

3 Cestodes of small mammals: Taxonomy and life cycles¹

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1 Introductory remarks

Cestodes are diverse, ubiquitous parasites of vertebrates. They are frequent parasites of small mammals. It is not possible to provide a concise description of their taxonomy and life cycles without omitting many of the complexities, controversies and fascinating novelties of such a diverse group. Therefore, this chapter is introductory and not exhaustive. Its aim is to introduce the reader to the biology of cestodes and to present the basic components of their diversity in rodents, insectivores, lagomorphs and chiropterans as well as the major patterns of cestode life cycles, in which these mammalian groups participate. The appearance of cestodes in their contemporary vertebrate host range comes as a result of multiple independent evolutionary invasions, host shifts and coevolutionary history with their hosts. Appearing well before the origin of mammals, cestodes have not failed to follow their vertebrate hosts wherever they have gone. Not least, whether as intermediate or definitive hosts, small mammals have provided significant opportunities for cestodes to diverge in space and time. Likewise, cestodes have played an integral role in the evolutionary ecology of small mammals.

¹ We are grateful to C. Vaucher (Natural History Museum, Geneva), V.V. Tkach (University of North Dakota, Grand Forks), T. Genov and G.P. Vasileva (Central Laboratory of General Ecology, Bulgarian Academy of Sciences, Sofia) for critical comments on the manuscript. This study was undertaken as part of a NERC award (NER/A/S/2003/00313) to DTJL and RAB. Additional funding was provided by the Natural History Museum, London.

2 General information on the class Cestoda

The tapeworms (cestodes) are considered a class within the phylum Platyhelminthes (flatworms). All are internal parasites, with only the egg (and, in some groups, a short-living larva hatching from the egg) existing outside a host. As a rule, adult cestodes are parasitic in vertebrates. The larvae occur in invertebrate and/or vertebrate hosts. Cestodes are distributed in almost all terrestrial, marine, brackish and freshwater habitats where vertebrate animals live.

2.1 Body organisation and life cycles

Typically, the body of the tapeworms is dorso-ventrally flattened and highly elongate, resembling tape. Its length ranges between 0.6 mm (some parasites of shrews) to 30 m (some parasites of cetaceans). Usually, the body of tapeworms consists of three distinct regions (Fig. 1): scolex (plural scoleces), neck and strobila (plural strobila).

The scolex is the most anterior part of the body. Its main function is the attachment of the parasite to the intestinal wall. It may bear spines, hooks, glands releasing adhesive secretions, grooves (bothria), suckers or tentacles, or various combinations of these depending on the systematic position of the species. The scoleces of the cestodes of several orders are characterised by the presence of an apical organ consisting mostly of muscular and/or glandular tissue. In the order Cyclophyllidea (which includes almost all cestodes parasitic in small mammal), the apical organ is typically a rostellum, which is characterised by an immense variability of structure (Fig. 2). It is protrusible and most commonly provided with one or two rows of hooks. In some families (e.g., Hymenolepididae, Dilepididae), the rostellum can be withdrawn in a special muscular pouch (rostellar sac). The protruded rostellum penetrates into the intestinal wall of the host, anchoring there by the hooks. Some cyclophyllideans (e.g. Anoplocephalidae) lack rostellar apparatus (Fig. 1).

The neck is the region just posterior to the scolex. It is a zone of proliferation giving rise to the strobila. The strobila consists of proglottides (singular proglottis) arranged in a linear series. Each proglottis contains a complete set of reproductive organs. The strobila may consist of few (2-3), several dozens (in the majority of species) or numerous (hundreds to thousands) proglottides. The development of each proglottis starts at the neck, resulting from the division of stem cells. Most commonly, the formation of proglottides at the neck is an enduring process lasting the entire life of the

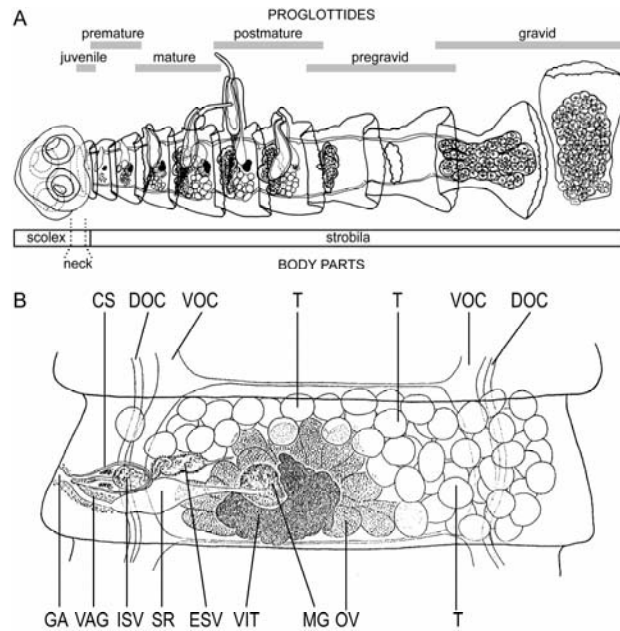


Fig. 1. **A.** Parts of the body of *Leporidotaenia pseudowimeroza* (Anoplocephalidae), a parasite of rabbits, *Oryctolagus cuniculus*, in Spain (the general view redrawn from Genov et al. 1990, reproduced with kind permission of Springer Science and Business Media). **B.** Mature proglottis of *Paranoplocephala aquatica* (Anoplocephalidae) (redrawn from Genov et al. 1996, reproduced with kind permission of Springer Science and Business Media), a parasite of aquatic voles *Arvicola terrestris* and *Ondatra zibethica*, demonstrating the structure of genital systems. Abbreviations: CS, cirrus sac; DOC, dorsal osmoregulatory canal; ESV, external seminal vesicle; GA, genital atrium, ISV, internal seminal vesicle; MG, Mehlis' gland; OV, ovary; SR, seminal receptacle; T, testes; VAG, vagina; VIT, vitellarium; VOC, ventral osmoregulatory canal.

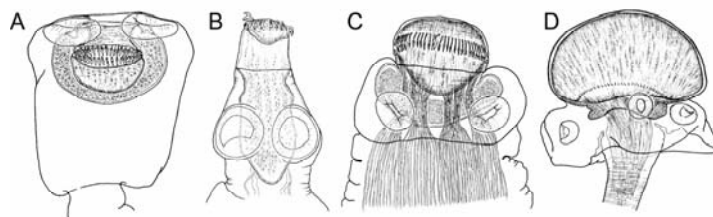


Fig. 2. Scoleces of cestodes of the family Hymenolepididae demonstrating the variability of the structure of the rostellar apparatus. *Coronacanthus magniharmatus* (A) and *Triodontolepis boyanensis* (B) from the water shrew *Neomys fodiens*; *Hymnilepis prokopici* (C) and *H. nagaty* (D) from *Crocidura* spp. (A, B, modified from Vasileva et al. 2005; C, D, modified from Vasileva et al. 2004)

cestode in the definitive host. Just posterior to the neck, the proglottides are short, containing undifferentiated cells (juvenile proglottides). With the appearance of a new proglottis at the neck, already formed proglottides move posteriorly. This coincides with growth and the gradual development of the reproductive organs. Posterior to the juvenile proglottides, each strobila typically contains premature (with primordia of genital organs), mature (with developed and functioning male and female genital systems), postmature (in which the uteri are filled with developing eggs and gonads gradually degenerate), pregravid (uterus well-developed but eggs not entirely formed) and gravid (containing uteri with ripe eggs) proglottides. As a rule, the gravid proglottides in the terminal position on the strobila detach. They pass to the environment with the host's excrement or disintegrate along their route and only eggs are released. Some cestodes (e.g., Pseudophyllidea) have uterine pores and eggs can be released one by one.

Out of 15 cestode orders, formation of proglottides occurs in 11. The representatives of three orders (Gyrocotylidea, Amphilinidea and Caryophyllidea) have only a single set of genital organs per body (i.e., no proglottides); they are often referred to as "monozoic" cestodes. The order Spathebothriidea exhibits an intermediate pattern of body organisation: an internal multiplication of reproductive organs down the strobila occurs but no externally distinct units are formed.

