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Dactylogyridae 2021: Seeing the forest through the (phylogenetic) trees

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Abstract

Dactylogyridae is one of the most studied families of parasitic flatworms with more than 1000 species and 166 genera described to date including ecto-, meso-, and endoparasites. Dactylogyrid monogeneans have been used as model organisms for host-parasite macroevolutionary and biogeographical studies due to the scientific and economic importance of some of their host lineages. Consequently, an array of phylogenetic research into different dactylogyrid lineages has been produced over the past years but the last family-wide study was published over a decade ago. Here, we provide a new phylogeny of Dactylogyridae including representatives of all the genera with available molecular data. First, we discuss morphological, host range, biogeographical, and freshwater-marine patterns. Second, we provide an overview of the current state of the systematics of the family, and its subfamilies and genera. Third, we elaborate on the implications of taxonomic, citation, and confirmation bias in past studies. We found two well-supported main lineages which we assigned to the subfamilies Dactylogyrinae and Ancyrocephalinae. The subfamilies further include 11 well-supported clades whose members share only few diagnostic morphological features. Our study highlights the discrepancy between morphological similarities and molecular phylogenetic relationships in some dactylogyrid lineages. Environmental changes might have induced morphological adaptation, e.g. changes in the attachment organ in response to marine-freshwater habitat switches or reduction of eyespots related to water turbidity. Moreover, synonymisation of some of the para- or polyphyletic genera is proposed. We conclude that a strong taxonomic bias further limits knowledge on biogeographical evolutionary patterns that can be inferred from these results. Finally, we propose addressing potential citation and confirmation biases through a 'level playing field' multiple sequence alignment as provided by this study.

Keywords: Monogenea, parasitic flatworms, biogeography, host-parasite interaction

Data availability statement

Phylogenetic trees and DNA alignments are openly available in TreeBase at https://treebase.org, accession number XXXXXX.

1. Introduction

Dactylogyridae (Monopisthocotylea, Monogenea, Neodermata) is one of the most studied neodermatan families with more than 1000 species described to date in 166 genera (Horton et al., 2021). The majority of dactylogyrid species are ectoparasites infecting the gills of fishes but several genera are ectoparasitic on the skin (Zago et al., 2020) or are endo- or mesoparasites. The latter can be found in the urinary system (Pariselle and Euzet, 2009; Fayton and Kritsky, 2013), in different regions of the digestive tract (Luus-Powell et al., 2020) and nasal cavity (Kritsky et al., 1992). Representatives of dactylogyrid monogeneans infect a broad range of fish hosts from a number of taxa including Anabantiformes, Anguilliformes, Aulopiformes, Centrarchiformes, Characiformes, Chaetodontiformes, Cichliformes, Clupeiformes, Cypriniformes, Ephippiformes, Gerreiformes, Gobiiformes, Gymnotiformes, Holocentriformes, Lutjaniformes, Mugiliformes, Perciformes, Syngnathiformes, Siluriformes, and Tetraodontiformes. The known distribution covers all biogeographic realms worldwide including the Arctic and Antarctic regions (Beverley-Burton, 1995; Rohde et al., 1998; Luque et al., 2017; Scholz et al., 2018; Kuchta et al., 2020). Due to the tremendous species richness and various levels of host-specificity, dactylogyrid monogeneans have been proposed as models to study general mechanisms of host-parasite interactions and distribution patterns of the host taxa. So far, they have been used to infer phylogenetic position (Benovics et al., 2017), biogeographical history (Boeger and Kritsky, 2003; Benovics et al., 2020b), anthropogenic introductions (Kmentová et al., 2019; Jorissen et al., 2020; Ondračková et al., 2021), and host population structure (Kmentová et al., 2020b). Moreover, cases of co-divergence on a host radiation have been reported for several dactylogyrid lineages (Vanhove et al., 2015; Benovics et al., 2020b; Cruz-Laufer et al., 2021b). Host biogeography and diversification patterns are key determinants of the current distribution of dactylogyrid monogeneans (Šimková et al., 2003; Braga et al., 2014). However, host repertoires were also reported to correlate with clades in the host phylogeny especially within younger parasite lineages (Braga et al., 2015). These patterns have to be seen in the context of oscillation of host repertoires (Janz and Nylin, 2008). As suggested by Brooks et al. (2019), oscillating host repertoires are enabled by ecological opportunities emerging from the rise and fall of ecological barriers (D'Bastiani et al., 2020) and ecological fitting as the capacity to infect new host species (Agosta et al., 2010).

Despite the versatility of dactylogyrid research, almost two decades have passed since the last assessment of dactylogyrid evolutionary history by Šimková et al. (2006). Biases in the selection of taxa and molecular markers potentially mask macroevolutionary patterns within dactylogyrids. For instance, phylogenetic positions are mostly inferred from subsets of taxa with DNA sequences available even though nowadays molecular data frequently accompany new descriptions of monogenean species and/or genera. Many taxonomic studies on dactylogyrid monogeneans have also targeted specific host taxa or geographic regions, e.g. species infecting siluriform fishes in Amazonia (Mendoza-Palmero et al., 2015, 2020) or Central America (Salgado-Maldonado, 2008), as well as host-parasite model systems, e.g. African cichlids and species of *Cichlidogyrus* (reviewed in Cruz-Laufer et al., 2021a). Furthermore, confirmation and citation paradigms might play in monogenean research. Confirmation bias arises from prior expectations of researchers driven by taxon selection, a problem that affects phylogenetic studies in general (see Jermiin et al., 2020). Citation bias emerges when the probability to be cited depends on the study outcome (positive vs. negative results) (Urlings et al., 2021) or author-related factors such as reputation (Bol et al., 2018), gender (Dworkin et al., 2020), and country of origin (Van der Stocken et al., 2016). The latter might affect the visibility of monogenean research especially from low-income countries, where most biodiversity hotspots of fish and their parasites are found (Jorge and Poulin, 2018).

Dactylogyridae sensu lato currently comprises 166 genera (Horton et al., 2021). However, two different designations have been used interchangeably for species belonging to this lineage: Dactylogyridae Bychowsky, 1933 and Ancyrocephalidae Bychowsky, 1937. Moreover, the status of several other families (Fig. 1a,b) has been put into question due to morphological similarities and phylogenetic relationships with members of Dactylogyridae (Kritsky and Boeger, 1989a; Bilong Bilong et al., 1994; Boeger and Kritsky, 2001; Lim et al., 2001; Šimková et al., 2006; Galli and Kritsky, 2008; Kritsky et al., 2009; Fayton and Kritsky, 2013; Mendoza-Palmero et al., 2015). A morphological assessment and cladistic study of Kritsky and Boeger (1989a) proposed Ancyrocephalidae sensu Bychowsky & Nagibina, 1978 as a junior synonym of Dactylogyridae and further suggested nine subfamilies for Dactylogyridae: Anacanthorinae Price, 1967, Ancylodiscoidinae Gussev, 1961, Ancyrocephalinae Bychowsky, 1937, Dactylogyrinae Bychowsky, 1937, Linguadactylinae Bychowsky, 1957, Linguadactyloidinae Thatcher & Kritsky, 1983, Hareocephalinae Young, 1968, Heterotesiinae Euzet & Dossou, 1979 and Pseudodactylogyrinae Ogawa, 1986. Yet the subfamily Ancyrocephalinae (Šimková et al., 2006; Mendoza-Palmero et al., 2015) is polyphyletic as Ancylodiscoidinae is nested in this group (Mendoza-Palmero et al., 2015). Therefore, Dactylogyridae is in need of a taxonomic revision.

Traditionally, partial DNA sequences of the nuclear ribosomal subunit genes together with internal transcribed spacers have been used for evolutionary reconstruction of monogenean and neodermatan lineages similar to other metazoan taxa (Jamy et al., 2020). The multiple copy nature of the nuclear rDNA operon facilitates amplification for Sanger sequencing as well as next-generation sequencing as the initial amount of DNA in these small organisms is often low (Strona et al., 2009). Studies deviate regarding the exact region used for phylogenetic reconstruction, e.g. some studies only used a portion of the large (Mendoza-Palmero et al., 2015) or the small (e.g. Soares et al., 2021) subunit rDNA genes. This inconsistency results in considerable gaps in multi-gene alignments and, hence, reduces the comparability of DNA sequence data across studies. Mitochondrial DNA regions can be incorporated. However, these sequences increase resolution mostly for recently diverged lineages because of their extremely low rate of recombination, maternal inheritance, and fast substitution rate (Hwang and Kim, 1999; Carvalho-Silva et al., 2017; Zhang et al., 2019; Nicolas et al., 2020).

Here, we aim to elucidate patterns of molecular evolution in Dactylogyridae by maximising the number of genera included in the phylogenetic reconstruction to minimise the bias towards certain lineages and geographic regions. To elucidate phylogenetic relationships across evolutionary time scale, a range of ribosomal markers with different rates of molecular evolution is applied. We further revise the classification of dactylogyrid lineages and genera to resolve paraphylies, and provide a new baseline for future taxonomic and phylogenetic studies on this parasite family.

2. Material and methods

2.1 Sequence selection and taxon coverage

Molecular data were obtained from GenBank (Clark et al., 2016). We searched for species of all genera that have so far been assigned to Ancylodiscoididae, Ancyrocephalidae, Dactylogyridae, Protogyrodactylidae, and Pseudodactylogyridae currently listed within Dactylogyridea in the WORMS database (Horton et al., 2021).

We selected only sequences released in peer-reviewed publications to assure that species identity and sequence quality had been verified. With the selected sequences, we compiled a three-locus concatenated multiple alignment including fragments of the large (28S rDNA) and small (18S rDNA) subunit ribosomal DNA, and the internal transcribed spacer 1 (ITS1). Taxon coverage was most complete for 28S rDNA but, for some genera, we found only 18S rDNA or ITS1 sequences e.g. *Diaphorocleidus* Jogunoori, Kritsky & Venkatanarasaiah, 2004, *Pavanelliella* Kritsky & Boeger, 1998, *Susanlimocotyle* Soares, Domingues & Adriano, 2020, and *Thylacicleidus* Wheeler & Klassen, 1988. Species of *Calceostoma* Van Beneden, 1858, *Neocalceostoma* Tripathi, 1959, *Neotetraonchus* Bravo-Hollis, 1968, and *Synodontella* Dossou & Euzet, 1993 were omitted as the available DNA sequences (Justine et al., 2002; Hayward et al., 2007; Raphahlelo et al., 2016; Mendoza-Franco et al., 2018) were unusually short or non-alignable. For genera with more than three species with available sequences, we only included two to three specimens to reflect the major clades of the genus based on previous phylogenetic studies including for *Anacanthorus* Mizelle & Price, 1965, *Ameloblastella* Kritsky, Mendoza-Franco & Scholz, 2000, *Bravohollisia* Bychowsky & Nagibina, 1970, *Characidotrema* Mendoza-Franco, Reina & Torchin, 2009, *Chauhanellus* Bychowsky & Nagibina, 1968, *Cichlidogyrus* Paperna, 1960, *Dactylogyrus* Diesing, 1850, *Euryhaliotrema* Kritsky & Boeger, 2002, *Haliotrematoides* Kritsky, Yang & Sun, 2009, *Hamatopeduncularia* Yamaguti, 1953, *Heteropriapulus* Kritsky, 2007, *Lethrinitrema* Lim & Justine, 2011, *Ligophorus* Euzet & Suriano, 1977, *Metahaliotrema* Yamaguti, 1953, *Nanayella* Acosta, Mendoza-Palmero, da Silva & Scholz, 2019, *Quadriacanthus* Paperna, 1961, *Scutogyrus* Pariselle & Euzet, 1995, *Thaparocleidus* Jain, 1952, and *Urocleidoides* Mizelle & Price, 1964 (Wu et al., 2007, 2008; Blasco-Costa et al., 2012; Sun et al., 2014; García-Vásquez et al., 2015; Acosta et al., 2017, 2019; Francová et al., 2017; Moreira et al., 2019; Řehulková et al., 2019; Soo, 2019; Zago et al., 2020; Mendoza-Palmero et al., 2020; Soo and Tan, 2021; Cruz-Laufer et al., 2021b). If possible, the type species of each genus was included. Full genus and species names including author citations can be found in Table 1.

Phylogenetic analyses

Phylogenetic analyses followed the procedures of Cruz-Laufer et al. (2021b). We aligned the sequences using the L-INS-I algorithm in MAFFT v7.409 (Katoh and Standley, 2013) as recommended for ribosomal DNA by the *MAFFT manual*, and removed poorly aligned positions and divergent regions with Gblocks v0.91b using the options for less stringent parameters (Talavera and Castresana, 2007). We partitioned the DNA sequence data by gene and selected the substitution models for each partition according to the Bayesian information criterion (BIC) through partition merging (Chernomor et al., 2016) as implemented in ModelFinder in IQ-Tree (Kalyaanamoorthy et al., 2017) (Table 1). For BI analyses, we only selected models implemented in MrBayes v3.2.6 (Ronquist and Huelsenbeck, 2003) (Table 1).

We estimated tree topologies through Bayesian inference (BI) and maximum likelihood (ML) methods applied to the individual loci and on the concatenated dataset using MrBayes v3.2.6 (Ronquist and Huelsenbeck, 2003) on the CIPRES Science Gateway online server (Miller et al., 2010) and IQ-Tree v1.6.12 (Nguyen et al., 2015). Species belonging to Diplectanidae Monticelli, 1903 were used to root the phylogenetic trees due to their well-documented relationship with dactylogyrid monogeneans (Mollaret et al., 2000; Zhang et al., 2020). For BI analyses, we used two parallel runs and four chains of Metropolis-coupled Markov chain Monte Carlo iterations, ran 100 million generations with a burn-in fraction of 0.25, and sampled the trees every 1000th generation. We checked convergence criteria by assessing the average standard deviation of split frequencies (< 0.01 in all datasets) and the effective sample size (> 200) using Tracer v1.7 For ML analyses (Rambaut et al., 2018). We estimated branch support values using ultrafast bootstrap approximation (Hoang et al., 2018) and Shimodaira-Hasegawa-like approximate likelihood ratio tests (SH-aLRT) (Guindon et al., 2010) with 1000 replicates following the recommendations of the IQ-TREE manual. We considered nodes with a BI posterior probability (PP) ≥ 0.95, ultrafast bootstrap values (UFBoot) ≥ 95, and SH-aLRT statistic ≥ 80 as well-supported (Hoang et al., 2018).

To compare the resulting tree topologies, we inferred the congruence between the single-locus trees and between the BI and ML concatenated trees using the Congruence Among Distance Matrices (CADM) test (Legendre and Lapointe, 2004; Campbell et al., 2011). To calculate the phylogenetic pairwise distance matrices and to conduct the CADM test, we used the ‘ape’ package v5.3 (Paradis and Schliep, 2019) in R v4.0.0 (R Core Team, 2021).

Morphological, ecological, biogeographical characterisation of clades and phylogenetic support in previous studies

Based on a survey of peer-reviewed literature, we characterised all clades in our tree (Fig. 2) according to their morphology, host range, occurrence in freshwater or marine habitats, and geographical distribution limited to the species included in the phylogenetic analysis (Table 2). We also reviewed the support from previous phylogenetic studies to assess the stability of the clades in phylogenetic reconstructions. We inferred morphological characters from the respective original and emended generic diagnoses (Table S1). For the host classification, we followed Betancur-R. et al. (2007). Habitat preferences of the hosts (marine vs. freshwater) and geographical distribution were inferred from FishBase (Froese and Pauly, 2000). The latter was defined as biogeographic realms according to Olson and Dinerstein (1998) and Spalding et al. (2007). Finally, we accessed information on the family-affiliation of all genera belonging to the order Dactylogyridea from the WORMS database (Horton et al., 2021) to infer temporal trends in the description of novel genera in this taxon.

Graphing

We plotted graphs and phylogenetic trees using the packages *ggplot2* 3.3.5 (Wickham, 2016) and *ggtree* v3.1.2 (Yu et al., 2017, 2018) in R v4.1.0 (R Core Team, 2021).

Results

Phylogenetic reconstruction

In total, specimens belonging to 66 dactylogyrid genera have been included in this analysis. An overview of all dactylogyridean genera described through time is presented in Fig. 1a. Phylogenetic reconstruction revealed the presence of two main lineages (further referred to as macroclades A and B), which comprise five and six well supported clades respectively (clades A1–A5 and B1–B6) (Fig. 2) (node support values: Bayesian posterior probabilities/ultrafast bootstrap values/Shimodaira-Hasegawa-like approximate likelihood ratios). Both macroclade A (99/99/1), which includes clades A1–A5, and macroclade B (99/94/1), which includes clades B1–B6 are well-supported. The phylogenetic positions of representatives of

Characidotrema, parasites of African alestid fishes, and *Kapentagyrus*, parasites of African freshwater clupeids, remain unresolved. Species of *Aphanoblastella,* parasites of neotropical pimeloid catfishes, form a sister group to species infecting various catfish families (clades B1–B5) with high support (100/100/1). Species of *Anacanthorus*, parasites of neotropical characid fishes, form the sister group to all other clades in macroclade B (clades B1–B6) with high support (100/100/1). Clade B6 also included several well or moderately supported subclades, which are further discussed below.

Morphological, ecological, biogeographical characterisation of clades

All taxa included here fit the morphological diagnosis of Dactylogyridae sensu Bychowsky, 1933. The presence of two pairs of anchors and a single dorsal and ventral bar, respectively, are considered plesiomorphic in dactylogyrid monogeneans (Kritsky and Boeger, 1989a). However, genera with a single pair of anchors and bar (*Dactylogyrus*, *Dactylogyroides*, *Dogielius*) or missing the anchors and bars entirely (*Anacanthorus*) are nested within macroclade A and B, respectively. A comparative overview of the morphological character states of all genera of which representatives were included in the phylogenetic reconstruction is presented in Table S1. An overview of the host repertoire, biogeography, phylogenetic support, and morphological features of the attachment organ (haptor) and male copulatory organ (MCO) of all 11 clades in our tree (Fig. 2) is provided below (restricted to the dactylogyrid species and lineages included in the phylogeny). The sclerotised parts of these organs are considered one of the most systematically informative structures in monogenean taxonomy (Kritsky and Boeger, 1989a).

Clade A1 – The 'global' group (*/100/*)

Habitat: marine/freshwater.

Site of infection: gills.

Distribution: Afrotropical, Central Indo-Pacific, Eastern Indo-Pacific, Neotropical, Palearctic, Temperate Northern Atlantic regions, Temperate Northern Pacific, and Temperate South America.

Host taxa: chaetodontiform, cichliform, gerreiform, gobiiform, lutjaniform, mugiliform, and perciform fishes as well as scatophagid fishes (*incertae sedis*).

Includes: *Cichlidogyrus, Ergenstrema, Euryhaliotrema, Gussevia, Haliotrematoides, Ligophorus, Metahaliotrema, Mexicana, Onchobdella, Parasciadicleithrum, Protogyrodactylus, Sciadicleithrum, Scutogyrus, Xenoligophoroides.*

Phylogenetic support in previous studies: The genera included here have previously not been placed in a single phylogenetic study. The clade includes a large array of species from different habitats from genera that infect non-siluriform hosts. Further subdivisions of the clade show no additional geographical or host taxon patterns except for the *Cichlidogyrus*-*Scutogyrus* subclade infecting mainly cichlids in the Afrotropical region. Species of the *Metahaliotrema*-*Protogyrodactylus* subclade included here inhabit the Central Indo-Pacific region but reports from the African coast indicate a wider distribution (Boeger et al., 2012).

Morphological features: eye spots present in 1 or 2 pairs. Two pairs of anchors are present associated with two bars except for representatives of *Xenoligophoroides*. Additional structures include well-developed auricles in the dorsal bar of *Cichlidogyrus* and *Scutogyru*s, two protrusions on the ventral bar in some species of *Ligophorus* and *Xenoligophoroides cobitis*, a fan-shaped plate on the ventral bar in species of *Scutogyrus*, flexible constrictions at the base of the marginal hooks in *Xenoligophoroides cobitis*, and a T-shaped ventral bar in representatives of *Ergenstrema*. The marginal hooks are of a similar size except the species of *Cichlidogyrus, Ergenstrema, Gussevia*, and *Scutogyrus*. The roots are well-developed in both anchor pairs except in species of *Haliotrematoides, Metahaliotrema, Mexicana*, and *Gussevia*. MCO (male copulatory organ) tubular or coiled, AP (accessory piece) present or absent.

<u>Clade A2 – *'Haliotrema'* type (100/100/1)</u>

Habitat: marine.

Site of infection: gills.

Distribution: Central Indo-Pacific, Eastern Indo-Pacific, Indo-Malayan, Temperate Northern Atlantic, and Western Indo-Pacific regions.

Host taxa: chaetodontiform, ephippiform, holocentriform, lutjaniform, perciform, spariform, syngnathiform, and tetraodontiform fishes as well as malacanthid and siganid fishes (*incertae sedis*).

Includes: *Bravohollisia, Caballeria, Glyphidohaptor, Haliotrema, Lethrinitrema, Parancyrocephaloides, Platycephalotrema, Pseudohaliotrema, Tetrancistrum, Thylacicleidus*.

Phylogenetic support in previous studies: many morphologically similar yet phylogenetically unrelated species of dactylogyrid monogeneans have previously been included in *Haliotrema*. Thus, taxonomic revisions have resulted in the creation of the genera *Euryhaliotrema* (Kritsky, 2012), *Haliotrematoides* (García-Vásquez et al., 2015b), *Ligophorus* (Euzet and Suriano, 1977), and *Metahaliotrema* (Kritsky et al., 2016). The well-supported '*Haliotrema*' group inferred in this study (1.00/100/100) captures multiple species of *Haliotrema* that have not been affected by these revisions. Recent phylogenetic studies confirm the monophyly of this clade (Dang et al., 2010; Soo, 2019; Al Jufaili et al., 2020). Nonetheless, *Haliotrema* remains a 'waste basket' (Klassen, 1994) as all other genera included in this group render the genus paraphyletic.

Morphological features: eye spots present in 1 or 2 pairs but absent in the species of *Glyphidohaptor, Pseudohaliotrema,* and *Tetrancistrum*, and sometimes absent in species of *Platycephalotrema*. Two bars present, associated with two pairs of anchors except for representatives of *Glyphidohaptor*. Vestigial dorsal bars only displayed in *Parancyrocephaloides.* Additional structures include haptor reservoirs in species of *Lethrinitrema,* short auricles on the ventral bar in representatives of *Thylacicleidus*, bifurcated ends of the dorsal bar in species of *Platycephalotrema*, and a canal in the point of the anchors present in species of *Parancylocephaloides*. Marginal hooks of similar size. The anchor roots are well developed. MCO tubular or coiled (unsclerotised sheath in species of *Thylacicleidus*), AP present or absent.

