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6

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By
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1. INTRODUCTION

The Cyclophyllidea are the largest order of cestodes with over 3,000 known species in 437 genera and 16 families (Georgiev, 2003; Caira and Littlewood, 2013; Table 1). Besides their high diversity, cyclophyllideans are also the quintessential cestodes because they are the most commonly known and the most pathogenic in humans and domestic animals. With rare exceptions, they are parasites of homeotherms and are particularly diverse in birds and mammals, although a few species also parasitize amphibians and "reptiles." Their known life-cycles include one or two, typically invertebrate, intermediate hosts; vertebrates rarely act as intermediate hosts.

Although cyclophyllideans are found on all continents, they have chiefly been studied in regions known to be home to strong schools of parasitology (i.e., Europe, North America, the territories of the former Soviet Union, and Japan). Data from other parts of the world, especially the tropics, remain patchy. Important biodiversity contributions focusing on the Cyclophyllidea are few and have predominantly concentrated on aquatic birds in eastern Europe, northern Asia, and the Far East. Synthetic studies covering a large diversity of hosts include Southwell and Lake (1939a, b), Mahon (1954), Baer (1959), Spasskaya and Spasskii (1971), Petrova (1977, 1978), Illescas-Gomez and Lopez-Roman (1979), Brglez (1981), Zhuk et al. (1982), Maksimova (1989), and Mariaux (1994) for birds, and Skrjabin and Matevosyan (1948), Gvozdev et al. (1970), Vaucher (1971), Hunkeler (1974), Kozlov (1977), Ryzhikov et al. (1978), Genov (1984), and Sawada (1997) for mammals. Most of these contributions were, however, geographically restricted.

One of the goals of the PBI project was to provide a more comprehensive global assessment of overall cestode diversity. Unfortunately, compared with the diversity of this order, the number of researchers who worked specifically on cyclophyllideans over the course of this project was limited. This meant that not all host groups could be targeted with equal effort. Furthermore, many birds and mammals are protected; therefore, opportunities to examine their parasite faunas are severely restricted in many areas. Despite these limitations, significant progress has been made in characterizing the cyclophyllidean fauna of a number of host groups from all continents (except Antarctica). These include terrestrial birds (mostly Passeriformes), and, among mammals, the Soricomorpha and Rodentia. Altogether, almost 3,500 bird specimens across more than 120 families, representing close to 10% of extant bird species, as well as over 1,000 mammal specimens across 32 families and 143 species were examined, making the present effort the largest cyclophyllidean diversity research program to date.

2. CYCLOPHYLLIDEA OVERVIEW

2.1. Morphological characteristics

Members of the Cyclophyllidea are variable in size (from less than 1 mm to several meters in length) but are usually easily recognizable by the presence of four circular suckers, a compact posterior vitellarium, and lateral genital pores. They are hermaphroditic (with rare exceptions). Furthermore a rostellum, armed or not, is usually present. The uterus may be persistent, or replaced by egg capsules or associated with one, or several, paruterine organs. However, all of these characters are variable and there are known deviations from these traits.

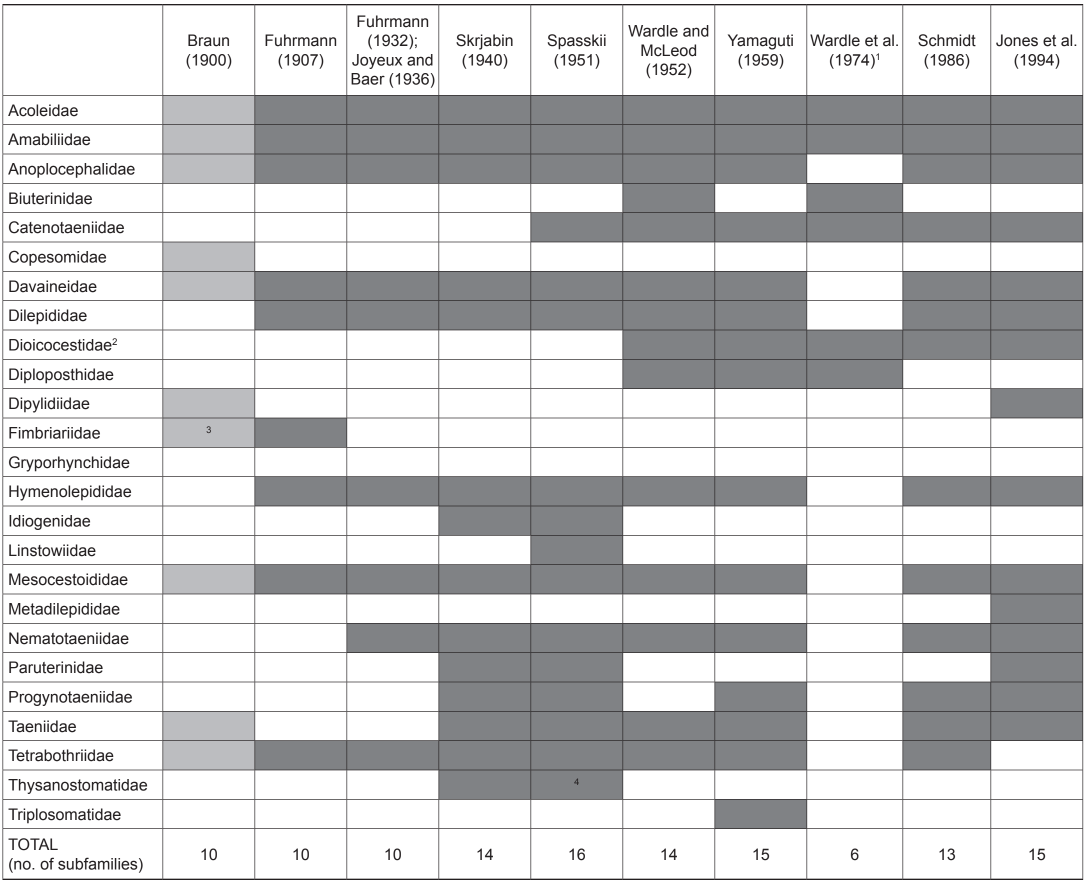
Within the order, the main differentiating characters are linked to the scolex (presence/absence/structure/retractibility of the rostellum; presence/absence/shape/organization of hooks, and presence of spine-like microtriches on tegument of scolex, especially of suckers and rhynchus, sometimes of proglottids); the genital organs (present in 1 or 2 sets per proglottid); number and disposition of testes; presence of internal and/or external seminal vesicles; shape and position of ovary; relative position of genital ducts to osmoregulatory canals; alternation of genital pores along the length of the strobila; presence of accessory structures to the copulatory organs (e.g., glands, sphincters, or spines); and development of gravid proglottids (shape and development of uterus, presence of paruterine organs, shape and peculiarities of eggs, nature of embryonic envelopes). Other characters, such as the shape and number of proglottids, the conspicuousness of proglottization, the shape of suckers are also used to discrimate among taxa.

2.2. Higher-level classification

The original establishment of the order remains a matter of controversy (see Wardle and McLeod [1952] and Hoberg et al. [1999] for short summaries). Jones et al. (1994) attributed the order to van Beneden (in Braun, 1900), although Braun (1900) himself is more often credited because it was one of the five orders of cestodes he recognized. Since then, the higher-level classification of the group has gone through numerous changes. Braun (1900) considered the order to include only the single family Taeniidae Ludwig, 1886, which he subdivided into ten subfamilies and 33 genera. The rapid discovery of numerous new taxa at the beginning of the 20th century prompted a number of refinements to that classification system (Fig. 1). Fuhrmann (1907) proposed a more complex scheme comprising ten families and 66 genera. A few years later, the Nematotaeniidae Lühe, 1910 were added to this scheme and the Fimbriariidae Wolffhügel, 1899 were reduced to subfamily level (Fuhrmann, 1932; Joyeux and Baer, 1936). Skrjabin (1940) proposed the order be subdivided into seven suborders, each with between one and four families. He believed that the presence of a paruterine organ was sufficiently distinct to justify erection of the family Idiogenidae Skrjabin, 1940 within the suborder Davaineata. He also recognized the Thysanosomatidae Skrjabin, 1933 as valid within the suborder Anoplocephalata and elevated the Paruterininae Fuhrmann, 1907 to the family level. Within families, he considered features of the uterus (sac-like or breaking down into egg capsules) as appropriate for recognizing subfamilies. Spasskii (1951) essentially followed Skrjabin (1940), but with some modifications in the membership of suborders and superfamilies. Most notably, he placed the Catenotaeniidae Spasskii, 1950, a family he had erected the previous year (Spasskii, 1950), in the suborder Anoplocephalata.

In their comprehensive book on cestodes, Wardle and McLeod (1952) included the Catenotaeniidae, Biuterinidae Meggitt, 1927, and Diploposthidae Poche, 1926 in Fuhrmann's classification scheme, thus recognizing 14 families. However, in the update of that book, Wardle et al. (1974) drastically reorganized the order, technically retaining only the families Catenotaeniidae, Biuterinidae, Acoleidae Fuhrmann, 1899, Amabiliidae Braun, 1900, Dioicocestidae Southwell, 1930, and Diploposthidae in the Cyclophyllidea *sensu stricto*. They elevated most of the other generally recognized families to ordinal level and further divided them into a total of 26 families, many of which had been recognized as subfamilies in other systems. However, Wardle et al.'s (1974) classification scheme was not generally accepted.

In his book, Yamaguti (1959) accepted the 15 families recognized by Wardle and McLeod (1952), to which he added the Triplotaeniidae Yamaguti, 1959. Freeman (1973) based his concept of cestode classification on ontogeny, proposing four lineages within the traditional Cyclophyllidea, with some traditionally recognized families split among them. However, he refrained from formally reorganizing the order. His proposals were summarized by Hoberg et al. (1999). Schmidt (1986) followed Yamaguti (1959) but treated the Diploposthidae as a synonym



	Braun (1900)	Fuhrmann (1907)	Fuhrmann (1932); Joyeux and Baer (1936)	Skrjabin (1940)	Spasskii (1951)	Wardle and McLeod (1952)	Yamaguti (1959)	Wardle et al. (1974)[1]	Schmidt (1986)	Jones et al. (1994)
Acoleidae	░	▓	▓	▓	▓	▓	▓	▓	▓	▓
Amabiliidae	░	▓	▓	▓	▓	▓	▓	▓	▓	▓
Anoplocephalidae	░	▓	▓	▓	▓	▓	▓		▓	▓
Biuterinidae						▓		▓		
Catenotaeniidae					▓	▓	▓	▓	▓	▓
Copesomidae	░									
Davaineidae	░	▓	▓	▓	▓	▓	▓		▓	▓
Dilepididae		▓	▓	▓	▓	▓	▓		▓	▓
Dioicocestidae[2]						▓	▓	▓	▓	▓
Diploposthidae						▓	▓	▓		
Dipylidiidae	░									▓
Fimbriariidae	░ 3	▓								
Gryporhynchidae										
Hymenolepididae		▓	▓	▓	▓	▓	▓		▓	▓
Idiogenidae				▓	▓					
Linstowiidae					▓					
Mesocestoididae	░	▓	▓	▓	▓	▓	▓		▓	▓
Metadilepididae										▓
Nematotaeniidae			▓	▓	▓	▓	▓		▓	▓
Paruterinidae				▓	▓					▓
Progynotaeniidae				▓	▓		▓		▓	▓
Taeniidae	░			▓	▓	▓	▓		▓	▓
Tetrabothriidae	░	▓	▓	▓	▓	▓	▓		▓	
Thysanostomatidae				▓	▓ 4					
Triplosomatidae							▓			
TOTAL (no. of subfamilies)	10	10	10	14	16	14	15	6	13	15

FIGURE 1. Higher cyclophyllidean classification through time. Braun's (1900) original subfamilies are in lighter gray.
[1] For comments on Wardle et al.'s (1974) families see Section 2.2.
[2] Sometimes spelled Dioecocestidae, see Section 5.7 for clarification.
[3] An "Annex" in Braun's system.
[4] Avitellinidae in Spasskii (1951).

of the Acoleidae and considered the Triplotaeniidae as a subfamily of the Anoplocephalidae Cholodkowsky, 1902, reducing the number of families to 13.

In the most recent authoritative treatment of the group, Jones et al. (1994) recognized 15 families. They transferred the Tetrabothriidae Linton, 1991 to their own order, and added the Metadilepididae Spasskii, 1959, Dipylidiidae Railliet, 1896, and Paruterinidae, to the order, the latter two of which had been treated as subfamilies in Schmidt's (1986) system. The current classification (see Table 1) also includes the Gryporhynchidae Spasskii & Spasskaya, 1973. Although doubts remain as to the status of the Mesocestoididae Perrier, 1897, which have repeatedly been proposed to be treated as a separate order, (e.g., Wardle et al., 1974; Brooks et al., 1991; Mariaux, 1998), they are treated as a family in the taxonomic framework presented here pending their ordinal status be more formally assessed in the context of the Cyclophyllidea overall.

3. PBI PROJECT RESULTS

3.1. Geographic sampling

This project resulted in the sampling of avian and mammalian hosts from areas of the planet that were among the most poorly known from the standpoint of cyclophyllidean diversity. Although we aimed to cover as many different regions as possible, the localities ultimately sampled were biased to some extent by logistical considerations. These included local administrative regulations, weather at the time of the scheduled expeditions, safety, as well as the participation of local academic counterparts. Thirty dedicated field trips (as well as a few more opportunistic smaller collecting trips) were organized between 2008 and 2015. These consisted of three to Australia, five to Africa, one to Europe, one to the Middle East, two to Madagascar, eight to Asia, three to North America, one to Central America, and six to South America. With the notable exceptions of Australia, the USA, the Ivory Coast, the Ukraine, Russia, and some South American countries, beyond some occasional mostly ancient reports, the cyclophyllidean fauna of all of these locations was very poorly known. A summary of our PBI expeditions is provided by country below. As noted above, owing to the limited number of individuals with taxonomic expertise in this, the largest cestode order, PBI project efforts emphasized collecting over the description of novelty in the hope of developing a resource for future taxonomic work.

Mist nets (and occasionally guns) were used to capture birds in the field. Mammals were trapped using Sherman live traps or pit fall traps. Birds were euthanized using chloroform or by thoracic compression, and mammals by exposure to isoflurane. All animals were dissected as soon as possible after their death. Cestodes were removed from the digestive tract, washed and relaxed in water, fixed with hot 4% formaldehyde, and preserved in 70% ethanol. Separate tissue fragments were kept in 95% ethanol for DNA extraction and sequencing. The worms were stained following various protocols; stains used included iron acetocarmine, hydrochloric carmine, aqueous alum carmine, Ehrlich's hematoxylin, and Mayer's hematoxylin. Some scoleces and fragments of strobila were mounted in Berlese's medium to facilitate detailed examination of the rostellar hooks, cirrus armature, and structure of the eggs (see Dubinina, 1971; Ivashkin et al., 1971; Georgiev et al., 1986; Miller et al., 2010).

Parasite specimens examined over the course of this project have been deposited in the collections of the HWML (Harold W. Manter Laboratory of the University of Nebraska, Lincoln, NE, USA); IBER-BAS (Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria); ISEA (Institute of Systematics and Ecology of Animals, Novosibirsk, Russia); MHNG (Natural History Museum of Geneva, Geneva, Switzerland); MZUSP (Museum of Zoology of the University of São Paulo, São Paulo, Brazil); NMNH (Smithsonian's National Museum of Natural History—Invertebrate Zoology Collection, Washington, D.C., USA); SAMA (South Australian Museum, Adelaide, Australia). Associated genomic DNA and ethanol-preserved tissue samples were deposited in the NHM (Natural History Museum, London, UK). Host vouchers (note that not all hosts specimens were preserved) have been deposited in the ISEA, MHNG, as well as the FMNH (Field Museum of Natural History, Chicago, IL, USA), KU (Biodiversity Institute, University of Kansas, Lawrence, KS, USA), NMPh (National Museum of the Philippines, Manila), and MPEG (Museu Paraense Emílio Goeldi, Belém, Brazil).

Host taxonomy follows Avibase (Lepage, 2014; Lepage et al., 2014) for birds and the online version of the Mammals Species of the World, 3rd edition (Wilson and Reeder, 2005) for mammals. Public databases ("Host-parasite database" [Gibson et al., 2005; http://www.nhm.ac.uk/research-curation/scientific-resources/taxonomy-systematics/host-parasites/

database/index.jsp]; “Zoological Records®” [Thompson Reuters]) were queried for known host-parasite associations. Molecular specimens collected over the course of the PBI project were assigned PBI-codes that are available from the corresponding author upon request.

AUSTRALIA (3 expeditions). **June 2010:** Arid pastoral lands, Western Australia; elevation 20 m. June 2011: Central desert, Northern Territory; elevation 650 m. **May 2013:** tropical coastal rainforest, Queensland; elevation 0–300 m. *Base camps:* Karratha (-20.74; 116.84), Mulga Park Station (-26.00; 131.59), and Cairns (-16.92; 145.77).

Vertebrates examined: 89 mammal specimens representing 13 species in seven families.

Cyclophyllideans encountered: Ten species; 40% overall prevalence.

Remarks: Cestodes of Australian mammals have been relatively well studied (see, e.g., Beveridge, 1976, 1985; Beveridge and Jones, 2002; Beveridge and Johnson, 2004) and no new species were collected. However, these new expeditions yielded material usable for molecular studies. For example, several species of *Bertiella* Stiles & Hassall, 1902 were preserved for the first time in ethanol and included in our molecular phylogenetic studies. In addition, collection of specimens of the anoplocephalids *Progamotaenia macropodis* Beveridge, 1976 and *Wallabicestus ewersi* Schmidt, 1975 from kangaroos will facilitate future analysis of both species complexes. A review of the cyclophyllidean holdings at the South Australian Museum in Adelaide did, however, yield taxa new to science.

BRAZIL (2 expeditions). **November 2011:** Atlantic rainforests in protected catchment areas, coastal massifs south of Salesopolis; elevation 800–900 m. Agricultural landscapes, north of Tremembe; elevation 500–600 m; both São Paulo Region. **July 2013:** Lowland tropical forest within Reserva Biologic do Gurupi, Maranhao State; elevation 0–100 m. *Base camps:* Estação Biológica de Boracéia, University of São Paulo (-23.65; -45.89), Fazenda Nabor (-22.92; -45.57), and Reserva Biológica do Gurupi (-3.70; -46.76).

Vertebrates examined: 413 bird specimens representing 173 species in 38 families.

Cyclophyllideans encountered: 57 species; 17% overall prevalence.

Remarks: The Neotropics, and specifically Brazil as its largest country, harbor one of the richest avifaunas in the world. Among other areas, we had excellent access to well-preserved patches of primary Atlantic coastal rainforests, in which few parasitological studies had been carried out previously. In the São Paulo Region, about one third of the species collected are likely new to science; the specimens belonging to known species are also important, since most of the species described from Brazil were based on poorly preserved specimens collected in the first half of 19th century by the Austrian naturalist and explorer J. Natterer. We have also examined birds in the southeastern-most area of the southern Amazon where helminths of birds had never been studied. Prevalence of cestode infections in the Amazonian Belem area of endemism (Gurupi) was lower (only 13%) than that in the Atlantic forest, which is considered a generally more disturbed habitat. The sources of these differences are yet to be determined. This region also yielded cestode taxa new to science.

CHILE (2 expeditions). **November 2008:** “Cathedral forests” on slopes of Andes and open land around estuaries in Fjord Comau, northern Patagonia, south of Puerto Montt, Los Lagos Region; elevation 0–100 m. **June 2015:** Lowland savannah, cattle pastures, and temperate deciduous forest outside of Chillán and wetland outside of Los Angeles, Biobio Region; elevation 100–200 m. *Base camps:* Huinay Scientific Field Station (-42.38; -72.41) and Universidad de Concepción, Chillán (-36.59; -72.08).

Vertebrates examined: 121 bird specimens of 27 species in 19 families, including some marine taxa, as well as ten mammal specimens of two species in two families.

Cyclophyllideans encountered in birds: Approximately 26 species, including at least ten which are new to science; 53% overall prevalence.

Cyclophyllideans encountered in mammals: One species; 10% prevalence.

Remarks: Cestode data are extremely limited for the birds and mammals of Chile, although a few localized contributions have been published (e.g., Babero et al., 1981; Torres et al., 1991; González-Acuña et al., 2000, 2011). In fact, in general, data on bird and mammal cestode diversity in the temperate latitudes of South America are not available. The late F. Bona collected extensively in Chile, including the Valdivia region, however most of his specimens have not yet been examined. Even though our collections in Chile were restricted to a very small area and the diversity of hosts examined was low, we obtained the highest relative diversity and proportion of new cestode taxa in terrestrial birds, including new genera from that country, than from any other country represented by our other expeditions. The second expedition to Chile targeted waterfowl and small mammals. The cestode fauna of three species of ducks and two species of coots turned out to be extremely depauperate. Morphological and molecular analyses have demonstrated that previous identification of mammalian hymenolepidids in Chile were likely incorrect. This locality yielded a member of a new cestode genus most closely related to another new cestode that we discovered in Central America (Guatemala; see below) found in the Chilean small mammals examined.

CHINA (1 expedition): **July 2011:** Mountainous area around Lanzhou City and in mixed forested, shrublands, and agricultural areas south of Yuzhong City, Xinglong Mountain; river valley and adjacent slopes, Lanzhou Shifogou National Forest Park; vicinities of the village of Dagoucun, Lanshan Forest Park; mountain slopes west of the city campus of the Northwest University for Nationalities (NWUN), as well as parks and grasslands on the new campus of NWUN and adjacent fields. Gansu Province; elevation 1,700–2,500 m. *Base camp:* Yuzhong campus of NWUN (35.93; 104.15).

Vertebrates examined: 129 bird specimens of 32 species in 16 families.

Cyclophyllideans encountered: 17 species; 33% overall prevalence.

Remarks: China's cyclophyllidean fauna remains extremely poorly known. Most previous data on the avian cestodes of China come from eastern parts of the country (e.g., Hsü, 1935). We explored some localities in the central parts of the country with relatively rich avifaunas—typical high altitude regions with continental climate. We mostly collected known Palaearctic species, which have been used widely in molecular phylogenetic analyses and ultrastructural studies. Furthermore, these specimens will be used for the redescription of species for which most of the morphology is poorly known.

ETHIOPIA (1 expedition): **November 2012:** Secondary open forests in Wondo Genet area; Southern Nations, Nationalities, and Peoples' Region; elevation 1,900–2,100 m. Shore of Lake Ziway in Ziway town; Oromia Region; elevation 1,650 m. *Base camps:* Wondo Genet (7.08; 38.63) and Ziway Fishery Resource Research Center (7.92; 38.73).

Cyclophyllideans encountered: 13 species; 19% overall prevalence.

Remarks: The only previous detailed taxonomic study of the cyclophyllideans of Ethiopia (Fuhrmann and Baer, 1943) was based on samples from the southern-most parts of the country, more specifically the region of the Sagan and Omo rivers. Over the course of the PBI project, we were able to examine areas in the Rift Valley that were home to a considerable diversity of birds. We found new species of the families Hymenolepididae, Dilepididae, and Paruterinidae as well as described species with poorly known morphology requiring the preparation of contemporary redescriptions.

GABON (1 expedition). **November 2009:** Mosaic savannah and river shores. Southeastern region, Franceville area, Haut-Ogooué Province; elevation 300–400 m. *Base camp:* Centre International de Recherches Médicales de Franceville (CIRMF) (-1.61; 13.58).

Cyclophyllideans encountered: 31 species; 24% overall prevalence.

Remarks: Although some neighboring countries, especially the Democratic Republic of Congo, had been explored for tapeworms in the first half of the 20th century (e.g., Baer, 1925, 1959; Southwell and Lake, 1939a, b; Mahon, 1954), basically nothing was known about cyclophyllideans from Gabon at the initiation of the project. The diverse landscapes of the Haut-Ogooué Province make it the richest part of the country for its avian diversity and allowed for the collection of cestodes that are representative of equatorial parts of Africa. Cestodes found included both new and described species of cyclophyllideans that were subsequently widely used in molecular and morphological studies carried out as part of the PBI project.

GUATEMALA (1 expedition). **January 2015:** Remnant, isolated, mixed-hardwood cloud forest in Cerro Cucurucho, Sacatepéquez Department; elevation 2,640 m. *Base camp:* Finca El Pilar, Cerro Cucurucho 11 km SE of Antigua Guatemala, Sacatepéquez, Guatemala (14.52; -90.69).

Vertebrates examined: 58 mammal specimens of ten species in four families.

Cyclophyllideans encountered: Approximately ten species with a combined overall prevalence of 43%.

Remarks: Almost all mammalian species collected on this trip had never been examined for helminths, including cyclophyllidean cestodes. All cyclophyllidean species appear to be new to science, including a member of a new genus in rodents that appears to be closely related to a new species from Chile. Cestodes parasitic in shrews belonged to several genera and besides being new, provided invaluable resource for phylogenetic studies of this group. This expedition provided the southern-most records of shrew-hosted cestodes so far in the Western Hemisphere. This material significantly complements material from higher latitudes in North America and Eurasia, and provides opportunities to obtain a more complete picture of several genera (e.g., *Skrjabinacanthus* Spasskii & Morosov, 1959, *Lineolepis* Spasskii, 1959, *Staphylocystoides* Yamaguti, 1959, *Cryptocotylepis* Skrjabin & Matevosyan, 1948) and also to inform historical biogeography (Hope et al., 2016; Cook et al., in press).

GUYANA (1 expedition). **April 2014:** Lowland savannah, cattle pastures, and deciduous tropical forest on the foothills of the Pakaraima Mts.; gallery forest on Ireng River near Karasabai; Region 9, Upper Takutu-Upper Essequibo; elevation 200–400 m. *Base camp:* Karasabai Amerindian Village (4.00; -59.53).

Vertebrates examined: 82 bird specimens of 47 species in 19 families.

Cyclophyllideans encountered: Approximately ten species with 15% overall prevalence.

Remarks: Collections focused on terrestrial birds. This work built on the knowledge gained during the Smithsonian sponsored program "Biological Diversity of the Guiana Shield", started in 1983, that included an extensive survey of the plants, insects, and vertebrates of Guyana (see http://botany.si.edu/bdg/index.html). While there have been a handful of studies on the helminths of amphibians and "reptiles" from Guyana, the cestodes of the country remain poorly known. The cyclophyllidean specimens collected during this trip were fixed appropriately for morphological and molecular work and represent several families.

IRAN (1 expedition). **December 2010:** Persian Gulf shore and Sea of Oman, intertidal areas, mangroves, area of the town of Minab, South of the city of Bandar Abbas, Hormozgan Province; elevation 0–20 m. *Base camp:* State Environmental Agency Office, Minab (27.13; 57.07).

Vertebrates examined: 54 bird specimens of 18 species in 11 families.

Cyclophyllideans encountered: Approximately 18 species; 50% overall prevalence.

Remarks: We studied mostly aquatic (shore and marine) birds. This resulted in a representative collection of cestode families that are specific to these hosts, which is of great value for both future morphological and molecular phylogenetic studies. Tetrabothriideans were also collected.

IVORY COAST (1 expedition). **April–June 2010:** Coastal lagoons near and east of Abidjan and southern Savannah. Grands Ponts, Belier and Sud Comoe Regions; elevation 10–150 m. *Base camps:* Centre Suisse de Recherches Scientifiques CSRS (5.33; -4.13) and its Bringakro field station (6.41; -5.09).

