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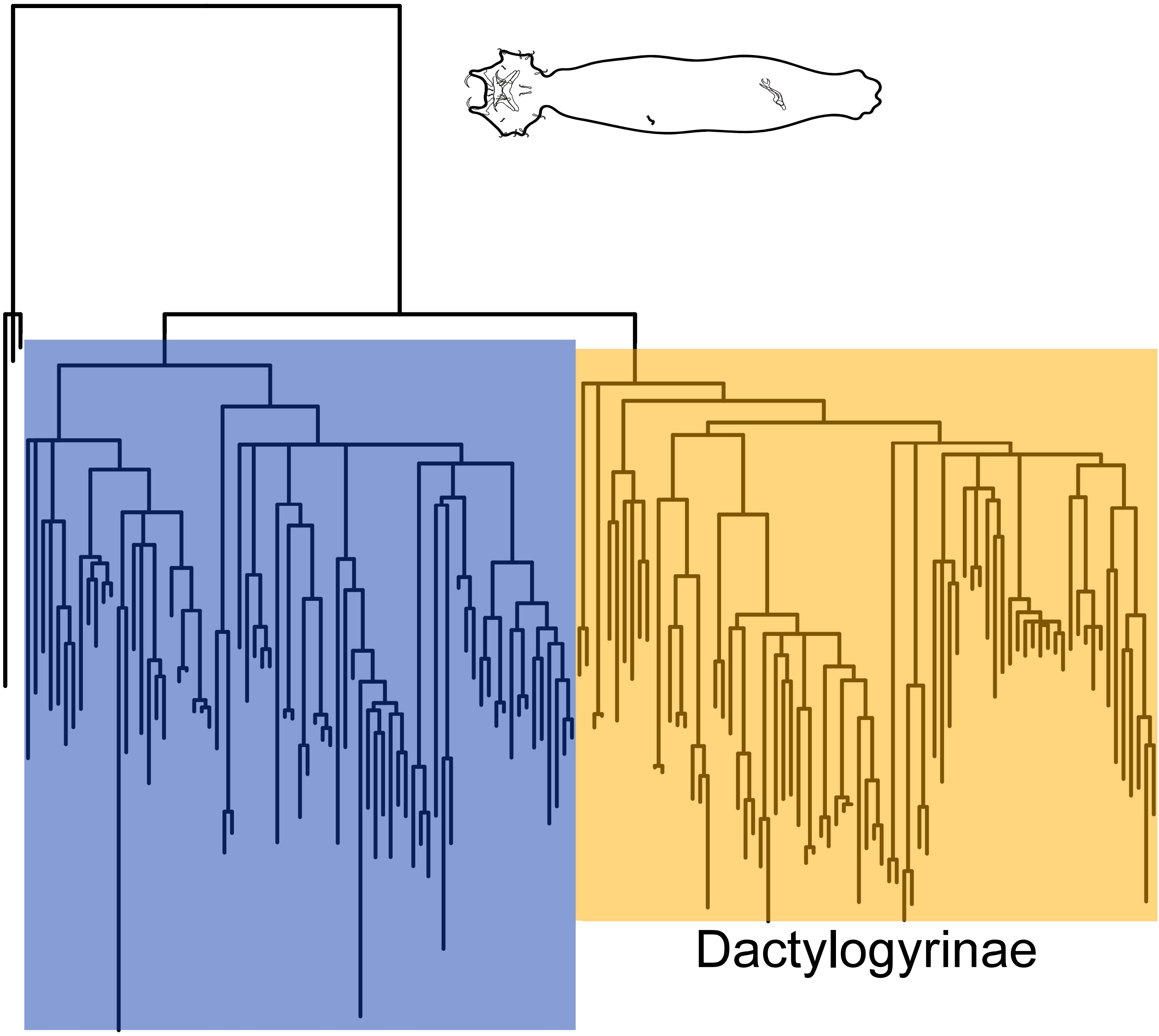
Dactylogyrinae
Ancyrocephalinae

Highlights

- Phylogenetic reconstruction of dactylogyrid monogeneans based on three ribosomal gene portions revealed two well-supported lineages and 16 well-supported clades.

- Re-evaluation of Dactylogyrinae and Ancyrocephalinae.

- Baseline multi-locus alignment to infer the phylogenetic position of new species and genera within Dactylogyridae.

Dactylogyridae 2022: a meta-analysis of phylogenetic studies and generic diagnoses of parasitic flatworms using published genetic and morphological data

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Abstract

Dactylogyridae are one of the most studied families of parasitic flatworms with more than 1000 species and 166 genera described to date including ecto- and endoparasites. Dactylogyrid monogeneans were suggested 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 16 years ago. Here, we provide a meta-analysis of the phylogenetic relationships of Dactylogyridae including representatives of all genera with available molecular data (n=67). First, we investigate the systematic informativeness of morphological characters widely used to diagnose dactylogyrid genera through a parsimony analysis of the characters, character mapping, and phylogenetic comparative methods. Second, we provide an overview of the current state of the systematics of the family and its subfamilies, and summarise potentially poly- and paraphyletic genera. Third, we elaborate on the implications of taxonomic, citation, and confirmation bias in past studies. Fourth, we discuss host range, biogeographical, and freshwater-marine patterns. We found two well-supported macroclades which we assigned to the subfamilies Dactylogyrinae and Ancyrocephalinae. These subfamilies further include 16 well-supported clades with only few synapomorphies that could be deduced from generic diagnoses in the literature. Furthermore, few morphological characters considered systematically informative at the genus level display a strong phylogenetic signal. Yet the parsimony analysis suggests that these characters provide little information on the relationships between genera. We conclude that a strong taxonomic bias and low coverage of DNA sequences and regions limit knowledge on morphological and biogeographical evolutionary patterns that can be inferred from these results. 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 interactions

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) are 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 some are ectoparasitic on the skin (e.g., *Uroleidoides falxus* Zago, Yamada, De Oliveira Fadel Yamada, Franceschini, Bongiovani & da Silva, 2020) or endoparasites. The latter can be found in the urinary system (e.g. species of *Urogyrus* Bilong Bilong, Birgi & Euzet, 1994 and *Acolpenteron* Fischthal & Allison, 1940) (Pariselle and Euzet, 2009; Fayton and Kritsky, 2013), in different regions of the digestive tract (e.g., species of *Enterogyrus* Paperna, 1963, *Paradiplectanotrema* Gerasev, Gayevskaya & Kovaleva, 1987, *Pseudempleurosoma* Yamaguti, 1965) (Luus-Powell et al., 2020) and nasal cavities (e.g., species of *Pavanelliella* and *Susanlimocotyle*) (Kritsky & Mendoza-Franco, 2003; Soares et al., 2021). Representatives of dactylogyrid monogeneans infect a broad range of fish hosts from a number of teleost 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 their hosts. So far, they have been used to study phylogenetic relationships (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 population structure (Kmentová et al., 2020) of the hosts. 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). 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 as a whole by Šimková et al. (2006). Biases in the selection of taxa and molecular markers potentially mask macroevolutionary patterns within dactylogyrids. For instance, phylogenetic relationships 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 the Amazon (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 biases arise 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 comprise 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, 1989; 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

(1989) 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 likely polyphyletic as members of Ancylodiscoidinae appear to be nested in this group (Mendoza-Palmero et al., 2015). The family 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 phylogenetic reconstructions 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 and next-generation sequencing as the initial amount of DNA in these rather 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. Only recently, studies have incorporated mitochondrial DNA regions into macroevolutionary analyses (Zago et al., 2020, 2021; Cruz-Laufer et al., 2021b). These sequences can increase resolution 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 (meta-analysis) to minimise the bias towards certain lineages and geographic regions. To elucidate phylogenetic relationships across evolutionary time scales, we employ a range of ribosomal and mitochondrial markers with different rates of molecular evolution. We further identify dactylogyrid lineages that should be the target of future taxonomic revisions based on the polyphylies and and paraphylies suggested by our analyses, and provide a new baseline multi-gene alignment 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, the internal transcribed spacer 1 (ITS1). The taxon coverage was highest for 28S rDNA but, for some genera, we found only 18S rDNA or ITS1 sequences e.g., *Pavanelliella* Kritsky & Boeger, 1998, *Susanlimocotyle* Soares, Domingues & Adriano, 2020, and *Thylacicleidus* Wheeler & Klassen, 1988. We also assembled an alignment for the mitochondrial gene coding for the cytochrome *c* oxidase subunit I (COI). Sequences of COI mtDNA were only selected for specimens with a corresponding 28S rDNA sequence. However, we excluded the COI sequence of *Urocleidoides tenuis* Zago, Yamada, De Oliveira Fadel Yamada, Franceschini, Bongiovani & da Silva, 2020 (GenBank accession number: MT594475) as this sequence was almost identical to a sequence of *Characithecium parapanemense* Zago, Franceschini, Abdallah, Müller, Azevedo & da Silva, 2021. Despite both sequences being published by some of the same authors the sequence of *U. tenuis* was omitted in the study on *C. paranapanemense* (Zago et al., 2021) unlike those of other species of *Urocleidoides* Mizelle and Price, 1964 letting us doubt its reliability. 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., 2019b; 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 authorities can be found in Table 1.

2.2. Phylogenetic analyses of molecular data

We aligned DNA 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). The 18S rDNA alignment contained sequences that only covered an anterior part of the alignment, i.e., members of *Chauhanellus*, *Cornudiscoides*, *Hamatopeduncularia*, and *Tetrancistrum*, a majority which covered the posterior parts, and some sequences that covered the entirety of the alignment. As, otherwise, *Gblocks* removes the anterior part (results not shown), we opted to split the alignment in two parts allowing us to trim both parts in *Gblocks* separately. We partitioned the DNA sequence data by gene for 28S and ITS1, by the anterior/posterior part for 18S, and by codon for COI 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 subsequent Bayesian Inference (BI) analyses, we only selected models implemented in *MrBayes* v3.2.6 (Ronquist and Huelsenbeck, 2003) (Table 2).

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 sister 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 BI and ML concatenated trees as well as the maximum parsimony tree (see below) using the Congruence Among Distance Matrices (CADM) test (Legendre and Lapointe, 2004; Campbell et al., 2011). We calculated phylogenetic pairwise distance matrices for each tee and to conduct the CADM test on the resulting matrices using the package *ape* v5.3 (Paradis and Schliep, 2019) in *R* v4.1.0 (R Core Team, 2021).

2.3. Ecological and 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 synapomorphies, host repertoire, 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. 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 (see Fig. 1).

2.4. Molecular vs. morphological phylogeny

To infer the systematic informativeness of morphological features mentioned in generic diagnoses, we assessed the congruence and compared the resolution of the phylogenies produced by the molecular and morphological characters (see Table 2). We inferred morphological characters from the respective original and emended generic diagnoses (Supporting Information S1). Character states reported diagnostic for the genus were treated as equivalent to the character state of the species due to the absence of the characters in a majority of species descriptions. Some of the characters were excluded from the analyses such as stable characters (e.g., 'subterminal and midventral' position of mouth are reported for all genera analysed here), characters with no comprehensive definition (e.g., the vitellaria are reported as 'scattered through trunk' or 'coextensive with gut', yet the presence/absence in the region of other reproductive organs being rarely mentioned; the position of the vagina is reported as 'dextroventral and submidventral', 'sinistrally submedian', or 'dextromarginal', characterisations that designed to reflect a range, which are challenging to code as unambiguous discrete characters) or characters being mentioned only in few out of the total number of generic diagnoses included (e.g., the oviduct). We conducted a CADM test (see above) on the molecular and morphological tree topologies estimated under maximum parsimony using *TNT* v1.5 (Goloboff et al., 2008b; Goloboff and Catalano, 2016).

