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Non Peer-reviewed author version

KMENTOVA, Nikol; CRUZ LAUFER, Armando; Pariselle, Antoine; SMEETS, Karen; ARTOIS, Tom & VANHOVE, Maarten (2022) Dactylogyridae 2022: a meta-analysis of phylogenetic studies and generic diagnoses of parasitic flatworms using published genetic and morphological data.

DOI: 10.32942/osf.io/5mh3d

Handle: <http://hdl.handle.net/1942/36897>

1 **This preprint is not a publication according to the ICZN, and especially according the emended Article 8 of**  
2 **the ICZN (ICZN, 2012).**

3 ICZN, 2012. Amendment of Articles 8, 9, 10, 21 and 78 of the International Code of Zoological  
4 Nomenclature to expand and refine methods of publication. Zootaxa.  
5 <https://doi.org/10.3897/zookeys.219.3994>  
6

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

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21

22 **Abstract**

23 Dactylogyridae are one of the most studied families of parasitic flatworms with more than 1000 species and  
24 166 genera described to date including ecto- and endoparasites. Dactylogyrid monogeneans were  
25 suggested as model organisms for host-parasite macroevolutionary and biogeographical studies due to the  
26 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., *Uroleioides 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, Ehippiiformes, 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

81 patterns have to be seen in the context of oscillation of host repertoires (Janz and Nylin, 2008). As  
 82 suggested by Brooks et al. (2019), oscillating host repertoires are enabled by ecological opportunities  
 83 emerging from the rise and fall of ecological barriers (D’Bastiani et al., 2020) and ecological fitting as the  
 84 capacity to infect new host species (Agosta et al., 2010).

85 Despite the versatility of dactylogyrid research, almost two decades have passed since the last assessment  
 86 of dactylogyrid evolutionary history as a whole by Šimková et al. (2006). Biases in the selection of taxa and  
 87 molecular markers potentially mask macroevolutionary patterns within dactylogyrids. For instance,  
 88 phylogenetic relationships are mostly inferred from subsets of taxa with DNA sequences available even  
 89 though nowadays molecular data frequently accompany new descriptions of monogenean species and/or  
 90 genera. Many taxonomic studies on dactylogyrid monogeneans have also targeted specific host taxa or  
 91 geographic regions, e.g., species infecting siluriform fishes in the Amazon (Mendoza-Palmero et al., 2015,  
 92 2020) or Central America (Salgado-Maldonado, 2008), as well as host-parasite model systems, e.g., African  
 93 cichlids and species of *Cichlidogyrus* (reviewed in Cruz-Laufer et al., 2021a). Furthermore, confirmation and  
 94 citation paradigms might play in monogenean research. Confirmation biases arise from prior expectations  
 95 of researchers driven by taxon selection, a problem that affects phylogenetic studies in general (see Jermini  
 96 et al., 2020). Citation bias emerges when the probability to be cited depends on the study outcome  
 97 (positive vs. negative results) (Urlings et al., 2021) or author-related factors such as reputation (Bol et al.,  
 98 2018), gender (Dworkin et al., 2020), and country of origin (Van der Stocken et al., 2016). The latter might  
 99 affect the visibility of monogenean research especially from low-income countries, where most biodiversity  
 100 hotspots of fish and their parasites are found (Jorge and Poulin, 2018).

101 Dactylogyridae *sensu lato* currently comprise 166 genera (Horton et al., 2021). However, two different  
 102 designations have been used interchangeably for species belonging to this lineage: Dactylogyridae  
 103 Bychowsky, 1933 and Ancyrocephalidae Bychowsky, 1937. Moreover, the status of several other families  
 104 (Fig. 1a,b) has been put into question due to morphological similarities and phylogenetic relationships with  
 105 members of Dactylogyridae (Kritsky and Boeger, 1989; Bilong Bilong et al., 1994; Boeger and Kritsky, 2001;  
 106 Lim et al., 2001; Šimková et al., 2006; Galli and Kritsky, 2008; Kritsky et al., 2009; Fayton and Kritsky, 2013;  
 107 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, Ancylo-discoidinae 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 Ancylo-discoidinae 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 Ancylo-discoididae, Ancyrocephalidae, Dactylogyridae, Protyrogodactylidae, 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. parapanemense* (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 &

161 Nagibina, 1970, *Characidotrema* Mendoza-Franco, Reina & Torchin, 2009, *Chauhanellus* Bychowsky &  
 162 Nagibina, 1968, *Cichlidogyrus* Paperna, 1960, *Dactylogyrus* Diesing, 1850, *Euryhaliotrema* Kritsky & Boeger,  
 163 2002, *Haliotrematoides* Kritsky, Yang & Sun, 2009, *Hamatopeduncularia* Yamaguti, 1953, *Heteropriapulus*  
 164 Kritsky, 2007, *Lethrinitrema* Lim & Justine, 2011, *Ligophorus* Euzet & Suriano, 1977, *Metahaliotrema*  
 165 Yamaguti, 1953, *Nanayella* Acosta, Mendoza-Palmero, da Silva & Scholz, 2019, *Quadriacanthus* Paperna,  
 166 1961, *Scutogyrus* Pariselle & Euzet, 1995, *Thaparocleidus* Jain, 1952, and *Urocleidoides* Mizelle & Price,  
 167 1964 (Wu et al., 2007, 2008; Blasco-Costa et al., 2012; Sun et al., 2014; García-Vásquez et al., 2015; Acosta  
 168 et al., 2017, 2019; Francová et al., 2017; Moreira et al., 2019b; Řehulková et al., 2019; Soo, 2019; Zago et  
 169 al., 2020; Mendoza-Palmero et al., 2020; Soo and Tan, 2021; Cruz-Laufer et al., 2021b). If possible, the type  
 170 species of each genus was included. Full genus and species names including authorities can be found in  
 171 Table 1.

## 172 2.2. Phylogenetic analyses of molecular data

173 We aligned DNA sequences using the L-INS-I algorithm in *MAFFT* v7.409 (Katoh and Standley, 2013) as  
 174 recommended for ribosomal DNA by the *MAFFT* manual, and removed poorly aligned positions and  
 175 divergent regions with *Gblocks* v0.91b using the options for less stringent parameters (Talavera and  
 176 Castresana, 2007). The 18S rDNA alignment contained sequences that only covered an anterior part of the  
 177 alignment, i.e., members of *Chauhanellus*, *Cornudiscoides*, *Hamatopeduncularia*, and *Tetrancistrum*, a  
 178 majority which covered the posterior parts, and some sequences that covered the entirety of the  
 179 alignment. As, otherwise, *Gblocks* removes the anterior part (results not shown), we opted to split the  
 180 alignment in two parts allowing us to trim both parts in *Gblocks* separately. We partitioned the DNA  
 181 sequence data by gene for 28S and ITS1, by the anterior/posterior part for 18S, and by codon for COI and  
 182 selected the substitution models for each partition according to the Bayesian information criterion (BIC)  
 183 through partition merging (Chernomor et al., 2016) as implemented in *ModelFinder* in *IQ-Tree*  
 184 (Kalyaanamoorthy et al., 2017) (Table 1). For subsequent Bayesian Inference (BI) analyses, we only selected  
 185 models implemented in *MrBayes* v3.2.6 (Ronquist and Huelsenbeck, 2003) (Table 2).