Vertebrates examined: 120 bird specimens of 31 species in 16 families.

Cyclophyllideans encountered: Six species; 13% overall prevalence.

Remarks: The Ivory Coast, and particularly the Adiopodoumé region, was extensively explored in the middle of the 20th century (Baer, 1972; Hunkeler, 1974) and again in the 1980s and 1990s (see Mariaux [1994] for a synthesis). This field trip allowed for some complementary collecting in the coastal and southern parts of the country and resulted in the collection of specimens of many taxa fixed appropriately for molecular work (see, e.g., Widmer et al., 2013).

MADAGASCAR (2 expeditions). **October 2013:** Secondary humid forests, east of Antananarivo; Toamasina Region; elevation 900–1,000 m. **December 2014:** Dry forests, Menabe region and Sofia region; elevation 20–50 m. *Base camps:* Sahambaky (-19.07; 48.34), Mahatsara (-18.85; 48.42), Maromizaha (-18.96; 48.47), Ankaraobato (-20.13; 44.64), and Ampombibe III (-15.54; 47.55).

Vertebrates examined: 132 bird specimens of 34 species in 22 families.

Cyclophyllideans encountered: 13 species; 15% overall prevalence.

Remarks: Despite the country's high bird diversity and the well-known high level of endemicity, Malagasy cyclophyllideans have barely been explored and only a dozen species, including some from domestic birds, have been recorded (i.e., Deblock et al., 1962; Rosé and Broussart, 1962; Quentin, 1963; Bona, 1975). Most of the collected specimens represent new taxa, probably endemic to the island.

MALAWI (1 expedition). **October 2009:** Vwaza Marsh Reserve (lowland marsh and plain); elevation 1,100–1,200 m Nyika National Park (highlands); elevation 1,800–2,000 m; both Rumphi District, northern Malawi. *Base camps:* Vwaza Marsh Reserve (-10.88; 33.46) and Nyika National Park (-10.79; 33.80).

Vertebrates examined: 438 bird specimens of 134 species in 28 families; 67 mammal specimens of 16 species in five families.

Cyclophyllideans encountered in birds: Approximately 50 species; 17% overall prevalence.

Cyclophyllideans encountered in mammals: Approximately ten species; 34% overall prevalence.

Remarks: This was the first major study of helminths (including cestodes) of birds and small mammals in Malawi. Rather little knowledge is available on the neighboring countries as well. Avian cestodes included a number of taxa known elsewhere in Africa as well as several putative new taxa. However, new, properly collected specimens of even previously described species provide material for redescriptions needed for many avian cestodes described from Africa. Mammalian cestodes, although not very diverse, have yielded a high level of novelty with one species from shrews already described (Greiman and Tkach, 2012) and additional new species descriptions from shrews and rodents (e.g., *Lophurolepis* sp.) underway. Some known species (e.g., a member of the anoplocephalid genus *Afrobaeria* Haukisalmi, 2008) will be very useful for broader phylogenetic analyses.

MALAYSIA (1 expedition). **August 2010:** Rainforest, including primary patches in northern vicinities of Kuala Lumpur, Selangor; elevation 200–500 m. *Base camp:* Gombak Field Station of the University of Malaya (3.32; 101.75).

Vertebrates examined: 90 bird specimens of 36 species in 14 families.

Cyclophyllideans encountered: 16 species; 19% overall prevalence.

Remarks: This expedition yielded specimens of avian cestodes from Peninsular Malaysia for the first time, which is of key importance due to the current lack of data on this group from Southeast Asian countries in general, the few exceptions being rather ancient (e.g., Burt, 1940a, b).

PERU (1 expedition). **November 2013:** Tropical lowland forests.

Vertebrates examined: 234 bird specimens of 104 species in 26 families.

Cyclophyllideans encountered: Approximately 25 species; 18% overall prevalence.

Remarks: This was the first significant collecting effort targeting cestodes of birds in that region of Peru and essentially in the whole country, especially considering the quality of collected material. Prevalence of cestode infections in birds inhabiting western slopes of the Andes was lower than that in Chile, but somewhat higher than in the Brazilian Amazonian forest obtained during the Gurupi collecting trip. This material includes several new species as well as interesting records of known species (e.g., only the second record of the dilepidid cestode *Arostellina reticulata* Neiland, 1955 in humming birds).

PHILIPPINES (3 expeditions). **May–July 2009:** Luzon Island, Aurora Province. Mostly mountain forests. Aurora Memorial National Park, near Sitio Dimani, elevation 400–600 m (15.70; 121.32); Barangay Casapsipan, Municipality of Casiguran, elevation 1–50 m (16.29; 122.19); Sitio Minoli, Barangay Real, Municipality of San Luis, elevation 600 m (15.68; 121.53); Barangay Lipimental, Municipality of San Luis; elevation 543 m (15.39; 122.19). **July 2011:** Luzon Island. Mostly mountain forests. Mt. Cagua, Barangay Magrafil, Gonzaga City, Cagayan Province, elevation 680 m (18.24; 122.10); Mt. Pao, Ilocos Norte Province, elevation 750 m (18.44; 120.88); Mt. Cabacan, Ilocos Norte Province, elevation 475 m (18.45; 120.90). **August 2013:** Mindoro Island, Sablayan Municipality, Occidental Province. Lowland rain forest and open land around Libuao Lake, elevation 100–200 m (Sablayan Prison and Penal Farm [12.79; 120.92] and Libuao Lake [12.82; 120.90]).

Vertebrates examined: 601 bird specimens of 96 species in 42 families; 324 mammal specimens of 40 species in 12 families.

Cyclophyllideans encountered in birds: Approximately 35 species; 17% overall prevalence.

Cyclophyllideans encountered in mammals: Approximately 20 species; 13% overall prevalence.

Remarks: Specimens collected in the Philippines represent a broad range of cyclophyllidean families. Cestodes of birds include several new species and rare findings of cestodes from doves and sunbirds, which will provide insight into their phylogenetic relationships, evolution, and systematics. Cestodes of small mammals were systematically studied in the Philippines for the first time as previous records contained only reports of *Hymenolepis diminuta* (Rudolphi, 1819) Weinland, 1858 (likely a misidentification) from the Norwegian rat, *Rattus norvegicus* (Berkenhout). We have discovered a rich, highly endemic fauna of cestodes in both rodents and insectivores. The cestode fauna of small mammals was represented by members of the families Hymenolepididae and Davaineidae. All collected cestodes from these hosts turned out to be new species. Remarkably, the Philippines (essentially, two islands of Luzon and Mindanao) yielded greater diversity of *Hymenolepis* Weinland, 1858, a well-known genus with cosmopolitan distribution, than the whole Palearctic and the whole Nearctic biogeographic realms (Makarikov et al., 2013a, b, 2015a). This can be attributed to the highly endemic fauna of hosts, complex landscape, and numerous colonization events due to the appearance of land bridges during periods of low sea level, coincident with glaciation at higher latitudes (Hopkins, 1973). There is no doubt that exploration of additional Philippine islands will allow for discovery of additional, yet unknown, species, and a better understanding of the island biogeography of parasites, as well as complex evolutionary trajectories of cestodes of small mammals in this part of the world.

RUSSIA/KAZAKHSTAN (3 expeditions). **Russian Federation August 2012:** Deciduous forest, Arkharinskiy Raion, Khinganskiy State Nature Reserve; Amurskaya Oblast′; elevation 100 m. **May 2014:** Steppe, Karasukskiy Raion, Novosibirskaya Oblast′; elevation 110 m. **Kazakhstan May 2012:** Semidesert, Ili River, Altyn-Emel State National Natural Park, Almaty Province; elevation 495 m. *Base camps:* Lake Dolgoe (49.37; 129.69); Karasuk Scientific Field Station (53.73; 77.87), Kalkan field station (43.85, 78.74).

Main results: Over 175 mammals, 14 species in four families; 5–25% prevalence; 12 cestode species and larval stages of four species.

Remarks: Collections targeted small mammals. Parts of our investigations were also based on previously collected cyclophyllidean specimens from the East Kazakhstan region and Russia (Novosibirskaya Oblast′, Amurskaya Oblast′ and south of Primorskiy Kray). Even though these localities had been documented by previous authors (e.g., Nadtochii, 1970; Fedorov, 1975, 1986; Shaikenov, 1981) the knowledge of the cestode fauna of mammals from Siberia and RussianFar East needed to be revised. Since many widespread species reported from this area are currently recognized as complexes of cryptic species, the existing data on cestodes do not reflect the actual species diversity. We found at least four species previously not reported from these regions and, at a minimum, three new species.

UGANDA (1 expedition). **March 2013:** Secondary forest and scrub and Dura River forest, Mainaro. Kibale National Park, Western Region, Kamwenge District; elevation 1,200–1,400 m. *Base camp:* Ngogo Research Camp (0.50; 30.43) and (0.36; 30.39).

Vertebrates examined: 224 bird specimens of 59 species in 28 families; 106 mammal specimens of 30 species in six families.

Cyclophyllideans encountered in birds: Approximately 25 species; 22% overall prevalence.

Cyclophyllideans encountered in mammals: Approximately 15 cestode species; 44% overall prevalence.

Remarks: Cestodes of birds were represented by members of several families, while the vast majority of cestodes parasitic in mammals belonged to the Hymenolepididae and the Davaineidae. Some previously unknown species, especially those collected from bats, provided unique morphological and molecular materials. They will significantly improve our understanding of the evolution of these cestode lineages and especially multiple host switching events recently demonstrated in several groups of mammalian cestodes, for instance, within the so-called *Rodentolepis* Spasskii, 1954 clade (Hymenolepididae) (Greiman and Tkach, 2012; Makarikov et al., 2015b)

UKRAINE (1 expedition). **August 2011.**

Vertebrates examined: 109 bird specimens of 52 species in 18 families.

Cyclophyllideans encountered: Approximately 35 species; 41% overall prevalence.

Remarks: These collections were focused on several groups of water birds (mostly Anseriformes, Charadriiformes, Ralliformes) as well as some passerine birds living near water. The Ukraine is a country in which the diversity of avian cestodes was already quite well known. Thus, collecting efforts were focused on taking advantage of the unique opportunity for obtaining of a broad diversity of avian cestodes from European avian hosts. This is important because, historically, a number of cestode genera were initially discovered in Europe but lack molecular vouchers. These taxa are thus important from a phylogenetic standpoint.

USA (Contiguous states). This dataset includes results from several smaller collections in various US states (California, Mississippi, Montana, North Dakota, Oklahoma, and Oregon) and more extensive collections in Texas (2 trips). Details for the trips to Texas are as follows: **September 2014:** Dry scrub forest, cattle pastures near Brackettville, Kinney County, elevation 300–430 m. Plains grassland and pinyon-juniper-oak woodlands near Fort Davis and Sky Mountains, Jeff Davis County, elevation 1,380–1,560 m. *Base camp:* Fort Clark Springs (29.30; -100.42) and Calamity Creek Ranch (30.53; -103.82). **May 2015:** Plains grassland, cattle pastures. Riparian and oak-mesquite-juniper hills near Brackettville, Kinney County, elevation 300–430 m. *Base camp:* Fort Clark Springs (29.30; -100.42) and Tularosa Nueces Ranch (29.48; -100.24).

Main results (Texas): 192 bird specimens of 70 species in 22 families; approximately 20 cestode species, 13% overall prevalence,

Main results (various states): 175 bird specimens of 67 species in 24 families; probably about 40 cestode species, greater than 55% overall prevalence. 144 mammal specimens of 20 species in ten families; approximately 25 cestode species including eight new to science; greater than 41% overall prevalence.

Remarks: In Texas, terrestrial birds were targeted; in the other states, targeted birds mostly belong to aquatic groups. Among the mammals, shrews of the genus *Sorex* L. (Soricidae Fischer) constitute the large majority of this material. Soricid hosts proved to be highly productive from the viewpoint of cestode prevalence, taxonomic diversity, and the number of the new species found. Several new species were found in the cestode genera *Skrjabinacanthus* Spasskii & Morozov, 1959, *Staphylocystoides* Yamaguti, 1952, *Soricinia* Spasskii & Spasskaya, 1954, *Urocystis* Villot, 1880, and *Staphylocystis* Villot, 1877 (see Tkach et al., 2013). All cyclophyllideans of *Sorex* shrews have been brought to North America with shrew hosts that colonized the continent over the Beringian land bridge that existed and disappeared several times in relatively recent geological history (Repenning, 1967; Prost et al., 2013). Despite the overall high similarity between the North American shrew cestodes and their counterparts in the eastern Palearctic at the level of cestode genera, the North American shrews are parasitized by an almost completely endemic cestode fauna at the level of species. This provides a unique opportunity to assess the timing and trends of the process formation of cestode fauna in North American shrews and possibly extrapolate these findings to other regions.

USA (Alaska). June 2011: Arctic tundra and boreal forest, north of Fairbanks, along the Dalton Highway, across the Brooks Range and beyond the Arctic Circle, elevation 100–300 m.

Main results: 17 bird specimens of nine spp. in two families; approximately ten cestode species, 53% overall prevalence. 124 mammal specimens of six species in four families; nine cestode species, 37% overall prevalence.

Remarks: Although all bird cestode species found during this expedition are known species, they constitute important comparative material. On the other hand, cestodes of small mammals, particularly shrews, proved to be highly diverse and little studied. Several new species were found in Alaskan shrews including members of the genera *Staphylocystoides* (e.g., Greiman et al., 2013), *Soricinia*, and a new as-of-yet undescribed genus. We have also found at least one trans-Beringian species of shrew cestodes belonging to the Dilepididae.

VIETNAM (2 expeditions). **June 2014:** Humid tropical forest in Tam Dao National Park. Vin Phuc Province; elevation 900–1,100 m. Dryer tropical forest in Xuan Son National Park. Phu Tho Province; elevation 400–500 m. Humid tropical forest in Cat Ba National Park, Cat Ba Island. Hai Phong Province; elevation 30–100 m. **October–November 2014:** Rainforest in Ba Be National Park, Bac Kan Province elevation 300–800 m. *Base camps:* Tam Dao (21.46; 105.64), Xuan Son (21.12; 104.96), Cat Ba Park headquarters (20.79; 106.99), and Quang Ke Commune (22.35; 105.71).

Vertebrates examined: 67 bird specimens of 22 species in nine families; 51 mammal specimens of ten species in six families.

Cyclophyllideans encountered in birds: Eight species; 21% overall prevalence.

Cyclophyllideans encountered in mammals: Approximately four species; 8% overall prevalence.

Remarks: Our collections focused on various types of protected tropical forests in the north of the country. Early data on the cyclophyllidean diversity of Vietnam were provided by foreign researchers (e.g., Joyeux and Baer, 1935, 1937; Oshmarin and Demshin, 1972). These, and the results of subsequent studies by Vietnamese authors, were provided in two monographic works by Nguyen (1994, 1995). Nevertheless, the knowledge of the cyclophyllidean fauna of the country remains incomplete, and includes much fewer cyclophyllidean taxa than expected given the rich vertebrate fauna of the country. This mostly reflects insufficient taxonomic and geographic coverage of collecting efforts. Nevertheless, several species of cestodes of small mammals were found for the first time in Vietnam. Several cestode species from bats and members of the shrew genus *Suncus* Ehrenberg are very important for phylogenetic inferences linking our richer materials from the Philippines with taxa distributed on continental Eurasia

3.2. Host groups and prevalences

The vast majority of cyclophyllideans use birds and mammals as definitive hosts. Exceptions to this include the Nematotaeniidae, which parasitize amphibians and "reptiles" (see Jones, 1987, 1994), the linstowiine anoplocephalids, some of which parasitize "reptiles" (see Beveridge, 1994), and a small number of records of Gryporhynchidae and Paruterinidae from amphibians and "reptiles" (Georgiev and Kornyushin, 1994; Pichelin et al., 1998). Nonetheless, our PBI project cyclophyllidean collecting efforts focused on birds and mammals, and within both groups we targeted specific taxa.

3.2.1. Birds

With respect to birds, we focused our collecting efforts almost exclusively on terrestrial taxa, mostly Passeriformes; however, some shore and marine birds were collected in Iran, Chile, the Ukraine, and some parts of the USA. All collections were opportunistic and were limited by logistical constraints and the various restrictions imposed by our collecting permits in each country visited. A total of 3,473 specimens consisting of 989 species (or 10% of the known bird diversity) in 122 families and 23 orders was examined across the more than 30 field expeditions conducted. A few additional isolated specimens were obtained opportunistically or through exchanges. Among the bird species examined, 417 (over 40%) were represented by only a single individual; only 41 or 4% were represented by samples of greater than ten specimens (Table 2). With the exception of the ratites and marine bird orders such as the Sphenisciformes and Procellariiformes, at least a few representatives of most terrestrial orders were examined. Among the Passeriformes, only a few important families were not represented, mostly because of their Australasian distribution (e.g., Acanthizidae Bonaparte, Meliphagidae Vigors, Paradisaeidae Vigors, and Petroicidae Mathews). The extent of our sampling in each order and family was, however, highly variable.

Concerning prevalences, in total, 749 individuals (21.6%) of 397 species were parasitized by at least one cyclophyllidean species. Among those, 234 bird species (58.9%) had never been reported to host cestodes prior to the start of the PBI project. These birds are distributed across most orders and about half of the families sampled in this project; the newly recorded hosts are especially numerous in the large Neotropical families Thamnophilidae Swainson (antbirds) and Tyrannidae Vigors (tryrant flycatchers) as well as in the Old World Pycnonotidae Gray (bulbuls) and Muscicapidae Fleming (Old World flycatchers). Other avian families with relatively numerous new host species records include the Cuculidae Vigors (cuckoos), Picidae Vigors (woodpeckers), Hirundinidae Vigors (swallows), Motacillidae Horsfield (wagtails and pipits), and Turdidae Rafinesque (thrushes) (Table 2). Of particular note are the six species of Trochilidae Vigors (hummingbirds) and four species of Nectariniidae Vigors (sunbirds) that were found to host cyclophyllideans, because they confirm that these birds harbor a diverse fauna of cyclophyllideans, despite their nectarivorous diet. Also of note was the single kingfisher (Alcedinidae Rafinesque) in Malaysia found to host cestodes, since the only previous record from this family was from Australia (Johnston, 1909). As expected, the new host records included very few aquatic birds. This is likely because not only are such species broadly distributed, but they have also been more frequently examined. Also not unexpected, was the higher infection prevalence seen in aquatic (Anseriformes, Charadriiformes [except Turnicidae], Gaviiformes, Gruiformes, Pelecaniformes, Podicipediformes, and Suliformes) than in terrestrial (especially Passeriformes) orders of birds (Table 2).

Although the following numbers may differ slightly once our newly collected material is fully identified, it is clear that most parasitized birds (76% in total; 79% in terrestrial birds; 66% in aquatic birds) were infected with a single species of cestode. Infections with two (16%, 15%, 21%), three (4%, 4%, 7%), or four or more cestode species (3%, 3%, 6%) were relatively rare. The latter category comprised two species each of Hirundinidae, Pycnonotidae, and Turdidae as well as one each of Apodidae Hartert (swifts) and Phasianidae Horsfield for terrestrial birds. Most aquatic birds harboring four or more cestode species belonged to the Charadriiformes.

The likelihood of detecting cestodes in a given host species is clearly linked to the number of individuals of that species examined. In terrestrial birds, a plateau of 60–70% of species parasitized (by 1 or more species of cestodes) was reached when over seven individuals of each species were examined. Below that threshold the chance of finding cestodes begins at 28% for a single specimen and increases almost linearly from there. These figures are higher for aquatic birds; the chance of finding cestodes begins at 55% for a single specimen and reaches 90–100% when six or more birds are examined. These data suggest that, globally, it is worth examining a minimum of five to seven specimens of each bird species in any locality in order to maximize the number of infected host species recovered in that area. While four to five specimens may be sufficient for each species of aquatic bird, six to eight specimens per species of terrestrial bird is needed. Larger sample sizes remain preferable in order to detect rare species of tapeworms.

3.2.2. Mammals

With the exception of marsupials (*sensu lato*) in Australia, among mammal hosts, no particular species were targeted. However, for practical reasons, rodents (Rodentia), bats (Chiroptera), and shrews (Soricomorpha) were the most abundant mammals captured during our PBI expeditions. Among the 143 species sampled, 56 (39%) were represented by only a single specimen—a percentage similar to that encountered in birds. However 29 (20%) species were relatively well sampled, with more than ten specimens necropsied of each.

A total of 1,160 mammal specimens belonging to 143 species in 32 families and 14 orders was necropsied over the course of the PBI project (Table 2). In addition, a few isolated specimens were obtained opportunistically or through exchanges. A total of 356 individuals (30.7%) representing 85 mammal species was found to be parasitized by at least one cyclophyllidean species. Among these, 36 (42.4%) were mammal species from which cestodes had not previously been reported. Half of the new host species belong to the Soricidae, while the majority of the others are rodents, mostly Muridae Illiger. Only three of the 40 bat species examined are new hosts of cestodes.

Most infected mammal species (70%) hosted only a single cestode species; infections with two (16%) or three (3%) species were similarly rare as compared to values observed in birds. In contrast, at 11%, infections with four or more species of cestodes were notably higher than seen in birds. This is mostly due to the extremely diverse hymenolepidid fauna found in the Soricidae, especially in the genera *Sorex* and *Crocidura* Wagler, 1832.

Not unexpectedly, as seen in birds, the probability of detecting cestodes in a given species of mammal increases with the number of specimens examined. At 37%, when only a single host specimen was necropsied, the prevalence of overall cestode infection observed was higher in

Table 2. Summary of collections for birds and mammals.

	No. of orders	No. of families	No. of species	No. of specimens	No. of species infected	No. of individuals infected	No. of new hosts for cestodes
BIRDS							
Terrestrial	16	104	866	3,131	307 (35.5%)	577 (17.8%)	229
Aquatic	7	19	123	342	90 (73.1%)	192 (56.1%)	5
Total	23	123	989	3,473	397 (40.1%)	749 (21.6%)	234
MAMMALS							
Total	14	32	143	1,160	85 (59.4%)	356 (30.7%)	36

mammals than in birds. However interordinal variation is high. The Chiroptera, for example, were conspicuously less parasitized than other mammal orders examined. When bats are removed from our calculation, almost all mammal species were found to be parasitized by one or more cyclophyllidean species when six specimens or more were studied.

3.3. Faunal composition and new taxa

3.3.1. Birds

Of all the cyclophyllideans collected over the course of the PBI project, approximately 70% were identified at least to family (Fig. 2A). The Hymenolepididae were the most frequently encountered family comprising 157 (38%) of the 415 identified records (Fig. 2B)—making them the most important family in many country datasets, with a tendency to be more abundant in Africa (Fig. 3B). At present, 17 new species and four new genera have been identified from among our hymenolepidid material (Fig. 3A). The Dilepididae are almost as numerous globally representing 115 (28%) of our identified records (Fig. 2B); that material likely includes six new genera and 18 new species (Fig. 3A). Dilepidids are particularly abundant in the Brazilian sample. Both the Paruterinidae and the Davaineidae are also well represented, although members of the latter family are clearly less abundant in the New World. The Metadilepididae are present in Africa and South America, but were notably absent from our Asian samples and were far less abundant than expected in our identified material overall. Taken together, all seven other cyclophyllidean families encountered represent only 8% of our identified records (Fig. 2B). This was, however, expected given the terrestrial emphasis of our collecting activities because most of these other families are specific to aquatic birds. In contrast, the surprisingly low prevalence of the Anoplocephalidae and the relatively common occurrence of the Mesocestoididae should be noted. In total, our newly collected material includes a minimum of 50 new species from birds (Fig. 3A) that have not yet been described; this figure is likely to increase substantially once all of this material has been examined in detail.

Previous studies in which family faunal compositions have been estimated have focused on particular geographic regions or countries and are thus far more limited than the present work. For example, in Bulgaria, Petrova (1977, 1978) found the Dilepididae to be more numerous than the Hymenolepididae (47% vs. 18% in 1,124 birds, and 44% vs. 22% in 1,200 birds, respectively). A similar result was obtained by Mariaux (1994) from the Ivory Coast with the relative proportion of Dilepididae and Hymenolepididae in the 1,252 bird specimens examined at 36% and 30%, respectively. However, that author also found an unusually high proportion of Metadilepididae (5%). In all three studies, the Paruterinidae, with 11–21%, was the third- or second-most commonly encountered family, and the Davaineidae (8–18%) was the fourth most common family. In contrast, in the 500 birds they examined in the Belgian Congo, Southwell and Lake (1939a, b) found the majority of cestodes to be Hymenolepididae (30%); they also found higher proportions of Paruterinidae and Davaineidae (27% each), and a relatively surprising low proportion of Dilepididae (2%). Most other significant faunal studies have concentrated on aquatic birds and are thus not directly comparable to ours.

3.3.2. Mammals

Representing over 75% of our records, the Hymenolepididae comprised an overwhelming majority of the cyclophyllideans found in mammals over the course of the PBI project (Fig. 4A). It is important to note, however, that this is likely due in part to the high proportion of shrews examined, as well as the fact that shrews host a diversity of hymenolepidids, and the mammal cestode taxonomists involved in the project (i.e., V. V. Tkach and A. Makarikov),

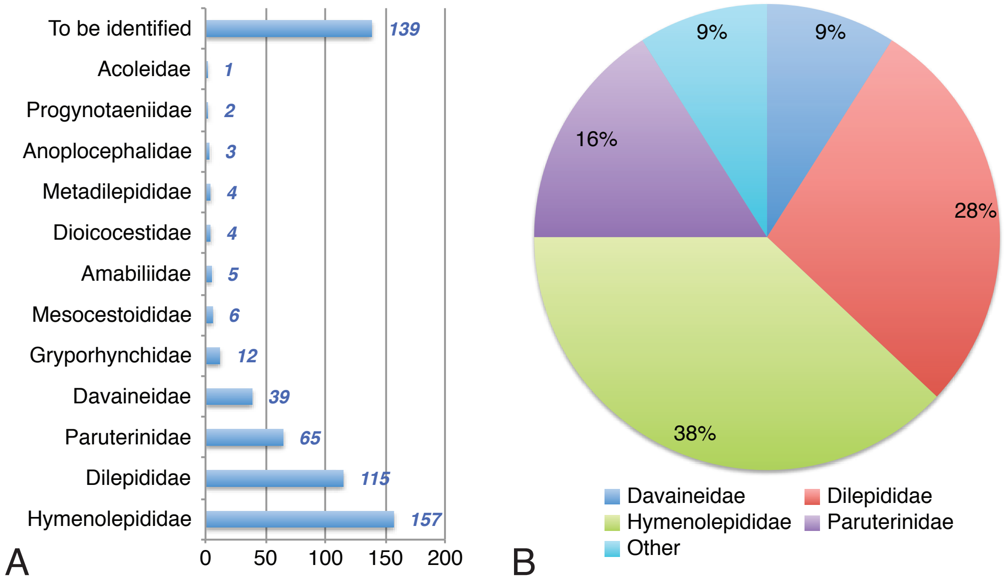


FIGURE 2. Bird cestodes encountered in PBI project collections. **(A)** Number of occurrences per family. **(B)** Relative proportion of cyclophyllidean families.

both have extensive expertise in that family. It is also party due to the fact that some samples of other families have not yet been fully identified. Nevertheless, previous studies have also demonstrated that the species-rich family Hymenolepididae is the primary groups of cestode parasitizing not only the Soricomorpha (see Vaucher, 1971; Genov, 1984), but also, together with the Anoplocephalidae and Catenotaeniidae, rodents overall (Ryzhikov et al., 1978; Genov, 1984; Haukisalmi et al., 2010a, 2014). In the present study, the greatest number of new cestode species discovered in mammals (i.e., more than 50 new species) were hymenolepidids (Fig. 4B). The Anoplocephalidae were also well represented in our material, but were mostly restricted to our samples from Australian marsupials, in which they were already known to dominate the cestode fauna (Beveridge and Jones, 2002). In combination, all other cyclophyllidean families composed only 14% of our records from mammals (Fig. 4A). Although higher numbers of Catenotaeniidae and Davaineidae might have been expected, the poor representation of other families is likely the result of the biased nature of the host taxa targeted here, particularly given the absence and/or underrepresentation of Carnivora and Lagomorpha in our sample.