<u>Clade A3 – ”Pseudodactylogyrids” and “heteronchocleidids” (100/99/1)</u>

Habitat: freshwater.

Site of infection: gills.

Distribution: Indo-Malayan and Palearctic region.

Host taxa: anabantiform, centrarchiform, gobiiform, anguilliform species.

Includes: *Ancyrocephalus mogurndae*, *Gobioecetes*, *Eutrianchoratus, Heteronchocleidus, Pseudodactylogyrus, Trianchoratus*.

Phylogenetic support in previous studies: recent phylogenetic studies show moderate ML and high BI support for this clade but include a two to three genera (Tan et al., 2011; Ogawa and Itoh, 2017).

Morphological features: eye spots present in 2 pairs. Variation in number of bars from none in *Trianchoratus*, one in *Eutrianchoratus, Gobioecetes, Ancyrocephalus morgundae* and *Pseudodactylogyrus* and two in *Heteronchocleidus*. Well supported lineage of *Eutrichanchoratus, Heteronchocleidus* and *Trianchoratus* (1/100/100) displaying unique haptoral arrangement with three developed and one vestigial anchors. Other genera and species with a single (*Ancyrocephalus mogurndae* and *Pseudodactylogyrus*) and two pairs of anchors (*Gobioecetes*), respectively. Representatives of all the reported genera of clade A3 have similar sized marginal hooks and anchors with developed roots. MCO tubular, AP present.

Clade A4 – Dactylogyrines (100/100/1)

Habitat: freshwater.

Site of infection: gills.

Distribution: Indo-Malayan and Palearctic region.

Host taxa: cypriniform species.

Includes: *Dactylogyrus*, *Dactylogyroides, Dogielius*.

Phylogenetic support: *Dactylogyroides*, and *Dogielius* have not been included in previous phylogenetic studies with other dactylogyrid genera beyond *Dactylogyrus*.

Morphological features: eye spots present in 2 pairs. A single pair of anchors is present accompanied by a ventral bar only in *Dogielius* and two bars in *Dactylogyrus* and *Dactylogyroides*. The anchor roots are well-developed with poorly differentiated shafts and points in *Dactylogyrus* and *Dactylogyroides* unlike in *Dogielius*. Marginal hooks of similar but also different sizes. MCO tubular, AP present.

<u>Clade A5 – Mesoparasitic dactylogyrids (100/100/1)</u>

Habitat: freshwater/marine.

Site of infection: oesophagus (*Paradiplectanotrema, Pseudempleurosoma*), pharynx (*Paradiplectanotrema*) and stomach (*Enterogyrus, Pseudempleurosoma*), rarely gills (*Paradiplectanotrema*, *Pseudempleurosoma*).

Distribution: Afrotropical and Central Indo-Pacific region.

Host taxa: aulopiform, cichliform, and sciaenid species.

Includes: *Enterogyrus, Paradiplectanotrema, Pseudempleurosoma*.

Phylogenetic support in previous studies: these genera have previously not been included in a phylogenetic study together.

Morphological features: eye spots present in 2 pairs. Two bars present accompanied by only a ventral pair of anchors in *Enterogyrus* (African representatives) compared to two pairs of anchors in *Enterogyrus* (Asian representatives, molecular data not available), *Pseudempleurosoma* and *Paradiplectanotrema.* The anchor roots are well developed. The ventral bar of *Paradiplectanotrema* and *Pseudempleurosoma* is divided in two and four parts, respectively. Marginal hooks of similar (*Enterogyrus*, *Paradiplectanotrema*) but also different sizes (*Pseudempleurosoma*). MCO tubular, coiled or straight, AP present or absent.

<u>Clade B1 – Parasites of siluriforms I: Pimelodidae (100/100/1)</u>

Habitat: freshwater.

Site of infection: gills.

Distribution: Neotropical region.

Host taxa: siluriform species (Pimelodidae).

Includes: *Boegeriella*, Dactylogyridae gen. sp. 9/13/18/23/26, *Demidospermus morthenthaleri*, *Demidospermus* sp. 11/23, *Nanayella*.

Phylogenetic support in previous studies: monophyly supported by several previous studies (Mendoza-Palmero et al., 2015, 2019; Acosta et al., 2019).

Morphological features: eye spots absent or reduced. Two pairs of variably shaped anchors accompanied by two robust, straight or slightly V- or U-shaped bars. Dorsal bar with median conjunction. Additional structures include two submedial projections on the dorsal bar directed anteriorly in the representatives of *Boegeriella.* Variation in the shank and base of marginal hook pairs 5 and 6. Marginal hooks of similar or different sizes. MCO tubular, J-shaped or coiled, AP present.

Clade B2 – Parasites of siluriforms II: Ariidae, Bagridae, and Schilbeidae (99/100/1)

Habitat: marine/freshwater.

Site of infection: gills.

Distribution: Afrotropical, Central Indo-Pacific, Temperate South America, Tropical Atlantic, and Western Indo-Pacific regions.

Host taxa: siluriform species (Ariidae,Bagridae, and Schilbeidae).

Includes: *Chauhanellus*, *Hamatopeduncularia*, *Schilbetrema, Susanlimocotyle*.

Phylogenetic support in previous studies: no study has previously included species of all four genera in a phylogenetic analysis. Previous studies have omitted species of at least one of the genera included here, e.g. *Hamatopeduncularia* (Franceschini et al., 2018; Acosta et al., 2019)*, Schilbetrema* (Soares et al., 2021), and *Susanlimocotyle* (Soo and Tan, 2021), and sometimes incorporated unpublished sequences of species of *Mizelleus* (see Illa et al., 2019; Soares et al., 2021).

Morphological features: two pairs of eye spots. Two pairs of anchors accompanied by two bars. Dorsal bar in two parts in *Susanlimocotyle narina.* Additional structures include a superficial knob on the ventral anchor base and submedial/subterminal projections on the ventral and/or dorsal bar in the representatives of *Schilbetrema,* accessory sclerites on both anchor pairs in the species of *Chauhanellus*, and an onchium in *Susanlimocotyle*. Variation in the development of anchor roots. Marginal hooks of similar but also different sizes. MCO tubular or not; AP present or absent.

Clade B3 – Parasites of siluriforms III: Bagridae and Siluridae (97/95/1)

Habitat: freshwater.

Site of infection: gills.

Distribution: Indomalayan and Palaearctic region.

Host taxa: siluriform species (Bagridae and Siluridae).

Includes: *Cornudiscoides, Pseudancylodiscoides, Thaparocleidus*.

Phylogenetic support in previous studies: no study has previously included all three genera in a phylogenetic analysis. However, close relationships between species of *Pseudancylodiscoides* and *Thaparocleidus* have previously been reported (Wu et al., 2008).

Morphological features: two pairs of eye spots. Two pairs of anchors accompanied by two bars. Dorsal bar straight to V-shaped. Ventral bar V-shaped or divided in two parts. Patches on dorsal anchors present. Additional structures include a long thin medial ligament in the ventral bar of *Cornudiscoides*. Variation in the development of anchor roots. Marginal hooks of similar but also different sizes. Straight or coiled MCO, AP present.

Clade B4 – Parasites of siluriforms IV: Doradidae and Loricariidae (96/89/0.98)

Habitat: freshwater.

Distribution: Neotropical region.

Site of infection: gills.

Host taxa: siluriform species (Doradidae and Loricariidae).

Includes: *Cosmetocleithrum*, *Demidospermus* sensu stricto.

Phylogenetic support in previous studies: our results confirm monophyly of this clade reported by recent studies (Acosta et al., 2019; Mendoza-Palmero et al., 2019) despite a lack of support for the clade in the first phylogenetic study including the two genera (Acosta et al., 2018).

Morphological features: eye spots absent or poorly developed in species of *Cosmetocleithrum* but present in species of *Demidospermus* sensu stricto. Two pairs of anchors accompanied by two bars. Bars robust and slightly bent in species of *Cosmetocleithrum* but elongated and V-, W- or U-shaped in species of *Demidospermus*. Additional structures include two submedial projections on the dorsal bar in the representatives of *Cosmetocleithrum.* Marginal hooks of similar or variable sizes. MCO tubular, coiled or straight, AP present.

Clade B5 – Parasites of siluriforms V: Bagridae and Clariidae (100/100/1)

Habitat: freshwater.

Site of infection: gills.

Distribution: Afrotropical and Indomalayan regions.

Host taxa: siluriform species (Bagridae and Clariidae).

Includes: *Bychowskyella, Quadriacanthus*.

Phylogenetic support: previous studies have indicated the close relationship of these two genera (Wu et al., 2008). Furthermore, sometimes unpublished sequences of species of *Mizelleus* (see Illa et al., 2019; Soares et al., 2021) were incorporated highlighting a close relationship of these species to species of *Bychowskyella*.

Morphological features: two pairs of eye spots, absent or dispersed in cephalic area. Two pairs of anchors accompanied by two bars. Dorsal bar with a conjunction in the middle in the representatives of

Bychowskyella. Ventral bar in two parts in species of *Quadriacanthus*. Additional structures include accessory two pairs of sclerites on both anchor pairs in the species of *Quadriacanthus* reminiscent of those in species of *Chauhanellus*, and an onchium in species of *Bychowskyella* similar to *Susanlimocotyle narina*. Marginal hooks of similar but also different sizes. MCO straight, curved, or coiled; AP present.

<u>Clade B6 – Ancyrocephalines (99/99/1)</u>

Habitat: freshwater.

Site of infection: gills.c

Distribution: Indo-Malayan, Neotropical, and Nearctic region (but some specimens used in this study co-introduced to Palearctic with centrarchid and ictalurid hosts, see Fig. 2).

Host taxa: centrarchiform, characiform, gymnotiform, perciform, and siluriform species

Includes: *Actinocleidus, Ameloblastella, Ancyrocephalus* sensu stricto, *Cacatuocotyle, Diaphorocleidus, Heteropriapulus*, *Ligictaluridus, Mymarothecium, Onchocleidus*, *Pavanelliella, Trinigyrus*, *Unibarra, Unilatus*, *Urocleidoides, Vancleaveus*.

Phylogenetic support: monophyly supported by previous studies (Moreira et al., 2019; Franceschini et al., 2020; Zago et al., 2020) but *Diaphorocleidus* and *Pavanelliella* hitherto not included.

- *Trinigyrus, Heteropriapulus, Unilatus* (*/99/*) - Parasites of siluriform hosts, family Loricariidae.

  Phylogenetic support in the previous studies: monophyly of the clade including the sister relationship of *Trinigyrus* and *Heteropriapulus* and the basal position of *Unilatus* was presented in Franceschini et al. (2020).

  Morphological features: eye spots absent or dissociated. Two pairs of anchors accompanied by two bars in species of *Heteropriapulus* and *Unilatus*, one anchor pair accompanied by a single bar in species of *Trinigyrus*. Both anchor pairs in species of *Unilatus* project dorsally, reminiscent of species belonging to *Actinocleidus*, where both pairs project ventrally (Beverley-Burton, 1981). Hooks are usually similar in shape and size, arranged in digits in representatives of *Trinigyrus* similar to species of *Hamatopeduncularia* (Lim, 1996). MCO tubular, straight or sigmoid, AP present.

- *Unibarra, Vancleaveus, Ameloblastella* (96/98/*) – Parasites of siluriform fishes, families Doradidae, Heptapteridae, and Pimelodidae.

Phylogenetic support in previous studies: previous studies show monophyly of the *Unibarra-Ameloblastella-Vancleaveus* group: Moderate support reported by Mendoza-Palmero et al. (2015) but high support reported in all follow-up studies (Acosta et al., 2019; Mendoza-Palmero et al., 2019; Franceschini et al., 2020; Zago et al., 2020) with exceptions (Mendoza-Palmero et al., 2017).

Morphological features: eye spots absent or incipient. Two pairs of anchors accompanied by two transverse bars in *Ameloblastella* and *Vancleaveus* with only a ventral bar being present in species of *Unibarra* (Suriano & Incorvaia, 1995). Dorsal anchors in species of *Vancleaveus* with superficial root and conspicuous basal fold. Dorsal bar of *Ameloblastella* with posteromedial projection. Marginal hooks of similar size but variable in shape and size between genera. MCO tubular and coiled, AP present.

- *Ancyrocephalus* sensu stricto*, Onchocleidus, Ligictaluridus, Actinocleidus* (99/99/0.97) – Parasites of centrarchiform, siluriform, and perciform hosts, families Centrarchidae, Ictaluridae, and Percidae.

Phylogenetic support: monophyly well-supported by previous studies (Moreira et al., 2019; Franceschini et al., 2020; Zago et al., 2020) but this is the first time all these genera have been included in a phylogenetic analysis together.

Morphological features: two pairs of eye spots. Two pairs of anchors accompanied by two transverse bars, both variable in shape and size. In species of *Actinocleidus*, both anchor pairs project ventrally similar to *Unilatus*, where both anchors project dorsally (Mizelle and Kritsky, 1967). Bars articulate in species of *Actinocleidus* to support the position of the anchors (Beverley-Burton, 1981). Species of *Ligictaluridus* possess a median lightly sclerotised flange at the bars (Beverley-Burton, 1984). Marginal hooks variable in shape and size. MCO tubular, curved or straight, AP present.

- *Urocleidoides, Cacatuocotyle* (*/87/*) - Moderately supported clade with unresolved internal topology. Parasites of characiform, centrarchiform, gymnotiform hosts, families Anostomidae, Gymnotidae, Parodontidae.

  Morphological features: eye spots present but may be dissociated. Two pairs of anchors accompanied by two transverse bars in species of *Mymarothecium* and *Urocleidoides* with only the ventral bar present in species of *Cacatuocotyle*. Dorsal bar of species of *Mymarothecium* with anteromedial projection. Marginal hooks are variable in shape and size between genera. MCO tubular, curved or straight, AP present.

Discussion

This study provides the most extensive phylogenetic analysis of dactylogyrid monogeneans to date. Based on representatives of 66 genera and a combination of three ribosomal gene markers, our phylogenetic reconstruction revealed the presence of two macroclades including five and six well-supported clades respectively. Our results highlight biological, biogeographical and habitat-type patterns that have shaped the evolutionary history of teleost-dactylogyrid interactions (Fig. 2). In the past, morphological and molecular data have resulted in multiple systematic revisions of species and clades in dactylogyrid monogeneans. We provide an overview of evolutionary patterns and systematic revisions at subfamily and genus levels within Dactylogyridae in the following discussion. Finally, we highlight how limited coverage of host taxa or distribution ranges and biases towards certain host groups and regions interfere with scientific exploration of the evolutionary history of Dactylogyridae.

Environment and biogeography: Molecular and morphological evolution occur at different rates

Monogenean evolution is often considered to closely mirror the evolutionary history of the host organisms (Pariselle et al., 2011). As dactylogyrid monogeneans occur in almost every biogeographic realm, their deep evolutionary history is likely shaped by large-scale biogeographical factors including continental drift, changes in salinity, and teleost diversification. Biogeographical, salinity (marine vs. freshwater) and host-related distinctions between the respective (macro)clades can be observed (Fig. 2). In general, environmental factors affect meso- and ectoparasites differently (Pariselle et al., 2011). Mesoparasites are more likely shielded from environmental changes. The phylogenetic tree presented here (Fig. 2) even suggests a common ancestor for all mesoparasitic dactylogyrid species sequenced to date. Meanwhile, ectoparasites are directly exposed to outside stressors. Sudden changes in salinity are deadly to many gill monogeneans, a fact used to treat these infections in aquaculture (Fajer-Ávila et al., 2007; Schelkle et al., 2011; Brazenor and Hutson, 2015). Hence, closely related ectoparasitic dactylogyrids are often exclusive to either freshwater or marine habitats (see Fig. 2). Dactylogyrid species infecting catfishes (Siluriformes) illustrate this adherence to freshwater and marine habitats. Catfishes constitute approximately 30% part of the world's ichthyofauna (Teugels, 1996) and have a Pangaean origin that dates back to the Early Cretaceous period (145 – 66 MYA) (Teugels, 1996; Chen et al., 2013). For these reasons, catfishes have been established as models for historical biogeography (e.g Agnèse and Teugels, 2005; Betancur-R. et al., 2007; Roxo et al., 2014). Several phylogenetic studies have focused on the evolutionary history of the Neotropical dactylogyrid lineages infecting siluriform hosts before. In the light of this importance and in comparison to the previous studies, our study shows that all molecularly characterised dactylogyrid monogenean genera infecting catfishes belong to a single lineage (macroclade B) with two nested clades (B1 and B4) specific to New World hosts and two others to Old World species (B3 and B5). This pattern suggests that certain dactylogyrid monogeneans have followed their hosts' evolution to spread to all continents before the time Pangaea separated 200 million years ago remaining in freshwater habitat except for a single mostly marine lineage (clade B2). Another example of the adherence to freshwater habitats, are the species infecting the cichlid fishes. All species (that have been sequenced) belong to the same clade (A1) including representatives of *Cichlidogyrus, Onchobdella,* and *Scutogyrus* from continental Africa (Pariselle and Euzet, 2009), and *Gussevia, Parasciadicleithrum,* and *Sciadicleithrum* from the Americas (Mendoza-Palmero et al., 2017). However, cichlids have a Gondwanan origin with the oldest lineages found in Madagascar (Matschiner, 2019c Matschiner et al., 2020). Dactylogyrid gill parasites on Neotropical and African cichlids constitute four different lineages that are not closely related including *Cichlidogyrus-Scutogyrus, Gussevia-Parasciadicleithrum, Onchobdella,* and *Sciadicleithrum* (Fig. 2). For this reason, previous studies suggested that cichlids must have crossed marine habitats (Pariselle et al., 2011; Vanhove et al., 2016) effectively removing the original cichlid gill parasites (*Insulacleidus* spp. from

Madagascar to Africa, or *Onchobdella*/*Cichlidogyrus* from Africa to South America) and opening the ecological niche to other new dactylogyrid lineages. Transatlantic dispersal of cichlids has since then been confirmed by ichthyological studies (Matschiner, 2019; Matschiner et al., 2020). However, to elucidate the origin and dispersal history of cichlid monogeneans, a more complete taxon coverage is needed. For instance, molecular data on mesoparasitic dactylogyrids infecting Neotropical cichlids would allow to evaluate whether mesoparasitic lineages indeed persisted after an alleged transatlantic dispersal in contrast to ectoparasitic dactylogyrids. In any case, marine-freshwater switches can be considered a major factor in teleost-dactylogyrid interactions.

Changes in environmental conditions such as marine-freshwater habitat switches can impact the morphology of the parasites (Brooks and McLennan, 1993; Joffe et al., 2001). These changes can tamper with genus diagnoses, which are traditionally based on common morphological features. This explains why morphologically and environmentally well-defined genera are rendered paraphyletic by some non-congeners, e.g. *Sciadicleithrum* for *Euryhaliotrema* or *Dogielius* and *Dactylogyroides* for *Dactylogyrus* (Fig. 2). We revealed multiple possible marine-freshwater switches within Dactylogyridae. *Sciadicleithrum* is a freshwater lineage nested in a group of mostly marine representatives of *Euryhaliotrema* (A1), species of *Thylacicleidus* are the only freshwater representatives in their clade (A2), and in macroclade B species of *Chauhanellus* and *Hamatopeduncularia* are the only marine representatives but, nonetheless, are still parasites of catfish hosts similar to most other species in this group. Furthermore, we found a remarkable pattern for the presence of eye spots in dactylogyrids. The *Glyphidohaptor-Pseudohaliotrema-Tetrancistrum* lineage in clade A2, all representatives of clade B1 (including *Demidospermus* spp., see below), species of *Aphanoblastella*, and several lineages in clade B6 have lost the four eyespots that are characteristic to dactylogyrid monogeneans, in their adult stage, or replaced them with many small eye granules (Table S1). Previous studies suggest that the eye spots might be linked to the larval development, i.e. helping the organism to travel through water to find a suitable host (Said and Abu Samak, 2008). Said and Abu Samak (2008) hypothesised that species of *Dactylogyrus* might use the eye spots to move on the host gills but their role in adult organisms remains uncertain (Cable and Tinsley, 1991). In the case of Neotropical dactylogyrids infecting siluriforms, the reduction of eye spots might reflect an adaptation to poorly lit environments where the parasites have no use for photoreceptors at least in their adult stage. For instance, white-, black-, and clearwater-type rivers are known to play an important role in allopatric speciation of aquatic communities in the Amazon basin (Paxiúba Duncan and Narciso Fernandes, 2010), which might explain the absence of eye spots in many adult Neotropical dactylogyrids. However, a majority of dactylogyrid genera and species lack molecular data, e.g. several species of *Demidospermus* present eye spots (Kritsky and Gutierrez, 1998) but DNA sequences remain unavailable. Evidently, a more complete molecular dataset is needed to shed light on the concordance between morphological and molecular data and the impact of environmental factors on dactylogyrid evolution.

The mismatch of rates of morphological and molecular evolution has consequences for dactylogyrid systematics. Rapid changes in shape and size may render morphological characters systematically uninformative at the level beyond the level of closely related species, e.g. in *Cichlidogyrus* (Pouyaud et al., 2006; Cruz-Laufer et al., 2021b) or *Thaparocleidus* (Wu et al., 2008). Similar patterns have been found for representatives of Diplectanidae (Poisot et al., 2011; Villar-Torres et al., 2019), a sister family to Dactylogyridae. Conversely, morphological similarities in more distantly related lineages may have led to the presence of several 'waste bucket' genera including *Ancyrocephalus* (Bychowsky and Nagibina, 1970), *Haliotrema* (Klassen, 1994), *Demidospermus*, *Urocleidoides* (Acosta et al., 2018), and to a smaller extent *Thaparocleidus*, which is rendered paraphyletic by the erections of *Pseudancylodiscoides* (Wu et al., 2008; this study) and *Cornudiscoides* (Fig. 2). Many species formerly considered part of these groups share morphological features but are otherwise unrelated. To address this issue, some studies based generic affiliations on monophyletic clades inferred from phylogenetic reconstructions (phylogenetic systematics). For instance, *Parasciadicleithrum octofasciatum* Mendoza-Palmero, Blasco-Costa, Hernández-Mena & Pérez-Ponce de León, 2017 is morphologically almost indistinguishable from species of *Sciadicleithrum* but belongs to a different evolutionary lineage (Mendoza-Palmero et al., 2017) (clade A1 in the present study). This approach has also led to the erroneous description of the genus *Paracosmetocleithrum* Acosta, Scholz, Blasco-Costa, Alves & da Silva, 2017. A lack of support for a monophyletic clade including the type species *P. trachydorasi* Acosta, Scholz, Blasco-Costa, Alves & da Silva, 2017 and other species of *Cosmetocleithrum* was misinterpreted as evidence for taxon separation in spite of the unresolved relationship between these taxa

(Acosta et al., 2018). Later, the genus was reassigned to *Cosmetocleithrum* as conclusions drawn from the phylogenetic analysis were questioned because of a lack of morphological differences (Cohen et al., 2020). Our results agree with this step as we found moderate support (95/*/*) for *Cosmetocleithrum* sensu Cohen et al. (2020). The need for strictly monophyletic taxa remains contested in the literature (Schmidt-Lebuhn, 2012; Stuessy and Hörandl, 2014). Yet we argue that all taxa should reflect phylogenetic hypotheses and consequently the evolutionary history (for an extensive discussion against the use of paraphyletic taxa, see Schmidt-Lebuhn, 2012). Hence, we propose the systematic revision of several poly- and paraphyletic genera in the following section to provide revised classification of molecularly characterised dactylogyrid genera consistent with taxon monophyly some of which were recognised in the previous phylogenetic studies.