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

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

### 205 2.3. Ecological and biogeographical characterisation of clades and phylogenetic support in previous studies

206 Based on a survey of peer-reviewed literature, we characterised all clades in our tree (Fig. 2) according to  
 207 their synapomorphies, host repertoire, occurrence in freshwater or marine habitats, and geographical  
 208 distribution limited to the species included in the phylogenetic analysis (Table 2). We also reviewed the  
 209 support from previous phylogenetic studies to assess the stability of the clades in phylogenetic  
 210 reconstructions. For the host classification, we followed Betancur-R. et al. (2007). Habitat preferences of  
 211 the hosts (marine vs. freshwater) and geographical distribution were inferred from FishBase (Froese and

212 Pauly, 2000). The latter was defined as biogeographic realms according to Olson and Dinerstein (1998) and  
213 Spalding et al. (2007). Finally, we accessed information on the family-affiliation of all genera belonging to  
214 the order Dactylogyridea from the WoRMS database (Horton et al., 2021) to infer temporal trends in the  
215 description of novel genera in this taxon (see Fig. 1).

#### 216 2.4. Molecular vs. morphological phylogeny

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

232 For the parsimony analyses in *TNT*, we used extended implied weighting (Goloboff, 2014) in a range of  
233 values for the concavity constant *K* (20, 21, 23, 26, 30, 35, 41, 48, 56). Unlike in the original implied  
234 weighting method (Goloboff, 1993), extended implied weighting avoids weighting characters with missing  
235 data artificially high (Goloboff, 2014). We also tested different weighting schemes for the molecular  
236 characters as suggested by Mirande (2019). Molecular characters were weighted separately (SEP) like the  
237 morphological characters or by the average homoplasy of their partition (BLK) as suggested by Goloboff et

238 al. (2008a). For COI mtDNA sequences, we also weighted characters by their codon position (COD). The final  
239 phylogenetic hypotheses were inferred from the parameters (k and weighting scheme) that produced the  
240 most stable consensus tree topology. The distortion coefficient and the subtree pruning and regrafting  
241 (SPR) distance served as selection criteria by calculating the similarity of all the consensus trees obtained  
242 under the different parameter combinations to the other consensus trees (Mirande, 2009). Tree searches  
243 involved rounds of tree fusing, sectorial searches, and tree drifting (Goloboff, 1999) under default settings  
244 and each round was stopped after three hits of the same optimum. Gaps were treated as missing data.  
245 Branch support was estimated through symmetric resampling with a probability of change of 0.33 and  
246 values expressed as differences in frequencies (GC: 'Groups present/Contradicted') as bootstrapping and  
247 jackknifing have been reported to be distorted by implied weighting methods (Goloboff, 2003).

## 248 2.5. Phylogenetic signal of morphological characters and character mapping

249 We also inferred the phylogenetic expressed by the morphological characters using phylogenetic  
250 comparative methods. The characters were fitted to 100 randomly selected tree topologies from the post-  
251 burn-in fraction of the Bayesian phylogenetic analysis using a continuous-time Markov model of trait  
252 evolution as implemented in the function *fitDiscrete* in the *R* package *geiger* v2.0 (Pennell et al., 2014). As  
253 we could make no inference on the transition costs between character states, all characters were modelled  
254 with an all-rates-different model (ARD) with a Pagel's  $\lambda$  tree transformation (Pagel, 1999). Model  
255 performance was assessed through the sample size-corrected Akaike information criterion (AICc) in  
256 comparison to a white noise model that assumes absolute phylogenetic independence (Pennell et al.,  
257 2014).

## 258 2.6. Graphing

259 We plotted graphs and phylogenetic trees using the packages *ggplot2* 3.3.5 (Wickham, 2016) and *ggtree*  
260 v3.1.2 (Yu et al., 2017, 2018) in *R* v4.1.0 (R Core Team, 2021). Character maps were produced with the  
261 function *asr\_max\_parsimony* in the *R* package *castor* (Louca and Doebeli, 2018).

## 262 3. Results

### 263 3.1. Phylogenetic reconstructions

264 In total, specimens belonging to 67 dactylogyrid genera were included in this analysis. An overview of all  
265 dactylogyridean genera described through time is presented in Fig. 1a. The COI mtDNA alignment included  
266 sequences of only 10 genera and was, thus, excluded from all downstream analyses. A more detailed  
267 discussion of the COI phylogeny can be found in Supporting Information S2. For the parsimony analysis of  
268 the molecular data, the BLK scheme with  $k = 23$  (SPR distance: 0.968) and  $k = 35$  (distortion coefficient:  
269 0.981) produced the most stable tree topologies and were used to infer the final consensus tree topology.  
270 The BI, ML, and MP trees were significantly congruent (Kendall's  $W = 0.691$ ,  $\chi^2 = 24115$ ,  $p < 0.01$ ).  
271 Phylogenetic reconstruction revealed the presence of two main lineages (further referred to as  
272 macroclades A and B), which comprise ten and six well-supported clades, respectively (clades A1–A10 and  
273 B1–B6) (Fig. 2) [node support values: Bayesian posterior probabilities/ultrafast bootstrap  
274 values/Shimodaira-Hasegawa-like approximate likelihood ratios/GC values; asterisk (\*) indicates low  
275 support below threshold (see Fig. 2)]. Both macroclade A (99/98/100/19), which includes clades A1–A10,  
276 and macroclade B (99/94/100/\*), which includes clades B1–B6 are well-supported. The phylogenetic  
277 positions of representatives of *Characidotrema*, parasites of African alestid fishes, and *Kapentagyryus*,  
278 parasites of African freshwater clupeids, remain unresolved within macroclade A, the same applies to  
279 representatives of *Anacanthorus*, parasites of South American serrasalmids, in macroclade B. Although DNA  
280 sequences of these three genera analysed here each form well-supported monophyletic clades, they were  
281 not assigned clade numbers as the intrageneric phylogenetic relationships are already discussed elsewhere  
282 (Kmentová et al., 2018; Moreira et al., 2019b; Řehulková et al., 2019).

### 283 3.2. Morphological, ecological, and biogeographical characterisation of clades

284 Most of the generic diagnoses analysed here fit the morphological diagnosis of Dactylogyridae *sensu*  
285 Bychowsky, 1933. The presence of two pairs of anchors and a single dorsal and ventral bar are considered  
286 plesiomorphic in dactylogyrid monogeneans (Kritsky and Boeger, 1989). Yet species of several genera  
287 deviating from this ancestral bauplan by displaying a single pair of anchors and bars (*Dactylogyrus*,  
288 *Dactylogyroides*, *Dogielius*) or no anchors and bars at all (*Anacanthorus*) form part of the macroclades A

289 and B, respectively. A comparative overview of the morphological character states of all genera of which  
290 representatives were included in the phylogenetic reconstruction is presented in Table 3. An overview of  
291 the host repertoire, biogeography, phylogenetic support, and synapomorphies of all 16 clades in our tree  
292 (Fig. 2) is provided in Table 4 (restricted to the dactylogyrid species and lineages included in the phylogeny).  
293 The sclerotised parts of the attachment and reproductive organs are considered one of the most  
294 systematically informative structures in monogenean taxonomy (Kritsky and Boeger, 1989). A list of the  
295 most recent original or emended generic diagnoses is available in Supporting Information S1.