4. PHYLOGENY

4.1. Overview

Hoberg et al. (1999) provided the first comprehensive family-level phylogenetic analyses of cyclophyllideans in a study based on 42 morphological, ultrastructural, and ontogenetic characters. The resulting trees supported the following affinities. The Mesocestoididae and Nematotaeniidae were sister taxa and together represented the earliest diverging lineage, followed by the Catenotaeniidae. The Metadilepididae and Paruterinidae, as well as the Taeniidae and *Dasyurotaenia* Beddard, 1912 were sister groups, respectively, and together composed a clade. The individual representatives of the four subfamilies of Davaineidae

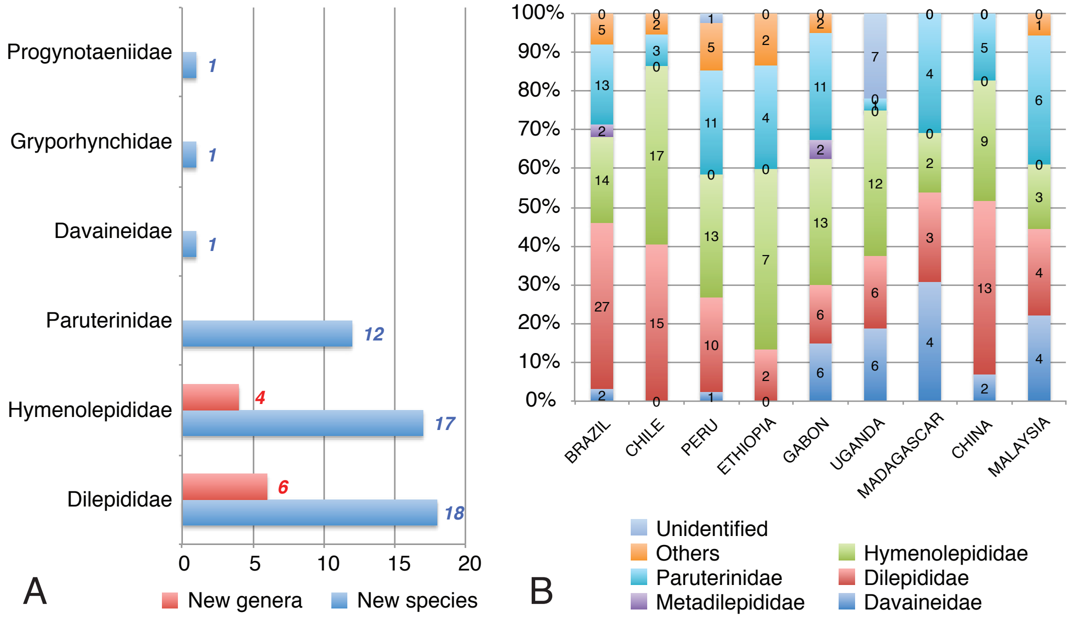


FIGURE 3. Bird cestodes encountered in PBI project collections. **(A)** Number of new species and genera by family. **(B)** Relative proportion of cyclophyllidean families by country (only countries from which a high proportion of cestodes collected were identified are shown).

were recovered as monophyletic. The Hymenolepididae, Amabiliidae, Dioicocestidae, Acoleidae, and Progynotaeniidae represented a clade, in which the latter three families composed a subclade. The Gryporhynchidae and Dipylidiidae were shown to represent independent families. The Anoplocephalidae grouped as two separate, non-related clades (i.e., the Linstowiinae Fuhrmann, 1907 + the Inermicapsiferinae Lopez-Neyra, 1943 and the Anoplocephalinae Blanchard, 1891 + the Thysanosomatinae Skrjabin, 1988). In a subsequent total evidence analysis, Hoberg et al. (2001) found a sister-group relationship between the Dilepididae and the Davaineidae (+ the Amabiliidae), and also between the Hymenolepididae and the Anoplocephalidae. They too found the Catenotaeniidae to be among the earliest diverging cyclophyllidean families. However, as their study was primarily aimed at resolving ordinal-level relationships among cestodes, their taxon sampling only partially covered cyclophyllidean diversity. It is of note that some of these phylogenetic relationships had been predicted by earlier authors on the basis of comparative morphology alone. For example, Spasskii (1951) combined Skrjabin's (1940) suborders Anoplocephalata and Hymenolepidata into a single suborder, and Spasskaya and Spasskii (1971) proposed the superfamily Paruterinoidea, which consisted of the families Paruterinidae and Metadilepididae.

Very few attempts had been made to resolve the phylogenetic relationships within the Cyclophyllidea using molecular sequence data prior to PBI project efforts (see Mariaux and Olson, 2001 for a summary)—a fact that is at least partly due to a lack of suitable molecular markers (Littlewood et al., 2008). Von Nickisch-Rosenegk et al. (1999) were the first to generate a molecular phylogenetic hypothesis specifically for the order. Their taxon sampling was, however, very limited and highly biased towards the Taeniidae. Furthermore, their analysis was based on only a very short fragment (314 bp) of the small mitochondrial

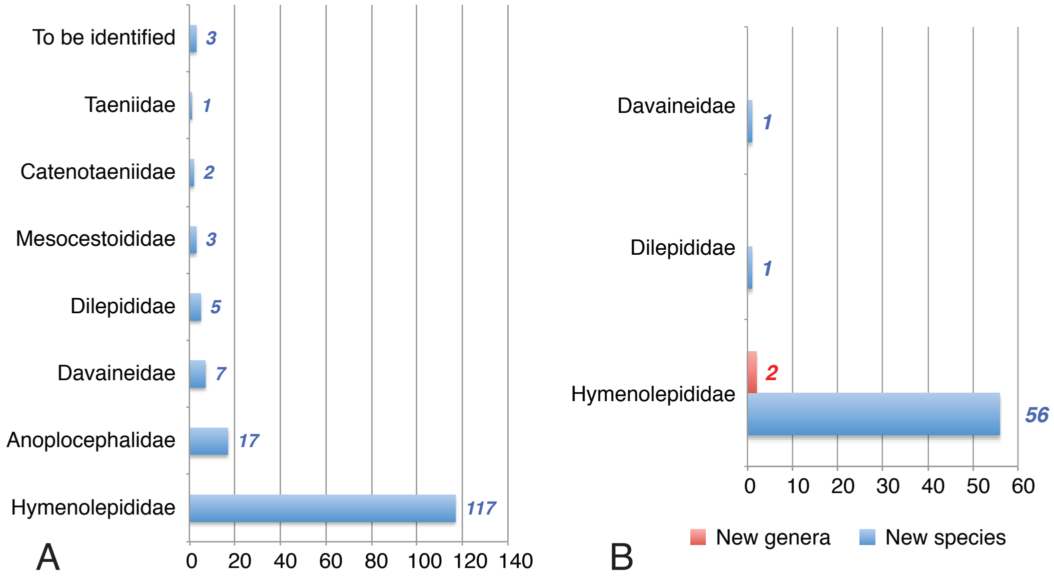


Figure 4. Mammal cestodes encountered in PBI project collections. **(A)** Number of occurrences by family. **(B)** Number of new species and genera by family.

ribosomal RNA subunit (12S rRNA), which may explain why most nodes in the resulting tree were not strongly supported. Mariaux's (1998) phylogeny, which was based on sequence data generated for the small subunit nuclear ribosomal RNA gene (18S rDNA), included a variety of cyclophyllideans, but was designed to study the phylogenetic structure of the class, and thus it too included representation of only a subset of cyclophyllidean families. Nonetheless, the monophyly of all families represented, including the Gryporhynchidae, and the sister-group relationship of Hymenolepididae and Anoplocephalidae were supported in that work. Subsequent major efforts in the field (e.g., Olson and Caira, 1999; Waeschenbach et al., 2007) also included limited representation of cyclophyllidean diversity and thus provide little insight into the phylogenetic relationships in the order overall.

4.2. PBI taxon coverage

Largely as a result of PBI-funded collecting expeditions, which were complemented by a few additional specimens obtained from various other sources, molecular data were generated for a total of 318 cyclophyllidean specimens from across the globe (i.e., Australia, Brazil, Bulgaria, Chile, China, Czech Republic, Ethiopia, France, Gabon, Guyana, Iran, Jordan, Malawi, Malaysia, Philippines, Russia, Slovakia, Sudan, Taiwan, Ukraine, USA, and Vietnam; see Section 3). The following four genes were targeted: small subunit nuclear ribosomal RNA (18S rDNA), partial large subunit nuclear ribosomal RNA (28S rDNA), partial large mitochondrial ribosomal RNA subunit (16S rDNA), and partial cytochrome *c* oxidase subunit I (COI). Sequence data for these genes were generated for 300, 296, 286, and 291 specimens, respectively (see Chapter 22 this volume). The concatenated alignment included representatives of the following 15 cyclophyllidean families (numbers in parentheses indicate the number of specimens and percent of known species diversity per family represented by these specimens): Acoleidae (1; 10%), Amabiliidae (2; 8%), Anoplocephalidae (12; 3%), Catenotaeniidae (4; 13%), Davaineidae

(39; 8%), Dilepididae (73; 10%), Dioicocestidae (9; 43%), Dipylidiidae (1; 7%), Gryporhynchidae (14; 16%), Hymenolepididae (111; 13%), Mesocestoididae (3; 10–20%), Metadilepididae (2; 13%), Paruterinidae (34; 28%), Progynotaeniidae (5; 14%), and Taeniidae (4; 8%).

4.3. PBI phylogenetic hypotheses

The molecular phylogeny generated as a result of the PBI project (see Fig. 5 for a schematic) is the most comprehensively sampled phylogeny of cyclophyllidean tapeworms to date. Unfortunately, the data from the four genes employed here do not provide sufficient signal to offer a well-resolved backbone to the phylogeny, nor do they unambiguously support the monophyly of the Davaineidae, the Paruterinidae + Metadilepididae + Taeniidae, the Dilepididae, and the Hymenolepididae + Anoplocephalidae. However, close relationships between the Progynotaeniidae + Acoleidae + Gyrocoeliinae Yamaguti, 1959, as well as between the Amabiliidae + Dioicocestinae were supported. Subfamilial components of the Anoplocephalidae (i.e., Linstowiinae vs. Anoplocephalinae) were shown to be unrelated confirming the non-monophyly of the family. In general, relationships towards the tips (not shown) of the phylogeny are more well-resolved than those of the deeper nodes. These relationships will be the subject of a later publication in which the backbone of the phylogeny will be based on almost complete mitochondrial genome sequences from 38 lineages across the Cyclophyllidea.

5. FAMILY SUMMARIES AND DISCOVERIES RESULTING FROM THE PBI PROJECT

This section outlines the history and diagnostic features of each of the 16 currently recognized cyclophyllidean families. In each case, novel insights gained over the course of the PBI project are also summarized. Information on life-cycles was retrieved from the literature and from the Cestode Life Cycle database of Lefebvre et al. (2009a) (see Lefebvre et al., 2009b).

5.1. Acoleidae Fuhrmann, 1899

Fuhrmann (1899) proposed the family Acoleidae for two newly erected genera, *Acoleus* Fuhrmann, 1899 and *Gyrocoelia* Fuhrmann, 1899; he based this decision mostly on the absence of a vagina and presence of the strobilar musculature consisting of two longitudinal and three transverse muscle layers. In a subsequent paper, Fuhrmann (1900) added the genera *Dioicocestus* Fuhrmann, 1900 and *Diplophallus* Fuhrmann, 1900 and demoted the group to a subfamily within the Taeniidae. He later reinstated family status for this taxon (Fuhrmann, 1907). In 1932, the same author considered eight genera to be part of the family, adding *Leptotaenia* Cohn, 1901, *Progynotaenia* Fuhrmann, 1909, *Proterogynotaenia* Fuhrmann, 1911, and *Shipleyia* Fuhrmann, 1907. Southwell (1930) erected the Dioicocestidae Southwell, 1930 for dioecious forms. After further study, Fuhrmann (1936) erected the Progynotaeniidae for the proterogynous forms. The validity of the Acoleidae is now generally accepted (Skrjabin, 1940; Yamaguti, 1959; Ryzhikov and Tolkacheva, 1981; Schmidt, 1986; Khalil et al., 1994).

The Acoleidae is one of the families of the suborder Acoleata Skrjabin, 1940 (together with the Progynotaeniidae, Amabiliidae, and Dioicocestidae) and includes cestodes that lack a vaginal pore (and vagina altogether) and reproduce by traumatic copulation (i.e., the cirrus penetrates through the body surface and strobilar parenchyma, and ejaculates sperm directly into the seminal receptacle). The current concept of the Acoleidae is that it includes cestodes that lack a vagina, are hermaphroditic (vs. Dioicocestidae), protandrous (vs. Progynotaeniidae), and that lack canals connecting the seminal receptacles of neighboring

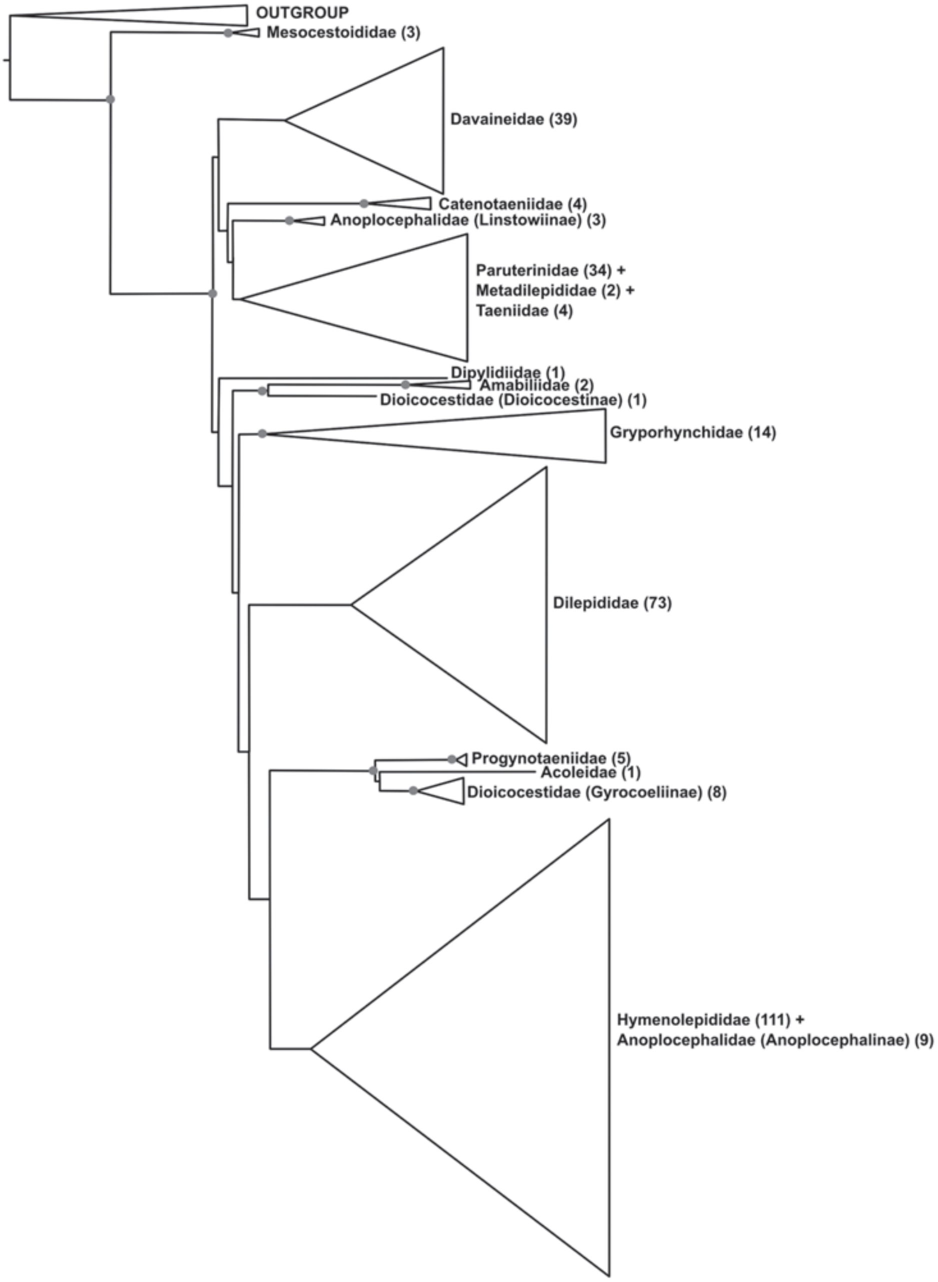


FIGURE 5. Diagrammatic representation of the PBI project cyclophyllidean phylogeny based on a concatenated dataset of small and large subunits nuclear ribosomal RNA (18S rDNA and 28S rDNA), large mitochondrial ribosomal RNA subunit (16S rRNA), and cytochrome c oxidase subunit I (COI) (number of terminals are given in parentheses for each family). Nodal support (≥ 0.95 posterior probability), as inferred from a Bayesian inference analysis using MrBayes 3.2.1 using the GTR+I+Γ model of nucleotide evolution, is indicated with gray dots.

proglottids (vs. Amabiliidae). Acoleids have strong, heavily armed cirri (Fig. 6B), and their scolex bears an armed or unarmed (Fig. 6A) rostellum. Only two genera, *Acoleus* (with a single set of male genital organs per proglottid; 3 species) and *Diplophallus* (with 2 sets of male genital organs per proglottid; 2 species) are now recognized in the family (Ryzhikov and Tolkacheva, 1981; Khalil, 1994a). Their host associations include charadriiform and, rarely, gruiform (rallid) birds (Ryzhikov and Tolkacheva, 1981). Both genera are cosmopolitan in distribution (Khalil, 1994a). No life-cycle is known (Beveridge, 2001).

Discoveries over the course of the PBI project. Only a single species of this group—an unidentified species of *Diplophallus* from *Recurvirostra americana* Gmelin in the USA—was collected over the course of PBI expeditions. A specimen of *Diplophallus polymorphus* (Rudolphi, 1819) Fuhrmann, 1900 from *R. americana*, collected from the USA on a pre-PBI expedition, was included in the molecular phylogenetic analyses. These analyses revealed a close relationship between acoleids, progynotaeniids, and the Gyrocoeliinae (all parasitic in Charadriiformes). However, our results indicate that this clade is only distantly related to a clade of grebe cestodes (i.e., Dioicocestinae plus several amabiliids), suggesting that the suborder Acoleata is polyphyletic.

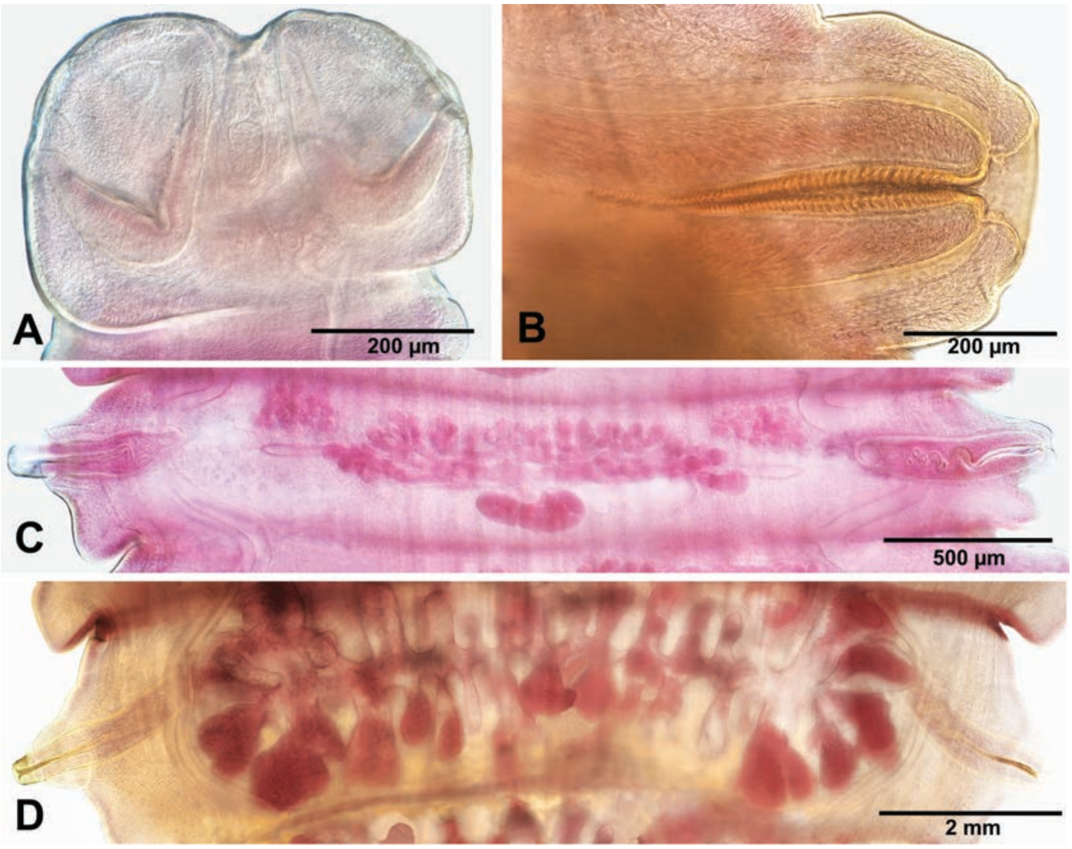


Figure 6. ACOLEIDAE: *Diplophallus andinus* from *Himantopus himantopus* from Paraguay. **(A)** Scolex. **(B)** Partly evaginated cirrus. **(C)** Mature proglottid. **(D)** Pre-gravid proglottid.

5.2. Amabiliidae Braun, 1900

This group was originally erected as a subfamily within the Taeniidae by Braun (1900). Fuhrmann (1907) subsequently raised it to the rank of family. Two subfamilies were erected by Johri (1959)—the Amabiliinae Braun, 1900 for *Amabilia* Diamare, 1893 and the Schistotaeniinae Johri, 1959 for *Schistotaenia* Cohn, 1900 and *Tatria* Kowalewski, 1904. Ryzhikov and Tolkacheva (1975) added a third subfamily, the Diporotaeniinae Ryzhikov & Tolkacheva, 1975, for *Diporotaenia* Spasskaya, Spasskii & Borgarenko, 1971. These three subfamilies were recognized by Ryzhikov and Tolkacheva (1981) but were not considered valid by Schmidt (1986) or Jones (1994a). The monophyly of the family has been called into question (Spasskii, 1992a; Gulyaev et al., 2010). In the taxonomic revision proposed by Spasskii (1992a), the family Amabiliidae included only *Amabilia*, a parasite of flamingos because he transferred all of the remaining genera, which parasitize grebes, to the family Schistotaeniidae, with the two subfamilies Schistotaeniinae and Diporotaeniinae. Spasskii (1992a) regarded the Amabiliidae and the Schistotaeniidae as sister taxa within the superfamily Amabilioidea. However, his rearrangement of the Amabiliidae has not been tested in a phylogenetic context and has not been generally accepted.

The main morphological characters of importance for identification of members of this family are the lack of a true vagina, the lack of a vaginal pore, the presence of an external seminal vesicle, and the presence of accessory or supplementary seminal ducts associated with the female reproductive organs (Fig. 7D). Copulation is traumatic and the cirrus is often destroyed in the process of copulation. A common accessory vaginal duct is not present in *Amabilia* and its presence in the Schistotaeniinae and the Diporotaeniinae (Gulyaev et al., 2010) appears to be a synapomorphy supporting the sister taxon status of these two subfamilies, as suggested by Spasskii (1992a). Amabiliids share the presence of an external seminal vesicle with the Hymenolepididae. They also typically have a scolex with a sac-like rostellar apparatus armed with a single row of rostellar hooks (Fig. 7A).

The host associations of the Amabiliidae, as adults, include aquatic birds of the order Phoenicopteriformes (*Amabilia*) and Podicipediformes (all 10 remaining amabiliid genera) (Ryzhikov and Tolkacheva, 1981; Jones, 1994a; Vasileva et al., 2003a, b; Gulyaev et al., 2010).

Life-cycles are known for seven amabiliid species parasitic in grebes. All seven have two-host life-cycles that include insect intermediate hosts of the orders Odonata, Ephemeroptera, or Hemiptera. The larval stage found in the intermediate host is a modification of the cysticercoid referred to as an "ascocercus" by some authors (e.g., Gulyaev, 1989). Chervy (2002), however, considered the "ascocercus" to be a synonym of the diplocysticercoid stage.

The geographical distribution of the family is cosmopolitan, coinciding with those of flamingos and grebes (Ryzhikov and Tolkacheva, 1981; Jones, 1994a).

Currently, the family houses 11 genera and 32 species. Major taxonomic works dealing with this family are those by Ryzhikov and Tolkacheva (1981) and Jones (1994a). Several papers present taxonomic revisions of the genera *Tatria* and *Joyeuxilepis* Spasskii, 1947 (see Gulyaev and Tolkacheva, 1987; Borgarenko and Gulyaev, 1990; Gulyaev, 1990, 1992; Vasileva et al., 2003a–d).