Cestodes lack a gut during all developmental stages. They feed through the body surface, i.e. the tegument. The latter is a syncytial tissue peculiar to parasitic flatworms. Its main functions are protective (against immune reactions and enzymes of the host) and digestive (as a major site of absorption, metabolic transformations and transport of nutrients). The tegument consists of a surface syncytial layer (distal cytoplasm) linked by cytoplasmic bridges with cell bodies (cytons) situated deep beneath the superficial muscle layers. The secretions of cytons continuously renovate the distal cytoplasm, which acts as a contact zone between the parasite body and the tissues and fluids of the host. Usually there are three layers of superficial musculature surrounding parenchyma. Strong longitudinal muscular bundles pass along the entire strobila and are responsible for the movements of the body. The nervous system is represented by paired ganglia situated in the scolex and arising from them major anterior and posterior longitudinal nerves; the latter run through the strobila. There are also numerous transverse commissures connecting longitudinal nerves and smaller nerves emanating from them and reaching to the musculature and the receptors. The osmoregulatory system comprises flame cells scattered in the parenchyma. Narrow ducts connect these cells with the major longitudinal canals of the system passing along the strobila (typically, two dorso-lateral

and two ventro-lateral, see Fig. 1). This system is responsible for the excretion of metabolic products and eliminates excess water from the body.

The majority of tapeworms, including all the species occurring in small mammals, are hermaphroditic. As a rule, each mature proglottis contains one male reproductive system and one female reproductive system, but two of each per proglottis is not rare.

The male reproductive system includes from one (some Hymenolepididae) to several hundreds (some Taeniidae) of testes. Each testis is provided with an outgoing duct (vas efferens). These ducts unite into a common wider duct (vas deferens), which transports the sperm to the male copulatory organ (cirrus). The latter is situated within a muscular pouch (cirrus-sac). Along its course, in order to have greater sperm storage capacity, vas deferens may form seminal vesicles before entering the cirrus sac (external seminal vesicle) and (or) within it (internal seminal vesicle), e.g. in the Hymenolepididae and Anoplocephalidae; in other cases, the same effect is achieved by a highly convoluted vas deferens (Dilepididae). The cirrus is a muscular (smooth or spinous) organ, which is able to invaginate (to be withdrawn) in the cirrus-sac or to evaginate (project) through its pore.

The female reproductive system includes the ovary, vitellarium, ootype, uterus, vagina, seminal receptacle and the ducts connecting them (Fig. 1). During copulation, sperm passes into the female system through the vagina and is stored in the seminal receptacle. As oocytes mature in the ovary, they pass from it into the oviduct. A duct coming from the seminal receptacle joins to the oviduct. The junction of these ducts forms a fertilization chamber. The vitellarium may be a compact organ (e.g., in Cyclophyllidea) or may consist of follicles scattered in the parenchyma, with outgoing ducts uniting into a common vitelline duct (in the majority of orders). The vitelline duct is linked with the oviduct where one or more vitelline cells become associated with each zygote. Together they pass into the ootype, which is normally surrounded by glandular tissue (Mehlis' gland) producing a secretion forming a thin envelope around the zygote and associated vitelline cells. The young eggs pass from the ootype through the uterine duct into the uterus where they complete their development.

The life cycle of cestodes involves at least two hosts, a final or definitive (harbouring the sexually reproducing, adult cestode) and an intermediate host (in which larvae, known also as metacestodes, develop). The two hosts are in ecological association making parasite transmission possible: the intermediate host occurs in habitats where the definitive host feeds and defecates. The intermediate host is a component of the diet of the definitive host. The principal scheme of the cestode life cycle is as follows. Parasite eggs are released with host's faeces into the environment. Each egg contains an embryo (oncosphere) provided with six embryonic hooks

and several glandular cells and is surrounded by several protective envelopes. The egg is eaten by the intermediate host. The oncosphere hatches in the gut of the latter and, using its hooks and glands, penetrates through the wall of the gut. It locates in the body cavity or in any internal organ. There, it metamorphoses into an infective metacestode possessing a fully- or an almost fully developed scolex. The definitive host is infested by eating infected intermediate hosts. The scolex of the metacestode attaches to the intestinal wall of the definitive host and the strobila is formed. Passage of cestodes from one host to another occurs universally through food chains.

There are some cestode species, which have life cycles differing from the above summary. For example, some species have two intermediate hosts or mobile embryos able to swim. Also, the embryos of the Amphilinidea and the Gyrocotylidea are not oncospheres but lycophores, which possess 10 embryonic hooks.

Metacestodes of various orders and families exhibit great morphological variability (Fig. 3). This resulted in a complex terminology associated with metacestode forms (Chervy 2002) and can make it difficult to compare and contrast developmental and ecological elements of life cycles. The proceroid is the metacestode in the first intermediate host, having an elongate body and a cercomer (e.g., in Pseudophyllidea). Entering into the second intermediate host, it develops into the plerocercoid. The latter possesses a differentiated scolex and is able to infect the definitive host. The most widespread type of metacestodes in the Cyclophyllidea is the cysticeroid, a metacestode with a developed scolex retracted (encysted) into the body. Among the Taeniidae, the most widespread metacestode is the cysticercus, which has a scolex introverted into the bladder-like posterior body part.

In terms of known intermediate host species and (or) described morphology of larval stages, the life cycles of only about 5% of cestode species are known. Having in view that each cestode occurs in at least two microhabitats during its life, i.e. in one definitive and in at least one intermediate host, this percentage exposes an enormous gap in the knowledge: for 95% of the cestode species, we know only one of at least two microhabitats (hosts) utilised by them.

Two major approaches have been used in cestode life-cycle studies, each characterised by a number of advantages and restrictions. The first approach is the experimental laboratory infection of potential intermediate hosts with eggs collected from an adult cestode. The main advantages are the reliable identification of the metacestodes studied (based on the adult specimens used as a source of infective eggs) and the possibility of describing the subsequent stages of metacestode development in an exact temporal scale. The main disadvantage of this approach is the lack of certainty that an animal species being successfully infected in experimental

conditions is really the intermediate host in natural conditions. The second approach is the examination of potential intermediate hosts in order to find naturally infected animals. These studies provide informative results for cyclophyllidean cestodes only because in this order the morphogenesis of the scolex mostly occurs in the intermediate host and the majority of the species possess rostellar hooks identical in adults and metacestodes. However, it is not applicable in numerous cases when congeneric species have identical rostellar hooks and have been differentiated on the basis of the strobilar morphology only. For the further development of these studies, the application of molecular markers can be of great value.

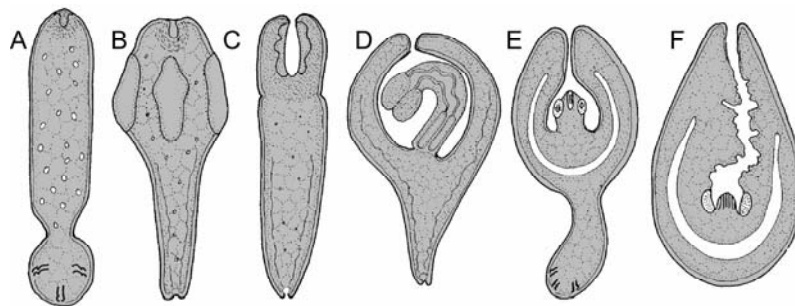


Fig. 3. Morphological types of metacestodes (redrawn from Chervy 2002, reproduced with kind permission of Springer Science and Business Media). A. Procercoid. B. Plerocercoid. C. Meroцерсoid. D. Plerocercus. E. Cysticercoid. F. Cysticercus

The present account contains basic information about the body organisation and the life cycles of tapeworms. The reader can obtain more detailed data from zoology textbooks (e.g., Ruppert and Barnes 1994), reference readings (Caira and Littlewood 2000; Georgiev 2003) or specialised monographs (Wardle and McLeod 1952; Joyeux and Baer 1962; Arme and Pappas 1984a, b; Smyth and McManus 1989; Coil 1991).