### 296 3.3. Systematic informativeness of morphological characters: Parsimony analysis, phylogenetic comparative 297 methods, and character mapping

298 For the parsimony analysis of the morphological data,  $k = 30$  produced the most stable trees (SPR distance:  
299 0.993, distortion coefficient: 0.972) and was used to compute the consensus tree (Fig. 3). The morphology-  
300 based phylogeny showed significant congruence with the molecular MP parsimony tree (Kendall's  $W =$   
301  $0.585$ ,  $\chi^2 = 12544$ ,  $p < 0.01$ ) 5(Fig. 3), but few larger clades were supported in the former resulting in a large  
302 polytomy including all taxa except for species of *Kapentagyris* and the outgroup.

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

## 310 4. Discussion

311 This study provides the most extensive phylogenetic meta-analysis of dactylogyrid monogeneans to date.  
312 Based on representatives of 67 genera and a combination of three ribosomal gene markers, our  
313 phylogenetic reconstruction revealed the presence of two major lineages, macroclades, including ten and

314 six well-supported smaller clades, respectively. In the past, morphological and molecular data have resulted  
315 in multiple systematic revisions of species and subfamilies in dactylogyrid monogeneans. Here, we provide  
316 an overview of evolutionary patterns, revise Dactylogyridae and its subfamilies, and summarise potential  
317 problematic areas at the genus level, i.e. potential polyphylies or paraphylies that call for a systematic  
318 revision in the future. Habitat types and host repertoires are illustrated alongside the phylogeny (Fig. 2).  
319 Our study also suggests that morphological characters contain little information on the phylogenetic  
320 relationships of dactylogyrids above the genus level as illustrated by the polytomy (i.e. low support) for  
321 most clades above the genus level (Fig. 3). Finally, we highlight how a limited coverage of host taxa or  
322 distribution ranges and biases towards certain host groups and regions interfere with scientific exploration  
323 of the evolutionary history of Dactylogyridae.

#### 324 *Taxonomic implications: Dactylogyridae and its subfamilies*

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

### 333 **Class Monogenea Bychowsky, 1933**

#### 334 **Subclass Monopisthocotylea Bychowsky, 1933**

#### 335 **Order Dactylogyridea Bychowsky, 1937**

#### 336 **Family Dactylogyridae Bychowsky, 1933**

337 *Junior synonyms:* Ancylo-discoididae Gusev, 1961, Ancyrocephalidae Bychowsky, 1937, Heteronchocleididae  
338 Tan, Fong & Lim, 2011, Protogyrodactylidae Johnston & Tiegs, 1922, Pseudodactylogyridae Gusev, 1965 and  
339 Urogyridae Bilong Bilong, Birgi & Euzet, 1994.

340     Remarks:

341     In the last decades, several studies have investigated phylogenetic relationships within Dactylogyridae  
342     (Šimková et al., 2003, 2006; Plaisance et al., 2005; Mendoza-Palmero et al., 2015). However, this research  
343     tradition required an update as DNA sequences are becoming available for an increasing number of species  
344     and species groups (see Fig. 1c). Overall, 53 and 30 families were recognised in the most recent systematic  
345     revision of Monogenea and Monopisthocotylea by Boeger and Kritsky (2001), respectively. The diagnoses  
346     of Ancyrocephalidae Bychowsky, 1937 and Dactylogyridae Bychowsky, 1935, which have been used  
347     interchangeably in the past, rely on the difference mainly in the number of seminal vesicles supported by a  
348     cladistic study of Bychowsky and Nagibina (1978) and the revision of Malmberg (1990). However, the  
349     revision of Kritsky and Boeger (1989) proposed Ancyrocephalidae *sensu* Bychowsky & Nagibina, 1978 as a  
350     junior synonym of Dactylogyridae as Ancyrocephalidae appeared paraphyletic with no unambiguous  
351     morphological evidence supporting the distinction between both families. As the difference in number of  
352     seminal vesicles is not consistent among the macroclades A and B and no other unambiguous  
353     morphological differences were identified in this study (see Supporting Information S1; Figs. 5 & 6), we  
354     follow the previously suggested synonymisation of Dactylogyridae and Ancyrocephalidae with  
355     Dactylogyridae having taxonomic priority.

356     Our results also confirm that *Protygodactylus* Johnston & Tiegs, 1922 is a genus within Dactylogyridae  
357     and as sister taxon to *Metahaliotrema*. Thus, we consider the family Protygodactylidae Johnston & Tiegs,  
358     1922 invalid and a synonym of Dactylogyridae as previously suggested by Price and Pike (1969).

359     Unlike Malmberg (1990), we conclude that *Ergenstrema mugilis* is nested within Dactylogyridae and  
360     representatives of this genus should be reassigned from Tetraonchidae to Dactylogyridae as proposed by  
361     Mendoza-Palmero et al. (2015) and Blasco-Costa et al. (2012). However, species of *Tetraonchus* Diesing,  
362     1858 are not transferred to Dactylogyridae and are kept in Tetraonchidae as this genus forms a separate  
363     lineage as supported by a recent phylogenetic reconstruction based on mitochondrial protein coding  
364     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 *Pseudodactylogyryus* 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 *Pseudodactylogyryus* 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 Ancylo-discoidinae to family level comprising monogeneans from siluriform and noto-pterid fishes of the Old World with four anchors. Although our results moderately support the monophyletic status of ancylo-discoidine monogeneans (clades B1–B5), the lineage is included in



392 macroclade B together with clade B6. Moreover, given that *Ancyrocephalus paradoxus* as type species is  
393 placed in clade B6, Ancyrocephalidae has taxonomic priority over Ancylo-discoididae. Hence, we propose  
394 that Ancylo-discoididae should be synonymised with Dactylogyridae.  
395 Neither representatives of the families Calceostomatidae, Fridericianellidae, Neocalceostomatidae, and  
396 Neotetraonchidae nor the subfamilies Linguadactylinae, Linguadactyloidinae, Hareocephalinae, and  
397 Heterotesiinae were included in the presented phylogenetic reconstruction due to the absence of  
398 published DNA sequence data. Therefore, the status of these taxa remains unresolved (Justine et al., 2002).

### 399 **Subfamily Dactylogyrinae Bychowsky, 1937**

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

402 *Diagnosis (based on diagnoses of genera with available molecular data available):* Two or four eye-spots;  
403 might be dissociated, incipient, or lacking. Body fusiform, pyriform, or uniform in width; compact or divided  
404 in cephalic region with trunk, peduncle, and haptor. Tegument smooth or striated. Two or three pairs of  
405 cephalic lobes; sometimes poorly developed. Three to five pairs of bilateral head organs; sometimes poorly  
406 developed. Cephalic glands unicellular, in two, three, or four pairs; might be dissociated or inconspicuous.  
407 Mouth subterminal. Intestinal caeca 2, confluent posterior to gonads or not united, diverticula present or  
408 absent. Common genital pore midventral or absent. Gonads in tandem or overlapping, intercaecal. Vas  
409 deferens looping left intestinal cecum or not looping; one or two seminal vesicles are a dilation of vas  
410 deferens. One or two prostatic reservoirs; might be absent. Vaginal aperture sclerotised or not sclerotised.  
411 Male copulatory organ sclerotised, tubular, coiled, or straight; accessory piece articulated or detached;  
412 might be weakly sclerotised or absent. Seminal receptacle present or absent. Vitellaria coextensive with the  
413 gut or scattered throughout the body. Haptor armed with single or paired dorsal and ventral anchor/bar  
414 sclerotised complexes; additional structures with various levels of sclerotisation might be present; 7 pairs of  
415 similar or dissimilar marginal hooks. Infecting the gills, skin, pharynx, oesophagus, intestines, urinary  
416 bladder, and kidneys of freshwater and marine fishes worldwide.

