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Recent advances and current state of knowledge of phylogenetics and systematics of the Diplostomoidea with a proposal of a new classification system and a key to genera

T.J. Achatz[1] and V.V. Tkach[2]

[1]Department of Natural Sciences, Middle Georgia State University, Macon, Georgia 31206, USA and [2]Department of Biology, University of North Dakota, Starcher Hall, 10 Cornell Street Stop 9019, Grand Forks, North Dakota 58202, USA

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Corresponding author:
V.V. Tkach;
Email: vasyl.tkach@und.edu

Abstract

The superfamily Diplostomoidea Poirier, 1886 is a large, globally distributed group of digeneans characterized by the presence of a unique holdfast organ and parasitic in most major groups of vertebrates (birds, mammals, reptiles, fishes) as definitive hosts. A number of diplostomoideans are associated with diseases in their intermediate and, more rarely, definitive hosts. Prior to this work and upon the recent synonymization of the Brauninidae Wolf, 1903, the Diplostomoidea included 5 families: Bolbocephalodidae Strand, 1935; Cyathocotylidae Mühling, 1896; Diplostomidae Poirier, 1886; Proterodiplostomidae Dubois, 1936; and Strigeidae Railliet, 1919. The separation of these families was based primarily on the structure and shape of prosoma and holdfast organ as well as the presence/absence of cirrus sac and paraprostate. More rarely, distinguishing among families was based on life cycles and types of larval stages, excretory system or even host specificity. However, due to the inconsistent nature of most of morphological and biological characters across the Diplostomoidea and nearly universal lack of agreement on their relative value, the systematic history of the group has been extremely tumultuous, and none of many classification systems proposed over the last 140 years has become broadly accepted or supported by phylogenetic analyses. Extensive molecular phylogenetic studies of the Diplostomoidea in the last 15 years helped to partly improve the classification system and resolve multiple taxonomic questions. Notably, practically all molecular phylogenies have clearly demonstrated non-monophyly of the two largest families, the Diplostomidae and the Strigeidae and indicated it as systematic problem. We provide a brief overview of the history and current state of knowledge of diplostomoidean systematics and re-evaluate the classification system of the Diplostomoidea based on morphological and molecular evidence. We propose changes in the classification system that reconciles the traditional morphological and life cycle data with molecular phylogenies. The major element of the proposed classification system is the synonymization of the families Proterodiplostomidae and Strigeidae with the Diplostomidae as the only feasible way to resolve the problem of consistent non-monophyly of the latter two families and provide stability to the classification system.

Introduction

The superfamily Diplostomoidea Poirier, 1886 (Digenea Carus, 1863: Diplostomida Olson, Cribb, Tkach, Bray et Littlewood, 2003) is a large, globally distributed group of digeneans that parasitize most major groups of vertebrates (fish, reptiles, birds, mammals) as definitive hosts. Diplostomoideans are characterized by the presence of a unique holdfast organ that most often appears sucker-like or as a distinctly bilobed structure (Blasco-Costa and Locke 2017; Niewiadomska 2002a–g). Members of a few genera, such as *Codonocephalus* Diesing, 1850 and *Nematostrigrea* Sandground, 1934, have more unusual holdfast organ anatomy that may consist of weakly developed or indistinct lobes (like crimped paper) (Achatz *et al.* 2019b; Gudla *et al.* 2023). A number of diplostomoideans are associated with diseases in their intermediate hosts, including humans. For instance, several genera, including *Cardiocephaloides* Sudarikov, 1959; *Crassiphiala* Van Haitsma, 1925; *Diplostomum* von Nordmann, 1832; *Posthodiplostomum* Dubois, 1936; *Tylodelphys* Diesing, 1850; and *Uvulifer* Yamaguti, 1934, are known to be causative agents of a variety of parasitic diseases in fishes (Chappell *et al.* 1994; Lemly and Esch 1984; Matisz *et al.* 2010; Overstreet and Curran 2004; Tăbăran *et al.* 2013; Tkach and Achatz 2025; Vermaak *et al.* 2021). Larval *Alaria* spp. infections, resulting from consumption of uncooked or undercooked frogs, may cause clinical disease or even death (Freeman *et al.* 1976; Möhl *et al.* 2009; Uhrig *et al.* 2015). Less frequently, diplostomoideans may cause disease in their definitive hosts; for example, *Cyathocotyle bushiensis* Khan, 1962 is associated with massive die-offs of

aquatic birds in the Midwestern United States (Gibson *et al.* 1972; Herrmann and Sorensen 2009; Hoeve and Scott 1988), *Cardiocephaloides physalis* (Lutz, 1927) caused mortality in penguins (e.g., Randall and Bray 1983), and *Ichthyocotylurus erraticus* (Rudolphi, 1809) caused heavy pathological effect and mortality in terns (Pieters *et al.* 2014). At present, the Diplostomoidea includes 5 families: Bolbocephalodidae Strand, 1935; Cyathocotylidae Mühling, 1896; Diplostomidae Poirier, 1886; Proterodiplostomidae Dubois, 1936; and Strigeidae Railliet, 1919.

The separation of these families is largely based on the structure and shape of a prosoma and holdfast organ as well as the presence/absence of a cirrus sac and paraprostate. Only the Cyathocotylidae possess a cirrus sac, while members of the other four families have a variety of modified reproductive structures. Only members of the Proterodiplostomidae have a paraprostate, although at least one member of the family (*Mesodiplostomum* Dubois, 1936) lacks this organ. According to the *Keys to the Trematoda* (Niewiadomska 2002f), the Strigeidae differ from the Bolbocephalodidae, Diplostomidae, and Proterodiplostomidae (Niewiadomska, 2002a,c,e) by the shape of the prosoma and holdfast organ. However, the nature of the prosoma and holdfast organ are rather inconsistent among many of these digeneans, including some diplostomids and strigeids as discussed below.

Over the previous approximately 140 years, there have been numerous publications dealing with the systematics of the Diplostomoidea to a smaller or greater extent. Brandes (1888), Yamaguti (1958, 1971), Shigin (1986, 1993), Sudarikov (1960a,b, 1984), Shoop (1989), and especially Dubois (1936a,1936b, 1938, 1944, 1953, 1968, 1970a,b, 1987, 1989) were among the most prominent researchers who advanced our knowledge on the group and attempted to create some sort of a classification system using traditional characters such as general anatomy, life cycles and types of larval stages, excretory system, or even host specificity. Due to the nearly universal lack of agreement on the relative value of one or another morphological character, the systematic history of the group has been extremely tumultuous.

Despite the availability of DNA sequencing, few studies produced DNA sequences of diplostomoideans until the early 2010s (Bell *et al.* 2001; Bell and Sommerville 2002; Olson *et al.* 2003; Overstreet *et al.* 2002). Starting in the early 2010s, molecular studies on diplostomoideans expanded in an explosive manner; numerous publications on molecular methods and datasets of diplostomoideans have been published in a short time span which continues until now, and hopefully will not slow down any time soon (e.g., Achatz *et al.* 2019a–d, 2020, 2021a–c, 2022a–e, 2023a,b, 2024a,b, in press; Blasco-Costa *et al.* 2016; Blasco-Costa and Locke 2017; Brabec *et al.* 2015; Cech *et al.* 2020; Chibwana *et al.* 2015; Faltýnková *et al.* 2023, 2024; González-García *et al.* 2024; Gudla *et al.* 2023; Heneberg *et al.* 2018, 2020; Hernández-Mena *et al.* 2014, 2017; Hoogendoorn *et al.* 2019, 2020; Huston *et al.* 2018; Keller *et al.* 2021; Locke *et al.* 2010a,b, 2011, 2018, 2021; López-Hernández *et al.* 2018, 2019; López-Jiménez *et al.* 2018, 2022, 2023; Marcogliese and Locke 2021; Montes *et al.* 2022; Moszczynska *et al.* 2009; Nakao and Sasaki 2021; Negrelli *et al.* 2020; Nguyen *et al.* 2012; Pérez-Ponce de León *et al.* 2022; Pernett *et al.* 2022; Pyrka *et al.* 2021; Queiroz *et al.* 2020; Rochat *et al.* 2020; Rosser *et al.* 2016; Schwelm *et al.* 2020; Sereno-Uribe *et al.* 2019; Shamsi *et al.* 2021; Soldánová *et al.* 2017; Steenrod *et al.* 2019; Stoyanov *et al.* 2017; Tkach *et al.* 2020; Van Steenkiste *et al.* 2015). However, despite increased attention and the use of DNA sequencing in nearly every work on the Diplostomoidea in the last 15 years or so, the majority of studies were based on larval stages, either those in snails or in the second intermediate hosts such as fish, amphibians, and some invertebrates like snails and leeches. Certainly, this is because obtaining larval stages is easier and typically does not require any special collecting permits or Institutional Animal Care and Use Committee (IACUC) protocols. Relatively few properly identified adult diplostomoideans were sequenced prior to the works by the present authors.