2.2 Classification, taxonomic diversity and phylogenetic relationships

According to a recent estimate (Georgiev 2003), the class Cestoda encompasses about 5100-5200 species, 680 genera, 72 families and 15 orders. Out of them, 3100 species, 380 genera and 18 families belong to the order Cyclophyllidea. A contemporary source on cestode classification at the ordinal, familial and generic level is the book by Khalil et al. (1994). The last

comprehensive source on the species diversity of tapeworms was by Schmidt (1986).

In the past, two subclasses have been recognised within this class: Cestodaria, including the monozoic orders Gyrocotylidea and Amphilinidea, and Eucestoda, comprising remaining orders (mostly polyzoic but also the monozoic Caryophyllidea). Some authorities consider Amphilinidea and Gyrocotylidea as distinct classes within the phylum Platyhelminthes (as Amphilinida and Gyrocotylida, respectively). Sometimes the order Caryophyllidea is placed out of the Eucestoda and believed to be close to the amphilinideans and gyrocotylideans. However, mostly as a result of recent extensive phylogenetic studies based on gene sequences and morphology, a wide consensus has been achieved on several points (e.g., Hoberg et al. 2001; Olson et al. 2001). The Cestoda, comprising Gyrocotylidea, Amphilinidea and Eucestoda are believed to form a monophyletic and highly derived flatworm group. The tapeworms, together with the monogeneans and the trematodes, belong to the monophyletic taxon Neodermata. The monogeneans are believed to be the closest relatives of the tapeworms; the two groups are included in the higher taxon Cercomeromorphae. Within the Cestoda, the Gyrocotylidea have a position basal to the branch containing the remaining taxa, i.e. Amphilinidea plus eucestode orders (Fig. 4). Among the Eucestoda, the monozoic Caryophyllidea are considered basal to the remaining groups. Among the polyzoic orders, these having as a rule four suckers or bothridia on the scolex (known as tetrafossate, e.g., Tetracyphylidea, Proteocephalidea and Cyclophyllidea) are considered more derived than those having two bothria or bothridia (difossate). For more detailed information on cestode phylogeny, see Hoberg et al. (2001) and Olson et al. (2001).

The representatives of 10 orders (Gyrocotylidea, Caryophyllidea, Spathebothriidea, Haplobothriidea, Diphyllidea, Trypanorhyncha, Tetracyphylidea, Litobothriidea, Lecanicephalidea and Nippotaeniidea) are entirely associated with fishes as definitive hosts. The majority of the species belonging to three other orders (Amphilinidea, Pseudophyllidea and Proteocephalidea) are also parasites of fishes; however, some taxa of these orders have colonised tetrapods. Among them, the Pseudophyllidea is relevant in the context of this volume because some species occur as larvae in small mammals. The order Tetrabothriidea includes parasites of marine birds and marine mammals only.

The most species-rich order is the Cyclophyllidea. Its members occur as adults in tetrapods, mostly in birds and mammals (a few species are parasites of reptiles and amphibians). All the species occurring as adults in small mammals belong to this order (Fig. 4). Intermediate hosts of cyclophyllideans include arthropods, annelids, molluscs or mammals (only in-

intermediate hosts or first intermediate hosts), fishes, amphibians, reptiles, birds or mammals (second intermediate hosts).

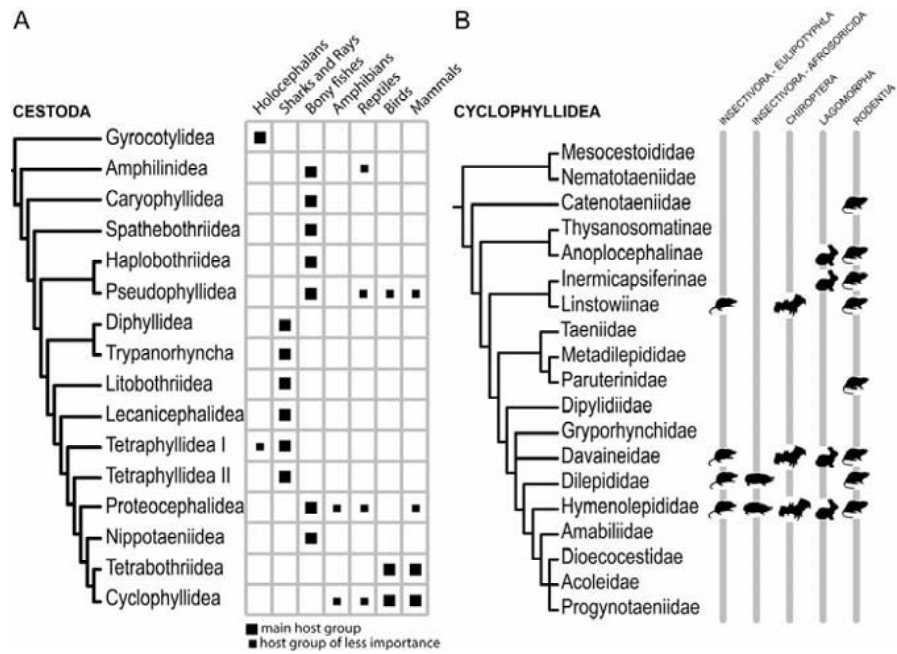


Fig. 4. **A.** Phylogeny of the class Cestoda drawn from multiple sources including morphological and molecular estimates both published (e.g. Hoberg et al. 2001; Olson et al. 2001) and unpublished. Range of definitive hosts is indicated. **B.** Phylogeny of the order Cyclophyllidea. Cladogram modified from Hoberg et al. (1999). The family-group taxa, for which small mammals are known as definitive hosts, are indicated. Their distribution across the tree suggests numerous events of colonisation and minor role of the co-diversification for the formation of the cestode fauna of the small mammal orders

3 Small mammals as definitive hosts of cestodes

The fauna of the cestodes of small mammals is relatively well studied in Europe, northern Asia and North America. These studies showed that adult cestodes are widespread and abundant in small mammals. In many areas, their species diversity is greater than that of their host groups. For example, Vaucher (1971) examined eight species of Soricidae from Europe and recorded 28 cestode species in them. Genov (1984) summarised data from the study of 33 species of insectivores and rodents in Bulgaria and reported

41 species of adult cestodes. Feliu et al. (1997) recorded 17 species of adult cestodes from 16 species of rodents from the Iberian Peninsula.

Unfortunately, even for the well-studied areas in the Northern Hemisphere, few reviews are available and those that are need updating (e.g., Stiles 1896; Baer 1927; Spasskii 1951; Gvozdev et al. 1970; Baer and Tenora 1970; Vaucher 1971; Rausch 1975, 1976; Beveridge 1978; Ryzhikov et al. 1978; Tenora and Murai 1978, 1980; Genov 1984; Tenora et al. 1985). Most primary information is scattered in numerous sources, mostly journal articles. Outside temperate latitudes, data are even more fragmentary, although detailed and comprehensive studies have been carried out in a few tropical areas (Hunkeler 1974; Quentin 1964, 1971).

No current estimate of the species diversity of cestodes from lagomorphs, rodents and insectivores has been made. According to Sawada (1997), 117 nominal cestode species have been described from bats. Even in well-studied areas in Europe and North America, new cestode species have been discovered from rodents and insectivores during the last few years (Haukisalmi et al. 2002; Tkach et al. 2003; Vasileva et al. 2005; Haukisalmi and Henttonen 2005). Considering that the diversity of small mammals in tropical areas is much greater than that in temperate latitudes, and that most of the cestodes described are genus- or species-specific to their definitive hosts, we predict that currently no more than half of the cestode species occurring in small mammals are described.

All cestodes occurring in small mammals as adults belong to the order Cyclophyllidea (Table 1, Appendix I). Currently, the validity of 15 families of this order is widely recognised (e.g., Khalil et al. 1994). Members of six families have been recorded in small mammals as definitive hosts (Fig. 4). One of them, the Catenotaeniidae, has a host range entirely restricted to rodents, which is indicative for the co-diversification of the two groups (Quentin 1971, 1994).