Systematics: not seeing the wood for the trees

Class Monogenoidea Bychowsky, 1937

Subclass Polyonchoinea Bychowsky, 1937

Order Dactylogyridea Bychowsky, 1937

Family Dactylogyridae Bychowsky, 1933

Junior synonyms: Ancylodiscoididae Gusev, 1961, Ancyrocephalidae Bychowsky, 1937, Heteronchocleididae Tan, Fong &Lim, 2011, Protogyrodactylidae Johnston & Tiegs, 1922, Pseudodactylogyridae Gusev, 1965 and Urogyridae Bilong Bilong, Birgi & Euzet, 1994.

Emended diagnosis: Two or four eye-spots; might be dissociated, incipient or lacking. Body fusiform, pyriform or uniform in width; compact or divided of cephalic region, trunk, peduncle and haptor. Tegument smooth or ciliated. Single, two or three pairs of cephalic lobes; sometimes poorly developed. Two to five pairs of bilateral head organs; sometimes poorly developed. Cephalic glands unicellular, in two, three or four pairs; might be dissociated or inconspicuous. Mouth subterminal. Intestinal caeca 2, confluent posterior to gonads or not united, diverticula present or absent. Common genital pore midventral or absent. Gonads in tandem or overlapping, intercaecal. Vas deferens looping left intestinal cecum or not looping; one or two seminal vesicles are a dilation of vas deferens. One or two prostatic reservoirs; might be absent. Vaginal aperture sclerotised or not sclerotised. Male copulatory organ sclerotised, tubular, coiled, or straight; accessory piece articulated or detached; might be weakly sclerotised or absent. Seminal receptacle present or absent. Vitellaria coextensive with gut or scattered throughout the body. Haptor armed with single or paired dorsal and ventral anchor/bar sclerotised complexes, sometimes absent; additional structures with various levels of sclerotisation might be present; 7 pairs of similar or dissimilar hooks. Parasites on the gills, skin, nasal cavities, intestines, urinal bladder, and kidneys of freshwater and marine fishes worldwide.

Remarks: In the most recent systematic revision of Monogenea and Monopisthocotylea by Boeger and Kritsky (2001) 53 and 30 families were recognised respectively. In the last decades, several studies have investigated phylogenetic relationships within Dactylogyridae (Šimková et al., 2003, 2006; Plaisance et al., 2005; Mendoza-Palmero et al., 2015). However, this research tradition required an update as DNA sequences are becoming available for an increasing number of species and species groups (see Fig. 1c).

- The diagnoses of Ancyrocephalidae Bychowsky, 1937 and Dactylogyridae Bychowsky, 1935 rely on the difference mainly in the number of seminal vesicles supported by the revision of Bychowsky and Nagibina (1978) and a cladistic study of Malmberg (1990). However, the systematic revision of Kritsky and Boeger (1989a) proposed Ancyrocephalidae sensu Bychowsky & Nagibina, 1978 as a junior synonym of Dactylogyridae as Ancyrocephalidae appeared paraphyletic with no unambiguous morphological evidence supporting the distinction between both families. As the difference in number of seminal vesicles is not consistent with the major lineages (macroclades A and B) and no other unambiguous morphological differences were identified in this study, we follow the previously suggested synonymisation of Dactylogyridae and Ancyrocephalidae with Dactylogyridae having the taxonomic priority.
- Our results also confirm species of *Protogyrodactylus* Johnston & Tiegs, 1922 as members of Dactylogyridae and as sister taxon to *Metahaliotrema*. Thus, we consider the family Protogyrodactylidae Johnston & Tiegs, 1922 invalid and a synonym of Dactylogyridae as previously suggested by Price and Pike (1969).
- Unlike Malmberg (1990), we conclude that *Ergenstrema mugilis* is nested within Dactylogyridae and representatives of this genus should be reassigned from Tetraonchidae to Dactylogyridae as

proposed by Mendoza-Palmero et al. (2015) and Blasco-Costa et al. (2012). However, species of *Tetraonchus* Diesing, 1858 are not transferred to Dactylogyridae as this genus forms a separate lineage as supported by a recent phylogenetic reconstructions based on mitochondrial protein coding regions (Zhang et al., 2020).

- Previous studies also recognised the subfamily Pseudodactylogyrinae Ogawa, 1986 (Šimková et al., 2003, 2006; Plaisance et al., 2005; Mendoza-Palmero et al., 2015) for species of *Pseudodactylogyrus* characterised by a reduced anchor-bar complex and supplementary needle-like pieces. Moreover, representatives of dactylogyrid genera with three well-developed anchors (*Eutrianchoratus*, *Heteronchocleidus,* and *Trianchoratus*) were placed in another subfamily, Heteronchocleidinae Price, 1968. Some studies even suggested raising Pseudodactylogyrinae (Le Brun et al., 1986) and Heteronchocleidinae (Tan et al., 2011) to family level. In the present study, pseudodactylogyrine and heteronchocleidine species form a well-supported clade (A3) within Dactylogyridae alongside species of *Gobioecetes* and *Ancyrocephalus mogurndae.* Additionally, Ogawa (1986) remarked on similarities of species of *Pseudodactylogyrus* and *Heteronchocleidus* concerning the haptor morphology. We propose that Pseudodactylogyridae Le Brun, Lambert & Justine, 1986 and Heteronchocleididae Tan, Fong & Lim, 2011 are synonyms of Dactylogyridae.
- Urogyridae Bilong Bilong, Birgi & Euzet, 1994 was proposed to accommodate species of Dactylogyridea with a single, asymmetric pair of anchors (i.e. one anchor is only rudimentarily developed) infecting the urinary bladder of cichlid fishes. As Bilong Bilong et al. (1994) provide only little information and even suggested a possible relationship with species of *Onchobdella*, the family was later synonymised with Dactylogyridae (Fayton and Kritsky, 2013). Indeed, the number of anchor pairs varies across dactylogyrid genera ranging from three pairs (e.g. in the 'heteronchocleidid' genera *Heteronchocleidus, Eutrianchoratus,* and *Trianchoratus*) to none (e.g. in species of *Anacanthorus* and *Pavanelliella*). Reduced anchor-bar complexes were suggested to result from morphological convergence of mesoparasitic dactylogyrids, in particular for dactylogyrids infecting the excretory system, e.g. species of *Acolpenteron* Fischthal and Allison, 1941, where the wide geographical range in the holarctic and neotropical realms indicates a potential polyphyly (Fayton

and Kritsky, 2013). Yet despite a limited taxon coverage, our results indicate a common ancestor for mesoparasitic dactylogyrids. The existence of this clade was previously reported but with only a limited number of other dactylogyrid lineages included in a phylogenetic analysis (Theisen et al., 2017, 2018).

- Lim et al. (2001) raised Ancylodiscoidinae to family level comprising monogeneans from siluriform and notopterid fishes of the Old World with four anchors. Although our results moderately support the monophyletic status of ancylodiscoidine monogeneans including clades B1–B5, the lineage is included in macroclade B together with clade B6. Ancylodiscoididae would, therefore, have to encompass all taxa from macroclade B including lineages basal to both of the clades (notably also representatives of *Anacanthorus* infecting characiform hosts). Moreover, given that *Ancyrocephalus paradoxus* as type species is placed in clade B6, Ancyrocephalidae has taxonomic priority over Ancylodiscoididae. Hence, we propose that Ancylodiscoididae should be synonymised with Dactylogyridae.
- No representatives of the families Calceostomatidae, Fridericianellidae, Neocalceostomatidae and Neotetraonchidae and the subfamilies Linguadactylinae, Linguadactyloidinae, Hareocephalinae, or Heterotesiinae could have been included in the presented phylogenetic reconstruction. Therefore, the status of these families remains unresolved (Justine et al., 2002).

Includes: Acolpenteron Fischthal & Allison, 1940; *Actinocleidus* Mueller, 1937; *Aethycteron* Suriano & Beverley-Burton, 1982; *Afrocleidodiscus* Paperna, 1969; *Ameloblastella* Kritsky, Mendoza-Franco & Scholz, 2000; *Amphithecium* Boeger & Kritsky, 1988; *Amphocleithrum* Price & Romero, 1969; *Anacanthoroides* Kritsky & Thatcher, 1974; *Anacanthorus* Mizelle & Price, 1965; *Anchoradiscoides* Rogers, 1967; *Anchoradiscus* Mizelle, 1941; *Anchylodiscus* Johnston & Tiegs, 1922; *Ancistrohaptor* Agarwal & Kritsky, 1998; *Ancylodiscoides* Yamaguti, 1937; *Ancyrocephaloides* Yamaguti, 1938; *Ancyrocephalus* Creplin, 1839; *Androspira* Suriano, 1981; *Annulotrema* Paperna & Thurston, 1969; *Annulotrematoides* Kritsky & Boeger, 1995; *Apedunculata* Cuglianna, Cordeiro & Luque, 2009; *Aphanoblastella* Kritsky, Mendoza-Franco & Scholz, 2000; *Archidiplectanum* Mizelle & Kritsky, 1969; *Aristocleidus* Mueller, 1936; *Atherinicus* Bychowsky & Nagibina, 1969; *Bagrobdella* Paperna, 1969; *Bicentenariella* Cruces, Chero, Sáez & Luque, 2021;

Bifurcohaptor Jain, 1958; *Biotodomella* Morey, Arimuya & Boeger, 2019; *Birgiellus* Bilong Bilong, Nack & Euzet, 2007; *Bivaginogyrus* Gusev & Gerasev, 1986; *Boegeriella* Mendoza-Palmero & Hsiao, 2020; *Bouixella* Euzet & Dossou, 1976; *Bravohollisia* Bychowsky & Nagibina, 1970; *Bychowskyella* Akhmerov, 1952; *Caballeria* Bychowsky & Nagibina, 1970; *Cacatuocotyle* Boeger, Domingues & Kritsky, 1997; *Calpidothecioides* Kritsky, Boeger & Jégu, 1997; *Calpidothecium* Kritsky, Boeger & Jégu, 1997; *Characidotrema* Paperna & Thurston, 1968; *Characithecium* Mendoza-Franco, Reina & Torchin, 2009; *Cichlidogyrus* Paperna, 1960; *Clavunculus* Mizelle, Stokely, Jaskoski, Seamster & Monaco, 1956; *Cleidodiscus* Mueller, 1934; *Cleithrarticus* Mizelle, 1963; *Constrictoanchoratus* Ferreira, Rodrigues, Cunha & Domingues, 2017; *Cornudiscoides* Kulkarni, 1969; *Cosmetocleithrum* Kritsky, Thatcher & Boeger, 1986; *Crinicleidus* Beverley-Burton, 1986; *Cryptocephalum* Vega, Viozzi & Brugni, 2011; *Curvianchoratus* Hanek, Molnár & Fernando, 1974; *Dactylogyrus* Diesing, 1850; *Dawestrema* Price & Nowlin, 1967; *Demidospermus* Suriano, 1983; *Diaphorocleidus* Jogunoori, Kritsky & Venkatanarasaiah, 2004; *Dicrodactylogyrus* Lu & Lang, 1981; *Diplectanotrema* Johnston & Tiegs, 1922; *Diversohamulus* Bychowsky & Nagibina, 1969; *Duplaccessorius* Viozzi & Brugni, 2004; *Enallothecium* Kritsky, Boeger & Jégu, 1998; *Enterogyrus* Paperna, 1963; *Ergenstrema* Paperna, 1964 ; *Eutrianchoratus* Paperna, 1969; *Glandulocephalus* Unnithan, 1972; *Glyphidohaptor* Kritsky, Galli & Yang, 2007; *Gobioecetes* Ogawa & Ito, 2017; *Gonocleithrum* Kritsky & Thatcher, 1983; *Guavinella* Mendoza-Franco, Scholz & Cabañas-Carranza, 2003; *Gussevia* Kohn & Paperna, 1964; *Haliotrema* Johnston & Tiegs, 1922; *Haliotrematoides* Kritsky, Yang & Sun, 2009; *Hamatopeduncularia* Yamaguti, 1953; *Hareocephalus* Young, 1968; *Helicirrus* Corlis, 2004; *Hemirhamphiculus* Bychowsky & Nagibina, 1969; *Heteronchocleidus* Bychowsly, 1957; *Heteropriapulus* Kritsky, 2007; *Heterotesia* Paperna, 1969; *Heterothecium* Kritsky, Boeger & Jégu, 1997; *Iliocirrus* Corlis, 2004; *Inserotrema* Viozzi, Marín, Carvajal, Brugni & Mancilla, 2007; *Insulacleidus* Rakotofiringa & Euzet, 1983; *Jainus* Mizelle, Kritzky & Crane, 1968; *Kapentagyrus* Kmentová, Gelnar & Vanhove, 2018; *Kriboetrema* Sarabeev, Rubtsova, Yang & Balbuena, 2013; *Kritskyia* Kohn, 1990; *Leptocleidus* Mueller, 1936; *Leptonchides* Chen, 1987; *Lethrinitrema* Lim & Justine, 2011; *Ligictaluridus* Beverley-Burton, 1984; *Ligophorus* Euzet & Suriano, 1977; *Linguadactyla* Brinkmann, 1940; *Linguadactyloides* Thatcher & Kritsky, 1983; *Longidigitis* Corlis, 2004; *Malayanodiscoides* Lim & Furtado, 1986; *Markewitschiana* Allamuratov & Koval, 1966; *Marumbius* Boeger, Ferreira, Vianna & Patella, 2014; *Mastacembelocleidus* Kritsky, Pandey, Agrawal &

Abdullah, 2004; *Metahaliotrema* Yamaguti, 1953; *Mexicana* Caballero & Bravo-Hollis, 1959; *Mexicotrema* Lamothe-Argumedo, 1969; *Microncocotyle* Kritsky, Aquaro & Galli, 2010; *Mizelleus* Jain, 1957; *Monocleithrium* Price & McMahon, 1966; *Mymarothecium* Kritsky, Boeger & Jégu, 1998; *Nanayella* Acosta, Mendoza-Palmero, da Silva & Scholz, 2019; *Nanotrema* Paperna, 1969; *Nasoancyrocephalus* Machida, 1979; *Neodiplectanotrema* Gerasev, Gaevskaja & Kovaleva, 1987; *Neohaliotrema* Yamaguti, 1965; *Notodiplocerus* Suriano, 1980; *Notothecioides* Kritsky, Boeger & Jégu, 1997; *Notopterodiscoides* Lim & Furtado, 1986; *Notothecium* Boeger & Kritsky, 1988; *Notozothecium* Boeger & Kritsky, 1988; *Octouncuhaptor* Mendoza-Franco, Roche & Torchin, 2008; *Odothecium* Kritsky, Boeger & Jégu, 1997; *Onchobdella* Paperna, 1968; *Onchocleidus* Mueller, 1936; *Palombitrema* Price & Bussing, 1968; *Paracolpenteron* Mendoza-Franco, Caspeta-Mandujano & Ramírez-Martínez, 2018; *Paradiplectanotrema* Gerasev, Gayevskaya & Kovaleva, 1987; *Pellucidhaptor* Price & Mizelle, 1964; *Pangasitrema* Pariselle, Euzet & Lambert, 2004; *Parancylodiscoides* Caballero & Bravo Hollis, 1961; *Parancyrocephaloides* Yamaguti, 1938; *Paraneohaliotrema* Zhukov, 1976; *Parasciadicleithrum* Mendoza-Palmero, Blasco-Costa, Hernández-Mena & Pérez-Ponce de León, 2017; *Paraquadriacanthus* Ergens, 1988; *Pavanelliella* Kritsky & Boeger, 1998; *Pennulituba* Řehulková, Justine & Gelnar, 2010; *Philocorydoras* Suriano, 1986; *Philureter* Viozzi & Gutiérrez, 2001; *Pithanothecium* Kritsky, Boeger & Jégu, 1997; *Placodiscus* Paperna, 1972; *Platycephalotrema* Kritsky & Nitta, 2019; *Pronotogrammella* Cruces, Chero, Sáez & Luque, 2020; *Protancyrocephaloides* Burn, 1978; *Protancyrocephalus* Bychowsky, 1957; *Protoancylodiscoides* Paperna, 1969; *Protogyrodactylus* Johnston & Tiegs, 1922; *Protorhinoxenus* Domingues & Boeger, 2002; *Pseudacolpenteron* Bychowsky & Gusev, 1955; *Pseudamphibdella* Yamaguti, 1958; *Pseudempleurosoma* Yamaguti, 1965; *Pseudancylodiscoides* Yamaguti, 1963; *Pseudodactylogyroides* Ogawa, 1986; *Pseudodactylogyrus* Gusev, 1965; *Pseudodiclidophora* Yamaguti, 1965; *Pseudodiplectanotrema* Gerasev, Gaevskaja & Kovaleva, 1987; *Pseudohaliotrema* Yamaguti, 1953; *Pseudotetrancistrum* Caballero & Bravo-Hollis, 1961; *Quadriacanthus* Paperna, 1961; *Recurvatus* Corlis, 200; *Rhinonastes* Kritsky, Thatcher & Boeger, 1988; *Rhinoxenoides* Santos Neto, Costa, Soares & Domingues, 2018; *Rhinoxenus* Kritsky, Boeger & Thatcher, 1988; *Salsuginus* Beverley-Burton, 1984; *Schilbetrema* Paperna & Thurston, 1968; *Schilbetrematoides* Kritsky & Kulo, 1992; *Sciadicleithrum* Kritsky, Thatcher & Boeger, 1989; *Sclerocleidoides* Agrawal, Yadav & Kritsky, 2001; *Sundatrema* Lim & Gibson, 2009; *Susanlimae* Boeger, Pariselle & Patella, 2015; *Susanlimocotyle* Soares, Domingues & Adriano, 2020; *Syncleithrium* Price, 1967; *Synodontella* Dossou & Euzet, 1993; *Telethecium* Kritsky, Van Every & Boeger, 1996; *Tereancistrum* Kritsky, Thatcher & Kayton, 1980; *Tetracleidus* Mueller, 1936; *Tetrancistrum* Goto & Kikuchi, 1917; *Thaparocleidus* Jain, 1952; *Thaparogyrus* Gusev, 1976; *Thylacicleidus* Wheeler & Klassen, 1988; *Triacanthinella* Bychowsky & Nagibina, 1968; *Trianchoratus* Price & Berry, 1966; *Tribaculocauda* Tripathi, 1959; *Trinibaculum* Kritsky, Thatcher & Kayton, 1980; *Trinidactylus* Hanek, Molnár & Fernando, 1974; *rinigyrus* Hanek, Molnár & Fernando, 1974; *Tucunarella* Mendoza-Franco, Scholz & Rozkošná, 2010; *Tylosuricola* Unnithan, 1964; *Unibarra* Suriano & Incorvaia, 1995; *Unilatus* Mizelle & Kritsky, 1967; *Urogyrus* Bilong Bilong, Birgi & Euzet, 1994; *Urocleidoides* Mizelle & Price, 1964; *Urocleidus* Mueller, 1934; *Vancleaveus* Kritsky, Thatcher & Boeger, 1986; *Volsellituba* Řehulková, Justine & Gelnar, 2010; *Williamsius* Rogers, 2016; *Xenoligophoroides* Dmitrieva, Sanna, Piras, Garippa & Merella, 2018.

Subfamily Dactylogyrinae Bychowsky, 1937

Junior synonyms: Ancyrocephalinae Bychowsky, 1937; Heteronchocleidinae Price, 1968 and Pseudodactylogyrinae Ogawa, 1986.

Includes (only genera with molecular data available mentioned): '*Ancyrocephalus*' *mogurndae* (Yamaguti, 1940); *Bravohollisia* Bychowsky & Nagibina, 1970; *Characidotrema* Paperna & Thurston, 1968; *Cichlidogyrus* Paperna, 1960; *Dactylogyrus* Diesing, 1850; *Enterogyrus* Paperna, 1963; *Ergenstrema* Paperna, 1964; *Eutrianchoratus* Paperna, 1969; *Glyphidohaptor* Kritsky, Galli & Yang, 2007; *Gobioecetes* Ogawa & Ito, 2017; *Gussevia* Kohn & Paperna, 1964; *Haliotrema* Johnston & Tiegs, 1922; *Haliotrematoides* Kritsky, Yang & Sun, 2009; *Heteronchocleidus* Bychowsky, 1957; *Kapentagyrus* Kmentová, Gelnar & Vanhove, 2018; *Lethrinitrema* Lim & Justin, 2011; *Ligophorus* Euzet & Suriano, 1977; *Metahaliotrema* Yamaguti, 1953; *Mexicana* Caballero & Bravo-Hollia, 1959; *Onchobdella* Paperna, 1968; *Paradiplectanotrema* Gerasev, Gayevskaya & Kovaleva, 1987; *Parancyrocephaloides* Yamaguti, 1938; *Parasciadicleithrum* Mendoza-Palmero, Blasco-Costa, Hernández-Mena & Pérez-Ponce de León, 2017; *Platycephalotrema* Kritsky & Nitta, 2019; *Protogyrodactylus* Johnston & Tiegs, 1922; *Pseudempleurosoma* Yamaguti, 1965; *Pseudodactylogyrus* Gusev, 1965; *Pseudohaliotrema* Yamaguti, 1953; *Sciadicleithrum* Kritsky, Thatcher & Boeger, 1989; *Tetrancistrum* Goto &

Kikuchi, 1917; *Thylacicleidus* Wheeler & Klassen, 1988; *Trianchoratus* Price & Berry, 1966; *Xenoligophoroides* Dmitrieva, Sanna, Piras, Garippa & Merella, 2018.