Brabec *et al.* (2015) were the first to sequence and annotate mitochondrial genomes of two *Diplostomum* spp. Their study was an early indication that mitochondrial genes and even complete mitogenomes are not ideal targets for higher level phylogenies, although they can be very useful at lower taxonomic levels. For instance, in their phylogeny, *Diplostomum* spp. ended up being closer to members of the Plagiorchiida, which does not make a biological sense. Otherwise, molecular phylogenetic studies, often based on large ribosomal subunit (28S) rDNA sequences, demonstrated non-monophyly of most diplostomoidean families (i.e., Cyathocotylidae + Brauninidae Wolf, 1903 and Diplostomidae + Strigeidae + Proterodiplostomidae) (Achatz *et al.* 2019d, 2021c, 2022e, 2023b; Blasco-Costa and Locke 2017; Gudla *et al.* 2023; Hernández-Mena *et al.* 2017; Locke *et al.* 2018; Tkach *et al.* 2020). In the present work, we briefly discuss the history and current state of knowledge of diplostomoidean systematics and re-evaluate the classification system of the Diplostomoidea based on morphological and molecular evidence. We propose changes in the classification system that reconcile the traditional morphological and life cycle data with molecular phylogenies, and provide stability to the classification system.

Materials and methods

Large ribosomal subunit (28S) rDNA sequences of 215 species/species-level lineages were gathered from GenBank. These sequences included 8 nominal genera and 21 species/species-level lineages of cyathocotylids, 20 nominal genera and 132 species/species-level lineages of diplostomids, 18 nominal genera and 22 species/species-level lineages of proterodiplostomids, and 9 genera and 39 species/species-level lineages of strigeids (Supplementary Table S1). Duplicate sequences from conspecific isolates were not included in the analysis if they were identical to other sequences. Based on the topology of Pérez-Ponce de León and Hernández-Mena (2019), *Harmotrema laticaudae* Yamaguti, 1933 was selected as the outgroup. Sequences were initially aligned using ClustalW as implemented in MEGA7 software (Kumar *et al.* 2016). The alignment was 1,056 nucleotides long upon trimming to the length of the shortest sequence; 102 sites with ambiguous homology were excluded from the analysis.

Bayesian inference (BI) as implemented in MrBayes v3.2.6 software was used for the phylogenetic analyses (Kumar *et al.* 2016; Ronquist and Huelsenbeck 2003). The general time-reversible model with estimates of invariant sites and gamma-distributed among-site variation (GTR + G + I) model was identified as the best-fitting nucleotide substitution model using MEGA7 (Kumar *et al.* 2016). The BI analysis was performed as follows: Markov chain Monte Carlo (MCMC) chains were run for 6,000,000 generations with sampling frequency set at 1,000. Log-likelihood scores were plotted, and only the final 75% of trees were used to produce the consensus trees. The number of generations in the analysis was considered sufficient since the standard deviation stabilized below 0.01.

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Results and discussion

Molecular phylogeny

The phylogeny resulting from the analysis of 28S demonstrated the monophyly of the Cyathocotylidae *sensu* Achatz *et al.* (2019d) and non-monophyly of the Diplostomidae and Strigeidae (Figures 1 and S1). Cyathocotylidae (100% supported) had well-resolved and strong supported topology. In contrast, the Diplostomidae, Strigeidae, and Proterodiplostomidae formed an extensive polytomy (100% supported) that consisted of 14 branches (albeit some with only a single species or lacking strong support). The Diplostomidae was split across 10 separate clades: (i) *Diplostomum* spp. + *Tylodelphys* spp. + *Austrodiplostomum* spp. + *Pulvinifer macrostomum* (Jägerskiöld, 1900) + *Alaria* spp. (93% supported), (ii) *Posthodiplostomum* spp. + an unknown diplostomid (94% supported), (iii) *Uvulifer* spp. + *Crassiphiala* spp. + *Pseudocrassiphiala* spp. + *Posthodiplostomoides kinsellae* Achatz, Chermak, Martens, Pulis et Tkach, 2021 + *Subuvulifer* spp. + *Cercocotyla* spp. (90% supported), (iv) *Neodiplostomum* spp. (100% supported), (v) *Dolichorchis* spp. + *Neodiplostomum* spp. + *Neofibricola* spp. (less than 80% supported), (vi) *Bolbophorus* spp. (100% supported), (vii) *Sphincterodiplostomum* spp. (98% supported), (viii) *Bolbophorus damnificus* Overstreet, Curran, Pote, King, Blend et Grater, 2002 (single sequence), (ix) an unknown genus (single sequence), and (x) *Hysteromorpha triloba* (Rudolphi, 1819) (single sequence). Two diplostomids (*Codonocephalus urniger* Diesing, 1850 and *Proalarioides* sp.) were positioned within a clade of strigeids (see below). The Strigeidae was split into two major clades: (i) a 100% supported clade of (*Strigea* spp. + *Apharyngostrigea* spp. + *Parastrigea* spp.) + (*Apatemon* spp. + *Australapatemon* spp.) and (ii) a very weakly supported clade of *Nematostrigea* spp. + *Codonocephalus urniger* + *Proalarioides* sp. + *Cardiocephaloides* spp. + (*Ichthyocotylurus erraticus* + *Cotylurus* spp.). Although the clade of (*Strigea* spp. + *Apharyngostrigea* spp. + *Parastrigea* spp.) was 100% supported, the support for the two sub-clades of *Strigea* Abildgaard, 1790 was low, and the two species of *Apharyngostrigea* Ciurea, 1927 appeared as independent branches (Figures 1 and S1). Overall, proximal nodes within the diplostomid and strigeids clades were not strongly supported, while the distal nodal supports (i.e., those at the genus level) were strongly supported. All current proterodiplostomids formed one strongly supported clade (100%) that was well resolved.

History of Diplostomoidean systematics

General remarks

The taxonomic history of the superfamily Diplostomoidea is highly complex. Numerous publications (e.g., Dubois 1938, 1953, 1968, 1970a, 1970b, 1982, 1987, 1989; Sudarikov, 1959, 1960a,b, 1961, 1997; Yamaguti 1958, 1971) have introduced and disputed changes to taxonomy, composition, and systematics of diplostomoideans based on morphology and host-associations. We provide an abbreviated history of the superfamily, without focus on generic composition of its constituent families, followed by histories and details for each family.

Diplostomoidea

Originally, Blanchard (1847) placed what are currently known as diplostomoideans into the family Holostomidae Blanchard, 1847. Poirier (1886) examined a series of digeneans from crocodilians to determine their relationship with *Diplostomum* spp. He used the name Diplostomidae but did not establish the superfamily Diplostomoidea in his work. Nicoll (1937) first proposed the name Diplostomatoidea Nicoll 1937, which was not broadly recognized until Sudarikov (1960a) and Gibson (1996) reintroduced the taxon as Diplostomoidea Poirier, 1886.

Railliet (1919) erected the superfamily Strigeoidea Railliet, 1919 and family Strigeidae; the family was further split into 5 subfamilies: the Strigeinae Railliet, 1919; Polyotylinae Monticelli, 1888 (which included diplostomids); Cyathocotylinae Mühling, 1898; Alariinae Hall et Wigdor, 1918; and Brauninninae Wolf, 1903. Poche (1925) provided an alternative classification system, which included Tribus Fascioloidae Poche, 1925 that contained 4 families, including the Strigeidae. In the same work, Poche (1925) erected the supersuperfamily Strigeida Poche, 1925 that consisted of the Strigeidae and Cyathocotylidae.

Dubois (1936b) accepted supersuperfamily Strigeida of Poche (1925) containing superfamilies Strigeides (amended spelling of Strigeoidea) of Railliet (1919) and Cyathocotylides Dubois, 1936. The Strigeides was further split into subsuperfamilies Strigeines Dubois, 1936; Diplostomines Dubois, 1936; and Bolbocephalodines Dubois, 1936. The Strigeines and Bolbocephalodines only included 1 family each, the family Strigeidae and Bolbocephalodidae, while the Diplostomines included the Diplostomidae and Proterodiplostomidae. It is worth noting that in this classification system, only species with a cup-shaped prosoma and bilobed holdfast organ belonged to the Strigeidae; all diplostomids of reptiles were included in the Proterodiplostomidae based on host association. The Cyatocotylides included the families Cyathocotylidae and Brauninidae. Dubois (1953) maintained this classification system, although the spelling of the Diplostomines was amended to Diplostomatines.

In contrast, La Rue (1957) maintained the superfamily Strigeoidea of Railliet (1919) with families Strigeidae, Diplostomidae, Cyathocotylidae, Proterodiplostomidae, Bolbocephalodidae, and Brauninidae. Shortly after, Sudarikov (1960a) recognized the superfamily Diplostomatoidea that contained the families Diplostomidae, Alariidae Tubangui, 1922, and Bolbocephalodidae. Further, Sudarikov (1960b) considered Proterodiplostomatoidea Sudarikov, 1960 as a separate superfamily containing two families, Proterodiplostomatidae and Ophiodiplostomatidae Sudarikov, 1960. The most recent major systematic re-evaluation of the group by Niewiadomska (2002a–g) in the *Keys to the Trematoda* recognized 6 families: Bolbocephalodidae, Brauninidae, Cyathocotylidae, Diplostomidae, Proterodiplostomidae, and Strigeidae. However, since its publication, Niewiadomska's classification system underwent several changes, mostly associated with the introduction of molecular phylogenetics (see overview below). Most notably, the family Brauninidae was synonymized with the Cyathocotylidae by Achatz *et al.* (2019d).

