticle, such as the gills. Further, he noted that upon contacting the gill, cercariae release mucous threads resulting in a capsule or cyst forming over the larval stage (Figure 4).

This has also been observed for other lecithodendriids and pleurogenids. Burns (1961) observed the cercaria of *Gyrbascus* (= *Allassogonoporus*) *vespertilionis* penetrate its second intermediate host. In this case no external cyst was formed but a mucous layer was secreted that covered the cercaria and appeared to enhance their chance of sticking to the gills of caddisfly larvae. Hall and Groves (1963) confirmed external cyst formation during penetration in several virgulate cercaria at the time of penetration but those cercaria have not been matched to adult worms; presumably they are lecithodendriids or pleurogenids.

Upon penetration, the cercaria of *Acanthatrium oregonense* does not encyst immediately but migrates through the insect's body and may not encyst until after metamorphosis (Brown, 1961). Brown (1961) reported that 31 days after exposure of caddisfly larvae to cercariae only insects that had metamorphosed into adults harbored encysted metacercariae. Those that were still in the larval stage or had developed into pupae harbored motile metacercariae. Etges (1960) found only unencysted metacercariae after exposure of mayfly naiads to cercariae of *A. anaplocami*. Although he never examined adult mayflies he assumed that metacercariae would encyst after metamorphosis. Brown (1933), although never observing the cercaria or performing laboratory studies, examined wild-caught caddisflies and found only unencysted metacercariae of *Paralecithodendrium chilostomum* in caddisfly larvae. However, he found encysted metacercariae in pupal and adult mayflies. On the other hand, El-Naffar and colleagues (1979) found encysted metacercariae in dipteran larvae after exposure to the cercariae of *Lecithodendrium granulosum*; however, only metacercariae from adult mosquitoes were infectious to the definitive host.

The life cycles of the virgulate pleurogenids do not appear to have delayed metacercarial encystment. Brown (1961) found *Gyrbascus* (= *Allassogonoporus*) *vespertilionis* to encyst shortly after entry into caddisfly larvae. Macy (1964) reported that metacercariae of *Pleurogenoides tener* encysted in odonate naiads at 5 days and that 5-day-old metacercariae from naiads were infectious to the lizard definitive host. Extended unencysted periods for other pleurogenid metacercariae have not been reported (for example, Grabda-Kazubaska, 1971; Brinesh and Janardanan, 2014).

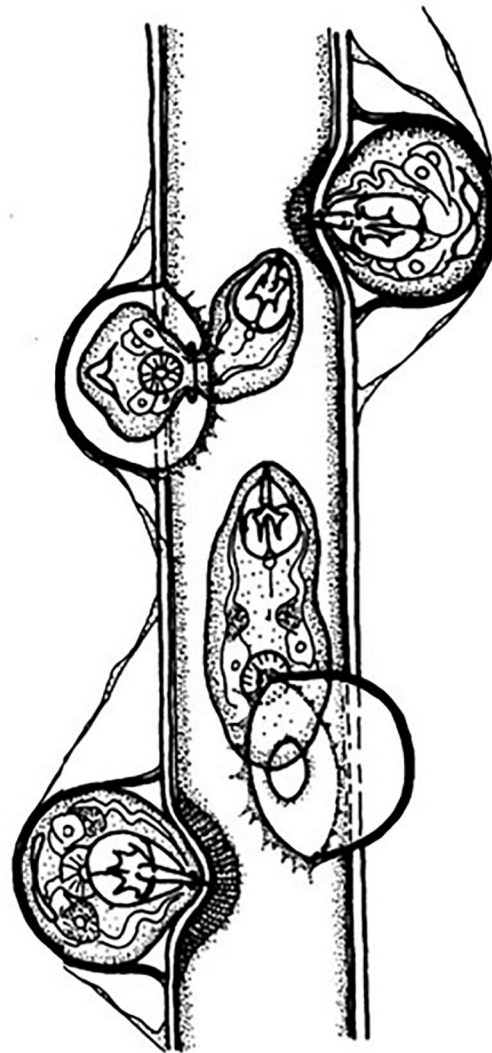


Figure 4. Cercaria of *Acanthatrium oregonense* encysting on and penetrating the gill of a larval caddisfly Source: Adapted from Burns, 1961b. License: CC BY-NC-SA 4.0.

Human Significance

Caprimulgorchis molenkampi (Lie Kian Joe, 1951) Lotz and Palmieri, 1985 was first described by Lie Kian Joe (1951) from 2 human necropsies in Indonesia. Manning and colleagues (1971) recovered this fluke from 14 human necropsies in Thailand. *Caprimulgorchis molenkampi* is not considered pathogenic, although high intensities may cause some symptoms. The prevalence of *C. molenkampi* is usually obtained coincidentally with surveys for the more pathogenic bile duct and gallbladder inhabitant, *Opisthorchis viverrini*. Chai and colleagues (2009) reported human infections with prevalences of 3.4–24.5% from Laos. They recovered worms after treating stool-sample-positive individuals with an anthelmintic, specifically, Paziquantel.

