

**PHYLOGENETIC SYSTEMATIC ANALYSIS OF THE NEODERMATA
(PLATYHELMINTHES) AND ASPIDOBOTHREA (TREMATODA,
NEODERMATA) WITH INVESTIGATION OF THE EVOLUTION OF THE
QUINONE TANNED EGGSHELL.**

By

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A thesis submitted in conformity with the requirements for the degree of M. Sc.

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ABSTRACT

Phylogenetic systematic analysis of the Neodermata (Platyhelminthes) and Aspidobothrea (Trematoda, Neodermata) with investigation of the evolution of the quinone tanned eggshell. Masters of Science, 2001. David Zamparo, Graduate Department of Zoology, University of Toronto.

A phylogenetic analysis of the Neodermata and their closest relatives (the Rhabdocoela) was undertaken in order to provide a robust estimate of phylogeny. This phylogenetic analysis incorporates new character information and addresses a number of methodological issues raised by recent phylogenetic systematic analyses of the Platyhelminthes. A phylogenetic analysis of the Aspidobothrea incorporates a new genus, *Sychnocotyle* Ferguson et al. 1999, and 16 new morphological characters. This analysis tests three previously proposed family-level hypotheses. The two phylogenetic systematic studies undertaken herein provides the basis for a study of the evolution of quinone-tanned eggshell among the parasitic platyhelminths. It has been hypothesized that quinone-tanned eggshell are a “pre-adaptation” (exaptation) to endoparasitism. I evaluate this hypothesis by means of the comparative phylogenetic approach, which provides both a test and suggests future research.

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Chapter One

GENERAL INTRODUCTION

THE IMPORTANCE OF PARASITES

Parasitism is a ubiquitous and highly successful mode of life. Most avid naturalists have surely, and most likely unexpectedly, encountered parasitic organisms as a byproduct of interest in their hosts. Parasitism has arisen independently at least once in most phyla, and by some accounts the majority of species on this planet are parasites (Price, 1980). Parasites have received considerable attention from scientists because many of their members are of medical and commercial importance as parasitic diseases of humans and their livestock. References to parasitic diseases of humans and their livestock date back to ancient Egyptian and Roman civilizations (Roberts & Janovy, 1996). The first major treatise devoted to the subject, *De lumbricus alvum occupantibus* by Hieronymus Gabuccini, was published in 1547 (Reinhard, 1957). The importance of parasitic diseases is reflected in direct socio-economic terms, such as annual deaths revenue losses in agriculture, and in public health costs (see Roberts & Janovy, 1996). In addition, parasites have and continue to influence humanity in indirect ways by shaping diverse social, economic and cultural facets of our daily lives (see Desowitz, 1997; Zimmer, 2000). Studies in ecology, population biology, systematics, and evolution suggests that parasites may have a tremendous ecological influence on the ecosystems in which they live, making them important components of biodiversity studies (Brooks & Hoberg, 2000).

Only recently have parasites begun to play a prominent role in Darwinian-based evolutionary biology. Most notable are the 'Red Queen Hypothesis' (Van Vallen, 1973;

and see Ridley, 1995) and the “Hamilton-Zuk Hypothesis” (Hamilton & Zuk, 1982; Andersson, 1994; see discussion in Brooks & McLennan, 1993c). These hypotheses suggest that parasites are imposing strong selection pressures on their hosts. Two major texts published during the 1990’s (Brooks & McLennan, 1993c; Poulin, 1998) were concerned wholly with the evolution of parasites and their use in general evolutionary biology.

The three most species-rich, and best-studied, groups of parasitic helminths are the phylum Acanthocephala, and members of the phyla Nematoda and Platyhelminthes. The parasitic platyhelminths (the Neodermata) are a diverse and species-rich group, with over 15,000 species having been described, and many potential hosts remaining unsampled. Of all the parasitic helminths, the Neodermata represents the most tractable model system for evolutionary studies because it is one of the most extensively studied and phylogenetically analyzed groups. This phylogenetic database, accumulated over the past 25 years, is approaching 2,500 morphological character states (in addition to a rapidly growing molecular database), which permits resolution of relationships at least to the family level (see Brooks & McLennan, 1993c; Brooks & Hoberg, 2000 and references therein). This information represents an excellent platform for integrating more than two centuries of investigations on the development, ecology, and behaviour of neodermatans into a modern evolutionary context, and may also help test general hypotheses concerning the evolution of parasitism.

INTRODUCING THE NEODERMATA

The phylum Platyhelminthes (*platy*, flat; *helminth*, worm), so called because they are characteristically dorso-ventrally flattened worms, comprises both a non-monophyletic assemblage of free-living organisms (referred to as the “Turbellaria”), many of which engage in varying degrees of commensalism, and a derived monophyletic group of parasitic organisms, the Neodermata Ehlers, 1984. The Neodermata are classified into three major clades, the Trematoda, Monogenea, and Cestodaria:

1. The Trematoda (*trema*, with holes) is comprised of two sub-clades; (1) the Aspidobothrea (*aspis*, shield; *bothros*, holes), so named because the type species *Aspidogaster conchicola* has an enlarged and loculate ventral sucker; and (2) the Digenea, a name derived to reflect the life cycles of these flatworms (an alternation of generations). Trematodes are characterized by having an oral and a ventral sucker, the latter being a modification of the posterior adhesive organ. Some digeneans have secondarily lost the ventral sucker and the aspidobothrean *Stichocotyle* has a series of ventral suckers. Trematodes plesiomorphically have a two-host life cycle involving a mollusc and a vertebrate. Some trematodes have secondarily lost the vertebrate host, while some digeneans have added hosts to the plesiomorphic life cycle. Digeneans are characterized by, among other traits, the developmental innovation of asexual multiplication, whereby several generations of larva are produced within the mollusc, ultimately producing many infective larva, called cercariae. The cercariae will infect the definitive host (plesiomorphic two-host life cycle) through ingestion of the mollusc by the vertebrate. Where a second intermediate host is involved (derived three or four host life cycle), the cercariae, plesiomorphically escape from the mollusc and encyst in the

open environment, while infection through penetration of the host is derived. The resulting encysted form, called a metacercaria, infects the definitive or second intermediate host via ingestion. The second intermediate host serves a source of infection for the next host (four-host life cycle) or the definitive host, which acquires the infection through ingestion of the second intermediate host along with its infectious agents. Adult digeneans typically live in the intestine and associated offshoots of the digestive tract like the bile ducts, stomach, esophagus, nasal cavity and eustachian tubes. Infections of the lungs, blood vessels and several other sites of their vertebrate hosts including the eyes and oviducts also occur. Perhaps the most famous of these worms are the schistosomes, blood parasites of birds and mammals, whose cercariae produce a dermatitis known as 'swimmers itch', caused by immune reaction to these invasive larvae of which the human is not the specific host. The eggs of these adults can cause serious pathology to the liver and other organs of the host (including humans) as they work their way through various internal structures to exit the host. This migration of eggs leaves a characteristic abdominal distension if left untreated. This distension, unfortunately, is commonly associated with developing countries and generally interpreted as a byproduct of malnutrition. Currently a great deal of effort is put into eradication of schistosomes through research into new chemotherapies and biological methods to control the intermediate hosts.

2. The Monogenea are characteristically ectoparasitic on fishes, attaching themselves to the gills or over the skin, although some have secondarily acquired internal habitats (see Euzet & Combes, 1998 for review to all known exceptions). The posterior adhesive organ

of both larva and adult are armed with hooks throughout their ontogeny. These worms, unlike the trematodes, have a direct life cycle, through loss of the sympletiomorphic neodermatan arthropod host. A ciliated larva, called an oncomiracidium hatches from the egg, actively seeks its vertebrate host, attaches itself and clings tenaciously while creeping along the body surface looking for the particular part of the host where it will mature into an adult. The aquaculture industry is all too familiar with monogeneans. The direct life cycle means that not only can a single infected fish infect an entire stock, but also parasite loads can become lethal as fish are confined to small rearing pens. As the parasite load increases, fish respond by secreting mucous that ultimately suffocates and kills the host.

3. The Cestodaria comprises the ((Gyrocotylea (Amphilinidea + Eucestoda))), the latter being true tapeworms. Except for the amphilinids, and some caryophyllid eucestodes, which are found in the body cavity of their host, these are strictly intestinal worms. Cestodarians have lost their gut and associated feeding apparatus, instead acquiring nutrients through their tegument. The gyrocotyliids and amphiliniids are species-poor, represented by only 10 and 8 nominal species, respectively. Amphiliniids are not as diverse as their hosts while the gyrocotyliids seem confined to their holocephalan hosts which are themselves extremely old and species poor (Brooks and Bandoni 1988: Brooks and McLennan 1993 b, c). The life cycle requires at least two hosts. The first host in the life-cycle is invariably an arthropod. Aquatic and terrestrial hosts have been colonized by cestodes both by releasing eggs that are able to withstand desiccation and by their use of appropriate intermediate hosts, like the trematodes but unlike the monogeneans.

Plesiomorphically the larva of cestodarians, like monogeneans, possess hooks on the posterior adhesive organ but these hooks are not retained by the adult cestodarians. (For good reviews of platyhelminth life cycles see Olsen, 1974; Yamaguti, 1975; Schell, 1985; for reviews of their general biology see Smyth, 1994; Roberts & Janovy, 1996).

THE FOCUS OF THIS THESIS

Chapter 2: Researchers have been studying the phylogenetic relationships among platyhelminths in general (Ehlers, 1985a,b, 1986; Jondelius & Tholleson, 1993; Littlewood et al., 1999a,b) and the Neodermata in particular (Brooks, 1982; Brooks et al., 1985; Brooks & McLennan, 1993; Rohde, 1990; Rohde et al., 1990; Litvatis & Rohde, 1999) for nearly 20 years. Although most of those studies have produced highly congruent results, there is still no general consensus on two matters. First, which platyhelminth clade is the sister-group to the parasitic Neodermata? Four candidates have been proposed: the Temnocephalida (Brooks, 1982; 1989a,b; Brooks et al., 1985a; Brooks & McLennan, 1993c), the Dalyelliidae + Typhloplanidae (Ehlers, 1984, 1985a,b, 1986, 1995; Ehlers & Sopott-Ehlers, 1993); the Fecampiidae (Rohde, 1990, 1991; Litvaitis & Rohde, 1999), and *Urasotoma* (Rohde et al., 1990; Williams, 1993; Watson, 1997; Kornakova & Joffe, 1999). Second, where does the enigmatic *Udonella* belong? Parasite taxonomists have debated whether *Udonella* is a derived monogenean (e.g. Furhman, 1928; Dawes, 1946; Sproston, 1946; Littlewood et al., 1999a,b) or whether the taxon is a basal member of the neodermatans (e.g. Ivanov, 1952; Ivanov & Mamkaev, 1973; Bychowsky, 1961; Brooks et al., 1985a and Kornakova, 1988). None of the preceding studies have evaluated the same set of data or the same set of relevant taxa. Understanding the evolution of life history traits within the Neodermata requires

information from outgroups, in particular the sister-group. In this chapter, therefore, I address the “sister-group” problem by combining all available data from all neodermatan taxa and potential sister group candidates to produce as robust an estimate of phylogenetic relationships as is presently possible.

Chapter 3: Within the Neodermata, questions have also arisen regarding the monophyly of, and relationships within, the Aspidobothrea. These questions revolve primarily around one group, the Aspidogastridae, which has been placed outside the aspidobothreans as the sister-group to the Digenea (Gibson 1987) or within a monophyletic Aspidobothrea as the most derived (Brooks et al. 1989) or basal most (Pearson, 1992) member. In this chapter I ask two questions, Is Aspidobothrea monophyletic? and, What are the relationships among the major subgroups within the clade? I will answer these questions by combining all of the available data from the previous literature, adding new characters to the data matrix, and adding a genus (*Sychnocotyle* Ferguson et al., 1999) that was previously not included in any analyses.

Chapter 4: Platyhelminth eggs are diverse. Some have an operculum, a lid-like structure, others have filaments at their pole(s), and the eggs may be deposited at various stages of development, from an uncleaved embryo to a fully developed larva. One of the most obvious features about the eggs is that they may be coloured, ranging from dark brown to pale yellow. Such coloured eggs are called ‘tanned’ because the colour is thought to reflect the presence of quinone-tanned (sclerotized) eggshell proteins. Llewellyn (1965) proposed that tanned eggs were a “pre-adaptation” to parasitism. The hypothesis contends

that without such an eggshell the free-living, ancestral platyhelminths could not have successfully colonized the intestine of a vertebrate. As such, the tanned egg is a “key innovation” that allowed for the passage of eggs through the vertebrate host’s gut. This hypothesis has thus far been uncritically accepted (e.g. Wharton, 1983; Kearn, 1998) or ignored. Recent advances in theoretical evolutionary biology allow for a revisiting of this macroevolutionary question. Such a hypothesis lends itself to the comparative phylogenetic approach (Brooks & McLennan, 1991) and will provide for both a test and guide to future research.

A comparative phylogenetic study requires a robust estimate of phylogeny upon which the evolution and diversification of traits can be deciphered. In this instance, a phylogeny for the Neodermata and their closest relatives within the Rhabdocoela, as well as detailed phylogenies for the parasitic groups themselves are needed. As noted above, previous phylogenetic hypotheses of the Neodermata have produced congruent results with the exception of the exact sister group of the Neodermata, the placement of *Udonella*, and the relationships among the aspidobothreans. I will use the results of the previous two chapters to provide the most up to date phylogenetic hypothesis with which to examine the question of the evolution of quinone tanning in these organisms.

Chapter Two

PHYLOGENETIC ANALYSIS OF THE RHABDOCOELA (PLATYHELMINTHES) WITH EMPHASIS ON THE NEODERMATA AND RELATIVES

INTRODUCTION

The phylogenetic relationships among members of the phylum Platyhelminthes have received extensive scrutiny for nearly twenty years. Ehlers (1984) published the first phylogenetic systematic treatment for the phylum at about the same time parasitologists were turning their attention towards intensive phylogenetic analysis of the parasitic groups within that phylum (the Neodermata and relatives: Brooks, 1982, 1989a,b; Brooks et al., 1985a,b). Although most of the studies since those initial attempts have produced remarkably congruent results, there have been some disagreements, especially about the identity of the sister group to the Neodermata (Ehlers, 1984, 1985a,b, 1986; Brooks, 1982, 1989a,b; Brooks et al., 1985a; Brooks & McLennan, 1993c; Rohde, 1990, 1991; Rohde et al., 1990; Williams, 1993; Jondelius & Tholleson, 1993; Watson, 1997).

Congruence notwithstanding, some parasite taxonomists (e.g., Rohde, 1990, 1994a, 1996) have objected to the hypothesized relationships among the parasitic groups, the choice of characters, and the evolutionary implications of the phylogenetic systematic analyses, which call into question a number of long-standing myths about parasite evolution (Brooks and McLennan, 1993a,b,c). More recently the debate has shifted to assertions that molecular data are inherently superior to morphological data as markers of phylogeny (e.g., Justine, 1998b; Littlewood et al., 1999a,b; Litvatis & Rohde, 1999). Recent molecular studies, for example, have either ignored (e.g., Baverstock et al., 1991;

Blair, 1993; Litvatis & Rohde, 1999) or minimized (Rohde et al., 1995; Littlewood et al., 1999a,b) the extensive morphological database that has been collected for the parasitic platyhelminths over the last 200 years. The assertion that morphological data are not as reliable as molecular data is a curious one, given that (1) morphological studies routinely produce fewer equally parsimonious trees with better goodness of fit values than their wholly molecular counterparts and (2) molecular studies have often produced results virtually identical to those already published by morphologists (e.g., Hoberg et al., 1997; Mariaux, 1997; Hoberg et al., in press). This same debate has been carried out by systematists working on many different taxa. The result of that debate has been widespread agreement that the goal of systematics should be the production of phylogenetic hypotheses based on the most parsimonious (i.e., most scientifically robust) arrangement of all available evidence (see Kluge, 1989, 1997, 1998a,b, 1999).

Jondelius & Tholleson (1993) provided the first direct phylogenetic systematic link between intense analysis of the parasitic groups and extensive analysis of the Platyhelminthes as a whole with their pioneering analysis of the Rhabdocoela. The emphasis of the present study is the Neodermata and their closest relatives, incorporating new character information that has been collected since the study by Jondelius & Tholleson (1993), with particular interest in answering two questions: What is the sister-group of the Neodermata?; and Do the new data support or refute previous hypotheses of phylogenetic relationships within the Neodermata? In doing so, discussion of the rationale for *a priori* exclusion of many morphological characters from recent phylogenetic analyses of these taxa is considered. In this regard, it will be shown that the

database of suitable morphological characters is far larger than that used in recent “total evidence” studies.

MATERIALS AND METHODS

Taxa.

The following 24 taxa were included in this study (see also Jondelius & Tholleson, 1993): Umagillidae, Pseudograffillinae, Graffillinae, Acholadidae, Pterastericolidae, Fecampiidae, Hypoblepharinidae, Dalyellidae, Provorticidae, Temnocephalida, Kytorrhynchidae, Promesostomidae, Solenopharyngidae, Trigonostomidae, Typhloplanidae, Kalyptorhynchidae, *Urastoma*, *Udonella*, Aspidogastrea, Digenea, Monogenea, Gyrocotylidea, Amphilinidea, and the Eucestoda.

Character List.

Characters were recorded based upon extensive descriptions in the literature: Aken'ova & Lester (1996); Bandoni & Brooks (1987a,b); Boeger & Kritsky (1993, 1997); Brooks (1982, 1989a,b); Brooks & McLennan (1993a,b,c); Brooks et al. (1985a,b, 1989, 1991); Bullock (1965); Cannon (1982, 1987); Ching & Leighton (1993); Christensen (1976); Christensen & Kanneworff (1965); DeClerk & Schockaert (1995); Ehlers (1984, 1985a,b, 1986, 1995); Ehlers & Sopott-Ehlers (1993); Fleming (1986); Fleming et al. (1981); Hoberg et al. (1997, in press); Hyman (1951); Ivanov (1952); Joffe & Kornakova (1998); Jondelius (1991, 1992); Jondelius & Tholleson (1993); Justine (1990, 1991, 1993, 1995, 1998a); Kanneworff & Christensen (1966); Kornakova & Joffe (1999); Koie & Bresciani (1973); Lee (1972); Littlewood et al. (1998, 1999a); Noury-Srairi et al. (1989a,b); Rohde (1986a,b, 1987, 1989, 1990, 1991, 1994b, 1998); Rohde & Watson (1993); Rohde et al.

(1987a,b, 1989a,b, 1992, 1995, 1999); Shinn & Christensen (1985); Sopott-Ehlers (1991, 1996, 1998, 2000); Sopott-Ehlers & Ehlers (1995, 1997, 1998); Watson (1997, 1998a,b); Watson & Jondelius (1995); Watson & L' Hardy (1995); Watson & Rohde (1994a,b, 1995a,b,c); Watson & Schockaert (1996, 1997); Watson et al. (1992, 1995); Williams (1993); Wirth (1984); Xylander (1986, 1987a,b,c,d, 1988a,b, 1989, 1990). Characters were polarized using information on platyhelminth groups other than the Rhabdocoela summarized primarily in Ehlers (1984, 1985a,b, 1986, 1995), Jondelius & Tholleson (1993) and Littlewood et al. (1998, 1999a). "?" indicates that the state of the character is unknown in a particular taxon. Higher taxa that are polymorphic for a character were coded with the plesiomorphic state, as per Jondelius & Tholleson (1993) and standard phylogenetic systematic practice (Wiley, 1981; Wiley et al., 1991, in press; Brooks & McLennan, 1991; McLennan & Brooks, in press). The data matrix is given in Table 2.1.

Spermatozoal Ultrastructure

1. Number of sperm axonemes. Two (0); none (1).
2. Axonemes. Free (0); incorporated into sperm cell body by proximo-distal fusion (1);
incorporated into sperm cell body by distal proximal fusion (2).
3. Dense bodies. Present (0); absent (1).
4. Reverting migration which leads to the nucleus occupying a more distal position
relative to the basal bodies. Absent (0); present (1).
5. Reverting migration includes a backward movement of the basal bodies and their
axonemes to a proximal position. Absent (0); present (1).
6. Basal bodies retain their proximal position. Absent (0); present (1).

7. Electron dense granules. Absent (0); present (1).
8. Spermatogenesis. Mature spermatozoa lacking dense heel, rotation of flagella, and spur (0); mature spermatozoa possessing dense heel, rotation of flagella, and spur (1).
9. Intercentriolar body during. present, well developed during spermatogenesis (0); present, weakly developed (1); absent (2).
10. Peripheral layer of microtubules in spermatozoa. Not spirally arranged (0); spirally arranged (1).
11. Mitochondria in sperm. Present (0); absent (1).

Protonephridia Ultrastructure

12. Longitudinal ribs (rods). Absent (0); present, in 2 rows, inner formed by terminal cell, outer formed by canal cell (1); present, in single row of longitudinal ribs formed by canal cell (2).
13. Interdigitating processes of weir. Absent (0); present (1).
14. Terminal perikaryon. Present (0); absent (not close to flame) (1).
15. Support structure of ribs (rods). Microtubules absent (0); microtubules present (1).
16. Pair of cytoplasmic cords from canal cell connected by a desmosome. Absent (0); present (1).
17. Surface of capillary. "Saccate"/simple (0); lamellae of connected spaces (1); microvilli (2).

Osmoregulatory System Micro-structure

18. Secondary protonephridial system of canals and pores. Absent (0); present (1).
19. Giant paranephrocytes. Absent (0); present (1).
20. Osmoregulatory system. Never reticulate (0); becomes reticulate in late ontogeny (1).

- 21. Osmoregulatory system in early ontogeny. Not reticulate (0); reticulate (1).
- 22. Protonephridia in larvae. In anterior end of body (0); in anterior and posterior end of body (1); in posterior end of body (2).
- 23. Desmosomes in the passage of the first excretory canal cell. Present (0); absent (1).

Tegument

- 24. Tegument. Cellular (0); syncytial, protruding to surface between epidermal cells (1); syncytial, not protruding to surface between epidermal cells (2).
- 25. Adult body ciliation. Completely ciliated (0); at least some body ciliation lost (1); all ciliation lost (2). Some umagillids have lost body ciliation (Jondelius, 1991); this will be considered a derived trait within the group the family is thus considered to be plesiomorphically ciliated.
- 26. Rhabdites. Present (0); absent (1).
- 27. Duo gland organ. Present (0); absent (1).
- 28. Rhabdomeric eyes. Two (0); none (1); four (2).
- 29. Lensing. Non-mitochondrial (0); mitochondrial (1); no lenses (2).
- 30. Rhabdoids (large granular and vesicular bodies in epidermis). Absent (0); present (1).
- 31. Spur projecting from the basal body opposite the horizontal rootlet of epidermal cilia. Absent (0); present (1).
- 32. Pharyngeal musculature. Circular muscle innermost (0); longitudinal muscle innermost; (1) circular muscle layer only (2); pharynx absent (3).
- 33. Dictyosomes and endoplasmic reticulum in larval/juvenile epidermis. Present (0); absent (1).
- 34. Larval epidermis. Not shed at end of larval stage (0); shed at end of larval stage (1)

35. Cilia of larval epidermis. With more than one rostrally-directed rootlet (0); with one rostrally-directed rootlet (1).
36. Specialized microvilli and microtubules in epithelium. Absent (0); present (1); modified into microtriches (2).
37. Epithelial sensory cells. EM-dense collars absent (0); EM-dense collars present (1).
38. Post-larval epidermis. Not syncytial (0); syncytial [neodermis] (1).
39. Excretory vesicles. Lateral, paired (0); single, medial opening postero-dorsally (1).
40. Cephalic tentacles. Absent (0); present (1).
41. Vitelloducts. Absent (0); present, lining not syncytial (1); present, lining syncytial (2).
42. Anterior and posterior nervous system commissures. Single bilobed units (0); two bilobed units (1).
43. Ciliary bands on embryo. Absent (0); present, in three rows (1).
44. Larval epidermis. Not syncytial (0); syncytial (1).
45. Endoderm. Present in embryos (0); absent in embryos (1).
46. Vitellogenic cells. With more than one kind of electron-dense vesiculated inclusions (0); with one kind of electron-dense vesiculated inclusion (1).
47. Inner longitudinal muscle layer. Poorly developed (0); well developed (1).
48. Antero-lateral notch. Absent (0); present (1).
49. Nuclei in larval epidermis. Present (0); absent (1).
50. Multi-ciliary nervous receptors. Present (0); absent (1).
51. Epithelial lining of genital ducts. Not syncytial (0); syncytial (1).
52. Protononephridial ductules. Ciliated (0); not ciliated (1).
53. Medullary and cortical distinction. Not apparent (0); apparent (1).

54. Protein embedments in larval epidermis. Absent (0); present (1).

Reproductive System

55. Male intromittent organ. Simple stylet (0); cirrus [sometimes mistakenly called a penis] (1); copulatory papilla (2); complex stylet (3); absent (4). Monogeneans do not have a copulatory stylet (the accessory piece in some Monogeneans is an independently evolved structure, and a cirrus is plesiomorphic for the group: Boeger & Kritsky, 1993, 1997). The copulatory papillae of Gyrocotylidea and Amphilinidea may be vestigial/reduced cirri.

56. Openings of male and female gonopores. Common genital atrium (0); separate (1); separate sexes (2).

57. Position of genital atrium or genital pores. Posterior (0); caudal (1); anterior (2); lateral (3).

58. Muscular copulatory bulb. Present (0); absent (1).

59. Testes. Paired (0); single (1); multiple, in two lateral bands (2). A single testis occurs convergently within Aspidogastrea, Digenea, Monogenea, but phylogenetic analyses (Brooks et al., 1985b, 1989; Boeger & Kritsky, 1993, 1997) have shown that paired testes are plesiomorphic in each case.

60. Female reproductive system. Simple oviduct (0); oviduct expanded to form antrum (functional uterus) without separate opening (1); oviduct coiled, with small secondary tube (Laurer's Canal) opening to the surface (not opening to surface or absent in derived taxa), used to vent excess material from oviduct (2); oviduct relatively straight, with secondary tube forming separate tubular uterus with uterine pore opening to surface (3); oviduct relatively straight, uterus highly coiled (4). Previous

phylogenetic analyses of the Cercomeria (Brooks et al., 1985a) and Rhabdocoela (Jondelius & Thollesson, 1993) have treated various portions of the female reproductive system as a series of separate characters. These include the presence or absence of a vagina, presence or absence of a uterus, and their position(s) relative to the male gonopore and to the body in general. This has been complicated in part by the fact that most neodermatans possess two (or even three) openings of the female reproductive tract.

The majority of Cercomerideans (Trematoda + Cercomeromorphae) exhibit a bifurcated oviduct, with each bifurcation forming a tube that opens to the exterior. These tubes have been functionally defined in the parasitic taxa, i.e., any egg-containing tube is called the uterus, and the alternative tube is called the vagina. Thus, in the trematodes the male gonopore and uterine pore are said to be proximate, with the vagina separate. The vagina (called the Laurer's Canal) is almost always short, narrow and relatively straight (in many cases it does not open to the exterior or is even lost) and the uterus is generally coiled. In the Monogenea, all three pores are separate plesiomorphically, with the apomorphic state "uterine and male pores proximate" being displayed by some taxa. The uterus and vagina are relatively well developed, short and straight. Doubling of the vagina (considered by Brooks et al., 1985a to be an autapomorphy for the Monogenea) appears to be an apomorphic trait within the Monogenea (Boeger & Kritsky, 1993, 1997). In the Gyrocotylidea, all three pores are proximal and separate (the plesiomorphic condition for the Monogenea). In the Cestoidea (Amphilinidea + Eucestoda), the male pore and the vaginal pore are proximal, with the uterine pore distantly situated. Finally, within the

Cestodaria (Gyrocotylidea + Amphilinidea + Eucestoda), the uterus is plesiomorphically highly coiled (it is apomorphically saccate in the Eucestoda: Brooks et al., 1991; Hoberg et al., 1997, in press). Such coiling also occurs convergently within the Monogenea (Boeger & Kritsky, 1993, 1997). Establishing homologies for these structures across taxa has been difficult, demanding complex evolutionary scenarios to explain the diversity of ducts, tubes, pores, and their positions relative to each other. It is suggested here that those scenarios have been unnecessarily complex and instead the following alternative is proposed.

The basic unit of the platyhelminth female reproductive system is an ovary (paired plesiomorphically) connected to a tubular oviduct, a canal which originates from the ovary and terminates in a genital pore that communicates with the external environment. Plesiomorphically, this canal functions as both vagina (receiving sperm) and uterus (delivering eggs to the external environment) and is situated proximate the male genital pore, either sharing a common atrium with the male pore or not (Figure 2.1). Within the Rhabdocoels, including fecampiids, *Urastoma* and *Udonella*, the oviduct is expanded, producing a functional uterus, or antrum. The antrum may be symmetrical or asymmetrical, it may be small, containing a single egg, or large, containing several eggs, and it may be saccate or somewhat tubular.

I propose that, regardless of the perceived function, the oviduct is that portion of the female reproductive system plesiomorphically proximal to the male genital pore, with which it may or may not share a common gonopore (genital atrium). The secondary duct may be proximal to (Monogenea, Gyrocotylidea) or distant from the openings of the oviduct and male genital pore (dorsal in the trematodes, ventral in the

Amphilinidea and Eucestoda). The Laurer's Canal is thus actually homologous with the uterus, not the vagina, of the Cercomeromorphae. The current function of the Laurer's Canal, expulsion or digestion of sperm and other debris from the fertilization and egg-making process (e.g. Juel's Organ in some hemiuriform digeneans), may well have been the original function of the duct. The widespread belief that the Laurer's Canal is a vestigial vagina stems from discussions of the presumed degenerate evolutionary nature of parasites beginning in the late 19th century. Actual evidence of the Laurer's canal use as a vagina is rare. For example, without sectioning his material, Cohn (1902) stated that he had found one specimen of *Liolope copulans* extruding its cirrus into the Laurer's Canal of another. Brooks & Overstreet (1978), however, noted that they never found any evidence of this behavior in a close relative of *L. copulans*, *Dracovermis occidentalis* Brooks & Overstreet, 1978. They stated that "...based on the narrow Laurer's Canal, wide cirrus, thick and large genital atrium, and uterus occasionally entirely packed with sperm in *Dracovermis occidentalis*, we doubt that Laurer's Canal in that species serves for more than elimination of excess products." Increased egg-holding capacity in the trematodes is made possible by extensive coiling of the oviduct, while in the cercomeromorphs it is due to the elongation (Monogenea) and coiling (Gyrocotylids, Amphilinids, and Eucestodes) of the Laurer's Canal, co-opted (an exaptation: Gould & Vrba, 1982) as a functional uterus distinct from the oviduct.