417 *Includes (only genera with molecular data available mentioned): 'Ancyrocephalus' mogurndae* (Yamaguti,  
418 1940); *Bravohollisia* Bychowsky & Nagibina, 1970; *Characidotrema* Paperna & Thurston, 1968; *Cichlidogyrus*  
419 Paperna, 1960; *Dactylogyrus* Diesing, 1850; *Enterogyrus* Paperna, 1963; *Ergenstrema* Paperna, 1964;  
420 *Eutrianchoratus* Paperna, 1969; *Glyphidohaptor* Kritsky, Galli & Yang, 2007; *Gobioecetes* Ogawa & Ito, 2017;  
421 *Gussevia* Kohn & Paperna, 1964; *Haliotrema* Johnston & Tiegs, 1922; *Haliotrematoides* Kritsky, Yang & Sun,  
422 2009; *Heteronchocleidus* Bychowsky, 1957; *Kapentagyrus* Kmentová, Gelnar & Vanhove, 2018;  
423 *Lethrinitrema* Lim & Justin, 2011; *Ligophorus* Euzet & Suriano, 1977; *Metahaliotrema* Yamaguti, 1953;  
424 *Mexicana* Caballero & Bravo-Hollia, 1959; *Onchobdella* Paperna, 1968; *Paradiplectanotrema* Gerashev,  
425 Gayevskaya & Kovaleva, 1987; *Parancyrocephaloides* Yamaguti, 1938; *Parasciadicleithrum* Mendoza-  
426 Palmero, Blasco-Costa, Hernández-Mena & Pérez-Ponce de León, 2017; *Platycephalotrema* Kritsky & Nitta,  
427 2019; *Protygyrodactylus* Johnston & Tiegs, 1922; *Pseudempleurosoma* Yamaguti, 1965; *Pseudodactylogyrus*  
428 Gusev, 1965; *Pseudohaliotrema* Yamaguti, 1953; *Sciadicleithrum* Kritsky, Thatcher & Boeger, 1989;  
429 *Tetrancistrum* Goto & Kikuchi, 1917; *Thylacicleidus* Wheeler & Klassen, 1988; *Trianchoratus* Price & Berry,  
430 1966; *Xenoligophoroides* Dmitrieva, Sanna, Piras, Garippa & Merella, 2018.

431 Remarks:

432 As mentioned in the result section, the two macroclades found here each include the type genera  
433 (*Dactylogyrus* and *Ancyrocephalus*) of two of the previously suggested subfamilies. Therefore, we reassign  
434 Ancyrocephalinae and Dactylogyrinae, subfamilies of Dactylogyridae, to these macroclades. As a  
435 consequence, Heteronchocleidinae, Protygyrodactylinae, and Pseudodactylogyrinae are synonymised with  
436 Dactylogyrinae. However, we could identify no apparent morphological differences between the genera  
437 belonging to these groups based on diagnostic features of internal organs and sclerotised structures in the  
438 literature (see Supporting Information S1 and Fig. 3). Given the lack of distinctive features for the  
439 subfamily, only genera with molecular data available are included here. Šimková et al. (2006) identified two  
440 sister groups within Dactylogyridae *sensu* Kritsky and Boeger (1989). The first group includes the freshwater  
441 species belonging to Ancyrocephalinae and Ancylo-discoidinae. The second group includes species belonging  
442 to Pseudodactylogyrinae, Dactylogyrinae, and marine representatives of Ancyrocephalinae. Kritsky and

443 Boeger (1989) proposed nine different subfamilies. We identified 16 well- or moderately supported clades  
444 (Fig. 2), which only partially confirm the proposed subfamilies/clades. Compared to previous studies  
445 (Mendoza-Palmero et al., 2015; Moreira et al., 2019b; Mendoza-Palmero et al., 2020), we report higher  
446 support values for the clade of predominantly marine dactylogyrids (A8).

#### 447 **Subfamily Ancyrocephalinae Bychowsky, 1937**

448 *Junior synonyms:* Anacanthorinae Price, 1967 and Ancylo-discoidinae Gussev, 1961.

449 *Includes (only genera with molecular data available mentioned):* *Actinocleidus* Müller, 1937; *Ameloblastella*  
450 Kritsky, Mendoza-Franco & Scholz, 2000; *Anacanthorus* Mizelle & Price, 1965; *Ancyrocephalus* Creplin,  
451 1839; *Aphanoblastella* Kritsky, Mendoza-Franco & Scholz, 2000; *Boegeriella* Mendoza-Palmero & Hsiao,  
452 2020; *Bychowskyella* Akhmerov, 1952; *Cacatuocotyle* Boeger, Domingues & Kritsky, 1997; *Cornudiscoides*  
453 Kulkarni, 1969; *Characithecium* Mendoza-Franco, Reina & Torchin, 2009, *Cosmetocleithrum* Kritsky,  
454 Thatcher & Boeger, 1986; *Demidospermus* Suriano, 1983; *Diaphorocleidus* Jogunoori, Kritsky &  
455 Venkatanarasaiah, 2004; *Hamatopeduncularia* Yamaguti, 1953; *Heteropriapulius* Kritsky, 2007; *Ligictaluridus*  
456 Beverley-Burton, 1984; *Mymarothecium* Kritsky, Boeger & Jégu, 1998; *Nanayella* Acosta, Mendoza-  
457 Palmero, da Silva & Scholz, 2019; *Pavanelliella* Kritsky & Boeger, 1998; *Pseudancylo-discoides* Yamaguti,  
458 1963; *Quadriacanthus* Paperna, 1961; *Schilbetrema* Paperna & Thurston, 1968; *Susanlimocotyle* Soares,  
459 Domingues & Adriano, 2020; *Thaparocleidus* Jain, 1952; *Trinigyrus* Hanek, Molnár & Fernando, 1974;  
460 *Unibarra* Suriano & Incorvaia, 1995; *Unilatus* Mizelle & Kritsky, 1967; *Urocleidoides* Mizelle & Price, 1964;  
461 *Vancleaveus* Kritsky, Thatcher & Boeger, 1986.

462 *Diagnosis (based on generic diagnoses of genera with available molecular data):* Two or four eye-spots;  
463 might be dissociated, incipient, or lacking. Body fusiform, pyriform, or uniform in width; compact or divided  
464 of cephalic region with trunk, peduncle, and haptor. Tegument smooth. Two or three pairs of cephalic  
465 lobes; sometimes poorly developed. Two to four pairs of bilateral head organs; sometimes poorly  
466 developed. Cephalic glands unicellular, in two, three, or four pairs; might be dissociated or inconspicuous.  
467 Mouth subterminal. Intestinal caeca 2, confluent posterior to gonads or not united, diverticula absent.  
468 Common genital pore midventral or inconspicuous. Gonads in tandem or overlapping, intercaecal. Vas

469 deferens looping left intestinal cecum or not looping; one or two seminal vesicles are a dilation of vas  
470 deferens. One or two prostatic reservoirs. Vaginal aperture sclerotised or not sclerotised. Male copulatory  
471 organ sclerotised, tubular, coiled, or straight; accessory piece articulated or detached; might be weakly  
472 sclerotised or absent. Seminal receptacle present or absent. Vitellaria coextensive with gut or scattered  
473 throughout the body. Haptor armed with single or paired dorsal and ventral anchor/bar sclerotised  
474 complexes, sometimes absent; additional structures with various levels of sclerotisation might be present;  
475 7 pairs of similar or dissimilar marginal hooks. Infecting the gills, skin, or nasal cavities of freshwater and  
476 marine fishes worldwide.