Remarks: Šimková et al. (2006) identified two sister groups within Dactylogyridae sensu Kritsky and Boeger (1989a). The first group includes the freshwater species belonging to Ancyrocephalinae and Ancylodiscoidinae. The second group includes species belonging to Pseudodactylogyrinae, Dactylogyrinae, and marine representatives of Ancyrocephalinae. Kritsky and Boeger (1989a) proposed nine different subfamilies. We identified 11 well- or moderately supported clades (Fig. 2), which only partially confirm the proposed subfamilies/clades. Compared to previous studies (Mendoza-Palmero et al., 2015; Moreira et al., 2019; Mendoza-Palmero et al., 2015) we report higher support values for the two clades of predominantly marine dactylogyrids (clades A1 and A2). As mentioned in the result section, the two macroclades found here each include the type genus of the respective two suggested subfamilies, *Dactylogyrus* and *Ancyrocephalus*. Therefore, we reassign Ancyrocephalinae and Dactylogyrinae to these macroclades as subfamilies of Dactylogyridae. As a consequence, Heteronchocleidinae, Protogyrodactylinae, and Pseudodactylogyrinae are synonymised with Dactylogyrinae. However, we could identify no apparent morphological differences between the genera belonging to these groups based on diagnostic features of internal organs and sclerotised structures in the literature (see Table S1). Given the lack of distinctive features for the subfamily, only genera with molecular data available are included here.

Bravohollisia Bychowsky & Nagibina, 1970

Junior synonyms: Caballeria Bychowsky & Nagibina, 1970

Emended diagnosis (based on Lim, 1995)*:* Four eye-spots; anterior pair smaller than posterior pair. Intestinal caeca unite posterior to testis. Peduncle present or absent. Haptor usually small with 4 haptoral glands sometimes with 3-4 pairs (each pair with one long and one short digit) of extensible haptoral digits in posterior region of haptor (*Caballeria*-type), associated with anchors, without marginal hooks on tips of digits; armed with 2 pairs of anchors, 2 bars, and 14 marginal hooks. Anchors usually with roots directed at equal to or less than 90˚ angles to each other (with exceptions); contain canal extending from shaft to point. Haptoral glands enter anterior aperture of canal on anchor shaft. Net-like structures occur near tip of anchors (probably represent secretions of haptoral glands). Ovary anterior to testis. Vagina opens ventrally at level of mid-body, slightly displaced to the right. Vas deferens loops left caecum, dilates twice forming 2 seminal vesicles. Copulatory organ without accessory piece. Integument forms rhombic plates in some species. Gill parasites of fishes belonging to Haemulidae.

Type species: Bravohollisia magna Bychowsky & Nagibina, 1970

Other species:

- *Bravohollisia geruti* Tan & Lim, 2013
- *Bravohollisia gussevi* Lim, 1995
- *Bravohollisia intermedius* (Lim, 1995) **comb. nov.**
- *Bravohollisia kritskyi* Lim, 1995
- *Bravohollisia liewi* (Lim, 1995) **comb. nov.**
- *Bravohollisia maculatus* (Venkatanarasaiah, 1984) Zhang, 2001
- *Bravohollisia parvianchoratus* (Venkatanarasaiah, 1984) Zhang, 2001
- *Bravohollisia pedunculata* (Bychowsky & Nagibina, 1970) **comb. nov.**
- *Bravohollisia pomadasis* Bychowsky & Nagibina, 1970
- *Bravohollisia reticulata* Lim, 1995
- *Bravohollisia robusta* (Bychowsky & Nagibina, 1970) **comb. nov.**
- *Bravohollisia rosetta* Lim, 1995
- *Bravohollisia tecta* Bychowsky & Nagibina, 1970

Remarks: Species of *Bravohollisia* and *Caballeria* were proposed for gill parasites of haemulid fishes (Lim, 1995). Both groups are morphologically similar, i.e. they present a simple copulatory tube without accessory pieces, anchors with canals running from shaft to point, similarly sized marginal hooks, haptoral glands, and a net-like structure near the tips of the anchors (Lim, 1995). Species of *Caballeria* differ regarding the presence of haptoral digits. However, phylogenetic studies demonstrate that *Caballeria* is nested in *Bravohollisia* and renders it paraphyletic (Wu et al., 2007; Sun et al., 2014), a result confirmed in the present study (Fig. 2). Therefore, we transfer all species belonging to *Caballeria* to *Bravohollisia* and consider *Caballeria* a junior synonym of *Bravohollisia*.

Cichlidogyrus Paperna, 1960

Junior synonyms: Scutogyrus Pariselle & Euzet 1995.

Emended diagnosis (based on Pariselle and Euzet (2009))*:* Three pairs of cephalic glands. Two posterior eyespots with crystalline lenses. Two small inconsistent anterior eyespots. Intestinal caeca unbranched, joined posteriorly. Haptor armed with 2 pairs of anchors, 2 bars, and 14 marginal hooks. Dorsal bar with two auricles. Ventral bar U-, V- or W-shaped, sometimes supporting 1 large, thin, oval plate marked by fan-shaped median thickenings (*Scutogyrus*-type). Median posterior testis. Vas deferens on the right side, not encircling intestinal caecum. Seminal vesicle present. One prostatic reservoir. Male copulatory complex with penis and accessory piece (the latter sometimes absent). Median pretesticular ovary. Submedian vaginal dextral opening. Vagina sclerotised or not. Seminal receptacle present. Gill parasites of African fishes belonging to Cichlidae, Nothobranchiidae, and Polycentridae.

Type species: Cichlidogyrus arthracanthus Paperna, 1960

Other species:

- *Cichlidogyrus acerbus* Dossou, 1982
- *Cichlidogyrus adkoningsi* Rahmouni, Vanhove & Šimková, 2018
- *Cichlidogyrus aegypticus* Ergens, 1981
- *Cichlidogyrus agnesi* Pariselle & Euzet, 1995
- *Cichlidogyrus albareti* Pariselle & Euzet, 1998
- *Cichlidogyrus amieti* Birgi & Euzet, 1983
- *Cichlidogyrus amphoratus* Pariselle & Euzet, 1996
- *Cichlidogyrus anthemocolpos* Dossou, 1982
- *Cichlidogyrus antoineparisellei* Rahmouni, Vanhove & Šimková, 2018
- *Cichlidogyrus arfii* Pariselle & Euzet, 1995

- *Cichlidogyrus aspiralis* Rahmouni, Vanhove & Šimková, 2017
- *Cichlidogyrus attenboroughi* Kmentová, Gelnar, Koblmüller & Vanhove, 2016
- *Cichlidogyrus bailloni* (Pariselle & Euzet, 1995) **comb. nov.**
- *Cichlidogyrus banyankimbonai* Pariselle & Vanhove, 2015
- *Cichlidogyrus berminensis* Pariselle, Bitja Nyom & Bilong Bilong, 2013
- *Cichlidogyrus berradae* Pariselle & Euzet, 2003
- *Cichlidogyrus berrebii* Pariselle & Euzet, 1994
- *Cichlidogyrus bifurcatus* Paperna, 1960
- *Cichlidogyrus bilongi* Pariselle & Euzet, 1995
- *Cichlidogyrus bixlerzavalai* Jorissen, Pariselle & Vanhove in Jorissen, Pariselle, Vreven, Snoeks, Decru, Kusters, Wamuini Lunkayilakio, Muterezi Bukinga, Artois & Vanhove, 2018
- *Cichlidogyrus bonhommei* Pariselle & Euzet, 1998
- *Cichlidogyrus bouvii* Pariselle & Euzet, 1997
- *Cichlidogyrus brunnensis* Kmentová, Gelnar, Koblmüller & Vanhove, 2016
- *Cichlidogyrus buescheri* Pariselle & Vanhove, 2015
- *Cichlidogyrus bulbophallus* Geraerts & Muterezi Bukinga in Geraerts, Muterezi Bukinga, Vanhove, Pariselle, Manda, Vreven, Huyse & Artois, 2020
- *Cichlidogyrus calycinus* Kusters, Jorissen, Pariselle & Vanhove in Jorissen, Pariselle, Vreven, Snoeks, Decru, Kusters, Wamuini Lunkayilakio, Muterezi Bukinga, Artois & Vanhove, 2018
- *Cichlidogyrus casuarinus* Pariselle, Muterezi Bukinga & Vanhove, 2015
- *Cichlidogyrus centesimus* Vanhove, Volckaert & Pariselle, 2011
- *Cichlidogyrus chikhii* (Pariselle & Euzet, 1995) **comb. nov.**
- *Cichlidogyrus chrysopiformis* Pariselle, Bitja Nyom & Bilong Bilong, 2014
- *Cichlidogyrus cirratus* Paperna, 1964
- *Cichlidogyrus consobrini* Jorissen, Pariselle & Vanhove in Jorissen, Pariselle, Huyse, Vreven, Snoeks, Volckaert, Chocha Manda, Kapepula Kasembele, Artois & Vanhove, 2017
- *Cichlidogyrus cubitus* Dossou, 1982

- *Cichlidogyrus dageti* Dossou & Birgi, 1984
- *Cichlidogyrus digitatus* Dossou, 1982
- *Cichlidogyrus dionchus* Paperna, 1968
- *Cichlidogyrus discophonum* Rahmouni, Vanhove & Šimková, 2017
- *Cichlidogyrus djietoi* Pariselle, Bitja Nyom & Bilong Bilong, 2014
- *Cichlidogyrus dossoui* Douëllou, 1993
- *Cichlidogyrus douellouae* Pariselle, Bilong Bilong & Euzet, 2003
- *Cichlidogyrus dracolemma* Řehulková, Mendlová & Šimková, 2013
- *Cichlidogyrus ecoutini* (Pariselle & Euzet, 1995) **comb. nov.**
- *Cichlidogyrus ergensi* Dossou, 1982
- *Cichlidogyrus euzeti* Dossou & Birgi, 1984
- *Cichlidogyrus evikae* Rahmouni, Vanhove & Šimková, 2017
- *Cichlidogyrus falcifer* Dossou & Birgi, 1984
- *Cichlidogyrus flagellum* Geraerts & Muterezi Bukinga in Geraerts, Muterezi Bukinga, Vanhove, Pariselle, Manda, Vreven, Huyse & Artois, 2020
- *Cichlidogyrus flexicolpos* Pariselle & Euzet, 1995
- *Cichlidogyrus fontanai* Pariselle & Euzet, 1997
- *Cichlidogyrus frankwillemsi* Pariselle & Vanhove, 2015
- *Cichlidogyrus franswittei* Pariselle & Vanhove, 2015
- *Cichlidogyrus gallus* Pariselle & Euzet, 1995
- *Cichlidogyrus georgesmertensi* Pariselle & Vanhove, 2015
- *Cichlidogyrus gillardinae* Muterezi Bukinga, Vanhove, Van Steenberge & Pariselle, 2012
- *Cichlidogyrus gillesi* Pariselle, Bitja Nyom & Bilong Bilong, 2013
- *Cichlidogyrus giostrai* Pariselle, Bilong Bilong & Euzet, 2003
- *Cichlidogyrus gistelincki* Gillardin, Vanhove, Pariselle, Huyse & Volckaert, 2012
- *Cichlidogyrus glacicremoratus* Rahmouni, Vanhove & Šimková, 2017
- *Cichlidogyrus gravivaginus* Paperna & Thurston, 1969

- *Cichlidogyrus guirali* Pariselle & Euzet, 1997
- *Cichlidogyrus habluetzeli* Rahmouni, Vanhove & Šimková, 2018
- *Cichlidogyrus halinus* Paperna, 1969
- *Cichlidogyrus halli* (Price & Kirk, 1967)
- *Cichlidogyrus haplochromii* Paperna & Thurston, 1969
- *Cichlidogyrus hemi* Pariselle & Euzet, 1998
- *Cichlidogyrus inconsultans* Birgi & Lambert, 1987
- *Cichlidogyrus irenae* Gillardin, Vanhove, Pariselle, Huyse & Volckaert, 2012
- *Cichlidogyrus jeanloujustinei* Rahmouni, Vanhove & Šimková, 2017
- *Cichlidogyrus karibae* Douëllou, 1993
- *Cichlidogyrus kmentovae* Jorissen, Pariselle & Vanhove in Jorissen, Pariselle, Vreven, Snoeks, Decru, Kusters, Wamuini Lunkayilakio, Muterezi Bukinga, Artois & Vanhove, 2018
- *Cichlidogyrus koblmuelleri* Rahmouni, Vanhove & Šimková, 2018
- *Cichlidogyrus kothiasi* Pariselle & Euzet, 1994
- *Cichlidogyrus kouassii* N'Douba, Thys van den Audenaerde & Pariselle, 1997
- *Cichlidogyrus lagoonaris* Paperna, 1969
- *Cichlidogyrus legendrei* Pariselle & Euzet, 2003
- *Cichlidogyrus lemoallei* Pariselle & Euzet, 2003
- *Cichlidogyrus levequei* Pariselle & Euzet, 1996
- *Cichlidogyrus lobus* Geraerts & Muterezi Bukinga in Geraerts, Muterezi Bukinga, Vanhove, Pariselle, Manda, Vreven, Huyse & Artois, 2020
- *Cichlidogyrus longicirrus* Paperna, 1965
- *Cichlidogyrus longicornis* Paperna & Thurston, 1969
- *Cichlidogyrus longipenis* Paperna & Thurston, 1969
- *Cichlidogyrus louipaysani* Pariselle & Euzet, 1995
- *Cichlidogyrus maeander* Geraerts & Muterezi Bukinga in Geraerts, Muterezi Bukinga, Vanhove, Pariselle, Manda, Vreven, Huyse & Artois, 2020

- *Cichlidogyrus makasai* Vanhove, Volckaert & Pariselle, 2011
- *Cichlidogyrus masilyai* Rahmouni, Vanhove & Šimková, 2018
- *Cichlidogyrus mbirizei* Muterezi Bukinga, Vanhove, Van Steenberge & Pariselle, 2012
- *Cichlidogyrus microscutus* Pariselle & Euzet, 1996
- *Cichlidogyrus milangelnari* Rahmouni, Vanhove & Šimková, 2017
- *Cichlidogyrus minus* Dossou, 1982
- *Cichlidogyrus mulimbwai* Muterezi Bukinga, Vanhove, Van Steenberge & Pariselle, 2012
- *Cichlidogyrus muterezii* Pariselle & Vanhove, 2015
- *Cichlidogyrus muzumanii* Muterezi Bukinga, Vanhove, Van Steenberge & Pariselle, 2012
- *Cichlidogyrus mvogoi* Pariselle, Bitja Nyom & Bilong Bilong, 2014
- *Cichlidogyrus nageus* Řehulková, Mendlová & Šimková, 2013
- *Cichlidogyrus nandidae* Birgi & Lambert, 1986
- *Cichlidogyrus njinei* Pariselle, Bilong Bilong & Euzet, 2003
- *Cichlidogyrus nshomboi* Muterezi Bukinga, Vanhove, Van Steenberge & Pariselle, 2012
- *Cichlidogyrus nuniezi* Pariselle & Euzet, 1998
- *Cichlidogyrus omari* Jorissen, Pariselle & Vanhove in Jorissen, Pariselle, Vreven, Snoeks, Decru, Kusters, Wamuini Lunkayilakio, Muterezi Bukinga, Artois & Vanhove, 2018
- *Cichlidogyrus ornatus* Pariselle & Euzet, 1996
- *Cichlidogyrus ouedraogoi* Pariselle & Euzet, 1996
- *Cichlidogyrus paganoi* Pariselle & Euzet, 1997
- *Cichlidogyrus papernastrema* Price, Peebles & Bamford, 1969
- *Cichlidogyrus philander* Douëllou, 1993
- *Cichlidogyrus polyenso* Jorissen, Pariselle & Vanhove in Jorissen, Pariselle, Vreven, Snoeks, Decru, Kusters, Wamuini Lunkayilakio, Muterezi Bukinga, Artois & Vanhove, 2018
- *Cichlidogyrus pouyaudi* Pariselle & Euzet, 1994
- *Cichlidogyrus pseudoaspiralis* Rahmouni, Vanhove & Šimková, 2017

- *Cichlidogyrus pseudozambezensis* Geraerts & Muterezi Bukinga in Geraerts, Muterezi Bukinga, Vanhove, Pariselle, Manda, Vreven, Huyse & Artois, 2020
- *Cichlidogyrus quaestio* Douëllou, 1993
- *Cichlidogyrus raeymaekersi* Pariselle & Vanhove, 2015
- *Cichlidogyrus ranula* Geraerts & Muterezi Bukinga in Geraerts, Muterezi Bukinga, Vanhove, Pariselle, Manda, Vreven, Huyse & Artois, 2020
- *Cichlidogyrus rectangulus* Rahmouni, Vanhove & Šimková, 2017
- *Cichlidogyrus reversati* Pariselle & Euzet, 2003
- *Cichlidogyrus rognoni* Pariselle, Bilong Bilong & Euzet, 2003
- *Cichlidogyrus salzburgeri* Rahmouni, Vanhove & Šimková, 2018
- *Cichlidogyrus sanjeani* Pariselle & Euzet, 1997
- *Cichlidogyrus sanseoi* Pariselle & Euzet, 2004
- *Cichlidogyrus schreyenbrichardorum* Pariselle & Vanhove, 2015
- *Cichlidogyrus sclerosus* Paperna & Thurston, 1969
- *Cichlidogyrus sergemorandi* Rahmouni, Vanhove & Šimková, 2018
- *Cichlidogyrus sigmocirrus* Pariselle, Bitja Nyom & Bilong Bilong, 2014
- *Cichlidogyrus slembroucki* Pariselle & Euzet, 1998
- *Cichlidogyrus steenbergei* Gillardin, Vanhove, Pariselle, Huyse & Volckaert, 2012
- *Cichlidogyrus sturmbaueri* Vanhove, Volckaert & Pariselle, 2011
- *Cichlidogyrus testificatus* Dossou, 1982
- *Cichlidogyrus teugelsi* Pariselle & Euzet, 2004
- *Cichlidogyrus thurstonae* Ergens, 1981
- *Cichlidogyrus tiberianus* Paperna, 1960
- *Cichlidogyrus tilapiae* Paperna, 1960
- *Cichlidogyrus vandekerkhovei* Vanhove, Volckaert & Pariselle, 2011
- *Cichlidogyrus vanhovei* (Pariselle, Bitja Nyom & Bilong Bilong, 2013) **comb. nov.**
- *Cichlidogyrus vealli* Pariselle & Vanhove, 2015

- *Cichlidogyrus vexus* Pariselle & Euzet, 1995
- *Cichlidogyrus yanni* Pariselle & Euzet, 1996
- *Cichlidogyrus zambezensis* Douëllou, 1993

Remarks: *Scutogyrus* has been proposed for parasites of cichlid fishes with a fan-shaped plate on the ventral bar missing in species of *Cichlidogyrus* (Pariselle and Euzet, 2009). Phylogenetic studies have shown that *Scutogyrus* is indeed monophyletic (e.g. Cruz-Laufer et al. 2021b) but also pointed out that *Scutogyrus* is nested within *Cichlidogyrus* (clade A1) (Wu et al., 2007; Cruz-Laufer et al. 2021b). The resulting paraphyly of *Cichlidogyrus* can be resolved in two ways: *Cichlidogyrus* could be divided into multiple genera, e.g. by the clades characterised in Cruz-Laufer et al. (2021b) or *Scutogyrus* could be synonymised with *Cichlidogyrus.* We prefer the latter option here to avoid splitting this well-recognisable genus into numerous genera with similar diagnoses. Hence, we consider *Scutogyrus* a junior synonym of *Cichlidogyrus*, revalidate the names of species of *Scutogyrus* that were previously considered species of *Cichlidogyrus* and transfer all other species to *Cichlidogyrus*.

Dactylogyrus Diesing, 1850

Junior synonyms: Dactylogyroides Gusev, 1963*, Dogielius* Bychowsky, 1936.

Emended diagnosis (based on Gussev, 1963; Rogers, 1967; Price and Yurkiewicz, 1968): Body elongate with smooth cuticule. Two pairs of eyespots present, component pigment granules may be dissociated and accessory granules may be scattered throughout body. Haptor unusually set off from body by distinct peduncle; possessing one pair of anchors connected by a bar; second bar present or absent; dorsal bar if present with different degrees of separation. 14 marginal hooks and sometimes two 4A's. Each anchor composed of base usually differentiated into deep and superficial roots, solid shaft, and solid point. Each hook usually composed of solid inflated base, elongate shaft, and solid point with a backward-projecting looping process and opposable piece. Gut bifurcated, united posteriorly, without diverticula. Copulatory complex composed of cirrus and accessory piece. Two prostates present. Testes two sometimes three (*Dactylogyroides*-type). Seminal vesicle a dilation of vas deferens. Ovary pretesticular but may partially overlap with testes. Vagina with or without sclerotised wall. Vitellaria coextensive with intestinal caeca. Parasites of freshwater fishes.

Type species: Dactylogyrus auriculatus (Nordmann, 1832).