The above proposal provides a succinct conception of the evolution of the number, nature, and position of the ducts and pores of the female reproductive system in the Cercomeridea. Interestingly, it is also the scheme proposed by Looss (1893) but

apparently forgotten until now. The above character coding reflects this new hypothesis. Finally, many trematodes have been described as exhibiting a glandular muscle surrounding the terminal end of the uterus called the “metatherm” (Smyth, 1994) or “metraterm” (Noble et al., 1989). Many eucestodes have been described as having a muscular structure at the terminal end of the vagina called a “vaginal sphincter”. If the hypothesis above is true, it is likely that these structures are homologous. At present, there is insufficient information to use this as a character.

61. Ovary. Paired (0); single and spherical (1); single and bilobed (2).
62. Mehlis' gland. Absent (0); present (1).
63. Vitellaria. Paired, compact, medial (0); lateral and follicular (1); compact and medial vitellarium (2). Compact vitellaria occur convergently in a number of digenean and eucestode groups, but are apomorphic within those taxa (Brooks et al., 1985b, 1989, 1991; Hoberg et al., 1997, in press).
64. Cirrus. Absent (0); present, muscular and aspinose (1); present, muscular and spinose (2).
65. Testes. Preovarian (0); postovarian (1); dioecious (2). Dioecy appears convergently in some digenean (e.g. Schistosomatidae) and some eucestode groups (e.g., *Dioecotaenia*, *Dioecocestus*, *Shipleya*, *Gyrocoelia*) (Brooks et al., 1985b, 1989, 1991; Hoberg et al., 1997, in press). Because the Fecampiidae are dioecious the character is inappropriate. There are two options available in this situation, either coding the Fecampiids as '9' - inappropriate, or as '2', as the condition is autapomorphic. Choice of coding in this instance does not affect the analysis and thus the latter is used.

66. Eggs, round adhesive disc at the end of filament where the substance of the disc is secreted later when the worm attaches the egg to the body of the host. Absent (0); present (1).
67. Vitellaria. Not encircling entire body (0); encircling entire body, extending along entire body length (1). The apomorphic state appears convergently in some eucestode groups (Hoberg et al., 1997, in press).
68. Permanent uterine pore. Absent (0); present, dorsal (1); present, ventral (2).
69. Uterine pore. Not proximal to pharynx (0); proximal to pharynx (1).
70. Uterus. Coiled, not N-shaped (0); "N"-shaped (1).

Digestive System

71. Mouth and pharynx. Present (0); absent (1). The apharyngeate condition exhibited by some Monogeneans and digeneans is convergently evolved within those groups (Boeger & Kritsky, 1993, 1997; Brooks et al., 1985b, 1989).
72. Doliiform pharynx (pharynx bulbosus of Jondelius & Tholleson, 1993). Present (0); absent (1).
73. Pharynx placement. In anterior half of worm (1); medial to posterior half of worm (2); absent (3). This is a difficult character to polarize because most outgroups are polymorphic. Jondelius & Tholleson (1993) proposed that anterior was plesiomorphic for the rhabdocoels, but their own argument can also be used to support the contention that a pharynx in the mid to posterior half of the body is plesiomorphic; therefore, I have coded the outgroup state as "?" and given each ingroup state a non-zero number.
74. Oral sucker. Lacking a capsule (0); with a capsule (1).

75. Gut shape. Saccate (0); bifurcate (1); lacking in adults (2). Convergent reversal to a saccate gut from a plesiomorphically bifurcate gut occurs within the Aspidogastreaans, digeneans and Monogeneans (Brooks et al., 1985b, 1989; Boeger and Kritsky, 1993, 1997).

76. Oral sucker. Absent (0); present (1).

Posterior Adhesive Organs

77. Posterior adhesive organ. Absent (0); present, not delimited by capsule (1); present, delimited by capsule (2).

78. Posterior adhesive organ. Absent (0); present, no hooks (1); present, with hooks (2).

79. Posterior adhesive organ. Absent (0); present throughout life (1); present only during early development, partially invaginated (2).

80. Posterior adhesive organ. Absent (0); present, terminal (1); present, ventral (2).

81. Posterior sucker. Without transverse septa (0); hypertrophy and linear subdivision of posterior sucker by transverse septa (1).

82. Hooks on posterior end of larva. Absent (0); 16 equal-sized hooks (1); 10 equal-sized hooks (2); 6 large and 4 small hooks (3); six hooks (4).

83. Posterior body invagination. Absent (0); present (1).

84. Rosette at posterior end of body. Absent (0); present (1).

Ontogeny

85. Miracidium. Absent (0); present (1).

86. Sporocyst. Absent (0); present (1).

87. Cercaria. Absent (0); present (1).

88. Proceroid. Absent (0); present (1).

89. Plerocercoid. Absent (0); present (1).

90. Cerebral development in larvae. Present (0); absent (1).

91. Extra embryonic membrane. Not formed by embryo (0); formed by embryo (1).

Analyses performed

Data were analyzed using standard Hennigian Argumentation (see Hennig, 1966; Wiley, 1981; Wiley et al., 1991, in press; Brooks & McLennan, 1991), and results were generated using the Branch and Bound option on the computer program PAUP 4*, implemented on Macintosh G3/400, G4/450, and G4/500 computers. Acctran and Deltran character optimization produced the same results. Bootstrap and Jackknife analyses were performed using 10,000 replicates, with the exception of the complete data set, for which only 100 replicates were performed due to computational constraints.

RESULTS

Analysis of all 91 characters, unordered, produces 98 MPTs, each 190 steps long with a CI of 67% and RCI of 55%. Forty-one of these MPTs place the Kytorrhynchidae, Promesostomidae, Trigonostomidae, Typhloplanidae, Dayellidae and Temnocephalida at the base of the tree, similar to results reported by Jondelius & Tholleson (1993) and Littlewood et al. (1999a,b). The remaining 57 MPTs suggest that those taxa are part of an inclusive clade also containing the Neodermata, a result more similar to the hypothesis proposed by Ehlers (1984, 1985a,b, 1986, 1995) and Brooks et al. (1985a; Brooks, 1989a,b; Brooks & McLennan, 1993). Figure 2.2 is the 50% majority rule consensus tree for those 98 MPTs. This “dichotomous” result in the placement of the Kytorrhynchidae,

Promesostomidae, Trigonostomidae, Typhloplanidae, Dayellidae and Temnocephalida seems to be the product of missing data for key taxa in characters 17 and 28. In computer-assisted phylogenetic studies, some configurations of missing data can produce effects similar to long branch attraction effects in analysis of nucleotide sequence data (see Nixon & Davis, 1991; Platnick et al., 1991; Maddison, 1993; Wilkinson, 1995). Other characters show low character consistencies on the tree as well, but their inclusion does not affect the stability of the results. Characters 17 and 28 would appear to be too poorly-documented at present to be useful.

Removing characters 17 and 28 produces two most parsimonious trees (MPT: Figure 2.3), 181 steps long with a consistency index (CI) of 0.69 and a rescaled consistency index (RCI) of 0.56, differing only in the degree of resolution of that portion of the tree containing the **Umagillidae, Achocladidae, Grafilliinae, Pseudograffillinae, Pterastercolidae** and **Hypoblepharinidae**. Characters 16, 22, 24, 41, 60, 61, 78, 79 and 82 are multistate transformation series produced by combining what were previously considered to be a series of binary characters (Brooks & McLennan, 1993c). The relationships shown in Figure 2.3 supported ordering those transformation series. Phylogenetic analysis with those 9 characters ordered produced the same results as Figure 2.3. Successive approximations re-weighting of the data produced the single tree shown in Figure 2.3a.

Six taxa in the present study, the **Acholadidae, Pseudograffillinae, Hypoblepharinidae, Solenopharyngidae, Promesostomidae, and Kytorrhynchidae** have substantial missing data entries, and the portion of the tree containing the **Umagillidae, Pseudograffillinae, Graffillinae, Acholadidae, Pterastercolidae, Hypoblepharinidae**

produces the two MPTs shown in figure 2.3. Not surprisingly, then, Bootstrap and Jackknife analyses indicate that only the groupings of ((Dalyelliidae + Temnocephalidae) Typhloplanidae) and of ((Fecampiidae + *Urastoma*) (*Udonella* ((Aspidbothrea + Digenea) (Monogenea (Gyrocotylidea (Amphilinidea + Eucestoda)))))) are robust (Figure 2.4). Given recent successes at finding many morphological traits for other platyhelminth groups (e.g., Lundin, 2000), there is reasonable confidence that sufficient characters are there to be discovered, and a fully robust assessment of the Rhabdocoela is feasible. The rest of this study will concentrate on the Neodermata and their closest relatives for which the results indicate the analysis is robust.

The placement of the Temnocephalida in this analysis precludes the interpretation that all posterior holdfast organs in this clade are homologous. The taxon *Cercomeria* Brooks, 1982 therefore cannot be maintained, as suggested by Ehlers & Sopott-Ehlers (1993) and Rohde & Watson (1995). The clade of Fecampiidae + *Urastoma* as the sister group of the Neodermata supports the monophyly of the Revertospermata Kornakova & Joffe, 1999 but not the Mediofusata Kornakova & Joffe, 1999.

DISCUSSION

Discussions of the phylogeny of the Neodermata revolve around two questions: (1) What is the sister group of the Neodermata and (2) how does the choice of sister groups affect hypotheses of relationships among taxa within the Neodermata? With regard to the first question, four taxa have been previously suggested as the sister group of the Neodermata: (1) the Dalyelliidae and Typhloplanidae (Ehlers, 1984, 1985a,b, 1986, 1995; Ehlers and Sopott-Ehlers, 1993), (2) the Temnocephalida (Brooks, 1982,

1989a,b; Brooks et al., 1985a; Brooks & McLennan, 1993c), (3) *Urastoma* (Rohde et al., 1990; Williams, 1993; Watson, 1997; Kornakova & Joffe 1999) and (4) the Fecampiidae (Rohde, 1990, 1991; Litvaitis & Rohde 1999). This study included all four candidates in the same analysis, and the results indicate that they comprise the four closest relatives of the Neodermata (Figure 2.3). With respect to the second question, the present analysis supports the monophyly of the Monogenea and the placement of *Udonella* as the basal member of the Neodermata as originally proposed by Brooks et al. (1985a). Re-analyzing the present data set using any number and combination of the four putative sister groups as outgroup taxa produces the same result. This occurs because the data for relationships within the Neodermata are highly robust (CI = 94%, RCI = 87%) making any combination of the four candidates suitable outgroups. The portion of the tree comprising the (Fecampiidae + *Urastoma*) + Neodermata is slightly less robust (CI=90%, RCI=82%) because the Fecampiidae + *Urastoma* clade is not as well-supported (see Bootstrap and Jackknife values on Figure 2.5).

Brooks et al. (1985a) used a data set of 39 transformation series in their initial analysis of the Neodermata; this produced a single MPT 41 steps long (CI=95%) depicting the same relationships as shown in Figure 2.3. In that analysis the authors used only attributes deemed informative by authors of numerous earlier studies in order to demonstrate that differences in results were due to differences in methods of analysis, not to choice of characters. Adding more morphological traits produced a data set of 127 binary characters (Brooks 1989a,b) corroborating the original phylogenetic hypothesis, producing a single MPT 131 steps long (CI = 97%). Brooks and McLennan (1993c) produced the same MPT 161 steps long for 153 apomorphic traits (CI = 95%). In the

present study, some characters were modified according to new findings, some redundant characters listed by Brooks and McLennan (1993c) were combined, and 47 fewer autapomorphies were used, resulting in the same MPT 107 steps long for 100 apomorphic traits (CI= 93%); including the 47 autapomorphies produces a single MPT for the Neodermata 154 steps long for 147 apomorphic traits (CI = 95%).

Despite consistent robust support for this hypothesis during the past 15 years, some researchers have felt uncomfortable with the results (Rohde, 1990, 1994a, 1996; Justine, 1998b; Littlewood et al., 1998, 1999a,b). It is suggested here that misunderstandings about phylogenetic systematics have been responsible for these differences of opinion. The most fundamental misunderstanding stems from the way in which phylogeneticists determine homologous character states. All systematists begin the search for homology by using a set of criteria, such as those proposed by Remane (1952), to determine whether two or more characters are “similar” (see discussion in de Pinna, 1991). These similarities apply to both identity (a finger is a finger) and also transformation (a bird’s wing is a tetrapod forearm). Assessing similarity based upon such biological criteria, without recourse to knowledge of underlying genealogical relationships, eliminates any hint of circularity in the process (see Eldredge & Cracraft, 1980; Wiley, 1981; Wiley et al., 1991, in press; Brooks & McLennan, 1991; McLennan & Brooks, in press). The difference among systematists begins with how those similarities are treated next. Phylogenetic systematists use assessments of similarity to construct *hypotheses* of homology “If a and b look the same (e.g., are in the same position, develop from the same tissue), then they are homologous”. This is called Hennig’s Auxiliary Principle (see Hennig, 1966; Wiley, 1981; Wiley et al., 1991, in

press; Brooks & McLennan, 1991; McLennan & Brooks, in press). These hypotheses are tested by using phylogenetic systematics and are ultimately corroborated or rejected. In the latter case one concludes that the similarity is due to homoplasy.

Some taxonomists, on the other hand, believe that they can make *a priori judgements* about which similarities are due to homology, and which are due to homoplasy, and thus eliminate some characters (the putative homoplasies) from the data set before the analysis begins. Such *a priori* judgements are valid only if they are supported by evidence. For example, experimental research has demonstrated that characters such as the number of vertebrae or fin rays in stickleback fishes are strongly influenced by the temperature under which the larvae develop (Lindsay, 1962; Hagen, 1967). Reporting number of vertebrae or fin rays without adjusting for developmental temperature, an almost impossible feat in wild caught fish, thus introduces a known source of homoplasy into the data set. In this case systematists are justified in eliminating these traits from their analysis *a priori*. Because such data are rare, however, it becomes important to ask “what supports the elimination of a particular character, or type of character, from an analysis?”.

With regard to the Neodermata, it has been asserted that complex characters are more likely to be homologous than simple characters (Rohde 1990, 1994a, 1996; Littlewood et al., 1999). What evidence is there to support this assertion? There is a large body of evidence documenting simple genetic bases for many homologous behavioral and morphological characters in *Drosophila* species. That alone would seem to falsify the hypothesis that simple characters are not likely to be homologous. This assertion stems, in part, from a misunderstanding of levels of homology. The presence of bristles may be

homologous across *Drosophila*, but the exact number of bristles may display some homoplasy. In other words, there is no evidence indicating that sweeping generalities can be made about the nature of homology versus homoplasy based upon a vague notion of simple versus complex character structure.

The hypothesis about the relative merits of simple versus complex characters as markers of genealogical relationships could be examined by assigning a “simple” versus “complex” status to characters *a priori*, running those characters through a phylogenetic systematic analysis, and then asking whether there is a significant difference in homoplasy among the two character classes. Once this process has been repeated for a substantial number of data sets from different groups of organisms, could we then begin to determine the validity of such a hypothesis. In lieu of this evidence, one should use all available characters, presuming maximum homology and character independence *a priori*, and relying on phylogenetic congruence among all characters *a posteriori* as the final arbiter of homology (Wiley, 1981; de Pinna, 1991; Kluge, 1989, 1997, 1998a,b, 1999).

While the primary function of phylogenetic analysis is to produce a robust hypothesis of phylogenetic relationships, it also provides a means for helping us know when our *a priori* presumptions are incorrect. Once we have a phylogenetic hypothesis based on as many characters as possible, we can move from homology presumptions to homology determinations. Hennig (1966) considered such “reciprocal illumination”, using the overall analysis to assess individual *a priori* presumptions of homology, to be a primary benefit of phylogenetic systematics. The homologies are the traits that are congruent with the phylogenetic tree, whether they are complex or superficial in nature;

homoplasies are those that are incongruent with the tree. For example, this study supports the proposal by Ehlers & Sopott-Ehlers (1993) and Rohde & Watson (1995) that the holdfast organ of the temnocephalids is not homologous with the holdfasts of neodermatans (characters 77-84). Brooks et al. (1985a) hypothesized that the various holdfasts, while demonstrably different, were all part of a homologous transformation series. Within phylogenetic systematic methodology, this hypothesis could not be falsified by reiterating that the holdfasts were different (Rohde & Watson, 1995) but could be falsified by including more taxa in the analysis, as was done herein.

Additionally, Rohde and co-workers (Rohde, 1990, 1994a, 1996; Littlewood et al., 1999a) suggested that protonephridial characters should be given high weight in phylogenetic analyses of the Platyhelminthes. This analysis considered 6 protonephridial characters. Three of them (12, 13, 16) have character consistencies of 100%, character 15 has a character consistency of 50%, 17 has a character consistency of 33%, and character 14 has a character consistency of 25%. The combined character consistencies for these traits is 68%, and their exclusion from the analysis produces the same tree topology as shown in Fig 3a and increases the CI slightly. In addition, character 17 is one of the characters producing marked instability due to missing data. Reciprocal illumination thus tells us that protonephridial characters are, at best, no better than any other character.

Phylogeneticists expect that analysis of a data set comprised of incorrect homology assessments will produce a distinctive result - many MPTs with low CIs. This is not the case with the Brooks et al. (1985; see also Brooks 1989a,b; Brooks & McLennan, 1993c) data sets, nor is it the case with the present data set. In the current study, 90% of the characters support the relationships indicated for the Revertospermata,

and these results strongly corroborate previous analyses. In the past, these results have been rejected because we are dealing with parasites (Neodermata) and symbiotic “turbellaria”, and adaptation to a common lifestyle is “known” to produce high degrees of correlated homoplasy (Rohde, 1990, 1994a, 1996; Littlewood et al., 1999a). To correct for this problem, characters “known” to be adaptations to parasitism/symbiosis should be discounted (eliminated from analysis *a priori*). For example, Rieger & Tyler (1985) suggested that similar structures in taxa sharing similar environments (e.g., exposed to similar selection pressures) should be coded *a priori* as homoplasious, or ambiguous as in Littlewood et al. (1999a,b).

Such suggestions ignore the basic Darwinian notion that homologies can be adaptations and that adaptation need not produce homoplasy. In the past decade a substantial amount of evidence has accumulated indicating that most similarities in structure, function, and preferred environment are due to common ancestry (Wanntorp et al., 1990; Harvey & Pagel, 1991; Brooks & McLennan, 1991). There is thus no reason to exclude, or manipulate, any “adaptive” character from any analysis (McLennan et al., 1988; Brooks & McLennan, 1991, 1993c, 1994; McLennan, 1993). In addition, Ronquist’s (1994) study on the evolution of inquilinism in cynipid hymenopterans, for example, showed that removal of characters associated with parasitic lifestyle did not alter the phylogenetic assessment that inquilinism had arisen only a single time in the group. And finally, Trouvé et al. (1998) showed that a suite of life-history traits for free-living and parasitic platyhelminths did not differ, suggesting that Neodermatans do not have a “parasitic mode of life” so much as a “platyhelminth mode of life” in a parasitic context.

In recent years, some have disparaged the morphological data upon which previous analyses of the Neodermata and their relatives had been performed because it is not compatible with molecular data (Rohde 1990, 1994a, 1996; Litvatis & Rohde, 1999; Mollaret et al. 2000; Littlewood et al., 1999a). It has also been suggested that the phylogenies based on morphological data have been highly variable and differ greatly among each other (Littlewood et al. 1999a). This has not actually been the case. First, the relationships among the Neodermatan groups have been the same in multiple studies using phylogenetic systematic methods beginning in 1985, with CI values remaining between 95% and 97% despite an increase in the number of characters used from 39 to 147. Second, differences in hypotheses of the sister group of the Neodermata have been based on differences in the taxa analyzed; the analysis herein accommodates all previously proposed sister groups in a manner that is congruent with all previous hypotheses.

In addition, Kornakova and Joffe (1999) pointed out that molecular results have failed to reproduce the monophyly of several firmly established taxa (based on morphology) and suggest that we consider sampling and long-branch attraction as serious effects in molecular analyses. For example, molecular studies suggest various combinations of para- or even polyphyly for the Monogenea, whereas morphological studies consistently suggest the group is monophyletic. Some take this as an indication that we should question all morphological traits used in phylogenetic studies of Monogeneans (Rohde 1990, 1994a, 1996; Litvatis & Rohde, 1999; Mollaret et al. 2000; Justine, 1998b). Littlewood et al. (1999b) showed that a combination of sequence data and only 50 of the 89 characters used herein supported a monophyletic Monogenea, and

accepted that grouping. Since the molecular data alone did not support Monogenean monophyly, the study by Littlewood et al. (1999b) provides evidence of insufficiencies in the sequence data as suggested by Kornakova and Joffe (1999).

This thinking needs to be carried through consistently in all future total evidence studies. Littlewood et al. (1999a) coded 9 characters shared uniquely by *Urastoma*, the Fecampiidae and the Neodermata as ambiguous for *Urastoma* and Fecampiidae, presumably based on Rohde's (1994a: 1104) assertion that "comparison of DNA sequences... suggests that the [fecampiids are] not a close relative of the Neodermata... thus the morphological similarities of the two groups appear indeed to be due to convergent evolution". Likewise, Littlewood et al. (1999a,b) made a number of *ad hoc* assumptions concerning *Udonella*. For example, the absence of larval hooks was coded *a priori* as apomorphic secondary loss, when the same absence of larval hooks in aspidobothreans and digeneans was coded as plesiomorphic absence. These added assumptions clearly demonstrate an *a priori* coding "preference" for regarding *Udonella* as a Monogenean. And finally, Littlewood et al. (1999a,b) utilized only slightly more than half of the available morphological characters that had been summarized in Brooks and McLennan (1993b). Many of those traits were characterized by Rohde (1990, 1994a, 1996; also Litvatis & Rohde 1999) as exhibiting a low probability of being homologous. The study herein does not support that characterization. In fact, the total morphological database provides very strong support not only for the monophyly of the Monogenea, which Littlewood et al. (1999b) accepted, but also for the Fecampiids + *Urastoma* as the sister group of the Neodermata and *Udonella* as the sister group of the Cercomeridea [Brooks, O'Grady & Glen, 1985 (Trematoda + Cercomeromorphae)].

Finally, this study corroborates the hypothesis that the ancestor of the Trematoda + Cercomeromorphae had a two-host life cycle involving the addition of a vertebrate host to the plesiomorphic arthropod host direct life cycle (Brooks et al., 1995a; Brooks, 1989b; Brooks & McLennan, 1993c), contrary to the proposal by Littlewood et al. (1999b) that the original life cycle was a single vertebrate host direct cycle. This is the most parsimonious explanation even if *Udonella* is a monogenean. It supports the notion that vertebrate endoparasitism in this group originated through predation of vertebrates on arthropods. It may also be an example supporting the hypothesis that alternation of hosts is an adaptive response to avoid the evolutionary costs of over-specialization (Moran, 1988, 1994; see also Kuris and Norton, 1985).

CONCLUSIONS

The morphological database for the Neodermata and close relatives is highly robust. This is partly due to the fact that the data themselves are numerous and unambiguous. More importantly, scientific hypotheses become more robust in proportion to the number of tests they have survived (Popper, 1960, 1968a,b, 1972, 1976, 1992), and the current database reflects the efforts of a number of specialists to refute the hypothesis first proposed by Brooks et al. (1985a). The current study also shows that phylogenetic systematic analysis is capable of uncovering instances in which our *a priori* presumption of homology is not supported. Thus, the selective removal of characters *a priori* is not necessary and indeed is counterproductive if our aim is always to produce the most robust hypothesis of phylogenetic relationships possible given all available evidence. The parasitic platyhelminths represent one of the most extensively studied animal groups,

with a database assembled over the past 200 years that will soon exceed 2500 morphological characters. This represents historical continuity in studies of flatworms, which comprises a formidable assemblage of knowledge about structure and biology. Results of the current study indicate that comparative morphology remains viable, tractable, and powerful. Phylogenetic analyses using morphological data provide an excellent framework for assessing a young but growing molecular database. It is with hopeful optimism that future total evidence studies will make full use of the large and robust morphological database documented herein.

This study also highlights two other benefits of a phylogenetic systematic approach: the ability, through reciprocal illumination, to falsify previous hypotheses of character evolution, and the ability to highlight areas where further research would be immediately beneficial. In this case, more studies on enigmatic groups (e.g., Acholadidae, Pseudograffillinae, Hypoblepharinidae, Solenopharyngidae, Promesostomidae, Trigonostomidae and Kytorrhynchidae) and poorly documented characters (e.g., 17 and 28) are clearly needed.

Figure 2.1: Schematic representation of diversity in the female reproductive system of Neodermatans. 0, 1, 2, 3, 4 refer to the character states used in this analysis. State 0 is the condition found among various Rhabdocoels. State 1 occurs in *Urastoma*, *Fecampiidae*, *Udonella*, and various Rhabdocoels. State 2 is the condition found in trematodes. State 3 is the condition among the Monogeneans. State 4 is the condition of the Cestodaria. A = antrum; L = Laurer's canal; M = Metraterm; OD = Oviduct; OV = Ovary; S = Sphincter; U = Uterus.

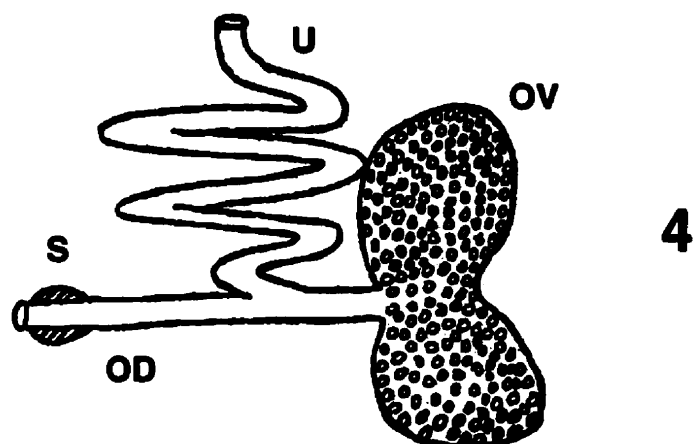
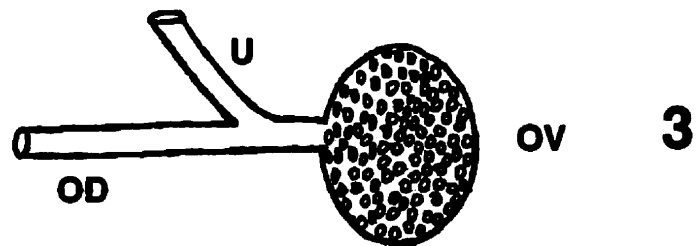
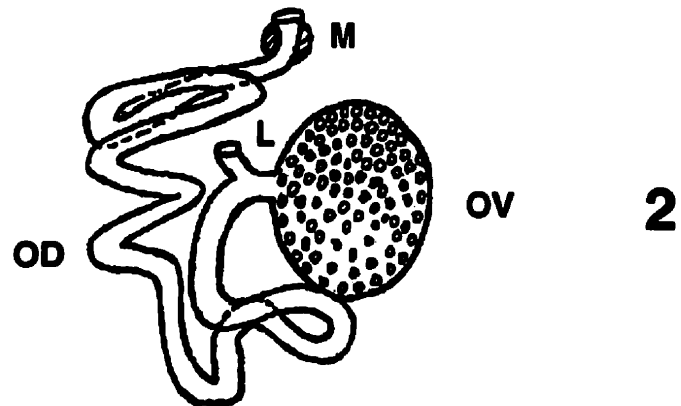
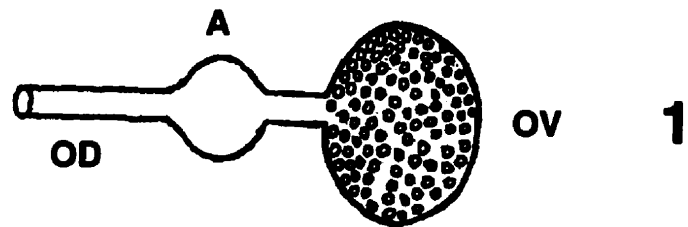
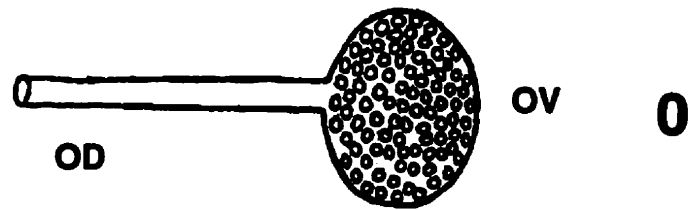


Figure 2.2: Majority Rule consensus tree for 24 Rhabdoceel taxa based on 98 MPTs (TL= 190, CI= 67%, RCI= 55%) produced by phylogenetic systematic analysis of 91 morphological characters.