The families Hymenolepididae and Anoplocephalidae are represented by considerable diversity in small mammals, containing ca. 45 and ca. 25 genera, respectively, with host ranges restricted to small mammal orders; however, these families exhibit higher diversity in other groups of tetrapods, i.e. hymenolepidids in birds (Czapliniski and Vaucher 1994) and anoplocephalids in other mammals (ruminants, macropodid marsupials), birds and reptiles (Beveridge 1994). Nevertheless, the considerable diversity of anoplocephalines in the lagomorphs and in murid rodents (Appendix I) and the restricted host specificity of the majority of the genera suggest the important role of these host groups for the diversification of the Anoplocephalinae (see also Wickström et al. 2005). Similarly, the co-diversification with the Soricidae seems to be the major event for the formation of the current diversity of mammalian hymenolepidids.

Table 1. Cestode genera occurring as adults in the main groups of small mammals (Insectivora, Chiroptera, Lagomorpha and Rodentia). The cestode genera marked by an asterisk (*) occur in this group of hosts only

Host group	Family	Genera	Source	
Insectivora	Anoplocephalidae (Linstowiinae)	<i>Mathevotaenia</i>	Schmidt (1986)	
	Davaineidae	<i>Raillietina</i>	Sawada (1999)	
	Dilepididae	<i>Dilepis</i> , <i>Hepatocestus</i> *	Bona (1994), Gulyaev and Kornienko (1998),	
		<i>Monocercus</i> * (= <i>Molluscotaenia</i>), <i>Multitesticulata</i> *, <i>Polycercus</i>	Sawada (1999)	
	Hymenolepididae	<i>Blarinolepis</i> *, <i>Brachylepis</i> *, <i>Coronacanthus</i> *, <i>Cryptocotylepis</i> *, <i>Ditestolepis</i> * (= <i>Sinuterilepis</i>), <i>Ecrinolepis</i> *, <i>Hilmylepis</i> *	(1997), Tkach (1998), Gulyaev and Kornienko (1999),	
		<i>Hymenolepis</i> , <i>Karpenolepis</i> *, <i>Lineolepis</i> *, <i>Lockerrauschia</i> *, <i>Mathevolepis</i> *, <i>Neomylepis</i> *, <i>Neoskrjabinolepis</i> *, <i>Protogynella</i> *, <i>Pseudhymenolepis</i> *, <i>Pseudobothrialepis</i> *, <i>Pseudodiorchis</i> *, <i>Skrjabinacanthus</i> *, <i>Soricinia</i> *, <i>Spalania</i> *, <i>Spasskylepis</i> *, <i>Staphylocystis</i> *, <i>Staphylocystoides</i> * (= <i>Zarnowskiella</i>), <i>Talpolepis</i> *, <i>Triodontolepis</i> *, <i>Urocystis</i> *, <i>Vaucherilepis</i> *, <i>Vigisolepis</i> *, <i>Vogelepis</i> *	Karpenko and Gulyaev (1999), Karpenko and Chechulin (2000), Tkach et al. (2003), Mel'nikova et al. (2004), Gulyaev et al. (2004), Gulyaev and Mel'nikova (2005)	
		Anoplocephalidae (Anoplocephalinae)	<i>Andrya</i> , <i>Cittotaenia</i> *, <i>Diuteriotaenia</i> *, <i>Ectopocephalum</i> *, <i>Leporidotaenia</i> *, <i>Mosgovoyia</i> *, <i>Neandrya</i> *, <i>Schizorchis</i> *	Beveridge (1994), Haukisalmi and Wickström (2005)
			Anoplocephalidae (Inermicapsiferinae)	<i>Inermicapsifer</i>
		Davaineidae	<i>Fuhrmannetta</i> , <i>Paroniella</i> , <i>Raillietina</i> , <i>Vadifresia</i>	Jones and Bray (1994), Movsesyan (2003a, b)
		Hymenolepididae	<i>Gvosdevilepis</i> *	Czaplinski and Vaucher (1994)
Chiroptera		Anoplocephalidae (Linstowiinae)	<i>Cycloskrjabinia</i> *, <i>Mathevotaenia</i> , <i>Oochoristica</i>	Beveridge (1994), Schmidt (1986)
		Davaineidae	<i>Raillietina</i>	
		Hymenolepididae	<i>Milina</i> * (= <i>Myotolepis</i>), <i>Gopalaia</i> (genus inquirendum), <i>Pseudoligorchis</i> *, <i>Rodentolepis</i> , <i>Vampirolepis</i> *	Czaplinski and Vaucher (1994)

Table 1. Continued.

Host group	Family	Genera	Source
Rodentia	Catenotaeniidae	<i>Catenotaenia</i> *, <i>Hemicatenotaenia</i> *, <i>Meggittina</i> *, <i>Pseudocataenotaenia</i> *, <i>Quentinia</i> *, <i>Skrjabina</i> taenia*	Quentin (1994)
	Anoplocephalidae (Anoplocephalinae)	<i>Andrya</i> , <i>Anoplocephaloides</i> (= <i>Paranoplocephaloides</i>), <i>Bertiella</i> lyaev (= <i>Indotaenia</i>), <i>Ctenotaenia</i> *, <i>Diandrya</i> *, <i>Gallegoides</i> *, <i>Hokkaidocephala</i> *, <i>Moniezia</i> , <i>Monoecocestus</i> *, <i>Parandrya</i> *, <i>Paranoplocephala</i> *, <i>Pseudocittotaenia</i> *, <i>Sdarikovina</i> *, <i>Viscachataenia</i> *	Beveridge (1994), Gulyaev and Chechulin (1996), Tenora et al. (1999), Denegri et al. (2003)
	Anoplocephalidae (Linstowiinae)	<i>Mathevotaenia</i> (= <i>Schizorchodes</i>), <i>Sinaiotaenia</i> *, <i>Witenbergitaenia</i> *	Beveridge (1994)
	Anoplocephalidae (Inermicapsiferinae)	<i>Inermicapsifer</i> , <i>Metacapsifer</i>	Beveridge (1994)
	Paruterinidae	<i>Orthoskrjabinia</i>	Georgiev and Kornysushin (1994)
	Davaineidae	<i>Delamuretta</i> *, <i>Dollfusoquenta</i> *, <i>Fuhrmannetta</i> , <i>Paroniella</i> , <i>Railietina</i> (= <i>Erchanella</i> , <i>Tenoretta</i>), <i>Skrjabinia</i> , <i>Vadifresia</i>	Jones and Bray (1994), Movsesyan (2003a, 2003b), Spasskii (1994)
	Dilepididae	<i>Alproma</i> *, <i>Dilepis</i> , <i>Hunkeleria</i> *	Bona (1994)

The families Dilepididae, Davaineidae and Paruterinidae include mostly parasites of birds, and individual taxa are associated with small mammals as definitive hosts, or occur accidentally in them (Bona 1994; Jones and Bray 1994; Georgiev and Kornysushin 1994; Movsesyan 2003a, 2003b).

3.1 Catenotaeniidae

This family contains about 35 species (Schmidt 1986). All are intestinal parasites of rodents: Sciuridae, Muridae, Heteromyidae, Geomyidae and Caviidae (Quentin 1994). The geographical range of the family includes all continents except Australia and Antarctica. Morphologically, catenotaeniids are diagnosed by a uterus consisting of a longitudinal stem and lateral branches (similar to that of the family Taeniidae). Their scolex is provided with suckers only. A rostellar apparatus is lacking, but sometimes adults have a vestigial “apical sucker” (metacestodes have apical organ).