477 Remarks:

478 As reported above, the two macroclades found here each include a type genus (*Dactylogyrus* and  
479 *Ancyrocephalus*) of the two suggested subfamilies. Therefore, we reassign Ancyrocephalinae and  
480 Dactylogyrinae to these macroclades as subfamilies of Dactylogyridae as presented by Bychowsky, 1937.  
481 Similar to Dactylogyrinae, we could identify no apparent morphological similarities between the genera  
482 belonging to the subfamily based on diagnostic features of internal organs and sclerotised structures in the  
483 literature (see Fig. 3, Figs. 5 & 6). Therefore, only genera with molecular data available are included.  
484 Anacanthorinae and Ancylo-discoidinae are synonymised with Ancyrocephalinae. Representatives of  
485 Anacanthorinae Price, 1968 sequenced to date form a monophyletic group (Moreira et al., 2019b) nested  
486 within Ancyrocephalinae as defined here and comprise species of *Anacanthorus* that are unique in lacking  
487 anchors and bars. Representatives of Ancylo-discoidinae are also nested within Ancyrocephalinae (see  
488 remarks for Dactylogyridae) albeit without representatives of the type genus *Ancylo-discoides* Johnston &  
489 Tiegs, 1922 being sequenced so far. Moreover, other genera formerly considered members of  
490 Ancylo-discoididae *sensu* Lim et al. (2001) and Anacanthorinae Price, 1968 also likely form also part of this  
491 subfamily as suggested by the morphological similarities observed with representatives so far included in  
492 phylogenetic analyses. These genera include *Anacanthoroides* Kritsky & Thatcher, 1974, *Anchylodiscus*  
493 Johnston & Tiegs, 1922, *Ancylo-discoides* Yamaguti, 1937, *Bagrobdella* Paperna, 1969, *Bifurcohaptor* Jain,  
494 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

521 *Demidospermus* and *Urocleidoides* (Acosta et al., 2018). Many species formerly considered part of these  
522 groups share morphological features but are otherwise unrelated. To address this issue, some studies  
523 based generic classification on monophyletic clades inferred from phylogenetic reconstructions  
524 (phylogenetic systematics) of ribosomal DNA regions. For instance, *Parasciadicleithrum octofasciatum*  
525 Mendoza-Palmero, Blasco-Costa, Hernández-Mena & Pérez-Ponce de León, 2017 is morphologically almost  
526 indistinguishable from species of *Sciadicleithrum* (Mendoza-Palmero et al., 2017) but appears to be more  
527 closely related to *Gussevia asota* (Fig. 2: Clade A3). However, the type species of *Sciadicleithrum*, *S.*  
528 *uncinatum* Kritsky, Thatcher & Boeger, 1989, has not been sequenced to date. Thus, the phylogenetic  
529 position of *P. octofasciatum* in relation to *S. uncinatum* remains unknown and it seems premature to have  
530 placed the former in a new genus. A similar approach has also led to the erroneous erection of the genus  
531 *Paracosmetocleithrum* Acosta, Scholz, Blasco-Costa, Alves & da Silva, 2017. A lack of support for a  
532 monophyletic clade including the type species *P. trachydorasi* Acosta, Scholz, Blasco-Costa, Alves & da Silva,  
533 2017 and other species of *Cosmetocleithrum* was misinterpreted as evidence for taxon separation in spite  
534 of the unresolved relationship between these taxa (Acosta et al., 2018). Later, the genus was reassigned to  
535 *Cosmetocleithrum* as conclusions drawn from the phylogenetic analysis were questioned because of a lack  
536 of morphological differences (Cohen et al., 2020). Our results agree with this decision as we found partial  
537 support (95/\*/\*/\*) for *Cosmetocleithrum sensu* Cohen et al. (2020). The need for strictly monophyletic taxa  
538 remains contested in the literature (Schmidt-Lebuhn, 2012; Stuessy and Hörandl, 2014; for an extensive  
539 discussion against the use of paraphyletic taxa, see Schmidt-Lebuhn, 2012). Yet we argue that all taxa  
540 should reflect phylogenetic hypotheses and, consequently, the evolutionary history (for an extensive  
541 discussion against the use of paraphyletic taxa, see Schmidt-Lebuhn, 2012). In the following section we  
542 provide a list of poly- and paraphyletic molecularly characterised dactylogyrid genera, to be revised in  
543 future systematic studies, with remarks on their host repertoires and morphological  
544 similarities/differences.

545 *Ancyrocephalus* Creplin, 1936

546 The diagnosis of *Ancyrocephalus* has been revalidated by Bychowsky & Nagibina, 1970 to include  
547 representatives infecting only percids, namely *A. paradoxus* and *A. percae* (Fig. 2: clade B6). Yet several  
548 other species remain classified under this genus. Therefore, the catch-all genus *Ancyrocephalus* has  
549 remained polyphyletic with, e.g., *A. mogurndae* being placed among the Dactylogyrinae (clade A9) rather  
550 than the Ancyrocephalinae (Fig. 2: clade B6). In the past, this polyphyly has resulted in the proposal of  
551 several genera whose members were previously assigned to *Ancyrocephalus* including *Kapentagyris*  
552 (Kmentová et al., 2018), *Ligophorus* (Euzet and Suriano, 1977; Marchiori et al., 2015), and  
553 *Xenoligophoroides* (Dmitrieva et al., 2018). Here however, we refrain from creating a new genus for *A.*  
554 *mogurndae* as sequences of a majority species of *Ancyrocephalus* are unavailable and systematic revision of  
555 the genus should be based on more extensive molecular and morphological datasets than used in the  
556 present study.

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

558 The genera *Bravohollisia* and *Caballeria* were proposed for gill parasites of haemulid fishes (Lim, 1995).  
559 Both groups are morphologically similar, i.e. they present a simple copulatory tube without accessory  
560 pieces, anchors with canals running from shaft to point, similarly sized marginal hooks, haptoral glands, and  
561 a net-like structure near the tips of the anchors (Lim, 1995). Species of *Caballeria* differ regarding the  
562 presence of haptoral digits. However, phylogenetic studies suggest that some species of *Caballeria* are  
563 nested within a clade of species *Bravohollisia* (Wu et al., 2007; Sun et al., 2014), a result confirmed in the  
564 present study (Fig. 2). However, the type species of both genera, *C. pedunculata* Bychowsky & Nagibina,  
565 1970 and *B. magna* Bychowsky & Nagibina, 1970 have not been sequenced to date. Future studies should  
566 investigate the phylogenetic position of the type species as well as a wider array of species from these  
567 genera to untangle the relationship of *Bravohollisia* and *Caballeria*.