For the parsimony analyses in *TNT*, we used extended implied weighting (Goloboff, 2014) in a range of values for the concavity constant K (20, 21, 23, 26, 30, 35, 41, 48, 56). Unlike in the original implied weighting method (Goloboff, 1993), extended implied weighting avoids weighting characters with missing data artificially high (Goloboff, 2014). We also tested different weighting schemes for the molecular characters as suggested by Mirande (2019). Molecular characters were weighted separately (SEP) like the morphological characters or by the average homoplasy of their partition (BLK) as suggested by Goloboff et al. (2008a). For COI mtDNA sequences, we also weighted characters by their codon position (COD). The final phylogenetic hypotheses were inferred from the parameters (k and weighting scheme) that produced the most stable consensus tree topology. The distortion coefficient and the subtree pruning and regrafting (SPR) distance served as selection criteria by calculating the similarity of all the consensus trees obtained under the different parameter combinations to the other consensus trees (Mirande, 2009). Tree searches involved rounds of tree fusing, sectorial searches, and tree drifting (Goloboff, 1999) under default settings and each round was stopped after three hits of the same optimum. Gaps were treated as missing data. Branch support was estimated through symmetric resampling with a probability of change of 0.33 and values expressed as differences in frequencies (GC: 'Groups present/Contradicted') as bootstrapping and jackknifing have been reported to be distorted by implied weighting methods (Goloboff, 2003).

2.5. Phylogenetic signal of morphological characters and character mapping

We also inferred the phylogenetic expressed by the morphological characters using phylogenetic comparative methods. The characters were fitted to 100 randomly selected tree topologies from the post–burn-in fraction of the Bayesian phylogenetic analysis using a continuous-time Markov model of trait evolution as implemented in the function *fitDiscrete* in the *R* package *geiger* v2.0 (Pennell et al., 2014). As we could make no inference on the transition costs between character states, all characters were modelled with an all-rates-different model (ARD) with a Pagel's λ tree transformation (Pagel, 1999). Model performance was assessed through the sample size–corrected Akaike information criterion (AICc) in comparison to a white noise model that assumes absolute phylogenetic independence (Pennell et al., 2014).

2.6. 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). Character maps were produced with the function *asr_max_parsimony* in the *R* package *castor* (Louca and Doebeli, 2018).

3. Results

3.1. Phylogenetic reconstructions

In total, specimens belonging to 67 dactylogyrid genera were included in this analysis. An overview of all dactylogyridean genera described through time is presented in Fig. 1a. The COI mtDNA alignment included sequences of only 10 genera and was, thus, excluded from all downstream analyses. A more detailed discussion of the COI phylogeny can be found in Supporting Information S2. For the parsimony analysis of the molecular data, the BLK scheme with $k = 23$ (SPR distance: 0.968) and $k = 35$ (distortion coefficient: 0.981) produced the most stable tree topologies and were used to infer the final consensus tree topology. The BI, ML, and MP trees were significantly congruent (Kendall's $W = 0.691$, $\chi^2 = 24115$, $p < 0.01$). Phylogenetic reconstruction revealed the presence of two main lineages (further referred to as macroclades A and B), which comprise ten and six well-supported clades, respectively (clades A1–A10 and B1–B6) (Fig. 2) [node support values: Bayesian posterior probabilities/ultrafast bootstrap values/Shimodaira-Hasegawa-like approximate likelihood ratios/GC values; asterisk (*) indicates low support below threshold (see Fig. 2)]. Both macroclade A (99/98/100/19), which includes clades A1–A10, and macroclade B (99/94/100/*), 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 within macroclade A, the same applies to representatives of *Anacanthorus*, parasites of South American serrasalmids, in macroclade B. Although DNA sequences of these three genera analysed here each form well-supported monophyletic clades, they were not assigned clade numbers as the intrageneric phylogenetic relationships are already discussed elsewhere (Kmentová et al., 2018; Moreira et al., 2019b; Řehulková et al., 2019).

3.2. Morphological, ecological, and biogeographical characterisation of clades

Most of the generic diagnoses analysed here fit the morphological diagnosis of Dactylogyridae *sensu* Bychowsky, 1933. The presence of two pairs of anchors and a single dorsal and ventral bar are considered plesiomorphic in dactylogyrid monogeneans (Kritsky and Boeger, 1989). Yet species of several genera deviating from this ancestral bauplan by displaying a single pair of anchors and bars (*Dactylogyrus*, *Dactylogyroides*, *Dogielius*) or no anchors and bars at all (*Anacanthorus*) form part of the macroclades 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 3. An overview of the host repertoire, biogeography, phylogenetic support, and synapomorphies of all 16 clades in our tree (Fig. 2) is provided in Table 4 (restricted to the dactylogyrid species and lineages included in the phylogeny). The sclerotised parts of the attachment and reproductive organs are considered one of the most systematically informative structures in monogenean taxonomy (Kritsky and Boeger, 1989). A list of the most recent original or emended generic diagnoses is available in Supporting Information S1.

3.3. Systematic informativeness of morphological characters: Parsimony analysis, phylogenetic comparative methods, and character mapping

For the parsimony analysis of the morphological data, k = 30 produced the most stable trees (SPR distance: 0.993, distortion coefficient: 0.972) and was used to compute the consensus tree (Fig. 3). The morphology-based phylogeny showed significant congruence with the molecular MP parsimony tree (Kendall's W = 0.585, $\chi^2 = 12544$, $p < 0.01$) 5(Fig. 3), but few larger clades were supported in the former resulting in a large polytomy including all taxa except for species of *Kapentagyrus* and the outgroup.

A phylogenetic comparative analysis revealed that all morphological characters investigated here expressed a phylogenetic signal when modelled against a randomly selected BI tree distribution (Fig. 4). However, for eight of these characters the difference in model fit compared to the white noise model was comparatively minor (ΔAICc > -20). Characters with the comparatively strongest phylogenetic signal are the number of cephalic lobes, the number of eyespot pairs, the position of the gonads, the number of prostatic reservoirs, the presence/absence of accessory piece, and the number of anchors (Fig. 4). Character maps of these characters are provided in Fig. 5 and Fig. 6 (for the input data matrix, see Table 3).

4. Discussion

This study provides the most extensive phylogenetic meta-analysis of dactylogyrid monogeneans to date. Based on representatives of 67 genera and a combination of three ribosomal gene markers, our phylogenetic reconstruction revealed the presence of two major lineages, macroclades, including ten and six well-supported smaller clades, respectively. In the past, morphological and molecular data have resulted in multiple systematic revisions of species and subfamilies in dactylogyrid monogeneans. Here, we provide an overview of evolutionary patterns, revise Dactylogyridae and its subfamilies, and summarise potential problematic areas at the genus level, i.e. potential polyphylies or paraphylies that call for a systematic revision in the future. Habitat types and host repertoires are illustrated alongside the phylogeny (Fig. 2). Our study also suggests that morphological characters contain little information on the phylogenetic relationships of dactylogyrids above the genus level as illustrated by the polytomy (i.e. low support) for most clades above the genus level (Fig. 3). Finally, we highlight how a 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.

Taxonomic implications: Dactylogyridae and its subfamilies

In the following section, we present a systematic revision of Dactylogyridae and its subfamilies. The clades suggested as the revised subfamilies, are well-supported across phylogenetic analyses (see Fig. 2) providing us with the confidence for the proposed taxonomic revision. However, we limit this revision to the genera of dactylogyrid monogeneans included in the present phylogenetic analyses as the low resolution of the morphology-based phylogeny above the genus level (Fig. 3) provides little confidence for classifying any of the genera without published DNA sequence data in the revised subfamilies. Future studies should further investigate the phylogenetic relationships of species groups and more morphological features should be inferred to help distinguish dactylogyrids belonging to these two proposed subfamilies.

Class Monogenea Bychowsky, 1933

Subclass Monopisthocotylea Bychowsky, 1933

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.

Remarks:

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). Overall, 53 and 30 families were recognised in the most recent systematic revision of Monogenea and Monopisthocotylea by Boeger and Kritsky (2001), respectively. The diagnoses of Ancyrocephalidae Bychowsky, 1937 and Dactylogyridae Bychowsky, 1935, which have been used interchangeably in the past, rely on the difference mainly in the number of seminal vesicles supported by a cladistic study of Bychowsky and Nagibina (1978) and the revision of Malmberg (1990). However, the revision of Kritsky and Boeger (1989) 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 among the macroclades A and B and no other unambiguous morphological differences were identified in this study (see Supporting Information S1; Figs. 5 & 6), we follow the previously suggested synonymisation of Dactylogyridae and Ancyrocephalidae with Dactylogyridae having taxonomic priority.

Our results also confirm that *Protogyrodactylus* Johnston & Tiegs, 1922 is a genus within 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 and are kept in Tetraonchidae as this genus forms a separate lineage as supported by a recent phylogenetic reconstruction 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 (A9) 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 endoparasitic 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 endoparasitic 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 (clades B1–B5), the lineage is included in macroclade B together with clade B6. 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.

Neither representatives of the families Calceostomatidae, Fridericianellidae, Neocalceostomatidae, and Neotetraonchidae nor the subfamilies Linguadactylinae, Linguadactyloidinae, Hareocephalinae, and Heterotesiinae were included in the presented phylogenetic reconstruction due to the absence of published DNA sequence data. Therefore, the status of these taxa remains unresolved (Justine et al., 2002).

Subfamily Dactylogyrinae Bychowsky, 1937

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

Diagnosis (based on diagnoses of genera with available molecular data available): Two or four eye-spots; might be dissociated, incipient, or lacking. Body fusiform, pyriform, or uniform in width; compact or divided in cephalic region with trunk, peduncle, and haptor. Tegument smooth or striated. Two or three pairs of cephalic lobes; sometimes poorly developed. Three 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 the gut or scattered throughout the body. Haptor armed with single or paired dorsal and ventral anchor/bar sclerotised complexes; additional structures with various levels of sclerotisation might be present; 7 pairs of similar or dissimilar marginal hooks. Infecting the gills, skin, pharynx, oesophagus, intestines, urinary bladder, and kidneys of freshwater and marine fishes worldwide.

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:

As mentioned in the result section, the two macroclades found here each include the type genera (*Dactylogyrus* and *Ancyrocephalus*) of two of the previously suggested subfamilies. Therefore, we reassign Ancyrocephalinae and Dactylogyrinae, subfamilies of Dactylogyridae, to these macroclades. 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 Supporting Information S1 and Fig. 3). Given the lack of distinctive features for the subfamily, only genera with molecular data available are included here. Šimková et al. (2006) identified two sister groups within Dactylogyridae *sensu* Kritsky and Boeger (1989). 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 (1989) proposed nine different subfamilies. We identified 16 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., 2019b; Mendoza-Palmero et al., 2020), we report higher support values for the clade of predominantly marine dactylogyrids (A8).

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; *Characithecium* Mendoza-Franco, Reina & Torchin, 2009, *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.

Diagnosis (based on generic diagnoses of genera with available molecular data): Two or four eye-spots; might be dissociated, incipient, or lacking. Body fusiform, pyriform, or uniform in width; compact or divided of cephalic region with trunk, peduncle, and haptor. Tegument smooth. Two or three pairs of cephalic lobes; sometimes poorly developed. Two to four 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 absent. Common genital pore midventral or inconspicuous. 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. 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 marginal hooks. Infecting the gills, skin, or nasal cavities of freshwater and marine fishes worldwide.

Remarks:

As reported above, the two macroclades found here each include a type genus (*Dactylogyrus* and *Ancyrocephalus*) of the two suggested subfamilies. Therefore, we reassign Ancyrocephalinae and Dactylogyrinae to these macroclades as subfamilies of Dactylogyridae as presented by Bychowsky, 1937. 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 Fig. 3, Figs. 5 & 6). Therefore, only genera with molecular data available are included. Anacanthorinae and Ancylodiscoidinae are synonymised with Ancyrocephalinae. Representatives of Anacanthorinae Price, 1968 sequenced to date form a monophyletic group (Moreira et al., 2019b) nested within Ancyrocephalinae as defined here and comprise species of *Anacanthorus* that are unique in lacking anchors and bars. Representatives of Ancylodiscoidinae are also nested within Ancyrocephalinae (see remarks for Dactylogyridae) albeit without representatives of the type genus *Ancylodiscoides* Johnston & Tiegs, 1922 being sequenced so far. Moreover, other genera formerly considered members of Ancylodiscoididae *sensu* Lim et al. (2001) and Anacanthorinae Price, 1968 also likely form also part of this subfamily as suggested by the morphological similarities observed with representatives so far included in phylogenetic analyses. These 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. Ancyrocephalinae Bychowsky, 1937 has served as a catch-all and, consequently, polyphyletic subfamily within Dactylogyridae (Šimková et al., 2003, 2006). Members of ancyrocephaline clades originate in freshwater, coastal, and marine origin, respectively. Moreover, Šimková et al. (2006) found the relationships between marine members of Ancyrocephalinae, Dactylogyrinae, and Pseudodactylogyrinae unresolved. 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., 2019b).