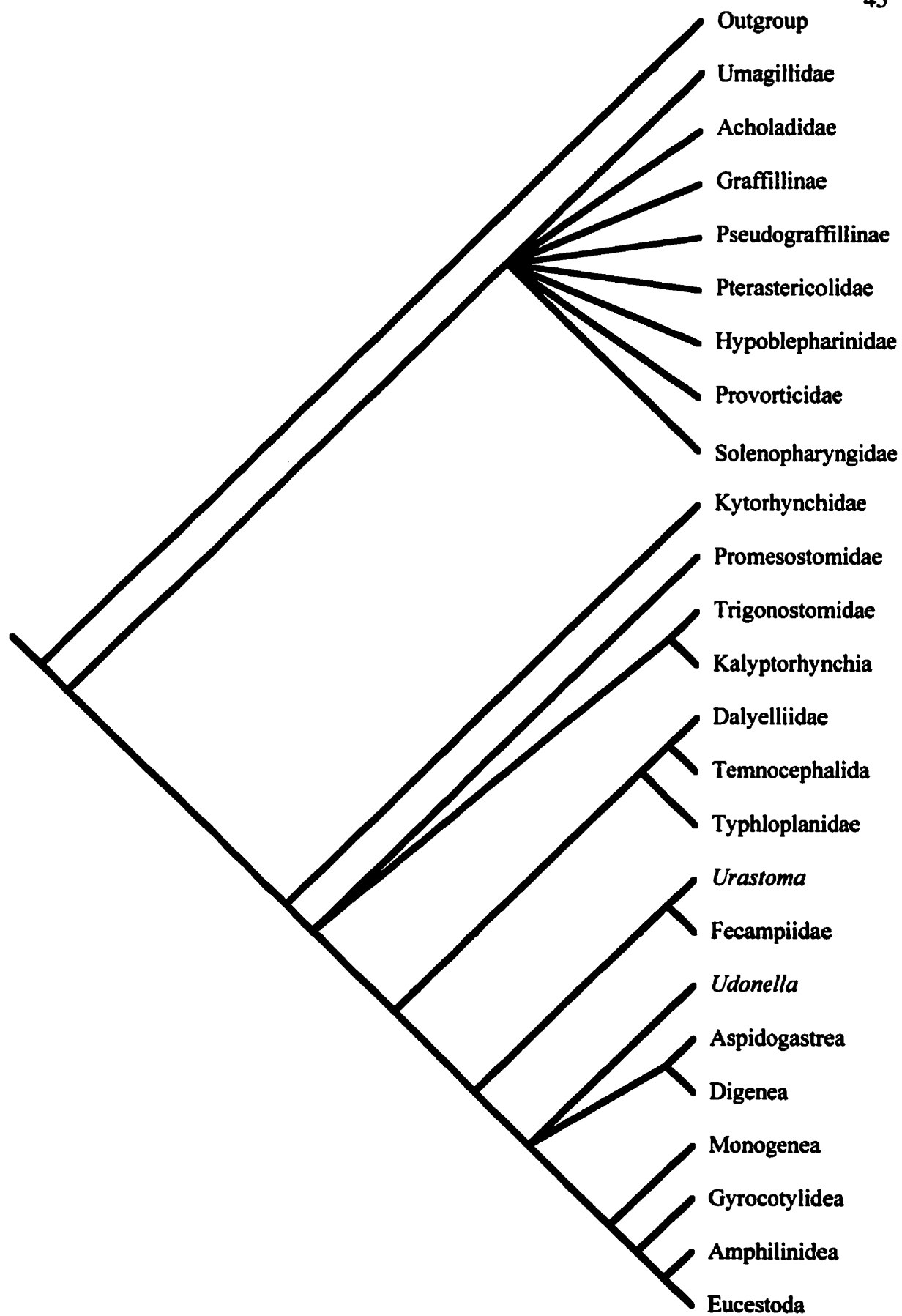


Figure 2.3: Two MPTs (TL= 181, CI= 69% , RCI= 56%) for 24 Rhabdocoel taxa produced by phylogenetic systematic analysis of 89 morphological characters. Ordering multistate characters 16, 22, 24, 41, 60, 61,78, 79 and 82 produces the same results.

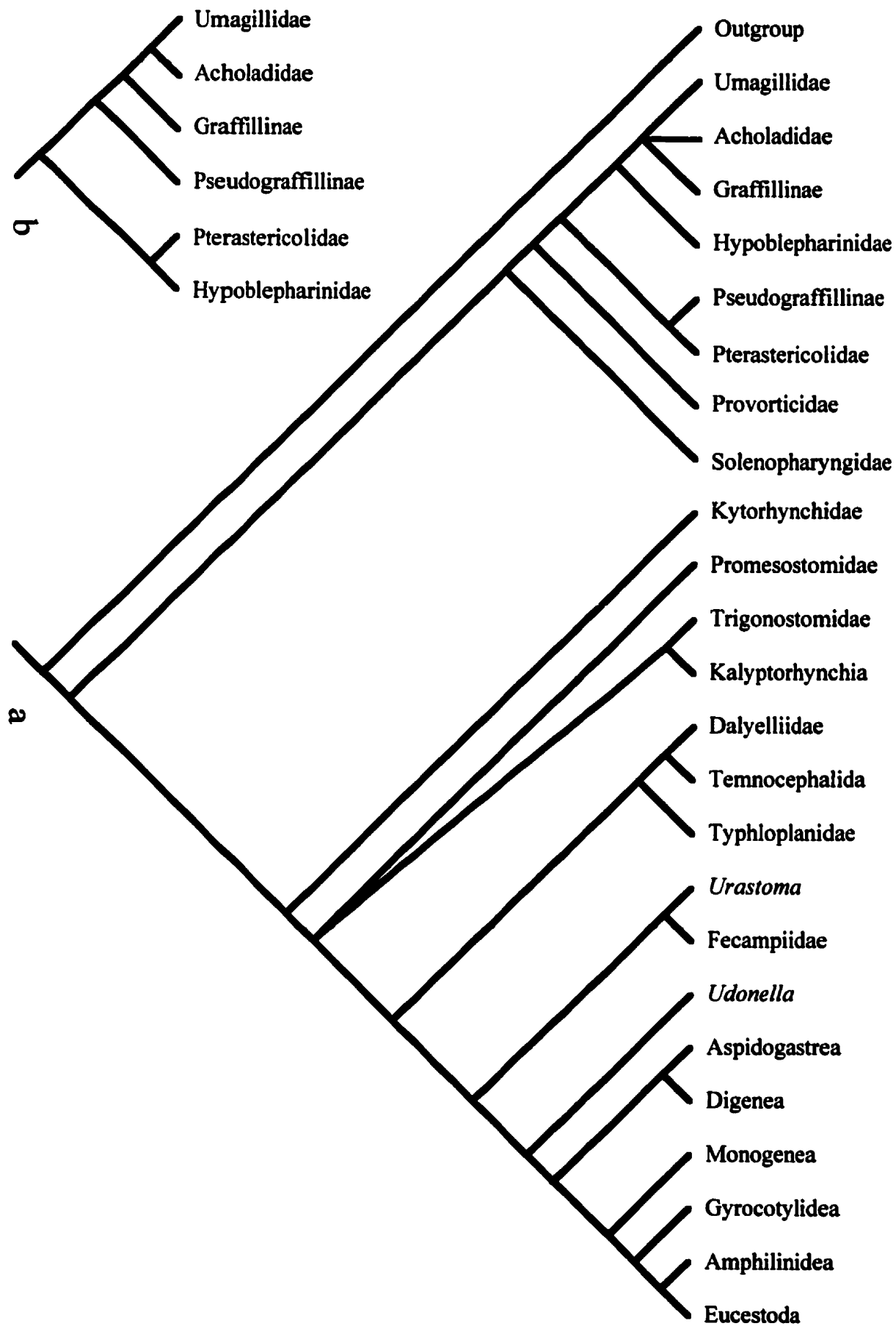


Figure 2.4: Bootstrap and Jackknife consensus tree for 24 rhabdocoel taxa based on 89 morphological characters, with multistate characters 16, 22, 24, 41, 60, 61, 78, 79 and 82 ordered. Bootstrap and Jackknife values appear on appropriate branches.

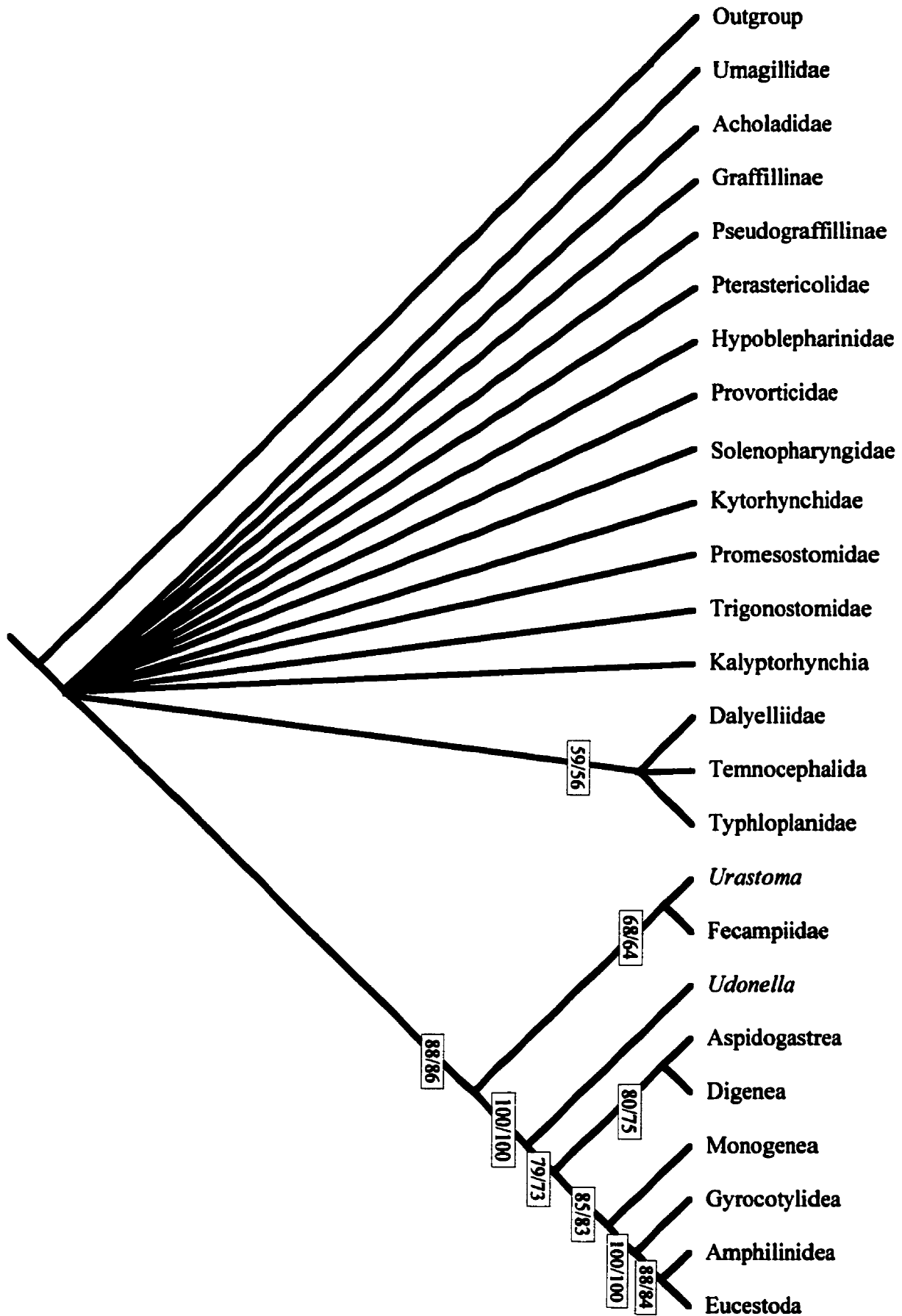


Figure 2.5: Bootstrap and Jackknife consensus trees for the Revertospermata Kornakova & Joffe (Neodermata (Fecampiidae + Urastoma)), based on 89 morphological characters, with multistate characters 16, 22, 24, 41, 60, 61, 78, 79 and 82 ordered. Bootstrap and Jackknife values appear on appropriate branches.

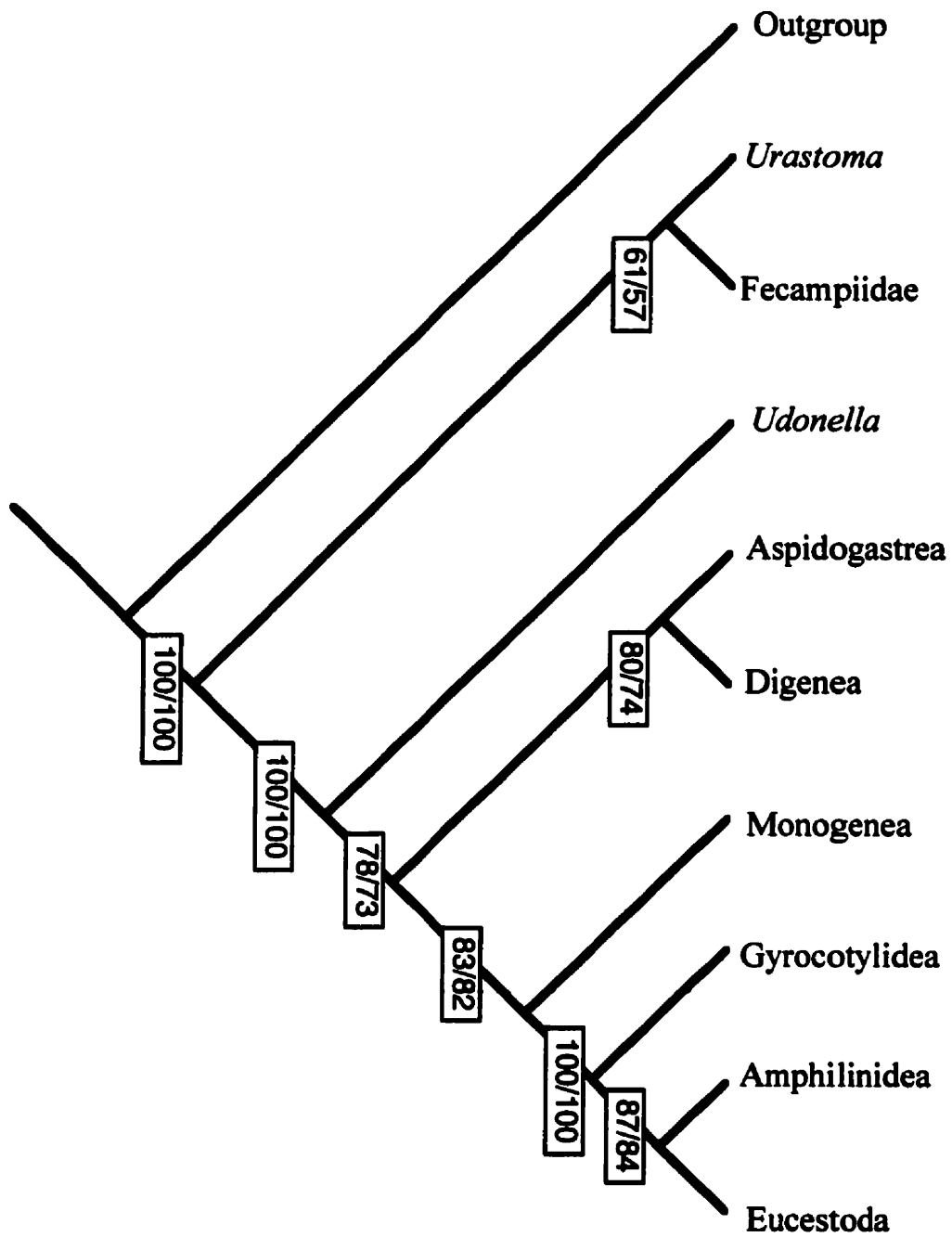


Table 2.1. Data matrix for phylogenetic analysis of the Rhabdocoels. In this study, 92 morphological transformation series were considered. The most robust and inclusive results are based on 90 transformation series (17 and 28 excluded) and with characters 16, 23, 25, 42, 61, 61, 76, 80, and 83 ordered. For identities of characters and states, refer to text. 0 = plesiomorphic state; 1,2,3,4,5 = apomorphic states; ? = unknown. OG= Outgroup function (composite outgroup based on character argumentations for each transformation series).

Taxa	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58
OUTGROUP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
UMAGILLIDAE	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
PSEUDOGRAFFILLINAE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
GRAFFILLINAE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1
ACHOLADIDAE	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
PTERASTERICOLIDAE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
HYPOBLEPHARINIDAE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	0
PROVORTICIDAE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
KYTORHYNCHIDAE	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PROMESOSTOMIDAE	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
SOLENOPHARYNGIDAE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
TRIGONOSTOMIDAE	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
KALYPTORHYNCHIA	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1	0	0
DALYELLIIDAE	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
TEMNOCEPHALIDA	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
TYPHLOPLANIDAE	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
URASTOMA	1	1	?	?	0	0	?	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
FECAMPIIDAE	1	1	3	?	0	0	1	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	0
UDONELLA	0	0	2	1	1	1	1	1	1	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	2	1
ASPIDOGASTREA	0	0	2	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0
DIGENEA	0	0	2	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0
MONOGENEA	0	0	2	1	1	1	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	2	0
GYROCOTYLIDEA	0	0	2	1	1	1	1	1	1	0	0	2	1	0	1	1	1	1	1	1	1	1	0	0	0	2	1	2	0
AMPHILINIDEA	0	0	2	1	1	1	1	1	1	0	0	2	1	0	1	1	1	1	0	0	0	1	1	1	0	2	1	3	0
EUCESTODA	0	0	2	1	1	1	2	1	1	0	0	2	1	0	1	1	1	1	0	0	0	1	1	1	1	1	0	0	0

Taxa		59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87
OUTGROUP		0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
UMAGILLIDAE		0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PSEUDOGRAFFILLINAE		0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GRAFFILLINAE		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ACHOLADIDAE		0	0	0	0	0	0	0	0	0	0	0	0	1	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PTERASTERICOLIDAE		0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HYPOBLEPHARINIDAE		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PROVORTICIDAE		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
KYTORHYNCHIDAE		0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PROMESOSTOMIDAE		0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SOLENOPHARYNGIDAE		0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TRIGONOSTOMIDAE		0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
KALYPTORHYNCHIA		0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DALYELLIIDAE		0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TEMNOCEPHALIDA		0	1	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0
TYPHLOPLANIDAE		0	1	1	0	0	0	0	1	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
URASTOMA		0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FECAPIIDAE		1	1	1	1	1	1	2	1	0	0	0	0	1	1	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0
UDONELLA		1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	1	1	1	2	1	1	0	0	0	0	0	0	0
ASPIDOGASTREA		0	2	1	1	1	1	1	1	0	1	0	0	0	0	1	0	1	1	1	2	1	1	2	0	0	0	0	0	0
DIGENEA		0	2	1	1	1	1	1	1	0	1	0	0	0	0	1	1	1	1	1	2	1	1	0	0	0	0	0	1	1
MONOGENEA		0	3	1	1	1	1	1	1	0	2	0	0	0	0	1	0	1	1	1	2	1	1	0	1	0	0	0	0	0
GYROCOTYLIDAE		2	4	2	1	1	1	1	0	0	2	0	0	0	0	1	0	2	0	1	1	2	1	0	2	1	0	0	0	0
AMPHILINIDAE		2	4	2	1	1	1	1	0	0	2	1	0	0	0	1	0	2	0	1	2	2	1	0	3	1	0	0	0	0
EUCESTODA		2	4	2	1	1	1	0	0	0	2	0	0	0	0	1	0	2	0	1	2	2	1	0	4	1	0	0	0	0

Taxa	88	89	90	91
OUTGROUP	0	0	0	0
UMAGILLIDAE	0	0	0	0
PSEUDOGRAFFILLINAE	0	0	0	0
GRAFFILLINAE	0	0	0	0
ACHOLADIDAE	0	0	0	0
PTERASTERICOLIDAE	0	0	0	0
HYPOBLEPHARINIDAE	0	0	0	0
PROVORTICIDAE	0	0	0	0
KYTORHYNCHIDAE	0	0	0	0
PROMESOSTOMIDAE	0	0	0	0
SOLENOPHARYNGIDAE	0	0	0	0
TRIGONOSTOMIDAE	0	0	0	0
KALYPTORHYNCHIA	0	0	0	0
DALYELLIIDAE	0	0	0	0
TEMNOCEPHALIDA	0	0	0	0
TYPHLOPLANIDAE	0	0	0	0
URASTOMA	0	0	0	0
FECAMPIIDAE	0	0	0	0
UDONELLA	0	0	0	0
ASPIDOGASTREA	0	0	0	0
DIGENEA	0	0	0	0
MONOGENEA	0	0	0	0
GYROCOTYLIDEA	0	0	0	0
AMPHILINIDEA	0	0	0	0
EUCESTODA	1	1	1	1

Chapter Three

PHYLOGENETIC SYSTEMATIC ASSESSMENT OF THE ASPIDOBOTHREA

(PLATYHELMINTHES, NEODERMATA, TREMATODA)

INTRODUCTION

Burmeister (1856) proposed the Aspidobothrii (*aspis*, shield; *bothros*, pit) for *Aspidogaster conchicola* Baer, 1827 to indicate an intermediate position between the Digenea and Monogenea within the Trematoda. Van Beneden (1858) used the term Aspidobothrea and considered *A. conchicola* and relatives to be closer to the digeneans than to the monogeneans. Monticelli (1892) suggested the name Aspidocotylea to reflect the inclusion of *Aspidocotylus mutabilis* Diesing, 1837 in the group. Faust and Tang (1936) agreed with Burmeister and Monticelli that *A. conchicola* and relatives should be removed from the Digenea and classified in an intermediate position between the Digenea and Monogenea. Furthermore, in an apparent effort to standardize terminology, Faust and Tang proposed the name Aspidogastrea for the group, stemming from the type genus *Aspidogaster*. Dollfus (1956) reported that *Aspidocotylus mutabilis* was a paramphistome digenean and, following Faust and Tang's nomenclature, referred to *Aspidogaster* and its relatives as the Aspidogastrea. Because there are no nomenclatural rules above the family group in zoological taxonomy, and favoring the maximum conservation of names as a means of preserving the maximum amount of taxonomic history, the older name Aspidobothrea will be used herein.

Current phylogenetic analyses place the Aspidobothrea as the sister group of the Digenea, each considered a sub-class of the class Trematoda (Ehlers, 1984, 1985a,b,

1986; Brooks et al. 1985b; Littlewood et al., 1999a,b; Chapter 2). Within the Aspidobothrea, most systematists (Gibson, 1987; Brooks et al., 1989; Pearson, 1992) accept four families, Aspidogastridae Poche, 1907, Stichocotylidae Faust and Tang, 1936, Rugogastridae Schell, 1973, and Multicalyicidae Gibson and Chinabut, 1984. Despite a long history of confusion regarding nomenclature there has not been an explicit phylogenetic analysis of relations within the group until recently. Gibson (1987) proposed the first phylogenetic hypothesis for the Aspidobothrea, based on a suite of 10 morphological characters. He considered the Aspidobothrea paraphyletic, with Aspidogastridae the sister group of the Digenea and the grouping ((Multicalyicidae (Rugogasteridae + Stichocotylidae))) as the sister group of Aspidogastridae + Digenea. Brooks et al. (1989) showed the most parsimonious arrangement of Gibson's (1987) characters supported a monophyletic Aspidobothrea, and familial relationships of (((Rugogastridae (Stichocotylidae (Multicalyicidae + Aspidogastridae))). Pearson (1992) suggested an additional 7 characters which he felt supported a monophyletic Aspidobothrea, with relationships of (((Aspidobothriidae (Multicalyicidae (Rugogasteridae + Stichocotylidae))), but he did not subject those characters to phylogenetic systematic analysis.

In this study, a phylogenetic systematic analysis of a suite of 33 morphological transformation series, comprising of the 10 original characters proposed by Gibson (1987), the 7 characters proposed by Pearson (1992), and 16 new characters is presented. This new data set allows consideration of 20 aspidobothrean taxa, including *Sychnocotyle* Ferguson et al, 1999 which has not been previously included in phylogenetic analyses of the Aspidobothrea.

MATERIALS AND METHODS:

Taxa.

The following taxa were included in this study: *Rugogaster*, Schell, 1973; *Stichocotyle*, Cunningham, 1884; *Multicalyx*, Olsson, 1868; *Cotylogaster michaelis*, Monticelli, 1892; *Cotylogaster basiri*, Siddiqi & Cable, 1960; *Cotylogasteroides occidentalis*, Yamaguti 1963; *Cotylogasteroides barrowi*, Huehner & Etges, 1972; *Aspidogaster conchicola*, Baer, 1827; *Aspidogaster*, Baer, 1827; *Lobatosoma manteri*, Rohde, 1973; *Lobatosoma hanumanthai*, Narasimhulu & Madhavi, 1980; *Lobatosoma*, Eckman, 1932; *Cotylospis*, Leidy, 1857; *Lissemysia*, Sinha, 1935; *Rohdella siamensis*, Gibson and Chinabut, 1985; *Multicotyle purvisi*, Dawes, 1941; *Sychnocotyle kholo*, Ferguson et al., 1999; *Lophotaspis vallei*, Stossich, 1899; *Lophotaspis interiora*, Ward & Hopkins, 1933; *Lophotaspis orientalis*, Faust & Tang, 1936. *Lophotaspis macdonaldi* and *L. margaritiferae* are excluded from the analysis because they are poorly described and specimens were not available for examination. *Cotylogaster dinosoides* is likewise excluded from the analysis because the taxon consists of only five juvenile specimens. Generic names appear where all species contained therein share the same states for all 33 characters used in this analysis. In the course of this study, it was found that all 33 transformations series could be used without resorting to coding some traits as polymorphic only if *Aspidogaster conchicola* was treated as distinct from the other members of *Aspidogaster*, *Lobatosoma manteri* and *L. hanumanthai* as distinct from the other members of *Lobatosoma*, *Cotylogaster basini* as distinct from *C. michaelis* and each of the three species of *Lophotaspis* as separate entities.

Character List.

Characters were coded based on discussions in Gibson (1987), Brooks et al. (1989; see also Brooks & McLennan, 1993c) and Pearson (1992) and the following primary literature, confirmed by examination of specimens of selected available taxa:

Aspidogaster conchicola (Bakker & Davids, 1973; Dollfus, 1958; Faust, 1922; Huehner & Etges, 1977; Stafford, 1896; Williams, 1942); *Aspidogaster* (Rai, 1964; Rawat, 1948); *Cotylogaster michaelis* (Monticelli, 1892); *Cotylogaster basini* (Hendrix & Overstreet, 1977); *Cotylogasteroides occidentalis* (Fredricksen, 1980; Nickerson, 1902) *Cotylogasteroides barrowi* (Huehner & Etges, 1972); *Cotylaspis* (Osborn, 1904; Rumbold, 1928; Cho & Seo, 1977); *Lissemysia* (Agarwal, 1978; Sinha, 1935; Tandon, 1948; Singh & Tewari, 1985); *Lobatostoma* (Caballero y Caballero & Hollis, 1965; Zylber & Ostrowski de Nunez, 1999; Oliva & Carvajal, 1984; MacCallum & MacCallum, 1913); *Lobatosoma manteri* (Rohde, 1973); *Lobatosoma hanumanthai* (Narasimhulu & Madhavi, 1980); *Lophotaspis interiora* (Hendrix & Short, 1972; Ward & Hopkins, 1931); *Lophotaspis vallei* (Stossich, 1899; Wharton, 1933); *Lophotaspis orientalis* (Faust & Tang, 1936); *Multicalyx* (Stunkard, 1962; Thoney & Burresson, 1987, 1988); *Multicotyle purvisi* (Dawes, 1941.; Rohde, 1972); *Rohdella siamensis* (Gibson & Chinabut, 1984); *Rugogaster* (Schell, 1973; Amato & Pereira, 1995); *Stichocotyle nephropis* (Nickerson, 1895); *Sychnocotyle kholo* (Ferguson et al., 1999). Characters were polarized using the Digenea as the primary outgroup, with the Cercomeromorphae, Udonellidea and Revertospermata Fecampiids + *Urastoma*, respectively, as secondary outgroups (Chapter 2). ‘?’ indicates that the state of the character is unknown in a particular taxon. As stated above, higher taxa that are polymorphic for a character had

species removed and treated separately to eliminate polymorphism from the higher level.

The data matrix is given in Table 3.1.

1. Transverse septum dividing body: absent (0); present (1).
2. Buccal lobes: absent (0); present pentalobate with two ventral lobes as largest (1); present with three lobes the ventral lobes larger (2); pentalobate with the dorsal lobe largest (3).
3. Gut: bifurcating (0); saccate (1).
4. Posterior zone of growth and transverse septation: absent (0); located within sucker (1), external to sucker (2).
5. Transverse septa separates membrane delimiting capsule: absent (0) present (1).
6. Longitudinal septa: absent (0); present, forming three rows of alveoli (1); present forming four rows of alveoli (2).
7. Marginal bodies: absent (0); present (1).
8. Papillae on ventral sucker: absent (0); present (1).
9. Ventral sucker extending beyond body proper: no (0); yes (1).
10. Septate oviduct: absent (0); present (1).
11. Ciliated oviduct: present (0); absent (1).
12. Common genital pore: present (0); absent (1).
13. Number of testes: two (0); one (1); multiple (2). *Lophotaspis vallei* & *Lophotaspis interiora* have a single testis with two vas efferentia, which we have coded as two testes. Dollfus (1958) reported *Aspidogaster conchicola* as having a second rudimentary testis and is therefore coded it as having two testes.

14. Genital sac: present inclosing pars prostatica and prostatic cells (0); absent (1);
present inclosing pars prostatica with prostatic cells both internal and external (2);
present inclosing only the pars prostatica with prostatic cells external (3); inclosing
prostatic cells but pars prostatica absent (4); pars prostatica and prostatic cells
external to genital sac (5).
15. Genital sac inclosing terminal end of uterus: absent (0); present (1).
16. Cirrus: present (0); absent (1).
17. Metraterm: present (0); absent (1).
18. Vitellaria: interrupted posteriorly (0); not interrupted posteriorly (1).
19. Vitellaria: interrupted anteriorly (0); not interrupted anteriorly (1).
20. Paired vitelline ducts (0); single (asymmetrical) duct (1).
21. Vitellaria: follicular (0); compact (as cord) (1).
22. Common vitelline duct: opens between ovary & Mehlis' gland (0); opening at
Mehliss' gland (1).
23. Orientation of ovary: oviduct opening posteriorly (0); opening anteriorly (1).
24. Ootype: posterior to ovary (0); anterior (1).
25. Proximal portion of uterus: passing posteriorly (0); passing anteriorly (1).
26. Laurer's canal: present, proceeding posteriorly, opening externally or not (0); absent
(1); present, proceeding anteriorly, opening externally (2). Agarwal (1978) states that
a Laurer's canal is present without any further information regarding this structure. It
should be noted that this is in disagreement with his statements regarding specific
differences. This structure may in fact be a uterine seminal receptacle and not a
Laurer's canal. However, being unable to locate specimens to confirm the description,

this character is coded as missing (“?”) in this analysis; its exclusion does not alter the hypothesized relationships.

- 27. Eggs naturally: partly embryonated (0); fully developed at deposition (1).
- 28. Ciliated larva: present (0); absent (1).
- 29. Eyespots: present (0); absent (1).
- 30. Mode of Infection: larval invasion (0); ingestion of egg (1).
- 31. Head gland: present (0); absent (1).
- 32. Caudal appendage: present (0); absent (1).
- 33. Yolk cells lie at one pole: present (0); absent (1).

Analyses performed.

Data were analyzed using standard Hennigian argumentation (Hennig 1966; Wiley 1981; Brooks & McLennan 1991, in press; Wiley et al., 1991, in press), and results were generated using the ‘branch and bound’ option implemented in the computer program PAUP* 4b8, implemented on a Macintosh G4/500 computer. All characters were run unordered. Acctran and Deltran character optimization produced the same results.