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

569 Both species of *Scutogyrus* and *Cichlidogyrus* are parasites of cichlids with in the latter genus a few  
570 exceptions infecting nothobranchiid and polycentrid hosts (Birgi and Euzet, 1983; Birgi and Lambert, 1986).  
571 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 *Dogieli* Bychowsky, 1936

*Dogieli* 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 *Dogieli* (Dash et al., 2014), the species included (*Dogieli catlai* (Jain, 1962) as '*Dactylogyrus catlai* Jain, 1961 [sic]') appeared nested in *Dactylogyrus*. Our phylogenetic analyses indicate that species of *Dactylogyroides* together with those of *Dactylogyrus* and *Dogieli* 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 *Dogieli* 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 *Dogieli*, *D. forceps* Bychowsky, 1936, should also be included in future studies alongside a wider array of species of *Dactylogyroides*, *Dactylogyrus*, and *Dogieli* 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*,

625 *Parancyrocephaloides*, *Pseudohaliotrema*, *Tetrancistrum*, and *Thylacicleidus* (Fig. 2: clade A8). The lack of  
626 distinctive morphological features of species of *Haliotrema* compared to the other genera in the clade and  
627 the lack of an apparent host-related pattern highlight the need for revising this genus as already suggested  
628 by Klassen (1994). In this context, Kritsky and Nitta (2019) created *Platycephalotrema* to encompass  
629 dactylogyrid parasites infecting platycephalid fishes but remarked that likely all dactylogyrid parasites of  
630 scorpaeniform fishes assigned to the *Ancyrocephalus* and *Haliotrema* might belong to this group. Yet recent  
631 phylogenetic studies show that the used host classification is outdated: Platycephalidae Gill, 1872 is now  
632 classified in the suborder Platycephaloidei within Perciformes (Betancur-R et al., 2017). Kritsky and Nitta  
633 (2019) did also not discuss phylogenetic relationships of the group despite the availability of molecular data  
634 for two species of *Platycephalotrema*, *P. macassarensis* and *P. platycephali* (both described under  
635 *Haliotrema*) (Wu et al., 2006; Sun et al., 2014). Therefore, they did not note that *Haliotrema johnstoni* is  
636 closely related to or even nested in *Platycephalotrema* as it appears according to a more recent study (Soo,  
637 2019) and the results here, which both include all available sequences of species of *Platycephalotrema*.  
638 *Haliotrema johnstoni* also presents a dorsal bar with bifurcating ends similar to species of  
639 *Platycephalotrema*, but does not lack the accessory piece in the male copulatory organ and has a different  
640 host repertoire (Syngnathiformes, Mullidae). The relationship of *H. johnstoni* with members of  
641 *Platycephalotrema* should be investigated further.

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

643 *Euryhaliotrema* encompasses gill parasites of lutjanid, sciaenid, sparid, and heamulid fishes in marine and  
644 freshwater environments (Kritsky, 2012). *Sciadicleithrum* was proposed for gill parasites of Neotropical  
645 cichlid fishes. It was proposed to be closely related to species of *Gussevia*, which also infect Neotropical  
646 cichlids, but differ regarding an unmodified hook pair 5, a ventral bar with anterior umbelliform  
647 membranes or cavities and unmodified anchors (Kritsky et al., 1989). Species of *Euryhaliotrema* and  
648 *Sciadicleithrum* have never been compared morphologically, most likely because their distinct host  
649 repertoires (cichlids vs. other fishes) and habitats (most species of *Sciadicleithrum* are limnic whereas a  
650 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

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

#### 678 *Environment and biogeography*

679 Monogenean evolution is often considered to reflect a co-divergence with the host lineages (Pariselle et al.,  
680 2011). As dactylogyrid monogeneans occur in almost every biogeographic realm, their deep evolutionary  
681 history is likely shaped by large-scale biogeographical factors including continental drift, changes in salinity,  
682 and teleost diversification. Biogeographical, salinity (marine vs. freshwater), and host-related distinctions  
683 between the respective (macro)clades can be observed (Fig. 2). Environmental factors affect endo- and  
684 ectoparasites differently (Pariselle et al., 2011). Endoparasites are more likely shielded from environmental  
685 changes although the egg/larval development might partly occur in an external environment (Theisen et al.,  
686 2018; Assane et al., 2021). Notably, the phylogenetic tree presented here (Fig. 2) suggests a common  
687 ancestor for all endoparasitic dactylogyrid species sequenced to date. In contrast, ectoparasites are directly  
688 exposed to external stressors. Sudden changes in salinity are deadly to many gill monogeneans and hence,  
689 are used to treat these infections in aquaculture (Fajer-Ávila et al., 2007; Schelkle et al., 2011; Brazenor and  
690 Hutson, 2015). This effect might explain why closely related ectoparasitic dactylogyrids appear often  
691 exclusive to either freshwater or marine habitats (see Fig. 2). However, interpretations of these patterns  
692 should be treated with caution as these observations are based on ribosomal genes and few species and  
693 genera only.

694 Despite these limitations, early evidence from previous studies indicates at least a partial adherence to  
695 freshwater and marine habitats in dactylogyrid species infecting catfishes (Siluriformes). Catfishes  
696 constitute approximately 30% part of the world's ichthyofauna in terms of species richness (Teugels, 1996)  
697 and have a Pangaeian origin that dates back to the Early Cretaceous period (145–66 MYA) (Teugels, 1996;  
698 Chen et al., 2013). For these reasons, catfishes have been established as models for historical biogeography  
699 (e.g. Agnèse and Teugels, 2005; Betancur-R. et al., 2007; Roxo et al., 2014; Van Steenberge et al., 2020).  
700 Several phylogenetic studies have focused on the evolutionary history of the Neotropical dactylogyrid  
701 lineages infecting siluriform hosts. Our study suggests that all molecularly characterised dactylogyrid

702 monogenean genera infecting catfishes belong to a single lineage (macroclade B) with two clades (Fig. 2:  
 703 B1, B2, and B4) specific to New World hosts and two others to Old World species (Fig. 2: B3 and B5). This  
 704 pattern appears to indicate that dactylogyrid monogeneans have followed their hosts' evolution to spread  
 705 to all continents before the time Pangaea separated 200 million years ago remaining in freshwater habitats  
 706 except for a single mostly marine dactylogyrid lineage (Fig. 2: clade B3). However, as many lineages and  
 707 species infecting siluriform hosts have not been sequenced to date, the pattern found here might also be  
 708 an artifact of a boom of studies investigating certain taxa among these parasites (e.g., Wu et al., 2008;  
 709 Mendoza-Palmero et al., 2015, 2019; Francová et al., 2017; Acosta et al., 2017, 2018; Franceschini et al.  
 710 2018, 2020; Soo and Tan, 2021).

711 Another example for possible adherence to freshwater habitats, are the species infecting the gills of cichlid  
 712 fishes. All species (that have been sequenced) belong to macroclade (A) including representatives of  
 713 *Cichlidogyrus*, *Onchobdella*, and *Scutogyrus* from continental Africa (Pariselle and Euzet, 2009), and  
 714 *Gussevia*, *Parasciadicleithrum*, and *Sciadicleithrum* from the Americas (Mendoza-Palmero et al., 2017).  
 715 However, cichlids have a Gondwanan origin with the oldest lineages found in Madagascar (Matschiner,  
 716 2019; Matschiner et al., 2020). Dactylogyrid gill parasites on Neotropical and African cichlids that we know  
 717 of constitute four different lineages that are not closely related including *Cichlidogyrus-Scutogyrus*,  
 718 *Gussevia-Parasciadicleithrum*, *Onchobdella*, and *Sciadicleithrum* (Fig. 2). Based on these lineages, previous  
 719 studies hypothesised that cichlids must have crossed marine habitats (Pariselle et al., 2011; Vanhove et al.,  
 720 2016) enabling multiple dactylogyrid freshwater lineages (*Insulacleidus* spp. in Madagascar, or *Onchobdella*  
 721 or *Cichlidogyrus* in Africa, and *Gussevia*, *Sciadicleithrum* or *Parasciadicleithrum* in South America) to infect  
 722 cichlids. Transatlantic dispersal of cichlids has since then been further discussed in ichthyological studies  
 723 (Matschiner, 2019; Matschiner et al., 2020). However, to elucidate the origin and dispersal history of cichlid  
 724 monogeneans, a more complete taxon coverage is needed. For instance, molecular data on endoparasitic  
 725 dactylogyrids infecting Neotropical cichlids would allow to evaluate whether endoparasitic lineages, indeed,  
 726 persisted after an alleged transatlantic dispersal in contrast to ectoparasitic dactylogyrids.