Systematics: problematic points (paraphyletic and polyphyletic genera)

As illustrated by the congruence of the morphology-based phylogeny with the molecular phylogeny, suggest a roughly matching of these two data types. Yet contradictions of character states suggested by generic diagnosis and the morphology of actual species do occur even though the placement of a species in a genus implies that this species displays the features listed in the most recent generic diagnoses. One example is *Demidospermus mortenthaleri*. This species was placed in *Demidospermus* despite a difference in the bar shape (Franceschini et al., 2018) and a difference in the number of eyespots that were reported (Table 3). We also observed a low resolution of the morphology-based phylogeny at higher nodes, which is unlikely the result of occasional mistakes made in generic diagnoses or species classification. Instead, rapid changes in shape and size may render morphological characters systematically uninformative beyond the level of closely related species as suggested for some dactylogyrid taxa before, e.g., *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 erection of several 'waste bucket' genera including *Ancyrocephalus* (Bychowsky and Nagibina, 1970), *Haliotrema* (Klassen, 1994), potentially *Thaparocleidus*, which is rendered paraphyletic by specimens belonging to *Pseudancylodiscoides* (Wu et al., 2008; this study) and *Cornudiscoides* (Fig. 2), and formerly

Demidospermus and *Urocleidoides* (Acosta et al., 2018). Many species formerly considered part of these groups share morphological features but are otherwise unrelated. To address this issue, some studies based generic classification on monophyletic clades inferred from phylogenetic reconstructions (phylogenetic systematics) of ribosomal DNA regions. For instance, *Parasciadicleithrum octofasciatum* Mendoza-Palmero, Blasco-Costa, Hernández-Mena & Pérez-Ponce de León, 2017 is morphologically almost indistinguishable from species of *Sciadicleithrum* (Mendoza-Palmero et al., 2017) but appears to be more closely related to *Gussevia asota* (Fig. 2: Clade A3). However, the type species of *Sciadicleithrum*, *S. uncinatum* Kritsky, Thatcher & Boeger, 1989, has not been sequenced to date. Thus, the phylogenetic position of *P. octofasciatum* in relation to *S. uncinatum* remains unknown and it seems premature to have placed the former in a new genus. A similar approach has also led to the erroneous erection 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 decision as we found partial 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; for an extensive discussion against the use of paraphyletic taxa, see Schmidt-Lebuhn, 2012). 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). In the following section we provide a list of poly- and paraphyletic molecularly characterised dactylogyrid genera, to be revised in future systematic studies, with remarks on their host repertoires and morphological similarities/differences.

Ancyrocephalus Creplin, 1936

The diagnosis of *Ancyrocephalus* has been revalidated by Bychowsky & Nagibina, 1970 to include representatives infecting only percids, namely *A. paradoxus* and *A. percae* (Fig. 2: clade B6). Yet several other species remain classified under this genus. Therefore, the catch-all genus *Ancyrocephalus* has remained polyphyletic with, e.g., *A. mogurndae* being placed among the Dactylogyrinae (clade A9) rather than the Ancyrocephalinae (Fig. 2: clade B6). In the past, this polyphyly has resulted in the proposal of several genera whose members were previously assigned to *Ancyrocephalus* including *Kapentagyrus* (Kmentová et al., 2018), *Ligophorus* (Euzet and Suriano, 1977; Marchiori et al., 2015), and *Xenoligophoroides* (Dmitrieva et al., 2018). 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.

Bravohollisia Bychowsky & Nagibina, 1970 and *Caballeria* Bychowsky & Nagibina, 1970

The genera *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 suggest that some species of *Caballeria* are nested within a clade of species *Bravohollisia* (Wu et al., 2007; Sun et al., 2014), a result confirmed in the present study (Fig. 2). However, the type species of both genera, *C. pedunculata* Bychowsky & Nagibina, 1970 and *B. magna* Bychowsky & Nagibina, 1970 have not been sequenced to date. Future studies should investigate the phylogenetic position of the type species as well as a wider array of species from these genera to untangle the relationship of *Bravohollisia* and *Caballeria*.

Cichlidogyrus Paperna, 1960 and *Scutogyrus* Pariselle & Euzet 1995

Both species of *Scutogyrus* and *Cichlidogyrus* are parasites of cichlids with in the latter genus a few exceptions infecting nothobranchiid and polycentrid hosts (Birgi and Euzet, 1983; Birgi and Lambert, 1986). The well-recognisable morphological difference lies in a fan-shaped plate associated with the ventral bar of species of *Scutogyrus*, missing in species of *Cichlidogyrus* (Pariselle and Euzet, 2009). Phylogenetic studies based on ribosomal and mitochondrial DNA markers (e.g., Caña-Bozada et al., 2021; Cruz-Laufer et al. 2021b) suggest that *Scutogyrus* is indeed monophyletic but also highlight that *Scutogyrus* is nested within *Cichlidogyrus* (clade A4) (Wu et al., 2007; Cruz-Laufer et al. 2021b). The resulting paraphyly of *Cichlidogyrus* could be resolved in several ways: *Cichlidogyrus* is divided into multiple (sub-)genera, e.g., by the clades characterised in Cruz-Laufer et al. (2021b), or *Scutogyrus* could be synonymised with *Cichlidogyrus.* However, due to the limited data included here, we refrain from taking any taxonomic decisions.

Dactylogyrus Diesing, 1850, *Dactylogyroides* Gusev, 1963 and *Dogielius* Bychowsky, 1936

Dogielius encompasses gill parasites of cyprinid fishes that differ from species of *Dactylogyrus* regarding the dorsal position of the anchor-bar complex (as opposed to a ventral position) and the absence of the loop around the intestinal caecum in the vas deferens (as opposed to its presence) (Price and Yurkiewicz, 1968). *Dactylogyroides* encompasses gill parasites of freshwater fishes that differ from *Dactylogyrus* through their paired, barely 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 suggested that *Dactylogyrus* is monophyletic (Šimková et al., 2003, 2006). Previous studies involving *Dactylogyroides* failed to resolve its phylogenetic position 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*. Our phylogenetic analyses indicate that species of *Dactylogyroides* together with those of *Dactylogyrus* and *Dogielius* form a monophyletic group (clade A10) of dactylogyrids with a single pair of anchors. However, *Dactylogyrus*, the most species-rich genus of monogeneans (Horton et al., 2021), is rendered paraphyletic by the representatives of *Dogielius* and *Dactylogyroides* sequenced to date (Fig. 2). We suggest that this observation calls for a deeper investigation of these closely related genera. The type species of *Dogielius*, *D. forceps* Bychowsky, 1936, should also be included in future studies alongside a wider array of species of *Dactylogyroides*, *Dactylogyrus*, and *Dogielius* to reconsider the current classification system of this species group.

Demidospermus Suriano, 1983

Species of *Demidospermus* alongside representatives of *Cosmetocleithrum* form a well-supported lineage (Fig. 2: clade B2). Our phylogenetic analysis shows that several specimens assigned to *Demidospermus* fall into separate lineages together with two other unassigned dactylogyrid specimens (Fig. 2: clade B1). These specimens should however not be considered members of *Demidospermus* as the type species falls within a separate clade (Fig. 2: clade B2). Moreover, *D. mortenthaleri* is situated within another dactylogyrid lineage suggesting that this species was either wrongly assigned to this genus or *Demidospermus*, as currently defined, is polyphyletic. These instances call for further systematic revisions 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 and *Chauhanellus* Bychowsky & Nagibina, 1968

Hamatopeduncularia sensu Lim (1996) encompasses gill parasites of ariid fishes with haptoral digitations. Although closely related to *Hamatopeduncularia,* species of *Chauhanellus*, also 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 protuberances 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 representatives 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. Moreover, phylogenetic analyses suggested that species of *Chauhanellus* sequenced so far are nested in a clade of species of *Hamatopeduncularia* (Soo and Tan, 2021; in this study Fig. 2: clade B3). The ambiguous delineation of the two genera and the close phylogenetic relationship of these species call for a thorough taxonomic revision in the future encompassing a wider array of species and also including the type species of *Chauhanellus* (*Chauhanellus oculatus* Bychowsky & Nagibina, 1968).

Platycephalotrema Kritsky & Nitta, 2019

In the present study, species of *Haliotrema* are placed in a well-supported lineages of clade A8 (‘*Haliotrema’* group) which also includes *Bravohollisia, Glyphidohaptor, Lethrinitrema,* *Parancyrocephaloides, Pseudohaliotrema, Tetrancistrum*, and *Thylacicleidus* (Fig. 2: clade A8). 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 *Ancyrocephalus* and *Haliotrema* might belong to this group. Yet recent phylogenetic studies show that the used host classification is outdated: Platycephalidae Gill, 1872 is now classified in the suborder Platycephaloidei within Perciformes (Betancur-R et al., 2017). Kritsky and Nitta (2019) did also not discuss phylogenetic relationships of the group despite the availability of molecular data for two species of *Platycephalotrema*, *P. macassarense* and *P. platycephali* (both described under *Haliotrema*) (Wu et al., 2006; Sun et al., 2014). Therefore, they did not note that *Haliotrema johnstoni* is closely related to or even nested in *Platycephalotrema* as it appears 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 the accessory piece in the male copulatory organ and has a different host repertoire (Syngnathiformes, Mullidae). The relationship of *H. johnstoni* with members of *Platycephalotrema* should be investigated further.

Sciadicleithrum Kritsky, Thatcher & Boeger, 1989 and *Euryhaliotrema* Kritsky & Boeger, 2002

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. It was proposed to be closely related to species of *Gussevia*, which also infect Neotropical cichlids, but differ regarding an unmodified hook pair 5, a ventral bar with anterior umbelliform membranes or cavities and unmodified anchors (Kritsky et al., 1989). Species of *Euryhaliotrema* and *Sciadicleithrum* have never been compared morphologically, most likely because their distinct host repertoires (cichlids vs. other fishes) and habitats (most species of *Sciadicleithrum* are limnic whereas a majority of species of *Euryhaliotrema* are marine). However, morphological comparison based on generic diagnoses reflects close morphological similarities with the main difference being the presence of membranes on the ventral bar in species of *Sciadicleithrum* with no such structure described in species of *Euryhaliotrema*. 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: clade A5). The most detailed study to date (Mendoza-Palmero et al., 2017) suggests that *Sciadicleithrum* is a monophyletic lineage but nested in *Euryhaliotrema* and renders it paraphyletic (Fig. 2: clade A5), similar to the situation of the *Scutogyrus*-*Cichlidogyrus* lineage. Yet only a fraction of species of *Euryhaliotrema* and *Sciadicleithrum* have been sequenced so far, among them the type species *E. chaoi* Kritsky & Boeger, 2002 and *S. uncinatum* Kritsky, Thatcher & Boeger, 1989. Future phylogenetic studies should aim for an increased coverage of species and DNA regions to resolve the relationship of these species.

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

Our phylogenetic study suggests that *Pseudancylodiscoides* and *Cornudiscoides* are nested in *Thaparocleidus* (Fig. 2: clade B4). *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 length of respective marginal hook pairs can differ substantially between congeners, e.g., in species of *Cichlidogyrus* (Cruz-Laufer et al., 2021b). Yet only few species of *Cornudiscoides* and *Pseudancylodiscoides* have been sequenced to date in comparison to the total number of species, the sequences available from *Pseudancylodiscoides* (Wu et al., 2008) were never attributed to any particular species, and only a fragment of the 18S rDNA gene has been sequenced to date for the type species of *Cornudiscoides* and

Thaparocleidus, *C. heterotylus*, and *T. wallagonius,* respectively. Thus, we refrain from any nomenclatural acts.

Environment and biogeography

Monogenean evolution is often considered to reflect a co-divergence with the host lineages (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). Environmental factors affect endo- and ectoparasites differently (Pariselle et al., 2011). Endoparasites are more likely shielded from environmental changes although the egg/larval development might partly occur in an external environment (Theisen et al., 2018; Assane et al., 2021). Notably, the phylogenetic tree presented here (Fig. 2) suggests a common ancestor for all endoparasitic dactylogyrid species sequenced to date. In contrast, ectoparasites are directly exposed to external stressors. Sudden changes in salinity are deadly to many gill monogeneans and hence, are used to treat these infections in aquaculture (Fajer-Ávila et al., 2007; Schelkle et al., 2011; Brazenor and Hutson, 2015). This effect might explain why closely related ectoparasitic dactylogyrids appear often exclusive to either freshwater or marine habitats (see Fig. 2). However, interpretations of these patterns should be treated with caution as these observations are based on ribosomal genes and few species and genera only.