RESULTS

The analysis of all 33 transformation series produces a single most parsimonious tree with a tree length (TL) of 70 steps, a Consistency Index (CI) of 62.86% and a Retention Index (RI) of 75.00% (figure 3.1). The tree indicates basal relationships of (Rugogastridae (Stichocotylidae (Multicalycidae+Aspidogastridae))). The tree also suggests a basal trichotomy of *Cotylogaster* + (*Aspidogaster* + *Lobatostoma*) +

(*Cotylogasteroides* [as *Cotylogaster basiri* + *Cotylogasteroides* spp.])((*Cotylaspis* + *Lyssemysia*) (*Rohdella* (*Lophotaspis* (*Multicotyle* + *Sychnocotyle*))))). Finally, *Aspidogaster conchicola*, type species of the genus, is the sister group of all other species currently placed in the genus + *Lobatosoma* spp., rendering *Aspidogaster* paraphyletic.

DISCUSSION

As noted in the introduction, Gibson (1987) provided the first formal phylogenetic hypothesis for the Aspidobothrea. He suggested 10 characters which he felt showed that the Aspidobothrea were paraphyletic with respect to the Digenea, proposing a phylogenetic hypothesis of (((Stichocotylidae (Multicalycidae + Rugogasteridae)) (Aspidogastridae + Digenea))). Brooks et al. (1989) subjected those 10 characters to phylogenetic systematic analysis and discovered that the most parsimonious hypothesis for Gibson's own data was a monophyletic Aspidobothrea with familial relationships of (((Rugogastridae (Stichocotylidae (Multicalycidae (Aspidogastridae)))). Pearson (1992) proposed seven additional characters that he felt supported the monophyly of the Aspidobothrea but suggested sister group relationships of (((Aspidogastridae (Multicalycidae (Stichocotylidae (Rugogastridae)))).

This study, in addition to recent molecular (e.g., Littlewood et al., 1999a,b) and morphological (e.g. Chapter 2) studies corroborating the hypothesis that the Aspidobothrea is a monophyletic group and the sister group of the Digenea, represents an empirical test of the three hypotheses of family-group relationships listed above, based on the 10 characters proposed by Gibson (1987) and used by Brooks et al. (1989) and Brooks & McLennan (1993c), the seven additional characters proposed by Pearson

(1992), and 16 new characters. The results unequivocally support the family relationships suggested by Brooks et al. (1989) and Brooks & McLennan (1993c). The analysis does not, however, support completely the current subfamilial classification of the Aspidogastridae, comprising Aspidobothriinae + Cotylaspinae + Rohdellinae (as shown by Brooks & McLennan, 1993c). Both the Aspidobothriinae [as (*Aspidogaster* + *Lobatostoma*) and the Cotylaspinae [as ((((*Cotylogasteroides* ((*Cotylaspis* + *Lissemysia*) (*Rohdella* (*Lophotaspis* (*Multicotyle* + *Sychnocotyle*)))))) are supported as monophyletic groups. Recognizing Rohdellinae, however, would make the Cotylaspinae paraphyletic. The tree suggests a basal trichotomy of *Cotylogaster michaelis* + Aspidobothriinae + Cotylaspinae; however, until a full revision of the entire group has been completed, proposing a new subfamily for a single species is not advisable and will not be done herein.

Hendrix & Overstreet (1977) redescribed *Cotylogaster basiri* Siddiqi & Cable, 1960, retaining it in *Cotylogaster* based on the possession of a Laurer's canal, paired vitelline ducts and follicular vitellaria. They also reported that the species lacks both a cirrus and a genital sac. This analysis suggests that the three traits used by Hendrix & Overstreet are plesiomorphies while the lack of a cirrus and genital sac are apomorphies linking *C. basiri* with *Cotylogasteroides*. This analysis thus places *C. basiri* as the sister species of the members of *Cotylogasteroides* Yamaguti, 1963. Within the Aspidogastrinae, *Aspidogaster conchicola*, type species of the genus, is the sister group of all other species currently placed in *Aspidogaster* + *Lobatosoma* spp., rendering *Aspidogaster* paraphyletic. Within the Cotylaspinae, neither *Lyssemysia*, with 11 nominal species, nor the monotypic *Multicotyle* have autapomorphies, based on the data currently

available. In the absence of a phylogenetic analysis for all species within these clades, taxonomic changes at this time are not advisable, but if future studies based on all species confirm the paraphyletic nature of these taxa, *Aspidogaster* + *Lobatosoma*, *Lysemysia* + *Cotylaspis*, and *Multicotyle* + *Sychnocotyle* may need to be synonymized.

Traditional classification of the Aspidobothrea was based primarily on differences in the structure of the ventral adhesive organ. This analysis is based on simultaneous assessment of many traits, including but not restricted to the ventral adhesive organ. The results support earlier findings by Brooks et al. (1989) and Brooks & McLennan (1993c) that *Rugogaster* and *Stichocotyle* are the two basal most members of the Aspidobothrea. The analysis supports part of the hypothesis of evolutionary diversification of the ventral adhesive organ suggested by Pearson (1992), namely that four longitudinal rows of alveoli arose from the *Multicalyx* condition. This study however, indicates that aspidogastrids with four rows of alveoli form a paraphyletic assemblage. This illustrates that grouping by plesiomorphies produces classifications that are logically inconsistent with phylogeny and are also inherently unstable with the addition of new taxa and new data (Wiley, 1981; Wiley et al., 1991, in press).

By definition, sister groups are of equal age (Mayden, 1986). All other things being equal, then, sister groups ought to comprise the same number of species. In evolution, however, all things are rarely equal. The Aspidobothrea and their sister group, the Digenea, occur worldwide, where they exhibit (plesiomorphically) a life cycle pattern involving a molluscan and a vertebrate host. Comparison with the phylogenetic relationships of their vertebrate hosts suggests that the common ancestors of aspidobothreans and digeneans diverged from each other at the same time as the common

ancestor of chondrichthyans and the rest of the gnathostome vertebrates diverged from each other (Brooks, 1989). This suggests that the aspidobothreans are at least 500 million years old. And yet, with 48 nominal species (see appendix 1), the Aspidobothrea is dwarfed by the Digenea, which has approximately 5,000 nominal species. Brooks & McLennan (1993b,c) suggested that this disparity in species richness might be due to the absence, in aspidobothreans, of a developmental innovation found in the digeneans, namely indirect development with one or more stages of asexual proliferation of larval forms permitting a single embryo to produce more than 1,000 infective larvae. This analysis provides additional indirect support for this interpretation. Aspidobothreans exhibit substantial ecological diversity, as indicated by their movement between marine and freshwater environments, and from chondrichthyans to actinopterygians to chelonians (figure 3.2), suggesting that ecological specialization has not been a major factor in limiting the diversification of the group. In this sense, the aspidobothreans resemble the Amphilinidea, sister group of the Eucestoda, and differ from the Gyrocotylidea, sister group of the Amphilinidea + Eucestoda.

CONCLUSIONS

Although there is considerable agreement on the monophyly of the Aspidobothrea and their placement as the sister group of the Digenea (e.g., Ehlers, 1984, 1985a,b, 1986; Brooks et al. 1985b; Littlewood et al., 1999a,b; Chapter 2) and for the basal relationships within the group, lower level relationships within the group have received little attention. This is reflected in the substantial amount of missing data for some characters, especially those associated with early ontogeny. Future studies documenting these missing data

should find substantial congruence between juvenile and adult traits as has been documented for other members of the Neodermata (summarized in Brooks & McLennan, 1993c).

The results presented herein also demonstrate that the fundamental difference between the hypotheses of Brooks et al. (1989) and those of Gibson (1987) and Pearson (1992) is not the result of the characters used; rather the differences lie in the method of analysis used. This point has been made before, beginning with Brooks et al. (1985). Effective progress in delineating these and all other phylogenetic relationships requires the addition of new characters from multiple sources, and the use of a common analytical procedure based on all available data.

Figure 3.1. Phylogenetic trees for 20 Aspidobothrean taxa produced by phylogenetic systematic analysis of 33 morphological transformation series. Letters on branches indicate the following apomorphies (transformation series number followed by state in parentheses): A= 4(1), 24(1), 26(1), 28(1); B= 4(2), 11(1), 13(2), 14(4), 20(2), 22(1), 23(1), 30(1); C= 3(1), 10(1), 27(1), 29(1); D= 5(1); E= 7(1); F= 13(1), 17(1); G= 1(1), 6(1); H= 2(2), 19(1), 20(1); I= 6(2), 14(3), 24(0); J= 13(1); K= 22(1); L= 2(1); M= 23(1); N= 14(2); O= 22(1); P= 14(1), 16(1), 27(0), 30(1), 31(1); Q= 2(3), 19(1); R= 21(1), 33(1); S= 9(1), 18(1), 22(1), 24(0), 32(1); T= 12(1), 13(1), 20(1); U= 14(0), 23(1); V= 6(2), 28(0); W= 14(5), 15(1), 16(2); X= 23(1); Y= 22(0), 25(1), 26(0); Z= 9(0), 13(1); AA= 8(1), 11(1), 14(4); BB= 17(1); CC= 22(0); DD= 13(1).

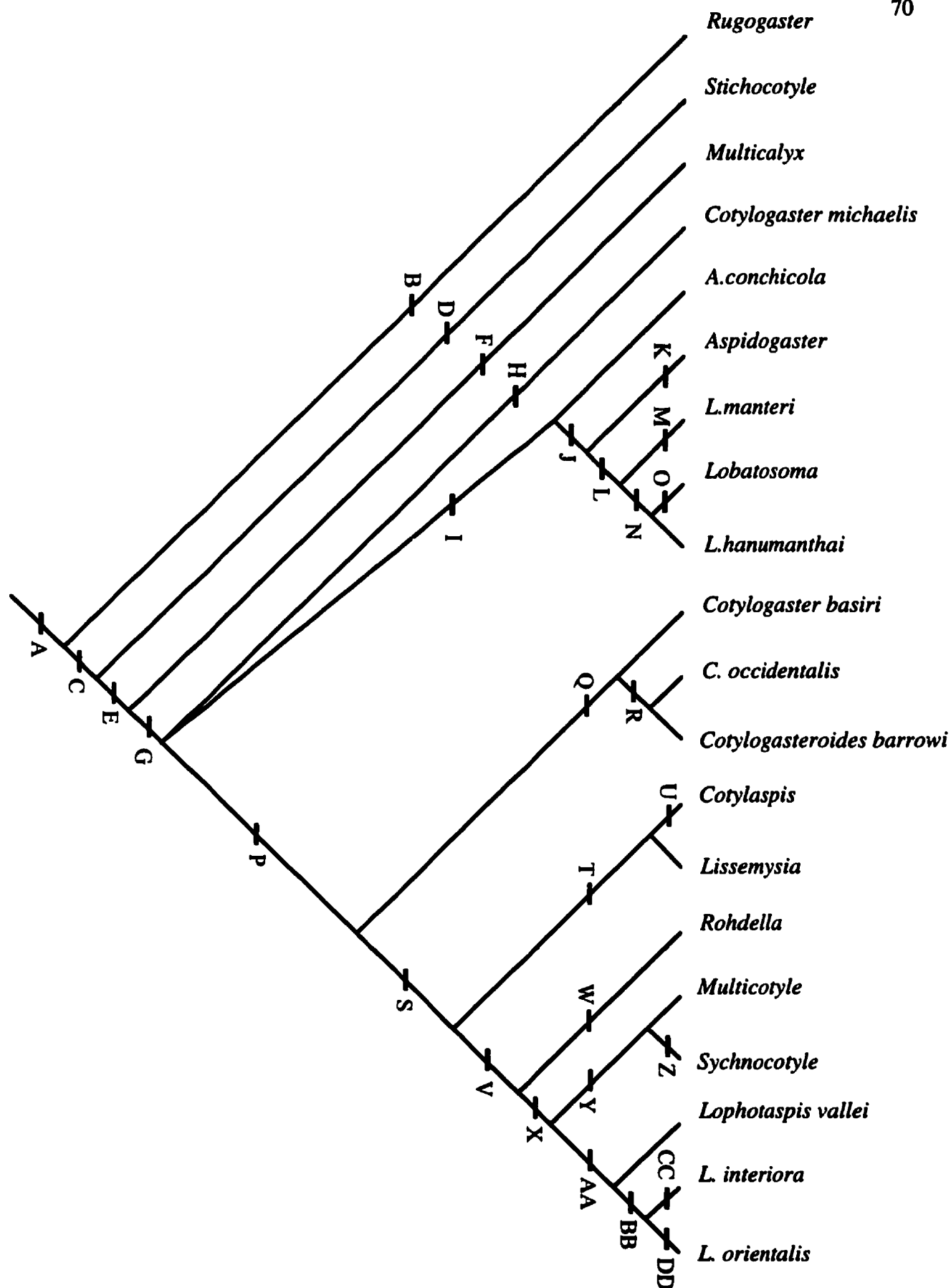


Figure 3.2. Phylogenetic optimization of major host and habitat shifts for 20 Aspidobothrean taxa. Clear boxes indicate marine habitats, black boxes indicate freshwater habitats. Alternative equally parsimonious optimizations include: (1) colonization of freshwater habitats associated with the host shift from chondrichthyans to actinopterygians, with secondary colonization of marine habitats in *Cotylogaster michaelis* and (2) host shift from actinopterygians to chelonians once, with a secondary shift back to actinopterygians in *Rohdella*.

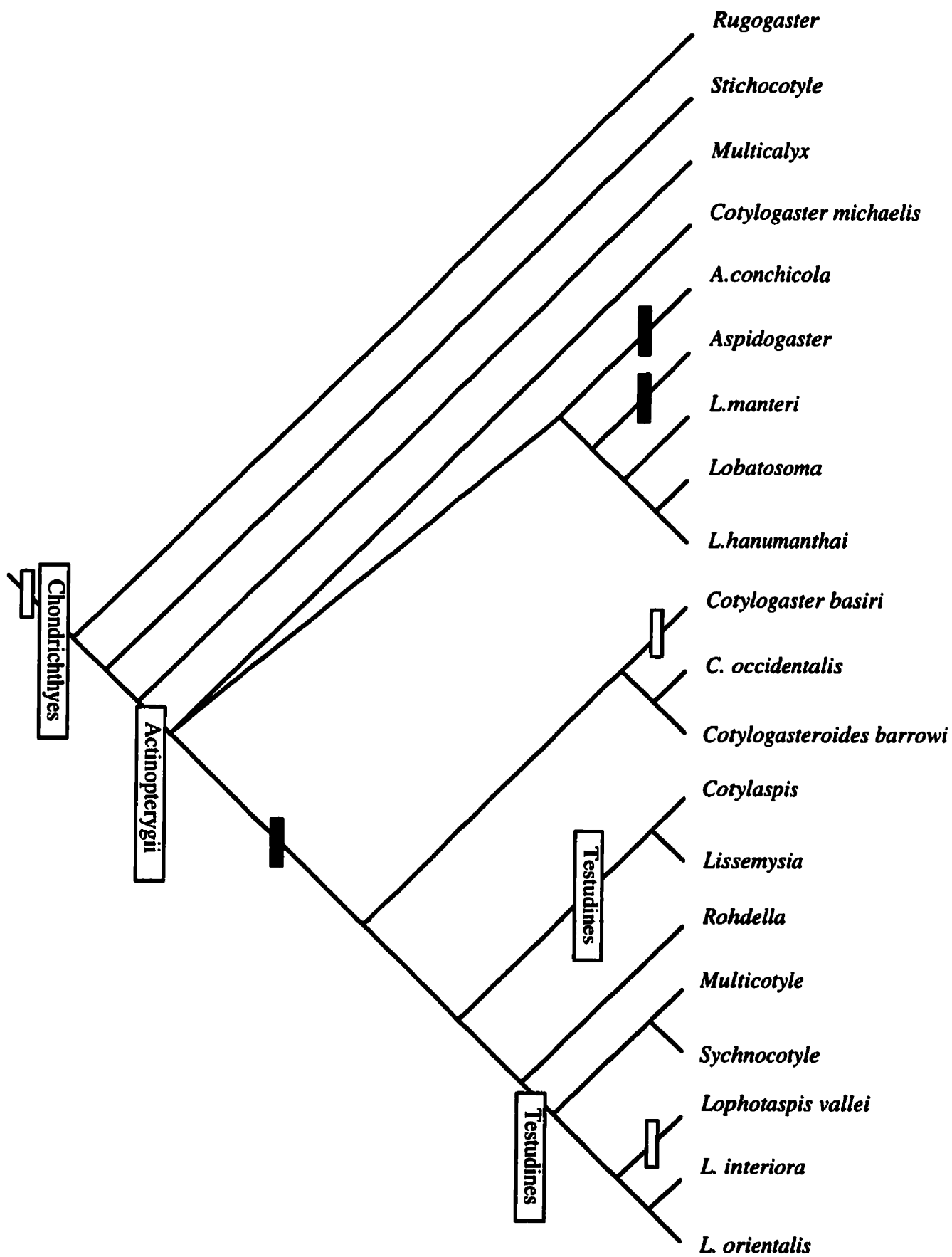


Table 3.1 Data matrix for phylogenetic analysis of the Aspidobothrea. In this study, 33 morphological transformation series were considered. For identities of characters and states, refer to text. 0 = plesiomorphic state; 1,2,3,4,5 = apomorphic states; ? = unknown. OG = Outgroup function (composite outgroup based on character argumentations for each transformation series).

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rugogaster</i>	0	0	0	2	0	0	0	0	0	0	1	0	2	4	0	0	0	0
<i>Stichocotyle</i>	0	0	1	1	1	0	0	0	0	1	?	0	0	?	0	0	?	?
<i>Multicalyx</i>	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	0	1	0
<i>Cotylogaster michaelis</i>	1	2	1	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0
<i>Cotylogaster basiri</i>	1	3	1	1	0	1	1	0	0	1	0	0	0	1	0	1	0	0
<i>Cotylogasteroides occidentalis</i>	1	3	1	1	0	1	1	0	0	1	0	0	0	1	0	1	0	0
<i>Cotylogasteroides barrowi</i>	1	3	1	1	0	1	1	0	0	1	0	0	0	1	0	1	0	0
<i>Aspidogaster</i>	1	0	1	1	0	2	1	0	0	1	0	0	1	3	0	0	0	0
<i>A.conchicola</i>	1	0	1	1	0	2	1	0	0	1	0	0	0	3	0	0	0	0
<i>Lobatosoma</i>	1	1	1	1	0	2	1	0	0	1	0	0	1	2	0	0	0	0
<i>L.hanumanthai</i>	1	1	1	1	0	2	1	0	0	1	0	0	1	2	0	0	0	0
<i>L.manteri</i>	1	1	1	1	0	2	1	0	0	1	0	0	1	3	0	0	0	0
<i>Cotylaspis</i>	1	0	1	1	0	1	1	0	1	1	0	1	1	0	0	1	0	1
<i>Lissemysia</i>	1	0	1	1	0	1	1	0	1	1	0	1	1	1	0	1	0	1
<i>Multicotyle</i>	1	0	1	1	0	2	1	0	1	1	0	?	0	?	0	?	0	1
<i>Sychnocotyle</i>	?	0	1	1	0	2	1	0	0	1	?	?	1	1	0	1	?	1
<i>Rohdella</i>	?	0	1	1	0	2	1	0	1	1	0	0	0	5	1	2	0	1
<i>Lophotaspis valleii</i>	1	0	1	1	0	2	1	1	1	?	?	0	0	4	0	1	0	1
<i>Lophotaspis interiora</i>	1	0	1	1	0	2	1	1	1	1	1	0	0	4	0	1	1	1
<i>Lophotaspis orientalis</i>	1	0	1	1	0	2	1	1	1	?	?	0	1	4	0	1	1	1

Taxa	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rugogaster</i>	0	0	0	1	1	1	?	2	1	0	1	0	1	0	?
<i>Stichocotyle</i>	0	0	0	?	?	?	?	?	1	1	?	?	?	?	?
<i>Multicalyx</i>	0	0	0	0	?	?	0	0	1	1	1	?	0	?	0
<i>Cotylogaster michaelis</i>	1	0	0	0	0	1	0	1	1	1	?	?	?	?	0
<i>Cotylogaster basiri</i>	1	0	0	0	0	1	0	0	1	0	?	?	?	?	?
<i>Cotylogasteroides occidentalis</i>	1	1	1	0	0	1	0	0	1	0	?	?	?	1	0
<i>Cotylogasteroides barrowi</i>	1	1	1	0	0	1	0	0	?	?	?	?	?	?	?
<i>Aspidogaster</i>	0	0	0	1	0	0	0	0	1	1	1	1	0	0	?
<i>A.conchicola</i>	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0
<i>Lobatosoma</i>	0	0	0	1	0	0	0	0	1	1	?	1	?	0	?
<i>L.hanumanthai</i>	0	0	0	0	0	0	0	0	1	1	?	1	?	0	?
<i>L.manteri</i>	0	0	0	0	1	0	0	0	1	1	1	1	?	0	?
<i>Cotyloaspis</i>	0	0	0	?	1	0	0	1	?	?	1	?	?	?	1
<i>Lissemysia</i>	0	0	0	1	0	0	0	1	?	?	?	?	?	?	?
<i>Multicotyle</i>	0	0	0	0	1	0	?	0	0	0	0	?	1	1	1
<i>Sychnocotyle</i>	0	0	0	?	1	0	1	0	0	0	?	?	?	?	?
<i>Rohdella</i>	0	0	0	1	0	0	0	0	?	?	?	?	?	?	?
<i>Lophotaspis vallei</i>	0	0	0	1	1	0	0	0	1	0	0	?	?	?	?
<i>Lophotaspis interiora</i>	0	0	0	0	1	0	0	0	1	0	0	?	?	?	?
<i>Lophotaspis orientalis</i>	0	0	0	1	1	0	0	0	1	0	0	?	?	?	?

Chapter Four

THE EVOLUTION OF QUINONE TANNED EGGS IN THE NEODERMATA

INTRODUCTION

Many species of parasitic platyhelminthes produce darkly colored eggs that are immediately visible through the integument of the adult worm. This colour, which can range from dark brown to pale yellow, is associated with the presence of quinone-tanned proteins. Pryor (1940) proposed the name “sclerotin” for such proteins that have aromatic cross linkages and are derived through the process of “tanning”; a term borrowed from then known industrial process of treating leather with vegetable tannins (i.e. polyphenols) resulting in physically tougher and chemically resistant leather (proteins). It has been demonstrated for both schistosomes (Seed et al., 1980) and fasciolids (Waite & Rice-Ficht, 1987) that tyrosine is oxidized to DOPA (dihydroxyphenylalanine) and packaged along with the enzyme phenol oxidase (also known as phenolase or catechol) in secretory vesicles within the vitelline cells that manufacture them. When the vesicles are released during eggshell formation, phenol oxidase further oxidizes DOPA to o-quinone, which in turn reacts with a free NH_2 group of another protein thereby covalently linking them together. This is referred to as “autotanning” because there are no free quinones (unlike in the treatment of leather) binding adjacent proteins but rather linkage occurs through oxidation of the phenolic side chain of the amino acid tyrosine.

Although the process of quinone tanning is widespread in nature (Waite, 1990) and other groups have quinone tanned eggs, and propagules, most researchers have sought explanations for its evolution by examining its presence in parasitic helminths. This bias stems, in part, from the observation that parasitic organisms tend to allocate a

substantial amount of their energy reserves to reproduction. Calow (1981) estimated that the average reproductive output of an individual parasitic platyhelminth represents as much as 35-40% of its total energy expenditure with eggshell production alone making up 27-30% of that total (Wharton, 1983). For example, according to Köster et al. (1988), the synthesis of eggshell precursor proteins for *Schistosoma mansoni* is one of the highest known at 4×10^4 molecules/cell/second which represents a daily production equal to 6% total adult mass. The investment in egg production in general, and quinone tanning in particular, is thus not trivial in these organisms. A number of hypotheses have been proposed to explain the amplification of reproductive output in parasites (see, e.g., Rogers 1962; discussion in Brooks and McLennan 1993a,b,c; but also see Trouvé et al., 1998). In this chapter, I will focus my attention on the evolution of quinone tanning in the parasitic platyhelminthes.

Why expend energy depositing eggshells that are rich in quinone-tanned proteins? Llewellyn (1965) proposed that quinone tanned eggs were a “pre-adaptation” (exaptation of Gould & Vrba, 1982) for endoparasitism. He used the term pre-adaptation to indicate that the quinone-tanned egg had originated prior to the origin of endoparasitism, but that the function of this eggshell had been co-opted by selection to fit the parasitic lifestyle. In particular, Llewellyn suggested that tanning protected the eggs from digestion as they passed through the newly acquired vertebrate host’s gut. He based this suggestion upon experimental demonstration that quinone tanned eggs were resistant to the digestive actions of pancreatin (eggs from *Fasciola hepatica* [Digenea], *Entobdella soleae*, *Diclidophora kuscae* [Monogenea]; *Schistocephalus solidus* [Eucestoda]) while eggs without quinone tanning were not resistant (eggs from *Gorgoderia vitelliloba* [Digenea];

Moniezia sp., *Hymenolepis diminuta* [Eucestoda]). This demonstrates that quinone tanned eggshells are a sufficient cause for resistance to pancreatin (cf. John Stuart Mill, 1843 *System of Logic*) although the samples are admittedly small. Llewellyn believed that the protective action of sclerotized eggshells represented a critical prerequisite for the evolution of endoparasitism. His hypothesis thus has two components. First, quinone tanning is older than the Neodermata. In order to address this component, we need to pinpoint the origin of quinone tanning. Questions of character origin fall within the domain of the comparative phylogenetic research program (see e.g., Brooks and McLennan 1991, in press and references therein). Two pieces of information are needed, a robust phylogenetic tree for the parasitic flatworms and their free living relatives, plus detailed information about the presence or absence of quinone tanning within these groups. The second component of Llewellyn's hypothesis concerns the relationship between the function of quinone tanning and the success of the Neodermata. Llewellyn proposed that quinone tanning was a "key innovation" (Miller, 1949) for these parasites; a trait (or one of several traits) that allowed the group to colonize a novel habitat (the interior of vertebrates) and speciate therein. In order to study this component further we need detailed studies of the possible functions of the quinone-tanned eggshell in both the ingroup and outgroup, as well as information about speciation patterns in the groups. Data about speciation are extremely rare in most groups, and parasitic platyhelminthes are no exception. I will therefore focus my attention on four questions in the remainder of this chapter: Is quinone tanning older than the Neodermata?; What are the possible functions of such tanning in these parasites and their free living relatives?; Has quinone tanning ever been lost in the Neodermata, and if so, are there any correlated changes in

the other aspects of the parasites' life history that could possibly compensate for its loss (assuming that quinone tanning has a demonstrable "function" to begin with)? Llewellyn felt that there was a direct coupling between the presence of quinone tanning and the habitat in which the parasite lived; that is, there was a direct correlation between having tanned eggs and having an intestinal route of egg emergence from the definitive vertebrate host. Given this, I would expect to see the following macroevolutionary patterns: (1) quinone tanned eggs are plesiomorphic for the Neodermata (the character originated before the origin of endoparasitism, (2) the plesiomorphic state for endoparasitism is an intestinal route of egg expulsion from the host, and (3) the presence or absence of quinone tanning should covary with the route of egg emergence (loss of eggs passing through the intestine should be correlated with loss of egg tanning).

MATERIALS & METHODS

The strength of a comparative phylogenetic analysis is dependent, in part, on the robustness of the phylogenetic tree used to trace the macroevolutionary patterns of character origin and diversification (Brooks and McLennan 1991). The Neodermata is currently one of the most extensively studied and phylogenetically analyzed groups, with a database comprising more than 2500 character states (see Brooks & McLennan, 1993c). Recent phylogenetic studies have added considerable resolution and support for overall systematic schemes among the parasitic flatworms (Chapter 2). Preliminary phylogenies exist for the three major clades within the Neodermata, the Digenea, Monogenea, and Cestodaria. There is a familial level phylogeny with a high consistency index for the Digenea (C. I.= 75% Brooks et al. 1985b, 1989; Brooks & McLennan, 1993c). The

Cestodaria is not resolved to familial level, however, the current estimate of phylogeny based on 49 morphological characters does have a high C. I. (87.2%) (Hoberg et al., 1997), indicating that the estimate of phylogeny is robust given the data set. The Monogenea is resolved to the familial level, but the phylogeny is not well supported (C. I. = 57.3%; Boeger & Kritsky, 1993, 1997). In fact, some authors question the monophyly of the group (Rohde, 1994; Justine, 1998b; Litvatis & Rohde, 1999; Mollaret et al, 1997, 2000). Given the importance of a robust phylogenetic hypothesis as a starting point in evolutionary studies, I decided to focus my attention on the Digenea and the Cestodaria in this preliminary investigation of the evolution of eggshell tanning. Hopefully future studies will resolve the status of the Monogenea, and provide a more rigorous template for investigating changes in quinone tanning within that clade.

Information on the presence or absence of quinone-tanned eggs was collected primarily from histochemical testing summarized in Smyth (1994) for the Neodermata and Gerzeli (1968) for the non-parasitic platyhelminthes, with Bunke (1972) and Isida and Teshirosi (1986) being the latest contributions to non-parasitic platyhelminthes. Information concerning cestodes was taken from Hoberg et al. (1997) and Swiderski & Xylander (2000). Successive sister taxa of the neodermatans, *Udonella* (Schell, 1985; Ivanov, 1952) and Fecampiidae (Shinn & Christensen, 1985), are coded absent for quinone tanning based on descriptions (see below). Histochemical evidence is compiled in Appendix 2. Most of the research that has been done on platyhelminth eggshells has been with the hope of being applied to control of helminthic infections, and thus most of the available information is concentrated on medically and commercially important groups such as the schistosomes and fasciolaids. There is currently very little information

available for the Aspidobothrea, the sister-group to the Digenea. The presence of quinone tanning has been confirmed using histochemical tests for only one species, *Aspidogaster conchicola* (Gerzeli, 1968), and anecdotal evidence for two others (*Multicotyle cristata*: Thoney & Bureson, 1987; *Sychnocotyle kholo*: Ferguson et al., 1999). No information, anecdotal or otherwise, exists for the other 10 genera of the order (Chapter 3); therefore I eliminated the Aspidobothrea from this analysis.

There are two caveats about the way in which this character (presence or absence of sclerotin) is scored. First, as mentioned above, the presence of quinone tanning has generally been inferred from the presence of colored eggs in gravid adults. The strongest line of evidence is generally considered to be histochemical testing for the components involved in tanning (i.e. protein precursors, phenols [free or as residue in an amino acid side chain] and phenolase [see Appendix 2] but also see Smyth & Halton, 1983 and Ramalingam, 1970 for non-specificity of some tests). Histochemical results were checked against available descriptions of the eggs and found to perfectly covary, that is, where histochemical tests indicate that sclerotin was ‘present’ for a particular species, that species was also described as having colored eggs, but where ‘absence’ was recorded no color has been reported (see Appendix 3). In general then, colour was assumed to be an accurate indicator of the presence of quinone-tanned proteins. For the purposes of this analysis, I will accept this assumption, with the caveat that a substantial amount of research is necessary in order to test the validity of the assumption.