Other species (only revalidations and comb. nov.):

- *Dactylogyrus anthocolpos* (Guégan, Lambert & Euzet, 1989) **comb. nov.**
- *Dactylogyrus bimaculati* (Gusev, 1963) **comb. nov.**
- *Dactylogyrus biradius* (Birgi & Lambert, 1987) **comb. nov.**
- *Dactylogyrus clavipenis* (Guegan, Lambert & Euzet, 1989) **comb. nov.**
- *Dactylogyrus complicitus* (Guegan, Lambert & Euzet, 1989) **comb. nov.**
- *Dactylogyrus djolibaensis* (Guegan & Lambert, 1990) **comb. nov.**
- *Dactylogyrus dorsali* (Agrawal, Pandey & Tripathi, 2002) **comb. nov.**
- *Dactylogyrus dorsalis* Gusev, 1963
- *Dactylogyrus dublicornis* (Paperna, 1973) **comb. nov.**
- *Dactylogyrus fernandoi* Gusev, 1963
- *Dactylogyrus flosculus* (Guégan, Lambert & Euzet, 1989) **comb. nov.**
- *Dactylogyrus forceps* (Bychowsky, 1936) **comb. nov.**
- *Dactylogyrus grandijugus* (Guegan, Lambert & Euzet, 1989) **comb. nov.**
- *Dactylogyrus grandiphallus* (Paperna, 1973) **comb. nov.**
- *Dactylogyrus gussevia* (Singh, Arya & Anuradha, 2003) **comb. nov.**
- *Dactylogyrus gyropetalum* (Lang, 1981) **comb. nov.**
- *Dactylogyrus harpagatus* (Guegan, Lambert & Euzet, 1989) **comb. nov.**
- *Dactylogyrus intorquens* (Crafford, Luus-Powell & Avenant-Oldewage, 2012) **comb. nov.**
- *Dactylogyrus junorstrema* (Price & Yurkiewicz, 1968) **comb. nov.**
- *Dactylogyrus kabaensis* (Guegan & Lambert, 1991) **comb. nov.**
- *Dactylogyrus likueichenae* (Zhang & Guo, 1981) **comb. nov.**
- *Dactylogyrus longicirrus* Tripathi, 1959

- *Dactylogyrus lucknowensis* (Agrawal & Sharma, 1988) **comb. nov.**
- *Dactylogyrus mahecoli* (Agrawal, Pandey & Tripathi, 2002) **comb. nov.**
- *Dactylogyrus malayensis* (Lim & Furtado, 1984) **comb. nov.**
- *Dactylogyrus martorellii* (Birgi & Lambert, 1987) **comb. nov.**
- *Dactylogyrus mokhayeri* (Jalali & Molnár, 1990) **comb. nov.**
- *Dactylogyrus neobicornis* (Luo & Long, 1982) **nom. nov.**
- *Dactylogyrus neocatlaius* (Jain, 1962) **nom. nov.**
- *Dactylogyrus neoflagellatus* (Guegan, Lambert & Euzet, 1989) **nom. nov.**
- *Dactylogyrus neogussevi* (Hossain, Chandra & Mohanta, 2001 nec Tripathi, 1977) **nom. nov.**
- *Dactylogyrus neoindicus* (Agrawal & Singh, 1984) **nom. nov.**
- *Dactylogyrus neomolnari* (Jalali, 1992) **nom. nov.**
- *Dactylogyrus neoorientalis* (Ma & Long in Wu, Long & Wang, 2000) **nom. nov.**
- *Dactylogyrus neosemilabeo* (Ma & Long in Wu, Long & Wang, 2000) **nom. nov.**
- *Dactylogyrus neosinilabe* (Zhao & Ma, 1991) **nom. nov.**
- *Dactylogyrus njinei* Birgi & Lambert, 1987
- *Dactylogyrus ogawai* (Mohanta, Chandra & Hossain, 2001) **comb. nov.**
- *Dactylogyrus osteobramii* (Agrawal, Pandey & Tripathi, 2002) **comb. nov.**
- *Dactylogyrus pedaloe* (Guegan & Lambert, 1990) **comb. nov.**
- *Dactylogyrus persicus* (Molnár & Jalali, 1992) **comb. nov.**
- *Dactylogyrus phrygieus* (Guegan & Lambert, 1990) **comb. nov.**
- *Dactylogyrus planus* (Bychowsky, 1957) **comb. nov.**
- *Dactylogyrus pseudobicornis* (Luo & Long, 1982) **nom. nov.**
- *Dactylogyrus pseudoflagellatus* (Guegan, Lambert & Euzet, 1989) **nom. nov.**
- *Dactylogyrus pseudoforceps* (Bychowsky, 1936) **nom. nov.**
- *Dactylogyrus pseudogussevi* (Singh & Jain, 1988) **nom. nov.**
- *Dactylogyrus pseudoparvus* (Guegan, Lambert & Euzet, 1989) **nom. nov.**
- *Dactylogyrus rectoris* (Tao & Lang, 1981) **comb. nov.**

- *Dactylogyrus rosumplicatus* (Guegan & Lambert, 1991) **comb. nov.**
- *Dactylogyrus sennarensis* (Pravdová, Ondračková, Přikrylová, Blažec, Mahmoud & Gelnar, 2018) **comb. nov.**
- *Dactylogyrus strombicinms* (Ma & Long in Wu, Long & Wang, 2000) **comb. nov.**
- *Dactylogyrus tripathii* Yamaguti, 1963
- *Dactylogyrus tropicus* (Paperna, 1969) **comb. nov.**
- *Dactylogyrus tubiformis* (Lang, 1981) **comb. nov.**
- *Dactylogyrus varicorhinis* (Long & Ma in Ma & Li, 1991) **comb. nov.**
- *Dactylogyrus vexillus* (Guegan & Lambert, 1990) **comb. nov.**
- *Dactylogyrus vittati* (Gusev, 1963) **comb. nov.**
- *Dactylogyrus wallagonius* (Singh & Jain, 1988) **comb. nov.**

Remarks: Dogielius encompasses gill parasites of cyprinid fishes that differ from species of *Dactylogyrus* regarding the dorsal position of the anchor-bar complex and the absence of the loop around the intestinal caecum in the vas deferens (Price and Yurkiewicz, 1968). *Dactylogyroides* encompasses gill parasites of freshwater fishes that differ from *Dactylogyrus* through their paired, weakly linked dorsal bar (Gussev, 1963). Despite these differences, both taxa are considered closely related to *Dactylogyrus* (Gussev, 1963; Price and Yurkiewicz, 1968). Phylogenetic studies have confirmed the monophyly of *Dactylogyrus* as a genus (Kritsky and Boeger, 1989a; Šimková et al., 2003, 2006) but studies involving *Dactylogyroides* failed to resolve its phylogenetic position in previous studies as DNA sequences of members of *Dactylogyroides* were used to root the tree (Singh and Chaudhary, 2010; Chiary et al., 2013). In the first molecular study on *Dogielius* (Dash et al., 2014), the species included (*Dogielius catlaius* (Jain, 1962) as "*Dactylogyrus catlaius* Jain, 1961 [sic]") appeared nested in *Dactylogyrus*. Here, we demonstrate that species of *Dactylogyroides* alongside those of *Dactylogyrus* and *Dogielius* form a monophyletic group (clade A4) of dactylogyrids with a single pair of anchors. *Dactylogyrus*, the most species-rich genus of monogeneans (Horton et al., 2021), is rendered paraphyletic by the erections of *Dogielius* and *Dactylogyroides* (Fig. 2). Hence, we consider *Dactylogyroides* and *Dogielius* junior synonyms of *Dactylogyrus* and all species belonging to the synonymised genera are transferred to *Dactylogyrus*. In several cases, species were renamed as the transfer would otherwise create junior homonyms of existing species. Therefore, *Dogielius bicornis* Luo & Long, 1982 is renamed *Dactylogyrus neobicornis* (Luo & Long, 1982) nom. nov., *Dogielius catlaius* (Jain, 1962) Gusev, 1976 is renamed *Dactylogyrus neocatlaius* (Jain, 1962) nom. nov., *Dogielius flagellatus* Guegan, Lambert & Euzet, 1989 is renamed *Dactylogyrus neoflagellatus* (Guegan, Lambert & Euzet, 1989) nom. nov., *Dogielius gussevi* Singh & Jain, 1988 is renamed *Dactylogyrus pseudogussevi* (Singh & Jain, 1988) comb. nov., *Dactylogyroides gussevi* Hossain, Chandra & Mohanta, 2001 nec Tripathi, 1977 is renamed *Dactylogyrus neogussevi* (Hossain, Chandra & Mohanta, 2001 nec Tripathi, 1977) comb. nov., *Dogielius indicus* Agrawal & Singh, 1984 is renamed *Dactylogyrus neoindicus* (Agrawal & Singh, 1984) comb. nov., *Dogielius molnari* Jalali, 1992 is renamed *Dactylogyrus neomolnari* (Jalali, 1992) comb. nov., *Dogielius orientalis* Ma & Long in Wu, Long & Wang, 2000 is renamed *Dactylogyrus neoorientalis* (Ma & Long in Wu, Long & Wang, 2000) comb. nov., *Dogielius parvus* Guegan, Lambert & Euzet, 1989 is renamed *Dactylogyrus pseudoparvus* (Guegan, Lambert & Euzet, 1989) comb. nov., *Dogielius semilabeo* Ma & Long in Wu, Long & Wang, 2000 is renamed *Dactylogyrus neosemilabeo* (Ma & Long in Wu, Long & Wang, 2000) comb. nov., and *Dogielius sinilabe* Zhao & Ma, 1991 is renamed *Dactylogyrus neosinilabe* (Zhao & Ma, 1991) comb. nov. In the case of *Dogielius forceps* Bychowsky, 1936, the transfer renders *Dactylogyrus forceps* Leuckart, 1858 a junior homonym of *Dactylogyrus forceps* (Bychowsky, 1936) comb. nov. However, *D. forceps* Leuckart, 1858 has already been transferred to *Ancyrocephalus*.

Sciadicleithrum Kritsky, Thatcher & Boeger, 1989

Junior synonyms: Aliatrema Plaisance & Kritsky, 2004; *Euryhaliotrema* Kritsky & Boeger, 2002; *Euryhaliotrematoides* Plaisance & Kritsky, 2004.

Emended diagnosis (based on Kritsky et al., 1989b; Kritsky, 2012)*:* Body fusiform or slightly flattened dorsoventrally, comprising body proper (cephalic region, trunk, peduncle) and haptor. Tegument usually smooth. Terminal and two bilateral cephalic lobes; three to four pairs of bilateral head organs; cephalic glands unicellular, lateral or posterolateral to pharynx. Eyespots two to four; granules small, ovate. Mouth subterminal, midventral; pharynx muscular; oesophagus present; intestinal ceca two, confluent posterior to gonads, lacking diverticula. Common genital pore midventral near level of intestinal bifurcation. Gonads intercaecal, tandem or slightly overlapping. Vas deferens looping left intestinal cecum; seminal vesicle a dilation of vas deferens; one or two prostatic reservoirs. Copulatory complex comprising MCO and accessory piece; accessory piece may be lacking. MCO tubular, coiled or meandering, with bulbous or funnel-shaped base; coil with anticlockwise rings (or clockwise for *Sciadicleithrum* sensu Kritsky et al., 1989b). Accessory piece, when present, serving as guide for distal portion of MCO, with or without articulation process attached to base of MCO. Seminal receptacle pregermarial; vaginal pore dextral, marginal or submarginal; vagina sclerotized. Vitellaria well developed, scattered throughout trunk. Haptor armed with dorsal and ventral anchor/bar complexes, seven pairs of similar hooks with ancyrocephaline distribution. Hooks with upright acute thumb, slender shank comprised of one subunit. Parasites of marine and freshwater teleosts.

Type species: Sciadicleithrum uncinatum Kritsky, Thatcher & Boeger, 1989.

Other species:

- *Sciadicleithrum adelpha* (Kritsky & Justine in Kritsky, 2012) **comb. nov.**
- *Sciadicleithrum aequidens* (Price & Schlueter, 1967) Kritsky, Thatcher & Boeger, 1989
- *Sciadicleithrum ambassisi* (Pan & Lu, 2005) **comb. nov.**
- *Sciadicleithrum amydrum* (Kritsky & Bakenhaster, 2011) **comb. nov.**
- *Sciadicleithrum anecorhizion* (Kritsky & Mendoza-Franco in Kritsky, 2012) **comb. nov.**
- *Sciadicleithrum anguiforme* (Zhang in Zhang, Yang & Liu, 2001) **comb. nov.**
- *Sciadicleithrum annulocirrus* (Yamaguti, 1968) **comb. nov.**
- *Sciadicleithrum aspistis* (Plaisance & Kritsky, 2004) **comb. nov.**
- *Sciadicleithrum atlanticum* (Kritsky & Boeger, 2002) **comb. nov.**
- *Sciadicleithrum berenguelae* (Plaisance & Kritsky, 2004) **comb. nov.**
- *Sciadicleithrum bravohollisae* Kritsky, Vidal-Martínez & Rodríguez-Canul, 1994
- *Sciadicleithrum bychowskyi* (Obodnikova, 1976) **comb. nov.**
- *Sciadicleithrum carbuncularium* (Kritsky & Bakenhaster, 2011) **comb. nov.**
- *Sciadicleithrum carbunculus* (Hargis, 1955) **comb. nov.**

- *Sciadicleithrum cardinale* (Kritsky & Justine in Kritsky, 2012) **comb. nov.**
- *Sciadicleithrum cavanaughi* (Price, 1966) Kritsky, Thatcher & Boeger, 1989
- *Sciadicleithrum chaoi* (Kritsky & Boeger, 2002) **comb. nov.**
- *Sciadicleithrum chrysotaeniae* (Young, 1968) **comb. nov.**
- *Sciadicleithrum cognatus* (Kritsky & Galli in Kritsky, 2012) **comb. nov.**
- *Sciadicleithrum cribbi* (Plaisance & Kritsky, 2004) **comb. nov.**
- *Sciadicleithrum cryptophallus* (Kritsky & Yang in Kritsky, 2012) **comb. nov.**
- *Sciadicleithrum diplops* (Kritsky, Yang & Justine in Kritsky, 2012) **comb. nov.**
- *Sciadicleithrum distinctum* (Kritsky & Galli in Kritsky, 2012) **comb. nov.**
- *Sciadicleithrum dontykoleos* (Fehlauer & Boeger, 2005) **comb. nov.**
- *Sciadicleithrum dunlapae* (Kritsky & Bakenhaster, 2011) **comb. nov.**
- *Sciadicleithrum ergensi* Kritsky, Thatcher & Boeger, 1989
- *Sciadicleithrum eukurodai* (Zhang, Ding, Lin & Yu, 1994) **comb. nov.**
- *Sciadicleithrum fajeravilae* (Kritsky & Mendoza-Franco in Kritsky, 2012) **comb. nov.**
- *Sciadicleithrum fastigatum* (Zhukov, 1976) **comb. nov.**
- *Sciadicleithrum fatuum* (Kritsky & Justine in Kritsky, 2012) **comb. nov.**
- *Sciadicleithrum ferocis* (Kritsky & Yang in Kritsky, 2012) **comb. nov.**
- *Sciadicleithrum frequens* Bellay, Takemoto, Yamada & Pavanelli, 2008
- *Sciadicleithrum geophagi* Kritsky, Thatcher & Boeger, 1989
- *Sciadicleithrum grande* (Mizelle & Kritsky, 1969) **comb. nov.**
- Sciadicleithrum griseus (Fuentes-Zambrano & Silva Rojas, 2006) **comb. nov.**
- *Sciadicleithrum guanduense* Carvalho, Tavares & Luque, 2008
- *Sciadicleithrum guangdongense* (Li, Yan, Yul, Lan & Huang, 2005) **comb. nov.**
- *Sciadicleithrum guangzhouense* (Li, 2005) **comb. nov.**
- *Sciadicleithrum hainanense* (Pan & Zhang, 2006) **comb. nov.**
- *Sciadicleithrum iphthimum* Kritsky, Thatcher & Boeger, 1989
- *Sciadicleithrum joanae* Yamada, Takemoto, Bellay & Pavanelli, 2009

- *Sciadicleithrum johni* (Tripathi, 1959) **comb. nov.**
- *Sciadicleithrum juruparii* Melo, Santos & Santos, 2012
- *Sciadicleithrum kritskyi* Bellay, Takemoto, Yamada & Pavanelli, 2009
- *Sciadicleithrum kurodai* (Ogawa & Egusa, 1978) **comb. nov.**
- *Sciadicleithrum lisae* (Kritsky & Diggles, 2014) **comb. nov.**
- *Sciadicleithrum lizardi* (Mendoza-Franco, Binning & Roche, 2017) **comb. nov.**
- *Sciadicleithrum longibaculoides* (Kritsky & Diggles, 2014) **comb. nov.**
- *Sciadicleithrum longibaculum* (Zhukov, 1976) **comb. nov.**
- *Sciadicleithrum lovejoyi* (Kritsky & Boeger, 2002) **comb. nov.**
- *Sciadicleithrum luisae* (Cruces, Chero & Luque, 2018) **comb. nov.**
- *Sciadicleithrum lutiani* (Yamaguti, 1953) **comb. nov.**
- *Sciadicleithrum lutjani* (Li, 2006) **comb. nov.**
- *Sciadicleithrum magnopharyngis* (Cruces, Chero & Luque, 2018) **comb. nov.**
- *Sciadicleithrum meekii* Mendoza-Franco, Scholz & Vidal-Martínez, 1997
- *Sciadicleithrum mehen* (Solar-Jiménez, Garcia-Gasca & Fajer-Ávila, 2012) **comb. nov.**
- *Sciadicleithrum mexicanum* Kritsky, Vidal-Martínez & Rodríguez-Canul, 1994
- *Sciadicleithrum microphallus* (Yamaguti, 1968) **comb. nov.**
- *Sciadicleithrum monacanthus* (Kritsky & Boeger, 2002) **comb. nov.**
- *Sciadicleithrum monoporosum* (Pan & Zhang, 2000) **comb. nov.**
- *Sciadicleithrum nanaoense* (Li, Yan, Yul, Lan & Huang, 2005) **comb. nov.**
- *Sciadicleithrum nicaraguense* Vidal-Martinez, Scholz & Aguirre-Macedo, 2001
- *Sciadicleithrum panamense* Mendoza-Franco, Aguirre-Macedo & Vidal-Martínez, 2007
- *Sciadicleithrum paracanthi* (Zhukov, 1976) **comb. nov.**
- *Sciadicleithrum paralonchuri* (Luque & Iannocone, 1989) **comb. nov.**
- *Sciadicleithrum paranaense* Bellay, Takemoto, Yamada & Pavanelli, 2009
- *Sciadicleithrum paululum* (Kritsky & Justine in Kritsky, 2012) **comb. nov.**
- *Sciadicleithrum perezponcei* (Garcia-Vargas, Fajer-Ávila & Lamothe-Argumedo, 2008) **comb. nov.**

- *Sciadicleithrum pirulum* (Plaisance & Kritsky, 2004) **comb. nov.**
- *Sciadicleithrum potamocetes* (Kritsky & Boeger, 2002) **comb. nov.**
- *Sciadicleithrum ramulum* (Kritsky & Galli in Kritsky, 2012) **comb. nov.**
- *Sciadicleithrum russellum* (Sun & Yang, 2015) **comb. nov.**
- *Sciadicleithrum sagmatum* (Kritsky & Boeger, 2002) **comb. nov.**
- *Sciadicleithrum satanopercae* Yamada, Takemoto, Bellay & Pavanelli, 2009
- *Sciadicleithrum seyi* (Kritsky, 2012) **comb. nov.**
- *Sciadicleithrum simplicis* (Kritsky & Justine in Kritsky, 2012) **comb. nov.**
- *Sciadicleithrum solenophallus* (Kritsky, 2019) **comb. nov.**
- *Sciadicleithrum spirotubiforum* (Zhang in Zhang, Yang & Liu, 2001) **comb. nov.**
- *Sciadicleithrum spirulum* (Kritsky & Bakenhaster, 2011) **comb. nov.**
- *Sciadicleithrum splendidae* Kritsky, Vidal-Martínez & Rodríguez-Canul, 1994
- *Sciadicleithrum succedaneus* (Kritsky & Boeger, 2002) **comb. nov.**
- *Sciadicleithrum tenuiaccessorium* (Sun & Yang, 2015) **comb. nov.**
- *Sciadicleithrum thatcheri* (Kritsky & Boeger, 2002) **comb. nov.**
- *Sciadicleithrum tormocleithrum* (Kritsky & Galli in Kritsky, 2012) **comb. nov.**
- *Sciadicleithrum torquecirrus* (Zhukov, 1976) **comb. nov.**
- *Sciadicleithrum tortrix* Kritsky, Thatcher & Boeger, 1989
- *Sciadicleithrum triangulovagina* (Yamaguti, 1968) **comb. nov.**
- *Sciadicleithrum tubocirrus* (Zhukov, 1976) **comb. nov.**
- *Sciadicleithrum umbilicum* Kritsky, Thatcher & Boeger, 1989
- *Sciadicleithrum variabile* (Mizelle & Kritsky, 1969) Kritsky, Thatcher & Boeger, 1989
- *Sciadicleithrum xinyingense* (Pan & Zhang, 2006) **comb. nov.**
- *Sciadicleithrum youngi* (Kritsky, 2012) **comb. nov.**
- *Sciadicleithrum zhangjianyingi* (Pan & Lu, 2005) **comb. nov.**

Remarks: *Euryhaliotrema* encompasses gill parasites of lutjanid, sciaenid, sparid, and heamulid fishes in marine and freshwater environments (Kritsky, 2012). *Sciadicleithrum* was proposed for gill parasites of neotropical cichlid fishes and characterised through the absence of typical traits of species belonging *Gussevia* (Kritsky et al., 1989b), which also infect neotropical cichlids. Euryhaliotrema and Sciadicleithrum have never been compared morphologically most likely because their distinct host repertoires (cichlids vs. other fishes) and habitats (all species of *Sciadicleithrum* are limnic whereas many species of *Euryhaliotrema* are marine) suggested no link. In contrast, phylogenetic studies (Mendoza-Palmero et al., 2017; Mendoza-Franco et al., 2018) indicated a close relationship between these two groups as observed in the present study (Fig. 2). The most detailed study to date (Mendoza-Palmero et al., 2017) suggests that *Sciadicleithrum* is nested in *Euryhaliotrema* and renders it paraphyletic (Fig. 2). Based on this evidence and the already wide morphological diagnosis of *Euryhaliotrema* (Kritsky, 2012) we propose synonymising the two genera. Thus, we consider *Euryhaliotrema* the junior synonym of *Sciadicleithrum* and transfer all species of *Euryhaliotrema* to *Sciadicleithrum*.

Platycephalotrema Kritsky & Nitta, 2019

Emended diagnosis (based on Kritsky and Nitta, 2019)*:* Body fusiform, slightly flattened dorsoventrally, comprising body proper (cephalic region, trunk, and peduncle) and haptor. Tegument smooth. Two terminal, two bilateral cephalic lobes; three pairs of bilateral head organs; bilateral groups of unicellular cephalic glands prepharyngeal, pharyngeal and/or postpharyngeal. Eyespots four, infrequently absent; granules small, ovate. Mouth subterminal, prepharyngeal; pharynx a muscular bulb; esophagus short to non-existent; intestinal ceca two, confluent posterior to gonads, lacking diverticula. Genital pore midventral, immediately posterior to intestinal bifurcation. Gonads intercecal, tandem (germarium pretesticular). Testis entire; vas deferens apparently looping dorsoventrally left intestinal cecum; seminal vesicle a simple dilation of distal vas deferens at level of male copulatory organ (MCO). Two generally large prostatic reservoirs; each having duct independently entering base of MCO; contents of anterior (or ventral) reservoir dense, usually comprising two zones of secretory material differing in density and stain preference; contents of posterior (or dorsal) reservoir nearly transparent, resisting stain. MCO a sclerotized tube, often with complex distal end; accessory piece frequently absent. Germarium entire; oviduct, uterus not observed; Mehlis' gland present. Vaginal pore dextral, submarginal; vagina comprising large distal vestibule often with sclerotized components and from which the vaginal canal extends posteriorly toward ootype. Seminal receptacle not observed or indistinct. Vitellarium throughout trunk, except absent from regions of other reproductive organs. Globose haptor with bilateral lobes and armed with dorsal and ventral anchor/bar complexes, seven pairs of similar hooks having normal dactylogyrid distribution; vesicle filled with granular product usually associated with each of ventral and/or dorsal anchor. Dorsal and ventral anchors similar in size, shape; each with elongate superficial root, large base, short slightly arcing shaft, elongate point. Ventral bar simple, with spatulate ends; dorsal bar with bifurcated ends. Each hook with protruding blunt thumb, slender shank comprised of one subunit. Parasites of fishes assigned to the Mullidae and Platycephalidae.

Type species: Platycephalotrema ogawai Kritsky & Nitta, 2019.