Bolbocephalodidae

Dubois (1934) erected the family Bolbocephalidae Dubois, 1934 for the lone species *Bolbocephalus intestiniforax* Dubois, 1934 parasitic in birds; however, since the original genus name was preoccupied, Strand (1935) amended the genus name to *Bolbocephalodes* and the family name to Bolbocephalodidae. Sudarikov (1960a) considered it to be one of the families within the Diplostomatoidea, where it has remained since. Currently, the Bolbocephalodidae is the smallest family in the superfamily consisting of a single monotypic genus, *Bolbocephalodes* Strand, 1935. The morphology of *Bolbocephalodes intestiniforax* Dubois, 1934 is highly similar to strigeids as recognized by Niewiadomska (2002a) (i.e., a cup-shaped portion of prosoma and bilobed holdfast organ). Despite these similarities, it

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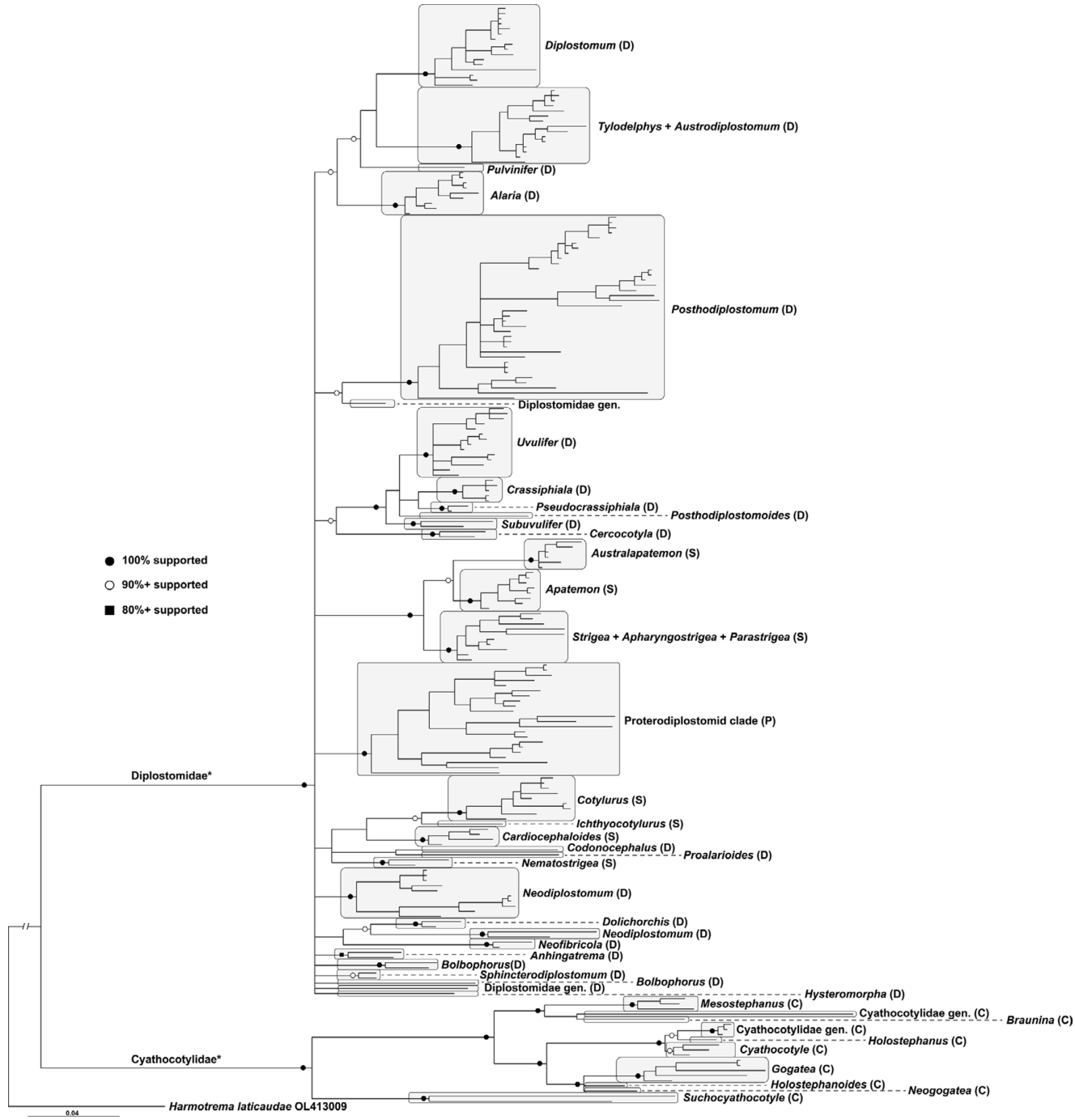

Figure 1. Phylogenetic interrelationships among 215 diplostomoidean taxa (see Supplementary Table S1) based on Bayesian Inference (BI) analysis of the partial 28S rDNA gene sequences. Bayesian inference posterior probability values lower than 80% are not shown. The scale-bar indicates the number of substitutions per site. * Families as recognized in the present study. Abbreviations for families as recognized prior to this work: C, Cyathocotylidae; D, Diplostomidae; P, Proterodiplostomidae; S, Strigeidae. Shaded rectangles indicate genera.

remains in its own family, with sequence data from this genus currently lacking.

Cyathocotylidae

The Cyathocotylidae has proven to be the least controversial family of diplostomoideans, in part because it contains the only diplostomoideans with a cirrus sac. Mühling (1896) initially established the Cyathocotyleae for the genus *Cyathocotyle* Mühling, 1896. Later, Poche (1925) amended the name to the Cyathocotylidae. More recently, Achatz *et al.* (2019d) synonymized the Brauninidae (containing a single genus *Braunina* Heider, 1900 also characterized by the presence of a cirrus sac) with the Cyathocotylidae based on morphological and molecular analyses. *Braunina* was transferred into the subfamily Braunininae of the Cyathocotylidae. At present, the Cyathocotylidae includes 6 subfamilies: Cyathocotylinae (3 genera), Muhlinginae Mehra, 1950 (1 genus), Prohemistominae Lutz, 1935 (5 genera), Prosostephaninae Szidat, 1936 (3 genera), Szidatiinae Dubois, 1938 (3 genera), and

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Suchocyathocotylinae Achatz, Pulis, Junker, Binh, Snyder et Tkach, 2019 (1 genus).

Few molecular phylogenetic studies have focused on cyathocotylids (Achatz *et al.* 2019d, 2024b; Sokolov *et al.* 2024). These studies have revealed somewhat contradictory evidence between morphology and molecular phylogenetic results. For instance, Achatz *et al.* (2019d) transferred *Holostephanoides* Dubois, 1983 from the Cyathocotylinae into the Szidatiinae based on strongly supported molecular evidence. At the same time, the adult morphology of *Holostephanoides* is highly similar to other cyathocotylines and quite different from the other 2 szidatiine genera, *Gogatea* Lutz, 1935 and *Neogogatea* Chandler et Rausch, 1947 (Achatz *et al.* 2019d, 2024b). Likewise, *Paracoenogonimus* Katsurada, 1914 (Prohemistominae) was shown to be nested among szidatiines, while *Georgduboisia* Sokolov, Vlasenkov, Bugmyrin, Kalmykov et Lebedeva, 2024 (Prosostephaninae) formed a strongly supported clade with cyathocotylines (Sokolov *et al.* 2024). Molecular phylogenies revealed similar problems with the subfamily classification systems among diplostomids and proterodiplostomids (Achatz *et al.* 2021c; Tkach *et al.* 2020; see discussion below) as well as in some other digenean families (Tkach *et al.* 2016, 2018). Hence, subfamily classification systems have been recently abandoned in several digenean families—for example Cryptogonimidae Ward, 1917; Dicrocoeliidae Looss, 1899; and Echinostomatidae Looss, 1899. Some of the recent authors (Achatz *et al.* 2021c; Tkach *et al.* 2018, 2020) pointed out that members of those subfamilies lack consistent differentiating morphological features. Based on these arguments and for the stability of the classification system, we do not recognize subfamilies of the Cyathocotylidae here and abandon the subfamily-based classification system of the family.

Diplostomidae

The history of the Diplostomidae was tumultuous. Poirier (1886) erected the family for *Diplostomum* spp. Railliet (1919) did not recognize the family and included diplostomids within the subfamily Polyotylinae in family Strigeidae. In Railliet's classification system, the subfamily Alariinae established by Hall and Wigdor (1918) for diplostomids of mammals (i.e., *Alaria* spp.) was maintained as a separate subfamily. Tubangui (1922) elevated its status to the family Alariidae.

Dubois (1936b, 1951) considered the Diplostomidae to be a separate family from the Strigeidae; in his classification system, the Diplostomidae included subfamilies Diplostominae (subsubfamilies Diplostomini Dubois, 1936 and Crassiphialini Dubois, 1936) and Alariinae; these subfamilies were almost entirely separated based on parasitism in avian or mammalian definitive hosts, respectively. Sudarikov (1960a,b) did not accept this arrangement and considered the family to include the subfamilies Diplostominae, Codonocephalinae Sudarikov, 1959, and Crassiphialinae Sudarikov, 1960. Later, Dubois (1970a,b) considered the Diplostomini and Crassiphialini, along with the Codonocephalini Sudarikov, 1959, to represent tribes of the Diplostomidae rather than subfamilies.