Discoveries over the course of the PBI project. Specimens of this family were collected in the USA from five species of grebes (Podicipedidae Bonaparte). These represented three genera and six species of cestodes. Two species from other sources (i.e., *Ryjikovilepis* sp. from *Podiceps nigricollis* Brehm, 1831 in the USA and *Schistotaenia colymba* Schell, 1955 from the same host species in the Ukraine) were incorporated into our molecular phylogenetic analyses. This allowed assessment of the position of the Schistotaeniinae and the Diporotaeniinae within the

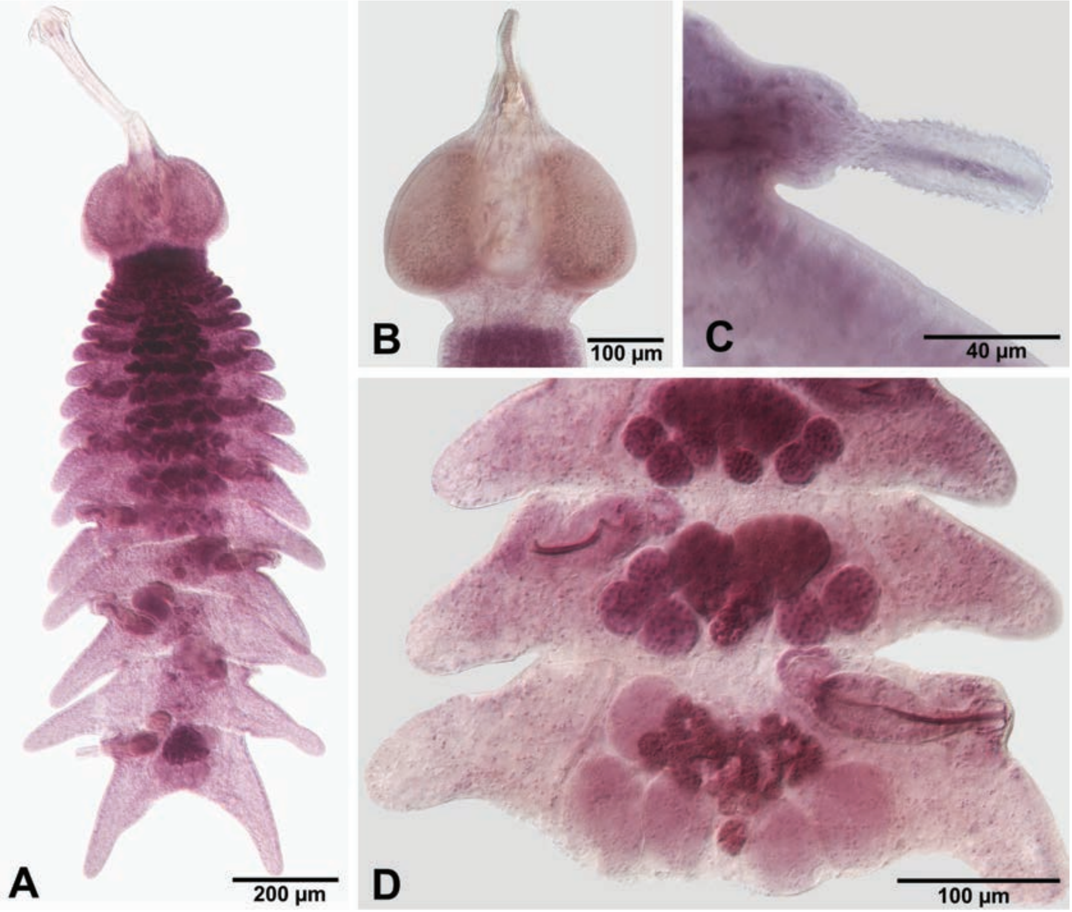


FIGURE 7. AMABILIIDAE: *Tatria biremis* from *Podiceps nigricollis* from Bulgaria. **(A)** Whole worm. **(B)** Scolex. **(C)** Evaginated cirrus. **(D)** Mature proglottids.

phylogeny of the Cyclophyllidea for the first time. In the context of our limited sampling of amabiliid genera, our results support a sister taxon relationship between these two genera. Furthermore, the sister group to the Amabiliidae appears to be the Dioicocestinae, while the Progynotaeniidae, Acoleidae, and Gyrocoeliinae grouped away from this clade.

5.3. Anoplocephalidae Blanchard, 1891

This family was erected by Blanchard (1891) (not Cholodkowsky, 1902 as erroneously reported by Spasskii [1951] and Beveridge [1994]) for cestodes lacking a rostellum, although species lacking such an organ also exist in the Davaineidae, Dilepididae, and Hymenolepididae. Because this character is obviously homoplasious, it has been recognized for some time that the family is almost certainly a polyphyletic assemblage. This view is reinforced by differences in proglottid anatomy (i.e., uterine structure) and life-cycles (Beveridge, 1994; Chervy, 2002).

Four subfamilies are currently recognized. The main morphological characters of importance for distinguishing among them are the single or double set of reproductive organs per proglottid (Fig. 8B), the structure of the uterus (with a paruterine organ in the

Thysanosomatinae), the presence of eggs in the uterine (Linstowiinae) or fibrous capsules (Inermicapsiferinae), and the unique modification of the egg envelopes into a pyriform apparatus (most Anoplocephalinae).

Anoplocephalids are primarily parasites of mammals (all 4 anoplocephalid subfamilies), birds (subset of Anoplocephalinae) and "reptiles" (subset of Linstowiinae). With the exception of the Inermicapsiferinae, which are restricted to Asia and Africa (Beveridge, 1994), the family is cosmopolitan. All known life-cycles involve two hosts. The intermediate host of the cysticercoids of anoplocephalines is usually an oribatid mite, whereas the linstowiines usual develop as precysticerci in coleopterans. Insects of the order Psocoptera (booklice or barklice) have been identified as intermediate hosts of the Thysanosomatinae (Chervy, 2002).

Major taxonomic works treating representatives of this family are those by Baer (1927), Spasskii (1951), and Beveridge (1994). Two principal systems of classification have been proposed. Spasskii (1951) utilized the suborder Anoplocephalata Skrjabin, 1933 with the families Anoplocephalidae (subfamilies Anoplocephalinae and Monieziinae Spasskii, 1951), Avitellinidae Spasskii, 1950 (subfamilies Avitellininae Gough, 1911 and Thysanosomatinae Fuhrmann, 1907), Linstowiidae Mola, 1929 (subfamilies Linstowiinae and Inermicapsiferinae), and Catenotaeniidae Spasskii, 1950. Yamaguti (1959), basing his classification on that of Fuhrmann (1907), recognized the single family, Anoplocephalidae, with five subfamilies: the Anoplocephalinae, Linstowiinae, Inermicapsiferinae, Thysanosomatinae (which included the Avitellininae), and the Rajotaeniinae Yamaguti, 1959. Beveridge (1994) recognized only the first four of the above subfamilies: the Anoplocephalinae, with a tubular uterus and a pyriform apparatus surrounding the embryo; the Linstowiinae with eggs surrounded by uterine capsules and scattered in the parenchyma; the Thysanosomatinae with paruterine organs; and the Inermicapsiferinae with fibrous egg capsules resembling those of davaineids. Beveridge (1994) also noted that the family Anoplocephalidae was clearly a non-monophyletic assemblage based not only on morphological but also on known life-cycle data, however molecular support was lacking. The Rajotaeniinae are now considered a synonym of the Skrjabinotaeniinae Genov & Tenora, 1979 within the Catenotaeniidae.

Discoveries over the course of the PBI project. Only three anoplocephalid species from birds, all in Africa, were found over the course of the PBI project expeditions. One of these has not yet been identified to species. In mammals, four species were collected from African rodents and one species from dermopteran mammals in the Philippines. Most of the newly collected material of this family came from Australian marsupials (10 cestode species); all of these specimens represent known species. In addition, a single species of the Linstowiinae, *Oochoristica fibrata* Meggitt, 1927, was collected from the colubrid snake *Boiga trigonata melanocephala* (Annandale) in the vicinity of Minab, southern Iran.

The most significant development of the PBI project has been the first molecular evidence confirming the non-monophyly of the Anoplocephalidae—more specifically, our phylogenetic results show that the Linstowiinae (represented by 3 species) and the Anoplocephalinae (represented by 9 species) are phylogenetically only distantly related (see Fig. 5). The Anoplocephalinae, as expected on the basis of larval development and the presence of true seminal vesicles, cluster with the Hymenolepididae (albeit with low nodal support), while the Linstowiinae cluster with the Paruterinidae, Metadilepididae, and Taeniidae (also with low nodal support). Although these results conform to those of previous morphological and life history work, the poorly supported nodes require resolution from mitogenome and other additional molecular data. No representatives of the Thysanosomatinae or Inermicapsiferinae were available for these analyses.

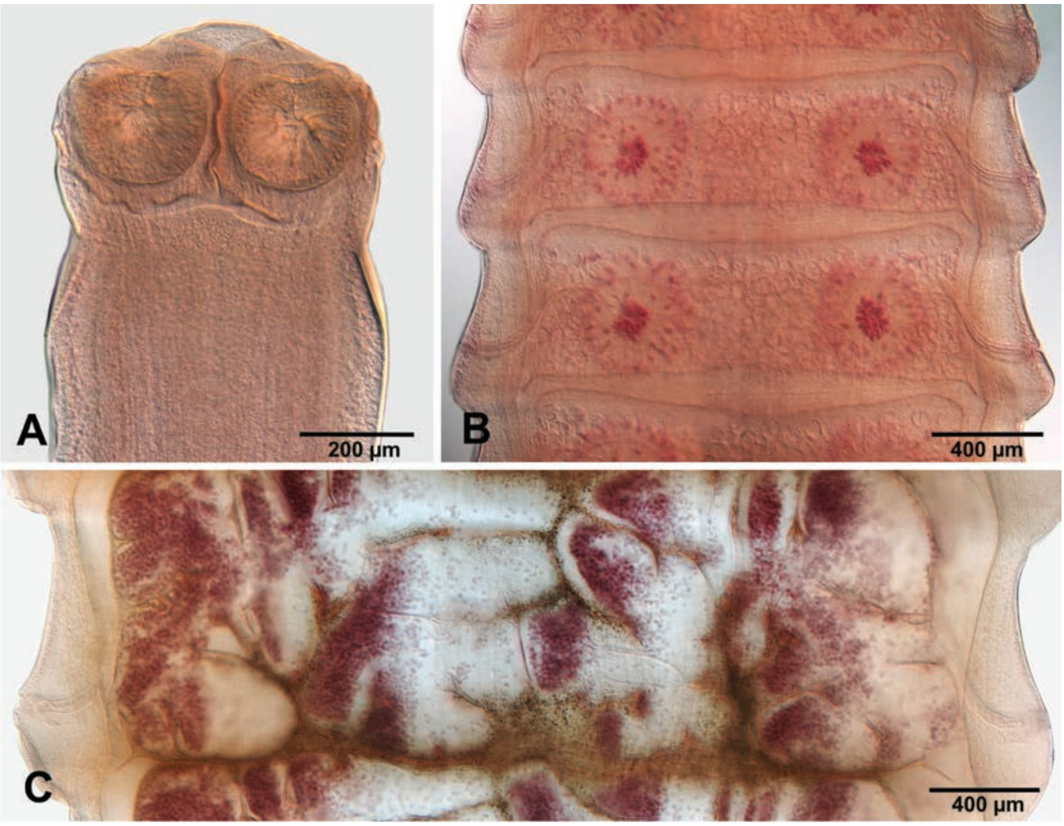


FIGURE 8. ANOPLOCEPHALIDAE: *Bulbultaenia calcaruterina* from *Pycnonotus tricolor* from Gabon. **(A)** Scolex. **(B)** Mature proglottids. **(C)** Pre-gravid proglottid.

Also resulting from the PBI project was the molecular phylogenetic study of Australian anoplocephalines by Hardman et al. (2012), which provided a firm molecular basis for a slightly revised generic arrangement of the subfamily. *Progamotaenia* Nybelin, 1917 was shown to be polyphyletic, resulting in the resurrection of *Wallabicestus* Schmidt, 1975; the other genera into which species of *Progamotaenia* had variously been placed (i.e., *Hepatotaenia* Nybelin, 1917, *Fuhrmannodes* Strand, 1942, and *Adelataenia* Schmidt, 1986) were not supported and are retained as synonyms. This study also showed that the single species in each genus occurring in wombats (Diprotodontia: Vombatidae) (i.e., *Phascolotaenia* Beveridge, 1976 and *Paramoniezia* Maplestone & Southwell, 1923) comprised a monophyletic group, prompting a review of *Paramoniezia* in general. In this review, Beveridge (2014) erected the new genus *Phascolocestus* Beveridge, 2014 for the only species formerly assigned to *Paramoniezia* found in wombats. The remaining valid species, *Paramoniezia phacochoeri* Baylis, 1927, found in African warthogs, was transferred to *Moniezia* Blanchard, 1891.

Haukisalmi and colleagues contributed substantially to the generic diversity of the anoplocephalids over the course of the PBI. In 2013, Haukisalmi erected two new genera (*Afrojoyeuxia* Haukisalmi, 2013 and *Hunkeleriella* Haukisalmi, 2013) for cestodes parasitizing African rodents and proposed two new combinations. Furthermore, he led a revision of the rather diverse and heterogeneous genus *Paranoplocephala* Lühe, 1910 from rodents based on morphological and molecular analyses (Haukisalmi et al., 2014). In that work, 12 additional new genera (i.e., *Arctocestus*, *Beringitaenia*, *Chionocestus*, *Cookiella*, *Douthittia*, *Eurotaenia*, *Gulyaevia*, *Lemminia*, *Microticola*, *Rauschoides*, *Rodentocestus*, and *Tenoraia*, all with authorship by Haukisalmi, Hardman, Hoberg & Henttonen, 2014) were erected and 23 new combinations were proposed. In addition, the new species *Beringitaenia nanushukensis* Haukisalmi, Hardman, Hoberg & Henttonen, 2014 from the singing vole, *Microtus miurus* Osgood was described. Several additional lineages, likely representing yet other independent species and genera, were identified, but not formally described because of the lack of good-quality specimens and/or absence of reliable morphological differences. Most recently, Haukisalmi et al. (2016) presented the results of phylogenetic and phygeographic analyses focused on members of the genus *Anoplocephaloides* from lemmings in the Holarctic.

At present, about 480 species in 81 genera are known in the family (Table 2); these consist of 258 species in 59 genera of Anoplocephalinae, 171 species in 13 genera of Linstowiinae, 27 species in four genera of Inermicapsiferinae, and 21 species in five genera of Thysanosomatinae.

5.4. Catenotaeniidae Spasskii, 1950

Spasskii (1950) erected the Catenotaeniidae for two genera previously assigned to the Anoplocephalidae (i.e., *Catenotaenia* Janicki, 1904 and *Skrjabinotaenia* Akhumyan, 1946) and confirmed this action in the first monographic treatment of the family (Spasskii, 1951). Subsequent studies added further species and genera. Currently, the family is subdivided into two subfamilies, the Catenotaeniinae Spasskii, 1950, characterized by two pairs of lateral osmoregulatory canals and testes situated posteriorly to the ovary, and the Skrjabinotaeniinae Genov & Tenora, 1979, characterized by numerous osmoregulatory canals and testes surrounding, at least posteriorly, the ovary (Genov and Tenora, 1979). Quentin (1994) recognized four genera in the Catenotaeniinae and two genera in the Skrjabinotaeniinae and provided emended diagnoses for each. Haukisalmi et al. (2010a) added one further genus to the former subfamily. Currently, the family consists of six genera and 36 species, 20 of which are members of the Catenotaeniinae (see Schmidt, 1986; Haukisalmi and Tenora, 1993; Haukisalmi et al., 2010a; Jrijer and Neifar, 2014).

Morphologically, catenotaeniids are diagnosed by their possession of a uterus consisting of a longitudinal stem with lateral branches (Fig. 9C), similar to that seen in the Taeniidae. Their scolex bears only suckers (Fig. 9A)—a rostellar apparatus is lacking, but adults occasionally have a vestigial "apical sucker" that appears to be a remnant of the apical organ of the metacestode.

Catenotaeniids are parasites of rodents, and specifically the families Sciuridae, Muridae, Heteromyidae Gray, Geomyidae Bonaparte, Dipodidae Fischer de Waldheim, and Caviidae Fischer de Waldheim. The geographic distribution of the family includes all continents except Australia (Quentin, 1994). Species diversity in the Catenotaeniinae peaks in cricetid rodents in the Holarctic region; species diversity in the Skrjabinotaeniinae peaks in murid rodents in Africa. The only South American species, *Quentinia mesovitellinica* (Rego, 1967) Quentin, 1994, from caviids, is morphologically divergent and its taxonomic position should be reconsidered.

The life-cycle of only one species, *Catenotaenia pusilla* (Goeze, 1782) Janicki, 1904, a common parasite of the house mouse, was described by Joyeux and Baer (1945). Tyroglyphid mites were reported to serve as intermediate hosts for its metacestode, which is a merocercoid that bears a large apical organ ("apical sucker") but no true suckers. The final stage of scolex development, which involves degeneration of the apical organ and differentiation of four suckers, is completed in the mouse definitive host.

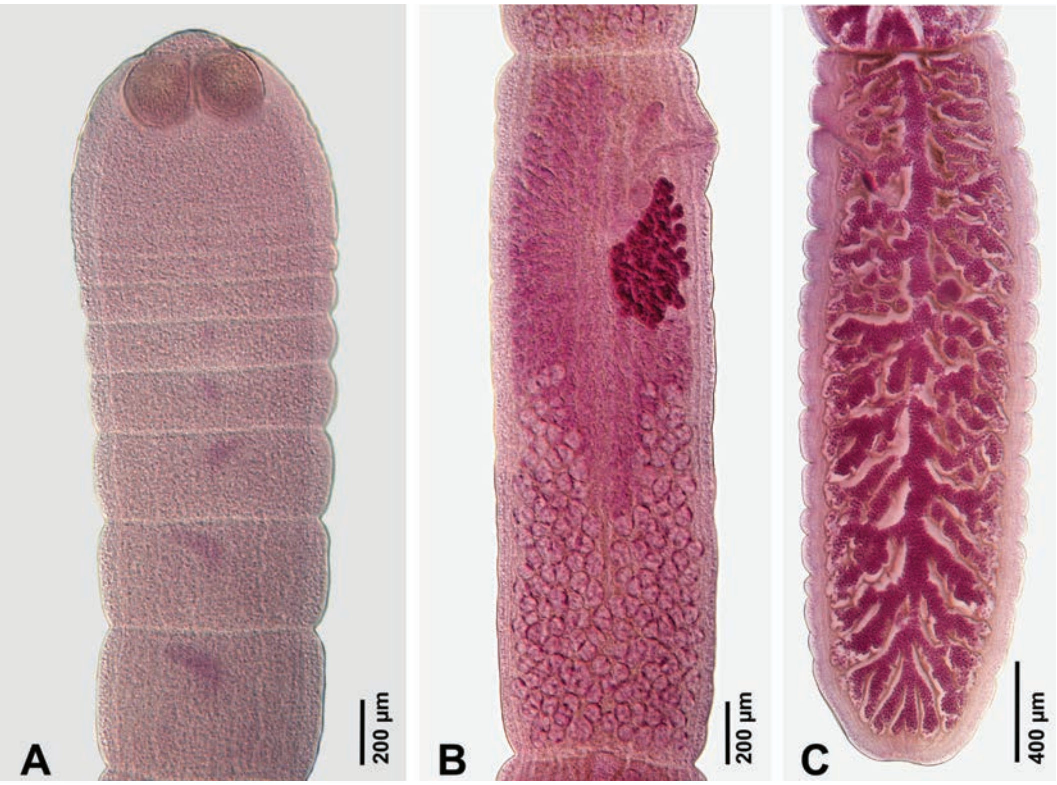


FIGURE 9. CATENOTAENIIDAE: *Catenotaenia indica* from *Tatera indica* from Iran. **(A)** Scolex. **(B)** Mature proglottid. **(C)** Gravid proglottid with branched uterus.

Discoveries over the course of the PBI project. One species of catenotaeniid (i.e., *Catenotaenia indica* Parihar & Nama, 1977) was collected from *Tatera indica* (Hardwicke) (Muridae: Gerbillinae) in Iran. Additional members of this family may be present in our unsorted samples of cestodes from rodents. A total of three species was included in our molecular phylogenetic analyses. The resulting tree supports the monophyly of the family as the sister of a clade composed of the Taeniidae, Paruterinidae, Metadilepididae, and Linstowiidae (albeit with low nodal support). However, these results require confirmation given the limited nature of our taxon sampling across the family.

5.5. Davaineidae Braun, 1900

This taxon was originally erected by Braun (1900) as a subfamily of the Taeniidae and then elevated to family status by Fuhrmann (1907) for those cyclophyllideans with a rostellum bearing numerous small hammer-shaped rostellar hooks, armed or unarmed suckers, and single or double genital systems per proglottid. Fuhrmann (1907) subdivided the family into three subfamilies: the Ophryocotylinae Fuhrmann, 1907 (for cestodes with a sac-like uterus), the Davaineinae Braun, 1900 (for cestodes with a uterus that, with maturity, breaks down into parenchymatous capsules, each containing 1 or several eggs), and the Idiogeninae Fuhrmann, 1907 (for cestodes with a uterus in the form of a paruterine organ). Additional key morphological features for identification of the Davaineidae include the number of rostellar hook rows, the duplication (or not) of genitalia, the position of the genital pores (unilateral or alternating), the number and position of the testes, the number of osmoregulatory canals, and the structure of gravid proglottids (Jones and Bray, 1994). Davaineids have a unique rostellar apparatus (Fig. 10A) consisting of a discoidal rostellum and a protrusible thick ring encircling the apical part of the scolex immediately posterior to the rostellum, termed the "pseudoproboscis" (see Stoitsova et al., 2001). Scale-like spines (considered to be spinitriches by Chervy et al. [2009]) on the pseudoproboscis (Fig. 10B) may be a synapomorphy for the family (Bâ et al., 1995).

Davaineids parasitize most bird orders (especially terrestrial birds) and many mammals, including marsupials, rodents, bats, primates, and others (Jones and Bray, 1994). Life-cycles are known for approximately 30 species (Artyukh, 1966; O'Callaghan et al., 2003). Davaineids have a single intermediate host that is typically an annelid, gastropod, or insect. Ants have been identified as intermediate hosts of davaineids parasitizing poultry. The larval stage is a cysticercoid (Chervy, 2002). The geographic distribution of the family is cosmopolitan; they are found mostly in terrestrial habitats, rarely in freshwater, or marine environments (Artyukh, 1966; Jones and Bray, 1994).

Major taxonomic works treating this family were published by Artyukh (1966), Schmidt (1986), Jones and Bray (1994), and Movsesyan (2003a, b). Subdivision of the family in two subfamilies is currently widely accepted; these are the Davaineinae (without a paruterine organ) and the Idiogeninae (with a paruterine organ). Some (e.g., Schmidt, 1986), but not all (e.g., Jones and Bray, 1994) authors also recognize the Ophryocotylinae, which differ from the Davaineinae in the presence of a persistent uterus, rather than a uterus that is replaced by a paruterine organ. Alternative classification schemes have been proposed by Russian authors. Artyukh (1966) recognized the Davaineidae and the Idiogenidae as distinct families; the former being subdivided into the Davaineinae and the Ophryocotylinae. Movsesyan (2003a, b) recognized three distinct families, all in the suborder Davaineata Skrjabin, 1940: the Davaineidae, with the subfamilies Davaineinae (for cestodes bearing a single set of genital organs per proglottid) and the Cotugniinae Movsesyan, 1969 (for cestodes with double sets of genital organs per proglottid), the Ophryocotylidae (using a much wider concept than previous authors), and the Idiogenidae. At present, 37 genera and 450 species are recognized in the family (Jones and Bray, 1994; Movsesyan, 2003a, b) (Table 1).

Jones and Bray (1994) considered the family, in its present form, to be polyphyletic. This was not supported by the work of Hoberg et al. (1999) who reached the opposite conclusion and favored its monophyly.

Discoveries over the course of the PBI. Davaineids were collected from 16 bird families from 12 countries, on all continents. They were notably absent from our Ethiopian and Chilean samples. The Pycnonotidae were found to host the highest diversity of davaineids, but davaineids were also well represented in the Piciformes (Picidae and Rhamphastidae Vigors) and Columbiformes. No members of the Idiogeninae were collected. Nine of the bird species hosting davaineids represent new host records for cestodes overall.

Our new collections included seven records of davaineids from mammals; six of these were from the Muridae and one was from the sciurid *Funisciurus pyrrhopus* (Cuvier) (a new host for cestodes) in Uganda. In total, over 30 species of at least four genera were collected. Our preliminary taxonomic work indicates the presence of at least two new species of *Raillietina*, one in birds and one in mammals.

Thirty-nine davaineid specimens were included in PBI project phylogenetic analyses; our preliminary results highly support the monophyly of the family to the exclusion of

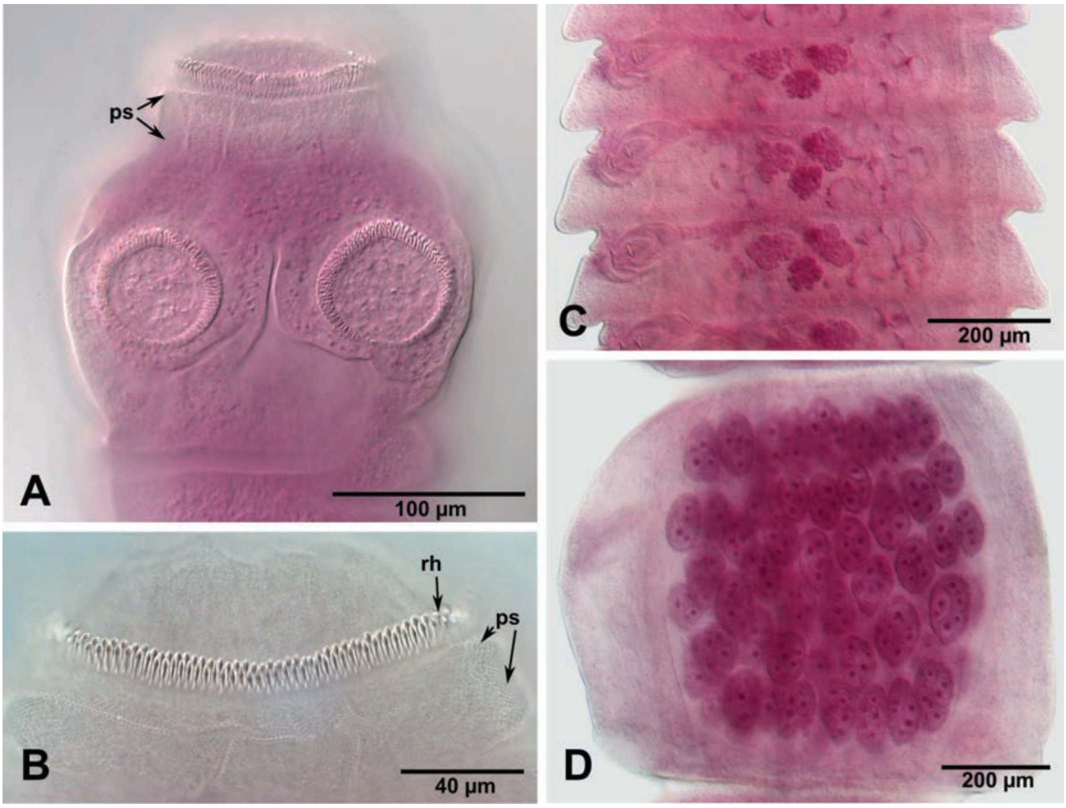


FIGURE 10. DAVAINEIDAE: *Raillietina* from *Colius striatus* from Gabon. **(A)** Scolex. **(B)** Armature of rostellum and pseudoproboscis. **(C)** Mature proglottids. **(D)** Gravid proglottid with parenchymatous multiovular capsules. *Abbreviations:* ps, pseudoproboscis; rh, rostellar hooks.

Ophryocotyle Friis, 1870 (result not shown in Fig. 5). However nodal support for the entire group (i.e., including *Ophryocotyle*) is currently weak (Fig. 5). Our results suggest the Davaineidae are a relatively early diverging group within the Cyclophyllidea, and are most closely related to the Catenotaeniidae, Linstowiinae, and a group consisting of the Paruterinidae, Metadilepididae, and Taeniidae (Fig. 5). However nodal support for this grouping is also weak.

5.6. Dilepididae Fuhrmann, 1907

This family was erected (under the incorrect spelling "Dilepinidae") by Fuhrmann (1907), who, nonetheless, must be credited as the authority of this taxon (ICZN, 1999, Article 19.2). Railliet and Henry (1909) used the correct spelling and thus these authors have since, albeit erroneously, been used as the authority of the family name, including by, for example, Schmidt (1986) and Khalil et al. (1994), but not, for example, by Matevosyan (1963) or Spasskaya and Spasskii (1977, 1978). This family is widely accepted as one of the most speciose cyclophyllidean families but its membership and classification have varied considerably throughout the last century (e.g., Ransom, 1909; Fuhrmann, 1932; Freeman, 1973). The most recent overview of the group was by Bona (1994), whose definition of the family (i.e., as excluding the Dipylidiinae, Paruterininae, and Metadilepididae) has been widely accepted. The exceptions are a number of genera with a three-host life-cycle that parasitize piscivorous birds and bear a unique rostellar configuration; these taxa are now considered members of the family Gryporhynchidae (see section 5.9.).