Other species:

- *Platycephalotrema austrinum* Kritsky & Nitta, 2019
- *Platycephalotrema bassense* (Hughes, 1928) Kritsky & Nitta, 2019
- *Platycephalotrema johnstoni* (Bychowsky & Nagibina, 1970) **comb. nov.**
- *Platycephalotrema koppa* Kritsky & Nitta, 2019
- *Platycephalotrema macassarense* (Yamaguti, 1963) Kritsky & Nitta, 2019
- *Platycephalotrema mastix* Kritsky & Nitta, 2019
- *Platycephalotrema ogawai* Kritsky & Nitta, 2019
- *Platycephalotrema platycephali* (Yin & Sproston, 1948) Kritsky & Nitta, 2019
- *Platycephalotrema sinense* (Yamaguti, 1963) Kritsky & Nitta, 2019
- *Platycephalotrema thysanophrydis* (Yamaguti, 1937) Kritsky & Nitta, 2019

Remarks: In the present study, species within *Haliotrema* are placed in different and well supported lineages of clade A2 (‘*Haliotrema’* group) which also includes *Bravohollisia, Glyphidohaptor, Lethrinitrema, Parancyrocephaloides, Pseudohaliotrema, Tetrancistrum*, and *Thylacicleidus* (Fig. 2). The lack of distinctive morphological features of species of *Haliotrema* compared to the other genera in the clade and the lack of an apparent host-related pattern highlight the need for revising this genus as already suggested by Klassen (1994). In this context, Kritsky and Nitta (2019) created *Platycephalotrema* to encompass dactylogyrid parasites infecting platycephalid fishes but remarked that likely all dactylogyrid parasites of scorpaeniform fishes assigned to the waste bucket genera *Ancyrocephalus* and *Haliotrema* might belong to this group. However, recent phylogenetic studies show that this classification is outdated: Platycephalidae Gill, 1872 is now classified in the suborder Platycephaloidei within Perciformes (Betancur-R et al., 2017). Kritsky and Nitta (2019) also did not discuss phylogenetic relationships of the group despite the availability of molecular data for two species of *Platycephalotrema*, *Platycephalotrema macassarense* and *P. platycephali* (both published as *Haliotrema*) (Wu et al., 2006; Sun et al., 2014). Therefore, they did not note that *Haliotrema johnstoni* even renders *Platycephalotrema* paraphyletic according to a more recent study (Soo, 2019) and the results here, which both include all available sequences of species of *Platycephalotrema*. *Haliotrema johnstoni* also presents a dorsal bar with bifurcating ends similar to species of *Platycephalotrema* but does not lack accessory piece in the male copulatory organ and has a different host repertoire (Syngnathiformes, Mullidae). Based on their phylogenetic relationship, we propose that *H. johnstoni* should be considered a member of *Platycephalotrema*. We transfer *H. johnstoni* to *Platycephalotrema* and emend the generic diagnosis to accommodate the additional species.

Subfamily Ancyrocephalinae Bychowsky, 1937

Junior synonyms: Anacanthorinae Price, 1967 and Ancylodiscoidinae Gussev, 1961.

Includes (only genera with molecular data available mentioned): Actinocleidus Müller, 1937; *Ameloblastella* Kritsky, Mendoza-Franco & Scholz, 2000; *Anacanthorus* Mizelle & Price, 1965; *Ancyrocephalus* Creplin, 1839; *Aphanoblastella* Kritsky, Mendoza-Franco & Scholz, 2000; *Boegeriella* Mendoza-Palmero & Hsiao, 2020; *Bychowskyella* Akhmerov, 1952; *Cacatuocotyle* Boeger, Domingues & Kritsky, 1997; *Cornudiscoides* Kulkarni, 1969; *Cosmetocleithrum* Kritsky, Thatcher & Boeger, 1986; *Demidospermus* Suriano, 1983; *Diaphorocleidus* Jogunoori, Kritsky & Venkatanarasaiah, 2004; *Hamatopeduncularia* Yamaguti, 1953; *Heteropriapulus* Kritsky, 2007; *Ligictaluridus* Beverley-Burton, 1984; *Mymarothecium* Kritsky, Boeger & Jégu, 1998; *Nanayella* Acosta, Mendoza-Palmero, da Silva & Scholz, 2019; *Pavanelliella* Kritsky & Boeger, 1998; *Pseudancylodiscoides* Yamaguti, 1963; *Quadriacanthus* Paperna, 1961; *Schilbetrema* Paperna & Thurston, 1968; *Susanlimocotyle* Soares, Domingues & Adriano, 2020; *Thaparocleidus* Jain, 1952; *Trinigyrus* Hanek, Molnár & Fernando, 1974;

Unibarra Suriano & Incorvaia, 1995; *Unilatus* Mizelle & Kritsky, 1967; *Urocleidoides* Mizelle & Price, 1964; *Vancleaveus* Kritsky, Thatcher & Boeger, 1986.

Remarks: As reported above, the two macroclades found here each include a type genus and species of the two suggested subfamilies, *Dactylogyrus* and *Ancyrocephalus*. Therefore, we reassign Ancyrocephalinae and Dactylogyrinae to these macroclades as subfamilies of Dactylogyridae as presented by Bychowsky, 1937. Because of the lack of distinctive morphological features for the subfamily, only genera with molecular data available are included here. Anacanthorinae and Ancylodiscoidinae are synonymised with Ancyrocephalinae. Anacanthorinae Price, 1968 is a monophyletic group (Moreira et al., 2019) nested within Ancyrocephalinae as defined here and comprise species of *Anacanthorus* that are unique in possessing 18 marginal hooks and lacking anchors and bars. Ancylodiscoidinae is also nested within Ancyrocephalinae (see remarks for Dactylogyridae). Ancyrocephalinae Bychowsky, 1937 has served as a catch-all and, consequently, polyphyletic subfamily within dactylogyrid monogeneans with different ancyrocephaline clades distinguished by freshwater, coastal and marine origin, respectively (Šimková et al., 2003, 2006). Moreover, Šimková et al. (2006) pointed out persistent unresolved relationships between marine members of Ancyrocephalinae, Dactylogyrinae and Pseudodactylogyrinae. Unresolved relationships between the lineages of freshwater clades within Ancyrocephalinae (macroclade B) are reported in the present study, which were not reported by Mendoza-Palmero et al. (2015). Several recent studies have pointed out the need for revision of Dactylogyridae and discussed the relevance of habitat type (marine vs. freshwater) and geographic origin as drivers of evolutionary processes (Mendoza-Palmero et al., 2015; Moreira et al., 2019). Similar to Dactylogyrinae, we could identify no apparent morphological similarities between the genera belonging to the subfamily based on diagnostic features of internal organs and sclerotised structures in the literature (see Table S1). Therefore, only genera with molecular data available are included. However, other genera formerly considered members of Ancylodiscoididae sensu Lim et al. (2001) and Anacanthorinae Price, 1967 also likely form also part of this subfamily as suggested by the phylogenetic position of all representatives from these groups included in the present study. This genera include *Anacanthoroides* Kritsky & Thatcher, 1974, *Anchylodiscus* Johnston & Tiegs, 1922, *Ancylodiscoides* Yamaguti, 1937, *Bagrobdella* Paperna, 1969, *Bifurcohaptor* Jain, 1958, *Malayanodiscoides* Lim & Furtado, 1986, *Mizelleus* Jain, 1957, *Notopterodiscoides*

Lim & Furtado, 1986 *Pangasitrema* Pariselle, Euzet & Lambert, 2004, *Paraquadriacanthus* Ergens, 1988, *Philureter* Viozzi & Gutiérrez, 2001, *Protoancylodiscoides* Paperna, 1969, *Schilbetrematoides* Kritsky & Kulo, 1992, and *Synodontella* Dossou & Euzet, 1993.

Ancyrocephalus Creplin, 1936

Remarks: The diagnosis of *Ancyrocephalus* has been revalidated by Bychowsky & Nagibina, 1970 to only include representatives infecting percids namely *A. paradoxus* and *A. percae* (clade B6 in Fig. 2). Yet several other species remain affiliated to this genus. Therefore, the catch-all genus *Ancyrocephalus* has remained polyphyletic with, e.g., *A. mogurndae* being placed among the Dactylogyrinae (clade A3) rather than the Ancyrocephalinae (B6) (Fig. 2). In the past, this polyphyly has resulted in creation of several genera whose members were previously assigned to *Ancyrocephalus* including *Kapentagyrus* (Kmentová et al., 2018), *Xenoligophoroides* (Dmitrieva et al., 2018), and *Ligophorus* (Marchiori et al., 2015). Here however, we refrain from creating a new genus for *A. mogurndae* as sequences of a majority species of *Ancyrocephalus* are unavailable and systematic revision of the genus should be based on more extensive molecular and morphological datasets than used in the present study. For now, we recommend referring to *A. mogurndae* as '*Ancyrocephalus*' *mogurndae* to highlight phylogenetic position outside *Ancyrocephalus* sensu stricto infecting percids.

Demidospermus Suriano, 1983

Remarks: Species of *Demidospermus* alongside representatives of *Cosmetocleithrum* form a well-supported lineage (clade B4). Our phylogenetic analysis shows that several unassigned and undescribed specimens assigned to *Demidospermus* fall into separate lineages together with two other unassigned dactylogyrid specimens (clade B1). These specimens should however not be considered *Demidospermus* as the type species falls withing a separate clade (clade B4). Moreover, *D. mortenthaleri* is situated within another dactylogyrid lineage causing the genus *Demidospermus* to be polyphyletic. These instances call for a systematic revision of the genus in a more extensive study covering a larger number of species than included here. In particular, the taxonomic position and generic status of *D. mortenthaleri* should be revised as suggested by Franceschini et al. (2018).

Hamatopeduncularia Yamaguti, 1953

Junior synonyms: Chauhanellus Bychowsky & Nagibina, 1969 and *Hargitrema* Tripathi, 1959.

Emended diagnosis (based on Lim, 1994 and Lim, 1996)*:* Three pairs of head organs. Haptor armed with two pairs of anchors, two bars and 14 hooks of which 6 pairs are sometimes located on digit-like extensions of the haptor. Anchors dissimilar: spines present or absent on main parts of dorsal anchors; outer roots of ventral anchors expanded or not; base of inner roots thickened. Bars usually simple, may possess protuberances such as spines on both ends; appendix present or absent. Hooks of two morphological types: one pair larval-type; 6 pairs adult-type; lengths may be variable. Four eye-spots; anterior pair smaller than posterior pair. Mouth subterminal. Muscular pharynx; long to medium-sized oesophagus; bifurcate intestine; intestinal caeca non-confluent posteriorly. Gonads and testis in tandem and intercaecal. Ovary pretesticular. Vaginal pore dextral; sclerotised vaginal tube entering seminal recepta- cle. Oviduct elongate, arises from ovary. Uterus receiving ducts from vagina and well-developed, follicular vitellarium. Uterine pore near copulatory organ. Testis single, post-ovarian. Vas deferens arises from anterior of testis, crosses along dorsal region, follows sinuous course anteriorly to loop around left intestinal caeca onto ventral side continuing anteriorly, or to reflex and dilate forming seminal vesicle. Copulatory organ consists of sclerotised tube (cirrus) with or without accessory piece. Parasites of marine fishes belonging to Ariidae.

Type species: Hamatopeduncularia arii Yamaguti, 1953

Other species:

- *Hamatopeduncularia alata* (Chauhan, 1945) **comb. nov.**
- *Hamatopeduncularia arabica* Paperna, 1977
- *Hamatopeduncularia aspinosa* (Lim, 1994) **comb. nov.**
- *Hamatopeduncularia auriculatum* (Lim, 1994) **comb. nov.**

- *Hamatopeduncularia australis* Young, 1967
- *Hamatopeduncularia bagre* Hargis, 1955
- *Hamatopeduncularia bifida* Illa, Shameem, Serra, Melai, Mangam, Basuri, Petroni & Modeo, 2019
- *Hamatopeduncularia boegeri* (Domingues & Fehlauer, 2006) **comb. nov.**
- *Hamatopeduncularia brisbanensis* Young, 1967
- *Hamatopeduncularia caelata* (Lim, 1994) **comb. nov.**
- *Hamatopeduncularia cangatae* Domingues, Soares & Watanabe, 2016
- *Hamatopeduncularia chauhani* (Venkatanarasaiah & Kulkarni, 1990) **comb. nov.**
- *Hamatopeduncularia digitalis* (Lim, 1994) **comb. nov.**
- *Hamatopeduncularia duriensis* (Lim, 1994) **comb. nov.**
- *Hamatopeduncularia elegans* Bychowsky & Nagibina, 1968
- *Hamatopeduncularia elongata* Lim, 1996
- *Hamatopeduncularia flexiosa* (Bychowsky & Nagibina, 1968) **comb. nov.**
- *Hamatopeduncularia forcipis* (Lim, 1994) **comb. nov.**
- *Hamatopeduncularia hamatopeduncularoidea* (Domingues, Soares & Watanabe, 2016) **comb. nov.**
- *Hamatopeduncularia heraldii* Mizelle & Price, 1964
- *Hamatopeduncularia hypenocleithrum* (Domingues, Soares & Watanabe, 2016) **comb. nov.**
- *Hamatopeduncularia indica* (Rastogi, Kumar & Singh, 2004) **comb. nov.**
- *Hamatopeduncularia indica* Siddiqui & Kulkarni, 1983
- *Hamatopeduncularia intermedia* (Lim, 1994) **comb. nov.**
- *Hamatopeduncularia isosimplex* Lim, 1996
- *Hamatopeduncularia longiangusticirrata* Soo & Tan, 2021
- *Hamatopeduncularia longicopulatrix* Lim, 1996
- *Hamatopeduncularia madhaviae* Illa, Shameem, Serra, Melai, Mangam, Basuri, Petroni & Modeo, 2019
- *Hamatopeduncularia major* Kearn & Whittington, 1994
- *Hamatopeduncularia malaccensis* Lim, 1996
- *Hamatopeduncularia malayana* (Lim, 1994) **comb. nov.**

- *Hamatopeduncularia malayana* Lim, 1996
- *Hamatopeduncularia manjungi* Lim, 1996
- *Hamatopeduncularia nagibinae* (Paperna, 1977) **comb. nov.**
- *Hamatopeduncularia nagibinae* Paperna, 1977
- *Hamatopeduncularia nanaoensis* Yao, Wang, Xia & Chen, 1998
- *Hamatopeduncularia nengi* (Tripathi, 1959) **comb. nov.**
- *Hamatopeduncularia neotropicalis* (Domingues & Fehlauer, 2006) **comb. nov.**
- *Hamatopeduncularia oculata* (Bychowsky & Nagibina, 1968) **comb. nov.**
- *Hamatopeduncularia osteogeneiosi* (Lim, 1994) **comb. nov.**
- *Hamatopeduncularia papernai* Lim, 1996
- *Hamatopeduncularia pearsoni* Kearn & Whittington, 1994
- *Hamatopeduncularia pedunculata* (Paperna, 1977) **comb. nov.**
- *Hamatopeduncularia petalumvaginata* Soo & Tan, 2021
- *Hamatopeduncularia pocula* (Lim, 1994) **comb. nov.**
- *Hamatopeduncularia pulchra* Bychowsky & Nagibina, 1969
- *Hamatopeduncularia pulutana* (Lim, 1994) **comb. nov.**
- *Hamatopeduncularia seenghali* (Kumar, 2013) **comb. nov.**
- *Hamatopeduncularia simplex* Bychowsky & Nagibina, 1969
- *Hamatopeduncularia spiralis* Kearn & Whittington, 1994
- *Hamatopeduncularia susamlimae* (Domingues, Soares & Watanabe, 2016) **comb. nov.**
- *Hamatopeduncularia thalassini* Bychowsky & Nagibina, 1968
- *Hamatopeduncularia trifida* (Lim, 1994) **comb. nov.**
- *Hamatopeduncularia tuberhamata* (Zhang & Ding, 1997) **comb. nov.**
- *Hamatopeduncularia velum* (Domingues, Soares & Watanabe, 2016) **comb. nov.**
- *Hamatopeduncularia venosus* Lim, 1996
- *Hamatopeduncularia youngi* (Kearn & Whittington, 1994) **comb. nov.**

Remarks: Hamatopeduncularia sensu Lim (1996) encompasses gill parasites of ariid fishes with haptoral digitations. Although closely related to *Hamatopeduncularia,* species of *Chauhanellus* infecting the gills of ariids, usually lack haptoral digitations and present wings on the anchors and a spine on the inner root of the dorsal anchors, a dorsal bar with spines, and a ventral bar with proturberances unlike species of *Hamatopeduncularia* (Lim, 1994). However, none of these characteristics provides an unambiguous separation of these two genera as they can also be present in representative of the other genus and, therefore, "the two genera are distinguished on a combination of characteristics" (Lim, 1994). For instance, Lim (1994) found several species of *Chauhanellus* with haptoral digitations. Phylogenetic analyses suggested that *Chauhanellus* is nested in *Hamatopeduncularia* (Soo and Tan, 2021; this study). Based on this paraphyly and the ambiguous generic diagnoses, we consider *Chauhanellus* a synonym of *Hamatopeduncularia*. All species of *Chauhanellus* are transferred to *Hamatopeduncularia.*

Thaparocleidus Jain 1952*, Pseudancylodiscoides* Yamaguti, 1963, and *Cornudiscoides* Kulkarni, 1969

Remarks: Our phylogenetic study demonstrates that *Pseudancylodiscoides* and *Cornudiscoides* are nested in *Thaparocleidus*. *Thaparocleidus* encompasses dactylogyrids infecting Old World siluriforms (Lim, 2001). In contrast, species of *Cornudiscoides* and *Pseudancylodiscoides* have only been reported from bagrids specifically in Southern and Eastern Asia (Lim, 2001). Species of *Cornudiscoides* differ from species of *Thaparocleidus* with regard to a single pair of elongated, needle-like marginal hooks and a divided ventral bar. Species of *Pseudancylodiscoides* differ only with regard to a divided ventral bar. However, Lim et al. (2001) remarked that some species of *Thaparocleidus* also present a divided ventral bar and *Pseudancylodiscoides* could be considered as synonym of *Thaparocleidus* as proposed by Gussev (1976) (cited as *Silurodiscoides*). Furthermore, studies on other dactylogyrid genera highlight that the marginal hook length can differ substantially between congeners, e.g. in species of *Cichlidogyrus* (Cruz-Laufer et al., 2021b). Therefore, we suggest that *Cornudiscoides* and *Pseudancylodiscoides* are both likely junior synonyms of *Thaparocleidus*. Yet we refrain from any nomenclatural acts unlike for other similar cases (see above) as few species of *Cornudiscoides* and *Pseudancylodiscoides* have been sequenced to date in comparison to the total number of species and the sequences available from *Pseudancylodiscoides* (Wu et al., 2008) were never attributed to any particular species.

Taxonomic biases and limitations

Despite the increasing number of described species and genera, and availability of DNA sequence data, taxonomic bias and limited data remain a major challenge for a comprehensive systematic revision of Dactylogyridae. Many phylogenetic studies in recent years have targeted specific taxa, clades, or geographic regions but omitted possibly related genera. For instance, phylogenetic publications investigating the parasite fauna of reef and littoral fish communities occasionally omit other taxa, e.g. much of the research focusing on species previously considered members of '*Haliotrema*' including *Euryhaliotrema*, *Haliotrema, Haliotrematoides,* and *Metahaliotrema* fails to include freshwater taxa such as *Cichlidogyrus, Enterogyrus,* or *Scutogyrus* (Plaisance et al., 2005; Mendoza-Franco et al., 2018) or other taxa altogether (Kritsky et al., 2009b) despite DNA sequences of these species groups being available at the time. Furthermore, a boom of molecular characterisations of monogenean parasites infecting neotropical siluriforms in recent years has produced many DNA sequence data included in Ancyrocephalinae (macroclade B), which now appears almost exclusive to siluriforms. Yet few studies have focused on other host groups such as cichliforms (Mendoza-Garfias et al., 2017), characiforms (Zago et al., 2018, 2020; Moreira et al., 2019), and gymnotiforms (Zago et al., 2020). Molecular data of many other lineages remain unavailable (Poulin et al., 2019) and many remain undiscovered (Jorge and Poulin, 2018), e.g. purely morphological studies on neotropical host taxa described new genera on non-siluriforms such as cichliforms, characiforms, and perciforms (Boeger et al., 2014; Morey et al., 2019; Cruces et al., 2020, 2021). Apparent biogeographical patterns might also be affected by this bias. For instance, species of clade A4 appear to be restricted to the Indo-Pacific region, species of clade A3 and A4 to the Palearctic and Indo-Malayan realms, and species of clade B4 and B5 to the Neotropics. Yet molecular data of dactylogyrine lineages (clade A4) are biased towards the Northern hemisphere, e.g. taxonomic studies show that species of *Dactylogyrus* are also present in the Afrotropical realm in sub-Saharan water bodies (e.g. Birgi and Euzet, 1983; Raphahlelo et al., 2020). Citation bias might also play a role in monogenean research. We observed that DNA sequences used in more prestigious studies are more likely to be included in follow-up studies leading to the omission of relevant molecular data published in journals with lower impact factors. Promotion on social media might address this shortfall but can likely not fully compensate this bias (Peoples et al., 2016; Marshall and Strine, 2019). Furthermore, confirmation biases might affect which taxa are included in phylogenetic studies as prior expectations of researchers could affect taxon selection (see Jermiin et al., 2020). For instance, DNA sequences of species of *Gobioecetes* and *Parancyrocephaloides* (Ogawa and Itoh, 2017) were absent from a study on species formerly and presently considered as belonging to '*Haliotrema*' (Soo, 2019) despite their close relationship to the '*Haliotrema*' group., Sequences of heteronchocleidine (Tan et al., 2011) and mesoparasitic (Theisen et al., 2017, 2018) worms were not considered in a study on the new genus *Characidotrema* and its phylogenetic position among Dactylogyrinae (macroclade A) (Řehulková et al., 2019) despite the importance these groups as major lineages within the subfamily. Omissions of taxa, intentional or not, can negatively impact the results of phylogenetic analyses. Taxon alongside gene sampling are key factors for improving phylogenetic accuracy (Nabhan and Sarkar, 2012) and even taxa with incomplete gene or sequence coverage can improve phylogenetic estimates (Wiens and Tiu, 2012). One step to address this issue could be a level playing field for multiple sequence alignments as provided by the present study.