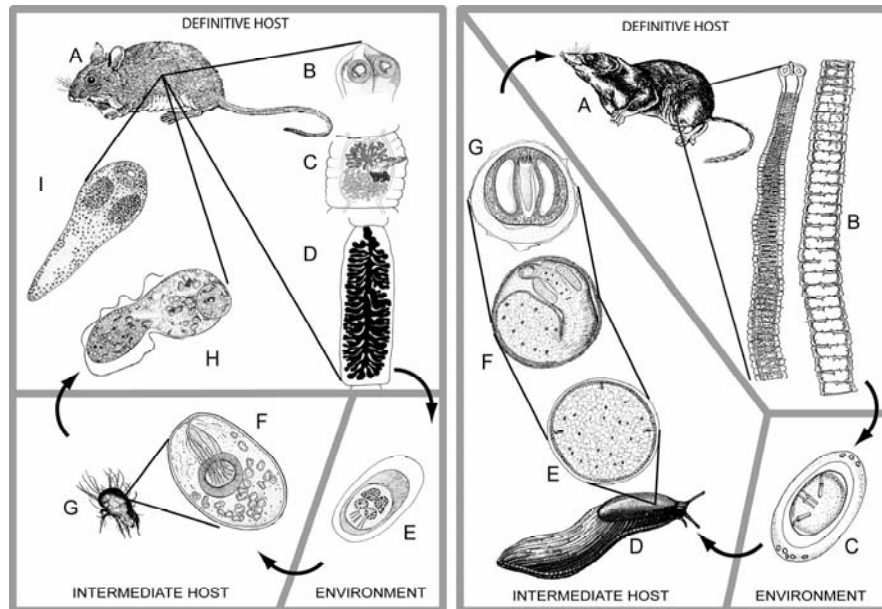


Fig. 5. Life cycles of *Catenotaenia pusilla* (Catenotaeniidae) and *Monocercus arionis* (Dilepididae). **Left.** *C. pusilla*. A. House mouse, *Mus musculus* (definitive host). B, C, D. Body parts of adult cestode (B, scolex; C, mature proglottis; D, gravid proglottis). E. Egg. F. Infective metacestode (merocercoid) in the body cavity of the intermediate host. G. Tyroglyphid mite, *Glycyphagus domesticus* (intermediate host). H. Merocercoid excysting under the action of digestive enzymes in the gut of the definitive host. I. Young cestode with developing scolex in the intestine of the definitive host. (B-F, H, I – modified from Joyeux and Baer 1945). **Right.** *M. arionis* (= *Molluscotaenia crassiscolex*) (Dilepididae). A. Common shrew, *Sorex araneus* (definitive host). B. Adult cestode. C. Egg. D. Slug, *Arion lusitanicus* (intermediate host). E-G. Gradual stages of metacestode development in the intermediate host. G. Infective monocysticercoid. (B – modified from Mel'nikova and Gulyaev 2004; C, E, F – modified from Jourdane 1972; G – modified from Kisielewska 1958a)

The life cycle of only one species has been described (Joyeux and Baer 1945). *Catenotaenia pusilla* is a common intestinal parasite of the house mouse and has been reported also from other rodents. Tyroglyphid mites have been demonstrated as its intermediate host (Fig. 5). The metacestode (merocercoid) develops to the infective stage within some 15 days. It has a large apical organ (“apical sucker”) but the suckers are not developed. The final stage of the scolex morphogenesis is in the intestine of the definitive host, where degeneration of the apical organ and differentiation of suckers occur.

3.2 Dilepididae

This family is characterised by great taxonomic diversity: the number of the valid genera exceeds 100 (Bona 1994) and the number of species is not less than 500 (Matevosyan 1963; Schmidt 1986). However, the dilepidids are widespread in birds and only few of them occur in small mammals (Table 1). The family has a cosmopolitan distribution.

The members of this family are usually characterised by a complex rostellar apparatus consisting of a rostellum, rostellar pouch and two (rarely one) rows of rostellar hooks. Usually, the testes in the mature proglottis are numerous, situated posteriorly to the female gonads or around them. They lack seminal vesicles and the function of sperm storage is carried out by a highly convoluted vas deferens.

The life cycles of about 30 species of Dilepididae are known in terms of recorded intermediate hosts and described metacestodes. However, almost all these are parasites of birds. The range of intermediate hosts includes annelids, molluscs and arthropods.

Monocercus arionis is an intestinal parasite of shrews of the genus *Sorex* throughout northern Eurasia (Fig. 5). Its metacestode has been recorded in more than 20 species of terrestrial gastropods (Kisielewska 1958a; Jourdane 1972; Genov 1984). *Monocercus estavarensis* has a similar life cycle, parasitizing terrestrial gastropods as intermediate hosts and shrews as definitive hosts (Jourdane 1972). Another species, *Multitesticulata filamentosa*, is a parasite of moles (*Talpa europaea*) in Europe; its intermediate hosts are myriapods (Genov 1984).

Sometimes immature specimens of the genera *Dilepis* (e.g. *Dilepis undula*) and *Polycercus* (e.g. *P. paradoxa*) have been recorded from insectivores. These are parasites of birds, typically occurring in thrushes and woodcocks, respectively. Their intermediate hosts are earthworms.

3.3 Hymenolepididae

With the number of species exceeding 900 (McLaughlin 2003), this is the most species-rich cestode family. The majority of hymenolepidids are parasites of birds (aquatic or terrestrial), but at least a quarter of the species have been described from mammals (Schmidt 1986; McLaughlin 2003). The family has a cosmopolitan distribution reflecting the broad geographical distribution of its hosts.

Morphologically, the hymenolepidids are characterised by a complex rostellar apparatus similar to that of dilepidids; however, generally they have only a single row of rostellar hooks. There are also some genera,

which have no rostellar hooks and the rostellum is lacking or rudimentary. The male reproductive system contains a small number of testes: usually three, sometimes two or even one, and only exceptionally more than three. The role of sperm storage is performed by seminal vesicles. The proglottides are typically much wider than long, which results in a higher number of proglottides relative to strobila size than in most other families (e.g., Dilepididae). It is possible that this strobilar organisation results in more frequent and more widespread dissemination of eggs by hymenolepidids.

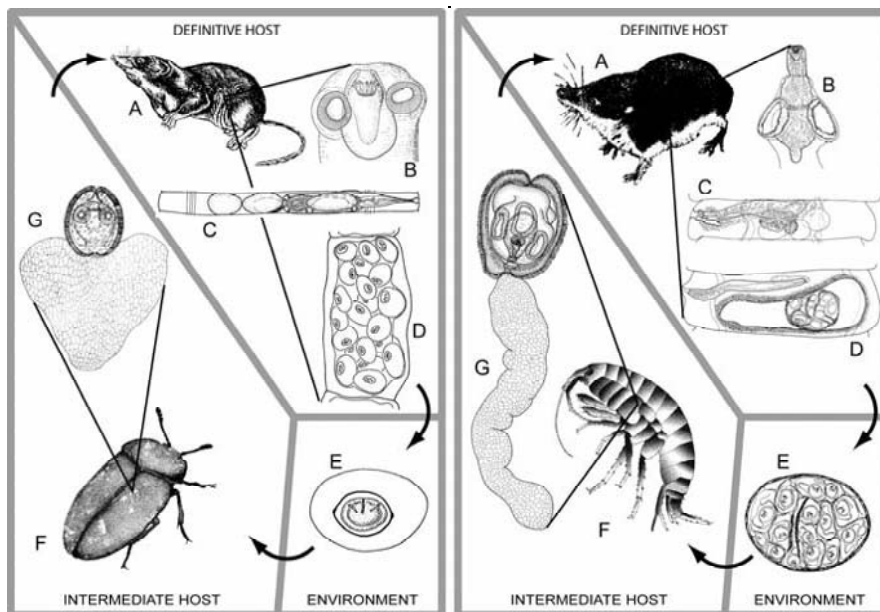


Fig. 6. Life cycles of hymenolepidids from soricids. **Left.** *Neoskrjabinolepis schaldybini*. A. Common shrew, *Sorex araneus* (definitive host). B-D. Adult cestode from the intestine of the definitive host (modified from Vaucher 1971). B. Scolex. C. Mature proglottis. D. Gravid proglottis. E. Egg (modified from Jourdan 1971). F. Red-breasted carrion beetle, *Oiceoptoma thoracica*, (intermediate host). G. Cysticercoid from the body cavity of the intermediate host (modified after Prokopič 1968b). **Right.** *Vaucherilepis trichophorus*. A. Water shrew, *Neomys fodiens* (definitive host). B-D. Adult cestode from the intestine of the definitive host. B. Scolex. C. Mature proglottis. D. Gravid proglottis. E. Eggs are distributed in the environment embedded in uterine capsule, adaptation for group transmission and possibly for attraction of the intermediate host. F. *Gammarus (Rivulogammarus) balcanius* (intermediate host). G. Cysticercoid from the body cavity of the intermediate host (B-D, E, G, modified from Tkach et al. 2003)