Shoop (1989) provided a substantial revision to the classification system of the Diplostomidae by breaking it up into 3 families: Bolbophoridae Shoop, 1989; Diplostomidae (subfamilies Alariinae and Diplostominae); and Neodiplostomidae Shoop, 1989 (Crassiphialinae and Neodiplostominae Shoop, 1989). Nieiwadomska (2002d) did not accept the classification system of Shoop (1989) and considered Diplostomidae comprising Alariinae, Codonocephalinae, Crassiphialinae, and Diplostominae. However, molecular phylogenetic studies (e.g., Achatz *et al.* 2019c, 2021a,c, 2022c–e, 2023b, 2024a; Blasco-Costa and Locke 2017; Hernández-Mena *et al.* 2017; Locke *et al.* 2018) revealed these subfamilies to be extensively non-monophyletic. This non-monophyly along with extensive morphological review led Achatz *et al.* (2021c) to reject the use of subfamilies within the Diplostomidae. Importantly, several prior studies (e.g., Achatz *et al.* 2021c, 2022e; Blasco-Costa and Locke 2017 and references therein) demonstrated that molecular phylogenies did not support host-based classification systems of diplostomoideans and emphasized the extensive amount of evolutionary host switching events between various host groups in this diverse, cosmopolitan digenean lineage.

Proterodiplostomidae

Dubois (1936a) erected the Proterodiplostomidae for diplostomids collected from reptiles, predominantly crocodilians. Most proterodiplostomids are characterized by the presence of a paraprostate that is associated with the male reproductive system. However, members of *Mesodiplostomum* and *Proalarioides* Yamaguti, 1933 lack this organ. The monophyly of this lineage, including *Mesodiplostomum*, has been demonstrated for most proterodiplostomids, with the exception of *Proalarioides* (Achatz *et al.* 2022a, 2024a; Tkach *et al.* 2020; Figures 1 and S1). Achatz *et al.* (2024a) transferred *Proalarioides* to the Diplostomidae. A brief systematic history of this family was published by Tkach *et al.* (2020); therefore, we are not presenting it in detail here. Among other systematic changes, Tkach *et al.* (2020) demonstrated the non-monophyly of the proterodiplostomid subfamilies and proposed to abandon their use. These findings were further supported by subsequent works on proterodiplostomids (Achatz *et al.* 2021b, 2022a, 2024a).

Recently, Achatz *et al.* (2022d) described the diplostomid *Neofibricola* Achatz, Martens, Kudlai, Junker, Boe et Tkach, 2022 from Nile crocodile *Crocodylus niloticus* Laurenti. Despite the host overlap, these new digeneans were demonstrated to be well separated from proterodiplostomids and lacked a paraprostate. This finding further demonstrates that host-based classification systems are not suitable for diplostomoidean systematics.

Strigeidae

The Strigeidae as originally recognized by Railliet (1919) was a mixture of contemporary strigeids, diplostomids, and cyathocotylids. Dubois (1936b) proposed the Strigeidae as it is currently accepted and split the family into the subfamilies Strigeinae with subsubfamilies Strigeini Dubois, 1936 and Cotylurini Dubois, 1936. Baer (1938) erected the subfamily Duboisiellinae Baer, 1938 for *Duboisiella proloba* Baer, 1938 collected from mammals, while all members of the Strigeinae only parasitize avian definitive hosts. Dubois (1953) accepted Duboisiellinae as a subfamily of the Strigeidae. Bisseru (1956) described a few species of *Neostrigea* Bisseru, 1956 and *Prostrigea* Bisseru, 1956 from crocodilians and placed them into a new family Neostrigeidae Bisseru, 1956 based primarily on parasitism in a specific group of hosts. Dubois (1968) considered the infection in crocodilians to be accidental and synonymized the family with the Strigeidae.

Sudarikov (1959) considered the Strigeini and Cotylurini to be subfamilies and separated *Pseudapatemon* Dubois, 1936 into a new subfamiliy, Pseudapatemoninae Sudarikov, 1959, based on its massive 'cork plug-like' holdfast organ. Dubois (1968) considered the Strigeini and Cotylurini to be tribes within the subfamily Strigeinae and rejected the Pseudapatemoninae. In turn, Sudarikov (1984) disagreed with Dubois (1968) and maintained the Pseudapatemoninae. Dubois (1968) separated his tribes based on the presence of vitellarium in prosoma and opisthosoma (Strigeini) or vitellarium

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entirely or tending to be confined to opisthosoma (Cotylurini). In *Keys to the Trematoda*, Niewiadomska (2002f) did not include the tribes into her key, but the first step of the key aligns with the separation of the former tribes.

More recently, molecular phylogenetic studies have demonstrated the Strigeidae to be clearly non-monophyletic (Achatz *et al.* 2019d, 2021c, 2022e, 2023b; Blasco-Costa and Locke 2017; Gudla *et al.* 2023; Hernández-Mena *et al.* 2017; Locke *et al.* 2018; Tkach *et al.* 2020). However, as subsequent studies have added a greater diversity of strigeid taxa, the family has broken up into multiple non-monophyletic clades/branches (Achatz *et al.* 2023b; Achatz *et al.* 2024a; Gudla *et al.* 2023; Figures 1 and S1). In some analyses, the diplostomid *Codonocephalus urniger* and *Proalarioides* sp. have clustered with strigeids (Figures 1 and S1). Furthermore, there are additional questions that may require attention at the genus level, as demonstrated by the apparent non-monophyly of *Apharyngostrigea* and weakly supported monophyly of *Strigea* in our analysis.

Proposal of a new classification system

The molecular phylogenies including the phylogeny obtained in the present work (Figures 1 and S1) consistently showed a clear separation between the Cyathocotylidae and Diplostomidae + Proterodiplostomidae + Strigeidae. This has been demonstrated in several recent molecular phylogenetic studies (Achatz *et al.* 2019d, 2021c, 2022e, 2023b; Blasco-Costa and Locke 2017; Gudla *et al.*2023; Hernández-Mena *et al.* 2017; Locke *et al.* 2018; Tkach *et al.* 2020), and it is not surprising as cyathocotylids possess a cirrus sac that is absent in members of the other 3 groups. There is no doubt that the Cyathocotylidae represents a distinct family. However, the highly non-monophyletic Diplostomidae and Strigeidae have not been supported in any of the larger studies. It is also clear that none of the historical classification systems of the Diplostomoidea is supported by either molecular data or morphology.

Strigeids, as commonly recognized, have a tubular, cup-shaped or bulbiform prosoma and a bilobed holdfast organ; diplostomids have a flattened, foliate, caliciform or bulbous prosoma with a sucker-like holdfast organ. However, for example, *Pseudapatemon aldousi* McIntosh, 1940 (a strigeid) has a concave, but not cup-shaped, prosoma. On the other hand, several diplostomids (e.g., *Codonocephalus urniger*, *Pseudocrassiphiala tulipifera* Achatz, Von Holten, Fecchio et Tkach, 2023, *Uvulifer elongatus* Dubois, 1988) have a cup-shaped prosoma, and numerous species have ventral concavities expressed to varying extents (e.g., *Alaria* Schrank, 1788, *Crassiphiala*, *Diplostomum*, *Neodiplostomum* Railliet, 1919, *Posthodiplostomum* Dubois, 1936) (see illustrations and photographs of Dubois (1968, 1970b, 1985, 1988), Niewiadomska (2002d) and Achatz *et al.* (2019a,b, 2022e, 2023a,b)).

The holdfast organ of strigeids is bilobed with ventral and dorsal lobes, while diplostomids and proterodiplostomids possess a sucker-like holdfast organ (Nieiwadomska 2002d–f; Figure 2). However, the holdfast organ of *Co. urniger* (a diplostomid) is weakly developed and appears almost bilobed. The holdfast organ of *Pseudapatemon* spp. (strigeids) is described as 'massive' (Dubois 1970b; Niewiadomska 2002d) or 'plug like' (Dubois 1970b). Diplostomids of the genera *Allodiplostomum* Yamaguti, 1935, *Parallelorchis* Harkema et Miller, 1961 and *Pseudoscolopacitrema* Palmieri, Krishnasamy et Sullivan, 1979 have holdfast organs that are trilobed or with 2 ventrolateral projections (Harkema and Miller 1961; Palmieri *et al.* 1979).

Bolbocephalodes intestiniforax (Bolbocephalodidae) adds further complexity. The prosoma of this species is bulbous with cup-shaped thickening at its base, which is not all too different as seen in the numerous diplostomids with a concave, but not cup-shaped, prosoma. The holdfast organ of *Bolbocephalodes intestiniforax* consists of 'two transverse lips' (Niewiadomska 2002a), which clearly appears to be a normal bilobed holdfast similar to that in most strigeids. Thus, *Bolbocephalodes intestiniforax* anatomy is consistent with both strigeids and diplostomids. The paraprostate organ of proterodiplostomids is not even consistently present in all members of the group; of known species, *Mesodiplostomum gladiolum* lacks this structure, while molecular phylogeny unequivocally supports its position among other proterodiplostomids (Figure 1; Achatz *et al.* 2022a; Tkach *et al.* 2020).