Despite these limitations, early evidence from previous studies indicates at least a partial adherence to freshwater and marine habitats in dactylogyrid species infecting catfishes (Siluriformes). Catfishes constitute approximately 30% part of the world's ichthyofauna in terms of species richness (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; Van Steenberge et al., 2020). Several phylogenetic studies have focused on the evolutionary history of the Neotropical dactylogyrid lineages infecting siluriform hosts. Our study suggests that all molecularly characterised dactylogyrid monogenean genera infecting catfishes belong to a single lineage (macroclade B) with two clades (Fig. 2: B1, B2, and B4) specific to New World hosts and two others to Old World species (Fig. 2: B3 and B5). This pattern appears to indicate that dactylogyrid monogeneans have followed their hosts' evolution to spread to all continents before the time Pangaea separated 200 million years ago remaining in freshwater habitats except for a single mostly marine dactylogyrid lineage (Fig. 2: clade B3). However, as many lineages and species infecting siluriform hosts have not been sequenced to date, the pattern found here might also be an artifact of a boom of studies investigating certain taxa among these parasites (e.g., Wu et al., 2008; Mendoza-Palmero et al., 2015, 2019; Francová et al., 2017; Acosta et al., 2017, 2018; Franceschini et al. 2018, 2020; Soo and Tan, 2021).

Another example for possible adherence to freshwater habitats, are the species infecting the gills of cichlid fishes. All species (that have been sequenced) belong to macroclade (A) 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, 2019; Matschiner et al., 2020). Dactylogyrid gill parasites on Neotropical and African cichlids that we know of constitute four different lineages that are not closely related including *Cichlidogyrus-Scutogyrus, Gussevia-Parasciadicleithrum, Onchobdella,* and *Sciadicleithrum* (Fig. 2). Based on these lineages, previous studies hypothesised that cichlids must have crossed marine habitats (Pariselle et al., 2011; Vanhove et al., 2016) enabling multiple dactylogyrid freshwater lineages (*Insulacleidus* spp. in Madagascar, or *Onchobdella* or *Cichlidogyrus* in Africa, and *Gussevia, Sciadicleithrum* or *Parasciadicleithrum* in South America) to infect cichlids. Transatlantic dispersal of cichlids has since then been further discussed in 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 endoparasitic dactylogyrids infecting Neotropical cichlids would allow to evaluate whether endoparasitic lineages, indeed, persisted after an alleged transatlantic dispersal in contrast to ectoparasitic dactylogyrids.

We also revealed multiple potential marine-freshwater switches within Dactylogyridae based on the limited selection of DNA sequence data included here. Several species of *Sciadicleithrum* form a freshwater lineage which appears closely related to a group of mostly marine representatives of *Euryhaliotrema* (Fig. 2: clade A5), a sequence of *Thylacicleidus* sp. represents the only freshwater lineage in the respective clade (Fig. 2: clade A8), and in macroclade B species of *Chauhanellus* and *Hamatopeduncularia* are the only marine representatives but, nonetheless, are still parasites of catfish hosts as most other species in this group. The number of possible marine-freshwater switches reported, indicates that these events might be a major factor in the evolution of teleost-dactylogyrid interactions.

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 formerly and presently 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 (e.g., Mendoza-Palmero et al., 2015) has produced many DNA sequence data of species belonging to Ancyrocephalinae (macroclade B), which now appears almost exclusive to siluriforms. Few studies have focused on other host groups such as cichliforms (Mendoza-Garfias et al., 2017), characiforms (Zago et al., 2018, 2020, 2021; Moreira et al., 2019b), and gymnotiforms (Zago et al., 2020) limiting the availability of molecular data from possibly related genera. In fact, molecular data of many parasite lineages remain unavailable (Poulin et al., 2019) and many species remain likely undiscovered (Jorge and Poulin, 2018), e.g., purely morphological studies on Neotropical host taxa described new genera on non-siluriform teleosts such as cichliforms, characiforms, and perciforms (Boeger et al., 2014; Morey et al., 2019; Cruces et al., 2020, 2021; de Oliveira et al., 2021). Apparent morphological and biogeographical patterns correlating with phylogenetic relationships might also be affected by discussed bias. For instance, species of clade A1 appear to be mostly restricted to the Indo-Pacific region, species of clade A10 to the Palaeartic and Indo-Malayan realms, and species of clade B1 and B2 to the Neotropics. Yet molecular data of dactylogyrine lineages are biased towards the Northern hemisphere, yet 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 some DNA sequences used in less prestigious studies are less likely to be included in follow-up studies (see examples discussed below) leading to the omission of relevant molecular data published in journals with lower impact factors. This pattern mirrors the citation biases observed in other fields such as behavioural biology (see, Taborsky, 2009). Promotion on social media might address this shortfall but can likely not fully compensate for 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 (clade A8). Sequences of heteronchocleidine (Tan et al., 2011) and endoparasitic (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 of 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 taxon sampling could be a level playing field for multiple sequence alignments as provided by the present study. Our phylogeny presents by no means a comprehensive or definite phylogenetic tree of Dactylogyridae as we included only a subset of all DNA sequences available on Genbank deemed representative of the main lineages within a genus. A majority of species and type species of genera have also not been sequenced to date, and new species are discovered every year. Furthermore, we cannot rule out that some DNA sequences were wrongly assigned. Our study also highlights several groups and studies that have previously been overlooked by phylogenetic analysis. We also point out general trends regarding the phylogenetic relationships that should be investigated in more detail in the future. Thus, we suggest that the DNA sequence alignments of ribosomal (Fig. 2) and mitochondrial (Supplementary Information S2) DNA regions we provide here could form a new starting point for studies aiming to infer the phylogenetic position of new species and genera within Dactylogyridae.

Concluding remarks

A phylogenetic reconstruction (meta-analysis) 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 endoparasitic species was reported as well as three well-supported clades infecting siluriform hosts. In cases of paraphyly and polyphyly suggested by our phylogenetic analyses, we discuss the morphological characters and propose steps for a systematic revision. 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 state-of-the-art phylogenetic trees. 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. Specimen data for DNA sequences used for phylogenetic reconstruction of Dactylogyridae including host species, GenBank accession numbers, locality by country, and reference.

Genera and species	Host	Isolate/Voucher	28S rDNA	18S rDNA	ITS1	COI mtDNA	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/ PR214a1[a]	MH843718			MK757436	Brazil	Moreira et al. (2019a, 2019b)
Anacanthorus paraxaniophallus Moreira, Carneiro, Ruz & Luque, 2019	*Serrasalmus marginatus* Valenciennes, 1837	PR50/ PR105b2[a]	MH843717			MK757438	Brazil	Moreira et al. (2019a, 2019b)
Anacanthorus penilabiatus Boeger, Husak & Martins, 1995	*Piaractus mesopotamicus* (Holmberg, 1887)	PR05/ PR228a3[a]	MH843719			MK757435	Brazil	Moreira et al. (2019a, 2019b)
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)

Characithecium Mendoza-Franco, Reina & Torchin, 2009								
Characithecium paranpanemense Zago, Franceschini, Abdallah, Müller, Azevedo & da Silva, 2021	*Psalidodon paranae* (Eigenmann, 1914)	2	MZ408902			MZ408251	Brazil	Zago et al. (2021)
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	MG970255	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	MW580361	MW580384	MW580384		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)
Cosmetocleithrum trachydorasi (Acosta, Scholz, Blasco-Costa, Alves & da Silva, 2017)	*Trachydoras paraguayensis* (Eigenmann & Ward, 1907)		MG001323				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 Suriano, 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 magnus Zago, Franceschini, Abdallah, Müller, Azevedo & da Silva, 2021	*Astyanax lacustris* (Lütgen, 1875)	1	MZ408903			MZ408253	Brazil	Zago et al. (2021)
Diaphorocleidus neotropicalis Zago, Franceschini, Abdallah, Müller, Azevedo & da Silva, 2021	*Astyanax lacustris* (Lütgen, 1875)	1	MZ408906			MZ408254	Brazil	Zago et al. (2021)
Dogielius Bychowsky, 1936								
Dogielius catlaius (Jain, 1962)	*Labeo rohita (*Hamilton, 1822)		KC687091				India	Dash et al. (2014)
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			MN095193	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 guttati (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. (2015)
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	MK598084	Dem. Rep. of the Congo	Kmentová et al. (2018, 2020b)
Kapentagyrus tanganicanus Kmentová, Gelnar & Vanhove 2018	*Stolothrissa tanganicae* Regan, 1907	LI8	MH071783	MH071807	MH071807	MK598180	Dem. Rep. of the Congo	Kmentová et al. (2018, 2020b)
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 auratus* (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. (2019b)
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)
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)
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 sp. 1	*Pseudobagrus fulvidraco* (Richardson, 1846)	HSY1	EF100542	EF100564			China	Wu et al. (2008)
Pseudancylodiscoides sp. 2	*Pseudobagrus fulvidraco*	HSY3	EF100543	EF100565			China	Wu et al. (2008)
Pseudancylodiscoides sp. 3	*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)
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	MT447060[b]	Senegal	Mendlová et al. (2010, 2012); Caña-Bozada et al. 2021
Scutogyrus vanhovei Pariselle, Bitja Nyom & Bilong Bilong, 2013	*Pelmatolapia mariae* (Boulenger, 1899)	AP385	MW580366				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			MN916719	Brazil	Franceschini et al. (2020)
Trinigyrus carvalhoi Franceschini, Acosta, Zago, Müller & da Silva, 2020	*Hypostomus ancistroides* (Ihering, 1911)		MN947608			MN922321	Brazil	Franceschini et al. (2020)
Trinigyrus peregrinus Nitta & Nagasawa, 2016	*Pterygoplychthys ambrosettii* (Holmberg, 1893)		MN944890			MN913212	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			MT594400	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			MT594473	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)
Outgroup: Diplectanidae Monticelli, 1903								
Dolicirroplectanum lacustre Kmentová, Gelnar & Vanhove, 2021	*Lates niloticus* (Linnaeus, 1758)	LN1	MK937579	MK937576	MK937576	MK908186	Uganda	Kmentová et al. (2021)
Paradiplectanum sillagonum (Tripathi, 1959)	*Sillago sihama* (Forsskål, 1775)		AY553626	AY553617			China	Wu et al. (2005)
Pseudorhabdosynochus grouperi (Bu, Leong, Wong, Woo & Foo, 1999)	*Epinephelus coioides* (Hamilton, 1822)		AY553628	AY553618			China	Francová et al. (2017)

[a] 28S and COI sequences with different isolate numbers but same author list, [b] authors report 100% similarity of 28S sequence with sequence published by Mendlová et al. (2010).

Table 2. 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	641	GTR + F + I + Γ4	GTR + F + R6
18S rDNA: part 1 + part 2	1320 + 496	SYM + I + Γ4	TIM3e + R3
ITS1 rDNA	238	GTR + F + Γ4	TVM + F + R2
COI mtDNA: 1st codon	828/3	GTR + F + I + Γ4	TN + F + Γ4
COI mtDNA: 2nd codon	828/3	GTR + F + Γ4	GTR + F + Γ4
COI mtDNA: 3rd codon	828/3	HKY + F + I + Γ4	HKY + F + R3

Table 3. List of morphological character states for each genus and reference of generic diagnoses used to infer these character states.