Manning and Lertprasert (1973) working in Thailand investigated part of the life cycle of *Caprimulgorchis molenkampii*. They found the rodent *Rattus rattus* and 2 species of bats (*Scotophilus kuhlii* and *Taphosous melanopogon*) to be naturally infected. Lotz and Palmieri (1985) found *T. melanopogon* infected with *C. molenkampii* in Malaysia. Manning and Lertprasert (1973) discovered metacercariae in naiads and adult dragon- and damselflies in Thailand. It is likely that human infections occur throughout southeast Asia, particularly where consumption of odonates is practiced. Manning and Lertprasert (1973) estimated that over a million people in Thailand and Laos may be infected.

Veterinary Significance

The Lecithodendriidae have been implicated in the transmission of Potomac horse fever (PHF), an acute inflammation of the digestive tract producing fever and diarrhea in horses of all ages, as well as abortion in pregnant mares. The causative agent is *Neorickettsia risticii* (order Rickettsiales, family Anaplasmataceae). The intracellular bacterium infects cells, particularly monocytes, of the small and large intestine. The infection results in acute colitis, which is one of the principal clinical signs of PHF (Madigan, 2010).

PHF occurs when horses ingest the reservoir host, a digenetic trematode, as is the case for other species of *Neorickettsia*. As early as 1924 insects (mayflies) were implicated in transmission of PHF, then called horse cholera (Baird and Arroyo, 2013). However, confirmation and the role of digeneans in the disease epidemiology would take some time to work out. Barlough and colleagues (1998) reported that the prosobranch snail, *Juga* spp., was positive for *N. risticii* but did not look for any trematode infections in those snails. However, they did suggest that the rickettsia might actually infect a trematode parasite of the snail, including *Acanthatrium oregonense*. Pusterla and colleagues (2000) successfully transmitted PHF to horses by feeding sporocysts and cercariae of an unidentified digenetic species isolated from naturally infected snails, *Juga yrekaensis*, and re-isolating the bacterium from them. Kanter and colleagues (2000) reported *N. risticii* from an unidentified virgulate cercaria and their sporocysts parasitizing the prosobranch, *Elimia livescens*. Chae and colleagues (2000) detected *N. risticii* (= *Ehrlichia risticii*) in metacercariae in the juveniles and adults of caddisflies, mayflies, damselflies, dragonflies, and stoneflies. Although it is likely that horses acquire infection from ingestion of insects, it is also possible infection could occur by ingestion of infected snail or even free-swimming infected cercariae.

Bats are important in the epidemiology of *Neorickettsia risticii*. Pusterla and colleagues (2003) found *N. risticii* in the lecithodendriids *Acanthatrium* spp. and *Lecithodendrium*

spp. inhabiting the intestine of the bat *Myotis yumanensis* collected in northern California, United States. Maintenance of *N. risticii* in the wild is likely enhanced by vertical transmission. Gibson and colleagues (2005) revealed that *N. risticii* is present in the eggs of *A. oregonense* infecting bats providing evidence that it is vertically transmitted in the trematode which contributes to the maintenance of *N. risticii*. Greiman and colleagues (2016) demonstrated that presence of *N. risticii* occurs in all stages of the life cycle of digeneans (*Plagiorchis elegans*) providing further evidence that transmission of the infection may occur from the adult to larvae through the egg and horizontal transmission is not required. Greiman et al. (2017) reported that *N. risticii* was likely worldwide in distribution and consisted of a number of recognizable genotypes.

Ecology

Species of Lecithodendriidae are important components of many parasite community ecology studies. Bats have elevated metabolism and require high caloric intake. As such they are voracious aerial insect feeders and may consume 25–100% of their body weight daily, most coming from insects (Tuttle, 2005; Kunz et al., 2011). The high rate of insect consumption consequently results in high recruitment rates of helminth species that are transmitted by insects to bats, such as Lecithodendriidae and related digeneans. This may result in high diversity and high worm burden in bat helminth infracommunities with up to 11 species in some infracommunities (Coggins et al., 1982; Lotz and Font, 1983; 1991; Pistole, 1988; Estaban et al., 2001; Lord et al., 2012; Warburton et al., 2016a).

A basic question in parasite community ecology is, “What processes structure infracommunity assemblages?” The Lecithodendriidae as components of bat helminth infracommunities have been used to attempt to answer that question. Lotz and Font (1983; 1991; 1994) concluded that infracommunities were most likely the result of random recruitment and within-host interactions were of little importance. The majority of pairs of co-occurring species exhibited no associations; however, of the pairs that did, they found that pairs were more likely to be positively associated rather than negatively associated. Lotz and colleagues (1995) suggested that the structure of helminth infracommunities might be best explained by co-transmission of intermediate stages.

Warburton et al. (2016a; 2016b) examined external factors that might influence infracommunity differences and found that environmental variables, especially amount of land used for human development, explained most differences within a set of helminth component communities. The component communities reflect the pool of helminth species available to

form infracommunities within a geographical site. At the infracommunity level they found that host body condition and host immune response significantly affected total worm burden and, likely, community structure.

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