Concluding remarks

A phylogenetic reconstruction of dactylogyrid monogeneans based on three ribosomal gene portions traditionally used in flatworm taxonomy revealed two well-supported lineages. Because of the phylogenetic positions of the type genera and species of two previously described subfamilies, we revised the classification of Dactylogyridae into two subfamilies Dactylogyrinae and Ancyrocephalinae sensu Bychowsky and Nagibina (1978). Comparison with previous phylogenetic reconstructions of dactylogyrid monogeneans revealed differences in tree topology within both subfamilies. For the first time a monophyletic clade of mesoparasitic species was reported as well as three well-supported clades infecting siluriform hosts. In cases of paraphyly and polyphyly, we conducted a systematic revision including the synonymisation of several genera and reclassification of some species. Moreover, we found that discrepancies between morphological similarities and phylogenetic relationships in some dactylogyrid lineages suggest an impact of environmental changes on morphological adaptation. Apparent biogeographical patterns in the evolution of dactylogyrid monogeneans might be explained by sampling bias towards certain biogeographical regions and host taxa. This study aims to provide a level playing field for future phylogenetic studies on Dactylogyridae by presenting an alignment accompanied by a state-of-the-art phylogenetic tree. We encourage researchers investigating dactylogyrid monogeneans to use the data offered here as a baseline for their respective studies. This approach could reduce researcher bias and enable a more balanced phylogenetic approach of one of the most species-rich families of fish parasites.

Author contributions

Conceptualization, N.K. and A.J.C.-L.; Methodology and data analyses, A.J.C.-L.; Writing–Original Draft Preparation, N.K. and A.J.C.-L.; Writing–Review & Editing, A.P., M.P.M.V., T.A., K.S., N.K., A.J.C.-L.; Supervision, M.P.M.V. All authors have read and agreed to the published version of the manuscript.

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Table 1. Substitution models of molecular evolution and partitions for Bayesian inference (BI) and maximum likelihood estimation (ML) of phylogeny of Dactylogyridae. For model specification see the IQ-TREE ModelFinder manual (Kalyaanamoorthy et al., 2017).

Partition	**Base pairs**	**Bayesian inference (BI)**	**Maximum likelihood estimation (ML)**
28S rDNA	655	GTR + F + I + Γ4	GTR + F + R6
18S rDNA	1815	SYM + Γ4	TIM3e + R3
ITS rDNA	259	HKY + F + Γ4	TPM2u + F + R2

Table 2. Specimen data for DNA sequences used for phylogenetic reconstruction of Dactylogyridae including host species, GenBank accession numbers, locality by country, and reference.

Species	Host	Isolate/Voucher	28S rDNA	18S rDNA	ITS	Locality	Reference
Actinocleidus Mueller, 1937							
Actinocleidus recurvatus Mizelle & Donahue, 1944	*Lepomis gibbosus* (Linnaeus, 1758)		AJ969951			Slovakia	Šimková et al. (2006)
Ameloblastella Kritsky, Mendoza-Franco & Scholz, 2000							
Ameloblastella chavarriai (Price, 1938)	*Rhamdia quelen* (Quoy & Gaimard, 1824)	AmchRq1	KP056251			Mexico	Mendoza-Palmero et al. (2015)
Ameloblastella edentensis Mendoza-Franco, Mendoza-Palmero & Scholz, 2016	*Hypophtalmus edentatus* Spix & Aggasiz, 1829	Am16He	KP056255			Peru	Mendoza-Palmero et al. (2015)
Ameloblastella unapioides Mendoza-Franco, Mendoza-Palmero & Scholz, 2016	*Sorubim lima* (Bloch & Schneider, 1901)	Am8SI	KP056254			Peru	Mendoza-Palmero et al. (2015)
Anacanthorus Mizelle & Price, 1965							
Anacanthorus lepyrophallus Kritsky, Boeger & Van Every, 1992	*Serrasalmus maculatus* Kner, 1858	PR04	MH843718			Brazil	Moreira et al. (2019)
Anacanthorus paraxaniophallus Moreira, Carneiro, Ruz & Luque, 2019	*Serrasalmus marginatus* Valenciennes, 1837	PR50	MH843717			Brazil	Moreira et al. (2019)
Anacanthorus penilabiatus Boeger, Husak & Martins, 1995	*Piaractus mesopotamicus* (Holmberg, 1887)	PR05	MH843719			Brazil	Moreira et al. (2019)
Ancyrocephalus Creplin, 1839							
Ancyrocephalus mogurndae (Yamaguti, 1940)	*Siniperca chuatsi* (Basilewsky, 1855)		DQ157667			China	Wu et al. (2006)
Ancyrocephalus paradoxus Creplin, 1839	*Sander lucioperca* (Linnaeus, 1758)		AJ969952			Czech Republic	Šimková et al. (2006)
Ancyrocephalus percae Ergens, 1966	*Perca fluviatilis* Linnaeus, 1758	Ac3	KF499080			Finland	Behrmann-Godel et al. (2014)
Aphanoblastella Kritsky, Mendoza-Franco & Scholz, 2000							

Aphanoblastella aurorae Mendoza-Palmero, Scholz, Mendoza- Franco & Kuchta, 2012	*Goeldiella eques* (Müller & Troschel, 1849)	ApauGe	KP056239			Peru	Mendoza-Palmero et al. (2015)
Aphanoblastella magna Yamada, Acosta, Yamada, Scholz & Da Silva, 2018	*Pimelodella avanhandavae* Eigenmann, 1917	1	MH688484			Brazil	Yamada et al. (2018)
Aphanoblastella travassosi (Price, 1938)	*Rhamdia guatemalensis* (Günther, 1864)	2	MK358458			Mexico	Acosta et al. (2019)
Boegeriella Mendoza-Palmero & Hsiao, 2020							
Boegeriella conica (Mendoza-Palmero, Mendoza-Franco, Acosta & Scholz, 2019)	*Platynematichthys notatus* (Jardine, 1841)	Ancy10Pn2	KP056225			Peru	Mendoza-Palmero et al. (2015)
Boegeriella ophiocirrus (Mendoza-Palmero, Mendoza-Franco, Acosta & Scholz, 2019)	*Platystomatichthys sturio* (Kner, 1858)	2	MK834511			Peru	Mendoza-Palmero et al. (2019)
Bravohollisia Bychowsky & Nagibina, 1970							
Bravohollisia maculatus (Venkatanarasaiah, 1984)	*Pomadasys maculatus* (Bloch, 1793)	SYSU20060429-3	KJ571008	KJ571018		China	Sun et al. (2014)
Bravohollisia plectorhynchus Li, Zhang, Chen & Chen, 2005	*Plectorhinchus* sp.	SYSU20060502-2	KJ571010	KJ571019		China	Sun et al. (2014)
Bravohollisia tecta Bychowsky & Nagibina, 1970	*Pomadasys maculatus*	SYSU20060429-4	KJ571012	KJ571020		China	Sun et al. (2014)
Bychowskyella Akhmerov, 1952							
Bychowskyella pseudobagri Akhmerov, 1952	*Tachysurus fulvidraco* (Richardson, 1846)		EF100541			China	Wu et al. (2008)
Caballeria Bychowsky & Nagibina, 1970							
Caballeria intermedius Lim, 1995	*Pomadasys argenteus* (Forsskål, 1775)	SYSU20060501-4	KJ571013			China	Sun et al. (2014)
Cacatuocotyle Boeger, Domingues & Kritsky, 1997							
Cacatuocotyle papilionis Zago, Franceschini, Müller & da Silva, 2018	*Astyanax lacustris* (Lütgen, 1875)		MG832889			Brazil	Zago et al. (2018)
Characidotrema Paperna & Thurston, 1968							
Characidotrema nursei Ergens, 1973	*Brycinus nurse* (Rüppell, 1832)	S	MK012540	MK014158	MK014158	Sudan	Řehulková et al. (2019)
Characidotrema vespertilio Kičinjaová & Řehulková, 2019	*Brycinus imberi* (Peters, 1852)	C	MK012543	MK014161	MK014161	Dem. Rep. of the Congo	Řehulková et al. (2019)

Chauhanellus Bychowsky & Nagibina, 1969							
Chauhanellus auriculatum Lim, 1994	*Plicofollis argyropleuron* (Valenciennes, 1840)	Ca1	MN108169	MN105020		Malaysia	Soo and Tan (2021)
Chauhanellus boegeri Domingues & Fehlauer, 2006	*Genidens genidens* (Cuvier, 1829)	ChboGg	KP056241			Brazil	Mendoza-Palmero et al. (2015)
Chauhanellus intermedius Lim, 1994	*Hexanematichthys sagor* (Hamilton, 1822)	Ci1	MN108172	MN105023		Malaysia	Soo and Tan (2021)
Chauhanellus sp.	*Genidens genidens*	ChGg	KP056242			Brazil	Mendoza-Palmero et al. (2015)
Cichlidogyrus Paperna, 1960							
Cichlidogyrus arthracanthus Paperna, 1960	*Coptodon guineensis* (Günther, 1862)	PC60	HQ010022	HE792783	HE792783	Senegal	Mendlová et al. (2010, 2012)
Cichlidogyrus attenboroughi Kmentová, Gelnar, Koblmüller & Vanhove, 2016	*Benthochromis tricoti* (Poll, 1948)	PB46 CiAt	MH708146	MH708153	MH708153	Burundi	Kmentová et al. (2018)
Cichlidogyrus halli (Price & Kirk, 1967)	*Oreochromis niloticus* x *mweruensis*	C ha	MG973075	MG973075	MG973075	Dem. Rep. of the Congo	Vanhove et al. (2018)
Cichlidogyrus pouyaudi Pariselle & Euzet, 1994	*Tylochromis intermedius* (Boulenger, 1916)	PC69	HQ010039	HE792793	HE792793	Senegal	Mendlová et al. (2010, 2012)
Cichlidogyrus sclerosus Paperna & Thurston, 1969	*Oreochromis niloticus* Linnaeus, 1758		DQ157660	DQ537359	DQ537359	China	Wu et al. (2006, 2007)
Cichlidogyrus zambezensis Douëllou, 1993	*Serranochromis macrocephalus* (Boulenger, 1899)	AP375	XXXXXXXX	XXXXXXXXX	XXXXXXXX	Zambia	Cruz-Laufer et al. (2021b)
Cornudiscoides Kulkarni, 1969							
Cornudiscoides geminus Gusev, 1976	*Mystus vittatus* (Bloch, 1794)	E07, EMBOSS gc	KU358727	KU358728		India	Verma et al. (2017)
Cornudiscoides Proximus Gusev, 1976	*Mystus vittatus*	C08, EMBOSS pc	KU358726	KU235550		India	Verma et al. (2017)
Cosmetocleithrum Kritsky, Thatcher & Boeger, 1986							
Cosmetocleithrum bifurcum Mendoza-Franco, Mendoza-Palmero & Scholz, 2016	*Hassar orestis* (Steindachner, 1875)	Co8H2	KP056216			Peru	Mendoza-Palmero et al. (2015)
Cosmetocleithrum bulbocirrus Kritsky, Thatcher & Boeger, 1986	*Pterodoras granulosus* (Valenciennes, 1821)		MG001326			Brazil	Acosta et al. (2018)
Dactylogyridae gen. sp. 13	*Hypophtalmus edentatus* Spix & Aggasiz, 1829	Ancy13He2	KP056230			Peru	Mendoza-Palmero et al. (2015)

Dactylogyridae gen. sp. 18	*Pseudoplatystoma fasciatum* (Linnaeus, 1766)	Ancy18Pf	KP056231			Peru	Mendoza-Palmero et al. (2015)
Dactylogyridae gen. sp. 23	*Platysilurus mucosus* (Vaillant, 1880)	Ancy23Pm	KP056232			Peru	Mendoza-Palmero et al. (2015)
Dactylogyridae gen. sp. 26	*Platynematichthys notatus* (Jardine, 1841)	Ancy26Pn	KP056234			Peru	Mendoza-Palmero et al. (2015)
Dactylogyridae gen. sp. 4	*Ageneiosus vittatus* Steindachner, 1908	Ancy4Av1	KP056218			Peru	Mendoza-Palmero et al. (2015)
Dactylogyridae gen. sp. 9	*Platynematichthys notatus*	Ancy9Pn5	KP056222			Peru	Mendoza-Palmero et al. (2015)
Dactylogyroides Gusev, 1963							
Dactylogyroides tripathii (Yamaguti, 1963)	*Pethia ticto* (Hamilton, 1822)		JX993982			India	Chiary et al. (2013)
Dactylogyrus Diesing, 1859							
Dactylogyrus bicornis Malevitskaja, 1941	*Rhodeus meridionalis* Karaman, 1924	ROME Bicornis	KY629345			Greece	Šimková et al. (2003)
Dactylogyrus extensus Mueller & Van Cleave, 1932	*Cyprinus caprio* Linnaeus, 1758		AJ969944	AJ564129	AJ564129	Czech Republic	Šimková et al. (2003, 2006)
Dactylogyrus lamellatus Akhmerow, 1952	*Ctenopharyngodon idella* (Valenciennes, 1844)		AJ969948	AJ564141	AJ564141	Czech Republic	Šimková et al. (2006)
Dactylogyrus mascomai El Gharbi, Renaud & Lambert, 1993	*Luciobarbus graellsii* (Steindachner, 1866)	LUGL Mascomai S13	MN338215	MN365680	MN365680	Spain	Benovics et al. (2020a)
Demidospermus Suriano, 1983							
Demidospermus anus uriano, 1983	*Loricariichthys platymetopon* Isbrücker & Nijssen, 1979	2	KY766957			Brazil	Franceschini et al. (2018)
Demidospermus mortenthaleri Mendoza-Palermo, Scholz, Mendoza-Franco & Kuchta, 2012	*Brachyplatystoma juruense* (Boulenger, 1898)	DemoBj1	KP056245			Peru	Mendoza-Palmero et al. (2015)
Demidospermus prolixus Franceschini, Zago, Müller, Francisco, Takemoto & da Silva, 2017	*Loricaria prolixa* (Isbrücker & Nijssen, 1978)		KY766955			Brazil	Franceschini et al. (2018)
Demidospermus rhinelepisi Acosta, Scholz, Blasco-Costa, Alves & da Silva, 2017	*Rhinelepis aspera* Spix & Agassiz, 1829		MG001324			Brazil	Acosta et al. (2018)

Demidospermus sp. *11*	*Brachyplatystoma vaillantii* (Valenciennes, 1840)	De11Bv	KP056235			Peru	Mendoza-Palmero et al. (2015)
Demidospermus sp. *23*	*Brachyplatystoma vaillantii*	De23Bv	KP056236			Peru	Mendoza-Palmero et al. (2015)
Diaphorocleidus Jogunoori, Kritsky & Venkatanarasaiah, 2004							
Diaphorocleidus armillatus Jogunoori, Kritsky & Venkatanarasaiah, 2004	*Gymnocorymbus ternetzi* (Boulenger, 1895)	HS/monogenea/2015/06		KT597997		India	Chaudhary et al. (2016)
Dogielius Bychowsky, 1936							
Dogielius catlaius (Jain, 1962)	*Labeo rohita (*Hamilton, 1822)		KC687091			India	Dash et al. (2014)
Dolicirroplectanum Kmentová, Gelnar & Vanhove, 2021							
Dolicirroplectanum lacustre Kmentová, Gelnar & Vanhove, 2021	*Lates niloticus* (Linnaeus, 1758)	LN1	MK937579	MK937576	MK937576	Uganda	Kmentová et al. (2020a)
Enterogyrus Paperna, 1963							
Enterogyrus coronatus Pariselle, Lambert & Euzet, 1991	*Tilapia dageti* Thys van den Audenaerde, 1967		HQ010030			Senegal	Mendlová et al. (2010)
Enterogyrus malmbergi Bilong, Bilong, 1988	*Oreochromis niloticus*	GZ-ZSDX	MN152976			China	Zhang et al. (2019)
Ergenstrema Paperna, 1964							
Ergenstrema mugilis Paperna, 1964	*Chelon ramada* (Risso, 1827)		JN996800	JN996835	JN996835	Spain	Blasco-Costa et al. (2012)
Euryhaliotrema Kritsky & Boeger, 2002							
Euryhaliotrema johnii Tripathi, 1959	*Lutjanus johnii* (Bloch, 1792)	ZSU 20060501-1	EU836193	EU836214		China	Sun et al. (2014)
Euryhaliotrema mehen (Solar-Jiménez, Garcia-Gasca & Fajer-Ávila, 2012)	*Lutjanus guttatus* (Steindachner, 1869)	LSJ-2011	HQ615997			Mexico	Soler-Jiménez et al. (2012)
Euryhaliotrema pirulum (Plaisance & Kritsky, 2004)	*Chaetodon lunula* (Lacepède, 1802)		AY820618	AY820607		French Polynesia	Plaisance et al. (2005)
Euryhaliotrema spirotubiforum (Zhang in Zhang, Yang & Liu, 2001)	*Lutjanus stellatus* (Akazaki, 1983)		DQ157656	DQ537347		China	Wu et al. (2006, 2007)
Eutrianchoratus Paperna, 1969							
Eutrianchoratus cleithrium Lim, 1989	*Belontia hasselti* (Cuvier, 1831)		HQ719224			Malaysia	Tan et al. (2011)

Glyphidohaptor Kritsky, Galli & Yang, 2007							
Glyphidohaptor safiensis Al Jufaili, Machkevsky, Kindi & Palm, 2020	*Siganus canaliculatus*	7	MN176409	MN213150	MN213150	Oman	Al Jufaili et al. (2020)
Gobioecetes Ogawa & Ito, 2017							
Gobioecetes biwaensis Ogawa & Ito, 2017	*Rhinogobius* sp. OM	M37	LC494515	LC494518	LC494518	Japan	Nitta and Nagasawa (2020)
Gobioecetes longibasis Nitta & Nagasawa, 2020	*Rhinogobius similis* Gill, 1859	M194	LC494516	LC494519	LC494519	Japan	Nitta and Nagasawa (2020)
Gussevia Kohn & Paperna, 1964							
Gussevia asota Kritsky, Thatcher & Boeger, 1989	*Astronotus ocellatus* (Agassiz, 1831)	DMS	MG596661			China	Xie et al. (2019)
Haliotrema Johnston & Tiegs, 1922							
Haliotrema angelopterum Plaisance, Bouamer & Morand, 2004	*Chaetodon kleinii* Bloch, 1790		AY820620	AY820609		Palau	Plaisance et al. (2005)
Haliotrema bilobatus (Yamaguti, 1953)	*Drepane punctata* (Linnaeus, 1758)		MG593837			Malaysia	Soo (2019)
Haliotrema chenhsintaoi Zhang, 2001	*Branchiostegus auratus* (Kishinouye, 1907)		DQ537371	DQ537345		China	Wu et al. (2007)
Haliotrema cromileptis Young, 1968	*Epinephelus coioides* (Hamilton, 1822)		EU523146	EU523144	EU523145	Vietnam	Dang et al. (2010)
Haliotrema johnstoni Bychowsky & Nagibina, 1970	*Upeneus luzonius* Jordan & Seale, 1907		DQ157664			China	Wu et al. (2007)
Haliotrema magnihamus Bychowsky & Nagibina, 1970	*Drepane punctata* (Linnaeus, 1758)		MG593838			Malaysia	Soo (2019)
Haliotrema scyphovagina Yamaguti, 1968	*Forcipiger flavissimus* Jordan & McGregor, 1898		AY820622	AY820611		French Polynesia	Plaisance et al. (2005)
Haliotrema susanae Soo, 2018	*Myripristis murdjan* (Forsskål, 1775)		MG518632			Malaysia	Soo (2019)
Haliotrematoides Kritsky, Yang & Sun, 2009							
Haliotrematoides guttate (García-Vargas, Fajer-Ávila & Lamothe-Argumedo, 2008)	*Lutjanus guttatus*		HQ615993	JN054406		Mexico	Soler-Jiménez et al. (2012)
Haliotrematoides plectridium Kritsky & Mendoza-Franco, 2009	*Lutjanus guttatus*		HQ615994			Mexico	García-Vásquez et al. (2015a)

Haliotrematoides spinatus Kritsky & Mendoza-Franco, 2009	*Lutjanus guttatus*		HQ615995	JN054404		Mexico	Soler-Jiménez et al. (2012)
Hamatopeduncularia Yamaguti, 1953							
Hamatopeduncularia arii Yaamaguti, 1953	*Arius jella* Day, 1877			KT252895		Mexico	Illa et al. (2019)
Hamatopeduncularia bagre Hargis, 1955	*Bagre marinus* (Mitchill, 1815)	5	MG586871			Mexico	Mendoza-Franco et al. (2018)
Hamatopeduncularia isosimplex Lim, 1996	*Arius maculatus* (Thunberg, 1792)	Hi1	MN108167	MN105018		Malaysia	Soo and Tan (2021)
Hamatopeduncularia petalumvaginata Soo & Tan, 2021	*Nemapteryx caelata* (Valenciennes, 1840)	Hp1	MN108164	MN105015		Malaysia	Soo and Tan (2021)
Heteronchocleidus Bychowsky, 1957							
Heteronchocleidus buschkieli Bychowsky, 1957	*Macropodus opercularis* (Linnaeus, 1758)		AY841876			China	Tan et al. (2011)
Heteropriapulus Kritsky, 2007							
Heteropriapulus heterotylus (Jogunoori, Kritsky & Venkatanarasaiah, 2004)	*Pterygoplichthys ambrosettii* (Holmberg, 1893)		MF116370			Brazil	Acosta et al. (2017)
Heteropriapulus simplex Li & Huang, 2012	*Pterygoplichthys ambrosettii*		MF116372			Brazil	Acosta et al. (2017)
Kapentagyrus Kmentová, Gelnar & Vanhove 2018							
Kapentagyrus limnotrissae (Paperna, 1973)	*Limnotrissa miodon* (Boulenger, 1906)	LI14	MH071782	MH071808	MH071808	Dem. Rep. of the Congo	Kmentová et al. (2018)
Kapentagyrus tanganicanus Kmentová, Gelnar & Vanhove 2018	*Stolothrissa tanganicae* Regan, 1907	LI8	MH071783	MH071807	MH071807	Dem. Rep. of the Congo	Kmentová et al. (2018)
Lethrinitrema Lim & Justine, 2011							
Lethrinitrema grossecurvitubum (Li & Chen, 2005)	*Lethrinus nebulosus* (Forsskål, 1775)	ZSU 20060522-1	EU836204	EU836225		China	Sun et al. (2014)
Lethrinitrema nebulosum Sun, Li & Yang, 2014	*Lethrinus nebulosus*	ZSU 20060524-1	EU836203	EU836224		China	Sun et al. (2014)
Ligictaluridus Beverley-Burton, 1984							
Ligictaluridus pricei (Mueller, 1936)	*Ameiurus nebulosus* (Lesueur, 1819)		AJ969939	AJ490168	AJ490168	Czech Republic	Šimková et al. (2003, 2006)
Ligophorus Euzet & Suriano, 1977							