Genus (diagnosis reference)	Clade (Fig. 2)	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14	C15	C16	C17	C18	C19	C20	C21	C22
Metahaliotrema (Kritsky et al., 2016)	A1	a	c	c	c	b	a		b	a	a	a	b	a	a	b	a	b	d	a	b	b	a
Protogyrodactylus (Galli and Kritsky, 2008)	A1	a	d	c	d	d	a	b	a	a	b	a		a	a	a	a	b	d	a	b	b	a
Parasciadicleithrum (Mendoza-Palmero et al., 2017)	A2	a	d		c	b	a	b		a		a	a	a	a	a	a	a	d	a		b	a
Gussevia (Kritsky et al., 1986)	A2	a			c		a	b	a	a	d	a	a	a	a	b	a	b	d	b		b	a
Ligophorus (Sarabeev et al., 2013)	A3	a	d	c	c		a	c	b	a		a		a	a	b	a	a	d	b	b	b	a
Xenoligophoroides (Dmitrieva et al., 2018)	A3	a	d		c		a	c	b	a	c	a	b	a	a	b	a	a	d	b	b	b	a
Ergenstrema (Paperna, 1964)	A3	a			c			d	b	a		a		a	b		a	a	d	b		b	a
Cichlidogyrus (Paperna, 1960; Pariselle and Euzet, 2009)	A4				c		a	b	b	a	b	a	b	b	a	a	a	b	d	b	b	b	a
Scutogyrus (Pariselle and Euzet, 2009)	A4				c		a	b	b	a	b	a	b	b	a	a	a	a	d	b	b	b	a
Euryhaliotrema (Kritsky, 2012)	A5	a	c	c	d	b	a	c	a	a	e	c	b	a	a	b	a	b	d	b	b	b	a
Sciadicleithrum (Kritsky et al., 1989)	A5	a	d	c	c	c	a	b	a	a	e	a		a	a	a	a	a	d	b	b	b	a
Haliotrematoides (Kritsky et al., 2009)	A6	a	c	c	c	b	a		a	a	b	b	b	a	a	b	a	a	d		b	b	a
Mexicana (Luque et al., 1992)	A6	a	c	a	c		a	b	b	a	b	b	b	a	a	b	a	a	d		b	b	a
Pseudempleurosoma (Yamaguti, 1965)	A7				c		a	a		a		b	b	b	a	b	a	a	d	b	a	b	a
Paradiplectanotrema (Theisen et al., 2018)	A7				c		a	a		a	b	a	b	a	a	b	a	a	d	b	a	b	a
Enterogyrus (Pariselle and Euzet, 2009)	A7	b			c		a	a	a	a	b	a	b	a	b		a	b	d	b	b	b	a
Onchobdella (Paperna, 1968)	A8	a	a		d		a	a			c	a	b	b	a	b	a	a	d	b		b	a
Caballeria (Lim, 1995)	A8	a			c		a	a	a	b	b	b		a	a	b	a	b	d	a		b	a
Bravohollisia (Lim, 1995)	A8	b			c		a	a	a	b	b	b		a	a	b	a	b	d	a		b	a
Platycephalotrema (Kritsky and Nitta, 2019)	A8	a	d	c	c	b	a	a	a	a	c	b	b	a	a	a	a	b	d	b	b	b	a
Lethrinitrema (Lim and Justine, 2011)	A8				c	b	a	a	a	a	c	c		a	a	b	a	b	d	a		b	a
Haliotrema (Adapted form Young, 1968)	A8				c		a	a	a	a	b	c		a	a	b	a	a	d	b		b	a
Thylacicleidus (Wheeler and Klassen, 1988)	A8	b	a		c		a	a				a		b	a	b	a	b	d	a		b	a
Parancyrocephaloides (Ogawa and Itoh, 2017)	A8				c		a	a	a	a	c	b	b	a	a	a	a	b	d	a		b	a
Tetrancistrum (Kritsky et al., 2007a)	A8	a	d	b	a	b	a	a		a	c	a	b	a	a	b	a	b	d	b		b	a
Glyphidohaptor (Kritsky et al., 2007b)	A8	a	d	c	a	b	a	a		a	c	a	b	a	a	b	a	a	d	b	b	b	a
Pseudohaliotrema (Kritsky and Galli, 2007)	A8	a	d	b	a	b	a	a	b	a	c	a	b	a	a	b	a	b	d	b	b	b	a
Gobioecetes (Ogawa and Itoh, 2017)	A9	a	a		c	b	a	a	a	a	c	a	b	a	b		a	b	d	a		b	a
Heteronchocleidus (Bychowsky, 1957)	A9				c		a	a				a			a	b	a	b	c	b		b	a
Eutrianchoratus (Paperna, 1969)	A9				c		a	a			c	a		a	a	b	b		c	b		b	a

Trianchoratus (Price and Berry, 1966)	A9	a	a		c	e	a	a		a	b	a	b		b		b		c	b	b	b	a
Pseudodactylogyrus (Ogawa et al., 2015)	A9				c	b	a	a	a	a	b	a		a	a	a	a	a	b	a	b	b	a
Dactylogyrus (Rogers, 1967)	A10	a			c		a		a	a	c	a	b		a	b			b	b	b	b	a
Dogielius (Price and Yurkiewics, 1968)	A10				c		a	c	b	a	c	a		a	b		a	b	b	b		b	a
Dactylogyroides (Gussev, 1963)	A10		d				a					a		a	a	a	a	b	b	a		b	a
Characidotrema (Kritsky et al., 1987)	A	a	b		c		a	b	a	a	b	a		a	a	b	a	a	d	b	b	b	a
Kapentagyrus (Kmentova et al., 2018)	A				c		b	a	b	a	b	a		b	a	b	a	b	d	b	b	b	a
Nanayella (Acosta et al., 2019)	B1	a			a		a	a	a	a		a	b		a	b	a	b	d	b	b	b	a
Boegeriella (Mendoza-Palmero et al., 2019)	B1	a	d	c	a	a	a	a	a	a	b	a	b		a	a	a	a	d	b	b	b	a
Demidospermus (Kritsky & Gutiérrez, 1998)	B2	a	d		b		a	a	a	a		a	b	b	a	b	a	b	d	b		b	a
Cosmetocleithrum (Kritsky et al., 1986)	B2	a			a		a	a	a	a	b	a	b	a	a	a	a	b	d	b	b	b	a
Chauhanellus (Lim, 1994)	B3				c	b	b	a	a	a		a	b	b	a		a		d	a		b	a
Hamatopeduncularia (Lim, 1996)	B3				c		b		a	a		c	b		a		a		d	b		b	a
Susanlimocotyle (Soares et al., 2021)	B3	a			c		a		a	a	b	a	a	a	a	a	a	b	d		b	b	a
Schilbetrema (Kritsky and Kulo, 1992)	B3	a	d	c	c		a	b	a	a	b	a	a		a	a	a	a	d	a		b	a
Pseudancylodiscoides (Lim et al., 2001)	B4				c		a			a		a		a	a	b	a	a	d	a		b	a
Cornudiscoides (Lim et al., 2001)	B4				c		a			a	c	a			a	b	a	a	d	a		b	a
Thaparocleidus (Lim et al., 2001; Lim, 1996)	B4				c	b	a		a	a		a	a	b	a	b	a	a	d	a		b	a
Quadriacanthus (Kritsky and Kulo, 1988)	B5	a	d	c		c	a	b	a	a	c	a	a		a	a	a	a	d	a		b	a
Bychowskyella (Lim et al., 2001)	B5				c		a			b		a		b	a	b	a	a	d	a		b	a
Aphanoblastella (Kritsky et al., 2000)	B	a	d	c	a	b	a	a	a	a		a	c	a	a	b	a	a	d	b	b	b	a
Anacanthorus (Kritsky et al., 1992)	B	a	e	c			a	c	a	a		c	c		b		b		a		b	b	a
Trinigyrus (Franceschini et al., 2020)	B6	a			a		a	b	a	a	c	a	a	a	b		a	b	b		b	b	a
Heteropriapulus (Acosta et al., 2017)	B6	a	d	c		b	a	b	a	a	c	a	a	a	a		a	b	d	b	b	b	a
Unilatus (Mizelle and Kritsky, 1967)	B6	a	d	c	a		a			a	e	a	c	a	a	b	a	b	d	b		b	a
Ameloblastella (Kritsky et al., 2000)	B6	a	d	c	a	b	a	b	a	a		a	a	a	a	b	a	a	d	b	b	b	a
Unibarra (Suriano and Incorvaia, 1995)	B6	a			a		a	b	a	a	c	a		a	b		a	b	d	b	b	b	a
Vancleaveus (Kritsky et al., 1986)	B6	a					a	b	a	a	b	a	a		a	b	a	b	d	a	b	b	a
Ancyrocephalus (Bychowsky and Nagibina, 1970)	B6						b		a	a	b	a	a	a	a	b	a	b	d	b	b	b	a
Onchocleidus (Wheeler and Beverley-Burton, 1989)	B6				c				a	a		a			a	b	a	b	d	b		b	a
Ligictaluridus (Beverley-Burton, 1984)	B6				c		a		a	a		a	b	b	a	b	a	b	d	b		b	a
Actinocleidus (Beverley-Burton, 1981)	B6				c	b	a		a	a		a	b	b	a	b	a	b	d	b		b	a
Urocleidoides (Zago et al., 2020)	B6	a					a	c	a	a		a		b	a		a		d	b	b	b	a
Cacatuocotyle (Boeger et al., 1997)	B6	a					a	a	a	a	b	a	b		b		a	b	d	b	b	b	a

Mymarothecium (Kritsky et al., 1996)	B6	a	d	c	c		a	b	a	a	c	a	a	a	a	b	a	a	d	b	b	b	a
Diaphorocleidus (Jogunoori et al., 2004)	B6	a	e	c	c	b	a	b	a		b	a	a	a	a	b	a	b	d	b	b	b	a
Pavanelliella (Kritsky and Mendoza-Franco, 2003)	B6	a			c	c	a	b	a	a	b	a		a	b		b		a		b	b	a
Characithecium (Mendoza-Franco et al., 2009)	B6	a	d	c	c	b	a	b	a	a	b	a	b	a	a	b	a	b	d	b	b	b	a
Pseudorhabdosynochus (Neifar and Euzet, 2007)	outgroup	c			c	b	b		b	a	b	b		a	a	a	a	b	d	b		c	b
Dolicirroplectanum (Kmentová et al., 2021)	outgroup	a			c		b		b	a	b	b		a	a	a	a	b	d	b		a	b
Paradiplectanum (Dominguez and Boeger, 2008)	outgroup	a			c		b			a	b	a		a	a	a	a	b	d	b		a	b

C1: Tegument - smooth (a), striated (b) or smooth/striated (c); C2: Number of cephalic lobes - 0 (a), 2 (b), 3 (c), 4 (d) or 5 (e); C3: Position of cephalic lobes: terminal (a), subterminal/bilateral (b) or terminal/bilateral (c); C4: Number of eyespot pairs - 0 (a), 1 (b), 2 (c) or 1/2 (d); C5: Number of head organ pairs - 2 (a), 3 (b), 4 (c), 3/4 (d) or 3/4/5 (e); C6: Intestinal caeca - confluent (a) or nonconfluent (b); C7: Mutual position of gonads - tandem (a), overlapping (b), tandem/overlapping (c) or beside (d); C8: Position of vas deferens - looping (a) or not looping left intestinal caecum (b); C9: Number of seminal vesicles: 1 (a) or 2 (b); C10: Number of prostatic reservoirs - 0 (a), 1 (b), 2 (c), 0/2 (d) or 1/2 (e); C11: Accessory piece: present (a), absent (b) or present/absent (c); C12: Position of testis - preovarian (a), postovarian (b) or beside (c); C13: Comparative size of hooks - similar (a) or dissimilar (b); C14: Dorsal bar - present (a) or absent (b); C15: Dorsal bar - modified (a) or unmodified (b); C16: Ventral bar - present (a) or absent (b); C17: Ventral bar - modified (a) or unmodified (b); C18: Number of anchors - 0 (a), 2 (b), 3 (c) or 4 (d); C19: Anchors - modified (a) or unmodified (b); C20: Diventricula - present (a) or absent (a); C21: Squamodiscs - present (a), absent (b) or present/absent (c); C22: MCO - tubular (a) or nested tube (b)

Table 4. Information reported in the literature for clades inferred through phylogenetic analyses including infection site, habitat, hosts repertoires, potential synapomorphies, and phylogenetic relationships as well as synapomorphies inferred from character maps in Fig. 5 and Fig. 6.