Second, I am scoring “quinone tanning present” as one state. If colour is a reliable indicator of the presence of quinone-tanned proteins, then the great variety of eggshell colors within the Neodermata hints that the character is much more complex than simply

“present”. For example, different groups may use different protein precursors, different concentrations of the same precursors resulting in different degrees of tanning, or differential production of melanins etc. It is not unusual for researchers to reduce complex characters such as nuptial colouration, parental care, and mating system type into simpler states in order to produce a preliminary hypothesis of character evolution (see e.g., McLennan, 1991; Sillén-Tullberg & Temrin, 1994; Temrin & Sillén-Tullberg 1994, 1995; Lindenfors & Tullberg, 1998; Ah-King & Tullberg, 2000). This process represents the beginning of a prolonged investigation; one that helps focus the researcher’s attention on areas that require further investigation in order to collect enough data to begin breaking the complex character into its component parts. The second caveat is that the evolutionary picture will probably turn out to be more complicated than this simple presence or absence mapping will show.

I collected data concerning the site of adult infection in the definitive host and route of egg emergence from the primary literature (see Appendix 3) and Schell (1985). The cues and mechanism of larval hatching are not fully understood and may be linked with the shell material itself in the parasitic Platyhelminthes (see Symth & Clegg, 1983). I therefore collected information about the following life history characters that might possibly be implicated in the secondary loss of quinone tanning: (1) the state of the egg when laid because the larval epidermis may confer protection; (2) whether the egg is operculate; (3) mode of hatching; (4) presence of a uterine pore (Cestodaria only). Characters were optimized onto the phylogenetic trees for the Neodermata, Digenea, and Cestodaria using both the Acctran and Deltran options in MacClade v. 4.0 (Maddison and Maddison, 2001).

RESULTS AND DISCUSSION

Being endoparasitic in the gut of a vertebrate host is a synapomorphy for the Cercomeridea (figure 4.1), confirming the second macroevolutionary prediction based on Llewellyn's hypothesis. Optimizing the presence or absence of quinone tanned eggs onto the phylogenetic tree for the Neodermata and its relatives (figure 4.2) indicates that quinone tanning is extremely old within the Platyhelminthes. There are two equally parsimonious hypotheses for its continued diversification: (1) tanning was lost independently in the Fecampiidae and *Udonella* (tanning is symplesiomorphic for the Neodermata) and (2) tanning was lost in the ancestor of the Revertospermata and reappeared in the ancestor of the Cercomeridea (Trematoda + Monogenea + Cestodaria). These results appear to indicate that quinone tanning has been lost at least once and possibly twice within this group but more data, especially from the rhabdocoels, are needed to test the hypotheses generated by the optimization. Given that we cannot determine the sequence of character evolution within a branch, scenario #2 above provides weaker support for Llewellyn's hypothesis than does scenario #1. However, either scenario confirms the first prediction from Llewellyn's hypothesis: the presence of quinone-tanned eggshells is plesiomorphic for the Neodermata.

As mentioned previously, quinone tanning is widespread throughout the Platyhelminthes, so its point of origin may be as old, if not older, than the phylum. In order to pinpoint that origin, we need data from basal members of the phylum (e.g. Acoela and Catenulida) as well as from successive sister-groups to the Platyhelminthes (e.g., deuterostomes, Riutort et al., 1993; Carranza et al., 1997). For the purposes of this

study, however, I have now answered my first question: quinone tanning arose, at least, concurrently if not before the evolution of endoparasitism

The next issue that needs to be addressed is the question of the functional significance, if any, of quinone tanning. Llewellyn suggested that sclerotin prevented the digestion of eggs as they passed through the vertebrate gut on their way to the external environment. The macroevolutionary patterns indicate that quinone tanning does appear to provide protection for the eggs of *Fasciola hepatica*, *Schistocephalus solidus* and the monogeneans *Entobdella soleae* and *Diclidophora luscae* from at least one digestive enzyme, pancreatin (Llewellyn, 1967). Protection from acids and digestive enzymes has also been demonstrated for parasitic protozoans with cysts comprising of quinone tanned proteins. Being impermeable to water soluble substances, the coccidian quinone tanned cyst wall is not injured by chemicals which normally damage the protoplasm (Monné & Hönig, 1954). Although these studies confirm the potential status of quinone tanning as an exaptation for endoparasitism (via protection of the eggs from digestion), this conclusion is tentative for two reasons. First, the experimental data base is extremely small for the group. Second, there are numerous physico-chemical properties associated with quinone tanned proteins; i.e. quinone tanning may serve more than one function in these organisms (or, alternatively different functions in different groups). For example, the antibacterial action of free quinones has been known since 1911 (See review in Colwell & McCall, 1945). While no free quinones are present during platyhelminth eggshell formation, fungal spores with quinone tanned protein coats demonstrate resistance to microbial lysis in soil (Kuo & Alexander, 1967; Potgieter & Alexander, 1966). Kearn (1998) suggested that quinone-tanned eggshells provide a sterile and tightly

sealed environment for the developing larva. Protection from bacterial invasion could thus hypothetically confer an adaptive benefit to organisms which provide no parental care to their eggs (i.e. do not clean or remove decaying eggs during development). The eggs are, in essence, on their own when released into water or onto soil, until they eventually hatch or are ingested by an intermediate host. Experimental investigations have also demonstrated that the quinone tanned protein coat of fungal spores confers protection from light, particularly damage from ultraviolet radiation. (Sussaman, 1968). This occurs as a side effect of melanin production via the oxidation of tyrosine to DOPA to DOPAquinone to melanin. Although melanins have been detected in a variety of quinone tanning systems (e.g. insect cuticle: Sugumaran, 1998); to date no one has looked for these compounds in parasitic platyhelminth eggshells. Tyrosine is oxidized to produce at least DOPA in platyhelminth eggshell production (Waite & Rice-Ficht, 1987) so it is possible that the entire melanin pathway exists in these organisms. Finally, the adhesive quality of quinone tanned proteins (Waite, 1990) is very important to ectoparasites and various symbionts in transmission via host contact (e.g. during mating). It has also been suggested that the presence of quinone tanned proteins causes eggs to sink, which may be important to interstitial turbellarians (Ginetsinskaya, 1988). Overall, then, quinone-tanned eggs might possibly be serving at least five adaptive functions within the parasitic platyhelminthes: protection from (1) macropredators (digestion of eggs by the definitive host), (2) micropredators (bacterial attack), and (3) the abiotic environment (radiation), as well as (4) increasing the likelihood of transmission and (5) aiding in dispersal. In order to determine whether these “intuitively obvious” benefits are indeed real, we would need substantially more experimental investigations into the

function of quinone tanned proteins. We would also need to demonstrate the function(s) of quinone tanned eggs in the closest free living relatives of the Neodermata in order to determine whether that function is apomorphic or plesiomorphic within neodermatans. These questions must be answered if we are ever to understand the complex nature of the evolution of quinone tanning. For example, quinone tanning may originally have been selectively advantageous in free living platyhelminthes because of functions 2, 3, 4, and 5 above. Function 1, protection from digestive enzymes, may be a side effect of quinone biochemistry that was never accessed before the association between flatworms and vertebrates appeared. In other words, the presence of quinone tanning may have allowed the ancestor of the Neodermata to develop and mature in a vertebrate's gut, but that function did not originate as an adaptation to or for endoparasitism.

It might be possible to shed a little light on the problem by looking for groups in which quinone tanning has been lost, then asking if any other characters changed that might permit such a loss (assuming that quinone tanning plays an important role in flatworm biology). Optimizing the character onto the more detailed phylogenetic trees for the two major neodermatan clades indicates that quinone tanning has been lost at least six times within the Digenea (figure 4.3) and once within the Cestodaria (figure 4.4). The convergent loss of quinone tanning within the Digenea is the perfect place to begin an investigation into the function of quinone tanning in these organisms. Repeated origins or losses of traits provides researchers with the evolutionary equivalent of replicated experimental trials; that is, this is a good place to test a hypothesis about the factors that might be influencing the evolution of a character (Coddington 1988; Arnold 1990; Brooks and McLennan 1991).

There are no obvious correlations between loss of quinone tanning and state of the egg when laid (figure 4.5), the presence of an operculum (figure 4.6), or the mode of first intermediate host infection (figure 4.7). There is, however, an association between loss of quinone tanning and changes in the plesiomorphic habitat (route of egg emergence [figure 4.8] + site of adult infection [figure 4.9]). All of the six groups in which quinone tanning has been lost are ones in which the route of egg emergence does not require the egg to spend any (*Sanguinicolidae*, *Gorgoderiidae*), or little (*Bucephalidae*, *Zoogonidae*, *Lepocreadiidae*, *Paramphistomatidae*) time in the presence of the host's digestive enzymes. The *Sanguinicolidae* live in the circulatory system of their hosts where they release their eggs which eventually mature in the gills. Here the miracidium hatches and penetrates to the exterior. The *Gorgoderiidae*, inhabit the urinary bladder and shed their eggs into the surrounding urine (figure 4.8). The remaining four groups are all found in the intestinal tract of their host, but they tend to prefer posterior locations within that available "habitat" (figure 4.9). However, more detailed information on both hosts and specific site of infection are needed to critically evaluate Llewellyn's hypothesis.

One interesting feature of paramphistomes is that derived members of the group have moved up into the rumen and bile ducts of homeothermic hosts. These taxa, as mentioned above, do not have quinone tanned eggs. At first glance, this appears to refute the hypothesis that quinone tanning is required to protect the eggs on their intestinal voyage. Paramphistomes, however, have heavily keratinized eggshells, and keratin has been shown to have similar resistant properties to digestive enzymes (Smyth & Halton, 1983). Interestingly, "some keratin may also be present in the eggs of [*Fasciola*]... previously thought to consist solely of sclerotin" (Smyth & Halton, 1983:99), while the

eggshells of *Orchispirium heterovitellatum* (a sanguinicolid) are composed of elastin (Madhavi & Rao, 1971). Most eggs increase in volume as they develop (Tinsley, 1983), which may suggest that elastin, which would permit eggshell expansion, is widespread in the neodermatans. It is thus tempting to speculate that the eggshells of Neodermatan eggs are plesiomorphically a composite of many different materials, including quinone-tanned proteins, elastin, and keratin. The composite nature of the eggshell would provide the raw materials on which selection could work; modifying the eggshell composition by emphasizing one component over another (e.g., loss of quinone-tanning and increase in keratin). In other words, it might be possible to select against the presence of quinone-tanned proteins in the plesiomorphic habitat (the gut) without the added Lamarckian stipulation that another functionally equivalent compound miraculously appear to counteract that loss. Re-echoing the sentiments of Smyth & Halton (1983), it is clearly important to determine whether both structural proteins (sclerotin and keratin) are present because tests for keratin have been employed only in those instances in which sclerotin was absent. I wish to add that according to this logic, tests for elastin are also needed.

Can keratin be formed from existing protein precursors in the absence, or inhibition, of phenol oxidase (one possible way to lose quinone tanning)? Recent, *in vivo* techniques to inhibit phenolase have been developed (Seed & Bennet, 1980) that would lend themselves to this very question. Keratins are formed by disulfide bonds between cysteines, which have thiol side-chains. These recent *in vivo* techniques use thiols to compete with phenolase for copper ions. This suggests that protein precursors with more cysteines may effectively inhibit phenolase preventing quinone tanning. So, we can use

these techniques to ask, If phenolase is inhibited, does keratin form instead? and Do these eggs remain viable after passage through the host?

Not all trematode groups whose eggs receive only minor or no exposure to digestive enzymes have lost quinone tanned eggs (for example, the lung fluke, *Heronimidae*; the blood flukes, *Schistosomatidae*). This does not falsify the hypothesis that quinone tanning has been co-opted to serve this protective role because there is nothing in Darwinian evolution that stipulates traits must be lost if they are no longer necessary. In fact, there are many explanations for why a “non-functional” trait may persist. The most obvious explanation is that evolution has not had time to eliminate it. This would appear to be unlikely in this case because the Neodermata is an extremely old group, at least 500 million years old. Alternatively, there may be no underlying genetic variability in the trait, so natural selection cannot work to modify its expression. Finally, there might be a greater cost incurred to eliminate the trait than to maintain it if the genetic/developmental basis for the trait is intertwined with the expression of other characters (e.g., through pleiotropy, developmental constraints, etc: see Maynard Smith et al. 1985; Rose and Lauder 1996; Kelly 1999). At the moment, then, all we can say is that neodermatan groups which have lost quinone tanning demonstrate a compensatory change in habitat (or egg shell composition), but not all groups that show a change in habitat lose quinone tanning. The two characters are not evolutionarily linked.

Overall, the macroevolutionary patterns of character loss and habitat modification in the Digenea support Llewellyn’s hypothesis. Clearly, however, until we can quantify concentration of enzymes in various parts of the intestinal tract and the time spent by the eggs in their passage out of that tract, this support is more suggestive than conclusive.

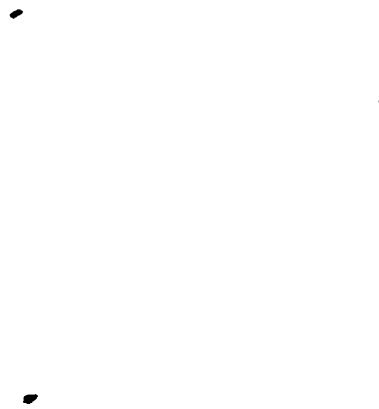
There are also a number of additional questions that must be answered: Do hosts that harbour species from any of these six groups also provide habitat for neodermatan species with quinone tanned eggs? If so, do the worms with quinone tanned eggshells occupy a more anterior position within the gut?

Quinone tanning has been lost only once within the Cestodaria (figure 4.4). This loss occurs following a series of evolutionary modifications within the Eucestoda (true tapeworms). The key step here would appear to be the loss of the uterine pore, and subsequent packaging of the eggs within the proglottis. This is the functional equivalent to changing a quinone-tanned eggshell for a keratinized eggshell; in this case the eggs are protected by the adult neodermis of the proglottis. As discussed previously, tanning was not lost immediately following the supposed usurping of its function by the change in egg retention biology. Nevertheless, the pattern is still consistent with Llewellyn's hypothesis. What is needed now is a series of studies documenting the actual mechanism(s) underlying sclerotin "loss". Is it the same in all groups? The macroevolutionary pattern hints that sclerotin, once lost, does not appear again. Is this truly an irreversible evolutionary step or an artifact of missing data?

The macroevolutionary analysis has thus provided tentative support for Llewellyn's hypothesis: quinone-tanned eggs are a plesiomorphy for the Neodermata (the character originated before, or concurrently with, the origin of endoparasitism), the plesiomorphic state for that endoparasitism is for the eggs to be released via an intestinal route in a vertebrate host, and the presence of quinone tanning is correlated with the requirement for eggs to pass through the harsh environment of the host intestinal tract. Relaxation of this requirement has been coupled with the loss of quinone tanning seven

out of seven times. The correlation between “quinone-tanning present” and “expel eggs through intestinal tract” is not, however, perfect. Some groups living outside of the intestine have quinone-tanned eggs (e.g. schistosomes), while others living in the intestine (e.g. paramphistomes) have lost quinone tanning without suffering any obvious fitness consequences. These observations hint that the system is more complex than simply “quinone-tanning present or absent”; that the state of the neodermatan eggshell represents the outcome of numerous selection vectors acting (possibly) upon the complex pathway producing keratin and quinone proteins in the eggshell (e.g., reduce quinone tanning, increase keratin content), in concert with other changes in the life history parameters (e.g., retention of eggs in proglottids) that affect egg expulsion. We also need to examine the suggestion that quinone tanning may have more than one function in these parasites (e.g., protecting the eggs from bacterial and/or radiation damage). Given the complexity of this system, it seems unlikely that there will be just one general explanation for the maintenance and modification of quinone tanning in the Neodermata.

Figure 4.1. Optimization of route of egg emergence onto the phylogenetic tree for the Neodermata and its relatives (strict consensus of figure 2.3) with Tricladida and Ploycladida placed at the base of the tree.



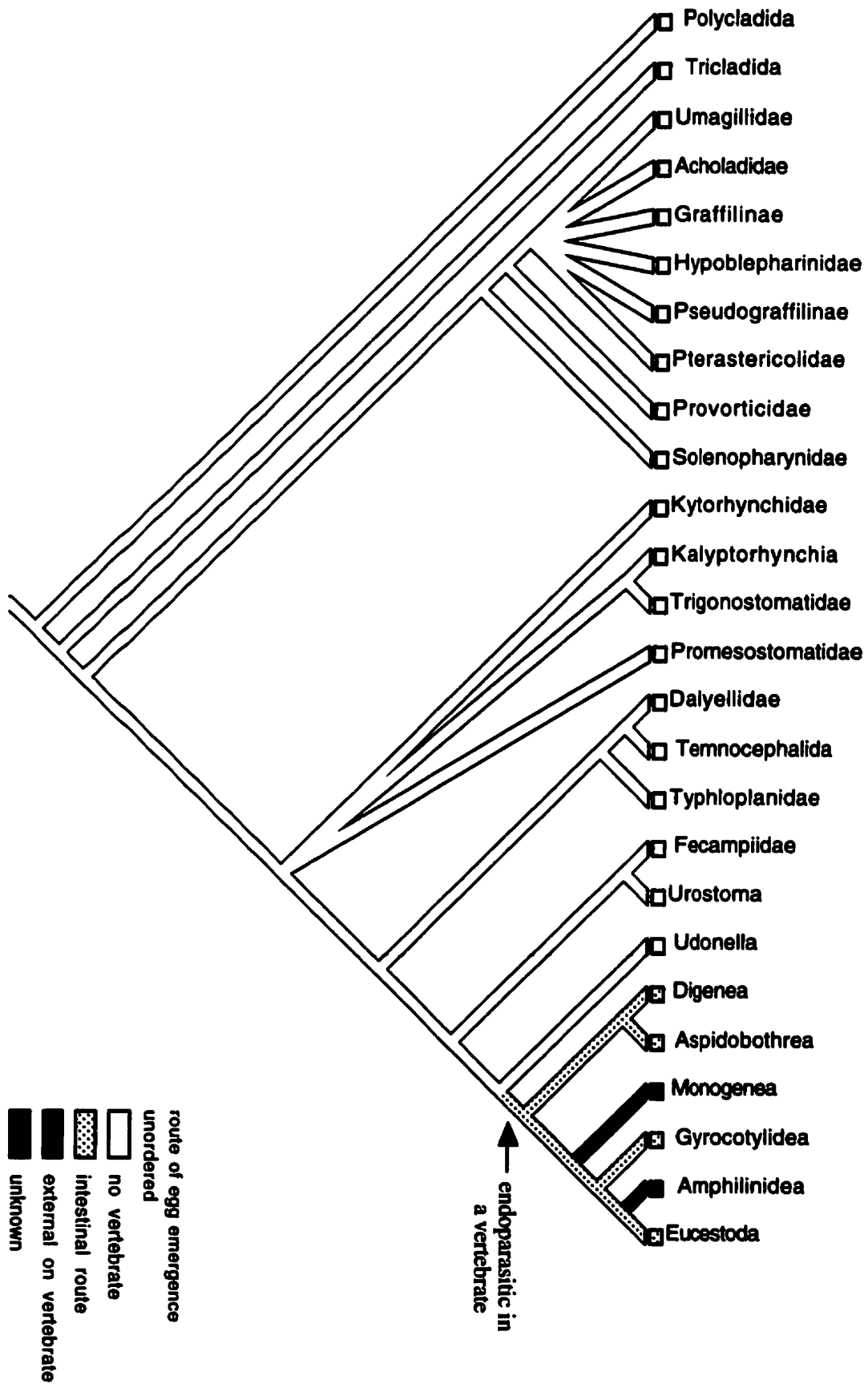


Figure 4.2. Optimization of presence or absence of quinone tanned eggs onto the phylogenetic tree for the Neodermata and its relatives (strict consensus of figure 2.3) with Tricladida and Ploycladida placed at the base of the tree. There are two equally parsimonious optimizations for this trait (as indicated by the hatched lines).

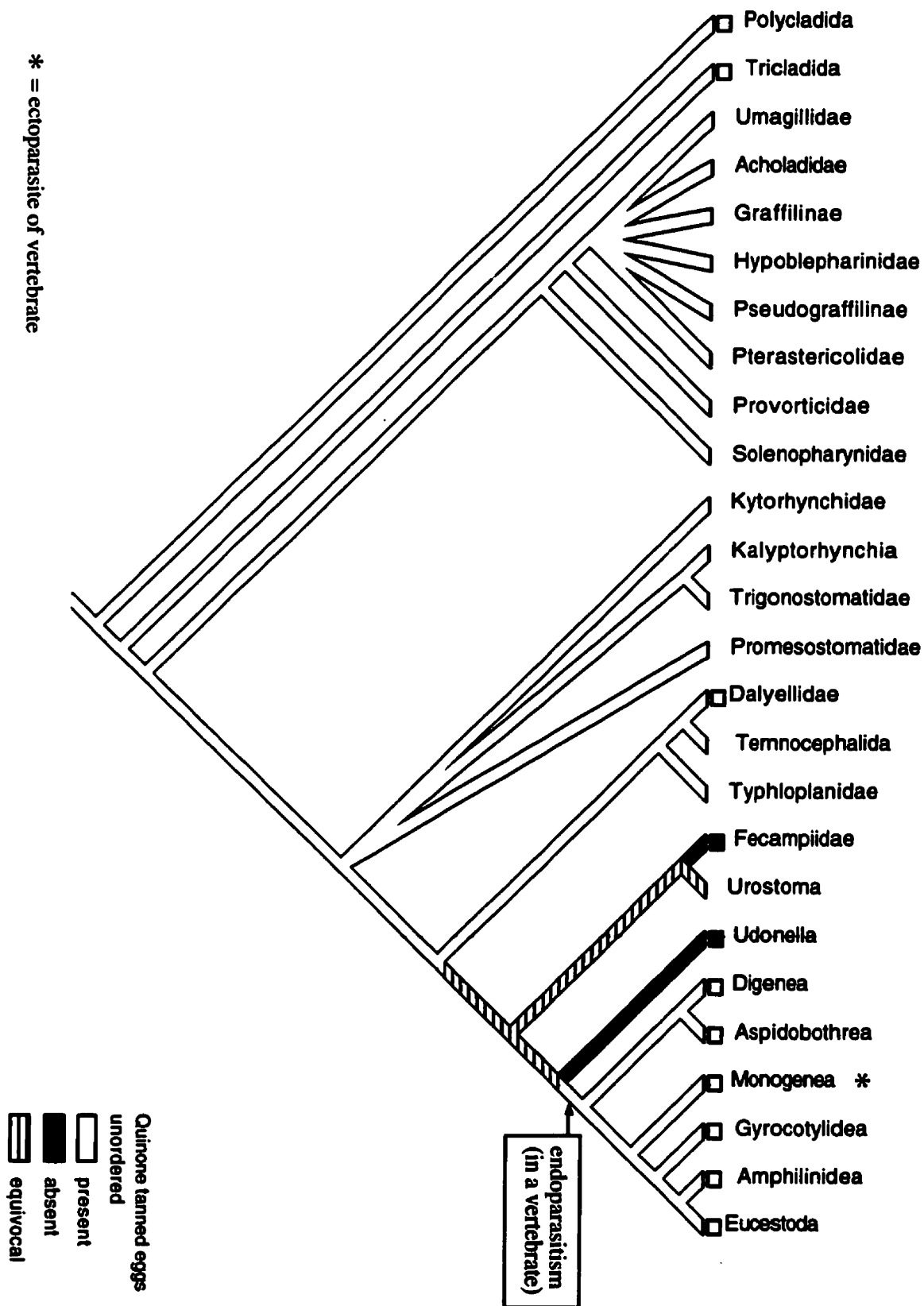


Figure 4.3. Optimization of presence or absence of quinone tanning onto the phylogenetic tree for the Digenea (Brooks and McLennan, 1993).

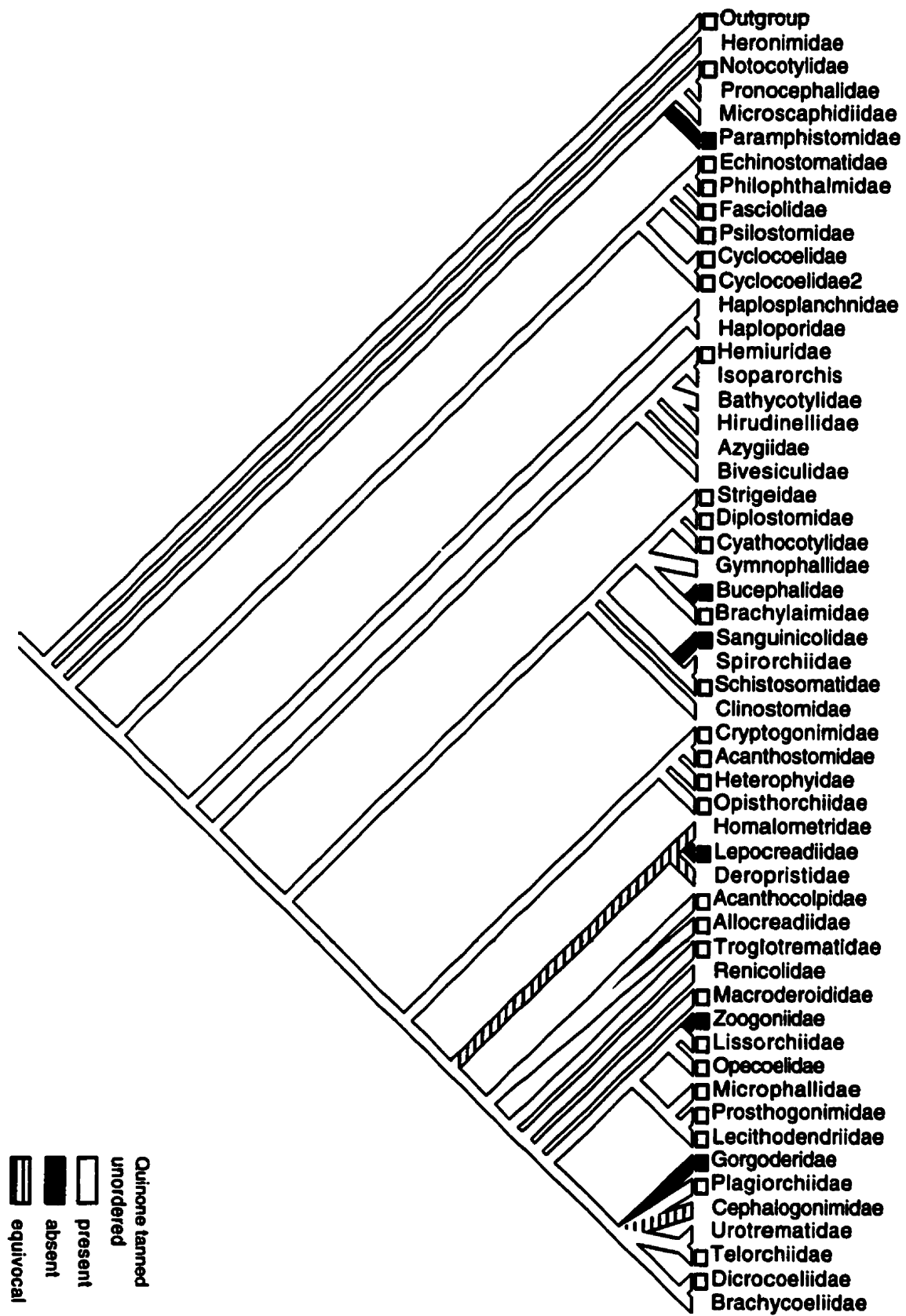


Figure 4.4. Optimization of four life history traits and the presence or absence of quinone tanning onto the phylogenetic tree for the Cestodaria (Hoberg et al., 1997).

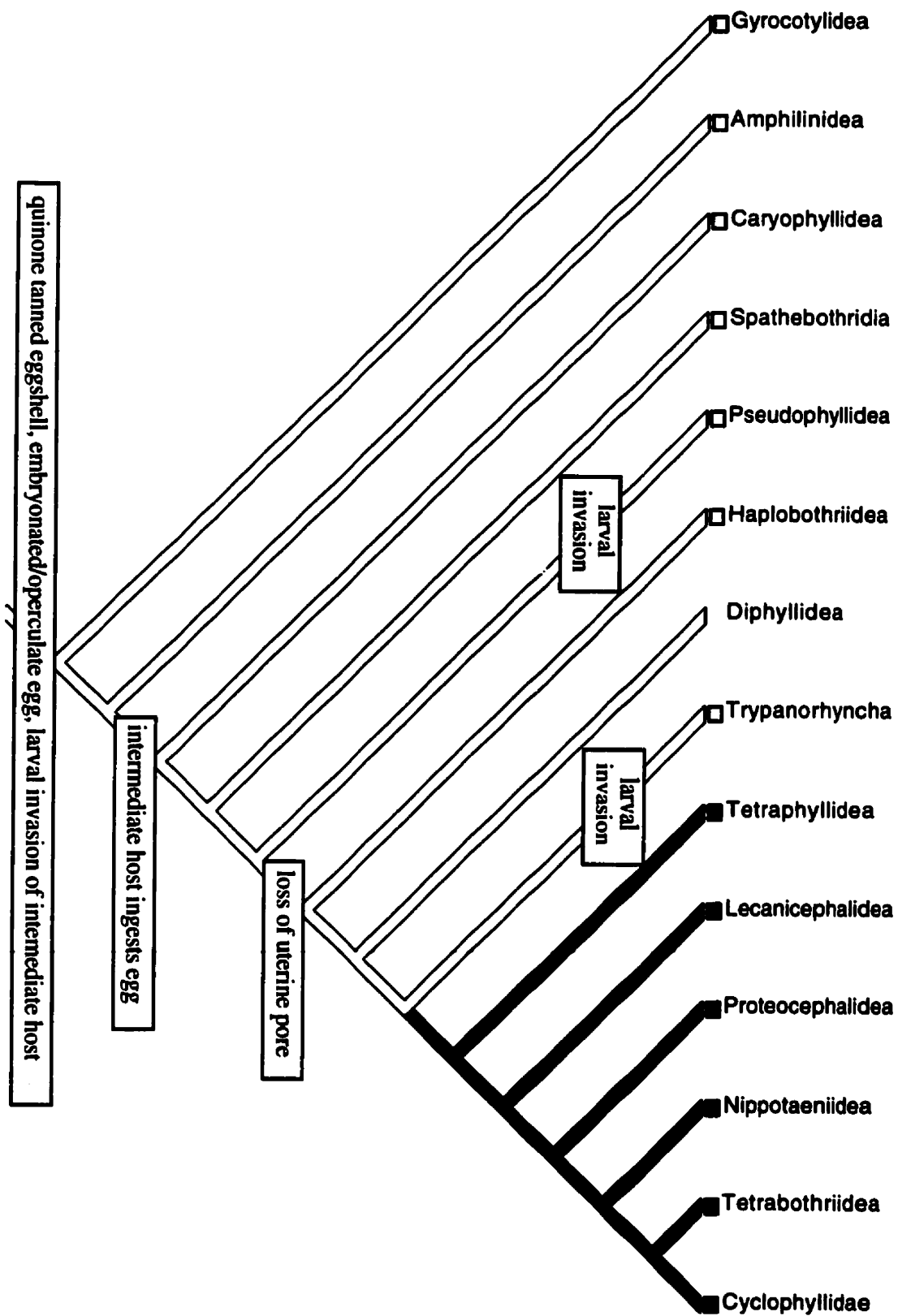


Figure 4.5. Optimization of the embryonic state of the egg when deposited onto the phylogenetic tree for the Digenea (Brooks and McLennan, 1993).