Ligophorus imitans Euzet & Suriano, 1977	*Chelon ramada* (Risso, 1827)		JN996813	JN996849	JN996849	Spain	Blasco-Costa et al. (2012)
Ligophorus leporinus (Zhang & Ji, 1981)	*Mugil cephalus* Linnaeus, 1758		DQ537380			China	Wu et al. (2007)
Ligophorus vanbenedenii (Parona & Perugia, 1890)	*Chelon auratua* (Risso, 1810)		JN996801	JN996836	JN996836	Spain	Blasco-Costa et al. (2012)
Metahaliotrema Yamaguti, 1953							
Metahaliotrema digyroides (Zhang in Zhang, Yang & Liu, 2001)	*Gerres macrosoma* Cuvier, 1830		DQ537377	DQ537349		China	Wu et al. (2007)
Metahaliotrema scatophagi Yamaguti, 1953	*Scatophagus argus* (Linnaeus, 1766)		DQ157646	DQ537352		China	Wu et al. (2006, 2007)
Metahaliotrema subancistroides (Zhang in Zhang, Yang & Liu, 2001)	*Gerres decacanthus* (Bleeker, 1864)	ZSU 20050917B-1	EU836210	EU836231		China	Sun et al. (2014)
Mexicana Caballero & Bravo-Hollis, 1959							
Mexicana rubra Camargo, Luque & Santos, 2017	*Orthopristis ruber* (Cuvier, 1830)	E514	KY553147	KY553146		Brazil	Camargo et al. (2017)
Mymarothecium Kritsky, Boeger & Jégu, 1998							
Mymarothecium viatorum Boeger, Piasecki & Sobecka, 2002	*Piaractus mesopotamicus* (Holmberg, 1887)	PR84	MH843723			Brazil	Moreira et al. (2019)
Nanayella Acosta, Mendoza-Palmero, da Silva & Scholz, 2019							
Nanayella aculeatrium Acosta, Mendoza-Palmero, da Silva & Scholz, 2019	*Sorubim lima* (Bloch & Schneider, 1801)	Ancy12Sl	KP056228			Peru	Mendoza-Palmero et al. (2015)
Nanayella amplofalcis Acosta, Mendoza-Palmero, da Silva & Scholz, 2019	*Hemisorubim platyrhynchos* (Valenciennes, 1840)		MG001325			Brazil	Acosta et al. (2018)
Nanayella fluctuatrium Acosta, Mendoza-Palmero, da Silva & Scholz, 2019	*Sorubim lima* (Bloch & Schneider, 1801)		MG001327			Brazil	Acosta et al. (2018)
Onchobdella Paperna, 1968							
Onchobdella aframae Paperna, 1968	*Hemichromis fasciatus* Peters, 1857		HQ010034				Mendlová et al. (2010)
Onchobdella bopeleti Bilong Bilong & Euzet, 1995	*Hemichromis letourneuxi* Sauvage, 1880		HQ010033				Mendlová et al. (2010)
Onchocleidus Mueller, 1936							

Onchocleidus similis Mueller, 1936	*Lepomis gibbosus*		AJ969938	AJ490167	AJ490167	Slovakia	Šimková et al. (2003, 2006)
Paracosmetocleithrum Acosta, Scholz, Blasco-Costa, Alves & da Silva, 2018							
Paracosmetocleithrum trachydorasi Acosta, Scholz, Blasco-Costa, Alves & da Silva, 2017	*Trachydoras paraguayensis* (Eigenmann & Ward, 1907)		MG001323			Brazil	Acosta et al. (2018)
Paradiplectanotrema Gerasev, Gayevskaya & Kovaleva, 1987							
Paradiplectanotrema klimpeli Theisen, Palm, Stolz, Al-Jufaili & Kleinertz, 2018	*Saurida tumbil* (Bloch, 1795)	ST-2018	MG763101			Indonesia	Theisen et al. (2018)
Paradiplectanum sillagonum (Tripathi, 1959)	*Sillago sihama* (Forsskål, 1775)		AY553626	AY553617		China	Wu et al. (2005)
Parancyrocephaloides Yamaguti, 1938							
Parancyrocephaloides daicoci Yamaguti, 1938	*Dactyloptena peterseni* (Nyström, 1887)		LC190513	LC176447	LC176447	Japan	Ogawa and Itoh (2017)
Parasciadicleithrum Mendoza-Palmero, Blasco-Costa, Hernández-Mena & Pérez-Ponce de León, 2017							
Parasciadicleithrum octofasciatum Mendoza-Palmero, Blasco-Costa, Hernández-Mena & Pérez-Ponce de León, 2017	*Rocio octofasciata* (Regan, 1903)	ExC9 15	KY305885			Mexico	Mendoza-Palmero et al. (2017)
Pavanelliella Kritsky & Boeger, 1998							
Pavanelliella takemotoi Aguiar, Ceccarelli & Luque, 2011	*Pimelodus maculatus* Lacepède, 1803	298		MF398305	MF398305	Brazil	Aguiar et al. (2017)
Platycephalotrema Kritsky & Nitta, 2019							
Platycephalotrema macassarense (Yamaguti, 1963)	*Ratabulus megacephalus* (Tanaka, 1917)	ZSU 20060523-1	EU836207	EU836228		China	Sun et al. (2014)
Platycephalotrema platycephali (Yin & Sproston, 1948)	*Platycephalus indicus* (Linnaeus, 1758)		DQ157662			China	Wu et al. (2006)
Protogyrodactylus Johnston & Tiegs, 1922							
Protogyrodactylus alienus Bychowsky & Nagibina, 1974	*Gerres filamentosus* Cuvier, 1829		DQ157650	DQ537355		China	Wu et al. (2006; 2007)
Protogyrodactylus hainanensis Pan, Ding & Zhang, 1995	*Therapon jarbua* (Forsskål, 1775)		DQ157653			China	Wu et al. (2006)
Pseudancylodiscoides Yamaguti, 1963							

Pseudancylodiscoides sp1	*Pseudobagrus fulvidraco* (Richardson, 1846)	HSY1	EF100542	EF100564		China	Wu et al. (2008)
Pseudancylodiscoides sp2	*Pseudobagrus fulvidraco*	HSY3	EF100543	EF100565		China	Wu et al. (2008)
Pseudancylodiscoides sp3	*Pseudobagrus fulvidraco*	HSY4	EF100544	EF100566		China	Wu et al. (2008)
Pseudempleurosoma Yamaguti, 1965							
Pseudempleurosoma haywardi Theisen, Palm, Al-Jufaili & Kleinertz, 2017	*Johnius amblycephalus*	worm 1 2698625 1 D2	MF115715			Indonesia	Theisen et al. (2018)
Pseudodactylogyrus Gusev, 1965							
Pseudodactylogyrus anguillae (Yin & Sproston, 1948)	*Anguilla anguilla* (Linnaeus, 1758)		AJ969950	AJ490162	AJ490162	Slovakia	Šimková et al. (2003, 2006)
Pseudodactylogyrus bini (Kikuchi, 1929)	*Anguilla Anguilla*		AJ969949	AJ490163	AJ490163	Austria	Šimková et al. (2003, 2006)
Pseudohaliotrema Yamaguti, 1953							
Pseudohaliotrema sphincteroporus Yamaguti, 1953	*Siganus doliatus* Guérin-Méneville, 1829-38		AF382058	AJ287568		Australia	Olson and Littlewood (2002)
Pseudorhabdosynochus Yamaguti, 1958							
Pseudorhabdosynochus grouperi (Bu, Leong, Wong, Woo & Foo, 1999)	*Epinephelus coioides* (Hamilton, 1822)		AY553628	AY553618		China	Francová et al. (2017)
Quadriacanthus Paperna, 1961							
Quadriacanthus clariadis Paperna, 1961	*Clarias gariepinus* (Burchell, 1822)		KX685952	KX713994	KX713994	Sudan	Francová et al. (2017)
Quadriacanthus fornicates Francová & Řehulková, 2017	*Clarias gariepinus*		KX685953	KX713995	KX713995	Sudan	Francová et al. (2017)
Quadriacanthus mandibulatus Francová & Řehulková, 2017	*Heterobranchus bidorsalis* Geoffroy Saint-Hilaire, 1809		KX685954	KX713996	KX713996	Sudan	Mendoza-Palmero et al. (2015)
Schilbetrema Paperna & Thurston, 1968							
Schilbetrema sp.	*Pareutropius debauwi* (Boulenger, 1900)	ScPd2	KP056244			West Africa	Mendoza-Palmero et al. (2017)
Sciadicleithrum Kritsky, Thatcher & Boeger, 1989							
Sciadicleithrum bravohollisae Kritsky, Vidal-Martínez & Rodríguez-Canul, 1994	*Vieja fenestrata* (Günther, 1860)	ExC2 3	KY305879			Mexico	Mendoza-Palmero et al. (2017)

Sciadicleithrum meekii Mendoza-Franco, Scholz & Vidal-Martínez, 1997	*Thorichthys meeki* Brind, 1918	ExC10 12	KY305889			Mexico	Mendoza-Palmero et al. (2017)
Scutogyrus Pariselle & Euzet, 1995							
Scutogyrus longicornis (Paperna & Thurston, 1969)	*Oreochromis niloticus*	PC105	HQ010035	HE792800	HE792800	Senegal	Mendlová et al. (2010, 2012)
Scutogyrus vanhovei Pariselle, Bitja Nyom & Bilong Bilong, 2013	*Pelmatolapia mariae* (Boulenger, 1899)	AP385	XXXXXXX			Cameroon	Cruz-Laufer et al. (2021b)
Susanlimocotyle Soares, Domingues & Adriano, 2020							
Susanlimocotyle narina Soares, Domingues & Adriano, 2020	*Sciades herzbergii* (Bloch, 1794)			MW144824	MW179606		Soares et al. (2021)
Tetrancistrum Goto & Kikuchi, 1917							
Tetrancistrum indicum (Paperna, 1972)	*Siganus canaliculatus* (Park, 1797)	Ti6	MN179335	MN179330		Oman	Al Jufaili et al. (2020)
Tetrancistrum labyrinthus Al Jufaili & Palm, 2017	*Siganus canaliculatus*	Tl6	MN179332	MN179334		Oman	Al Jufaili et al. (2020)
Tetrancistrum sp.	*Siganus fuscescens* (Houttuyn, 1782)		AF026114			Australia	Mollaret et al. (1997)
Thaparocleidus Jain, 1952							
Thaparocleidus siluri (Zandt, 1924)	*Silurus glanis* Linnaeus, 1758		AJ969940	AJ490164	AJ490164	Czech Republic	Šimková et al. (2003, 2006)
Thaparocleidus vistulensis (Sivak, 1932)	*Silurus glanis*		AJ969941	AJ490165	AJ490165	Czech Republic	Šimková et al. (2003, 2006)
Thylacicleidus Wheeler & Klassen, 1988							
Thylacicleidus sp.	*Dichotomyctere fluviatilis* (Hamilton, 1822)	Malaysia-AS-2002		AJ490169	AJ490169	Malaysia	Šimková et al. (2003)
Trianchoratus Price & Berry, 1966							
Trianchoratus gussevi Lim, 1986	*Anabas testudieus* (Bloch, 1792)		AY841875			China	Tan et al. (2011)
Trinigyrus Hanek, Molnár & Fernando, 1974							
Trinigyrus anthus Franceschini, Acosta, Zago, Müller & da Silva, 2020	*Hypostomus regani* (Ihering, 1905)		MN947622			Brazil	Franceschini et al. (2020)
Trinigyrus carvalhoi Franceschini, Acosta, Zago, Müller & da Silva, 2020	*Hypostomus ancistroides* (Ihering, 1911)		MN947608			Brazil	Franceschini et al. (2020)

Trinigyrus peregrinus Nitta & Nagasawa, 2016	*Pterygoplychthys ambrosettii* (Holmberg, 1893)		MN944890	Brazil	Franceschini et al. (2020)
Unibarra Suriano & Incorvaia, 1995					
Unibarra paranoplatensis Suriano & Incorvaia, 1995	*Aguarunichthys torosus* Stewart, 1986	UnpaAt1	KP056219	Peru	Mendoza-Palmero et al. (2015)
Unilatus Mizelle & Kritsky, 1967					
Unilatus unilatus Mizelle & Kritsky, 1967	*Pterygoplychthys ambrosettii*	Unilatus unilatus P ambrosettii 5 Jan/15	MF102106	Brazil	Acosta et al. (2017)
Urocleidoides Mizelle & Price, 1964					
Urocleidoides digitabulum Zago, Yamada, De Oliveira Fadel Yamada, Franceschini, Bongiovani & da Silva, 2020	*Leporinus friderici* (Bloch, 1794)	d ACZ-2020	MT556796	Brazil	Zago et al. (2020)
Urocleidoides tenuis Zago, Yamada, De Oliveira Fadel Yamada, Franceschini, Bongiovani & da Silva, 2020	*Apareiodon* sp.	1	MT556797	Brazil	Zago et al. (2020)
Urocleidoides uncinus Zago, Yamada, De Oliveira Fadel Yamada, Franceschini, Bongiovani & da Silva, 2020	*Gymnotus sylvius* Albert & Fernandes-Matioli, 1999	u ACZ-2020	MT556798	Brazil	Zago et al. (2020)
Vancleaveus Kritsky, Thatcher & Boeger, 1986					
Vancleaveus janauacaensis Kritsky, Thatcher & Boeger, 1986	*Pterodoras granulosus* (Valenciennes, 1821)	VajaPg1	KP056247	Peru	Mendoza-Palmero et al. (2015)
Xenoligophoroides Dmitrieva, Sanna, Piras, Garippa & Merella, 2018					
Xenoligophoroides cobitis (Ergens, 1963)	*Gobius cobitis* Pallas, 1814	B9	MG194744	Russia	Dmitrieva et al. (2018)

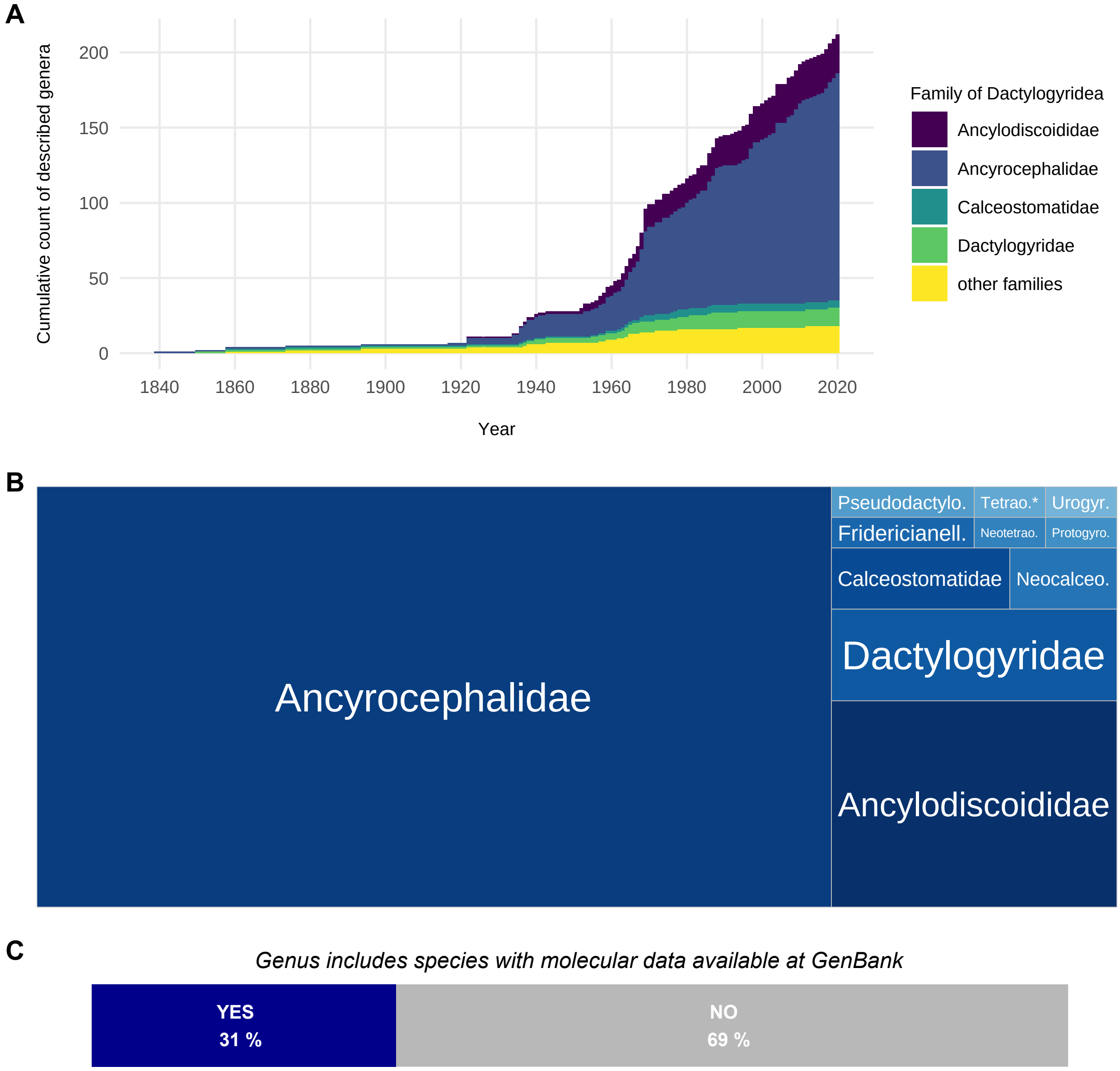

Figure 1. Overview of genera previously included in Dactylogyridea with family affiliations as listed on the WORMS database (Horton et al., 2021): (A) cumulative count of genera described over time, (B) families recognised in WORMS that were previously hypothesised as synonyms of Dactylogyridae with the surface area proportionate to the number of genera, and (C) availability of molecular data in GenBank. Full names of families: Ancylodiscoididae Gusev, 1961, Calceostomatidae Parona & Perugia, 1890, Fridericianellidae Gupta & Sachdeva, 1990, Neocalceostomatidae Lim, 1995, Neotetraonchidae Bravo-Hollis, 1968, Protogyrodactylidae Johnston & Tiegs, 1922, Pseudodactylogyridae Johnston & Tiegs, 1922, Tetraonchidae Monticelli, 1903, Urogyridae Bilong Bilong, Birgi & Euzet, 1994. *Only species of *Ergenstrema* were suggested to form part of Dactylogyridae.

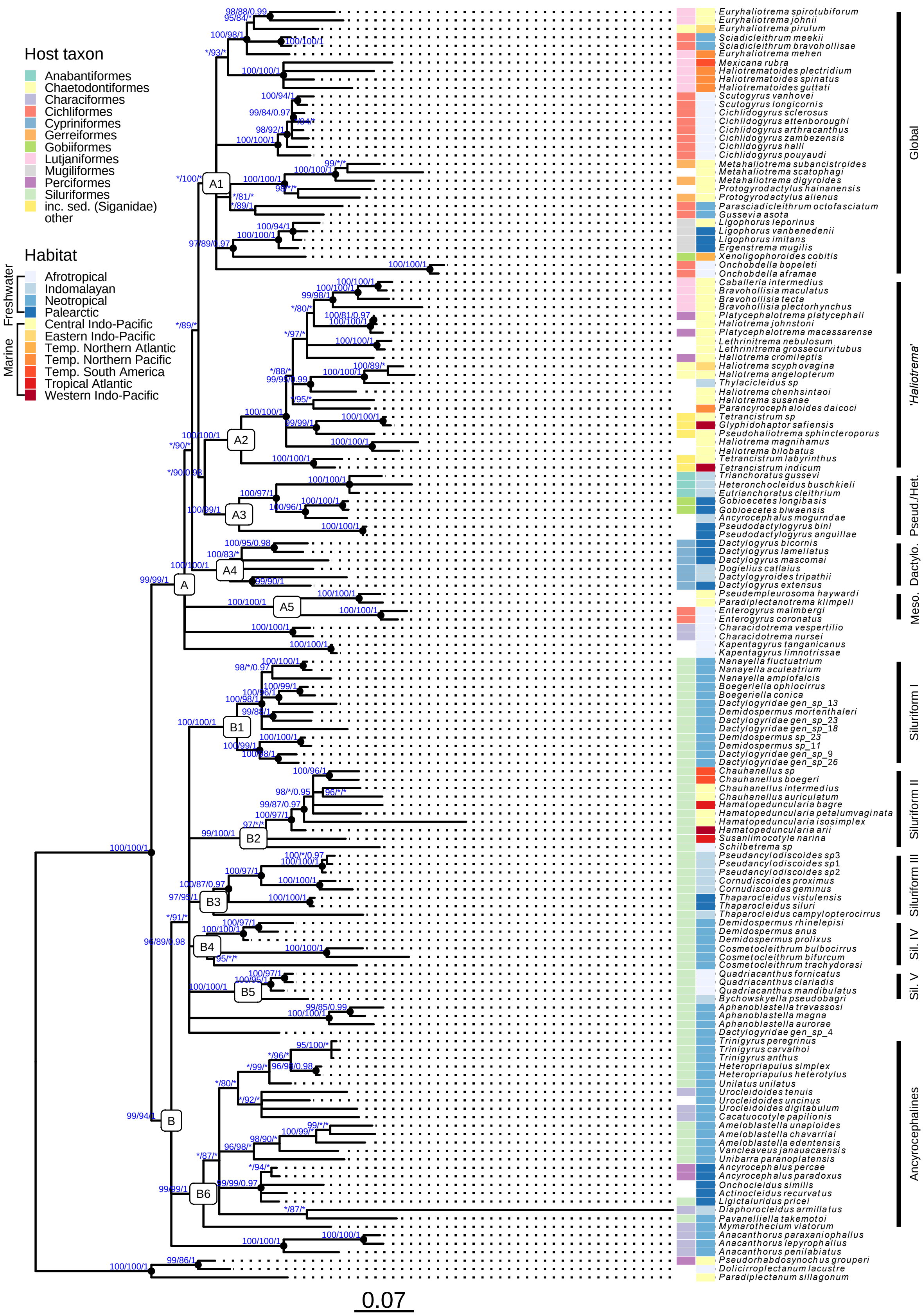

Figure 2. Bayesian inference phylogram of monogenean flatworms belonging to Dactylogyridae (Platyhelminthes: Monogenea). The phylogram was inferred from three nuclear DNA portions (18S, 28S, and ITS rDNA). Node support values include Bayesian posterior probabilities (PP) followed by ultrafast bootstrap

values (UBoost) and Shimodaira-Hasegawa-like approximate likelihood ratios (SH-aLRT) inferred from maximum likelihood estimation; asterisk (*) indicates low support below threshold (PP < 0.95, UBoost < 95, SH-aLRT < 80); black dots indicate internal nodes with strong support across all analyses; highlighted clades indicate monophyletic clades considered strongly supported ([A1–A5], [B1–B6]); heatmaps indicate the order of the infected host species and the biogeographic realm of the sampling location.