#	Clade name	Node support	Genera/species included	Site of infection	Habitat	Ecoregions	Host repertoire	Synapomorphies	Results of previous phylogenetic studies
A1	*Metahaliotrema–Protogyrodactylus*	100/100/100/*	*Metahaliotrema* *Protogyrodactylus*	gills	marine	Central Indo-Pacific	Centrarchiformes Gerreiformes Scatophagidae	-	Wu et al. (2006): *Metahaliotrema* and *Protogyrodactylus* reported as sister taxa.
A2	*Gussevia* – *Parasciadicleithrum*	99/95/100/*	*Gussevia* *Parasciadicleithrum*	gills	freshwater	Neotropical	Cichliformes	Preovarian position of testis (present study), coiled copulatory tube (Kritsky et al., 1986; Mendoza-Palmero et al., 2017)	-
A3	'*Ligophorus*'-like	95/87/98/*	*Ligophorus* *Ergenstrema* *Xenoligophoroides*	gills	marine	Central Indo-Pacific Temperate Northern Atlantic	Gobiiformes Mugiliformes	Vas deferens not looping caecum and modified ventral bar (present study), vas deferens not looping (Dimitrieva et al., 2018)	Dimitrieva et al. (2018): *Ergenstrema* and *Ligophorus* closely related but relationship with *X. cobitis* unresolved
A4	'*Cichlidogyrus*'-like	100/100/100/100	*Cichlidogyrus* *Scutogyrus*	gills	freshwater	Afrotropical	Cichliformes	Vas deferens not looping caecum, dissimilar size of hooks, modified dorsal bar (present study), auricles associated with dorsal bar (Pariselle and Euzet, 2009)	Wu et al. (2006): *Scutogyrus* nested in *Cichlidogyrus*
A5	*Euryhaliotrema–Sciadicleithrum*	100/96/100/*	*Euryhaliotrema* *Sciadicleithrum*	gills	marine and freshwater	Central Indo-Pacific Eastern Indo-Pacific Neotropical	Chaetodontiformes Cichliformes Lutjaniformes	copulatory tube coiled or meandering (Kritsky et al, 1989; Kritsky, 2012)	Mendoza-Palmero et al. (2017): *Sciadicleithrum* nested in a clade of species now considered members of *Euryhaliotrema*

A6	*Haliotrematoides* – *Mexicana*	100/100/100/77	*Haliotrematoides* *Mexicana*	gills	marine	Temperate Northern Pacific Temperate South America	Lutjaniformes	Overlapping gonads, modified ventral bar and absence of accessory piece (present study), absence of accessory piece in the male copulatory organ (Luque et al., 2002; Kritsky et al., 2009)	-
A7	Mesoparasitic dactylogyrids	100/100/100/87	*Enterogyrus* *Paradiplectanotrema* *Pseudempleurosoma*	oesophagus pharynx stomach rarely gills	marine and freshwater	Afrotropical Central Indo-Pacific	Aulopiformes Cichliformes Scianidae	-	-
A8	‘*Haliotrema*’-like	100/100/100/74	*Haliotrema* *Bravohollisia* *Caballeria* *Glyphidohaptor* *Lethrinitrema* *Parancyrocephaloides* *Platycephalotrema* *Pseudohaliotrema* *Tetrancistrum* *Thylacicleidus*	gills	marine	Central Indo-Pacific Eastern Indo-Pacific Indo-Malayan Temperate Northern Atlantic Western Indo-Pacific	Chaetodontiformes Ephippiformes Holocentriformes Lutjaniformes Perciformes Spariformes Syngnathiformes Tetraodontiformes Malacanthidae Siganidae	-	Monophyly of the ‘*Haliotrema*’ group [without species now considered as members of *Euryhaliotrema* (Kritsky, 2012), *Haliotrematoides* (García-Vásquez et al., 2015), *Ligophorus* (Euzet and Suriano, 1977), and *Metahaliotrema* (Kritsky et al., 2016)] supported by Dang et al. (2010), Soo (2019), and Al Jufaili et al. (2020)
A9	‘pseudodactylogyrids’ – ‘heteronchocleidids’	99/99/100/39	*Heteronchocleidus* ‘*Ancyrocephalus*’ *mogurndae* *Eutrianchoratus* *Gobioecetes* *Trianchoratus* *Pseudodactylogyrus*	gills	freshwater	Indo-Malayan Palaearctic	Anabantiformes Centrarchiformes Gobiiformes Anguilliformes	-	Moderate to high support for monophyly in Tan et al. (2011) and Ogawa and Itoh (2017) but representatives of only two to three genera belonging to A9 included.
A10	dactylogyrines	100/100/100/*	*Dactylogyrus* *Dactylogyroides* *Dogielius*	gills	freshwater	Indo-Malayan Palaearctic	Cypriniformes	Two prostatic reservoirs and single pair of anchors	-
B1	Parasites of siluriforms I: Pimelodidae	100/100/100/*	*Boegeriella* ‘*Demidospermus*’ *mortenthaleri* *Nanayella*	gills	freshwater	Neotropical	Siluriformes (Pimelodidae)	-	Clade reported as monophyletic by Acosta et al. (2018). Clade reported as monophyletic by Mendoza-Palmero et al. (2015, 2019) and Acosta et al. (2019).
B2	Parasites of siluriforms II: Doradidae and Locariidae	97/86/96/*	*Cosmetocleithrum* *Demidospermus*	gills	freshwater	Neotropical	Siluriformes (Doradidae and Locariidae)	-	Acosta et al. (2019), Mendoza-Palmero et al. (2019): clade reported as monophyletic.

B3	Parasites of siluriforms III: Ariidae, Bagridae, and Schilbeidae	100/99/100/*	*Chauhanellus* *Hamatopeduncularia* *Schilbetrema* *Susanlimocotyle*	gills	marine and fresh-water	Afrotropical Central Indo-Pacific Temperate South America Tropical Atlantic Western Indo-Pacific	Siluriformes (Ariidae,Bagridae, and Schilbeidae)	Modified dorsal bar	Monophyly supported by previous studies but omission of at least one of the following genera: *Hamatopeduncularia* (Franceschini et al., 2018; Acosta et al., 2019), *Schilbetrema* (Soares et al., 2021), and *Susanlimocotyle* (Soo and Tan, 2021)
B4	Parasites of siluriforms IV: Bagridae and Siluridae	99/94/100/*	*Cornudiscoides* *Pseudancylodiscoides* *Thaparocleidus*	gills	fresh-water	Indo-Malayan Palaearctic	Siluriformes (Bagridae and Siluridae)	-	Close relationship between species of *Pseudancylodiscoides* and *Thaparocleidus* reported in Wu et al. (2008)
B5	Parasites of siluriforms V: Bagridae and Clariidae	100/100/100/*	*Bychowskyella* *Quadriacanthus*	gills	fresh-water	Afrotropical and Indo-Malayan	Siluriformes (Bagridae and Clariidae)	-	Wu et al. (2008): Close relationship of the two genera reported.
B6	ancyrocephalines	98/99/99/*	*Actinocleidus* *Ameloblastella* *Ancyrocephalus* *Cacatuocotyle* *Characithecium* *Diaphorocleidus* *Heteropriapulus* *Ligictaluridus* *Mymarothecium* *Onchocleidus* *Pavanelliella* *Trinigyrus* *Unibarra* *Unilatus* *Urocleidoides* *Vancleaveus*	gills	fresh-water	Indo-Malayan Neotropical Nearctic *Palaearctic**	Centrarchiformes Characiformes Gymnotiformes Pericformes Siluriformes	-	Reported as monophyletic in Moreira et al. (2019b), Franceschini et al. (2020), Zago et al. (2020), and Zago et al. (2021) but *Pavanelliella* not included.

Figure captions

Figure 1. Classification system 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 for these genera. 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 (BI) phylogram of monogenean flatworms belonging to Dactylogyridae (Platyhelminthes: Monogenea) with node support inferred from BI, Maximum Likelihood (ML), and Maximum Parsimony (MP). 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 ML estimation and GC values inferred from symmetric resampling ($p = 0.33$) during MP analysis; asterisk (*) indicates low support below threshold ($PP < 0.95$, $UBoost < 95$, $SH\text{-}aLRT < 80$); 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.

Figure 3. Final phylogenetic hypotheses inferred from molecular and morphological data under maximum parsimony. (A) Molecular phylogram inferred from three nuclear DNA portions (18S, 28S, and ITS rDNA) under extended implied weighting. (B) Morphological phylogram based 22 morphological characters (Table 3). Node support constitutes GC values inferred from symmetric resampling ($p = 0.33$).

Figure 4. Phylogenetic signal of morphological characters widely used in generic diagnoses of dactylogyrid monogeneans assessed through the model fit (all-rates-different model) in comparison to a white noise

model that absolute assumes phylogenetic independence. Model fits were assessed through the difference between the sample size–corrected Akaike information criterion (ΔAICc) values. For character codes (C1–C22) see Table 3.

Figures 5. Character maps of morphological character widely used in generic diagnoses of dactylogyrid monogeneans estimated under maximum parsimony. For character codes (C1–C11) and respective character states (a–e) see Table 3.

Figures 6. Continuation of Fig. 5. Character maps of morphological character widely used in generic diagnoses of dactylogyrid monogeneans estimated under maximum parsimony. For character codes (C12–C22) and respective character states (a–e) see Table 3.

Supplementary material

Supporting Information S1. Table of morphological features reported in generic diagnoses of species of Dactylogyridae.

Supporting Information S2. Results and discussion of the phylogenetic analyses of mitochondrial cytochrome oxidase subunit I (COI) gene.

Figure 1

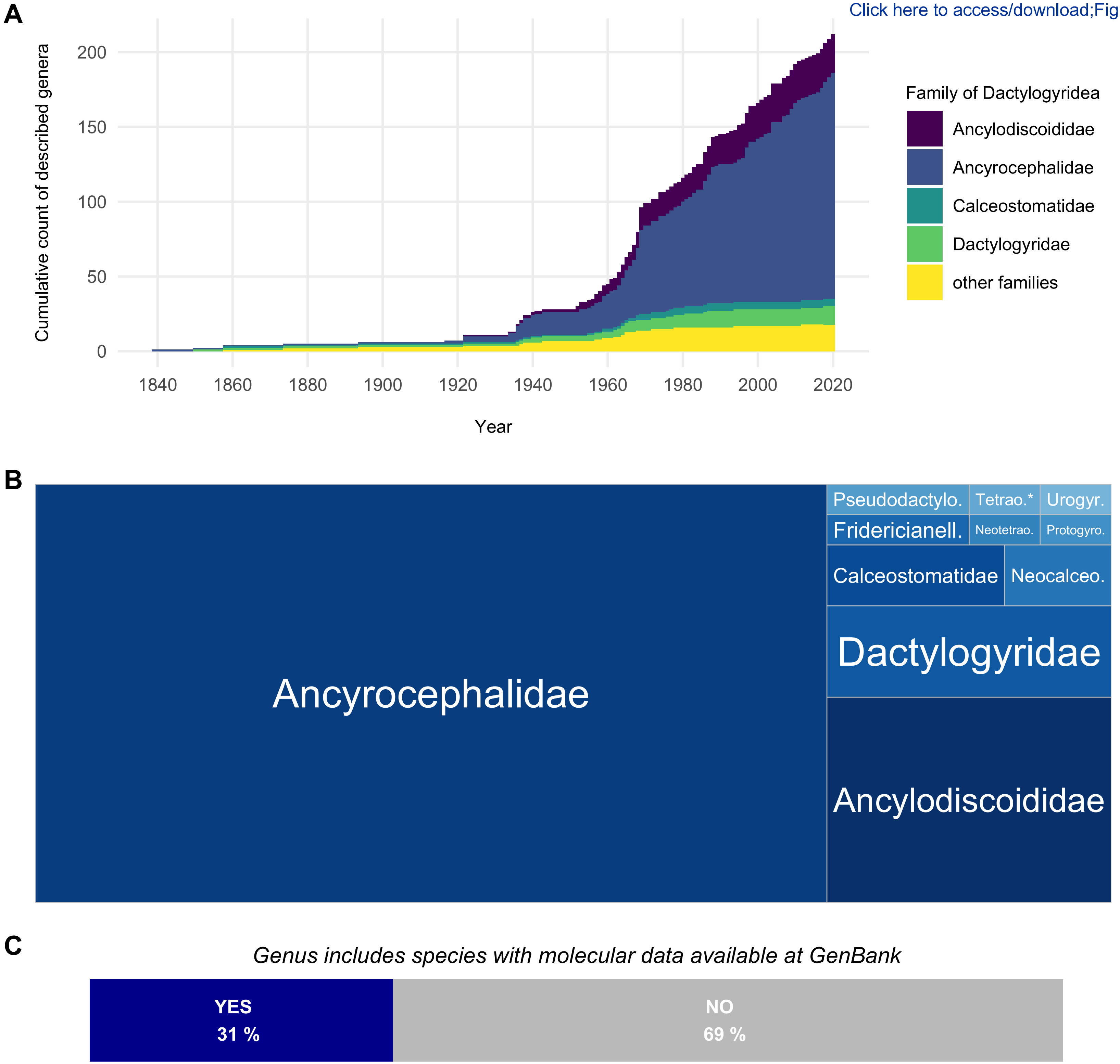
A
Cumulative count of described genera
0
50
100
150
200
1840
1860
1880
1900
1920
1940
1960
1980
2000
2020
Year
Family of Dactylogyridea
Ancylodiscoididae
Ancyrocephalidae
Calceostomatidae
Dactylogyridae
other families
B
Ancyrocephalidae
Pseudodactylo.
Tetrao.*
Urogyr.
Fridericianell.
Neotetrao.
Protogyro.
Calceostomatidae
Neocalceo.
Dactylogyridae
Ancylodiscoididae
C
Genus includes species with molecular data available at GenBank
YES
31 %
NO
69 %