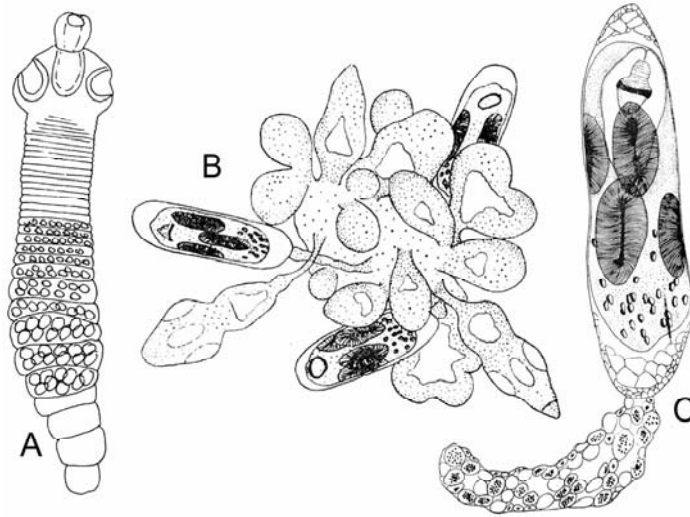


Fig. 7. *Urocystis prolifer* (Hymenolepididae). A. Adult worm from the intestine of a shrew (redrawn from Baer and Della Santa 1960). Adults (up to 20,000 specimens per host) are 0.25-0.55 mm long (Baer and Della Santa 1960) and their gravid proglottides contain few eggs (7-14, according to Kisieleska 1960). B. Early stage of metacystode development in the body cavity of the myriapod *Glomeris connexa*. The development of the oncosphere gives the beginning of cellular mass of irregular shape producing cysticercoids by budding. C. Fully developed cysticercoid. (B and C modified from Kisieleska 1960)

The life cycles of about 200 hymenolepidid species are known. Arthropods and annelids are their intermediate hosts in both aquatic and terrestrial environments.

The number of the hymenolepidid genera occurring in insectivores exceeds 30; almost all are specific parasites to the families or the genera. A number of taxa occurring in *Sorex* spp. as definitive hosts use insects as intermediate hosts. These include, e.g., *Vigisolepis spinulosa* recorded in the collembolans *Tomocerus flavesvens* (see Prokopič 1968a), *Lineolepis scutigera* in fleas of the genus *Ctenophthalmus* (see Quentin and Beaucournu 1966), *Neoskrjabinolepis schaldybini* in coleopterans of the genera *Catops* (Leiodidae) and *Oiceoptoma* (Silphidae) (see Kisieleska 1958b; Prokopič 1968b; Vaucher 1971) (Fig. 6), *Staphylocystis furcata* in a wide range of coleopterans (Geotrupidae, Carabidae and Silphidae) and orthopterans (Ryšavý and Prokopič 1965; Ryšavý 1989). *Urocystis prolifer* (Fig. 7) is another widespread intestinal parasite of *Sorex* spp. in Europe (Baer and Della Santa 1960; Genov 1984). Its intermediate hosts are glomerid diplo-

Pods in the body cavities of which metacestodes reproduce asexually by budding (Joyeux 1922; Kisieleska 1960).

Similarly, hymenolepidids parasitizing *Crocidura* spp. also use insects and myriapods as intermediate hosts. For example, *Staphylocystis brusatae* has been recorded in sand flies *Phlebotomus* spp. (Quentin et al. 1972), *S. uncinata* in coleopterans *Silpha* spp. (Vaucher 1971; Genov 1984), *S. scalaris* and *S. pistillum* in glomerids (Joyeux and Baer 1936). Asexual reproduction of metacestodes has been recorded in the latter species (Joyeux and Baer 1936). *Pseudhymenolepis redonica* is hyperapolytic (Fig. 7), i.e. its proglottides are detached before reaching maturation and live separately in the intestine (Joyeux and Baer 1936). Fleas (Quentin and Beaucourou 1966) and opiliones (Gabrion 1977) serve as its intermediate hosts.

About 20 hymenolepidid species of the genera *Coronacanthus*, *Triodontolepis*, *Neomylepis*, *Pseudobothrialepis* and *Vaucherilepis* occur in water shrews of the genus *Neomys* (Vaucher 1971; Tkach et al. 2003; Vasileva et al. 2004). For all these genera, use of freshwater amphipods as intermediate hosts in the life cycles has been demonstrated (Fig. 6).

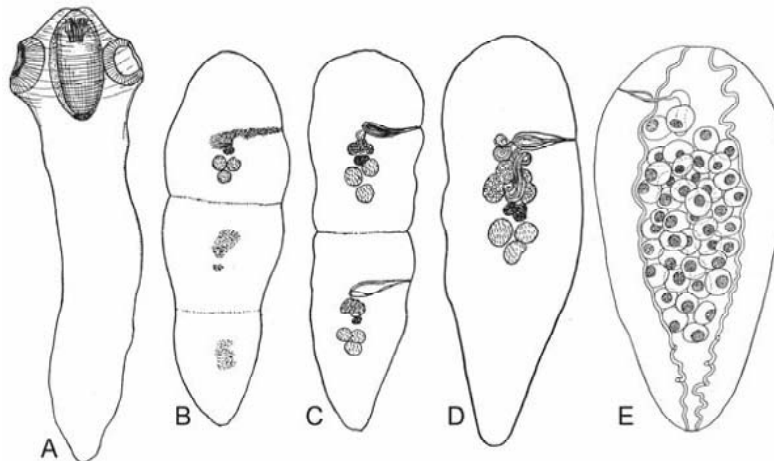


Fig. 8. *Pseudhymenolepis redonica* (Hymenolepididae), a hyperapolytic intestinal parasite of *Crocidura* spp. The scolex and the neck (A) are attached at the intestinal wall. The neck forms strobilar segments (B-E), which detach from it before their maturation and continue their development in intestine. Modified after Joyeux and Baer (1936)

The hymenolepidid cestodes of rodents are also characterised by considerable taxonomic diversity (Table 1). *Hymenolepis diminuta* has a cosmopolitan distribution, frequently recorded in rats. Burt (1980) presented a list

of 99 definitive host species (93 rodent species) and 66 species of intermediate hosts (29 coleopterans, 2 dermapterans, 2 embiopterans, 11 lepidopterans, 9 orthopterans, 11 siphonapterans and 2 diplopods).

Rodentolepis fraterna occurs mostly in the domestic mouse, sometimes also in other rodents; its metacestodes have been shown to develop in fleas and tenebrionid beetles. However, this species is unique among tapeworms in that eggs swallowed by the definitive host may give rise to cysticercoids located in the intestinal villi. Therefore, the life cycle can be completed in the same host, without participation of invertebrate intermediate host.

The metacestodes of *Rodentolepis asymmetrica* (a parasite mostly of voles) have been recorded in acarines *Archipteria coleoptera* (see Prokopič and Mauer 1969) and *Ceratozetella sellnicki* (see Pavlichenko et al. 1992).

Hymenolepidids are the main cestode group occurring in bats (Table 1). However, no life cycle is known for any species.