The main morphological characters of importance for identification of the Dilepididae include the structure of the (usually) armed rostellum (Fig. 11A), rostellar hooks (Fig. 11B), post-ovarian position of the compact vitellarium, bilobed ovary, single set of reproductive organs per proglottid, lack of seminal vesicles, numerous testes, and ventral position of the uterus. It should be noted, however, that most of these features are found in many states within the family and thus the Dilepididae are presently defined by a set of semi-exclusive characters rather than by one or more unambiguous morphological synapomorphies.

The Dilepididae are found in most orders of birds; they are particularly diverse in the Passeriformes, and to a lesser extent, in the Ciconiiformes and the Charadriiformes. They are also known from various mammal groups, primarily the Soricomorpha and Rodentia, but also marsupials (Bona, 1994). "Reptiles" are no longer considered among their potential hosts, given the single species reported from Australian turtles (Pichelin et al., 1998) now belongs to the Gryporhynchidae.

Life-cycles are known for approximately 25 species (Matevosyan, 1963; Spasskaya and Spasskii, 1977, 1978). Dilepidids use only one intermediate host, which is generally an arthropod, but annelids or molluscs are also known to serve as intermediate hosts. The larval stage is a cysticercoid (existing in several variants, but generally a monocysticercoid, see Chervy, 2002). Their geographic distribution is cosmopolitan, including Antarctica (Bona, 1994).

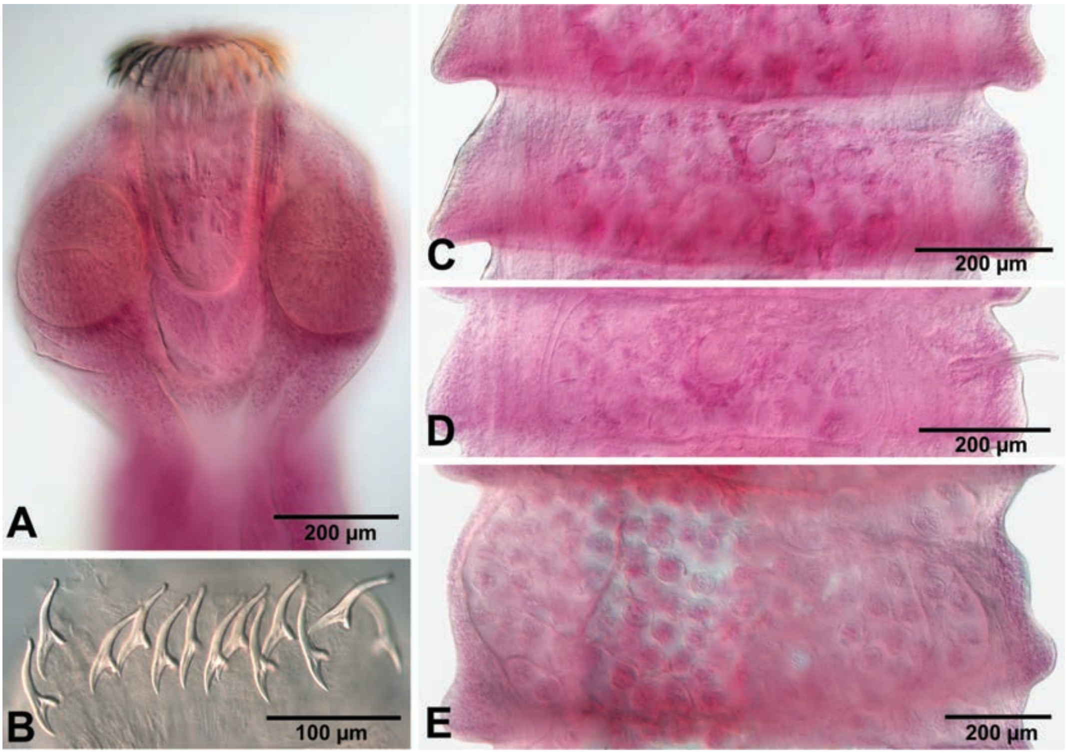


FIGURE 11. DILEPIDIDAE: *Dilepis undula* from *Turdus mupinensis* from China. **(A)** Scolex. **(B)** Rostellar hooks. **(C, D)** Mature proglottids. **(E)** Gravid proglottid.

Major taxonomic works dealing with representatives of this family are those by Matevosyan (1963), Spasskaya and Spasskii (1977, 1978), and Bona (1994). Although the family has historically been divided into a number of subfamilies, these are no longer recognized. The family currently includes 90 valid genera (Table 1) and about 750 species.

Discoveries over the course of the PBI. Specimens of this family were collected from all countries visited, from a total of 44 bird families. This material yielded approximately 107 species and at least 36 genera. In all countries except Ethiopia, dilepidids represented over 20% of the avian cyclophyllidean fauna collected. The Dilepididae were particularly well represented in the Turdidae and Hirundinidae. One new genus (*Gibsonilepis* Dimitrova, Mariaux & Georgiev, 2013) was erected and one new species (*Pseudangularia gonzalezi* Dimitrova, Mariaux & Georgiev, 2013) was described (Dimitrova et al., 2013). The descriptions of an additional two new genera and species from Chile as well as one new species from the Philippines are in preparation. An additional two new genera and approximately 18 new species are represented among the material that has been sorted, but not formally described. In mammals, four known species of *Monocercus* Villot, 1882 were collected from North American shrews of the genus *Sorex*, and one new species was collected from the eastern mole, *Scalopus aquaticus* (L.) (Talpidae).

Although Bona (1994) suggested that the family was not monophyletic, even once genera belonging to the Gryporhynchidae were removed, the results of our preliminary molecular analyses, which included 73 dilepidid specimens, tend to support the monophyly of the family. The highly nested position of the Dilepididae within the order Cyclophyllidea and its position as sister taxon to a clade composed of the Progynotaeniidae, Acoleidae, Gyrocoeliinae, and Hymenolepididae + Anoplocephalinae is, however, not strongly supported (Fig. 5). The results of our molecular analyses confirm the Gryporhynchidae as a taxon distinct from the Dilepididae.

5.7. Dioicocestidae Southwell, 1930

Southwell (1930) proposed the family Dioicocestidae (erroneously spelled Dioecocestidae) for the single genus *Dioicocestus* Fuhrmann, 1900 (erroneously spelled *Dioecocestus*) on the basis of the separation of sexes (i.e., some individuals have proglottids with only male genital organs, and others have proglottids with only female organs). The spelling *Dioecocestus* [sic] is recognized here as an unjustified emendation of this generic name (ICZN, 1999, Article 33.2.3) and, therefore, the spelling Dioicocestidae is adopted as a derivate of the generic name originally proposed by Fuhrmann (1900) and as used in the only monograph on the family (Ryzhikov and Tolkacheva, 1981).

Fuhrmann (1932) rejected the validity of the Dioicocestidae, transferring all of its species to the Acoleidae. In a subsequent paper (Fuhrmann, 1936), he accepted the group as a subfamily within the acoleids. Burt (1939) recognized the family and added three additional genera. Yamaguti (1959) divided the Dioicocestidae into two subfamilies: the Dioicocestinae (for *Dioicocestus*) with female individuals without male copulatory apparatus and possessing a transverse tubular uterus, and male individuals with two reproductive systems per proglottid; and the Gyrocoeliinae Yamaguti, 1959 (for *Gyrocoelia* Fuhrmann, 1899, *Shipleya* Fuhrmann, 1908, and *Infula* Burt, 1939) with female individuals possessing vestigial (non-functional) male copulatory apparatus and a ring-shaped uterus, and male individuals with one set of reproductive systems per proglottid. Ryzhikov and Tolkacheva (1981) elevated both subfamilies to family level, expanding existing recognized morphological differences between them to include the fact that, while the dioicocestids are specific to grebes and ibises, the gyrocoeliids parasitize only charadriiform hosts. Schmidt (1986) recognized the single family Dioicocestidae (including gyrocoeliids) without subfamilies. In contrast, Jones (1994b) recognized the two subfamilies (Dioicocestinae with 1 genus, and Gyrocoeliinae with 4 genera) and followed the generic assignments of Yamaguti (1959), placing *Echinoshipleya* Tolkacheva, 1979 in the Gyrocoeliinae. The main characteristics used for distinguishing among genera are the presence (Fig. 12A) or absence of a rostellum, and the presence and arrangement of rostellar hooks (e.g., in festoons [Fig. 12A] or many rows). In total, 21 species in five genera are currently considered members of the family (Ryzhikov and Tolkacheva, 1981; Schmidt, 1986).

Host associations of the family include grebes (Podicipedidae) and ibises (Threskiornithidae Poche) for the Dioicocestinae, and charadriiform birds for *Gyrocoelia*, *Shipleya*, *Infula*, and *Echinoshipleya* (Ryzhikov and Tolkacheva, 1981; Jones, 1994b). The geographic distribution is cosmopolitan (Jones, 1994b). No life-cycle is known for any member of the family.

Discoveries over the course of the PBI. Specimens of this family were collected from Brazil, Iran, and the USA, in numerous host species of the Charadriidae and one species of the Podicipedidae. These consisted of two species of *Gyrocoelia* and one species of *Dioicocestus*, none of which were new.

Dioicocestids were included in a molecular phylogenetic study for the first time. Five of the eight specimens analyzed were collected during PBI project expeditions. Our results (Fig. 5) do not support the monophyly of the family, instead they suggest that *Dioicocestus* is closely related to amabiliid genera from grebes and that the gyrocoeliines belong to a clade that also includes the acoleids and progynotaeniids (Fig. 5). These relationships are in agreement with the taxonomic concept of Ryzhikov and Tolkacheva (1981) who recognized the Dioicocestidae and Gyrocoeliidae as distinct families.

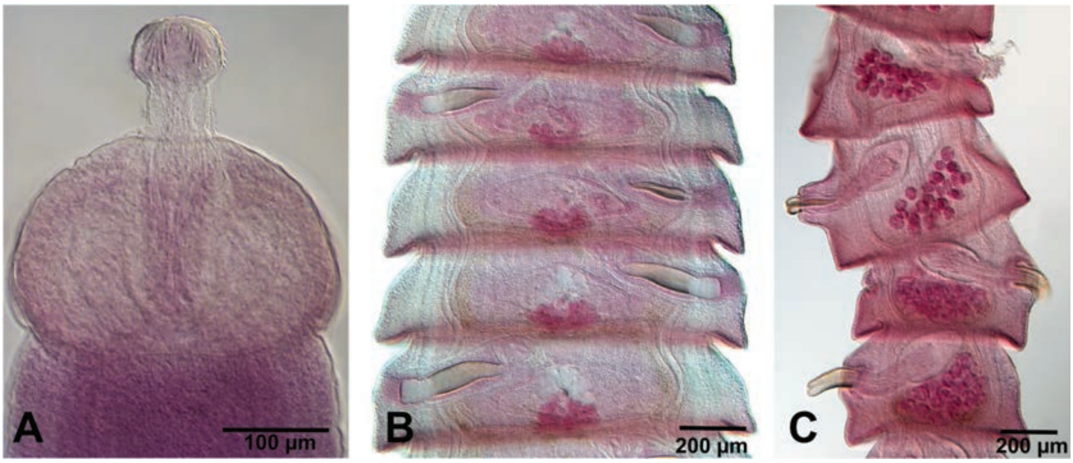


FIGURE 12. DIOICOCESTIDAE: *Gyrocoelia perversa* from *Charadrius alexandrinus* from Iran. **(A)** Scolex. **(B)** Mature proglottids of female strobila. **(C)** Mature proglottids of male strobila.

5.8. Dipylidiidae Railliet, 1896

The taxonomic history of the Dipylidiidae is among the most complex of all cyclophyllidean families. The name was first proposed by Railliet (1896) (and not Stiles [1896] as is frequently reported) as a subfamily of the Taeniidae (as Taeniadae). Although periodically considered as a family (e.g., Matevosyan, 1963; Wardle et al., 1974), its subfamilial status in the Dilepididae was adopted by the majority of earlier authors, including Schmidt (1986). However, Khalil et al. (1994) subdivided the Dilepididae *sensu lato* into several families, including the Dipylidiidae, which were thus treated in that same volume as a separate family by Jones (1994c). The subsequent morphology-based phylogenetic analysis of Hoberg et al. (1999) supported the status of the group as an independent family.

The main character differentiating the Dipylidiidae from the Dilepididae, and other cyclophyllideans, is the replacement of the uterus by mono- or multi-ovular egg capsules. Other characters of importance are the armature of the rostellum, which consists of several (3 or more) rows of hooks (Fig. 13A), the lack of a rostellar pouch, and the presence of a double set of genital organs in each proglottid (Fig. 13B). However, Hoberg et al. (1999) noted the homoplasious nature of all of these characters.

Membership in, and thus the concept of, the family have varied substantially over time. This is largely due to its imprecise original definition, with up to 20 genera parasitic in mammals and birds having been assigned to the group. Taxonomic treatments over time have progressively led to the assignment of most of these genera to other families, keeping only eight (Meggitt, 1924), five (Matevosyan, 1963), and only three (Witenberg, 1932) genera in the Dipylidiidae. Jones (1994c) followed the latter scheme, recognizing only *Dipylidium* Leuckart, 1863, *Diplopylidium* Beddard, 1913, and *Joyeuxiella* Fuhrmann, 1935 (reviewed by Jones, 1983) as valid members of the family. Collectively these three genera are considered to house a total of 15 valid species today.

The definitive hosts of the Dipylidiidae consist of carnivorous mammals (Jones, 1994c), mostly Canidae and Felidae. The life-cycle appears to include two hosts, with an insect, "reptile," or small mammal serving as the intermediate host. However, vertebrate paratenic hosts are common. *Dipylidium caninum* (L.), a common species in domestic dogs, uses fleas (Siphonaptera) and lice (Phthiraptera) as intermediate hosts. A list of both definitive

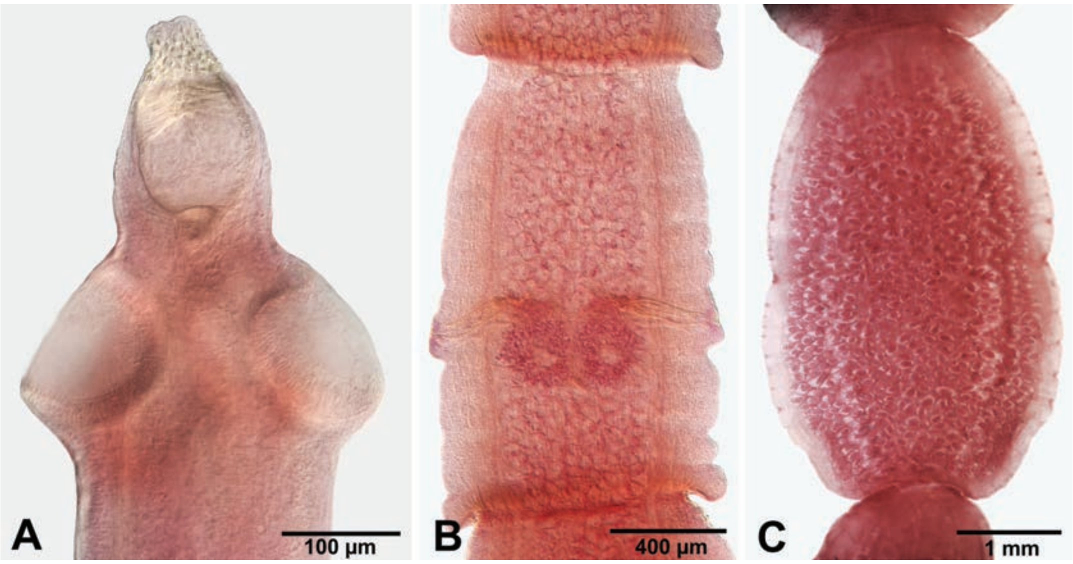


FIGURE 13. DIPYLIDIIDAE: *Dipylidium caninum* from *Canis familiaris* from Bulgaria. **(A)** Scolex. **(B)** Mature proglottid. **(C)** Gravid proglottid with multiovular egg capsules.

and intermediate hosts can be found in Matevosyan (1963). The larval stage is a modified cysticercus termed a cryptocysticercus (Chervy, 2002). Dipylidiids have a cosmopolitan distribution (Jones, 1994c).

The phylogenetic position of the family has been studied by Hoberg et al. (1999). Their morphological analysis placed the group as the sister to a large clade composed of seven families, including the Davaineidae, but clearly showed the Dipylidiidae to represent a lineage independent from the latter family.

Discoveries over the course of the PBI. Although no members of this family were collected during any of the PBI field trips, a specimen that had been obtained from a previous collecting trip in Werribee, Victoria, Australia was included in our molecular phylogenetic analyses. That specimen grouped as the sister taxon to a large clade including all the families with a sac-like rostellar apparatus (Fig. 5), albeit with low nodal support.

5.9. Gryporhynchidae Spasskii & Spasskaya, 1973

This taxon was originally erected by Spasskii and Spasskaya (1973) as a subfamily within the Dilepididae, primarily on the basis of the three-host life-cycle. In 1980, these authors elevated it to the family level. Its genera were treated as members of the Dilepididae (see Bona, 1994) in the most recent comprehensive treatment of the order by Khalil et al. (1994). However, the phylogenetic analyses of the Cyclophyllidea of Mariaux (1998) and Hoberg et al. (1999) supported its validity as an independent family.

Although similar to dilepidids in overall morphology, gryporhynchids can be distinguished from them in that their rostellar apparatus bears a rostellar sheath with strong muscular walls consisting of longitudinal and oblique fibers. As a consequence, when the rostellum is retracted, the tips of the rostellar hooks are directed anteriorly (Fig. 14A). Furthermore, the hooks of gryporhynchids are typically robust and large and are arranged in two concentric circles (Bona, 1975, 1994).

Definitive hosts of gryporhynchids are fish-eating birds, mostly belonging to the Ciconiiformes, although they are also found in other aquatic bird orders including the Pelecaniformes, Anseriformes, Gruiformes (Rallidae Vigors), and Accipitriformes (Bona, 1975, 1994). One species has been reported to use Australian turtles as definitive hosts (Pichelin et al., 1998).

The gryporhynchids have a three-host life-cycle which, as noted earlier, is a key biological character differentiating them from the dilepidids with their two-host life-cycles. Only a few life-cycles are completely known. It appears that crustaceans (copepods, experimentally) serve as first intermediate hosts and freshwater (rarely brackish) fish, and especially the Perciformes, serve as second intermediate hosts (reviewed by Scholz et al. [2004]). The larval stage found in the second intermediate host is a merocercoid (Chervy, 2002). The family is cosmopolitan in distribution with the majority of known species occurring in the Holarctic region (Bona, 1975, 1994).

Major taxonomic works dealing with representatives of this family are those by Bona (1975, 1994) and Scholz et al. (2004). Presently, 16 genera and approximately 76 species are recognized (Matevosyan, 1963; Bona, 1975, 1994; Schmidt, 1986; Pichelin et al., 1998; Scholz et al., 2004; Kornyushin and Greben, 2014).

Discoveries over the course of the PBI project. Specimens of this family were collected from Gabon (1 species), Brazil (4 species), Chile (1 species), and the USA (6 species). Brazil as "an unending source" of cestodes of ciconiiforms was already noted by Bona (1975; p. 11) as a major center of diversification for the group. The majority of gryporhynchid

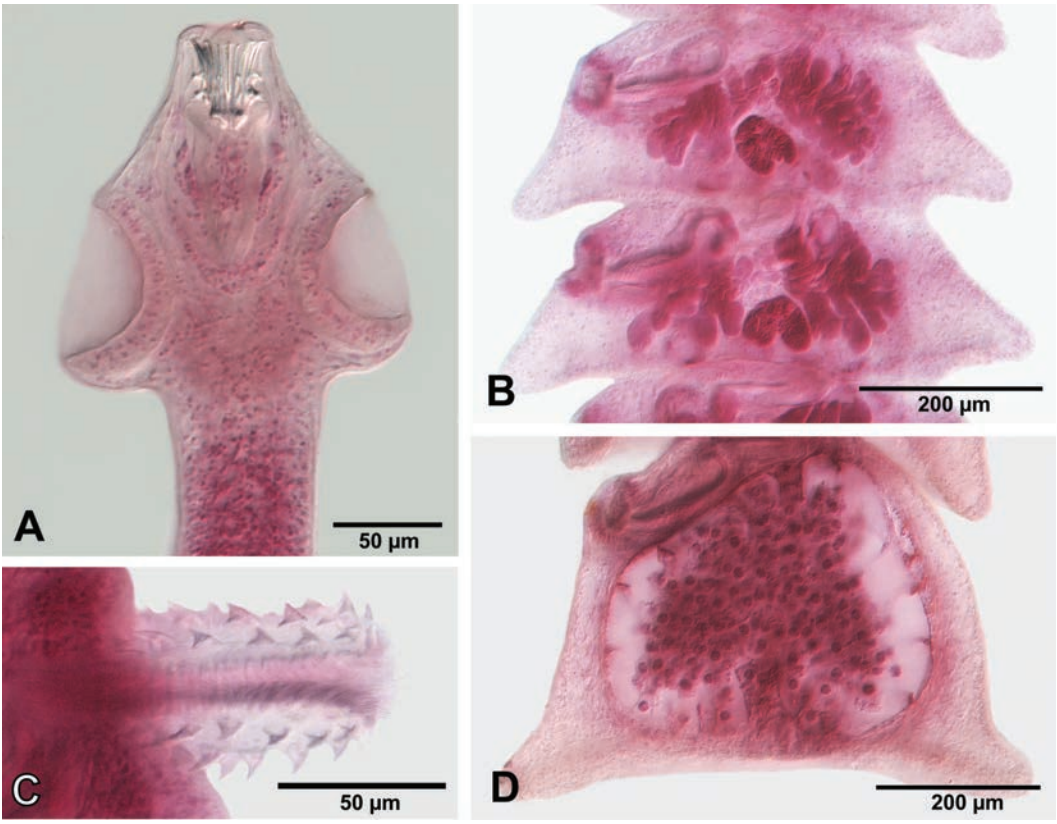


FIGURE 14. GRYPORHYNCHIDAE: *Parvitaenia macropeos* from *Nycticorax nycticorax* from Bulgaria. **(A)** Scolex. **(B)** Mature proglottids. **(C)** Evaginated cirrus. **(D)** Pre-gravid proglottid.

specimens collected over the course of the PBI project were from the Ardeidae (herons) and the Threskiornithidae (ibises and spoonbills)—both of which were already known to host a diversity of gryporhynchids. Our Gabonese sample from *Ixobrychus sturmii* (Wagler) appears to be a new species of *Valipora* Linton, 1927. Other records of this genus from Africa are limited (Bona, 1975); the closest in terms of greographic proximity are those of Mettrick (1967) in Zambia and Zimbabwe, and Mariaux (1994) in the Ivory Coast. Other preliminary identifications are of a species of *Dendrouterina* Fuhrmann, 1912 in Brazil and of *Paradilepis* Hsü, 1935 in Chile. The latter is a new locality record for this genus.

In total, 14 specimens of this family were included in our phylogenetic analyses. The monophyly of the family Gryporhynchidae is well supported (Fig. 5), however, their relationships within the Cyclophyllidea remain uncertain. The family appears to represent the sister-group of a large clade consisting of the Dilepididae, Hymenolepididae, Anoplocephalinae, and a well-supported subclade consisting of the Progynotaeniidae + Acoleidae + Gyrocoeliinae.

5.10. Hymenolepididae Perrier, 1897

This family was erected as the tribe Hymenolepinae within the Taeniidae by Perrier (1897) and elevated to family rank as the Hymenolepidae by Ariola (1899). Fuhrmann (1907) provided the first detailed diagnosis of the family Hymenolepinidae (later emended to Hymenolepididae by Railliet and Henry [1909]), including four genera within the family. Fuhrmann (1932) subdivided the family into the two subfamilies, Hymenolepidinae Perrier, 1897 and Fimbriariinae Wolffhügel, 1898. Joyeux and Baer (1936) and later Skrjabin and Matevosyan (1945) recognized four subfamilies on the basis of the structure of the uterus and the number of the sets of genital organs per proglottid. The latter classification was essentially the one followed by Wardle and McLeod (1952) and Yamaguti (1959).

Spasskii (1954) and Spasskii and Spasskaya (1954) proposed significant changes to the systematics of hymenolepidids at the generic level, employing many characters that had not previously been applied, such as peculiarities of life-cycles and associations with specific host groups. Over the next 40 years, Spasskii and his colleagues modified the classification of hymenolepidids further following that same approach (e.g., Spasskii, 1963; Spasskaya, 1966; Kornyushin, 1983, 1995; Bondarenko and Kontrimavichus, 2004).

Skrjabin (1940) erected the suborder Hymenolepidata Skrjabin, 1940, to which he attributed four families, one of which was the Hymenolepididae. However, Spasskii (1992b, 2003a–c, 2004) proposed a new higher-level classification dividing the suborder Hymenolepidata into three superfamilies in which he collectively recognized more than 25 family-group taxa. This classification resulted in an inefficient dismantling of the Hymenolepididae and although it has not been generally accepted, subsequently some authors have followed this scheme in part (e.g., Bondarenko and Kontrimavichus, 2006).

In the latest taxonomic revision of the family, Czapliński and Vaucher (1994) recognized four subfamilies within the Hymenolepididae of birds. In contrast, no subfamilies have been recognized within the hymenolepidids of mammals. Czapliński and Vaucher (1994) also proposed numerous new generic synonymies, which included the suppression of a number of well-defined genera, especially from birds. Their concepts of avian hymenolepidid genera were based on few morphological criteria and ignored numerous distinguishing morphological and life-cycle characteristics. This approach was in stark contrast to the criteria they used to define hymenolepid genera from mammals employed in the same publication.

The validity of the family Hymenolepididae is now generally accepted. However, despite numerous attempts to develop an effective classification at the subfamily level, a generally accepted unified scheme has yet to emerge. In addition, until now, a comprehensive phylogenetic analysis of the family, based on either morphological or molecular data, has not been conducted and, as a consequence, the interrelationships among the genera remain unclear.

This is the most speciose cestode family—currently containing at least 923 valid species (565 species from birds and 358 species from mammals) and 130 valid genera (Schmidt, 1986; Czapliński and Vaucher, 1994; McLaughlin, 2003; Gibson et al., 2014) (see Table 1). The most important morphological traits characterizing the family include the sac-like rostellar apparatus (Fig. 15A), typically with one, or exceptionally two, rows of rostellar hooks (although a rostellum may be lacking [Fig. 15C] or present in only rudimentary form), proglottids that are usually wider than long (Figs. 15B, D, E), genital pores that are typically unilateral (Fig. 15B), a single or rarely double set of reproductive organs per proglottid, small number of testes (typically 1 to 4, rarely up to 32), and the presence of both external and internal seminal vesicles. Additional diagnostic characters at the generic level include the number of longitudinal osmoregulatory canals, the number of the inner longitudinal muscle bundles, the presence of a pseudoscolex, the presence of an accessory sac and stylet, and the structure and pattern of development of the uterus. Of key importance at the generic level, however, are the number and shape of the rostellar hooks (see Skrjabin and Matevosyan

[1945] for the generally accepted classification of hymenolepidid hook shapes) (e.g., Khalil et al., 1994). It is of note that the presence of an external seminal vesicle is a character the hymenolepidids share with both the Anoplocephalidae and the families placed in the, albeit controversial, suborder Acoleata.