Figure 2

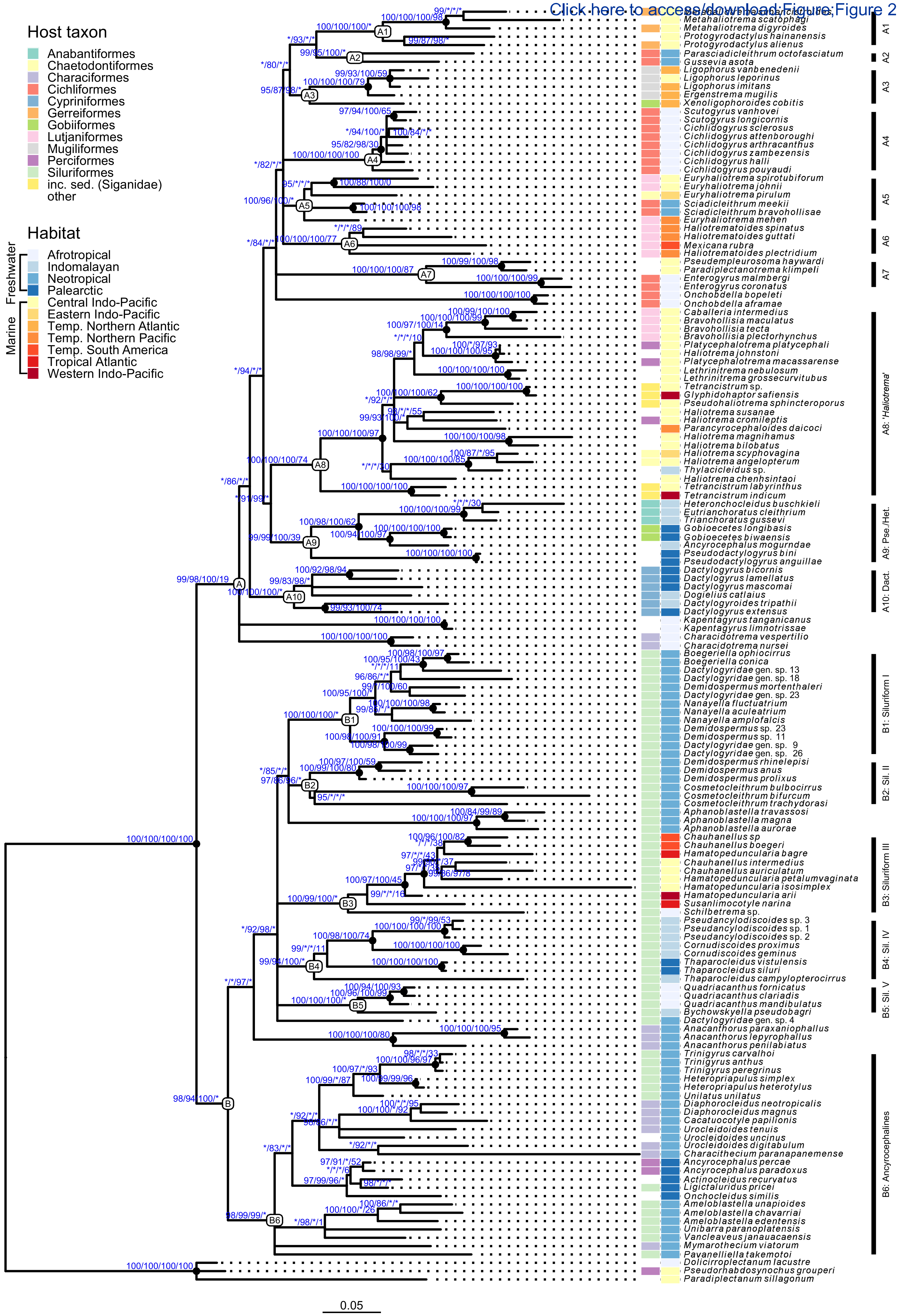
Host taxon
Anabantiformes
Chaetodontiformes
Characiformes
Cichliformes
Cypriniformes
Gerreiformes
Gobiiformes
Lutjaniformes
Mugiliformes
Perciformes
Siluriformes
inc. sed. (Siganidae)
other
Habitat
Freshwater
Afrotropical
Indomalayan
Neotropical
Palearctic
Marine
Central Indo-Pacific
Eastern Indo-Pacific
Temp. Northern Atlantic
Temp. Northern Pacific
Temp. South America
Tropical Atlantic
Western Indo-Pacific
99/*/*/*
100/100/100/98
100/100/100/*
A1
99/87/98/*
/93//*
99/95/100/*
A2
/80//*
99/93/100/59
100/100/100/79
95/87/98/*
A3
97/94/100/65
/94/100/
100/84/*/*
95/82/98/30
100/100/100/100
A4
/82//*
95/*/*/*
100/88/100/0
100/96/100/*
A5
100/100/100/98
//*/89
/84//*
100/100/100/77
A6
100/99/100/98
100/100/100/87
A7
100/100/100/99
100/100/100/100
100/99/100/100
100/100/100/99
100/97/100/14
//*/10
100/*/97/93
98/98/99/*
100/100/100/95
/94//*
100/100/100/100
100/100/100/100
100/100/100/62
/92//*
98/*/*/55
99/93/100/*
100/100/100/97
100/100/100/98
100/87/*/95
100/100/100/74
A8
100/100/100/85
//*/30
/86//*
100/100/100/100
/91/99/
//*/30
100/100/100/99
100/98/100/62
100/100/100/100
100/94/100/97
99/99/100/39
A9
100/100/100/100
100/92/98/94
99/98/100/19
A
99/83/98/*
100/100/100/*
A10
99/93/100/74
100/100/100/100
100/100/100/100
100/98/100/97
100/95/100/43
//*/11
96/86/*/*
99/*/100/60
100/95/100/*
100/100/100/98
99/85/*/*
100/100/100/*
B1
100/100/100/99
100/98/100/91
100/98/100/99
100/97/100/59
100/99/100/80
/85//*
97/86/96/*
B2
100/100/100/97
95/*/*/*
100/84/99/89
100/100/100/97
100/100/100/100
100/96/100/82
//*/38
97/*/*/43
99/90/*/37
97/*/*/35
99/86/97/8
100/97/100/45
99/*/*/16
100/99/100/*
B3
99/*/99/53
100/100/100/100
/92/98/
100/98/100/74
100/100/100/100
99/*/*/11
99/94/100/*
B4
100/100/100/100
100/94/100/93
100/96/100/99
//97/*
100/100/100/*
B5
100/100/100/95
100/100/100/80
98/*/*/33
100/100/96/97
100/97/*/93
100/99/*/87
100/99/99/96
98/94/100/*
B
100/*/*/95
100/100/*/92
/92//*
98/86/*/*
/83//*
/92//*
97/91/*/52
//*/6
97/99/96/*
98/*/*/*
100/86/*/*
100/100/*/26
98/99/99/*
B6
/98//1
100/100/100/100
0.05
Metahaliotrema subancistroides
Metahaliotrema scatophagi
Metahaliotrema digyroides
Protogyrodactylus hainanensis
Protogyrodactylus alienus
Parasciadicleithrum octofasciatum
Gussevia asota
Ligophorus vanbenedenii
Ligophorus leporinus
Ligophorus imitans
Ergenstrema mugilis
Xenoligophoroides cobitis
Scutogyrus vanhovei
Scutogyrus longicornis
Cichlidogyrus sclerosus
Cichlidogyrus attenboroughi
Cichlidogyrus arthracanthus
Cichlidogyrus zambezensis
Cichlidogyrus halli
Cichlidogyrus pouyaudi
Euryhaliotrema spirotubiforum
Euryhaliotrema johnii
Euryhaliotrema pirulum
Sciadicleithrum meekii
Sciadicleithrum bravohollisae
Euryhaliotrema mehen
Haliotrematoides spinatus
Haliotrematoides guttati
Mexicana rubra
Haliotrematoides plectridium
Pseudempleurosoma haywardi
Paradiplectanotrema klimpeli
Enterogyrus malmbergi
Enterogyrus coronatus
Onchobdella bopeleti
Onchobdella aframae
Caballeria intermedius
Bravohollisia maculatus
Bravohollisia tecta
Bravohollisia plectorhynchus
Platycephalotrema platycephali
Haliotrema johnstoni
Platycephalotrema macassarense
Lethrinitrema nebulosum
Lethrinitrema grossecurvitubus
Tetrancistrum sp.
Glyphidohaptor safiensis
Pseudohaliotrema sphincteroporus
Haliotrema susanae
Haliotrema cromileptis
Parancyrocephaloides daicoci
Haliotrema magnihamus
Haliotrema bilobatus
Haliotrema scyphovagina
Haliotrema angelopterum
Thylacicleidus sp.
Haliotrema chenhsintaoi
Tetrancistrum labyrinthus
Tetrancistrum indicum
Heteronchocleidus buschkieli
Eutrianchoratus cleithrium
Trianchoratus gussevi
Gobioecetes longibasis
Gobioecetes biwaensis
Ancyrocephalus mogurndae
Pseudodactylogyrus bini
Pseudodactylogyrus anguillae
Dactylogyrus bicornis
Dactylogyrus lamellatus
Dactylogyrus mascomai
Dogielius catlaius
Dactylogyroides tripathii
Dactylogyrus extensus
Kapentagyrus tanganicanus
Kapentagyrus limnotrissae
Characidotrema vespertilio
Characidotrema nursei
Boegeriella ophiocirrus
Boegeriella conica
Dactylogyridae gen. sp. 13
Dactylogyridae gen. sp. 18
Demidospermus mortenthaleri
Dactylogyridae gen. sp. 23
Nanayella fluctuatrium
Nanayella aculeatrium
Nanayella amplofalcis
Demidospermus sp. 23
Demidospermus sp. 11
Dactylogyridae gen. sp. 9
Dactylogyridae gen. sp. 26
Demidospermus rhinelepisi
Demidospermus anus
Demidospermus prolixus
Cosmetocleithrum bulbocirrus
Cosmetocleithrum bifurcum
Cosmetocleithrum trachydorasi
Aphanoblastella travassosi
Aphanoblastella magna
Aphanoblastella aurorae
Chauhanellus sp
Chauhanellus boegeri
Hamatopeduncularia bagre
Chauhanellus intermedius
Chauhanellus auriculatum
Hamatopeduncularia petalumvaginata
Hamatopeduncularia isosimplex
Hamatopeduncularia arii
Susanlimocotyle narina
Schilbetrema sp.
Pseudancylodiscoides sp. 3
Pseudancylodiscoides sp. 1
Pseudancylodiscoides sp. 2
Cornudiscoides proximus
Cornudiscoides geminus
Thaparocleidus vistulensis
Thaparocleidus siluri
Thaparocleidus campylopterocirrus
Quadriacanthus fornicatus
Quadriacanthus clariadis
Quadriacanthus mandibulatus
Bychowskyella pseudobagri
Dactylogyridae gen. sp. 4
Anacanthorus paraxaniophallus
Anacanthorus lepyrophallus
Anacanthorus penilabiatus
Trinigyrus carvalhoi
Trinigyrus anthus
Trinigyrus peregrinus
Heteropriapulus simplex
Heteropriapulus heterotylus
Unilatus unilatus
Diaphorocleidus neotropicalis
Diaphorocleidus magnus
Cacatuocotyle papilionis
Urocleidoides tenuis
Urocleidoides uncinus
Urocleidoides digitabulum
Characithecium paranapanemense
Ancyrocephalus percae
Ancyrocephalus paradoxus
Actinocleidus recurvatus
Ligictaluridus pricei
Onchocleidus similis
Ameloblastella unapioides
Ameloblastella chavarriai
Ameloblastella edentensis
Unibarra paranoplatensis
Vancleaveus janauacaensis
Mymarothecium viatorum
Pavanelliella takemotoi
Dolicirroplectanum lacustre
Pseudorhabdosynochus grouperi
Paradiplectanum sillagonum
A1
A2
A3
A4
A5
A6
A7
A8: 'Haliotrema'
A9: Pse./Het.
A10: Dact.
B1: Siluriform I
B2: Sil. II
B3: Siluriform III
B4: Sil. IV
B5: Sil. V
B6: Ancyrocephalines