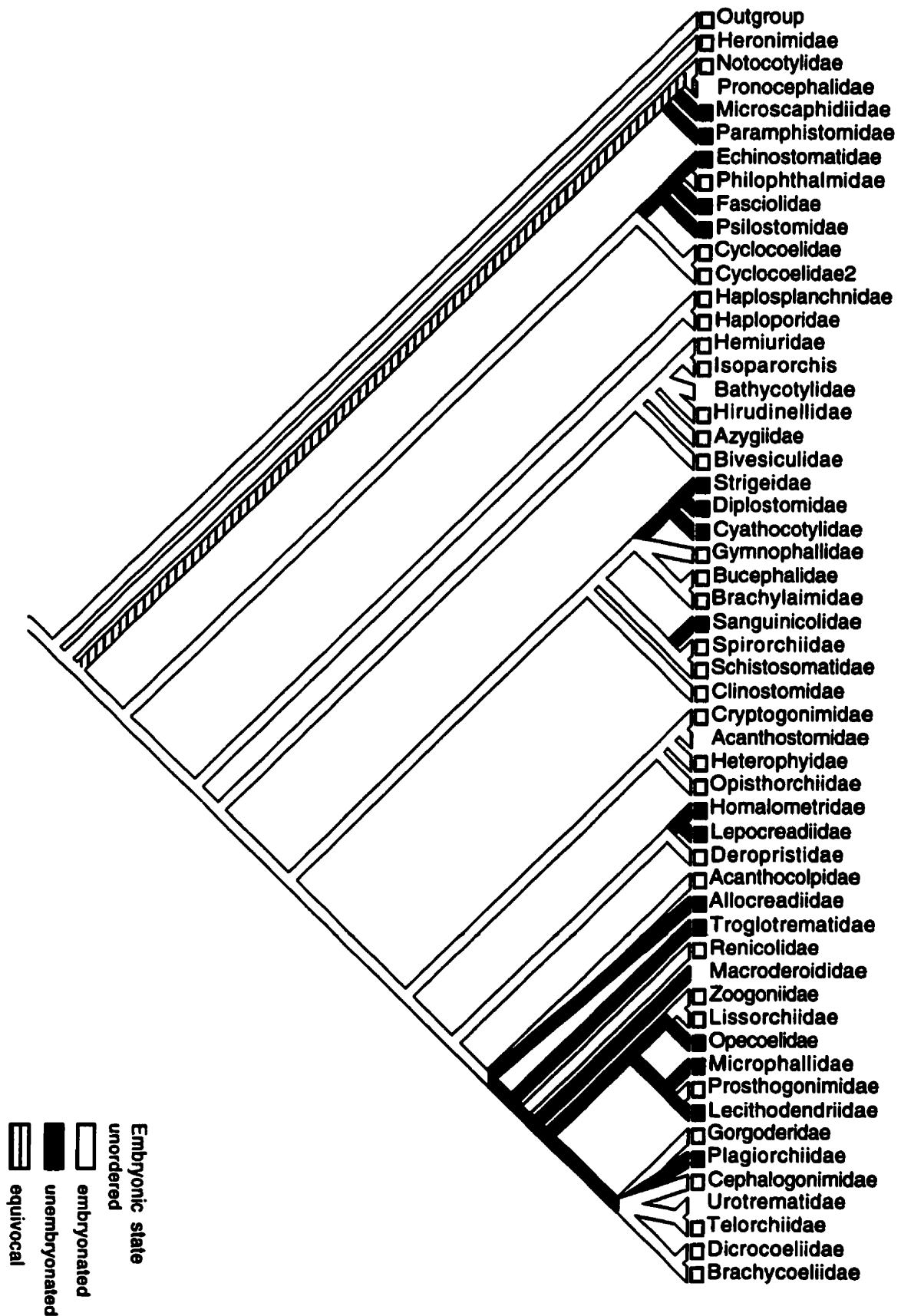


Figure 4.6. Optimization of the presence or absence of an operculum on the egg onto the phylogenetic tree for the Digenea (Brooks and McLennan, 1993).

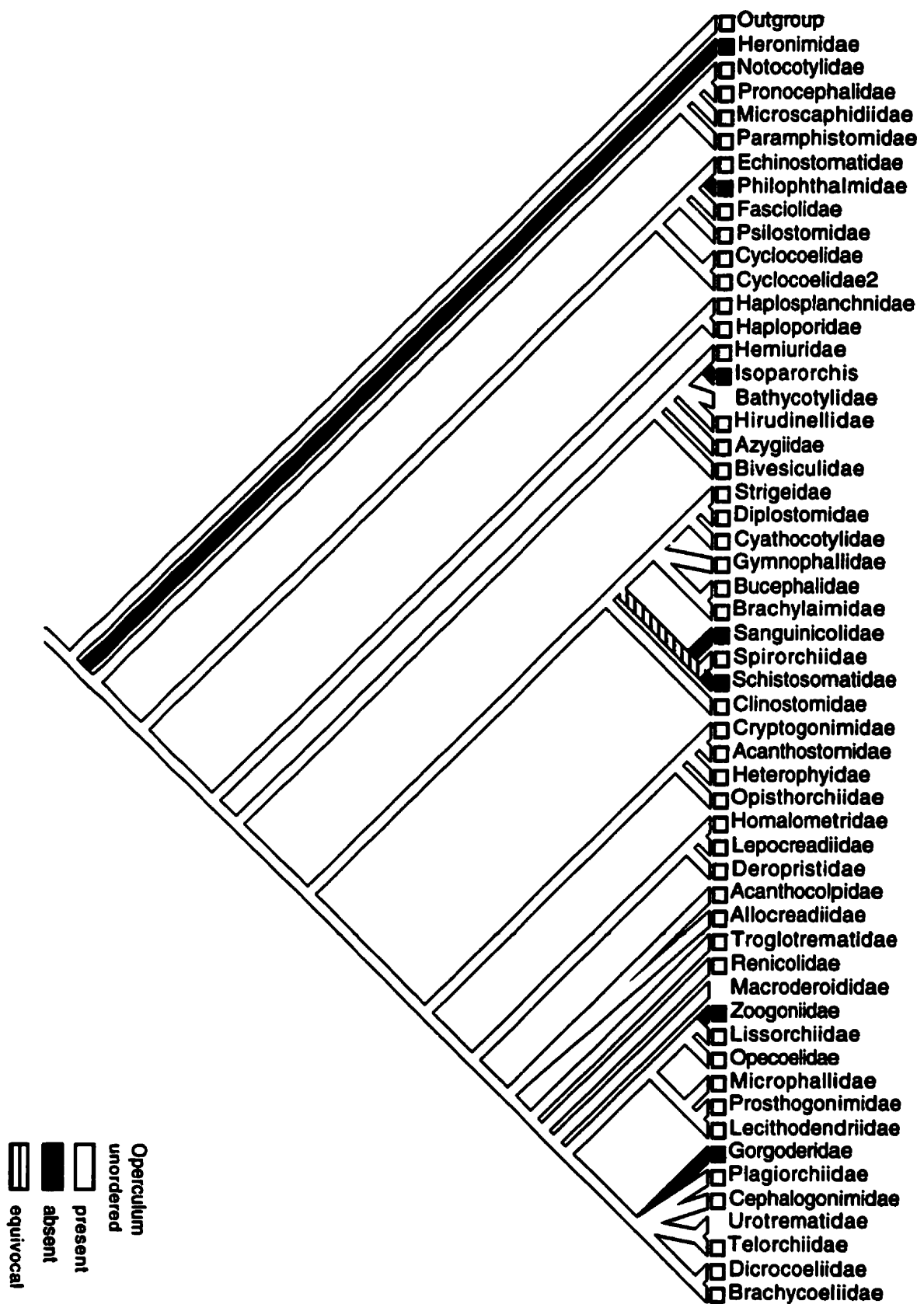


Figure 4.7. Optimization of the mode of infection of the intermediate host onto the phylogenetic tree for the Digenea (Brooks and McLennan, 1993).

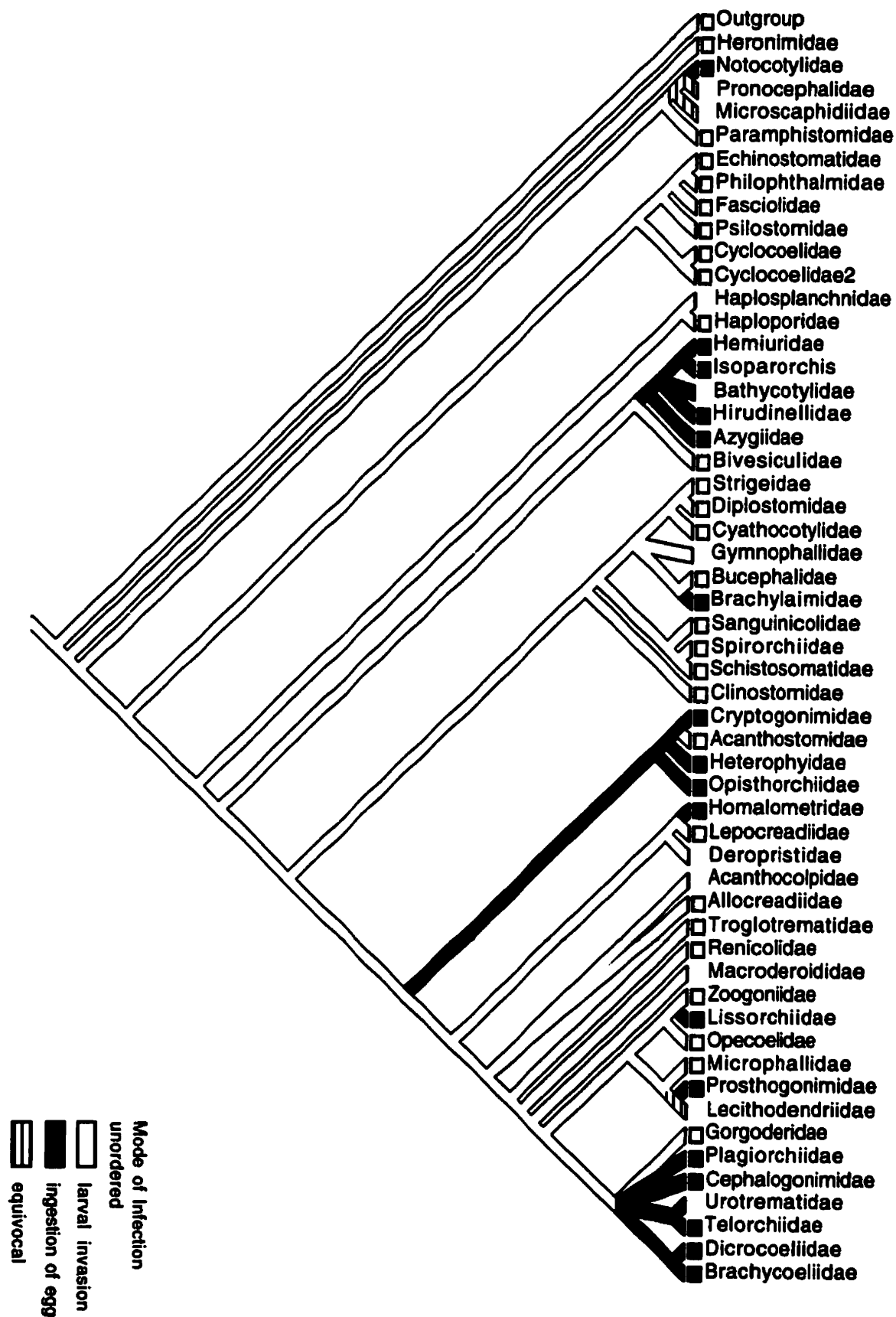


Figure 4.8. Optimization of the route of egg emergence from the definitive host onto the phylogenetic tree for the Digenea (Brooks and McLennan, 1993).

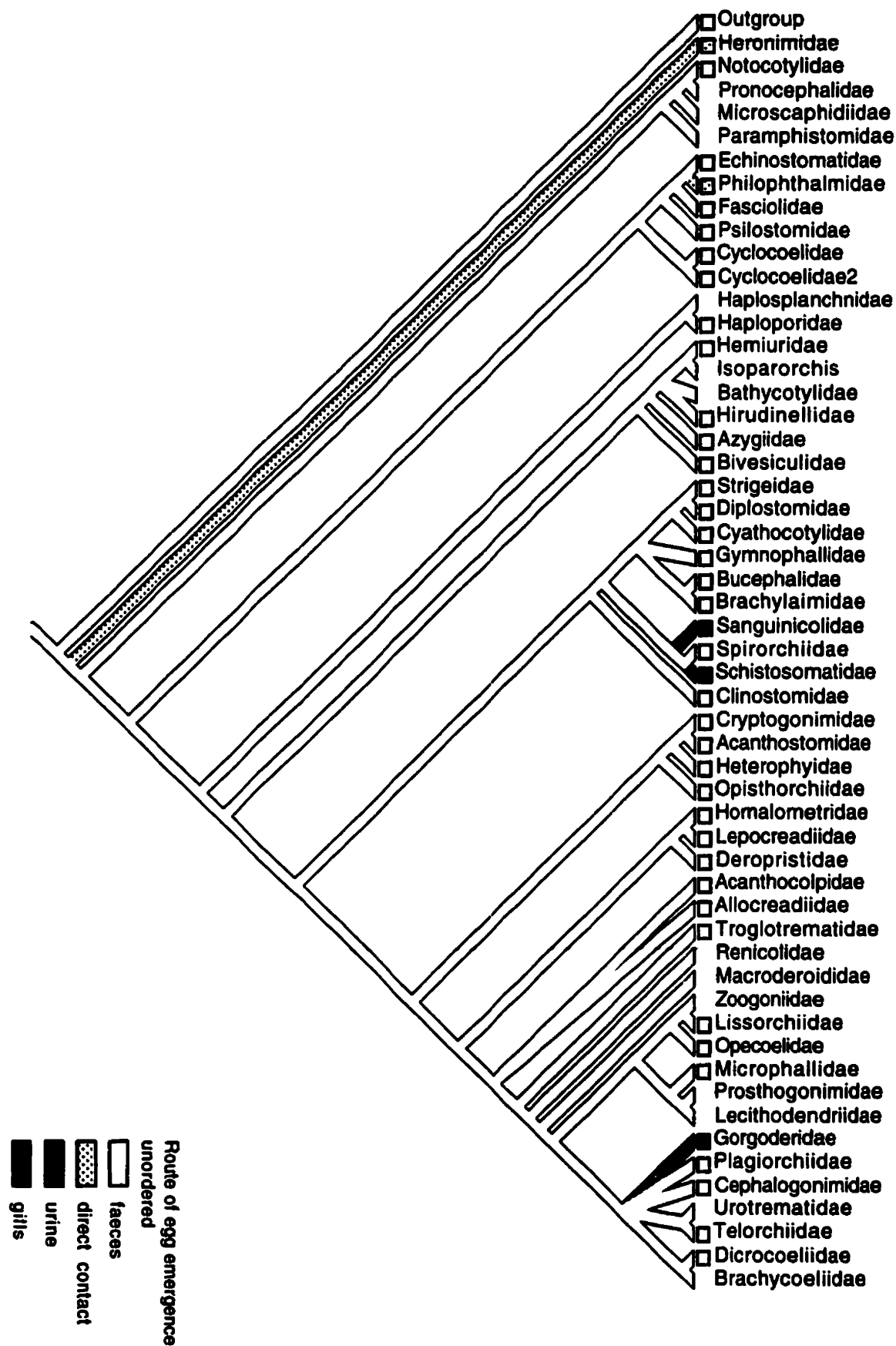
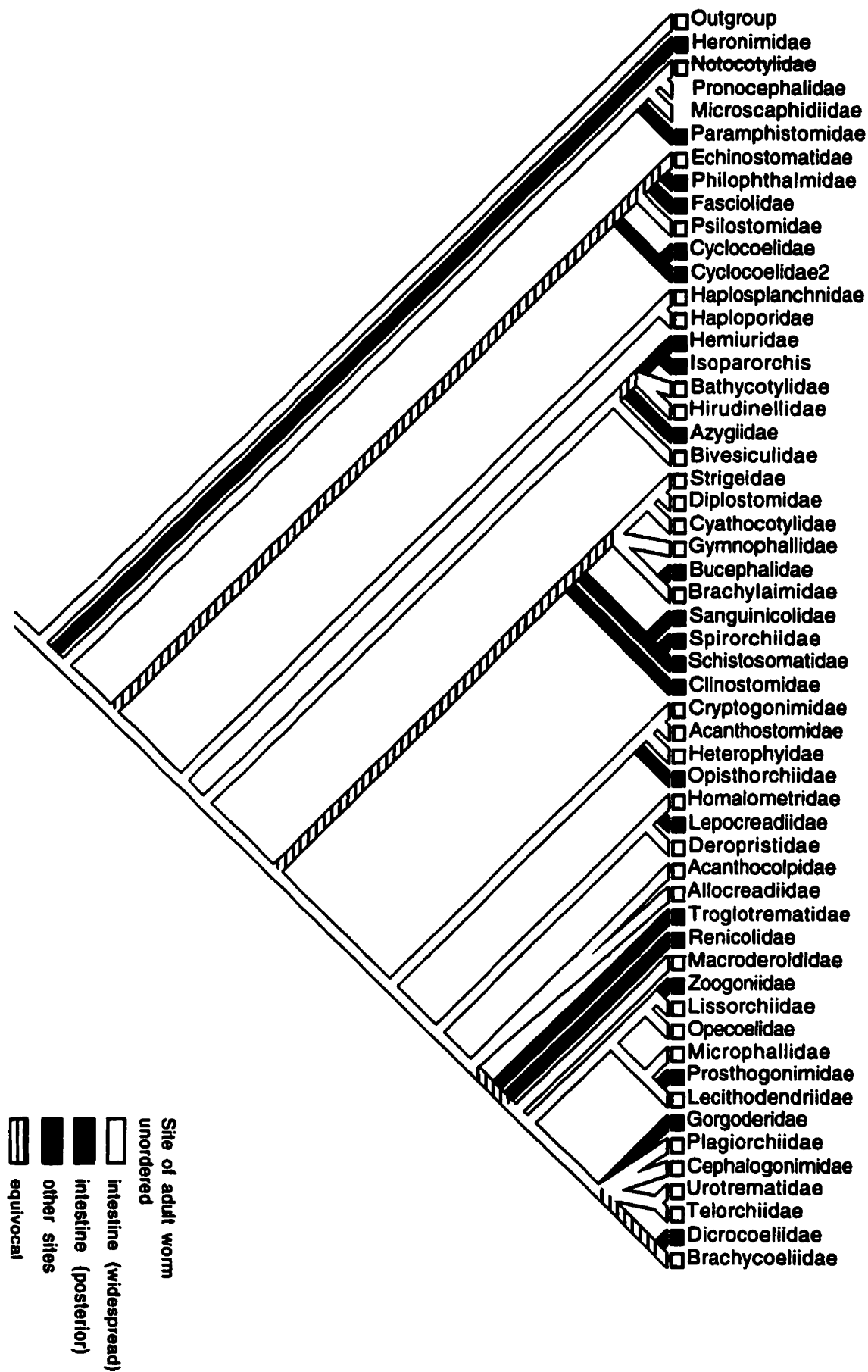


Figure 4.9. Optimization of the part of the definitive host inhabited by the adult parasite onto the phylogenetic tree for the Digenea (Brooks and McLennan, 1993).



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<i>Taxa</i>	Vertebrate Host	Site of Adult Worm	Geographic Location	Reference
<i>Stichocotyle nephropis</i>	Elasmobranchii <i>Raja clavata</i>	biliary ducts	Atlantic Ocean N.A.	Linton (1940)
<i>Multicalyx cristata</i>	Elasmobranchii <i>Rhinoptera quadriloba</i> <i>Mustelus canis</i> <i>Scoliodon tertiae-novae</i> <i>Rhinobatus cemiculus</i> <i>Pristis pectinata</i> <i>Dasyatis sayi</i> <i>Dasyatis centroura</i> <i>Cephaloscyllium ventriosum</i> <i>Sphyrna lewini</i> <i>Odontaspis taurus</i>	biliary ducts spiral valve?	Senegal Gulf of Mexico Massachusetts Santa Barbara California Natal, South Africa East Cape, South Africa	Reviewed in Thoney & Burreson (1988)
<i>Multicalyx elegans</i>	Holocephalii <i>Chimaera monstosa</i> <i>Callorhynchus milii</i>		North Sea Mississippi (Atlantic) Argentina (Atlantic)	Reviewed in Thoney & Burreson (1988)

	<i>Hydrolagus collei</i>		NE Atlantic New Zealand NE Pacific Mediterranean	
<i>Cotylogaster michaelis</i>	Sparidae- porgies <i>Cantharus orbicularis</i> <i>Sparus auratus</i>	intestine		Monticelli (1892) Montecelli (1906)
<i>Cotylogasteroides occidentalis</i>	Sciaenidae- drums <i>Aplodinotus grunniens</i>	intestine	N.A.	Nickerson (1902) Sogandares-Bernal (1955)
<i>Cotylogasteroides barrowi</i>	N/R		N.A	Huehner & Etges (1972)
<i>Cotylogaster dinosoides</i>	Sciaenidae- drums <i>Pogonias cromis</i>	intestine	Gulf of Mexico (Mississippi & Louisiana)	Hendrix & Overstreet (1977)
<i>Cotylogaster basiri</i>	Sparidae-porgies <i>Calamus calamus</i> <i>Rhabdosargus sarba</i>	intestine rectum	Peurto Rico Durban Natal, South Africa	Siddiqi & Cable (1960) Bray (1984)
	<i>Archosargus probatocephalus</i> Sciaenidae- porgies <i>Micropogonias undulatus</i> <i>Menticirrhus americanus</i> Carangidae- pompano <i>Trachinotus carolinus</i> <i>Tracghinotus falcatus</i>		Gulf of Mexico (Mississippi & Louisiana)	Hendrix & Overstreet (1977)
<i>Rugogaster callorhinchii</i>	Holocephalii <i>Callorhinchus callorhinchus</i>	rectal glands	Atlantic Ocean S.A.	Amato & Pereira (1995)
<i>Rugogater hydrolagi</i>	Holocephalii <i>Hydrolagus colliei</i>	rectal glands	Pacific Ocean N.A.	Shell (1973)
<i>Asidogaster conchicola</i>	<i>Amyda sinensis</i> (Turtle)	intestine	Wuchang	Reviewed in Dollfus (1958)

	Cyprinidae <i>Leuciscus aethiops</i> <i>Cyprinus carpio</i>		(China) Wuchang (China) N.A.	
<i>Aspidogaster limacoides</i>	Cyprinidae <i>Leuciscus idus</i> <i>Leuciscus cephalus</i> <i>Aspius aspius</i> <i>Blicca bjoerkna</i> <i>Abramis sapa</i> <i>Abramis ballerus</i> <i>Abramis brama</i> <i>Rutilus frisii</i> <i>Rutilus rutilus</i> <i>Barbus brachycephalus</i> <i>Vimba vimba</i> Gobiidae <i>Gobius fluviatilius</i> Siluridae <i>Siluris</i>	intestine		Reviewed in Dollfus (1958)
<i>Asidogaster decatis</i>	Cyprinidae <i>Cyprinus carpio</i>	intestine	Lake Antioche	Reviewed in Dollfus (1958)
<i>Aspidogaster enneatis</i>	Cyprinidae <i>Barbus</i> sp.	intestine	Lake Tiberiade	Reviewed in Dollfus (1958)
<i>Aspidogaster piscicola</i>	Cyprinidae <i>Labeo rhoita</i>	intestine	India	Rawat (1948)
<i>Aspidogaster indicum</i>	Cyprinidae <i>Barbus tor</i>	intestine	India	Dayal (1943)
<i>Lobatosoma manteri</i>	Carrangidae- pompanos	intestine	Australia	Rohde (1973)

<i>Lobatosoma kemostoma</i>	<i>Trachinotus blochi</i>		Florida	
	Carrangidae- pompanos			
	<i>Trachinotus carolinus</i>			
<i>Lobatosoma ringens</i>	Carrangidae- pompanos	intestine		Summarized in Hendrix &
	<i>Trachinotus carolinus</i>		North	Overstreet (1977);
	<i>Trachinotus falcatus</i>		Carolina	Narasimhulu & Madhavi (1980)
	Sciaenidae- drums		Gulf of	
	<i>Micropogonias furnieri</i>		Mexico	
	<i>Micropogonias opercularis</i>			
	<i>Micropogonias undulatus</i>		Jamaica	
	<i>Menticirrhus americanus</i>		Argentina	
	Sparidae- porgies		North	
	<i>Calamus calamus</i>		Carolina	
	<i>Calamus bajonado</i>		Mississippi	
	<i>Stenstomus chrysops</i>			
	Ephippidae- spadefishes		Florida	
	<i>Chaetodipterus faber</i>			
	Labridae- wrasses		Bermuda	
	<i>Halichoeres radiatus</i>			
	<i>Iridio radiatus</i>		Florida	
	Pleuronectidae- flounder			
	<i>Oncopterus darwini</i>		Bermuda	
	Exocoetidae- halfbeaks			
	<i>Hyporhamphus roberti</i>		Argentina	
	Pomatomidae- bluefishes			
	<i>Pomatomous saltatrix</i>		Gulf of	
			Mexico	
			Bermuda	

<i>Lobatosoma ansiotremum</i>	Haemulidae <i>Ansiotremus scapularis</i>	intestine	Chile	Oliva & Carvajal (1984)
<i>Lobatosoma albulae</i>	Albulidae <i>Albula vulpes</i>		Hawaii	Yamaguti 1968
<i>Lobatosoma hanumanthai</i>	Carangidae- pompanos <i>Trachinotus blochi</i>	intestine	Bay of Bengal	Narasimhulu & Madhavi (1980)
<i>Lobatosoma jungwirthi</i>	Cichilidae <i>Geophagus brachyurus</i> <i>Cichlasoma facetum</i>	intestine	Brazil Argentina	Zylber & Ostrowski de Nunez (1999)
<i>Lobatosoma pacificum</i>	Carangidae- pompanos <i>Trachinotus paloma</i>	intestine	Galapagos	
<i>Lophotaspis vallei</i>	<i>Thalassochelys</i>	esophagus & stomach	Gulf of Mexico	
<i>Lophotaspis interiora</i>	<i>Macrochelys</i>	intestine	N.A.	
<i>Lophotaspis orientalis</i>	<i>Amyda tuberculata</i> (mud turtle)	stomach & intestine	China	Faust & Tang (1936)
<i>Multicotyle purvisi</i>	<i>Siebenrockiella</i>	?	Malaya	Dawes (1941)
<i>Lissemysia ovata</i>	N/R		India	Tandon (1949)
<i>Lissemysia indica</i>	<i>Lissemys punctata</i>		India	Sinha (1935)
<i>Lissemysia bipini</i>	<i>Lissemys punctata</i>		India	Agarwal (1973)
<i>Lissemysia mehrai</i>	<i>Lissemys punctata</i>		India	Srivastava & Singh (1959)
<i>Lissemysia sinha</i>	<i>Lissemys punctata</i>		India	Srivastava & Singh (1959)
<i>Lissemysia macrorchis</i>	N/R			Siddiqui (1965)
<i>Lissemysia pandei</i>	Cyprinidae <i>Puntius sarana</i>		India	Rai (1970)
<i>Lissemysia hepatica</i>	<i>Lissemys punctata</i>	liver	India	Dandotia (1972)
<i>Lissemysia jagatai</i>	<i>Lissemys punctata</i>	intestine	India	Gwalior & Singh (1973)
<i>Lissemysia agarwali</i>	Cyprinidae <i>Puntius ticto</i>	intestine	India	Singh & Tewari (1985)

<i>Lissemysia ocellata</i>	N/R		India	Ramachandru & Agarwal (1984)
<i>Cotylaspis stunkardi</i>	<i>Chelydra serpentina</i>	intestine	N.A.	Rumbold (1928)
<i>Cotylaspis cokeri</i>	<i>Malacoclemys leseurii</i>	intestine	N.A.	Reviewed in Faust & Tang (1936)
<i>Cotylaspis lenoiri</i>	<i>Tetrathyra vaillanti</i>	intestine	Senegal	
<i>Cotylaspis insignis</i>	N/R		N.A.	
	<i>Tetrathyra</i> (turtle)	intestine	Africa	
<i>Cotylaspis coreensis</i>	<i>Amyda sinensis</i> (mud turtle)	intestine	Korea	Cho & Seo (1977)
<i>Cotylaspis sinensis</i>	<i>Amyda tuberculata</i> (mud turtle)	intestine	China	Faust & Tang (1936)
<i>Cotylaspis anodontae</i>	N/R		N.A.	Stunkard (1917)
<i>Rohdella siamensis</i>	Cyprinidae	intestine	Thailand	Gibson & Chinabut (1987)
	<i>Osteochilus melanopleurus</i>			
	<i>Barbus daruphani</i>			
<i>Sychnocotyle kholo</i>	<i>Emydura macquarii</i> (freshwater turtle)	intestine	Australia	Ferguson et al. (1999)