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

#### 735 *Taxonomic biases and limitations*

736 Despite the increasing number of described species and genera, and availability of DNA sequence data,  
737 taxonomic bias and limited data remain a major challenge for a comprehensive systematic revision of  
738 Dactylogyridae. Many phylogenetic studies in recent years have targeted specific taxa, clades, or  
739 geographic regions but omitted possibly related genera. For instance, phylogenetic publications  
740 investigating the parasite fauna of reef and littoral fish communities occasionally omit other taxa, e.g.,  
741 much of the research focusing on species formerly and presently considered members of *Haliotrema*  
742 including *Euryhaliotrema*, *Haliotrema*, *Haliotrematoides*, and *Metahaliotrema* fails to include freshwater  
743 taxa such as *Cichlidogyrus*, *Enterogyrus*, or *Scutogyrus* (Plaisance et al., 2005; Mendoza-Franco et al., 2018)  
744 or other taxa altogether (Kritsky et al., 2009b) despite DNA sequences of these species groups being  
745 available at the time. Furthermore, a boom of molecular characterisations of monogenean parasites  
746 infecting Neotropical siluriforms in recent years (e.g., Mendoza-Palmero et al., 2015) has produced many  
747 DNA sequence data of species belonging to Ancyrocephalinae (macroclade B), which now appears almost  
748 exclusive to siluriforms. Few studies have focused on other host groups such as cichliforms (Mendoza-  
749 Garfias et al., 2017), characiforms (Zago et al., 2018, 2020, 2021; Moreira et al., 2019b), and gymnotiforms  
750 (Zago et al., 2020) limiting the availability of molecular data from possibly related genera. In fact, molecular  
751 data of many parasite lineages remain unavailable (Poulin et al., 2019) and many species remain likely  
752 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 Palaearctic 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).

778 One step to taxon sampling could be a level playing field for multiple sequence alignments as provided by  
779 the present study. Our phylogeny presents by no means a comprehensive or definite phylogenetic tree of  
780 Dactylogyridae as we included only a subset of all DNA sequences available on Genbank deemed  
781 representative of the main lineages within a genus. A majority of species and type species of genera have  
782 also not been sequenced to date, and new species are discovered every year. Furthermore, we cannot rule  
783 out that some DNA sequences were wrongly assigned. Our study also highlights several groups and studies  
784 that have previously been overlooked by phylogenetic analysis. We also point out general trends regarding  
785 the phylogenetic relationships that should be investigated in more detail in the future. Thus, we suggest  
786 that the DNA sequence alignments of ribosomal (Fig. 2) and mitochondrial (Supplementary Information S2)  
787 DNA regions we provide here could form a new starting point for studies aiming to infer the phylogenetic  
788 position of new species and genera within Dactylogyridae.

#### 789 Concluding remarks

790 A phylogenetic reconstruction (meta-analysis) of dactylogyrid monogeneans based on three ribosomal gene  
791 portions traditionally used in flatworm taxonomy revealed two well-supported lineages. Because of the  
792 phylogenetic positions of the type genera and species of two previously described subfamilies, we revised  
793 the classification of Dactylogyridae into two subfamilies Dactylogyrinae and Ancyrocephalinae *sensu*  
794 Bychowsky and Nagibina (1978). Comparison with previous phylogenetic reconstructions of dactylogyrid  
795 monogeneans revealed differences in tree topology within both subfamilies. For the first time, a  
796 monophyletic clade of endoparasitic species was reported as well as three well-supported clades infecting  
797 siluriform hosts. In cases of paraphyly and polyphyly suggested by our phylogenetic analyses, we discuss  
798 the morphological characters and propose steps for a systematic revision. Apparent biogeographical  
799 patterns in the evolution of dactylogyrid monogeneans might be explained by sampling bias towards  
800 certain biogeographical regions and host taxa. This study aims to provide a level playing field for future  
801 phylogenetic studies on Dactylogyridae by presenting an alignment accompanied by state-of-the-art  
802 phylogenetic trees. We encourage researchers investigating dactylogyrid monogeneans to use the data



803 offered here as a baseline for their respective studies. This approach could reduce researcher bias and  
804 enable a more balanced phylogenetic approach of one of the most species-rich families of fish parasites.

#### 805 **Author contributions**

806 Conceptualization, N.K. and A.J.C.-L.; Methodology and data analyses, A.J.C.-L.; Writing—Original Draft  
807 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.;  
808 Supervision, M.P.M.V. All authors have read and agreed to the published version of the manuscript.

#### 809 **Acknowledgements**

810 This research was funded by Czech Science Foundation (GAČR) standard project GA19-13573S. N.K.  
811 (BOF21PD01), A.J.C.L. (BOF19OWB02) and M.P.M.V. (BOF20TT06) are financed by the Special Research  
812 Fund of Hasselt University. Walter A. Boeger (Universidade Federal do Paraná, Brazil) is thanked for fruitful  
813 discussions on this matter.

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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
<i>Actinocleidus</i> Mueller, 1937								
<i>Actinocleidus recurvatus</i> Mizelle & Donahue, 1944	<i>Lepomis gibbosus</i> (Linnaeus, 1758)		AJ969951				Slovakia	Šimková et al. (2006)
<i>Ameloblastella</i> Kritsky, Mendoza-Franco & Scholz, 2000								
<i>Ameloblastella chavarriai</i> (Price, 1938)	<i>Rhamdia quelen</i> (Quoy & Gaimard, 1824)	AmchRq1	KP056251				Mexico	Mendoza-Palmero et al. (2015)
<i>Ameloblastella edentensis</i> Mendoza-Franco, Mendoza-Palmero & Scholz, 2016	<i>Hypophtalmus edentatus</i> Spix & Aggasiz, 1829	Am16He	KP056255				Peru	Mendoza-Palmero et al. (2015)
<i>Ameloblastella unapioides</i> Mendoza-Franco, Mendoza-Palmero & Scholz, 2016	<i>Sorubim lima</i> (Bloch & Schneider, 1901)	Am8SI	KP056254				Peru	Mendoza-Palmero et al. (2015)
<i>Anacanthorus</i> Mizelle & Price, 1965								
<i>Anacanthorus lepyrophallus</i> Kritsky, Boeger & Van Every, 1992	<i>Serrasalmus maculatus</i> Kner, 1858	PR04/ PR214a1 <sup>a</sup>	MH843718			MK757436	Brazil	Moreira et al. (2019a, 2019b)
<i>Anacanthorus paraxaniophallus</i> Moreira, Carneiro, Ruz & Luque, 2019	<i>Serrasalmus marginatus</i> Valenciennes, 1837	PR50/ PR105b2 <sup>a</sup>	MH843717			MK757438	Brazil	Moreira et al. (2019a, 2019b)
<i>Anacanthorus penilabiatus</i> Boeger, Husak & Martins, 1995	<i>Piaractus mesopotamicus</i> (Holmberg, 1887)	PR05/ PR228a3 <sup>a</sup>	MH843719			MK757435	Brazil	Moreira et al. (2019a, 2019b)
<i>Ancyrocephalus</i> Creplin, 1839								
<i>Ancyrocephalus mogurndae</i> (Yamaguti, 1940)	<i>Siniperca chuatsi</i> (Basilewsky, 1855)		DQ157667				China	Wu et al. (2006)
<i>Ancyrocephalus paradoxus</i> Creplin, 1839	<i>Sander lucioperca</i> (Linnaeus, 1758)		AJ969952				Czech Republic	Šimková et al. (2006)
<i>Ancyrocephalus percae</i> Ergens, 1966	<i>Perca fluviatilis</i> Linnaeus, 1758	Ac3	KF499080				Finland	Behrmann-Godel et al. (2014)