Figure 3

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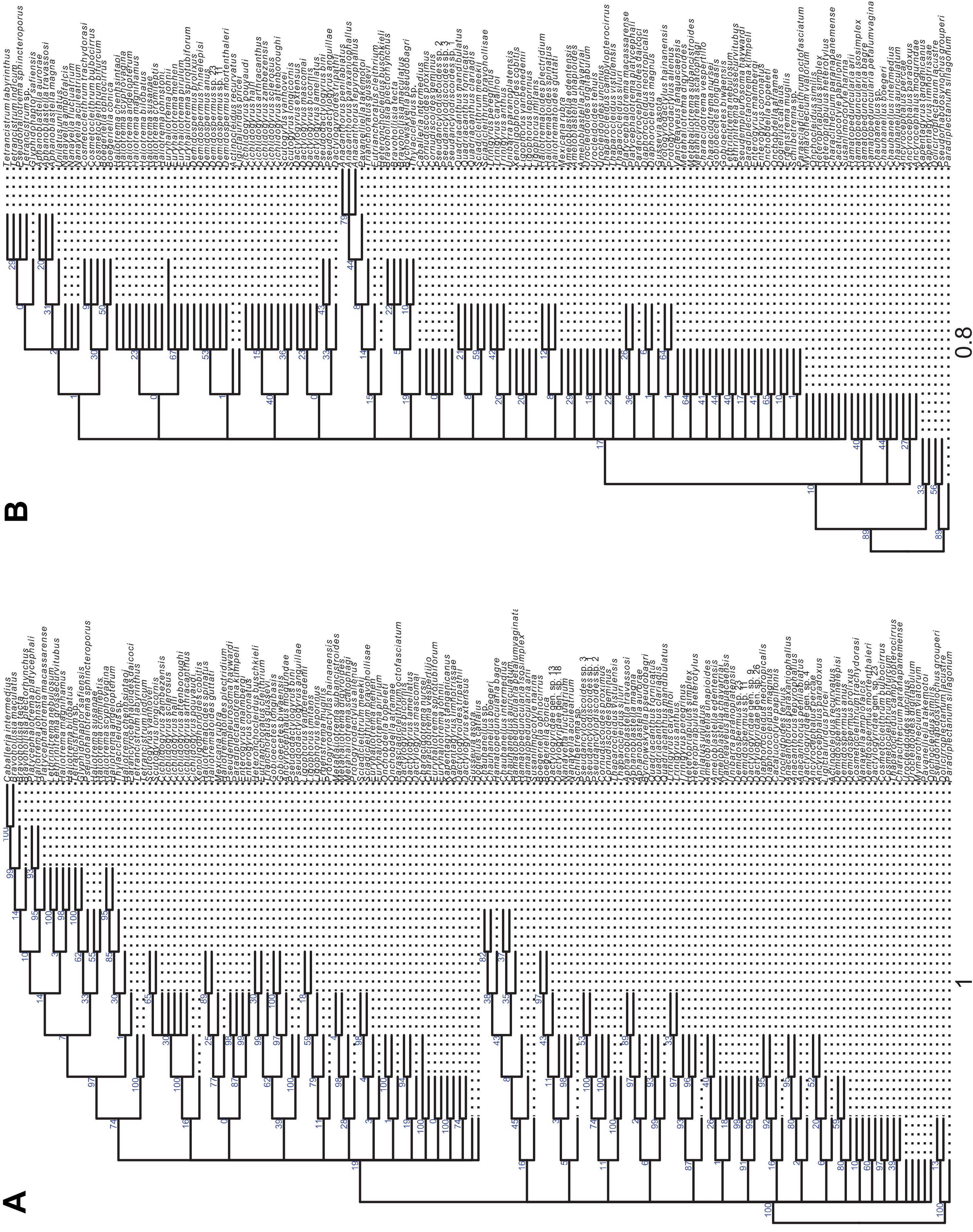

Figure 4

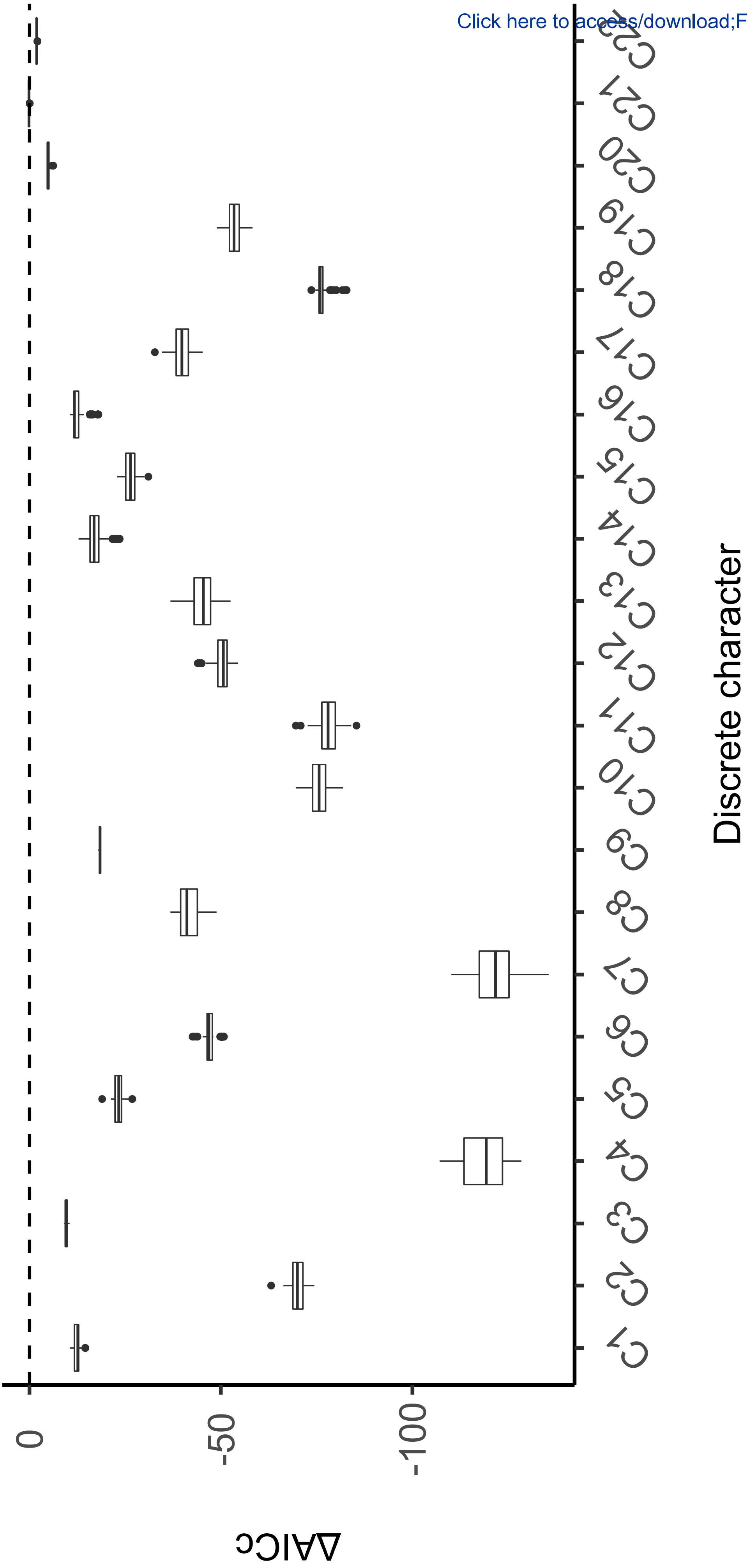
ΔAICc
0
-50
-100
Discrete character
C1
C2
C3
C4
C5
C6
C7
C8
C9
C10
C11
C12
C13
C14
C15
C16
C17
C18
C19
C20
C21
C22

Figure 5

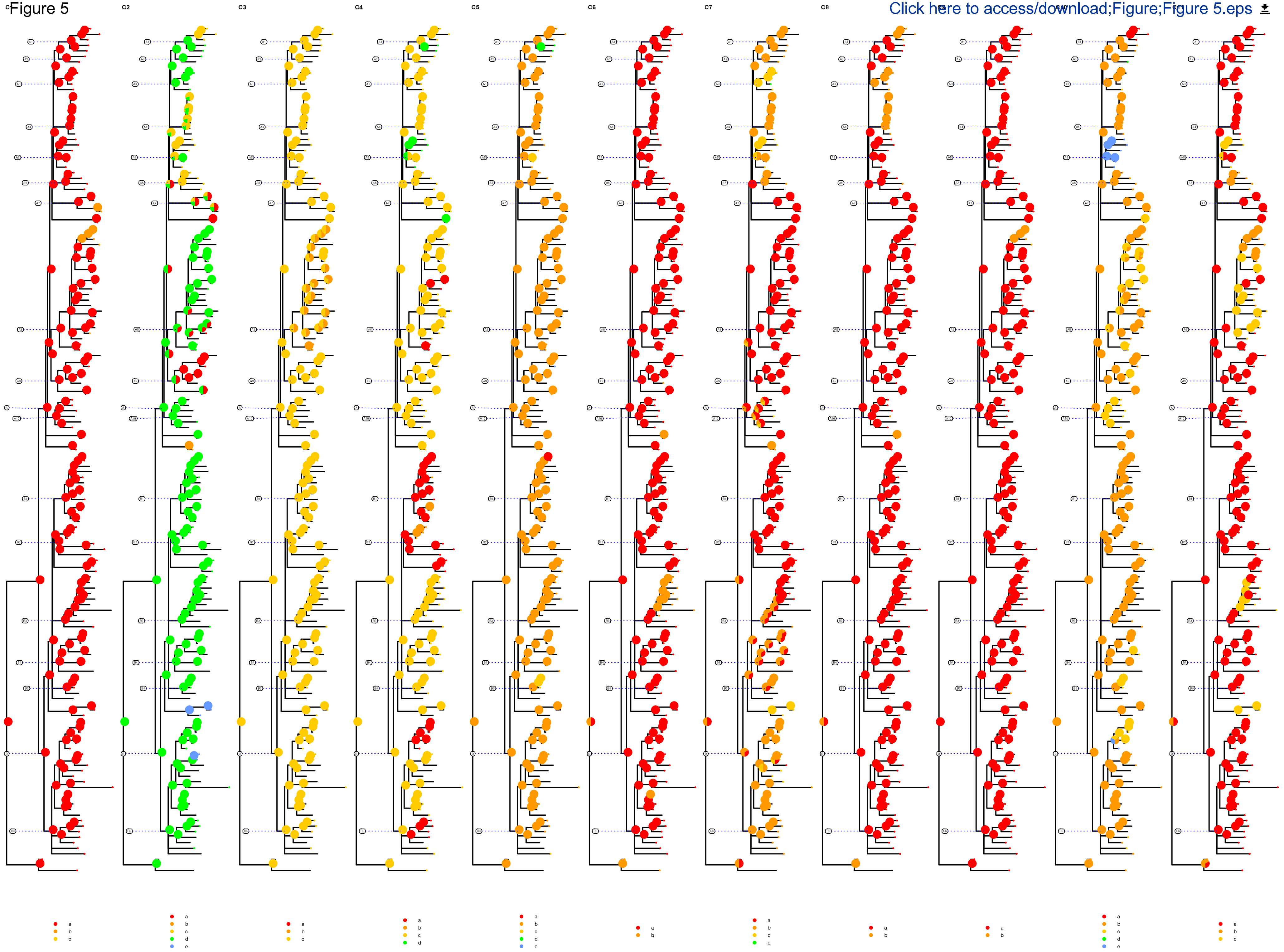

Figure 6