The host associations of the Hymenolepididae include almost all orders of birds, both aquatic and terrestrial taxa (Schmidt, 1986; Czapliński and Vaucher, 1994), and many groups of mammals, with an emphasis on the orders Soricomorpha, Rodentia, Lagomorpha, Chiroptera, and Marsupialia (see Czapliński and Vaucher, 1994; Georgiev et al., 2006; Binkienė et al., 2011). Of note is the fact that humans are also among the hosts of hymenolepidids (which otherwise are mainly parasites of rodents) (Fan, 2005; Magalhaes et al., 2013; Nkouawa et al., 2016).

Life-cycles are known for 230 species of hymenolepidids (Lefebvre et al., 2009a, b). Most have a two-host life-cycle that involves an invertebrate intermediate host and a vertebrate definitive host. Intermediate host taxa differ depending on the habitat. Intermediate hosts of terrestrial taxa are generally arthropods (i.e., Insecta, Entognatha, Myriapoda, Arachnida) or annelids. Intermediate hosts of aquatic taxa are generally aquatic crustaceans, insects, or annelids (Skrjabin and Matevosyan, 1945; Lefebvre et al., 2009a, b). In exceptional cases, the life-cycles of aquatic taxa may have a snail paratenic host. The larval stage developing in the intermediate host is a cysticercoid, with eight recognized variants (Chervy, 2002). A notable exception to this scenario is the life-cycle of *Pararodentolepis fraterna* (Stiles, 1906) Tkach, Makarikov & Kinsella, 2013, which may be entirely completed within the mammalian definitive host alone—a strategy that is considered to represent a secondary simplification of the two-host life-cycle (Skrjabin and Matevosyan, 1948). The family is cosmopolitan (including Antarctica) in distribution (Czapliński and Vaucher, 1994).

Major taxonomic works treating this family are those of Mayhew (1925), Skrjabin and Matevosyan (1945, 1948), Spasskii and Spasskaya (1954), Spasskii (1954, 1963), Spasskaya (1966), Vaucher (1971), Czapliński and Vaucher (1994), Sawada (1997), and Bondarenko and Kontrimavichus (2006).

Discoveries over the course of the PBI project. Hymenolepidids from birds were collected from 17 countries and 49 bird families (10 families of aquatic and 39 of terrestrial birds). In total, 141 species of at least 30 genera of this cestode family were collected. In addition to taxa from aquatic birds (35 species), these collections revealed a substantial diversity in terrestrial birds (77 hymenolepidid species). The Hymenolepididae are particularly well represented in the Passeriformes, especially in the Turdidae (10 species) and Thamnophilidae (7 species). One new genus (*Colibrilepis* Widmer, Georgiev & Mariaux, 2013) and one new species from Chile (*Colibrilepis pusilla* Widmer, Georgiev & Mariaux, 2013) and one new species (*Diorchis thracica* Marinova, Georgiev & Vasileva, 2015) from Bulgaria were described (Widmer et al., 2013; Marinova et al., 2015). Preliminary taxonomic work on other newly collected material suggests it includes an additional three new genera and at least 17 new species, most of which are members of *Passerilepis* Spasskii & Spasskaya, 1954.

Hymenolepidids from mammals were collected from 12 countries and nine families representing four orders of hosts. In total, 106 species and 33 genera of Hymenolepididae were collected. Hymenolepidids are known to be very well represented in Soricidae, with more than 60 species parasitizing the family. One new genus (*Sawadalepis* Makarikova & Makarikov, 2013) and 22 new species were described: *Potorolepis gulyaevi* Makarikova & Makarikov, 2012 (see Makarikova and Makarikov, 2012), *Pararodentolepis gnoskei* (Greiman & Tkach, 2012) Tkach, Makarikov & Kinsella, 2013 (see Greiman and Tkach, 2012), *Sawadalepis prima* Makarikova

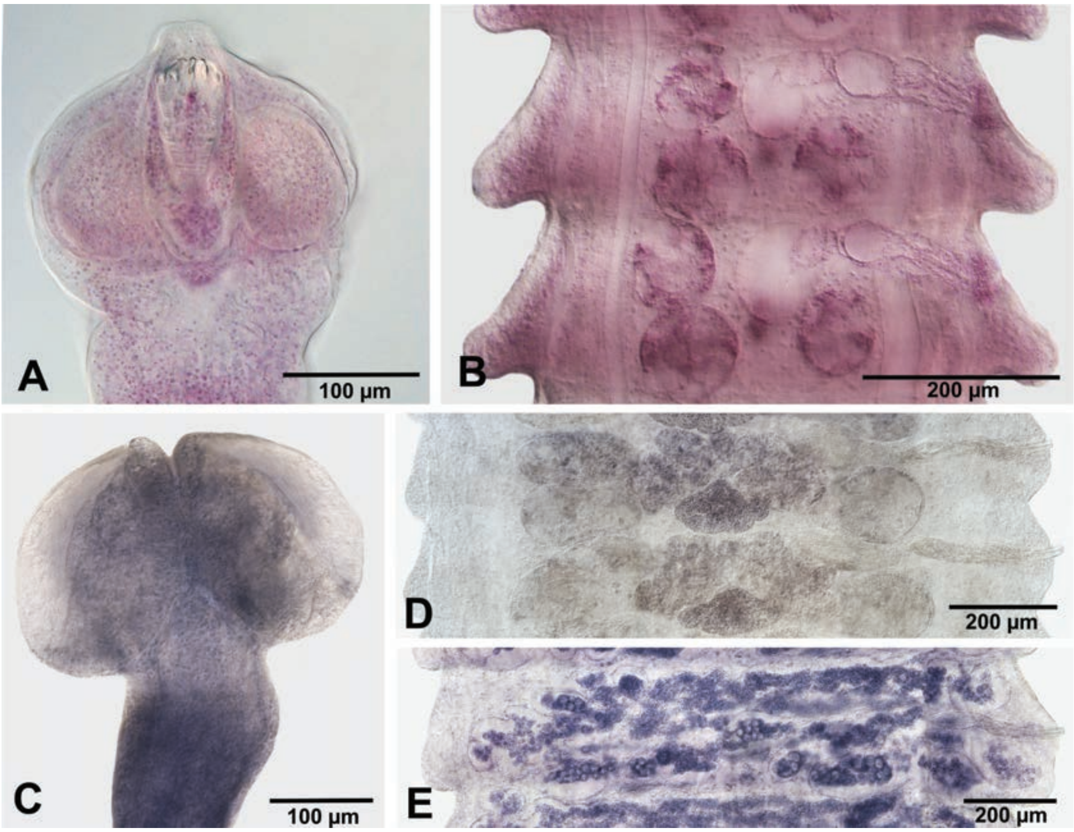


FIGURE 15. HYMENOLEPIDIDAE: **(A–B)** *Passerilepis crenata* from *Turdus mupinensis* from China. **(A)** Scolex. **(B)** 'Male' mature proglottids. **(C–E)** *Arostrilepis intermedia* from *Myodes rufocanus* from Russia. **(C)** Scolex. **(D)** Mature hermaphroditic proglottids. **(E)** Pre-gravid proglottid.

& Makarikov, 2013 (see Makarikova and Makarikov, 2013), *Staphylocystis clydesengeri* Tkach, Makarikov & Kinsella, 2013 (see Tkach et al., 2013), *Staphylocystoides gulyaevi* Greiman, Tkach & Cook, 2013 (see Greiman et al., 2013), *Arostrilepis intermedia* Makarikov & Kontrimavichus, 2011, *A. janickii* Makarikov & Kontrimavichus, 2011 (see Makarikov and Kontrimavichus, 2011), *A. mariettavogeae* Makarikov, Gardner & Hoberg, 2012, *A. schilleri* Makarikov, Gardner & Hoberg, 2012 (see Makarikov et al., 2012), *A. cooki* Makarikov, Galbreath & Hoberg, 2013, *A. gulyaevi* Makarikov, Galbreath & Hoberg, 2013, *A. rauschorum* Makarikov, Galbreath & Hoberg, 2013 (see Makarikov et al., 2013a), *Hymenolepis apodemi* Makarikov & Tkach, 2013, *H. rymzhanovi* Makarikov & Tkach, 2013 (see Makarikov and Tkach, 2013), *H. bicauda* Makarikov, Tkach & Bush, 2013, *H. haukisalmii* Makarikov, Tkach & Bush, 2013 (see Makarikov et al., 2013b), *H. folkertsi* Makarikov, Nims, Galbreath & Hoberg, 2015 (see Makarikov et al., 2015c), *H. alterna* Makarikov, Tkach, Villa & Bush, 2015, *H. bilaterala* Makarikov, Tkach, Villa & Bush, 2015 (see Makarikov et al., 2015a), *Soricinia genovi* Binkienė, Kornienko & Tkach, 2015 (see Binkienė et al., 2015), *Nomadolepis fareasta* Makarikov, Mel'nikova & Tkach, 2015, and *N. shiloi* Makarikov, Mel'nikova & Tkach, 2015 (see Makarikov et al., 2015b), and two species of *Armadolepis* Spassky, 1954 (Makarikov, 2017). In addition, albeit not as part of the PBI project, Makarikov and Hoberg (2016) recently described another new species of *Arostrilepis*, *A. kontrimavichusi* Makarikov & Hoberg, 2016. Preliminary taxonomic work on other material collected from mammals over the course of the PBI project leads us to believe it includes one additional new genus and 34 new species.

This family was the most well represented of all cyclophyllidean families in our molecular phylogenetic analyses. The sample consisted of a total of 111 specimens (41 of which were collected on PBI expeditions) of 91 identified species (66 species from birds and 25 from mammals) in at least 38 genera. The hymenolepidids were found to nest deeply among the cyclophyllideans, in a clade that also includes the anoplocephaline cestodes (Fig. 5). Although nodal support for this relationship was not high, it is interesting to note that all taxa in this clade have a sac-like rostellar apparatus. In terms of relationships to other families, our results suggest that the Hymenolepididae may be phylogenetically most related to Progynotaeniidae, Acoleidae, and the dioicocestid subfamily Gyrocoeliinae but nodal support for these relationships is also weak. One further molecular outcome from the PBI project was the examination of the distribution and genetic variation of three hymenolepidid species from rodents from the Canary Islands (Foronda et al., 2011).

5.11. Mesocestoididae Perrier, 1897

This family was erected by Perrier (1897) for the genus *Mesocestoides* Vaillant, 1863 and has been widely accepted as a monophyletic group by later authors. Skrjabin (1940) elevated it to subordinal status, as the Mesocestoidata Skrjabin, 1940 within the order Cyclophyllidea (see also Chertkova and Kosupko, 1978). Wardle et al. (1974) recognized it as the independent order Mesocestoididea on the basis of its lack of a rostellar apparatus, and its possession of median genital pores, a pair of vitelline glands, a paruterine organ, and vermiform oncospheres. However, the status of the group as an independent order has not generally been accepted by subsequent authors, most of whom considered the Mesocestoididae as a family within the Cyclophyllidea (e.g., Schmidt, 1986; Khalil et al., 1994). Nonetheless, discussion of the position of the group within or outside of the Cyclophyllidea has been revitalized by the wider application of molecular phylogenetic approaches to the classification of cestodes—a topic that is treated in more detail below.

The main morphological characters of importance for identification of this family include the lack of a rostellum (Fig. 16A) and the mid-ventral position of the genital atrium (Fig. 16C), as well as the presence of a paruterine organ (Fig. 16C) and typically also possession of a pair, rather than a single, vitelline gland (Fig. 16B). The exception is the monotypic *Mesogyna* Voge, 1952, which has a transversely elongated vitellarium and a saccular uterus without a paruterine organ.

Definitive hosts of the family are carnivorous mammals, and more rarely birds of prey (Rausch, 1994a). The geographic distribution is cosmopolitan with the exception of Australia (James, 1968). No complete life-cycle is known for the family. However, they are thought to have a three-host life-cycle. Mites have been suspected, but not proven, to serve as the first intermediate host because the first larval stage has never been found. The second larval stage, known as a tetrathyridium, is commonly found in a wide array of tetrapods, in which it can asexually reproduce, usually by longitudinal fission (Chertkova and Kosupko, 1978; Galan-Puchades et al., 2002).

Major taxonomic monographs dealing with representatives of this family are those of Witenberg (1934), Chertkova and Kosupko (1978), and Rausch (1994a). The family is typically subdivided into the subfamilies Mesocestoidinae and Mesogyninae, each with a single genus (Rausch, 1994a). Host-induced morphological variation makes the identification of species

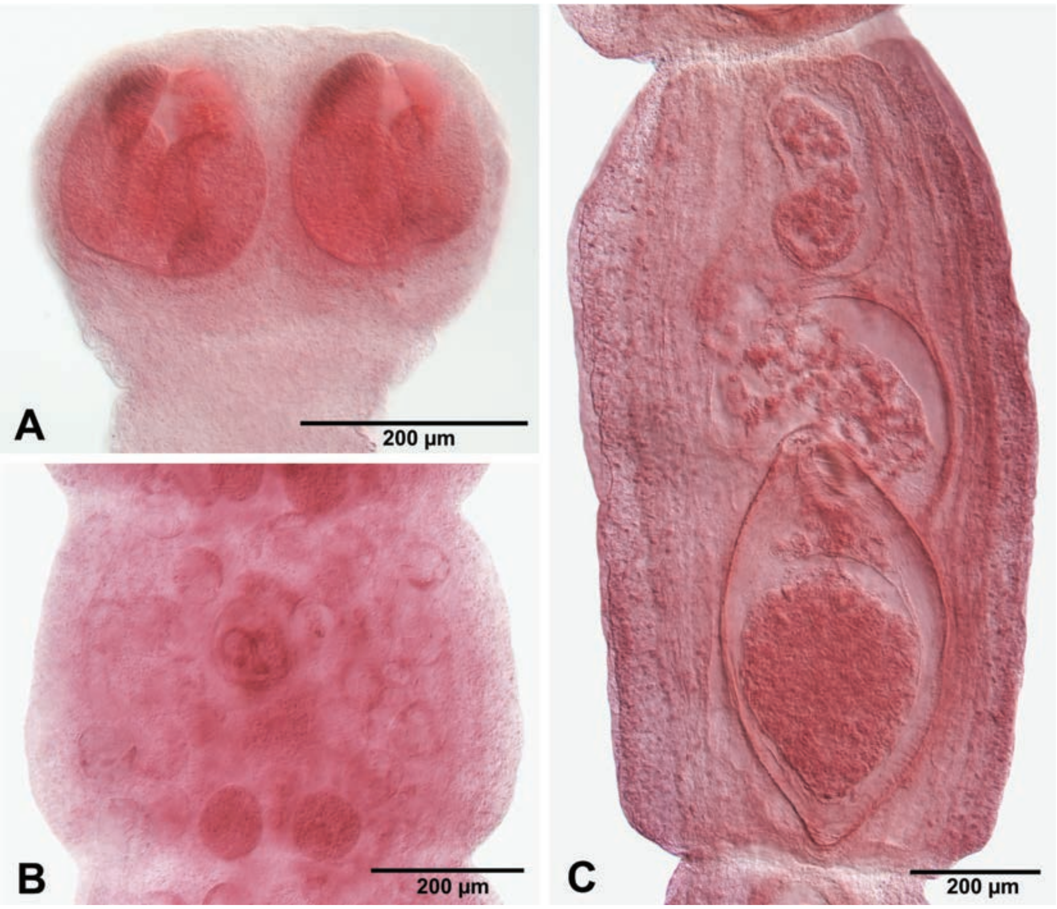


FIGURE 16. MESOCESTOIDIDAE: *Mesocestoides lineatus* from *Vulpes vulpes* from Bulgaria. **(A)** Scolex. **(B)** Mature proglottid (ventral view). **(C)** Pre-gravid proglottid with paruterine capsule formation.

difficult (Rausch, 1994a). To date, approximately 30 nominal species have been proposed in *Mesocestoides* but only a subset of these (i.e., 12 according to Chertkova and Kosupko [1978] and 17 according to Wardle et al. [1974]) can be distinguished with confidence. *Mesogyna* is monotypic.

Hoberg et al. (1999), as a result of their morphology-based phylogenetic analysis, believed the Mesocestoididae to be the earliest diverging group of cyclophyllideans. Molecular phylogenetic studies are almost unanimous in suggesting that the Mesocestoididae should be removed from the Cyclophyllidea and recognized as an indepentent order (Mariaux, 1998; Olson et al., 2001; Waeschenbach et al., 2007; Caira et al., 2014) although its exact phylogenetic affinities have never been strongly supported. The only divergent view is that of von Nickisch-Rosenegk et al. (1999) who found the Mesocestoididae to be highly nested within the cyclophyllidean evolutionary tree as the sister group to the most derived families or of the Anoplocephalidae, depending on the type of analysis employed. Their work was, however, based on data from only a very short fragment of a single gene (i.e., 12S rDNA) and thus support for this hypothesis is limited.

Discoveries over the course of the PBI project. Collections from PBI expeditions emphasized tetrathyridia of *Mesocestoides*. In birds, five occurrences were seen in Peru (including 3 in thamnophilid birds and 1 each in members of the Emberizidae Vigors and Formicariidae Gray), with one occurrence each in Ethiopia (in a turdid) and Malaysia (in a vangid). In mammals, two adults were found, one each in a procyonid and a didelphid in USA, and one tetrathyridium was collected from a soricid in Malawi. All eight of these represent new host and locality records. However, this is not surprising as tetrathyridia are known from a large variety of intermediate hosts, including passerine birds of various families (Witenberg, 1934; Chertkova and Kosupko, 1978) and nothing is known about their host specificity.

Recent molecular studies by Waeschenbach et al. (2007, 2012) and Caira et al. (2014) failed to resolve the phylogenetic position of this group among the acetabulate cestode taxa, although significant support was found for its exclusion from the Cyclophyllidea. Waeschenbach et al.'s (2012) 516 mitochondrial amino acid analysis provided strong support for a sister-group relationship between the Mesocestoididae and Cyclophyllidea (Waeschenbach et al., 2012). In a larger analysis of acetabulate taxa, although with limited sampling of cyclophyllideans, Caira et al. (2014) found the Mesocestoididae to group as sister to the order Tetrabothriidea, which in turn was sister to a clade consisting of the Cyclophyllidea + Nippotaeniidea.

Our molecular phylogenetic analyses included three specimens of tetrathyridia of *Mesocestoides*. They were indeed found to comprise a clade that grouped as the sister taxon of the remaining cyclophyllideans (Fig. 5). However, as the Nippotaeniidea and Tetrabothriidea were not represented in our analyses, the inferences about the position of the Mesocestoididae that can be drawn from these analyses are limited.

5.12. Metadilepididae Spasskii, 1959

This taxon was originally established as a subfamily within the family Dilepididae by Spasskii (1959) for three genera with a sucker-like rostellar apparatus, a sac-like uterus, and genital ducts that were usually located ventral to the osmoregulatory canals. It was elevated to family level by Spasskaya and Spasskii (1971) who considered it to be a close relative of the Paruterinidae and who proposed the superfamily Paruterinoidea to house the two families. For decades, the metadilepidids were recognized as a distinct family solely in the Russian-language literature (Borgarenko, 1981; Kornyushin, 1989). It was not until they were "rediscovered" through the description of several African metadilepidid taxa by Mariaux and his collaborators (e.g., Mariaux and Vaucher, 1989; Mariaux, 1991; Mariaux et al., 1992) that the group regained family-level status more globally. Kornyushin and Georgiev (1994) treated the family and the eight genera then recognized; Georgiev and Vaucher (2003) subsequently established two new genera in the family.

The main morphological features characterizing metadilepidids include a sucker-like rostellar apparatus, which is typically armed with triangular rostellar hooks with epiphyses (Figs. 17A, B). Based on these characters, metadilepidids are similar to paruterinids but can be distinguished from them by their possession of a sacciform uterus positioned dorsal to the ovary (Figs. 17 C, D), rather than paruterine organs.

The host associations of this family consist of terrestrial birds of the orders Caprimulgiformes, Coraciiformes, and Passeriformes (Kornyushin and Georgiev, 1994). No complete life-cycle is known for any metadilepidid cestode. Since the definitive hosts are insectivorous birds, it seems likely that arthropods serve as intermediate hosts of this group. The Metadilepididae exhibit the narrowest geographic distribution of any of the cyclophyllidean families. They are generally restricted to tropical regions, although a few

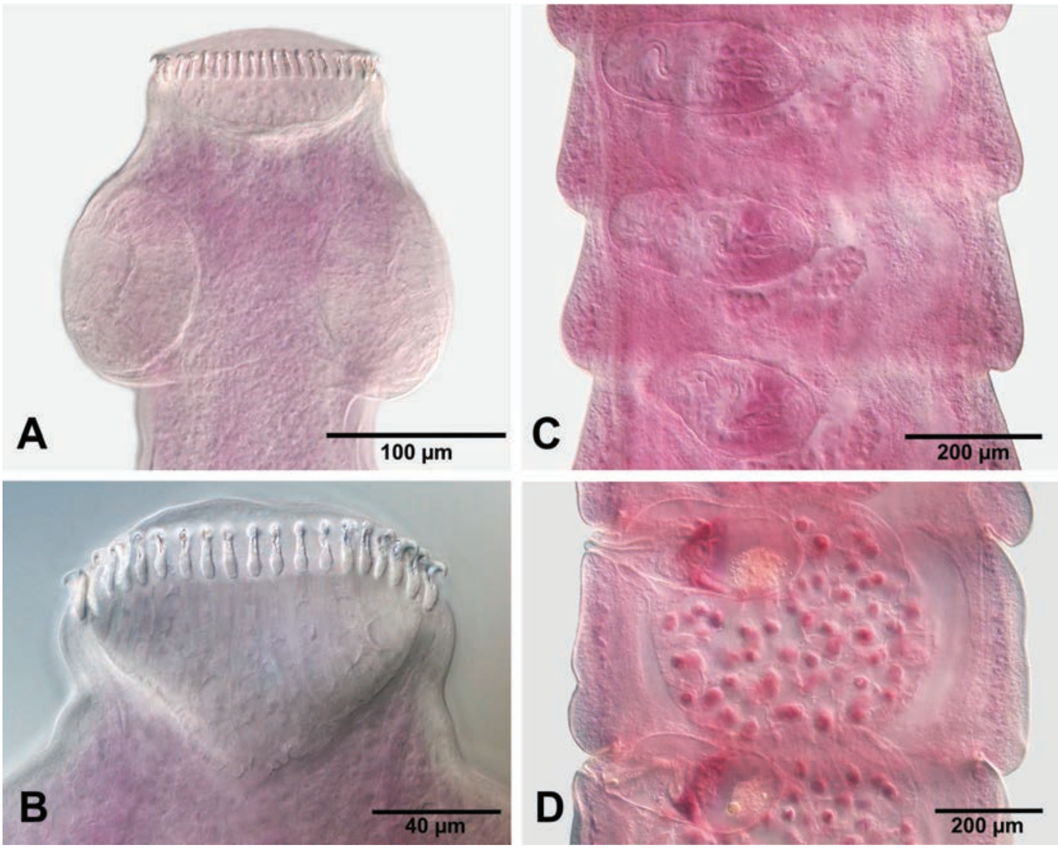


FIGURE 17. METADILEPIDIDAE: *Pseudadelphoscolex eburnensis* from *Terpsiphone rufiventer* from Gabon. **(A)** Scolex. **(B)** Sucker-like rostellar apparatus. **(C)** Mature proglottids. **(D)** Gravid proglottids.

species also occur in migrating birds in their summer nesting grounds in temperate latitudes (Kornyushin and Georgiev, 1994).

Currently, the family includes ten genera and 15 species (Kornyushin and Georgiev, 1994; Georgiev and Vaucher, 2003).

Discoveries over the course of the PBI project. Specimens of this family were collected from two countries and three bird families (2 passeriforms and 1 coraciiform). This material consisted of four species, only two of which (i.e., *Pseudadelphoscolex eburnensis* Mariaux, Bona & Vaucher, 1992 and *Skrjabinoporus merops* [Woodland, 1928] Spasskii & Borgarenko, 1960), both from Gabon, have been identified. Both of the latter species were included in our molecular phylogenetic analyses. They were found to be composed of a well-supported subclade within the Paruterinidae suggesting that the lack of the paruterine organ is likely the result of a secondary loss in the metadilepidids, but also calling into question the independence of the two families.

5.13. Nematotaeniidae Lühe, 1910

This family was erected by Lühe (1910) for *Nematotaenia dispar* (Goeze, 1782) Lühe, 1899. It is one of the least speciose families of the Cyclophyllidea with only about 20 valid species.

The main features characterizing nematotaeniids include the weakly segmented cylindrical strobila (Fig. 18C), the simple scolex devoid of apical structures (Fig. 18A), the reduced number of testes (2 or 3) and the presence of multiple paruterine organs in each gravid proglottid (Fig. 18C). A particularly useful list of characters for identifying nematoteniids was provided by Jones (1987).

Nematotaeniids are among the few cyclophyllidean groups that use amphibians as definitive hosts. Host groups include both Anura and Caudata, and "reptiles" (Sauria), mostly the Anguidae Gray, Gekkonidae Oppel, and Scincidae Gray. In addition, one species has been reported from a turtle (Jones, 1987). No life-cycle is known for the family (Beveridge, 2001). The geographic distribution is cosmopolitan (Jones, 1994).

Major taxonomic monographs dealing with representatives of this family are those by Douglas (1958) and Jones (1987, 1994). Jones (1987) recognized 18 species in four genera. Since that work, a few more species have been described (e.g., Buriola et al., 2005) and one genus (*Lanfrediella* Melo, Giese, Furtado, Soares, Gonçalves, Vallinoto & Santos, 2011; see Melo et al., 2011) has been erected. The group however remains very small. Jones (1987) provided a preliminary phylogeny and biogeographical history on the basis of morphological characters.

Mariaux (1998) included one nematotaeniid specimen in his analysis of 18S rDNA sequence data, but his results served only to confirm it as a member of the Cyclophyllidea. Beyond that work, the family has not been represented in other phylogenetic contributions based on molecular data.

Discoveries over the course of the PBI project. Only a few amphibians and "reptiles" were collected in our field trips and no nematotaeniids were found.