Taxa	Phenol	Protein	Phenolase	Reference
TRICLADIDA				
<i>Gunda segmentata</i>	+	?	?	Vialli (1933)
<i>Dendrocoelum lacteum</i>	+	+	+	Nurse (1950)
<i>Polycelis nigra</i>	+	+	+	Gerzeli & Pedrazzi (1965)
<i>Planaria torva</i>	+	+	+	Gerzeli & Pedrazzi (1965)
<i>Dugesia lugubris</i>	+	+	+	Gerzeli & Pedrazzi (1965)
POLYCLADIDA				
<i>Leptoplana tremellaris</i>	+	?	?	Vialli (1933)
<i>Thysanozoon brocchii</i>	+	+	?	Gerzelli (1960)
<i>Pseudoceros velutinus</i>	+	+	?	Gerzelli (1960)
<i>Pseudostylochus sp.</i>	+	+	+	Ishida & Teshirogi (1986)
RHABDOCOELA				
<i>Macrostomum tuba</i>	+	+	?	Gerzeli (1966)
<i>Microdalyellia fairchildi</i>	+	+	+	Bunke (1972)
<i>Microdalyellia sp.</i>	+	+	?	Gerzeli (1966)
<i>Mesocastrada furhmanni</i>	+	+	?	Gerzeli (1966)
<i>Rhynchomesostoma</i>	+	+	?	Gerzeli (1966)
rostratum				
<i>Mesostoma benazii</i>	+	+	?	Gerzeli (1966)
<i>Mesostoma craci</i>	+	+	?	Gerzeli (1966)
<i>Mesostoma lingua</i>	+	+	?	Gerzeli (1966)

<i>Gyratrix hermaphroditus</i>	+	+	?	Gerzeli (1966)
ASPIDOBOTHREA				
<i>Aspidogaster conchicola</i>	+	+	+	Gerzeli (1968)
DIGENEA				
Allocreadiidae				
<i>Macrolecithus papilliger</i>	+	+	+	Rees (1936)
Aporocotylidae				
<i>Orchispirium heterovitellatum</i>	-	+	-	Madhavi & Rao (1971)
Bucephalidae				
<i>Bucephaloides gracilescens</i>	+	?	-	Symth & Clegg (1959)
Cyathocotylidae				
<i>Cyathocotyle bushiensis</i>	+	+	+	Erasmus (1972)
<i>Holostephanus lehei</i>	+	+	+	Erasmus (1972)
Echinostomatidae				
<i>Artyfechinostomum mehrai</i>	+	+	+	Madhavi (1971)
<i>Echinoparyphium recurvatum</i>	+	+	+	Fried & Stromberg (1971)
<i>Isoparorchis hypselobagri</i>	+	+	+	Srivasta & Gupta (1978)
Fasciolidae				
<i>Fasciola hepatica</i>	+	+	+	Symth & Clegg (1959)
<i>Fasciola indica</i>	+	+	+	Lal & Johri (1967)
Fellodistomatidae				
<i>Lintonium vibex</i>	+	+	+	Coil (1972)
<i>Proctoeces subtenuis</i>	?	?	-	Freeman & Llewellyn (1958)

Gorgoderidae				
<i>Gorgoderina attenuata</i>	+	+	?	Nollen (1971)
<i>Gorgoderina sp.</i>	+	+	-	Symth & Clegg (1959)
Halipegidae				
<i>Halipegus eccentricus</i>	+	+	+	Guilford (1961)
Hemiuridae				
<i>Syncoelium spathulatum</i>	+	+	?	Coil & Kuntz (1963)
Heterophyidae				
<i>Cryptocotyle lingua</i>	+	?	+	Symth & Clegg (1959)
Lecithodendriidae				
<i>Brandesia turgida</i>	+	+	?	Gerzeli (1968)
<i>Ganeo tigrinum</i>	+	+	+	Kandhaswami (1980)
<i>Pleurogenes claviger</i>	+	+	?	Gerzeli (1968)
Notocotylidae				
<i>Ogmocotyle indica</i>	+	+	+	Coil (1966)
Opisthorchiidae				
<i>Clonorchis sinensis</i>	+	+	+	Ma (1963)
Paramphistomidae				
<i>Carmyerius spatiosus</i>	?	+	?	Madhavi (1966)
<i>Carmyerius synethes</i>	-	+	-	Eduardo (1976)
<i>Diplodiscus amphichurus</i>	-	+	-	Kanwar & Agarwal (1977)
<i>Diplodiscus mehrai</i>	-	+	?	Madhavi (1968)
<i>Gastrodiscus secundus</i>	-	+	?	Madhavi (1966)
<i>Gastrothylax crumenifer</i>	?	+	-	Eduardo (1976)
<i>Megalodiscus temperatus</i>	-	+	-	Nollen (1971)
<i>Paramphistomum cervi</i>	?	+	?	Madhavi (1966)

Philophthalmidae				
<i>Philophthalmus megalurus</i>	?	+	+	Nollen (1971)
Plagiorchiidae				
<i>Dolichosaccus rastellus</i>	?	?	+	Symth (1954)
<i>Glypthelmins sp.</i>	+	+	+	Fried & Stromberg (1971)
<i>Haematoloechus medioplexus</i>	+	+	+	Fried & Stromberg (1971)
<i>Haplometra cylindraca</i>	+	+	+	Symth (1954)
<i>Macrodera longicollis</i>	+	+	?	Gerzeli (1968)
Schistosomatidae				
<i>Schistosoma japonicum</i>	+	+	+	Ho & Yang (1973)
<i>Schistosoma mansoni</i>	+	+	+	Clegg & Symth (1968)
Strigeidae				
<i>Apatemon gracilis</i>	+	+	+	Erasmus (1972)
<i>Diplostomum phoxini</i>	+	+	+	Bell & Symth (1958)
<i>Diplostomum spathaceum</i>	+	+	+	Erasmus (1972)

Appendix 3

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
Acanthostomidae							
<i>Acanthostomum burniniis</i>	intestine of snakes		ingestion-could not induce hatching	yes		yellowish brown eggs	Roope & Janardanan (1998)
<i>Acanthostomoides apophelliformis</i>	intestine of fishes						Ostrowski de
<i>Timoniella praetentum</i>	intestine of marine fish		miracidial invasion	yes		yellowish brown eggs.	Nunez et al. (1989)
<i>Acanthostomum imbutiforme</i>	rectum of marine fish		miracidial invasion	yes			Mallard (1974)
Acanthocolpidae							
<i>Deropristis infiale</i> (<i>Stephanostomum tenue</i> - Martin 1939)	intestine of eel			yes	embryonated	Eggs are brown in older ones	Cable & Humninen (1942a)
Stephanostomidae							
<i>Stephanostomum tenue</i> (Stunkard 1983 <i>Acanthocolpidae</i>)	intestine of puffer- <i>Spherooides</i> . Stripped bass probable natural host						Martin 1939
<i>Stephanostomum baicalium</i> in <i>Acanthocolpidae</i>	intestinal parasites of piscivorous marine teleosts						Woitgang (1955); Mackenzie & Liversidge (1975)
<i>Stephanostomum caducum</i>	pyloric caeca of cod						Stunkard (1961)
Allocreadilidae							
<i>Allocreadium neotenicum</i>	hemocoel of beetle		miracidial invasion	yes		Dark brown, thin shelled eggs.	Peters (1957)
<i>Allocreadium alloneotenicum</i>			miracidial invasion	yes	eggs hatch only after being ingested by snails and passing out of faeces	Dark brown, thin shelled eggs. Eggs left in caddis fly remains encouraged bacterial & protozoan growth.	Wootton (1957b)
<i>Allocreadium ictalur</i> *	intestine of freshwater fish		probably miracidial invasion- experimental results were not published. But miracidia do hatch in 10 days and are active swimmers.	yes	undeveloped, small embryonic mass discernible after 2 days- unembryonated		Seitner (1951) (See Peters (1957)- probably <i>Skrejabinosolus marineri</i> a leprocreadid)
<i>Allocreadium fasciatus</i>			miracidial invasion	yes	unembryonated	amber colored	Madhavi (1978a)

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
<i>Bunoderella mettri</i>	intestine of tailed frog		ingestion		unembryonated may be embryonated, embryonation proceeds in water only at suitable temperatures.	eggs are amber but by the time miracidium is fully developed the shell is transparent	Anderson et al. (1965)
<i>Bunodera luciopercae</i>	intestine of fish		miracidial invasion	yes	may be embryonated, embryonation proceeds in water only at suitable temperatures.		Cannon (1971)
<i>Bunodera sacculata</i>	intestine		miracidial invasion	yes	unembryonated	Eggs dark brown	Cannon (1971)
<i>Crepidostomum cooperi</i>	pyloric ceca	faeces	miracidial invasion	yes			Choquette (1954)
<i>Crepidostomum cornutum</i>	intestine of fish		miracidial invasion- empty eggshells	yes		eggs light yellowish-brown color	Ameel (1937) Crawford (1943) & Brown, F. (1927)
<i>Azygiidae</i>	intestine of trout						
<i>Azygia acuminata</i>	stomach of fishes & eel		ingestion ingestion-snail faeces examined. Eggs passed as a string in mucous		fully embryonated, miracidium present		Wooton (1957a)
<i>Azygia sebago</i>	stomach of eels		ingestion. Note eggs stored for several weeks at 7C readily hatched when placed in room temp. These were assumed to be non-infective.	yes	non-cliated miracidium is present	Eggs are light yellow in color.	Stunkard (1956)
<i>Azygia longa</i>	stomach of fish						Sillman (1960)
<i>Proterometra dickermanni</i>	pharynx/esophagus of fishes	faeces	ingestion-snail faeces examined	yes	miracidium present		Anderson & Anderson (1963)

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
<i>Proterometra macrostoma</i> (syn. <i>P. sagittaria</i>)	pharynx/esophagus	faeces		yes	contain unciliated miracidium		Dickerman (1934; 1945)
<i>Proterometra catenaria</i>	pharynx/esophagus	faeces	ingestion				See Schell (1985) for reference
<i>Proterometra hodgeiana</i> Bivesiculidae	pharynx/esophagus	faeces	ingestion				See Schell (1985) for reference
<i>Paucivitellosus hanumanthai</i>	digestive tract of marine fish			yes		eggs amber color, thin shelled	Mani (1989)
<i>Bivesicula hepsetiae</i>	intestine of marine fishes		miracidial invasion- based on morphology. However, did not hatch.	yes	Eggs were teased from adult and required 2 weeks to develop. contain miracidium that hatches minutes after		LeZotte (1954)
<i>Paucivitellosus fragilis</i> <i>Bivesicula caribensis</i> Brachylaemidae	stomach of fish pyloric ceca of marine fish			yes			Pearson (1968) Cable & Nahhas (1962)
<i>Postharmostomum heliciis</i>	cecum of mice	faeces	ingested. Could not induce hatching. ingested stated, but no hatching exp. or obs. made	yes	well embryonated (miracidia present)		Ulmer (1951a,b)
<i>Brachylaemus virginianus</i> <i>Brachylaemus recurvus?</i>	intestine of mammals posterior part of intestine and caecum						Krull (1935) Timon-David (1959)
<i>Postharmostomum gallinum</i> <i>Brachylaemus mesostomus?</i>	ceca of chickens		ingestion- snail faeces checked	yes	miracidium present	dark brown	Alicata (1940) Pavlov (1947) Krull (1934a,1935b); Reynolds (1938)
<i>Panopistus pricei</i>	intestine of mammals		ingestion-unspecified probably ingestion-hatching attempts failed				
<i>Leucochloridiomorpha constantiae</i>	bursa Fabricii of birds & intestine of mammal	faeces		yes	embryonated	golden brown eggs	Allison (1943)

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
<i>Leucochloridium macrostomum</i> †	rectum	faeces	ingested probably ingestion-hatching attempts failed				Heckert (1887)
<i>Leucochloridium paradoxum</i>					unembryonated- Note eggs were probably not viable due to inappropriate host	eggs thick & brown	Robinson (1947)
<i>Leucochloridium fuscostriatum</i>	cloaca of birds pancreatic duct of mammal	faeces	ingestion experiments failed- eggs obtained from inappropriate host & thus not viable ingestion- snail faeces checked	yes	mature miracidia	dark brown colored eggs.	Jensen (1972)
<i>Scaphiostomum pancreaticum</i>							
<i>Neoleucochloridium problematicum</i>	cloaca of birds	faeces	ingestion	yes	mature miracidia partially developed miracidium	dark brown eggs eggs golden brown as they mature	Kagan (1951, 1952)
<i>Hasstilesia tricolor</i>	intestine of rabbits		ingestion ingestion- snail faeces examined	yes			Rowan (1955) Timon-David (1957e)
<i>Urotocus tholonetensis</i>	bursa Fabricii of birds						
Bucephalidae							
<i>Bucephalus elegans</i>	cecum	faeces	likely swept siphon	yes	fully formed miracidium		Woodhead (1930)
<i>Bucephalus papillosus</i>				yes	fully formed miracidium	colorless eggs, hatch immediately on contact with water	Woodhead (1929)
			did not hatch, eggshells with open opercula found in snail faeces but no primary sporocysts were found 2 weeks later- natural infection can not be excluded. Miracidia are quiescent within egg.	yes	embryonated fully developed, hatch immediately upon contact with water	Eggshell is thick, yellow & opaque. Not permeable to stains.	Stunkard (1976)
<i>Rhipidocotyle transversale</i>	intestine of fish						
<i>Rhipidocotyle septapapillata</i> <i>Rhipidocotyle lintoni</i>	pyloric ceca of fish		miracidial invasion	yes			Kniskern (1952) Stunkard (1976)
<i>Proserhynchus crucibulum</i> = <i>Rudolphinus</i> (Stunkard, 1974) <i>Bucephalus haimeanus</i>							Matthews (1973b) Matthews (1973)
<i>Bucephaloides gracilescens</i>	intestine of fishes		miracidium swept into siphon		embryonation takes place in water	not quinone tanned	Matthews (1974)

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
Cephalogonimidae							
<i>Cephalogonimus vesicaudus</i>	intestine of turtle		ingestion (snails exposed to eggs)	yes	? eggs obtained through teasing apart adults		Dronen & Underwood (1977)
<i>Cephalogonimus americanus</i>	intestine of frogs		ingestion	yes	fully embryonated		Lang (1968)
<i>Cephalogonimus salamandrus</i>	intestine of salamander		ingestion	yes	fully embryonated		Dronen & Lang (1974)
Clinostomatidae							
<i>Clinostomum complanatum</i> *	mouth	swallowed and voided	miracidial invasion	yes	both		Liao (1993)
<i>Clinostomum marginatum</i>	oral cavity & esophagus of birds	faeces, but eggs also found in heron uterus.					Osborn (1890); Hopkins (1933); Krull (1934b)
<i>Clinostomum sinensis</i> \$	bile duct		ingestion	yes	contain miracidium		
<i>Clinostomum giganticum</i>			hatching obs.				Agarwal (1959, 1963)
<i>Odhneriotrema incommodum</i>	buccal cavity		hatching obs.				Leigh (1978)
Cryptogonimidae							
<i>Caecicola parvulus</i>	intestine, pyloric ceca & stomach of bass	faeces	ingestion-couldn't induce hatching. Active penetration not obs. Snail faeces not checked.	yes	fully developed miracidia	egg opaque, thick, yellowish-brown	Lundahl (1941)
<i>Siphodera vinaledwardsii</i>	intestine of toadfish					brown eggs	Cable & Hunninen (1942b)
<i>Caecicola latostoma</i>	intestine of fishes		miracidia obtain through pressure= ingestion?	yes	fully embryonated	thick shelled	Greer & Corkum (1979)
<i>Stemmatosoma pearsoni</i>	intestine of fish	faeces	ingestion - exposed to eggs, empty shells in stomach & intestine. Did not hatch within 4 weeks.	yes	partially embryonated-mass of cells with the form of the miracidium	eggs thick shelled.	Cribb (1986)
Cyathocotylidae							
<i>Cyathocotyle bushiensis</i>	caecum birds & mammals	faeces	miracidial invasion	yes	unembryonated-develop in 8-10 days hatch in 14 days	Egg light yellow. Thin shelled.	Khan (1962b)
<i>Cyathocotyle graviori</i>	intestine of birds		miracidial invasion				Mathias (1935)
<i>Mesostephanus appendiculatoides</i>	intestine of birds & mammals						Hutton & Sogandares-Bernal (1960)
<i>Mesostephanus appendiculatus</i>	intestine of birds & mammals			yes		eggs yellowish color	Martin (1961)
<i>Mesostephanus yedeae</i>	intestine	faeces					Dennis (1973)

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
<i>Neogogatea kentunkiensis</i>	intestine of fish & watersnake						Hoffman & Dunbar (1963)
<i>Prohemistomum chandleri</i>							Vernberg (1952) Anderson & Cable (1950)
<i>Linstowiella szidati</i>				yes	unembryonated	light yellow	Stang & Cable (1966)
<i>Holostephanus ictaluri</i>	intestine of catfish						
Cyclocoelidae	air sacs. Migration through intestine into body cavity then into liver by direct penetration then carried to air sac.	ingested and passed through faeces	miracidial attachment and redial invasion miracidial invasion-eggs hatch quickly in water	yes	redia in miracidia present hatches in hours	eggs brown.	McLaughlin (1976, 1977)
<i>Cyclocoelum mutabile</i>							
<i>Cyclocoelum jaenschi</i>	abdominal air sacs		ingestion- eggs placed with snails and a few hours later the moist paper and eggs were devoured. Experimentally induced egg laying by putting adults in water, eggs hatched after only and hour or two.	no	miracidia with redia present in uterus		Johnston & Simpson (1940)
<i>Pseudhypthiasmus dollfusi</i>	air sacs and body cavity.	In a specimen- eggs were found in mucous of trachea but all other specimens were negative.			miracidia with redia present in uterus		Timon-David (1955)
<i>Typhlocoelum cymbium</i>	nasal cavity	Sreekumaran & Peters (1973) Ind. Vet. J. 50:1060 could not find eggs in faeces assumed to emerge from nasal excretions into water while bird is drinking.	redia within miracidium bores into snail	yes	miracidia present-hatch immediately when emersed in water		Stunkard (1934)
<i>Cyclocoelum obscurum</i>	air sacs of birds		miracidia attach to snail & redia penetrates	yes	miracidium present	eggs light brown in color	Taft (1973)
<i>Cyclocoelum vanelli</i>	air sacs of birds		miracidia hatch in utero & contain redia		hatch in utero		Taft (1974)
<i>Cyclocoelum brasilianum</i>	air sacs of birds		miracidia attach to snail & redia penetrates	yes	miracidium present	eggs golden-brown in color	Taft (1975)

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
<i>Ophthaimophagus singularis</i>	nasal cavity		miracidia attach to snail and redia penetrates		miracidia hatch in uterus with redia present inside		Taft & Heard (1978)
Cyclocoelum microstomum Dicrocoelidae	abdominal cavity		miracidial attachment and redial invasion	yes	redia present in miracidium		reference in Schell (1985)
<i>Platyngostomum cordatum</i>	intestine of cats	faeces	hatching not observed		embryonated- 20 days for miracidia to appear		Wallace (1939)
<i>Dicrocoelium dendriticum</i>	bile duct	faeces	ingestion	yes	embryonated		Krull & Mapes (1952) Carney (1967, 1970)
<i>Brachylecithum mosquensis</i>	bile ducts		ingestion				Timon-David (1957b)
<i>Brachylecithum alfordense</i>	bile ducts		ingestion				Denton (1945)
<i>Brachylecithum americanum</i> *	bile duct of birds		ingestion				
<i>Brachylecithum orfi</i>	bile duct		ingestion	yes	fully developed miracidium	dark brown eggs. Eggs coated with a lipid that prevents uptake of water and hatching until eaten.	Kingston (1965); Kingston & Freeman (1959); Carney (1966b)
<i>Mesocoelium monodi</i>	interlobular ducts of the pancreas of raccoon		ingestion	yes	embryonated	Tanned eggs	Carney (1966b)
<i>Eurytrema procyonis</i>	pancrease of mammals		ingestion- faeces checked	yes	miracidium present	yellow color, shell is fairly thick but transparent	Thomas (1985)
<i>Eurytrema pancrealicum</i>	gall bladder	faeces		yes	fully embryonated	dark brown, thick shelled eggs	Denton (1944)
<i>Conspicuum icteridorum</i> *	biliary ducts		ingestion				Basch (1965); Tang (1950)
<i>Dicrocoeloides petiolatum</i>	bile duct & gall bladder		ingestion (eggs placed with snails)	yes	?	brown eggs	Patten (1952)
<i>Brachylecithum stunkardi</i>	gall bladder & bile ducts of birds		ingested (fecal exam of snail)	yes	fully embryonated	yellowish to dark brown eggs.	Timon-David (1960)
<i>Lutztrema morenleron</i>						eggshell is dark in vitro exp. with gastric juice and intestinal contents failed to hatch snail. Osmotic forces suspected.	Carney (1966a); Krüssinger (1994)
<i>Platyosomum fastosum</i>	bile duct	faeces	ingestion- observed	yes	fully embryonated		Maldonado (1945)
Diplostomatidae							Erasmus (1958)
<i>Uvulifer ambloplitis</i> *	intestine of kingfisher	faeces	miracidial invasion	yes	unembryonated		Summary of stigelid life-cycles Hoffman & Putz (1965)

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
<i>Crassiphiala bulboglossa</i> *	intestine	faeces	miracidial invasion	yes	unembryonated unembryonated - 10 days for miracidium to appear & 12 to hatch @ 23C		Hoffman & Hundley (1957)
<i>Diplostomum beeri eucaliae</i> *	intestine of mallard	faeces	miracidial invasion miracidial invasion - snails exposed to miracidia	yes	unembryonated*		Pearson (1956) Arvy & Buttner (1954)
<i>Alaria canis</i> *	intestine	faeces		yes	unembryonated	Quinone tanned eggshell	Stunkard (1973)
<i>Diplostomum phoxini</i> \$ <i>Diplostomum nassa</i>	duodenum of duck	faeces	miracidial invasion	yes	unembryonated		Ganapati & Rao (1962)
<i>Diplostomum spathaceum</i> \$	duodenum	faeces	miracidial invasion		unembryonated		Ferguson (1944)
<i>Diplostomum ketupanensis</i> <i>Diplostomum flexicaudum</i>	intestine of birds	faeces	miracidial invasion miracidial invasion	yes	hatch in 6 days @ 38C		
<i>Alaria arisaemoides</i> <i>Alaria mustelae</i>	intestine	faeces	miracidial invasion - exposed snails to miracidia	yes	ova with two nuclei in contrast to A. Intermedia which re ij the two cell stage when passed (uncleaved). Hatch in 2 weeks at 21-24C		Pearson (1956) Bosma (1934)
<i>Ornithodiplostomum pychocheilus</i> <i>Diplostomulum scheuringi</i>			miracidial invasion (stimulated hatching)	yes	? many eggs hatched when incubated in dark at 30 degrees C for 8 days were brought into the light	golden brown eggs transparent	Hendrickson (1986) Etges (1953a)
<i>Procyotrema marsupiformis</i>	pancreatic duct	faeces	miracidial invasion - obs.				Harris et al (1970)
<i>Pharyngostomoides spp.</i>	intestine		miracidial invasion (stimulated hatching) miracidial invasion, eggs passed through snail intact. Miracidia died. Eggs had to be placed with snail. No obs.		? adults were teased apart for eggs		Beckerdite (1971)
<i>Fibricola texensis</i> Echinostomatidae		faeces		yes	12 days for miracidia to develop and 18 to hatch		Chandler (1942)
<i>Acanthoparyphium paracherardii</i>	intestine		miracidial invasion - hatching	yes	16-27 to hatch	yellow eggs when mature	Velasquez (1964a) Martin & Adams (1961)
<i>Acanthoparyphium spinulosum</i>	intestine					yellow eggs when mature large ova with heavy shells amber in color	Beaver, (1941b)
<i>Euparyphium melis</i>	intestine						

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
<i>Echinoparyphium elegans</i> (syn= <i>E. bioccalerouxii</i> , <i>E. ralphaudyi</i> , <i>E. combesi</i>)			miracidial invasion	yes	unembryonated unembryonated. 10 days at 28C	yellowish-brown eggs	Mouahid & Mone (1988)
<i>Echinoparyphium combesi</i>	intestine			yes		eggs ocre coloured	Kechemir (1980)
<i>Echinoparyphium flexum</i>	intestine	faeces	ingestion-unsuccessful hatching, snails exposed to eggs- no obs.			brown eggs	McCoy (1928)
<i>Echinoparyphium rubrum</i>	intestine	faeces	miracidial invasion	yes	uncleaved condition uncleaved- 28C 9days for miracidium to develop	eggs yellow-brown in color	Kanev et al (1998)
<i>Echinoparyphium cinctum</i>	intestine		miracidial invasion	yes	uncleaved- may hatch within 8 days at 28C	eggs yellow-brown in color.	Kanev et al. (1994a)
<i>Echinoparyphium dunni</i>		faeces	miracidial invasion	yes		Eggs are yellowish-brown.	Lie & Umathevy (1965b)
<i>Echinoparyphium ralphaudyi</i>	intestine		miracidial invasion	yes		Eggs are yellowish-brown.	Lie et al. (1975)
<i>Echinostoma audyi</i> (Kanev 1994 syn. of <i>E. revolutum</i>)	rectum	faeces	miracidial invasion	yes	uncleaved condition- miracidia develop in 7 days hatch on 8th	yellow/brown eggs	Lie & Umathevy (1965a)
<i>Echinostoma murinum</i>	intestine		miracidial invasion (obs)	yes	uncleaved condition do not develop in the worm-quickly passed through uterus 2-5 weeks development	yellow/brown eggs	Lie (1967)
<i>Himasthia quissetensis</i>	intestine	faeces	miracidial invasion- hatched eggs but no experimental infection conducted	yes			Stunkard, H. (1938)
<i>Himasthia compacta</i>			miracidial invasion - hatching not observed	yes	four cell stage-4 weeks to develop		Stunkard (1960)
<i>Himasthia littorinae</i>					undeveloped, hatch in a week @ 26C	thin, transparent shelled eggs.	Stunkard (1966)
<i>Paryphostomum mehrai</i>	intestine	faeces	miracidial invasion				Jain (1958a,b)
<i>Paryphostomum bubulcusi</i>	intestine of bird		miracidial invasion	yes	embryonated	brownish eggs	Agarwal & Tiwari (1968)
<i>Paryphostomum radium</i> (syn. <i>P.</i> <i>tenuicollis</i>)	intestine of Comorant		miracidial invasion	yes	incubated 16-18 days from uterus.	Eggs are yellowish-brown.	Nasincova et al. (1993); Johnston & Angel (1942)
<i>Hypoderaeum rhigedana</i>	ilium of exp. chicken reported from a willet		miracidial invasion because hatched not observed	doesn't appear so from figure	require 17 days to hatch unembryonated- 7 to 8 days to develop start to hatch on 11th day		Adams & Martin (1963)
<i>Hypoderaeum essexensis</i>		faeces	miracidial invasion	yes	2 cell stage. 18 days at 20C minimum incubation	Eggs light yellow in colour.	Khan (1962a)
<i>Hypoderaeum conoideum</i>	intestine	faeces	miracidial invasion	yes		yellow eggs	Mathias (1925)

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
<i>Pelatesiger chandleri</i>	duodenum & cloaca						Abdel-Malek (1953)
<i>Echinostoma ilocanum</i>	intestine	faeces	miracidial invasion	yes	undeveloped condition- hatch in 9 days at 27 C	yellow/brown eggs	Lie (1973)
<i>Echinostomus macrocaudatus</i>	intestine			yes	unembryonated- start to hatch in 9 days	golden-yellow eggs	Ditrich et al (1996)
<i>Echinostoma revolutum</i>	ilium	faeces	miracidial invasion (hatched)	yes	undeveloped condition	yellow-brown eggs.	Karnev (1994)
<i>Echinostoma lindoense</i>	intestine	faeces	miracidial invasion- exposed snails to miracidia	yes	67% of eggs hatched in 18days at 26C	yellow/brown yellowish color	Lie (1968) Nasir (1961)
<i>Echinostoma cinetorchis</i>	intestine	faeces					Chung & Jung (1999)
<i>Echinostoma caproni</i>	intestine	faeces	miracidial invasion	yes	no embryonic development- 10days in 28C for miracidium. Light seems necessary	amber colored eggs	Fried & Huffman (1996); Richard & Brygoo (1978)
<i>Pelatesiger varospinosus</i>	intestine	faeces	miracidial invasion	yes	unembryonated- hatch 6-9 days	light brown color	King, P. H. & Van As, J.G (2000) Johnston & Angel (1941)
<i>Pelatesiger australis</i>	intestine						Nassi (1980)
<i>Pelatesiger caribensis</i>	intestine						Kostadinova & Chiprev (1992)
<i>Pelatesiger grandivesticularis</i>	intestine						
<i>Echinostoma londonensis</i>	intestine (only large intestine)	faeces	miracidial invasion	yes	unembryonated- 4 weeks at room temp for miracidium to develop 2 cell stage, 10 days at 26C minimum incubation	eggs brown-yellow in color.	Khan (1961)
<i>Echinostoma parvocirrus</i>	rectum	faeces	miracidial invasion				Nassi & Dupouy (1986)
<i>Fasciolidae</i>							
<i>Fasciola hepatica</i> *	liver	faeces	miracidial invasion	yes	unembryonated		Ogumbo-Ongoma & Goodman (1976)
<i>Fasciola gigantica</i> *			miracidial invasion	yes	unembryonated		
<i>Heronimidae</i>							
<i>Heronimus chelydrae</i>	lungs of turtles	adults migrate up tracheae	miracidial invasion	no	miracidia present, hatches immediately in water.		Crandall (1960); Lynch (1933); Uimer & Sommer (1957)