3.4 Anoplocephalidae

The Anoplocephalidae are characterised by the lack of a rostellum, i.e. the scolex has four suckers only. Currently, four subfamilies are recognised in it, i.e. Anoplocephalinae, Linstowiinae, Inermicapsiferinae and Thysanosomatinae. The former three subfamilies occur in small mammals. However, in this concept the Anoplocephalidae seems unlikely to be monophyletic (Beveridge 1994; Hoberg et al. 1999). The representatives of the subfamily Anoplocephalinae are characterised by the presence of eggs containing a conically-elongate envelope (modification of the embryophore) termed the “pyriform apparatus” (Fig. 9).

Typically, as with hymenolepidids, they have well-expressed seminal vesicles (external and internal). The intermediate hosts are mostly mites and definitive hosts (mostly herbivorous mammals) accidentally ingest them while grazing. The Anoplocephalinae has a cosmopolitan distribution occurring in equids, ruminants, rodents, lagomorphs, marsupials, dermapterans, primates and some birds (Spasskii 1951; Beveridge 1994).

Most of the life cycle information about anoplocephaline cestodes comes from studies on the genera and species occurring in ruminants and equids, where oribatean mites are implicated intermediate hosts. Data on life cycles of anoplocephalids from small mammals are scarce. However, the life cycles of *Cittotaenia denticulata* and *Mosgovoyia ctenoides*, occurring in rabbits, have been studied in detail (Stunkard 1941). Their intermediate hosts are oribatean mites of various families (Fig. 9). The life cycle of the species of the genus *Monoecocestus*, parasitic in porcupines, is similar (Freeman 1952). There are data that collembolans participate as inter-

mediate hosts in the life cycle of *Paranoplocephala omphalodes*, a parasite of voles, in the Russian tundra (Smirnova and Shalayeva 1986).

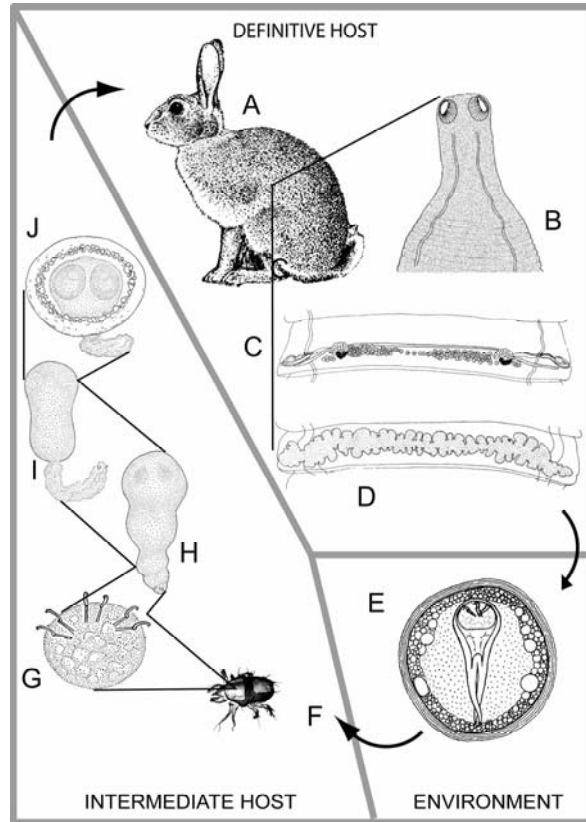


Fig. 9. Life cycle of *Mosgovoyia ctenoides*. A. Rabbit, *Oryctolagus cuniculus* (definitive host). B-D. Parts of the adult worm from the intestine of the definitive hosts (modified from Beveridge 1978). B. Scolex. C. Mature proglottis. D. Gravid proglottis. E. Egg. Note the pyriform apparatus (modified from Stunkard 1941). F. Mite *Scutovertex minutus* (intermediate host). G-J. Gradual stages of the metacestode development from the body cavity of the intermediate host (modified from Stunkard 1941). G. Oncosphere. H, I. Gradual stages of body differentiation. J. Infective cysticercoid. According to Stunkard (1941), about 70 days are needed for the metacestode to reach the infective encysted stage

4 Small mammals as intermediate and paratenic hosts of cestodes

Small mammals participate as intermediate and paratenic hosts in the life cycles of pseudophyllidean cestodes (Diphyllbothriidae), as the only intermediate hosts in the life cycles of cyclophyllidean cestodes of the families Taeniidae and Paruterinidae, as intermediate and paratenic hosts in the life cycles of the Mesocestoididae (*Mesocestoides*) and as host of metacestodes (whether as intermediate or paratenic disputed) of the Dipylidiidae (*Joyeuxiella*). Definitive hosts of all these cestodes are carnivorous mammals and/or birds of prey.

4.1 Diphyllbothriidae

According to the taxonomic concept adopted here (Bray et al. 1994), the family includes pseudophyllideans occurring as adults in reptiles, birds and mammals; their life cycles typically include copepods as hosts of proceroids (first intermediate host) and fishes as hosts of plerocercoids (second intermediate host). However, the species of the cosmopolitan genus *Spirometra*, which includes intestinal parasites of carnivorous mammals, use tetrapods as second intermediate and paratenic hosts, i.e. amphibians, reptiles and mammals (Dubinina 1951; Mueller 1974; Uchida 2003). Their life cycles have been studied in detail, mostly because plerocercoids (termed spargana, singular sparganum) are agents of the disease human sparganosis and because they were found to secrete a hormone-like factor stimulating an overgrowth of mammals (Mueller 1974; Hirai 2003).

S. erinaceieuropaei is widespread in the Old World, in many parts of its geographical range (e.g., in Europe) exhibiting a focal pattern of distribution. Its life cycle was studied in the Volga Delta (Dubinina 1951), where mostly frogs (*Rana* spp.) and grass snakes (*Natrix* spp.) were infected with plerocercoids. However, rodents also participated, supposedly being infested either by ingesting crustaceans with proceroids (i.e. as a second intermediate host) or by swallowing developed plerocercoids with the flesh of intermediate hosts (i.e. as a paratenic host). Dubinina (1951) believed that the transmission route using rodents had secondary importance in the Volga Delta region. In contrast, a study carried out in the Srebarna Reserve, a wetland associated with the lower Danube in Bulgaria (Genov 1969), showed that two species of frogs and nine species of mammals (rodents, insectivores and mustelid carnivores) were infected with plerocercoids of *S. erinaceieuropaei*. Two carnivore species, stray domestic cats and wild cats (*Felis silvestris*), were recorded as definitive hosts. While the

most abundant frog species, *Rana ridibunda*, had a prevalence of plerocercoid infection of 8.6%, the prevalence in the most abundant insectivores *Crocidura leucodon* and *C. suaveolens* reached 29.6 and 25.0%, respectively. Therefore, the importance of the small mammal transmission route in that ecosystem was comparable with, or perhaps of more importance, than that of the amphibian route. Use of small mammals (rodents) was also demonstrated for the life cycle of the North American *Spirometra mansonioides* (see Mueller 1938).

4.2 Taeniidae

This family includes about 50 species, which are intestinal parasites of carnivorous mammals or humans as adults and their metacestodes occur in the internal organs, musculature, body cavity, connective tissue or other parenteral sites (“external to gut”) of mammals (Abuladze 1964; Verster 1969; Loos-Frank 2000). The family includes five species of primary medical importance and about 20 species of basic veterinary importance. The main intermediate hosts of taeniids are two groups of mammals: the ruminants and small mammals (mostly rodents). They all become infected by eating food contaminated with taeniid eggs. Abuladze (1964) listed 112 species of rodents, 16 species of lagomorphs and two species of insectivores as intermediate hosts of taeniids.

Currently, the validity of two genera, *Taenia* and *Echinococcus*, is widely accepted (see Rausch 1994). The former genus exhibits a morphological uniformity of the adult cestodes but diverse morphology of metacestodes; their structural peculiarities have sometimes been used as characters for splitting *Taenia* into several genera, e.g. *Hydatigera*, *Multiceps*, *Taeniarhynchus* and *Tetratirotaenia* (see Abuladze 1964). We adopt here the concept of Verster (1969) and Rausch (1994) recognising the latter generic names as synonyms of *Taenia*, a course of action in line with a recent phylogenetic study (Hoberg et al. 2000).