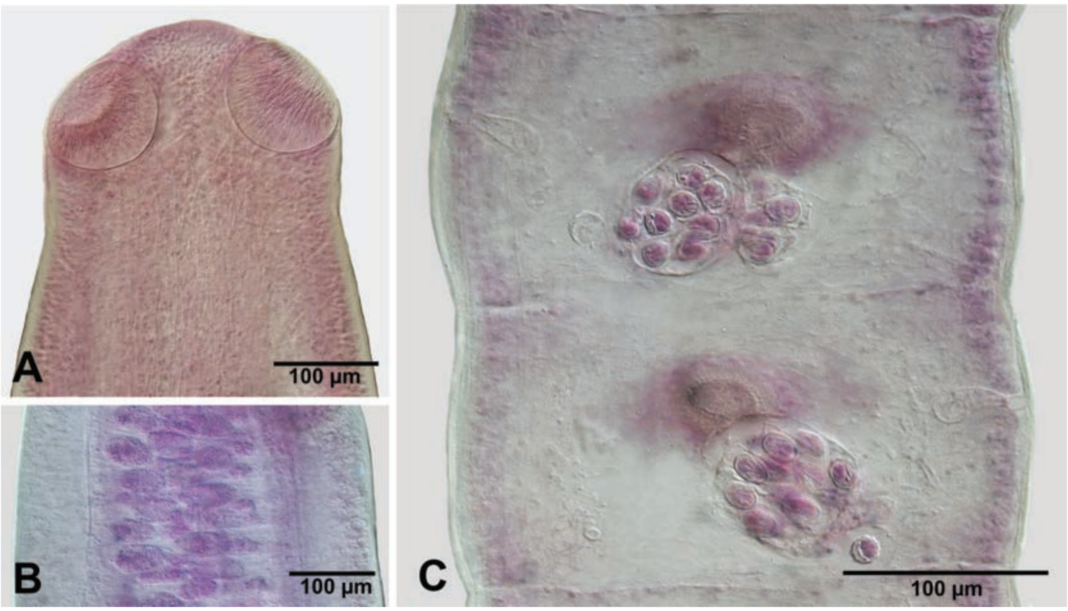


FIGURE 18. NEMATOTAENIIDAE: *Cylindrotaenia americana* from *Rhinella marina* from Peru. **(A)** Scolex. **(B)** Mature proglottids. **(C)** Pre-gravid proglottids with early paruterine capsule formation.

5.14. Paruterinidae Fuhrmann, 1907

This group was established as a subfamily within the family Dilepididae by Fuhrmann (1907). This concept was embraced by some subsequent authors (e.g., Yamaguti, 1959; Schmidt, 1986), however others have considered the group to represent a distinct family (e.g., Mola, 1929; Skrjabin, 1940; Spasskaya and Spasskii, 1971; Georgiev and Kornyushin, 1994). Yet other authors elevated it to superfamilial rank and included one or two other families (e.g., Matevosyan, 1969; Kornyushin, 1989).

A key morphological feature characterizing the paruterinids is the presence of a single paruterine organ in the form of a fibrous or granular appendage to the uterus that usually receives the eggs and retains them in a common capsule (Figs. 19B, C). This structure is believed to serve to protect against desiccation of eggs allowing them to be disseminated in terrestrial habitats, and/or to have a propagative function perhaps attracting intermediate hosts and thereby facilitating the simultaneous transmission of groups of eggs (Georgiev and Kornyushin, 1994). Another key character of the paruterinids is the position of the developing uterus dorsal to the ovary—a feature the group shares only with the family Metadilepididae (Kornyushin and Georgiev, 1994). The scolex of paruterinids typically bears a sucker-like rostellar apparatus (Fig. 19A) armed with two rows of rostellar hooks that usually bear epiphyseal thickenings on the handle and guard. However, some genera are characterized by either the presence of a rudimentary (unarmed) rostellum or by their lack of a rostellum entirely (see Georgiev and Kornyushin, 1994).

The host associations of members of this family, as adults, consist mostly of terrestrial birds of the orders Passeriformes, Coraciiformes, Piciformes, Trogoniformes, Strigiformes, Accipitriformes, Galliformes, Cuculiformes, and Apodiformes; a few species have been recorded from mammals and amphibians (Yamaguti, 1959; Matevosyan, 1969; Schmidt, 1986; Georgiev and Kornyushin, 1994). The few species for which life-cycles are known use two hosts. For species of the genera *Paruterina* Fuhrmann, 1906 (parasitic in owls) and *Cladotaenia* Cohn, 1901 (parasitic in eagles, hawks, and falcons), rodents and soricomorph mammals serve as intermediate hosts (Freeman, 1957, 1959). For species of *Metroliasthes* Ransom, 1900 and *Lyruterina* Spasskii & Spasskaya, 1971 (parasitic in galliform birds), insects serve as intermediate hosts (Jones, 1936; Smigunova, 1991). The larval stage developing in the intermediate host is a merocercoid (Chervy, 2002).

With the exception of the Antarctic, paruterinids are cosmopolitan in distribution, occurring in habitats spanning the range of tundra to equatorial forests (Yamaguti, 1959; Matevosyan, 1969; Schmidt, 1986).

The only taxonomic monograph on the Paruterinidae is that of Matevosyan (1969). The more recent work by Georgiev and Kornyushin (1994) considered the taxonomy of the family at the generic level. The family currently includes 24 genera (Georgiev and Kornyushin, 1994; Phillips et al., 2012) and 125 species, the majority of which were either listed by Matevosyan (1969) and Schmidt (1986) or described in subsequent publications (Bona et al., 1986; Kornyushin, 1989; Georgiev and Vaucher, 2001; Georgiev and Gibson, 2006; Georgiev and Mariaux, 2007; Phillips et al., 2012, 2014).

Discoveries over the course of the PBI project. Specimens of this family were collected from 12 countries and from 38 bird families. The Pycnonotidae and Thraupidae Cabanis (tanagers) were found to host the richest paruterinid faunas, with seven and five species, respectively. In total, 61 species of at least 12 genera were collected. Genera that were especially well represented in our collections are *Anonchotaenia* Cohn, 1900 (16 species), *Biuterina* Fuhrmann, 1902 (12 species), and *Sphaeruterina* Johnston, 1914 (5 species). Work on

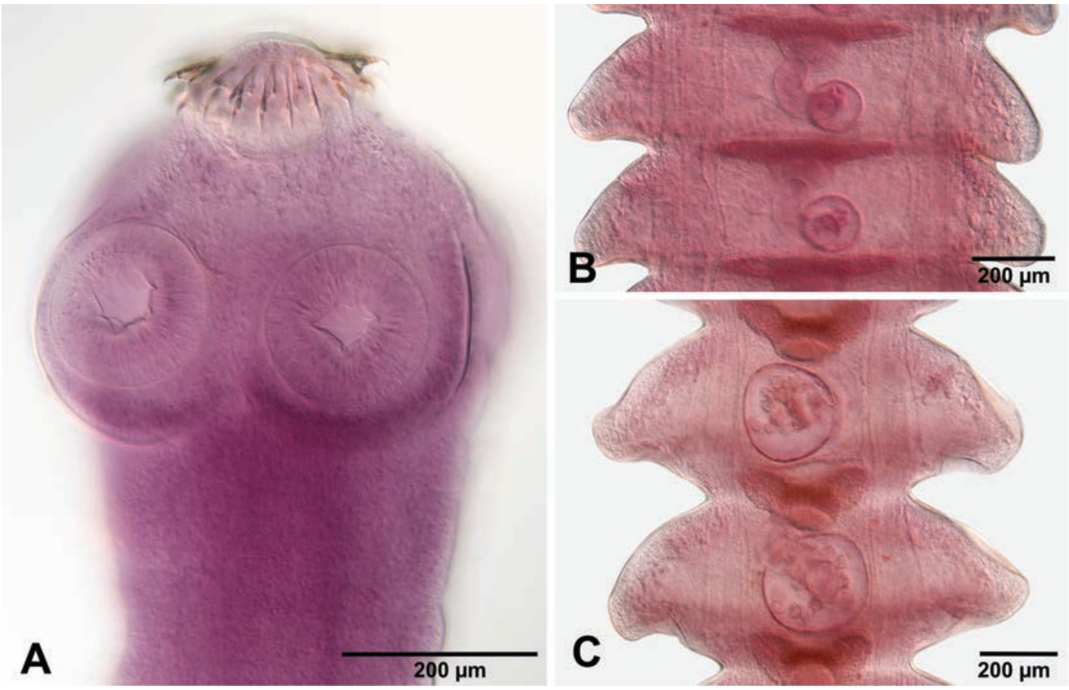


FIGURE 19. PARUTERINIDAE: *Sphaeruterina* sp. from *Mixornis gularis* from Vietnam. **(A)** Scolex. **(B)** Post-mature proglottids. **(C)** Pre-gravid proglottids.

this material continues. To date, the new genus *Cucolepis* Phillips, Mariaux & Georgiev, 2012 was erected (Phillips et al., 2012). Three new species have been described: *Cucolepis cincta* Phillips, Mariaux & Georgiev, 2012 from Paraguay, *Anonchotaenia vaslata* Phillips, Georgiev, Waeschenbach & Mariaux, 2014 also from Paraguay, and *A. prolixa* Phillips, Georgiev, Waeschenbach & Mariaux, 2014 from Chile (Phillips et al., 2012, 2014). Redescriptions of five species have also been published (Phillips et al., 2014; Dimitrova et al., in press). At least nine additional new species appear to be represented among this material. Additionally, specimens of *Dictyterina cholodkowskii* (Skrjabin, 1914) Spasskii in Spasskaya & Spasskii, 1971 collected in China were used to study the vitellogenesis of a paruterinid for the first time (Yoneva et al., 2016).

In total, 33 specimens of 25 species were included in our molecular phylogenetic analyses; 27 of these had been collected during PBI project expeditions. The paruterinids were found to group with the taeniids and metadilepidids, albeit in a clade with relatively poor nodal support (Fig. 5). As the metadilepidids grouped among the paruterinids, it is possible that, based on traditional concepts (i.e., Khalil et al., 1994), one or possibly both of these families may not be monophyletic, although nodal support for these inferences is currently weak.

5.15. Progynotaeniidae Fuhrmann, 1936

Fuhrmann (1936) erected the family Progynotaeniidae for four genera, three of which were initially considered to belong to the Acoleidae (see Khalil, 1994a). The criteria he applied to distinguish his new family from the acoleids included their proterogyny (i.e., maturation of the female gonads before the male genital system), small body size (strobila consisting of only few proglottids), and weak body musculature. Fuhrmann (1936) subdivided the family into the subfamilies Progynotaeniinae with hermaphroditic proglottids exhibiting proterogyny (i.e., with each proglottid initially functioning as female and later becoming simultaneously gravid and male) and Gynandrotaeniinae, characterized by a strobila with regularly alternating male and female proglottids. Skrjabin (1940), Yamaguti (1959), Ryzhikov and Tolkacheva (1981), Schmidt (1986), and Khalil et al. (1994) also recognized the family Progynotaeniidae as valid but the subfamilies were recognized only by a subset of these authors (i.e., Skrjabin, 1940; Yamaguti, 1959; Ryzhikov and Tolkacheva, 1981).

The only monograph on the Progynotaeniidae was that of Ryzhikov and Tolkacheva (1981), who recognized six genera and 15 valid species. Khalil (1994b) provided emended diagnoses and a key to the genera. More recent taxonomic developments include redescriptions of known and descriptions of new species (Macko and Špakulová, 1995, 1998; Nikolov and Georgiev, 2002; Nikolov et al., 2005) as well as revisions of the genera *Leptotaenia* Cohn, 1901 (see Nikolov et al., 2004) and *Paraprogynotaenia* Rysavy, 1966 (see Nikolov and Georgiev, 2008). Currently, 24 species are recognized in the family's six valid genera.

The diagnostic features of the family are the sac-like rostellar apparatus with a highly protrusible rhynchus that is armed with one or two rows of rostellar hooks (Fig. 20B), and the lack of a vaginal pore (Fig. 20D). Whereas the Progynotaeniinae exhibit monoecious proglottids and testes arranged in two groups positioned lateral to the uterus (Fig. 20D), the Gynandrotaeniinae bear dioecious proglottids, and an enormous, heavily armed cirrus.

The host associations of the family include flamingos for *Leptotaenia* and *Gynandrotaenia* Fuhrmann, 1936, and waders (Charadriiformes) for the remaining genera (Ryzhikov and Tolkacheva, 1981). *Gynandrotaenia stammeri* Fuhrmann, 1936 is the only species for which a complete life-cycle is known. This parasite of flamingos uses brine shrimp (*Artemia* spp.) as an intermediate host, with cysticercoids developing in the body cavity (Gvozdev and Maksimova, 1979; Georgiev et al., 2005). Progynotaeniids are generally distributed along seashores and wetlands, mostly in tropical areas, throughout the world, although some species occur in aquatic birds in temperate latitudes (Ryzhikov and Tolkacheva, 1981).

Discoveries over the course of the PBI project. A single undescribed species of *Proterogynotaenia* was collected from the American oystercatcher (*Haematopus palliatus* Temminck) in Chile, and an unidentified genus and species was obtained from *Charadrius vociferus* L. in the USA. The former is the first record of a progynotaeniid from South America, although a member of the family has been reported from Cuba (Rysavy, 1966).

For the first time, progynotaeniids were included in a molecular phylogenetic study (5 specimens representing 3 species). These specimens were found to compose a monophyletic group, which appears to be the sister group of a clade consisting of the Acoleidae and Gyrocoeliinae (all parasitic in Charadriiformes). Our results question the monophyly of the suborder Acoleata, for this clade appears to be only distantly related to the clade of grebe parasites (i.e., Dioicocestinae plus several amabiliid genera).

5.16. Taeniidae Ludwig, 1886

The family Taeniidae was erected by Ludwig (1886) for nine species of *Taenia* L., 1758, which then included the most common large tapeworms from humans and domestic animals, as well as a species that is now placed in the genus *Echinococcus* Rudolphi, 1801. The features he identified as characterizing the family were rostellar armature, proglottid shape, position of the genital pores, and lack of a uterine pore. Other typical characteristics of the group are the long ribbon-like strobila, the shape of the rostellar hooks (Fig. 21A) (when present), and

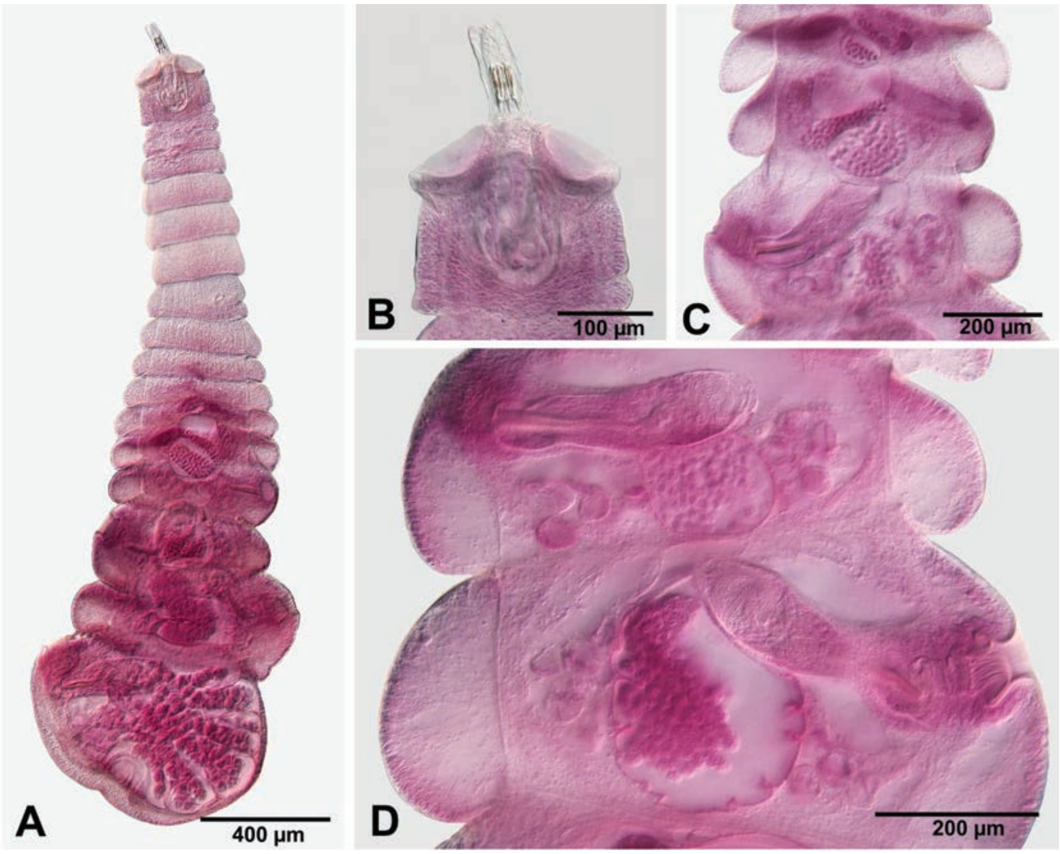


Figure 20. PROGYNOTAENIIDAE: *Proterogynotaenia* sp. from *Haematopus palliatus* from Chile. **(A)** Whole worm. **(B)** Scolex. **(C)** Mature proglottids. **(D)** Post-mature and pre-gravid proglottids. Note the functional male genitalia in the latter..

possession of numerous testes, a bilobed ovary (Fig. 21B), a sacciform uterus with lateral branches (Fig. 21C), and thick-walled eggs. The family includes both some of the largest tapeworms, with some species reaching several meters in length, and some of the smallest tapeworms, with adults of *Echinococcus* reaching only a few millimeters in length.

The family has been unanimously accepted since its erection. Skrjabin (1940) and Wardle et al. (1974) proposed elevating it to subordinal or ordinal status, respectively, however, neither proposal has been generally embraced. The number of genera attributed to the Taeniidae has varied widely. For example, Wardle and McLeod (1952) recognized seven, Abuladze (1964) recognized 13, Wardle et al. (1974) recognized 11, and Schmidt (1986) only five genera. The source of much of this confusion is the variation seen in the metacestode stage across the family, because a number of genera were originally erected on the basis of metacestode characters alone and have subsequently been synonymized or attributed to other families (see Rausch [1994b] for a review). In fact, in his major revision, Rausch (1994b) considered only *Taenia* and *Echinococcus* as valid genera, placing each in its own subfamily (i.e., Taeniinae Stiles, 1896 and Echinococcinae Abuladze, 1960). Nevertheless, the taxonomic position of a few genera formerly assigned to the Taeniidae, and *Dasyurotaenia* Beddard, 1912 in particular, remains doubtful. The most important taxonomic treatments of the family are those of Abuldaze (1964), Verster (1969), Rausch (1994b), and Loos-Frank (2000); Lavikainen (2014) provided a particularly detailed summary of the taxonomic history of the family.

Given their importance for humans, human activities, and domesticated animals, taeniids have been studied more intensely than any other group of tapeworms. This also applies to their diversity and systematics with what turn out to be a large number of synonyms, both at the generic and specific level, having been established over time. Quite unusual for tapeworms is the fact that many studies have led to the recognition of subspecies, "genotypes" or "strains," particularly for the most pathogenic taxa and especially within *Echinococcus* (see Lymbery, 2017).

The life-cycles of many taeniid species are known. In general, mammals serve both as herbivorous intermediate (Rodentia, Artiodactyla, and Lagomorpha) and carnivorous definitive (Carnivora, humans) hosts (Rausch, 1994b). Since the introduction of *Echinococcus* to Australia, the family is present on all continents, although it is poorly represented in South America (Rausch, 1994b; Jenkins and Macpherson, 2003). Several species have been dispersed by anthropogenic activities (Rausch, 1995).

The Taeniidae are largely considered to represent a monophyletic group and, in fact, most phyogenetic studies focused on either *Taenia* or *Echinococcus* use the other genus as an outgroup (Lavikainen, 2014). Hoberg et al. (1999) formally studied the phylogenetic position of the family based on analyses of morphological data. They found it to be the well-supported sister group to a clade consisting of the Paruterinidae plus Metadilepididae, with the "epiphyseal structure" of hooks serving as a synapomorphy for this three-family group. They also found these taxa (+ *Dasyurotaenia*) to be early diverging within the order and to represent the sister group of all other cyclophyllidean families, with the exception of the Catenotaeniidae, Mesocestoididae, and Nematotaeniidae. In contrast, the molecular analysis of von Nickisch-Rosenegk et al. (1999) placed the Taeniidae (+ Dipylidiidae) as the sister group to the Anoplocephalidae and Mesocestoididae, although with weak support.

Prior to the PBI project, the interrelationships among *Taenia* species based on morphological features have been examined in some detail (e.g., Verster, 1969; Hoberg et al., 2000; Hoberg, 2006). A number of molecular studies have also focused on the genus (e.g., Okamoto et al., 1995; Lavikainen et al., 2008). But, in general there has been poor congruence between results from morphological and molecular analyses (see Lavikainen [2014] for a summary). *Echinococcus* has received much less attention in terms of morphological contributions beyond that of Lymbery (1992), and also fewer molecular studies (e.g., Bowles et al., 1995; Le et al., 2002; Saarma et al., 2009) have examined the inter- and intraspecific relationships among species of *Echinococcus*. Nakao et al. (2013a) and Lymbery (2017) published recent comprehensive reviews of this topic.

Discoveries over the course of the PBI project. No new adult material of this family was collected during the PBI expeditions; this was largely because their definitive hosts are primarily Carnivora and are thus difficult to collect for obvious legal and logistical reasons. A single larva was collected from a cricetid rodent in Alaska as part of the PBI project. The bulk of the material examined came from other sources.

Recent molecular phylogenies (some unrelated to the PBI project) (e.g., Lavikainen et al., 2008; Knapp et al., 2011) confirmed the monophyly of *Echinococcus* and the paraphyly of *Taenia* as traditionally defined, leading to the latter genus being split by Nakao et al. (2013b). However, these studies did not consider the placement of the Taeniidae within the Cyclophyllidea. To clarify the interrelationships among species of *Taenia*, molecular phylogenies were constructed using nuclear and mitochondrial genes (Nakao et al., 2013a).

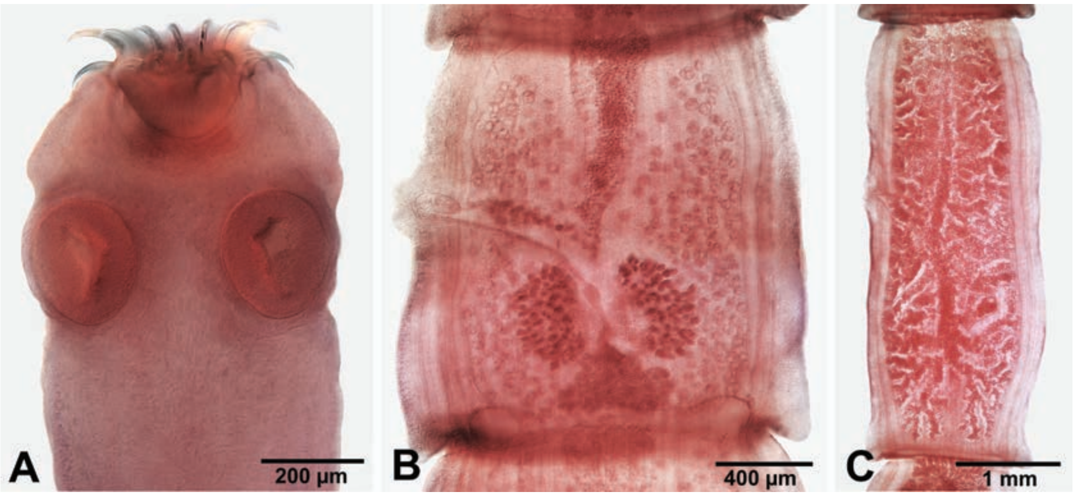


Figure 21. TAENIIDAE: *Taenia crassiceps* from *Vulpes vulpes* from Bulgaria. **(A)** Scolex. **(B)** Post-mature proglottid. **(C)** Gravid proglottid with branched uterus.

The resulting phylogenetic trees demonstrated that both *Taenia mustelae* Gmelin, 1790, and a clade consisting of *Taenia parva* Baer, 1924, *Taenia krepkogorski* (Schulz & Landa, 1934) Verster, 1969, and *Taenia taeniaeformis* (Batsch, 1786) Wolffügel, 1911 are only distantly related to the other species of *Taenia*. Based on these results, the resurrection of *Hydatigera* Lamarck, 1816 for *T. parva* Baer, 1924, *T. krepkogorski*, and *T. taeniaeformis* was proposed. They also erected a new genus, *Versteria* Nakao, Lavikainen, Iwaki, Haukisalmi, Konyaev, Oku, Okamoto & Ito, 2013 with *T. mustelae* Gmelin, 1790, thereby establishing the new combination *V. mustelae* (Gmelin, 1790) Nakao, Lavikainen, Iwaki, Haukisalmi, Konyaev, Oku, Okamoto & Ito, 2013. Due to obvious morphological and ecological similarities, *Taenia brachyacantha* Baer & Fain, 1951 was also included in *Versteria* (thus establishing *V. brachyacantha* [Baer & Fain, 1951] Nakao, Lavikainen, Iwaki, Haukisalmi, Konyaev, Oku, Okamoto & Ito, 2013), although molecular evidence was not available. Furthermore, although historically regarded as a single species, these authors clearly demonstrated that *Taenia taeniaeformis* comprises two cryptic species. One of these was described as the new species *Taenia arctos* Haukisalmi, Lavikainen, Laaksonen & Meri, 2011, from the brown bear *Ursus arctos* L., 1758 (definitive host) and moose/elk *Alces* spp. (intermediate hosts) from Finland (type locality) and Alaska by Haukisalmi et al. (2011). The independent status of this new species and the conspecificity of its adults and metacestodes had previously been confirmed with mitochondrial sequence data (Lavikainen et al., 2011). Haukisalmi et al. (2011) also identified potentially useful morphometric features that had not been previously applied to *Taenia* taxonomy.

Recently, molecular approaches have been used effectively to help with the detection of additional new species in this group (Haukisalmi et al., 2011; Lavikainen et al., 2011, 2013), as a consequence, at present a total of 56 species, including the recently described *Hydatigera kamiyai* Iwaki, 2016 (in Lavikainen et al. [2016]) and *Taenia lynciscapreoli* Haukisalmi, Konyaev, Lavikainen, Isomursu & Nakao, 2016, are recognized in four genera, with a few others awaiting formal description (Lavikainen, 2014; Haukisalmi et al, 2016a; Lavikainen et al., 2016).

Our more comprehensive phylogenetic analyses of the Cyclophyllidea overall, which included the above and other published sequences of taeniids, yielded topologies in which the taeniids grouped together in a clade with the paruterinids and metadilepidids, in which the taeniids formed the sister group of two paruterinid genera known to use vertebrates as intermediate hosts (results not shown in Fig. 5).

6. DISCUSSION AND CONCLUSIONS

The global collecting efforts of this project likely represent the largest such collective undertaking ever conducted for cyclophyllideans both in their magnitude and diversity, involving the examination of 4,633 host individuals from 1,132 host species (avian and mammalian) across 21 countries. Specimens of about 10% of all known bird species were examined; among those, 234 species of birds were reported to host cestodes for the first time. A smaller proportion of the mammalian fauna was studied but it nevertheless revealed 36 new cestode hosts. As expected, no new taxa at the familial level were found, which confirms that all of the primary evolutionary lineages of the order have likely already been discovered. Material of approximately 108 species and 12 genera of Cyclophyllidea that are new to science was collected, that is about 16% of all identified species found during the course of this project, and even close to 40% of those found in mammals. Globally, this represents an estimated 3% increase in the total number of species in Cyclophyllidea, which is a particularly significant contribution considering the size of the order. This indicates that the specific diversity in the Cyclophyllidea is still far from being fully documented.

Our results indicate that at least 40% of all studied bird species host cestodes. Approximately 75% of these host at least one cestode species while the remaining 25% host two or more species of cestode. Although higher species richness may have been present, our sampling methodology did not allow us to uncover it. As was already known (see, e.g., Fuhrmann, 1932), aquatic bird species generally host a relatively high diversity of cestodes, while terrestrial bird species mostly host a single and rarely a few species of cestodes. Most bird species that were not found to host cestodes were represented by only one to three individuals in our captures (81%); those for which no cestodes were found, despite the examination of five birds or more, were only few and mostly distributed in families that either have particular diets (Alcedinidae, Fringillidae Leach) or seem to represent exceptions (Cisticolidae Sundevall, Asian Muscicapidae). As expected (e.g., Fuhrmann, 1932; Bona, 1975), host-specificity was high and each cestode species was only rarely found in more than a single host species. This leads us to estimate that the total number of cyclophyllidean species parasitizing birds globally may be as high as 8,000.