Host association-based differentiation was historically used by some authors to separate diplostomoidean families and genera (see Dubois (1936a,b, 1968, 1970a,b) and Niewiadomska (2002c–g)). However, molecular phylogenetic studies have consistently rejected these classification systems. For instance, Achatz *et al.* (2022e) demonstrated that *Neodiplostomum* (historically viewed as parasites of birds with a single exception of a species parasitic in bat host) and *Fibricola* Dubois, 1932 (historically viewed as parasites of mammals) represented a single genus, *Neodiplostomum*. In the case of reptiles, Dubois (1936a) placed all diplostomids described from reptiles (primarily crocodilians) into the Proterodiplostomidae. Achatz *et al.* (2022d) erected the genus *Neofibricola*, a diplostomid, from crocodile. Their molecular phylogenetic analysis, along with the present study, clearly placed that genus in the phylogeny separately from proterodiplostomids. The former *Didelphodiplostomum* Dubois, 1944, a parasite of mammals, was revealed to be synonymous with *Tylodelphys* (Achatz *et al.* 2022b). Obviously, host associations do not withstand criticism as the basis for the classification system of diplostomoideans.

As seen in several recent studies, our molecular phylogeny clearly demonstrates the extensive non-monophyly of the Diplostomidae and Strigeidae (Figure 1; see discussion above). The Proterodiplostomidae was nested as a part of the polytomy consisting of many clades of diplostomids and strigeids. Unfortunately, no DNA sequences of *Bolbocephalodes intestiniforax* (the only member of the Bolbocephalodidae) are currently available. The fact that the major features used to discern between these families are not consistent among their members, coupled with the extensive non-monophyly of families, clearly suggests that the current classification system is not supported and renders it unstable as exemplified by the taxonomic history of family-group diplostomoidean level taxa above. This leaves two possibilities: (i) each independent lineage/branch has to be considered a separate family that will require the erection of more than 10 new families, or (ii) the Proterodiplostomidae and Strigeidae should be synonymized with the Diplostomidae. This will resolve the non-monophyly, finally provide stability for the classification system of the Diplostomoidea at the family level, and allow focus on the enhancement of the classification system of the group at the level of genera. Even if we decide to establish multiple new families, a number of monophyletic groups do not possess morphological or biological characteristics that may clearly separate them from all other monophyletic groups. Therefore, we strongly favor the latter solution and synonymize the Strigeidae, Proterodiplostomidae, and Bolbocephalodidae (based on morphology) with the Diplostomidae. Upon synonymization, the Diplostomidae includes 77 genera. This action leaves only the families Cyathocotylidae and Diplostomidae within the Diplostomoidea. We provide amended diagnoses of the Diplostomidae and Cyathocotylidae below.

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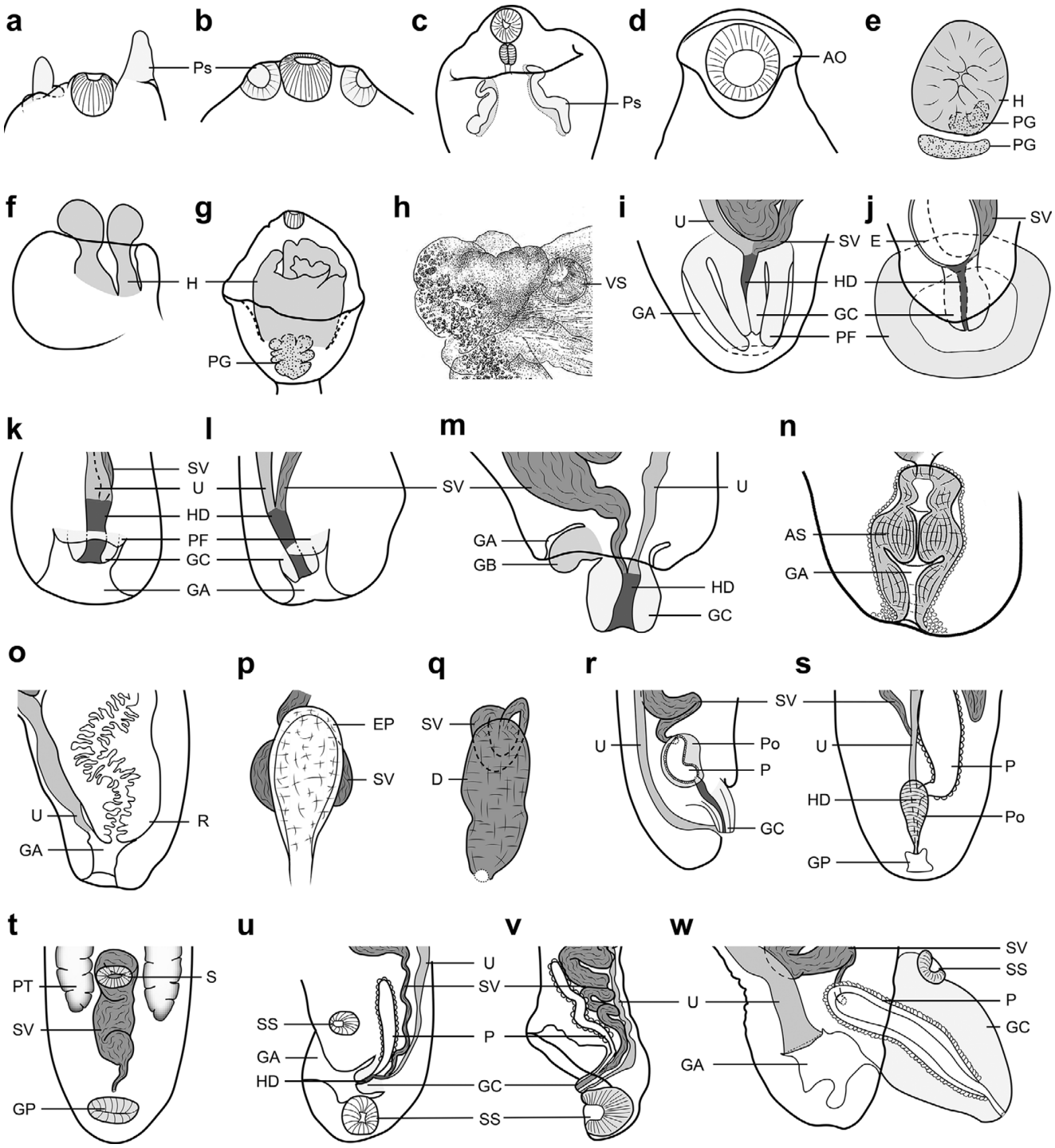

Figure 2. Some of the major morphological features of diplostomids. (a) *Alaria marcianae*, anterior part of prosoma with horn-like pseudosuckers, ventral view (after Young *et al.* in press); (b) *Alaria trashpandae*, anterior part of prosoma with invaginated pseudosuckers, ventral view (after Young *et al.* in press); (c) *Schwartzitrema* sp., anterior part of prosoma with pseudosuckers with auricular expansions, ventral view; (d) *Neodiplostomum nephrocystis*, anterior part of prosoma with apical organ, ventral view (after Achatz *et al.* in press); (e) *Herpetodiplostomum vogti*, sucker-like holdfast organ, ventral view (after Achatz *et al.* 2021b); (f) *Cotylurus cornutus*, bilobed holdfast organ, lateral view (after Dubois 1968); (g) *Nematostrigea annulata*, bilobed holdfast organ with thin, crimped lobes, ventral view (after Gudla *et al.* 2023); (h) *Allodiplostomum scolopacis*, holdfast organ with 3 massive lobes (from Dubois 1970b); (i, j) *Posthodiplostomum dawnsherryae*, posterior part of opisthosoma with genital cone and preputial fold in genital atrium (i) and everted (j), ventral view (after Achatz *et al.* 2025); (k, l) *Pseudocrassiphiala tulipifera*, posterior part of opisthosoma with genital cone and preputial fold in genital atrium, ventral (k) and lateral (l) views (after Achatz *et al.* 2023b); (m) *Bolbophorus indianus*, posterior part of opisthosoma with genital cone and bulb, lateral view (after Dubois 1970b); (n) *Neofibricola smiti*, genital atrium with atrial sphincter (after Achatz *et al.* 2022d); (o) *Australapatemon intermedius*, posterior part of opisthosoma with well-developed genital cone with internal rugae, lateral view (after Dubois 1968); (p) *A. marcianae*, seminal vesicle and ejaculatory duct with muscular pouch-like part, ventral view (after Young *et al.* in press); (q) *Crassiphiala jeffreybelli*, seminal vesicle with dilated part, ventral view (after Achatz *et al.* 2023b); (r) *Dungalabatrema kostadinovae*, posterior part of opisthosoma with pouch surrounding paraprostate, lateral view (after Achatz *et al.* 2022a); (s) *Pseudocrocodilicola americaniense*, posterior part of opisthosoma with muscular pouch surrounding hermaphroditic duct, ventral view (after Tkach *et al.* 2020); (t) *Sphincterodiplostomum joaopinhoi*, posterior part of opisthosoma with muscular sphincter and genital pore, dorsal view (after Achatz *et al.* 2021a); (u) *Polycotyle ornata*, posterior part of opisthosoma with sucker-like structures on body wall, lateral view (after Tkach *et al.* 2020); (v) *Proterodiplostomum longum*, posterior part of opisthosoma with well-developed sucker-like structure in genital atrium, lateral view (after Tkach *et al.* 2020); (w) *Afroproterodiplostomum ingwenyae*, posterior part of opisthosoma with massive genital cone with sucker-like structure, lateral view (after Achatz *et al.* 2022a). Abbreviations for structures: AO, apical organ; AS, atrial sphincter; D, dilated part of seminal vesicle; E, egg; EP, pouch like part of ejaculatory duct; GA, genital atrium; GB, genital bulb; GC, genital cone; GP, genital pore; HD, hermaphroditic duct; H, holdfast organ; P, paraprostate; Po, pouch; PF, preputial fold; PG, proteolytic gland; Ps, pseudosucker; R, genital cone with rugae; SV, seminal vesicle; S, sphincter; SS, sucker-like structure; PT, posterior testis; U, uterus; VS, ventral sucker.