According to a recent review (Loos-Frank 2000), out of 44 species of *Taenia*, 20 use small mammals as intermediate hosts: metacestodes of 16 occur in rodents, of eight in lagomorphs and of two in insectivores. The following morphological modifications of metacestodes of *Taenia* spp. are found in small mammals (terminology follows Hoberg et al. 2000 and Chervy 2002, see Figs. 3 and 10):

- Cysticercus. This is the basic modification of metacestode in the Taeniidae, and is characterised by a scolex introverted (invaginated) during the development into the posterior bladder-like body part. This modification is widespread among *Taenia* spp. Examples for species having cysti-

cerci in their life cycles are *T. crassiceps* with a wide range of carnivores as definitive hosts (frequent in European foxes) and a wide range of rodents and lagomorphs as intermediate hosts, in which it occurs in connective tissue and in the musculature; *T. pisiformis* with range of definitive hosts similar to that of the previous species and metacestodes occurring mostly in rabbits and hares. Hoberg et al. (2000) considered the cysticercus as plesiomorphic and the other metacestode modifications in taeniids as its derivatives.

- Strobilocercus. This is similar to the cysticercus but has, in addition to a scolex and neck, a segmented region (“metacestode strobila”). This metacestode occurs in several species previously referred to *Hydatigera*, e.g. *T. taeniaeformis*, which as an adult is found mostly in cats and as a metacestode in the liver of a wide range of rodents.
- Fimbriocercus (armatetrathyridium). This type of cysticercus is characterised by having an elongated unsegmented body. It occurs in the life cycle of several species, e.g. *Taenia martis*, which as an adult parasitizes martens (*Martes* spp.) and as a metacestode occurs in the thoracic cavity of bank voles (has been referred to the genus *Fimbriotaenia*).
- Coenurus. This metacestode forms a large bladder, which is full of liquid and is internally lined by a special layer (termed germinative membrane), which buds off multiple scoleces. It occurs in the species previously recognised as members of *Multiceps*, e.g. *T. serialis*, a tapeworm widespread in canids and having a metacestode occurring mostly in the intermuscular and subcutaneous connective tissue of rabbits and hares.
- Polycephalic. In this metacestode, several scoleces are situated on elongate stalks arising by exogenous budding from a central bladder, which later regresses. It is known for several species, e.g. for *T. twitchelli* from the wolverine in North America, with the metacestode found in the pleural and abdominal cavity of various rodents, mostly voles.

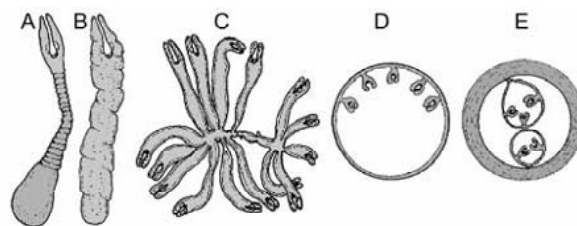


Fig. 10. Schematic presentation of the types of taeniid larvae (from Chervy 2002, reproduced with kind permission of Springer Science and Business Media). A. Strobilocercus. B. Fimbriocercus. C. Polycephalic. D. Coenurus. E. Echinococcus or hydatid (for cysticercus, see Fig. 3).

As seen from the above descriptions, the metacestodes belonging to the modifications “coenurus” and “polycephalic” are able to reproduce asexually in the intermediate host.

The second genus of the Taeniidae, *Echinococcus*, includes cestodes, which as adults are minute, only few millimetres long and consist of a few proglottides. They also occur in intestines of carnivores. Their metacestode is known as an echinococcus (= hydatid) and is located in the internal organs of herbivorous animals. Structurally, it resembles a coenurus but its germinative membrane is capable of producing daughter bladders, which, on their turn, can also form both daughter bladders and scoleces. Thus, the rate of the asexual reproduction of metacestodes is greatly increased, resulting in the proliferation of thousands of scoleces from a single oncosphere. Humans can also become infected as intermediate hosts. This disease is one of the major current problems of the medical parasitology.

The validity of four species is recognised (Rausch 1995; Thompson 1995). These are (after Rausch 1995): (1) *E. granulosus*, a cosmopolitan parasite occurring as an adult mostly in canids and as a metacestode in a wide range of ungulates. This species exhibits an immense genetic diversity associated with various life-cycle patterns (including the range of intermediate hosts) and, to a lesser extent, with the geographical distribution (for a survey, see McManus and Thompson 2003); the ‘strains’ perhaps deserve to be given subspecies or species status. (2) *E. multilocularis*, a species occurring in the Northern Hemisphere only, with a circumpolar distribution in the tundra and focal distribution in temperate latitudes, mostly in highland areas. Its definitive hosts are canids and felids, and its intermediate hosts are rodents, insectivores and lagomorphs. (3) *E. oligarthus*, a Neotropical species occurring from Central America (Costa Rica) to the subantarctic areas of Argentina, with wild felids as definitive hosts and rodents (mostly dasyproctids) as intermediate hosts. (4) *E. vogeli*, having a restricted geographical range in Central America and northern South America, with the bush dog (*Speothos venaticus*, Canidae) as definitive host and the paca (*Cuniculus paca*, Dasyproctidae) and few other rodent species as intermediate hosts; the participation of hunters’ dogs in its life cycle as definitive hosts is possible. Recently, a fifth species (*E. shiquicus*) was proposed, occurring in Tibet and having a life cycle associated with the Tibetan fox *Vulpes ferrilata* and the plateau pika *Ochotona curzoniae*, distinguished mostly on the basis of genetic differences (see Xiao et al. 2005); however, its validity needs further confirmation, especially because its morphology is poorly described.

4.3 Paruterinidae

The number of the genera included in this family exceeds 20. Most of them are parasites of insectivorous birds. For two genera only, *Paruterina* (parasites of owls) and *Cladotaenia* (parasites of birds of prey), small mammals (rodents and insectivores) are known as intermediate hosts (Georgiev and Korniyushin 1994). Life cycles of several species of these two genera have been described in detail (Freeman 1957, 1959). The metacestodes were found in the liver and mesenteric lymph of various experimentally and naturally infected rodents. They have elongated body, their scolex is invaginated within the body and a cercomer and bladder are lacking. The terms “plerocercoids” (Freeman 1957, 1959), “cladothyridia” (Abuladze 1964) and “merocercoids” (Chervy 2002) have been used for them.

5 Concluding remarks

Cestodes are widespread in small mammals. Their taxonomic diversity is rather well studied in the Holarctic but poorly known in tropical areas. All cestodes using small mammals as definitive hosts belong to the order Cyclophyllidea. The numbers of the families and the genera occurring in each major group of small mammals (i.e., insectivores, bats, lagomorphs and rodents) are 4 and 37, 3 and 9, 3 and 14, and 6 and 47, respectively. Studies on the life cycles of the cestodes from small mammals are relatively few. No life cycle is known for any cestode species occurring in bats. As a rule, cestode species occurring in small mammals as definitive hosts are characterised by two-host life cycles, involving invertebrates as intermediate hosts. Most of the invertebrate hosts are terrestrial arthropods (insects, acari, myriapods, in some cases arachnids), rarely molluscs; only the species parasitizing water shrews are known to have life cycles involving crustaceans as intermediate hosts. Some life cycles demonstrate adaptations for group infestation, asexual reproduction within the intermediate host or even a possibility of infestation without the participation of an intermediate host. Small mammals participate as the only intermediate host in the life cycles of taeniid species parasitic in carnivore mammals (*Taenia*, *Echinococcus*) and paruterinid species parasitic in birds of prey (*Paruterina*, *Cladotaenia*). They can also provide alternative transmission routes as second intermediate hosts of some pseudophyllidean cestodes (*Spirometra*) and as (second?) intermediate hosts or paratenic hosts of some cyclophyllidean cestodes (*Mesocestoides*, *Joyeuxiella*).

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