The number of cyclophyllideans infecting mammals is even more difficult to estimate. However, our results lead us to predict that the highly-parasitized Soricomorpha alone, probably host a greater number of species of cyclophyllideans than are presently known for the entire class Mammalia. This is due to the strict nature of the specificity of their cestodes (Hunkeler, 1974; Genov, 1984; Vaucher, 1992; Haukisalmi et al., 2010b). However, as has been shown in recent studies, rodents also are likely to harbor a greater cestode diversity than currently appreciated (Haukisalmi et al., 2008, 2009, 2014, 2016b). The genus *Arostrilepis* has been recently shown to contain at least 13 genetically and morphologically distinguishable species in high latitudes of Eurasia and North America (Makarikov et al., 2012, 2013a; Makarikov and Hoberg, 2016).

New taxa were identified from all major geographic regions surveyed. In the case of birds, the Neotropics remain a important source of novel cestode taxa, largely because of the rich diversity of the candidate host taxa and comparatively limited number of previous survey work that has been done in this region. However non-tropical areas—even those with a cold climate and relatively low candidate host diversity—such as Chilean Patagonia, were found to be home to a surprisingly diverse and very poorly known cestode fauna. We thus recommend that such regions should not be overlooked in future avian cestode surveys.

The unknown diversity of cestodes of mammals is likely to be high in all areas of the world. For example, the single Luzon island of the Philippine archipelago sampled as part of the PBI project was found to be home to a remarkably high number of new species of *Hymenolepis* from rodents; in fact that number equals the total number of species of the genus known so far from whole continents like Eurasia or North America (Makarikov et al., 2013b, 2015a). Considering that large regions of the planet and a very large number of small mammals have yet to be examined for cestodes, we anticipate that the number of tapeworms described from these hosts to continue to grow steadily. This is true even in those regions where a strong parasitological tradition exists, as shown by our results from Russian and North American collections. However, further exploration in tropical regions where mammal parasite faunas remain poorly known, especially in Asia, is likely to yield substantial additional novelty.

Beyond the discovery of new taxa, specimens collected on our PBI expeditions facilitated the redescription and revision of numerous cyclophyllidean taxa. This was especially important because the descriptions of most of the species described in the 19th and the first half of the 20th century were based on single specimens, often collected by non-specialists, and improperly fixed and preserved. As consequence, descriptions based on these specimens are frequently vague and do not allow morphological interpretations according to current taxonomic standards. The newly collected material was of extremely high quality as it was fixed, preserved, and mounted according to a standardized protocol. It is of high scientific value, since taxonomic revisions and redescriptions are a substantial part of the work associated with understanding the global cestode diversity.

The majority of the samples collected and preserved for morphological studies was complemented by specimens preserved for molecular analyses. In combination, our collections yielded the most diverse molecular tissue collection of cyclophyllidean cestodes in existence, with over 340 specimens representing over 250 species. These specimens have been, and will continue to be, essential for confirming species identifications and identifying cryptic species. In a larger context, apart from the Gyrocoeliinae needing to be extracted from the Dioicocestidae, the paraphyly of the Anoplocephalidae, and possibly also of the Paruterinidae, our molecular results, to date, confirm the validity of the majority of the morphologically defined cyclophyllidean families, and preliminarily support a sister group relationship between the Mesocestoididae and all other Cyclophyllidea. The molecular data generated over the course of the PBI project, in conjunction with almost complete mitochondrial genome data for key lineages, will be crucial for strengthening the phylogenetic framework and enabling the study of cyclophyllidean evolution at a scale that was not possible before the implementation of this project.

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TABLE 1. List of 437 valid cyclophyllidean genera by family. New taxa resulting from PBI project activities indicated in bold.

VALID HIGHER TAXA

FAMILY ACOLEIDAE FUHRMANN, 1899 [2 GENERA]
- *Acoleus* Fuhrmann, 1899
- *Diplophallus* Fuhrmann, 1900

FAMILY AMABILIIDAE BRAUN, 1900 [11 GENERA]
- *Amabilia* Diamare, 1893
- *Decarabia* Konyaev & Gulyaev, 2005
- *Diporotaenia* Spasskaya, Spasskii & Borgarenko, 1971
- *Isezhia* Gulyaev & Koyaev, 2004
- *Joyeuxilepis* Spasskii, 1947
- *Laterorchites* Fuhrmann, 1932
- *Mircia* Konyaev & Gulyaev, 2006
- *Pseudoschistotaenia* Fotedar & Chishti, 1976
- *Ryjikovilepis* Gulyaev & Tolkacheva, 1987
- *Schistotaenia* Cohn, 1900
- *Tatria* Kowalewski, 1904

FAMILY ANOPLOCEPHALIDAE BLANCHARD, 1891 [81 GENERA]
- Subfamily Anoplocephalinae Blanchard, 1891
  - *Afrobaeria* Haukisalmi, 2008
  - ***Afrojoyeuxia* Haukisalmi, 2013**
  - *Andrya* Railliet, 1893
  - *Anoplocephala* Blanchard, 1848
  - *Anoplocephaloides* Baer, 1923
  - *Aporina* Fuhrmann, 1902
  - ***Arctocestus* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
  - ***Beringitaenia* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
  - *Bertiella* Stiles & Hassell, 1902
  - *Bulbutaenia* Beveridge, 1994
  - ***Chionocestus* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
  - *Cittotaenia* Riehm, 1881
  - ***Cookiella* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
  - *Crossotaenia* Mahon, 1954
  - *Ctenotaenia* Railliet, 1893

Diandrya Darrah, 1930
Diuterinotaenia Gvozdev, 1961
***Douthittia* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
Ectopocephalium Rausch & Ohbayashi, 1974
Equinia Haukisalmi, 2009
***Eurotaenia* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
Flabelloskrjabinia Spasskii, 1951
Gallegoides Tenora & Mas-Coma, 1978
Genovia Haukisalmi, 2009
***Gulyaevia* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
Hemiparonia Baer, 1925
Hokkaidocephala Tenora, Gulyaev & Kamiya, 1999
***Hunkeleriella* Haukisalmi, 2013**
Killigrewia Meggitt, 1927
***Lemminia* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
Leporidotaenia Genov, Murai, Georgiev & Harris, 1990
Marmotocephala Gvozdev, Zhigileva & Gulyaev, 2004
Microcephaloides Haukisalmi, Hardman, Hardman, Rausch & Henttonen, 2008
***Microticola* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
Moniezia Blanchard, 1891
Moniezoides Fuhrmann, 1918
Monoecocestus Beddard, 1914
Mosgovoyia Spasskii, 1951
Neandrya Haukisalmi & Wickström, 2005
Neoctenotaenia Tenora, 1976
Parandrya Gulyaev & Chechulin, 1996
Paranoplocephala Lühe, 1910 (syn. *Aprostatandrya* Kirshenblat, 1938)
Paranoplocephaloides Gulyaev, 1996
Parasciurotaenia Haukisalmi, 2009
Paronia Diamare, 1900
***Phascolocestus* Beveridge, 2014**
Phascolotaenia Beveridge, 1976
Progamotaenia Nybelin, 1917
Pseudocittotaenia Tenora, 1976
Pulluterina Smithers, 1954
***Rauschoides* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
***Rodentocestus* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
Schizorchis Hansen, 1948
Stringopotaenia Beveridge, 1978
***Tenoraia* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
Triplotaenia Boas, 1902
Triuterina Fuhrmann, 1922
Viscachataenia Denegri, Dophic, Elissondo & Beveridge, 2003
Wallabicestus Schmidt, 1975

Subfamily Linstowiinae Fuhrmann, 1907
Atriotaenia Sandground, 1926
Cycloskrjabinia Spasskii, 1951
Echidnotaenia Beveridge, 1980
Gekkotaenia Bursey, Goldberg & Kraus, 2005
Linstowia Zschokke, 1899
Mathevotaenia Akhumyan, 1946
Oochoristica Lühe, 1898
Panceriella Stunkard, 1969
Paralinstowia Baer, 1927
Pritchardia Gardner, Agustín Jimenez & Campbell, 2013
Sinaiotaenia Wertheim & Greenberg, 1971
Tupaiataenia Schmidt & File, 1977
Witenbergitaenia Wertheim, Schmidt & Greenberg, 1986

Subfamily Inermicapsiferinae Lopez-Neyra, 1943
Inermicapsiper Janicki, 1910
Metacapsifer Spasskii, 1951
Pericpasifer Spasskii, 1951
Thysanotaenia Beddard, 1911
Subfamily Thysanosomatinae Fuhrmann, 1907
Avitellina Gough, 1911
Stilesia Ralliet, 1893
Thysaniezia Skryabin, 1926
Thysanosoma Diesing, 1835
Wyominia Scott, 1941

FAMILY CATENOTAENIIDAE SPASSKII, 1950 [6 GENERA]
Subfamily Catenotaeniinae Spassky, 1950
Catenotaenioides Haukisalmi, Hardman & Henttonen, 2010
Catenotaenia Janicki, 1904
Hemicatenotaenia Tenora, 1977
Pseudocatenotaenia Tenora, Mac-Coma, Murai & Feliu, 1980
Subfamily Skrjabinotaeniinae Genov & Tenora, 1979
Meggittina Lynsdale, 1953
Skrjabinotaenia Akhumyan, 1946

FAMILY DAVAINEIDAE BRAUN, 1900 [37 GENERA]
Subfamily Davaineinae Braun, 1900
Abuladzugnia Spasskii, 1973
Baerfainia Yamaguti, 1959
Calostaurus Sanders, 1957
Cotugnia Diamare, 1893
Davainea Blanchard, 1891
Davaineoides Fuhrmann, 1920
Delamuretta Spasskii, 1977
Demidovella Spasskii & Spasskaya, 1976
Diorchiraillietina Yamaguti, 1959
Dollfusoquenta Spasskii, 1973
Fernandezia López-Neyra, 1936
Fuhrmannetta Stiles & Orleman, 1926
Gvosdevinia Spasskii, 1973
Houttuynia Furhmann, 1920
Idiogenoides López-Neyra, 1929
Manitaurus Spasskaya & Spasskii, 1971
Metadavainea Baer & Fain, 1955
Multicotugnia Lópex-Neyra, 1943
Numidella Spasskaya & Spasskii, 1971
Ophryocotyle Friis, 1870
Ophryocotyloides Fuhrmann, 1920
Ophryocotylus Srivastava & Capoor, 1977
Paroniella Fuhrmann, 1920
Paspalia Spasskaya & Spasskii, 1971
Pentocoronaria Matevosyan & Movsesyan, 1966
Pluviantaenia Jones, Khalil & Bray, 1992
Porogynia Railliet & Henry, 1909
Raillietina Fuhrmann, 1920
Skrjabinia Fuhrmann, 1920
Soninotaurus Spasskii, 1973
Vadifresia Spasskii, 1973
Subfamily Idiogeninae Fuhrmann, 1907
Chapamania Monticelli, 1893
Idiogenes Krabbe, 1868
Otiditaenia Beddard, 1912
Pseudoidiogenes Movsesyan, 1971

- *Satyanarayana* Khan, 1984
- *Sphyroncotaenia* Ransom, 1911

FAMILY DILEPIDIDAE FUHRMANN, 1907 [90 GENERA]

- *Acanthocirrus* Fuhrmann, 1907
- *Aelurotaenia* Cameron, 1928
- *Alcataenia* Spasskaya, 1971
- *Alproma* Spasskii, 1982
- *Amoebotaenia* Cohn, 1899
- *Angularella* Strand, 1928
- *Anomolepis* Spasskii, Yurpalova & Kornyushin, 1968
- *Anomotaenia* Cohn, 1900
- *Apokrimi* Bona, 1994
- *Apoliga* Bona, 1994
- *Arctotaenia* Baer, 1956
- *Arlenelepis* Georgiev & Vaucher, 2004
- *Arostellina* Neiland, 1955
- *Bakererpes* Rausch, 1947
- *Birovilepis* Spasskii, 1975
- *Bonaia* Mariaux & Vaucher, 1990
- *Bucerolepis* Spasskii & Spasskii, 1967
- *Burhinotaenia* Spasskii & Spasskaya, 1965
- *Capsulata* Sandeman, 1959
- *Chimaerula* Bona, 1994
- *Chitinorecta* Meggitt, 1927
- *Choanotaenia* Railliet, 1896
- *Cinclotaenia* Macy, 1973
- *Cotylorhipis* Blanchard, 1909
- *Cuculincola* Bona, 1994
- *Dictymetra* Clark, 1952
- *Dilepidoides* Spasskii & Spasskaya, 1954
- *Dilepis* Weinland, 1858
- *Eburneotaenia* Bona, 1994
- *Echinotaenia* Mokhehle, 1951
- *Emberizotaenia* Spasskaya, 1970
- *Ethiopotaenia* Mettrick, 1961
- *Eugonodaeum* Beddard, 1913
- *Eurycestus* Clark, 1954
- *Fuhrmannolepis* Spasskii & Yurpalova, 1967
- ***Gibsonilepis* Dimitrova, Mariaux & Georgiev, 2013**
- *Glanduluncinata* Bona, 1994
- *Gruitaenia* Spasskii, Borgarenko & Spasskya, 1971
- *Hepatocestus* Bona, 1994
- *Himantaurus* Spasskaya & Spasskii, 1971
- *Hirundinicola* Birova-Volosinovicova, 1969
- *Hunkeleria* Spasskii, 1992
- *Imparmargo* Davidson, Doster & Prestwood, 1974
- *Ivritaenia* Singh, 1962
- *Kintneria* Spasskii, 1968
- *Kotlanolepis* Murai & Georgiev, 1987
- *Kowalewskiella* Baczynska, 1914
- *Krimi* Burt, 1944
- *Laritaenia* Spasskaya & Spasskii, 1971
- *Lateriporus* Fuhrmann, 1907
- *Liga* Weinland, 1857
- *Malika* Woodland, 1929
- *Megacirrus* Beck, 1951
- *Megalacanthus* Moghe, 1926
- *Mirandula* Sanders, 1956

Molluscotaenia Spasskii & Andreiko, 1971
Monoliga Bona, 1994
Monopylidium Fuhrmann, 1899
Monosertum Bona, 1994
Multitesticulata Meggitt, 1927
Neoliga Singh, 1952
Neovalipora Baer, 1962
Neyralla Johri, 1955
Nototaenia Jones & Williams, 1967
Onderstepoortia Ortlepp, 1938
Ovosculpta Bona, 1994
Paraliga Belopolskaya & Kulachkova, 1973
Paricterotaenia Fuhrmann, 1932
Parorchites Fuhrmann, 1932
Platyscolex Spasskaya, 1962
Polycercus Villot, 1883
Prochoanotaenia Meggitt, 1924
Pseudangularia Burt, 1938
Pseudochoanotaenia Burt, 1938
Ptilotolepis Spasskii, 1969
Rallitaenia Spasskii & Spasskaya, 1975
Rauschitaenia Bondarenko & Tomilovskaja, 1979
Reticulotaenia Hoberg, 1985
Sacciuterina Matevosyan, 1963
Sobolevitaenia Spasskaya & Makarenko, 1965
Spasskytaenia Oshmarin, 1956
Spasspasskya Bona, 1994
Spiniglans Yamaguti, 1959
Spinilepis Oshmarin, 1972
Spreotaenia Spasskii, 1969
Stenovaria Spasskii & Borgarenko, 1973
Trichocephaloidis Sinitzin, 1896
Tubanguiella Yamaguti, 1959
Unciunia Skrjabin, 1914
Vitta Burt, 1938

FAMILY DIOICOCESTIDAE SOUTHWELL, 1930 [5 GENERA]
Subfamily Dioicocestinae Southwell, 1930
Dioicocestus Fuhrmann, 1900
Subfamily Gyrocoeliinae Yamaguti, 1959
Gyrocoelia Fuhrmann, 1899
Infula Burt, 1939
Shipleya Fuhrmann, 1908
Echinoshipleya Tolkacheva, 1979

FAMILY DIPYLIDIIDAE RAILLIET, 1896 [3 GENERA]
Dipylidium Leuckart, 1863
Diplopylidium Beddard, 1913
Joyeuxiella Fuhrmann, 1935

FAMILY GRYPORHYNCHIDAE SPASSKII & SPASSKAYA, 1973 [16 GENERA]
Amirthalingamia Bray, 1974
Ascodilepis Guildal, 1960
Baerbonaia Deblock, 1966
Bancroftiella Johnston, 1911
Clelandia Johnston, 1909
Cyclorchida Fuhrmann, 1907
Cyclustera Fuhrmann, 1901
Dendrouterina Fuhrmann, 1912
Glossocercus Chandler, 1935
Mashonalepis Beverley-Burton, 1960

Neogryporhynchus Baer & Bona, 1960
Paradilepis Hsü, 1935
Parvitaenia Burt, 1940
Proorchida Fuhrmann, 1908
Proparadilepis Kornyushin & Greben, 2014
Valipora Linton, 1927

FAMILY HYMENOLEPIDIDAE PERRIER, 1897 [130 GENERA]
Allohymenolepis Yamaguti, 1956
Amazilolepis Schmidt & Dailey, 1992
Amphipetrovia Spasskii & Spasskaya, 1954
Anatinella Spasskii & Spasskaya, 1954
Aploparaksis Clerc, 1903
Armadolepis Spasskii, 1954
Armadoskrjabinia Spasskii & Spasskaya, 1954
Arostrilepis Mas-Coma & Tenora, 1997
Arvicolepis Makarikov, Gulyaev & Chechulin, 2005
Avocettolepis Spasskii & Kornyushin, 1971
Biglandatrium Spasskaya, 1961
Blarinolepis Tkach & Kornyushin, 1997
Branchiopodataenia Bondarenko & Kontrimavichus, 2004
Calixolepis Macko & Hanzelova, 1997
Capiuterilepis Oschmarin, 1962
Chimaerolepis Spasskii & Spasskaya, 1972
Chitinolepis Baylis, 1926
Cladogynia Baer, 1938
Cloacotaenia Wolffhügel, 1938
***Colibrilepis* Widmer, Georgiev & Mariaux, 2013**
Confluaria Ablasov in Spasskaya, 1966
Coronacanthus Spasskii, 1954
Cryptocotylepis Skrjabin & Mathevossian, 1948
Debloria Spasskii, 1975
Dicranotaenia Railliet, 1892
Diorchilepis Lykova, Gulyaev, Melnikova & Karpenko, 2006
Diorchis Clerc, 1903
Diplogynia Baer, 1925
Diploposthe Jacobi, 1896
Ditestolepis Soltys, 1952
Dollfusilepis Vasileva, Georgiev & Genov, 1998
Drepanidotaenia Railliet, 1892
Dubininolepis Spasskii & Spasskaya, 1954
Echinatrium Spasskii & Yurpalova, 1965
Echinocotyle Blanchard, 1891
Echinolepis Spasskii & Spasskaya, 1954
Echinorhynchotaenia Fuhrmann, 1909
Ecrinolepis Spasskii & Karpenko, 1983
Fimbriaria Fröhlich, 1802
Fimbriariella Wolffhügel, 1936
Fimbriarioides Fuhrmann, 1932
Fimbriasacculus Alexander & McLaughlin, 1996
Flamingolepis Spasskii & Spasskaya, 1954
Fuhrmannacanthus Spasskii, 1966
Gastrotaenia Wolffhügel, 1938
Geraldolepis Czapliński & Vaucher, 1994
Globarilepis Bondarenko, 1966
Gulyaevilepis Kornienko & Binkienė, 2014
Gvosdevilepis Spasskii, 1953
Hamatolepis Spasskii, 1962
Helicoductus Deblock & Canaris, 2001

Hilmylepis Skrjabin & Mathevossian, 1942
Hispaniolepis López-Neyra, 1942
Hunkelepis Czapliński & Vaucher, 1994
Hymenandrya Smith, 1954
Hymenolepis Weinland, 1858
Jardugia Southwell & Hilmy, 1929
Lineolepis Spasskii, 1959
Lobatolepis Yamaguti, 1959
Lockerrauschia Yamaguti, 1959
Lophurolepis Spasskii, 1973
Mackoja Kornyushin, 1983
Mackolepis Spasskii, 1962
Mathevolepis Spasskii, 1948
Matiaraensis Dixit & Capoor, 1988
Microsomacanthus López-Neyra, 1942
Milina van Beneden, 1873
Monogynolepis Czapliński & Vaucher, 1994
Monorcholepis Oshmarin, 1961
Monotestilepis Gvosdev, Maksimova & Kornyushin, 1971
Nadejdlepis Spasskii & Spasskaya, 1954
Nematoparataenia Maplestone & Southwell, 1922
Neodiorchis Bilqees & Fatima, 1984
Neoligorchis Johri, 1960
Neomylepis Tkach, 1998
Neoskrjabinolepis Spassky, 1947
Nomadolepis Makarikov, Gulyaev & Krivopalov, 2010
Novobrachylepis Özdikmen, 2010
Octacanthus Spasskii & Spasskaya, 1954
Oligorchis Fuhrmann, 1906
Ortleppolepis Spasskii, 1965
Oschmarinolepis Spasskii & Spasskaya, 1954
Parabisaccanthes Maksimova, 1963
Paradicranotaenia López-Neyra, 1943
Parafimbriaria Voge & Read, 1954
Paramilina Makarikova, Gulyaev, Tiunov & Feng, 2010
Paraoligorchis Wason & Johnson, 1977
Pararetinometra Stock & Holmes, 1982
Pararodentolepis Makarikov & Gulyaev, 2009
Passerilepis Spasskii & Spasskaya, 1954
Pentorchis Meggitt, 1927
Podicipitilepis Yamaguti, 1959
Polytestilepis Oshmarin, 1960
Potorolepis Spasskii, 1994
Profimbriaria Wolffhügel, 1936
Protogynella Jones, 1943
Pseudandrya Fuhrmann, 1943
Pseudanoplocephala Baylis, 1927
Pseudhymenolepis Joyeux & Baer, 1935
Pseudobotrialepis Schaldybin, 1957
Pseudodiorchis Skrjabin & Mathevossian, 1948
Pseudoligorchis Johri, 1934
Relictolepis Gulyaev & Makarikov, 2007
Retinometra Spasskii, 1955
Rodentolepis Spasskii, 1954
***Sawadalepis* Makarikova & Makarikov, 2013**
Schmelzia Yamaguti, 1959
Skrjabinacanthus Spasskii & Morozov, 1959
Skrjabinoparaxis Krotov, 1949
Sobolevicanthus Spasskii & Spasskaya, 1954

Soricinia Spasskii & Spasskaya, 1954
Spasskylepis Schaldybin, 1964
Staphylepis Spasskii & Oschmarin, 1954
Staphylocystis Villot, 1877
Staphylocystoides Yamaguti, 1952
Sternolepis Dixit & Capoor, 1988
Sudarikovina Spasskii, 1951
Talpolepis Gulyaev & Melnikova, 2005
Thaumasiolepis Mariaux & Vaucher, 1989
Triodontolepis Yamaguti, 1959
Tschertkovilepis Spasskii & Spasskaya, 1954
Urocystis Villot, 1880
Vampirolepidoides Yamaguti, 1959
Vampirolepis Spasskii, 1954
Variolepis Spasskii & Spasskaya, 1954
Vaucherilepis Tkach, Vasileva & Genov, 2003
Vigisolepis Mathevossian, 1945
Vogelepis Czapliński & Vaucher, 1994
Wardium Mayhew, 1925
Wardoides Spasskii, 1963

FAMILY MESOCESTOIDIDAE PERRIER, 1897 [2 GENERA]
  Subfamily Mesocestoidinae Perrier, 1897
    Mesocestoides Vaillant, 1863
  Subfamily Mesogyninae Tschertkova & Kosupko, 1977
    Mesogyna Voge, 1952

FAMILY METADILEPIDIDAE SPASSKII, 1959 [10 GENERA]
Cracticotaenia Spasskii, 1966
Hamatofuhrmania Spasskii, 1969
Mariauxilepis Georgiev & Vaucher, 2003
Metadilepis Spasskii, 1949
Proparuterina Fuhrmann, 1911
Pseudadelphoscolex Mariaux, Bona & Vaucher, 1992
Schmidneila Spasskii & Spasskaya, 1973
Skrjabinoporus Spasskii & Borgarenko, 1960
Urutaulepis Georgiev & Vaucher, 2003
Yapolepis Mariaux, 1991

FAMILY NEMATOTAENIIDAE LÜHE, 1910 [5 GENERA]
Bitegmen Jones, 1987
Cylindrotaenia Jewell, 1916
Distoichometra Dickey, 1921
Lanfrediella Melo, Giese, Furtado, Soares, Gonçalves, Vallinoto & Santos, 2011
Nematotaenia Lühe, 1899

FAMILY PARUTERINIDAE FUHRMANN, 1907 [24 GENERA]
Anonchotaenia Cohn, 1900
Ascometra Cholodkowsky, 1912
Biuterina Fuhrmann, 1902
Cladotaenia Cohn, 1901
***Cucolepis* Phillips, Mariaux & Georgiev, 2012**
Culcitella Fuhrmann, 1906
Dictyterina Spasskii in Spasskaya & Spasskii, 1971
Francobona Georgiev & Kornyushin, 1994
Laterotaenia Fuhrmann, 1906
Lyruterina Spasskaya & Spasskii, 1971
Matabelea Mettrick, 1963
Metroliasthes Ransom, 1900
Mogheia López-Neyra, 1944
Neyraia Joyeux & Timon-David, 1934
Notopentorchis Burt, 1938

- *Octopetalum* Baylis, 1914
- *Orthoskrjabinia* Spasskii, 1947
- *Paruterina* Fuhrmann, 1906
- *Parvirostrum* Fuhrmann, 1908
- *Rhabdometra* Cholodkowsky, 1906
- *Spasskyterina* Kornyushin, 1989
- *Sphaeruterina* Johnston, 1914
- *Triaenorhina* Spasskii & Shumilo, 1965
- *Troguterina* Spasskii, 1991

FAMILY PROGYNOTAENIIDAE FUHRMANN, 1936 [6 GENERA]

- Subfamily Progynotaeniinae Fuhrmann, 1936
  - *Leptotaenia* Cohn, 1901
  - *Paraprogynotaenia* Rysavy, 1966
  - *Progynotaenia* Fuhrmann, 1909
  - *Proterogynotaenia* Fuhrmann, 1911
- Subfamily Gynandrotaeniinae Fuhrmann, 1936
  - *Gynandrotaenia* Fuhrmann, 1936
  - *Thomasitaenia* Ukoli, 1965

FAMILY TAENIIDAE LUDWIG, 1886 [4 GENERA]

- Subfamily Taeniinae Stiles, 1896
  - *Hydatigera* Lamarck, 1816
  - *Taenia* Linnaeus, 1758
  - ***Versteria* Nakao, Lavikainen, Iwaki, Haukisalmi, Konyaev, Oku, Okamoto & Ito, 2013**
- Subfamily Echinococcinae Abuladze, 1960
  - *Echinococcus* Rudolphi, 1801

FAMILY *INCERTAE SEDIS* [5 GENERA]

- *Quentinia* Spasskii, 1969
- *Deltokeras* Meggitt, 1927
- *Anoplotaenia* Beddard, 1911
- *Dasyurotaenia* Beddard, 1912
- *Insinuarotaenia* Spasskii, 1948