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Family Diplostomidae Poirier, 1886

Diagnosis: Body composed of prosoma and opisthosoma, separation of body parts may be indistinct. Prosoma flattened, concave or cup-shaped, bulbous, caliciform, foliate, or spatulate; opisthosoma claviform, coniform, cylindrical, or subovate, rarely with thick-walled capsule or series of suckers. Prosoma with or without pseudosuckers. Oral sucker typically present. Ventral sucker present or absent. Holdfast organ variable in size and shape, sucker-like or bilobed, rarely trilobed, with or without papillae, compact gland at base present or absent. Compact proteolytic gland often present, near prosoma-opisthosoma junction. Pharynx typically present. Esophagus short, ceca usually reaching close to posterior end of body. Testes two, variable in shape and arrangement, typically in opisthosoma. Ovary pretesticular or opposite to anterior testis. Seminal vesicle post-testicular; paraprostate present or absent. Cirrus-sac and cirrus absent. Genital cone or bulb often present, variable in level of development. Genital atrium often well developed, muscular, rarely with sucker or sucker-like structures. Genital pore terminal or dorso-subterminal. Vitellarium follicular, variable in extent. Uterus typically in opisthosoma, sometimes extends into prosoma. Parasites of reptiles, birds, and mammals. Afrotropics, Australasia, Indomalaya, Nearctic, Neotropics, and Palearctic. Type-genus *Diplostomum* von Nordmann, 1832.

Cyathocotylidae Mühling, 1896

Diagnosis: Body composed of unipartite or prosoma and opisthosoma, oval, cordiform, linguiform, or pyriform. Oral and ventral suckers typically present; pseudosuckers absent. Holdfast organ round or oval, may be massive. Pharynx typically present. Esophagus short; ceca usually reaching close to posterior end of body. Position and shape of ovary and testes variable. Cirrus-sac present, occasionally rudimentary, enclosing seminal vesicle and pars prostatica. Cirrus typically present. Genital pore terminal or dorso-subterminal. Vitellarium follicular, variable in extent. Uterus variable in extent. Parasites of fishes, reptiles, birds, and mammals. Afrotropics, Australasia, Indomalaya, Nearctic, Neotropics, and Palearctic. Type-genus *Cyathocotyle* Mühling, 1896.

Key to diplostomoidean genera

We provide a new key to genera of the Diplostomoidea to follow the new classification system. The removal of the inconsistent features separating the former family-group taxa, including host associations, allows this key to be more suitable for separation among genera. The key provided is based, in part, on the keys of Niewiadomska (2002a–g), Tkach *et al.* (2020), and Achatz *et al.* (2022a,d). The terminology for the structures aligns with the definitions provided in Achatz *et al.* (2022d). Some of the structures found at the anterior and posterior ends of diplostomids as well as various modifications of the terminal genitalia organization are illustrated in Figure 2.

1a. Cirrus sac ..... **2** (Cyathocotylidae Mühling, 1896)
1b. Cirrus sac absent ..... **17** (Diplostomidae Poirier, 1886)
2a. Prosoma cup-shaped or with well-developed concavity **3**
2b. Prosoma flattened, lateral margins may be somewhat concave **9**
3a. Concavity opens anteriorly **4**
3b. Concavity opens ventrally **6**
4a. Body with small cup-shaped prosoma and large opisthosoma region. Holdfast organ elongated, with cavity reduced to narrow slit, prolonged deep into opisthosoma ..... *Muhlingina* Mehra, 1950
4b. Prosoma much larger. Opisthosoma small. Holdfast organ broad, only in prosoma **5**
5a. Body bulbous, prosoma with deep cavity containing holdfast organ. Holdfast organ massive, occupying essentially entire prosoma. Parasites of dolphins ..... *Braunina* Heider, 1900
5b. Body oval or pyriform, with less deep cavity. Holdfast organ not occupying entire prosoma. Parasites of birds ..... *Georduboisia* Sokolov, Vlasenkov, Bugmyrin, Kalmykov et Lebedeva, 2024
6a. Ventral concavity nearly entirely filled by massive holdfast organ. In fishes and mammals **7**
6b. Holdfast organ smaller, not occupying entire ventral concavity. In birds **8**
7a. Opisthosoma absent. In fishes ..... *Holostephanoides* Dubois, 1983
7b. Short opisthosoma present. In mammals ..... *Prosostephanus* Lutz, 1935
8a. Vitellarium distributed along most of body length. Testes opposite or diagonal. Holdfast organ occupies at least half of body length ..... *Holostephanus* Szidat, 1936
8b. Vitellarium limited to around the level of holdfast organ, in about half of body length. Testes tandem. Holdfast organ occupying less than half of body length ..... *Prohemistomum* Odhner, 1913
9a. Vitellarium distributed throughout most of body length **10**
9b. Vitellarium limited in distribution, usually only posterior part of prosoma at level of holdfast organ **12**
10a. Holdfast organ not massive, does not occupy most of body. Ventral sucker and opisthosoma present. In birds ..... *Pseudhemistomum* Szidat, 1936
10b. Holdfast organ typically massive, often occupying most of body. Ventral sucker and opisthosoma present or absent. In birds and crocodilians **11**
11a. Testes typically opposite. Eggs generally smaller (typically about 100 μm or less) ..... *Cyathocotyle* Mühling, 1896
11b. Testes tandem. Eggs generally larger (typically around 130 μm or greater) ..... *Suchocyathocotyle* Dubois, 1984
12a. Opisthosoma present, may be small or weakly separated from prosoma **13**
12b. Opisthosoma absent **16**
13a. Vaginal sphincter present, may be weakly developed **14**
13b. Vaginal sphincter absent **15**