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
Hemiluridae						eggs of all hemiluridae are tapered (Gibson & Bray (1979) Bull. Br. Mus. Nat. Hist. (Zool.) 36(2):35-146]	
<i>Lecithaster confusus</i>	intestine						Huuninen & Cable (1943a)
<i>Tubulovesicula pinguis</i>	stomach of fish		ingestion				Stunkard (1980a)
<i>Halipegus ovocaualatus</i>	buccal cavity esophagus & stomach of frogs		ingestion ingestion- faeces checked	yes, filamented at anopercular end yes, filamented at anopercular end	miracidium present	yellow eggs	Kechenir (1976) Krull (1935c); Macy et al. (1960)
<i>Halipegus eccentricus</i>	Eustachian tube of frog Eustachian tube & mouth of frog		checked ingestion- faeces checked	yes, filamented at anopercular end yes, filamented at anopercular end	miracidium present		Thomas (1938)
<i>Halipegus emherstensis</i>	stomach of fish		ingestion	yes, filamented at anopercular end	miracidium present	yellow eggs	Rankin (1944)
<i>Gemarchopsis goppo</i>	gut of fish						Madhavi (1978b)
<i>Hirudinella ventricosa</i>							Maenakshi & Madhavi (1980)
<i>Isoparorchis hypselobagri</i>	air bladder of fish		ingestion	yes	development occurs outside worm	brown, released as string	Devaraj (1972); Siddiqi & Nizami (1978)
Gorgoderidae							
<i>Gorgodera amplicava*</i>	urinary bladder of frogs & salamander	urine	miracidium drawn into siphon	no	fully embryonated- hatch immediately ripe eggs obtained from teasing apart adults- hatched in 10mins to 2 hours contain miracidium		Krull (1934c) ; Goodchild (1946;1948)
<i>Gorgodera attenuata</i>	urinary bladder of fish		miracidium drawn into siphon-obs.	no		eggs colorless	Rankin (1939b) Schell (1967)
<i>Phylodistomum stoffordii*</i>	urinary bladder of fish		miracidial invasion (exposed clams to miracidia)	no	contain miracidium		Uebelaker & Olson (1972)
<i>Phylodistomum bufoinis</i>	urinary bladder of fish				contain miracidium- hatch immediately	eggs yellow in color	Rai (1964)
<i>Phylodistomum srivastavaei</i>	urinary bladder of fish				contain miracidium- hatch immediately		Beitkus (1954)
<i>Phylodistomum kohrenzi</i>	urinary bladder of fish	urine	miracidium drawn into siphon				Beitkus (1954)
<i>Phylodistomum caudatum</i>	urinary bladder of fish	urine	miracidium drawn into siphon				Beitkus (1954)
<i>Gorgoderina rochalimai</i>			miracidial invasion				Jourdane & Theron (1975)
Haploporidae							

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
<i>Saccocoeloides pearsoni</i>	intestine		ingestion	yes	undeveloped- development did not proceed (3 weeks) without ingestion	yellow eggs	Martin (1973) Shameen & Madhavi (1991)
<i>Saccocoeloides martini</i>			N/A but hatched in 7 days	yes	undergoing cleaving	light amber colour	
<i>Saccocoelium obesum</i>		faeces		yes	miracidium present, hatch immediately in the presence of light, so found free in uterus.		Fares & Mailland (1974)
<i>Saccocoelium tensum</i>	intestine of fish	faeces	miracidial invasion	yes	miracidium present, hatch immediately in the presence of light, so found free in uterus.		Fares & Mailland (1974)
<i>Haploporus benedeni</i>		faeces	miracidial invasion	yes	miracidium present, hatch immediately in the presence of light, so found free in uterus.		Fares & Mailland (1974) Fares & Mailland (1974)
<i>Dicogaster contractus</i>	intestine of fish			yes	miracidium present, miracidia may hatch in utero or shortly after being laid		Martin (1973) Shameen & Madhavi (1991)
<i>Lecithobolys sprelli</i>							
<i>Cerassotrema bengalensis</i>			N/A				
Heterophyidae							
<i>Apophailus venustus*</i>	intestine	faeces	ingestion	yes	fully embryonated		Nieml & Macy (1974)
<i>Apophailus imperator*</i>	intestine	faeces	ingestion	yes	fully embryonated	golden brown eggs	Anderson & Pratt (1985) Arneel (1938)
<i>Apophailus denticus</i>	intestine			yes	fully embryonated		Stunkard (1930)
<i>Eurythelmis squamula</i>	intestine of mammals			yes	undeveloped		
<i>Eurythelmis monorchis</i>	intestine of mammals				embryonate in water	rich dark brown color	Arneel (1938) Stunkard (1930)
<i>Cryptocotyle lingua</i> §	intestine	faeces	miracidial invasion	yes	embryonate in water contain miracidium		Stunkard (1930)
<i>Fam. Heterophyidae</i> §	intestine		ingestion- didn't hatch	yes			
<i>Heterophyes heterophyes</i> §	intestine		ingestion				Kinsella & Heard (1974) Leigh (1974) Stein (1968)
<i>Stictodora curstians</i>	intestine of mammals						
<i>Ascocotyle mcintoshi</i>	intestine of bird	faeces	ingestion				
<i>Ascocotyle (Phagicola) ampullacea</i>	intestine						

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
<i>Ascocotyle (Phagicola) diminuta</i> <i>Heterophyes yokogawai</i> †	intestine intestine		ingestion		contain miracidium	Eggshells become darker in color & those in the terminal loop are bright yellow	Ostrowski de Nunez (1993); Stunkard & Uzman (1955)
<i>Monorchotrema taihokui</i>			miracidial invasion- not obs. Miracidia obs to die within minutes of being popped out	yes	contain viable miracidium	eggs yellow-brown color	Faust & Nishigori (1926) Schroeder & Leigh (1965)
<i>Ascocotyle pechycystis</i>	intestine of raccoon	faeces	ingestion- did not hatch	yes	miracidia present	amber-coloured eggs	Shameen & Madhavi (1988)
<i>Haplorchoides mehrai</i> Homalometridae <i>Anelocreadium armatum</i> <i>Homalometron pallidum</i>	intestine of fishes		ingestion		unembryonated		Hopkins (1937) Stunkard (1964)
Gymnophallidae <i>Gymnophallus nereicola</i> <i>Gymnophallus fossarum</i> <i>Parvatrema homoeotecnium</i> (Gymnophallidae)	intestine of birds intestine of birds			no			Bartoli (1972) Bartoli (1972)
<i>Meiogymnophallus minutus</i> Lepocreadiidae				yes	embryonated		James (1964) Bowers & James (1967)
<i>Tetracerasta blepta</i>	intestine of fish		miracidial invasion	yes	embryonated (zygote)		Watson (1984)
<i>Stegodexamene callista</i> <i>Neopechona pyriforme</i>	intestine of fish intestine of fish		miracidial invasion	yes yes	embryonated (zygote) embryonated	colourless eggs	Watson (1984) Stunkard (1969)
<i>Neopechona cablei</i>	intestine of fish			yes	unembryonated	colourless eggs	Stunkard (1980b)
<i>Lepocreadium areolatum</i> Monorchilidae <i>Asymphyiodora amnicolae</i> (Monorchilidae- see Stunkard (1983))	intestine of fish		ingestion (snails exposed to eggs)	yes	contain miracidia	yellow eggs. Reviewed in Stunkard (1983).	Stunkard (1980c) Stunkard (1959)
<i>Asymphyiodora tincae</i> <i>Neopalaeorchis catostomi</i>	intestine of fish intestine of fish		ingestion	yes yes	contain miracidia embryonated	yellow brown eggs colorless eggs	Van den Broek & de Jong (1979) Schell (1973)
<i>Palaeorchis problematicus</i> Lissorchiidae <i>Lissorchis</i> (<i>Tripanodistomum mutabile</i>)	intestine of fish intestine of fish					brownish eggs	Macy & English (1975)
				yes			Wallace (1941)

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
<i>Lissoorchis fairporti</i> Omphalometridae	intestine of fish			yes			Magaath (1917)
<i>Rubensstrema exasperatum</i>	intestine of rodents						Busta & Nashedova (1981a)
<i>Rubensstrema opisthovitellinum</i>	intestine of rodents						Nashedova & Busta (1981b)
<i>Opisthophryxe localis</i> Opisthorchidae	intestine of shrew	faeces	ingestion- eggs did not hatch	yes	unembryonated- miracidia develops within 8 weeks	Eggs are light brown in color.	Bock (1982)
<i>Metorchis conjunctus*</i> <i>Opisthorchis sinensis</i> † <i>Opisthorchis felinus</i> ‡	liver bile duct bile duct	faeces faeces faeces	ingestion ingestion	yes yes	embryonated		
<i>Opisthorchis viverrini</i>	human hepatic parasite		stated ingestion but not observed				Wykoff et al (1965) Bourgat & Kulo (1977b)
<i>Opisthorchis chaubaudi</i> Microphallidae	biliary ducts of cats			yes			
<i>Carneophallus brevicaeca</i> <i>Microphallus hoffmanni</i>	intestine of exp. rat; naturally in fish intestine of birds			yes yes	miracidium present unembryonated, at most 1 division. 35 days to develop miracidium at room temp. unembryonated	yellow eggs brown eggs	Velasquez (1975) Rebecq (1964)
<i>Maritrema obstipum</i> <i>Levinseniella amnicolae</i>	intestine, ceca, yolk sac & cloaca of ducks & intestine of mice ceca of ducks & mice		ingestion- no hatching observed. Experiments failed	yes yes		eggs light yellow to brown in color	Elges (1953b) Elges (1953b)
<i>Levinseniella minuta</i> <i>Microphallus abortivus</i>	intestine, ducts but also experimentally in mice		ingestion- states "fed to"	yes	miracidia present		Stunkard (1958) Delblock (1974)
<i>Microphallus opacus</i> <i>Microphallus gracilis</i>		faeces	ingestion		32 cell stage		Caveny & Elges (1971) Jourdaire (1977) Cable & Hurninen (1940)
<i>Speiotrema nicoli</i> <i>Microphallus</i> (<i>Speiotrema</i>) <i>limulif</i> <i>M. claviformis</i> (Biguet et al., 1958)	intestine of gulls			yes		Eggs become yellow	Stunkard (1951; 1968)
<i>Maritrema arenaria</i>	intestine			yes		eggs become bright yellow	Hadley & Castle (1941) Prevot et al (1976); Bartoli & Prevot (1976) Rebecq (1964)
<i>Maritrema misenensis</i> <i>Speiotrema papilionobusta</i>	intestine intestine of birds						

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
<i>Gynaecotyla nassicola</i> <i>Maritrema laricola</i> <i>Levinseniella cruzi</i>	intestine of gulls intestine of gulls intestine		miracidial invasion- evidence not given N/A	No- only immature egg is figured N/R	N/R		Rankin (1939, 1940); Stunkard (1983) Ching (1963) Young (1938)
<i>Microphallus similis</i>		faeces	ingestion	yes	miracidia present	eggs become thicker, tougher & bright yellow in color	Stunkard (1957)
<i>Odhneria odhneri</i> Lecithodendriidae <i>Mosesia chordeilesia</i> & <i>Lecithodendrium chilostomum</i> respectively	intestine of heron intestine of birds					eggs become thicker, tougher & opaque	Stunkard (1979)
<i>Lecithodendrium pyramidium</i> <i>Acanthatrium</i>	intestine of bats			yes	fully embryonated		McMullen (1936); Brown (1933) Azim (1936)
<i>Allassogonoporus vespertilionis</i>	intestine of bats					yellowish brown eggs	Cheng (1957) Knight & Pratt (1955)
<i>Cephalophallus obscurus</i>	intestine of mammal			yes	fully embryonated	brownish eggs	Macy & Moore (1954)
<i>Cephalouterina dicamptodoni</i>	intestine of salamander						Anderson et al (1966)
<i>Metolophilius uaticus</i> <i>Pleurogenoides tener</i> <i>Prosthodendrium anaplocami</i> Microscaphidiidae	intestine of birds intestine of lizard			yes yes yes	unembryonated	yellow-brown eggs	Macy & Bell (1968b) Macy (1964) Etges (1960)
<i>Dictyangium chelydrae</i> Notocotylidae	intestine of turtle			yes	unembryonated (one cell condition)		Stunkard (1937); Lotz & Corkum (1984)
<i>Quinqueserialis hassalli</i>	ceca of mice, also found in a woodchuck & gopher			yes			Smith (1954)
<i>Quinqueserialis quinqueserialis</i> *	cecum	faeces	ingestion	yes & filamented	embryonated		Herber (1942)
<i>Notocotylus tadomae</i>	waterfowl- ceca & intestine			yes & filamented		eggs are colorless	Bisset (1977)
<i>Notocotylus gippyensis</i>	waterfowl- ceca & cloaca						Bisset (1977)
<i>Notocotylus stagnicolae</i>	intestine & ceca of birds & mammals				immediately infective		Acholonu & Olsen(1967)
<i>Notocotylus urbanensis</i> *	intestine & ceca of birds & mammals		ingestion				Acholonu & Olsen (1967)

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
<i>Diplodiscus temperatus</i>	rectum of frogs			yes	miracidium present	transparent eggs	Krull & Price (1932); Herber (1939)
<i>Diplodiscus subclavatus</i>	intestine of amphibians		miracidial invasion	yes	3-5 cell stage, hatch 12-13 days		Bourgat & Kulo (1977a)
<i>Opisthodiscus nigrivasis</i>	cloaca of frogs		miracidial invasion-hatched		3-5 cell stage, hatch 15-18 days @ 29C		Simon-Vincent et al. (1974)
<i>Carymyerius dollfusi</i>	rumen of bovines			yes			Gretillat (1960)
<i>Allesostoma parvum</i>	cloaca of frogs & turtle						Beaver (1929)
<i>Wardius zibethicus</i>	cecum of muskrat				unembryonated		Murrel (1963, 1965)
Plagiorchiidae							
<i>Plagiorchis muris</i> *	intestine of birds	faeces	ingested ingestion (eggs placed with snails)	yes	morula stage		McMullen (1937)
<i>Plagiorchis noblei</i>	intestine of birds			yes	?		Blankespoor (1977)
<i>Plagiorchis jaenschi</i> *	intestine of birds	faeces	ingestion	yes	unembryonated		
<i>Plagiorchis parorchis</i> *	intestine of birds	faeces	ingestion	yes	unembryonated		
<i>Plagiorchis vespertilionis</i>	intestine of bats						Macy (1960)
<i>Plagiorchis goodmani</i>	intestine of birds	faeces	ingestion-hatching not obs	yes	uncleaved	4-5 days at room temp. for miracidia to develop.	Najarian (1961)
<i>Plagiorchis ameurensis</i>	intestine of catfish		ingestion-unsuccessful at hatching				McCoy (1928)
<i>Plagiorchis megalorchis</i>	intestine (ex. Turkey)					yellowish brown eggs	Rees (1953)
<i>Plagiorchis neomidis</i>	rectum	faeces	ingestion			cercarial body covered with spines	Theron (1976)
<i>Plagiorchis dilimanensis</i>	intestine (exp. Mouse)						Velasquez (1964b)
		Ova deposited in the lungs and conveyed to the mouth by ciliary action, swallowed and passed with faeces.	ingestion- exp. eggs hatch only in specific snail gastric juices. No miracidia in snail faeces or seen swimming.				McCoy (1928); Byrd (1935); Owen (1946); Talbot (1933); Goodman (1949)
<i>Reniferinae, Dasymetra, & Pneumatophilus</i>	mouth, air passages, lungs, esophagus and stomach of snakes			yes	miracidia present fully mature miracidium	thin dark brown elastic shells	Byrd & Maples (1963)
<i>Dasymetra conferta</i>			ingestion	yes			
			ingestion- didn't hatch in water. miracidia found in gut after exposure to eggs				
<i>Dolichopera macalpini</i>	trachea & upper lungs of snake				miracidia present miracidia but not active or infective when passed need 4 days in water	dark brown eggs	Johnston & Angel (1940)
<i>Plagitura salamandra</i>	intestine	faeces	ingested- failed to hatch but did in snail gastric juices	yes		dark brown, thin pliable shell	Owen (1946)

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
<i>Haematoloechus medioxiplexus</i>	lungs	swallowed & voided	ingestion-obs. No hatching could be induced.	no?/yes	fully embryonated	brown egg shells.	Krull (1930, 1931)
<i>Haematoloechus parviplexus</i>							
<i>Haematoloechus longiplexus</i> *	lungs	swallowed & voided	ingestion-obs. No hatching could be induced.		mature miracidia		Krull (1931)
<i>Haematoloechus breviplexus</i>	lungs		ingestion ingestion-obs. No hatching could be induced.	yes	mature miracidia miracidium present	dark brown eggs.	Schell (1965)
<i>Haematoloechus complexus</i>	lungs				miracidium present fully embryonated*		Krull (1934d)
<i>Haplometra utahensis</i> *	intestine of frogs	faeces	ingestion-empty shells in snail faeces	yes	fully developed miracidia	yellowish brown eggs in thin transparent shell	Olsen (1937)
<i>Haplometra cylindracea</i> §	lungs		ingestion	?	contain miracidium	tanned eggs	Cheng (1961)
<i>Glypheleminis pennsylvanicensis</i> *	intestine of frogs		ingestion	yes	contain miracidium		
			ingestion-anails placed with embryonated eggs			brown egg shells. Use of temporary ponds. Eggs do not survive desiccation or nor fall temperatures	Schell (1962a); Leigh (1946); Martin (1969)
<i>Glypheleminis quieia</i>	intestine of frogs			yes	embryonated		
<i>Glypheleminis hyloareus</i>	intestine of tree frog					brown egg shells elastic	Tatbot (1933)
<i>Lechthorichis prinus</i> *	lungs of water snakes	swallowed & voided	ingestion	yes	fully embryonated		Sogandares-Bernal & Grenier
<i>Ochetosoma kansensis</i> & O. laterotremia	mouth		ingestion-obs under scope				Crawford (1937); McCallen (1935)
<i>Alloglossidium cortei</i> P. ameliuensis McCoy (1928)	intestine of fish		ingestion- hatching not observed				Krull (1937)
<i>Eustoma cheydræ</i>	intestine of turtle						McCallen (1935)
<i>Macroderoides typicus</i>	intestine of fish						McCallen (1935)
<i>Macroderoides spiniferus</i>	intestine of fish		ingestion- hatching not observed	yes	fully embryonated		Leigh (1958)
<i>Paramacroderoides echinus</i>	intestine of fish		ingestion		fully embryonated		Leigh (1975)
<i>Paramacroderoides pseudoechinus</i>	intestine of fish						Leigh (1975)
Philophthalmidae							
<i>Philophthalmus gralli</i>	eyes of birds	direct contact of eyes with water, or through nasal or oral passages during drinking		no	fully developed miracidium		Alicata (1962); West (1961)
<i>Philophthalmus lucipetus</i>	eye		radial penetration miracidia attaches and passes sporocyst through	no	fully developed miracidium		Radev et al. (1999)
<i>Philophthalmus distomatosa</i>	eye			no	fully developed miracidium		Radev et al. (2000)
<i>Philophthalmus negeneri</i>	eyes of birds				miracidium		Fried & Grigo (1976)

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
<i>Clacostema philippinum</i> <i>Echinocephalus palellae</i>	cloaca intestine of birds						Velasquez (1969) Kollén (1986)
<i>Parorchis acanthus</i>	medium, bursa Fabricii		miracidial invasion		miracidia present in uterus	eggs yellowish color	
<i>Parorchis avitus</i>	cloaca of gulls		miracidial invasion		miracidium develops in utero, and hatching may even occur there. viviparous-miracidia also contain redia	eggs are brown in color	Stunkard & Cable (1932)
Pallastomidae							
<i>Sphaerodotema spinoscelabulum</i>	ceca of ducks			yes			
<i>Asclatermatula macrocyla</i>	intestine (exp. Chick)						Burns (1961a) Macy & Bell (1968a)
<i>Psilostomum brevicole</i>	intestine of bird				unembryonated		Loos-Frank (1968a)
<i>Psilostomum aglyptorchis</i>	intestine of bird						
<i>Psilostomum ondalrae</i>	intestine of bird & mammals	faeces	miracidial invasion	yes	undeveloped	eggs have heavy shell, pale brown color.	Loos-Frank (1968b)
<i>Psilostomum spiculigerum</i>	intestine	faeces	miracidial invasion-obs.	yes	undeveloped - hatch in 22-23 days at 23-24°C	pale yellow eggs	Beaver (1939)
<i>Ribeiroia marini</i>	proventriculus of birds	faeces	miracidial invasion-obs.	yes	2 cell stage	colorless & sticky	Mathias (1925) Basch & Sturrock (1969)
Pronoccephallidae							
<i>Neurogonius maleclemys</i> <i>Neopronoccephalus triangularis</i> <i>Macraesitubium obtusicaudum</i>	intestine duodenum of turtles						Hunter (1967) Thapar (1968) Horstall (1935)
Prosthogonimidae							
<i>Prosthogonimus macrorchis</i> *	oviducts or bursa Fabricii	faeces	ingestion		embryonated		Macy (1934)
<i>Prosthogonimus ovatus</i> (syn. <i>P. cuneata</i>)	oviduct & bursa Fabricii of fowl	faeces	ingestion	yes	embryonated	brown colored eggs when fully developed	Boddeke (1960a,b,c); Macy (1965)
Opecoelidae							
<i>Anisoporus marteni</i> (Stunkard 1963- <i>Opecoeloides vitellus</i> in Opecoelidae, Meenakshi et al. 1993)	intestine of marine fish						Hunninen & Cable (1941)
<i>Plagioporus leporis</i> <i>Plagioporus (Podocotyle) shawi</i> <i>Nezpercella lewisi</i>	intestine of fish intestine of fish intestine of fish		miracidial invasion miracidial invasion	yes yes yes	unembryonated unembryonated unembryonated	amber colored eggs	Dobrowolny (1939a) Schell (1975) Schell (1976)
<i>Podocotyle atomon</i>	intestine of fish						Hunninen & Cable (1943b)

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
<i>Plagioporous sinitsini</i>	gall bladder of fish	faeces & from sporocyst	miracidial invasion-hatch immediately both from sporocyst and fish host Hatching not observed, but light stimulated "rotary movement typical of hatching"		2-4 cell stage 12-14 days @ room temp.		Dobrovolsky (1939b); Berger & Esch (2000)
<i>Helicometra gibsoni</i>	intestine of fish		miracidial invasion-miracidia placed with with snails	yes & filamented (unipolar)	unembryonated, eggs collected by teasing apart gravid worms.		Meenakshi et al. (1993) S
<i>Opecoelus variabilis</i>	intestine of freshwater fishes	faeces		yes	unembryonated- hatch 8-10 days @ 22-27C	eggs yellow-brown	Cribb (1985)
<i>Nematobothrium texomensis</i>	ovaries of fish		presumably ingestion	yes	embryonated	eggs dark yellow color.	Self et al (1963)
Telorchidae							
<i>Telorchis sp.</i>				yes	miracidium present		Agarwal & Pandey (1979)
<i>Telorchis bonnerensis</i>	intestine of salamander		ingestion	yes	embryonated	light brown in color	Schell (1962)
<i>Cercorchis medius</i>							McMullen (1933)
<i>Telorchis robustus</i>	intestine of turtle		ingestion				Krull (1935d, 1936)
Troglotremitidae							
<i>Paragonimus kellicotti</i> *	lungs of mammals	swallowed & voided	miracidial invasion	yes	unembryonated		
<i>Paragonimus westermani</i> †	lungs of mammals	swallowed & voided	miracidial invasion	yes		Eggs have brown color	
<i>Paragonimus spp.</i>	lungs of mammals						Ameel (1932)
<i>Paragonimus ohirai</i>	lungs of mammals		miracidial invasion				Bruce et al. (1971)
<i>Nanophyetus salmincola</i> *	intestine of mammals	faeces	miracidial invasion	yes	unembryonated		Bennington & Pratt (1960)
<i>Sellacotyle mustelae</i>	intestine of mammals	faeces		yes	unembryonated		Wallace (1935)
Transversotremitidae							
<i>Prototransversotrema steeri</i>	beneath scales of fish		miracidial invasion		hatch 12-15 days after deposition		Cribb (1988)
<i>Transversotrema larvae</i>					miracidia present	yellow eggs	Velasquez (1961)
<i>Transversotrema patialense</i>						yellow to dark brown eggs	Cruz & Ratnayake (1964)
Renicolidae							
<i>Renicola thaidus</i>	kidney (renal tubules) of birds		ingestion	yes	fully embryonated	Eggs dark in color	Stunkard (1964b)
<i>Renicola lari</i>	kidney (renal tubules) of birds						Prevot & Bartoli (1978)
<i>Cercaria parvicaudata</i>			ingestion		embryonated		Stunkard (1974)
Sanguinicolidae							
<i>Aporocotyle simplex</i>	blood vessels of marine fish		miracidial invasion, eggs hatch in gill filaments		intramiracidial sporocyst		Koie (1982)

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
<i>Cardicola davis</i> [*] <i>Cardicola kiamathensis</i> [*]	blood vessels blood vessels	hatch in gills and penetrate main gill capillaries	miracidial invasion miracidia possibly ingested as found in intestine when exposed to free swimming miracidia	no			Meade (1967)
<i>Cardicola elseae</i>	blood vessels- freshwater salmonids	secondary lamellae gills		no	All stages found in gills eggs mature in gills before miracidium is completed. No elastin (McMichael et al, 1982)		Meade & Pratt (1965)
<i>Sanguinicola ihermsi</i> [*] Schistosomatidae	blood vessels	miracidia penetrate gills	miracidia invasion	no			Kirk & Lewis (1993)
<i>Schistosomatum douvillei</i> [*] <i>Schistosomatum pathocopicum</i> [*]	blood vessels	penetrate gut and voided	miracidial invasion	no	unembryonated		
<i>Schistosoma japonicum</i> [#]	blood vessels	penetrate gut and voided	miracidial invasion				
<i>Schistosoma haematobium</i> [#]	blood vessels	penetrate gut and voided	miracidial invasion				
<i>Schistosoma mansoni</i> [#]	blood vessels	penetrate gut and voided	miracidial invasion	no\$	mature miracidium\$		
<i>Pseudobilharzia filiformis</i>	blood vessels		miracidial invasion		fully developed miracidia		Brackett (1940)
<i>Pseudobilharzia yokogawai</i>	blood vessels		miracidial invasion		fully developed miracidia		Brackett (1940)
<i>Pseudobilharzia waubesensis</i>	blood vessels		miracidial invasion		fully developed miracidia		Brackett (1940)
<i>Pseudobilharzia kegonsensis</i>	blood vessels		miracidial invasion		fully developed miracidia		Brackett (1940)
<i>Pseudobilharzia quercetulae</i>	blood vessels	penetrate gut and voided	miracidial invasion		fully developed miracidia		Brackett (1940)
<i>Gigantobilharzia gyraui</i>	blood vessels		miracidial invasion			Straw colored eggs & no spine. Up to 7 eggs seen in uterus.	Brackett (1940)
<i>Gigantobilharzia huronensis</i>	blood vessels	penetrate gut and voided	miracidial invasion		fully developed miracidia		Najim (1956)
<i>Trichobilharzia cameroni</i>	blood vessels	penetrate gut and voided	miracidial invasion- hatched	no	embryonated*	spindel shaped egg, colourless	Wu (1953)
<i>Trichobilharzia oregonensis</i> [*] <i>Trichobilharzia stagnicola</i> [*]	blood vessels	penetrate gut and voided	miracidial invasion- placed with snails	no	miracidia present		Macy et al. (1955)
<i>Heterobilharzia americana</i> [#]	blood vessels	penetrate gut and voided	miracidial invasion				

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
<i>Austrobilharzia terrigalensis</i>	blood vessels	penetrate gut and voided	miracidial invasion		miracidium present by the time it is in the faeces		Bearup (1956) Stunkard & Hinchliffe (1952)
<i>Microbolharzia variglandis</i>	blood vessels of birds						
Spirorchidae							
<i>Spirorchis elegans</i>	blood vessels of turtle	faeces penetrate gut and voided	miracidial invasion		fully embryonated	light amber to reddish brown	Goodchild & Kirk (1960)
<i>Spirorchis parvus</i> *	blood vessels of turtle	penetrate gut and voided	miracidial invasion	no	fully embryonated well developed miracidia	older eggs are dark yellowish-brown	Wall (1941)
<i>Spirorchis elephantis</i>	blood vessels of turtle	penetrate gut and voided	miracidial invasion	yes			
Gen. <i>Spirorchis</i> †	blood vessels	penetrate gut and voided	miracidial invasion				
<i>Vesotrema robustum</i>	blood vessels	5-8 weeks between deposition and appearance in faeces	miracidial invasion	yes	eggs taken from host tissues were seen in various stages of development-unembryonated to miracidia present	yellowish brown eggs	Wall (1951)
Strigidae							
<i>Cotylurus flabelliformis</i> *	intestine	faeces	miracidial invasion	yes	unembryonated		
<i>Cotylurus erraticus</i>	intestine	faeces	miracidial invasion-snails exposed to miracidia	yes	unembryonated- hatch as early as 12, usually 15-16 days at 24C.	eggs amber color	Olsen (1970)
<i>Cotylurus lutzi</i>	intestine	faeces	miracidial invasion-snails exposed to miracidia but also eggs that did not hatch and also became infected	yes	uncleaved condition-hatch as early as 16 days usually between 24-28 days at 28C	eggs light orange brown color the outer surface becomes sticky after a few days	Basch (1969)
<i>Cotylurus michiganensis</i> - Note the cercaria used were diplostomum describe as <i>Cercaria emarginata</i> .	bursa Fabricii	faeces	miracidial invasion-hatched in 19 days exposed snails to miracidia although watched carefully didn't obs. penetration. Eggs may have been present		were allowed to embryonate (Oliver & Cort, 1942) uncleaved- 24hrs 1st cleavage, 4 cell stage in 2-3 days. 21 days to hatch at 20C 8 days at 27C		Van Haitsma (1930); Olivier & Cort (1942)
<i>Strigea tarda</i> (cited by Cort & Olivier, 1942)	intestine	faeces	miracidial invasion	yes		Eggs are dark yellow	Mathias (1925)
<i>Strigea elegans</i> †	intestine		miracidial invasion				

Taxa	Site of adult worm	Route of egg emergence	Mode of infection	Operculum present	Developmental state of egg when laid	Egg Colour	Reference
<i>Hysteromorpha triloba</i>	intestine of bird		miracidial invasion	yes	unembryonated- hatch in 20-25days at 19-22C, 6-8 days at 37C	eggs amber color	Huggins (1954) Stunkard et al. (1941); Blair (1976); Vojtek et al. (1967); Hoffman (1959) Martin (1945); Stunkard (1973)
<i>Apatemon gracilis</i> <i>Cercaria nassa</i> (Stunkard 1983- <i>Diplostomum nassa</i>) Zoogonidae <i>Diphterostomum brusinae</i> <i>Zoogonoides viviparus</i>	intestine	faeces					Prevot (1966) Kole (1976)
<i>Zoogonus rubellus</i>	intestine of fishes		miracidia probably enter siphon of snail			Eggs have no shell, mature miracidia are in membranous sacs	Stunkard (1938)
<i>Zoogonoides laevis</i>	intestine of fish		penetration not observed- probably enter the branchial cavity with water & then invade the tissue		miracidium present, emerge in a few hours	Eggs have no shell, mature miracidia are in membranous sacs.	Stunkard (1943)

§=Smyth (1994)

*= Noble et al. (1989)

#=Olsen (1974)