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14a. Ventral sucker apparent ..... *Mesostephanus* Lutz, 1935
(Syn. *Gelanocotyle* Sudarikov, 1961)
14b. Ventral sucker weakly developed or apparently absent ..... *Neogogatea* Chandler et Rausch, 1947
15a. Vitellarium distributed as almost a ring near outer margin of holdfast organ. In birds ..... *Paracoenogonimus* Katsurada, 1914
15b. Vitellarium distributed as horseshoe-shape or 2 lateral fields around holdfast organ. In snakes ..... *Gogatea* Lutz, 1935
16a. Vitellarium distributed around holdfast organ, does not enter the holdfast organ itself. In birds ..... *Linstowiella* Szidat, 1933
16b. Vitellarium mainly inside holdfast organ. In snakes ..... *Serpentostephanus* Sudarikov, 1961
17a. Prosoma bulbous with cup-shaped thickening at base ..... *Bolbocephalodes* Strand, 1935
17b. Prosoma otherwise structured **18**
18a. Holdfast organ not sucker-like **19**
18b. Holdfast organ sucker-like when not everted. When everted it may protrude significantly above the ventral surface **34**
19a. Holdfast organ bilobed, lobes may be thin, crimped **20**
19b. Holdfast organ not bilobed **31**
20a. Vitellarium only in prosoma. In mammals ..... *Duboisiella* Baer, 1938
20b. Vitellarium primarily in opisthosoma or prosoma and opisthosoma. In birds **21**
21a. Vitellarium in prosoma and opisthosoma **22**
21b. Vitellarium in, or mainly in, opisthosoma **24**
22a. Prosoma with vitelline follicles in two symmetrical masses localized in lateral expansions of dorsal lobe of holdfast organ ..... *Parastrigea* Szidat, 1928
(Syns *Prostrigea* Bisseru, 1956; *Chaseostrigea* Ukoli, 1967; *Brasiliana* Ukoli, 1967)
22b. Vitelline follicles uniformly distributed in both parts of body **23**
23a. Pharynx absent ..... *Apharyngostrigea* Ciurea, 1927
(Syn. *Ridgeworthia* Verma, 1936)
23b. Pharynx present ..... *Strigea* Abildgaard, 1790
(Syns *Holostomum* Nitzsch, 1819; *Gongylura* Lutz, 1933; *Neoalaria* Lal, 1939; *Neostrigea* Bisseru, 1956; *Chabaustrigea* Sudarikov, 1959)
24a. Body highly elongated; opisthosoma 5–25 times longer than prosoma. Anterior 50–90% of opisthosoma devoid of gonads .. **25**
24b. Body less elongated; opisthosoma < 6 times longer than prosoma. Ovary either entirely or partially in the anterior 50% of opisthosoma **27**
25a. Vitellarium in opisthosoma and holdfast organ ..... *Ophiosoma* Szidat, 1928
25b. Vitellarium in opisthosoma. A few sparse follicles may be in prosoma, but not in the holdfast organ **26**
26a. Prosoma ventrally concave, small. Holdfast organ lobes thin, crimped ..... *Nematostrigea* Sandground, 1934
26b. Prosoma cup-like, broad/bulky. Holdfast organ lobes thick ..... *Cardiocephaloides* Sudarikov, 1959
(Syn. *Cardiocephalus* Szidat, 1928 *nec* Broili, 1904)
27a. Genital bulb present **28**
27b. Genital bulb absent **29**
28a. Proteolytic gland disperse. Testes lobes generally smooth ..... *Cotylurus* Szidat, 1928
(Syns *Choanodiplostomum* Vigueras, 1944; *Cotylurostrigea* Sudarikov, 1961)
28b. Proteolytic gland compact. Main lobes of testes with rough, globular outlines ..... *Ichthyocotylurus* Odening, 1969
29a. Pseudosuckers strongly developed, with auricular expansions ..... *Schwartzitrema* Pérez Vigueras, 1941
(Syn. *Schwartziella* Pérez Vigueras, 1940)
29b. Pseudosuckers not readily discernible **30**
30a. Genital cone small, not or poorly delimited from parenchyma; ejaculatory duct without internal rugae .. *Apatemon* Szidat, 1928
(Syn. *Pseudostrigea* Yamaguti, 1933)
30b. Genital cone large, well delimited from parenchyma; ejaculatory duct with internal rugae ... *Australapatemon* Sudarikov, 1959
31a. Pseudosuckers present. Holdfast organ distinct **32**
31b. Pseudosuckers absent. Holdfast organ indistinct ..... *Codonocephalus* Diesing, 1850
32a. Holdfast organ with 3 massive lobes (2 lateral and 1 posteromedian) ..... *Allodiplostomum* Yamaguti, 1935
32b. Holdfast organ with only 2 lateral projections **33**
33a. Muscular vaginal sphincter present ..... *Pseudoscolopacitrema* Palmieri, Krishnasamy et Sullivan, 1979
33b. Muscular vaginal sphincter absent ..... *Parallelorchis* Harkema et Miller, 1961
34a. Paraprostate present **35**
34b. Paraprostate absent **56**
35a. Paraprostate surrounded by muscular pouch. Paraprostate duct eversible. Ejaculatory duct and metraterm open side by side, neither enclosed in a muscular pouch. In snakes. In Neotropics ..... *Heterodiplostomum* Dubois, 1936
35b. Paraprostate not surrounded by muscular pouch; alternatively, muscular pouch surrounds other terminal elements of reproductive system in addition to paraprostate **36**
36a. Entire paraprostate, ejaculatory duct, and metraterm enclosed in muscular pouch. Ejaculatory duct and metraterm open separately. In crocodilians. In India ..... *Capsulodiplostomum* Dwivedi, 1966
36b. Entire paraprostate, ejaculatory duct, and metraterm not enclosed together in muscular pouch. Ejaculatory duct and metraterm open separately or have a common opening **37**
37a. Vitellarium confined to opisthosoma. In crocodilians. In Neotropics ..... *Massoprostatum* Caballero, 1948

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37b. Vitellarium distributed differently **38**
38a. Holdfast organ relatively massive, typically occupying about half of prosoma **39**
38b. Holdfast organ not as massive, typically occupying about 25–30% of prosoma **40**
39a. Ejaculatory duct joins distal part of paraprostate. Genital atrium wall with two muscular pits, occasionally sucker-like. In crocodilians. In Australasia ..... *Pseudoneodiplostomoides* Yamaguti, 1934
39b. Ejaculatory duct and paraprostate do not join/unite. Muscular pits in wall of genital atrium absent. In snakes. In Neotropics ..... *Ophiodiplostomum* Dubois, 1936
40a. Metraterm, ejaculatory duct and paraprostate join to form a common duct or all three share common opening **41**
40b. Metraterm, ejaculatory duct and paraprostate do not form common duct. Ejaculatory duct and paraprostate or ejaculatory duct and metraterm may join or share common opening **45**
41a. Opisthosoma with longitudinal row of sucker-like structures on dorsal side. In crocodilians. In Nearctic ..... *Polycotyle* Willemoes-Suhm, 1870
41b. Opisthosoma without dorsal sucker-like structures **42**
42a. Terminal part of paraprostate, ejaculatory duct and metraterm enclosed in muscular pouch **43**
42b. Terminal part of paraprostate, ejaculatory duct, and metraterm not enclosed in muscular pouch **44**
43a. Ejaculatory duct joins paraprostate near its midpoint. In crocodilians. In Nearctic .... *Pseudocrocodilicola* Byrd et Reiber, 1942
43b. Ejaculatory duct joins paraprostate near its proximal end. In crocodilians. In Nearctic ..... *Neocrocodilicola* Tkach, Achatz et Pulis, 2020
44a. Vitelline follicles confined to area around holdfast organ. Separation between prosoma and opisthosoma indistinct. In crocodilians. In Nearctic ..... *Crocodilicola* Poche, 1926
44b. Vitelline follicles distributed in both prosoma and opisthosoma, extending well beyond area around holdfast organ. Separation between prosoma and opisthosoma distinct. In crocodilians. In Nearctic ..... *Archaeodiplostomum* Dubois, 1944
45a. Paraprostate opens separately from ejaculatory duct and metraterm. Ejaculatory duct and metraterm may join or share common opening **46**
45b. Metraterm opens separately from ejaculatory duct and paraprostate. Ejaculatory duct and paraprostate may join or share common opening **49**
46a. Genital cone present **47**
46b. Genital cone absent **48**
47a. Genital cone massive, equal to about 1/4 of total body length. In crocodilians. In Neotropics ... *Paradiplostomum* La Rue, 1926
47b. Genital cone much smaller, not more than 1/8 of total body length. In crocodilians and chelonians. In Neotropics ..... *Herpetodiplostomum* Dubois, 1936
48a. Thick-walled, sucker-like dorsal invagination of body present near midpoint of opisthosoma or slightly more posterior. In crocodilians. Neotropics ..... *Cystodiplostomum* Dubois, 1936
48b. No thick-walled, sucker-like dorsal invagination of body present. In crocodilians. In Neotropics ..... *Prolecithodiplostomum* Dubois, 1936
49a. Sucker-like muscular structure or distinct muscular bundles in the wall of the genital atrium present **50**
49b. Genital atrium without sucker-like structure or distinct muscular bundles **51**
50a. Sucker-like muscular structure in the wall of the genital atrium present. In crocodilians. In Neotropics ..... *Proterodiplostomum* Dubois, 1936
50b. Distinct muscle bundles in the wall of the genital atrium present. In crocodilians. In Neotropics ..... *Nattererodiplostomum* Achatz et Tkach, 2022
51a. Genital cone with sucker-like muscular structure. In crocodilians. In Afrotropics ..... *Afroproterodiplostomum* Achatz, Chermak, Junker et Tkach, 2022
51b. Genital cone without sucker-like muscular structure **52**
52a. Genital atrium with well-developed glandular papilla. In crocodilians. In Australasia ..... *Australiadiplostomum* Achatz, Chermak et Tkach, 2022
52b. Genital atrium without a well-developed glandular papilla. Smaller papillae may be present in genital atrium **53**
53a. Ejaculatory duct does not join paraprostate. Ejaculatory duct and paraprostate share common opening. In crocodilians and snakes. In Neotropics ..... *Proteroduboisia* Tkach, Achatz et Melo, 2020
53b. Ejaculatory duct joins paraprostate **54**
54a. Glandular muscular pouch surrounding paraprostate and terminal portion of ejaculatory duct. In crocodilians. In Australasia ..... *Dungalabatrema* Achatz, Chermak et Tkach, 2022
54b. Glandular muscular pouch surrounding paraprostate absent **55**
55a. Ejaculatory duct joins paraprostate near its distal end. Paraprostate well-developed. In crocodilians. In Nearctic. ..... *Paraproterodiplostomum* Tkach, Achatz et Pulis, 2020
55b. Ejaculatory duct joins proximal half of paraprostate. Paraprostate weakly developed. In crocodilians. In Africa, Australasia and Neotropics ..... *Pseudoneodiplostomum* Dubois, 1936
56a. Pseudosuckers present **57**
56b. Pseudosuckers absent **79**
57a. Dorsal tubular invagination at level of posterior testis equipped with muscular sphincter present. ..... *Sphincterodiplostomum* Dubois, 1936
57b. Dorsal tubular invagination of body wall at level of posterior testis equipped with muscular sphincter absent **58**

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58a. Genital cone with semicircular ventral pad projecting from dorsal region of anterior wall of genital atrium. Large unicellular gland-cells with ducts opening on ventral surface around ventral sucker present ..... *Adenodiplostomum* Dubois, 1937
58b. Genital cone without semicircular ventral pad. Large unicellular gland-cells with ducts opening around ventral sucker absent **59**
59a. Muscular pouch surrounding hermaphroditic duct present. In snakes. In Palearctic and Indomalaya ..... *Proalarioides* Yamaguti, 1933
59b. Muscular pouch surrounding hermaphroditic duct absent. In birds and mammals **60**
60a. Genital cone with a preputial or prepuce-like fold **61**
60b. Genital cone without a preputial or prepuce-like fold or genital cone absent **63**
61a. Prosoma elongated, generally flattened, without deep concavity ..... *Posthodiplostomoides* Williams, 1969
61b. Prosoma oval or cochleariform, concave (bowl-like) **62**
62a. Body strongly retroflexed. Prosoma similar in length to opisthosoma ..... *Neoharvardia* Gupta, 1963
62b. Body not strongly retroflexed. Prosoma much shorter than opisthosoma ..... *Subuvulifer* Dubois, 1952
(Syns *Choanochenia* Yang, 1959; *Cotylostoma* Yang, 1965; *Neochoanochenia* Yang, 1965) .....
63a. Prosoma pouch-shaped. Holdfast organ is located inside pouch formed by prosoma ..... *Procyotrema* Harkema et Miller, 1959
63b. Prosoma not pouch-shaped **64**
64a. Muscular bulb in genital atrium present ..... *Bolbophorus* Dubois, 1935
64b. Muscular bulb in genital atrium absent **65**
65a. Vitellarium only distributed within opisthosoma ..... *Pulvinifer* Yamaguti, 1933
(Syn. *Laterostrigea* Yang, 1962)
65b. Vitellarium in prosoma and opisthosoma or only prosoma **66**
66a. Body strongly retroflexed ..... *Harvardia* Baer, 1932
66b. Body not strongly retroflexed **67**
67a. Ventral sucker present **68**
67b. Ventral sucker absent **77**
68a. Genital atrium with internal muscular sphincter ..... *Cynodiplostomum* Dubois, 1936
68b. Genital atrium without internal muscular sphincter **69**
69a. Vitellarium mainly in prosoma, some follicles may extend into opisthosoma as far as level of ovary or near anterior margin of posterior testis **70**
69b. Vitellarium well-distributed in both parts of the body, typically reaching to near posterior end of opisthosoma **72**
70a. Genital cone well-developed. Anterior testis horseshoe-shaped or bilobed, oriented sagittaly, almost perpendicular to posterior testis ..... *Anhingatrema* Achatz, Burkman, Fecchio, Pulis et Tkach, 2023
70b. Genital cone weakly developed, or seemingly absent. Anterior testis otherwise structured and/or oriented **71**
71a. Pseudosuckers horn-like (testes tandem) or invaginated (typically testes opposite). Pouch-like portion of ejaculatory duct present or absent ..... *Alaria* Schrank, 1788
(Syns *Conchosomum* Railliet, 1896; *Pharyngostomoides* Harkema, 1942)
71b. Pseudosuckers invaginated (testes tandem). Pouch-like portion of ejaculatory duct absent ..... *Paralaria* Krause, 1914
..... (Syn. *Enhydridiplostomum* Dubois, 1944)
72a. Genital cone relatively large, occupies approximately 25% of body length. Anterior testis asymmetrical .....
..... *Glossodiplostomoides* Bhalerao, 1942
(Syn. *Pseudoglossodiplostomum* Dubois, 1944)
72b. Genital cone smaller or absent. Anterior testis symmetrical or asymmetrical **73**
73a. Pouch-like portion of ejaculatory duct present. Anterior testis asymmetrical. Body distinctly bipartite. .....
..... *Tylodelphys* Diesing, 1850, part.
(Syns *Didelphodiplostomum* Dubois, 1944; *Glossodiplostomum* Dubois, 1932; *Prodiplostomum* Ciurea, 1933)
73b. Pouch-like portion of ejaculatory duct absent. Anterior testis symmetrical or asymmetrical. Body distinctly or indistinctly bipartite **74**
74a. Genital cone distinct **75**
74b. Genital cone indistinct **76**
75a. Body distinctly bipartite. Anterior testis asymmetrical ..... *Dolichorchis* Dubois, 1961
75b. Body typically indistinctly bipartite. Anterior testis symmetrical ..... *Tylodelphys* Diesing, 1850, part.
(Syns *Didelphodiplostomum* Dubois, 1944; *Glossodiplostomum* Dubois, 1932; *Prodiplostomum* Ciurea, 1933)
76a. Body usually distinctly bipartite. Anterior portion of prosoma not trilobate or weakly trilobate *Diplostomum* von Nordmann, 1832
(Syns *Hemistomum* Diesing, 1850; *Proalaria* La Rue, 1926)
76b. Body indistinctly bipartite. Anterior portion of prosoma strongly trilobate ..... *Hysteromorpha* Lutz, 1931
77a. Genital atrium bell-shaped ..... *Bursatintinnabulus* Tehrany, Dronen et Wardle, 1999
77b. Genital atrium not bell-shaped **78**
78a. Vitellarium digitiform. Genital atrium sucker-like ..... *Bursacetabulus* Dronen, Tehrany et Wardle, 1999
78b. Vitellarium follicular. Genital atrium not sucker-like ..... *Austrodiplostomum* Szidat et Nani, 1951
79a. Ventral sucker absent **80**
79b. Ventral sucker present **82**
80a. Genital atrium contains large, muscular sucker-like structure. Genital cone absent ..... *Cercocotyla* Yamaguti, 1939
(Syn. *Pseudocercocotyla* Yamaguti, 1971)

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80b. Genital atrium without muscular sucker-like structure. Genital cone present **81**
81a. Prosoma distinctly cup-like with deep cavity that opens anteriorly. Holdfast organ positioned entirely within concavity. Tegument of prosoma armed ..... *Pseudocrassiphiala* Achatz, Von Holten, Fecchio et Tkach, 2023
81b. Prosoma not distinctly cup-like, flattened or with shallow concavity that opens ventrally. When concavity present, holdfast organ not positioned entirely within it. Tegument of prosoma unarmed ..... *Crassiphiala* Van Haitsma, 1925
82a. Vitellarium only in opisthosoma, some follicles may enter holdfast organ **83**
82b. Vitellarium in both prosoma and opisthosoma or primarily in prosoma **85**
83a. Genital cone inconspicuous, typically situated inside genital atrium ..... *Pseudapatemon* Dubois, 1936 (Syn. *Eroliostrigea* Yamaguti, 1971)
83b. Genital cone apparent, more strongly developed **84**
84a. Genital cone without preputial fold. Genital atrium width less than one third of opisthosoma width ..... *Pseudodiplostomum* Yamaguti, 1934
84b. Genital cone half-enclosed in preputial fold. Genital atrium width greater than one third of opisthosoma width, often occupies most of opisthosoma width at level of genital atrium ..... *Uvulifer* Yamaguti, 1934 (Syn. *Prochoanochenia* Yang, 1965)
85a. Posterior part of opisthosoma consists of ventral and dorsal conical protuberances ..... *Podospathalium* Dubois, 1932
85b. Posterior part of opisthosoma not divided into 2 conical protuberances **86**
86a. Genital atrium with muscular, sucker-like structure ..... *Scolopacitrema* Sudarikov et Rykovsky, 1958
86b. Genital atrium without sucker-like structure **87**
87a. Genital cone surrounded by a preputial fold ..... *Posthodiplostomum* Dubois, 1936 (Syns *Choanouvulifer* Lung, 1966; *Mesoophorodiplostomum* Dubois, 1936; *Ornithodiplostomum* Dubois, 1936; *Prolobodiplostomum* Baer, 1959)
87b. Genital cone without a preputial or prepuce-like fold or genital cone absent **88**
88a. Genital cone large, occupies about half of opisthosoma width. Body bottle-shaped ..... *Bursotrema* Szidat, 1960
88b. Genital cone smaller or absent. Body not bottle-shaped **89**
89a. Pouch-like portion of ejaculatory duct present. Genital atrium with well-developed internal muscular sphincter ..... *Neofibricola* Achatz, Martens, Kudlai, Junker, Boe et Tkach, 2022
89b. Pouch-like portion of ejaculatory duct absent. Genital atrium without internal muscular sphincter **90**
90a. Prosoma cup-shaped. Holdfast organ linguiform ..... *Prudhoella* Beverley-Burton, 1960
90b. Prosoma not cup-shaped. Holdfast organ not linguiform **91**
91a. Testes opposite. Holdfast organ massive, occupying almost entire concavity of prosoma ..... *Pharyngostomum* Ciurea, 1922
91b. Testes tandem. Holdfast organ not massive, does not typically occupy most of prosoma **92**
92a. Genital atrium distinct, with small, dilated secondary chamber formed by invagination of atrium wall near its posterior end. Prosoma much longer than opisthosoma. In crocodilians ..... *Mesodiplostomum* Dubois, 1936
92b. Genital atrium small, often nearly unobservable, without a secondary chamber. Prosoma typically the same length or shorter than opisthosoma. In birds **93**
93a. Oral sucker with or without apical organ. Metacercaria of diplostomulum/neodiplostomulum type. Second intermediate hosts are amphibians ..... *Neodiplostomum* Railliet, 1919 (Syns *Conchogaster* Lutz, 1928; *Conodiplostomum* Dubois, 1937; *Fibricola* Dubois, 1932; *Lophosicyadiplostomum* Dubois, 1936; *Neodiplostomoides* Vidyarthi, 1938; *Neoparadiplostomum* Bisseru, 1957; *Theriodiplostomum* Dubois, 1944; *Triplostomum* Lutz, 1928)
93b. Oral sucker without apical organ. Metacercaria of neascus type. Second intermediate hosts are fishes ..... *Ciureatrema* Heneberg, Sitko et Těšínský, 2020

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