<i>Aphanoblastella</i> Kritsky, Mendoza-Franco & Scholz, 2000						
<i>Aphanoblastella aurorae</i> Mendoza-Palmero, Scholz, Mendoza- Franco & Kuchta, 2012	<i>Goeldiella eques</i> (Müller & Troschel, 1849)	ApauGe	KP056239		Peru	Mendoza- Palmero et al. (2015)
<i>Aphanoblastella magna</i> Yamada, Acosta, Yamada, Scholz & Da Silva, 2018	<i>Pimelodella</i> <i>avanhandavae</i> Eigenmann, 1917	1	MH688484		Brazil	Yamada et al. (2018)
<i>Aphanoblastella travassosi</i> (Price, 1938)	<i>Rhamdia guatemalensis</i> (Günther, 1864)	2	MK358458		Mexico	Acosta et al. (2019)
<i>Boegeriella</i> Mendoza-Palmero & Hsiao, 2020						
<i>Boegeriella conica</i> (Mendoza- Palmero, Mendoza-Franco, Acosta & Scholz, 2019)	<i>Platynematchthys</i> <i>notatus</i> (Jardine, 1841)	Ancy10Pn2	KP056225		Peru	Mendoza- Palmero et al. (2015)
<i>Boegeriella ophiocirrus</i> (Mendoza-Palmero, Mendoza- Franco, Acosta & Scholz, 2019)	<i>Platystomatchthys sturio</i> (Kner, 1858)	2	MK834511		Peru	Mendoza- Palmero et al. (2019)
<i>Bravohollisia</i> Bychowsky & Nagibina, 1970						
<i>Bravohollisia maculatus</i> (Venkatanarasaiah, 1984)	<i>Pomadasys maculatus</i> (Bloch, 1793)	SYSU200604 29-3	KJ571008	KJ571018	China	Sun et al. (2014)
<i>Bravohollisia plectorhynchus</i> Li, Zhang, Chen & Chen, 2005	<i>Plectorhynchus</i> sp.	SYSU200605 02-2	KJ571010	KJ571019	China	Sun et al. (2014)
<i>Bravohollisia tecta</i> Bychowsky & Nagibina, 1970	<i>Pomadasys maculatus</i>	SYSU200604 29-4	KJ571012	KJ571020	China	Sun et al. (2014)
<i>Bychowskyella</i> Akhmerov, 1952						
<i>Bychowskyella pseudobagri</i> Akhmerov, 1952	<i>Tachysurus fulvidraco</i> (Richardson, 1846)		EF100541		China	Wu et al. (2008)
<i>Caballeria</i> Bychowsky & Nagibina, 1970						
<i>Caballeria intermedius</i> Lim, 1995	<i>Pomadasys argenteus</i> (Forsskål, 1775)	SYSU200605 01-4	KJ571013		China	Sun et al. (2014)
<i>Cacatuocotyle</i> Boeger, Domingues & Kritsky, 1997						
<i>Cacatuocotyle papilionis</i> Zago, Franceschini, Müller & da Silva, 2018	<i>Astyanax lacustris</i> (Lütgen, 1875)		MG832889		Brazil	Zago et al. (2018)

<i>Characithecium</i> Mendoza-Franco, Reina & Torchin, 2009								
<i>Characithecium paranpanemense</i> Zago, Franceschini, Abdallah, Müller, Azevedo & da Silva, 2021	<i>Psolidodon paranae</i> (Eigenmann, 1914)	2	MZ408902			MZ408251	Brazil	Zago et al. (2021)
<i>Characidotrema</i> Paperna & Thurston, 1968								
<i>Characidotrema nursei</i> Ergens, 1973	<i>Brycinus nurse</i> (Rüppell, 1832)	S	MK012540	MK014158	MK014158		Sudan	Řehulková et al. (2019)
<i>Characidotrema vespertilio</i> Kičinjaová & Řehulková, 2019	<i>Brycinus imberi</i> (Peters, 1852)	C	MK012543	MK014161	MK014161		Dem. Rep. of the Congo	Řehulková et al. (2019)
<i>Chauhanellus</i> Bychowsky & Nagibina, 1969								
<i>Chauhanellus auriculatum</i> Lim, 1994	<i>Plicofollis argyroleuron</i> (Valenciennes, 1840)	Ca1	MN108169	MN105020			Malaysia	Soo and Tan (2021)
<i>Chauhanellus boegeri</i> Domingues & Fehlaue, 2006	<i>Genidens genidens</i> (Cuvier, 1829)	ChboGg	KP056241				Brazil	Mendoza-Palmero et al. (2015)
<i>Chauhanellus intermedius</i> Lim, 1994	<i>Hexanematichtys sagor</i> (Hamilton, 1822)	Ci1	MN108172	MN105023			Malaysia	Soo and Tan (2021)
<i>Chauhanellus</i> sp.	<i>Genidens genidens</i>	ChGg	KP056242				Brazil	Mendoza-Palmero et al. (2015)
<i>Cichlidogyrus</i> Paperna, 1960								
<i>Cichlidogyrus arthracanthus</i> Paperna, 1960	<i>Coptodon guineensis</i> (Günther, 1862)	PC60	HQ010022	HE792783	HE792783		Senegal	Mendlová et al. (2010, 2012)
<i>Cichlidogyrus attenboroughi</i> Kmentová, Gelnar, Koblmüller & Vanhove, 2016	<i>Benthochromis tricoti</i> (Poll, 1948)	PB46 CiAt	MH708146	MH708153	MH708153		Burundi	Kmentová et al. (2018)
<i>Cichlidogyrus halli</i> (Price & Kirk, 1967)	<i>Oreochromis niloticus x mweruensis</i>	C ha	MG973075	MG973075	MG973075	MG970255	Dem. Rep. of the Congo	Vanhove et al. (2018)
<i>Cichlidogyrus pouyaudi</i> Pariselle & Euzet, 1994	<i>Tylochromis intermedius</i> (Boulenger, 1916)	PC69	HQ010039	HE792793	HE792793		Senegal	Mendlová et al. (2010, 2012)
<i>Cichlidogyrus sclerosus</i> Paperna & Thurston, 1969	<i>Oreochromis niloticus</i> Linnaeus, 1758		DQ157660	DQ537359	DQ537359		China	Wu et al. (2006, 2007)

<i>Cichlidogyrus zambezensis</i> Douëllou, 1993	<i>Serranochromis macrocephalus</i> (Boulenger, 1899)	AP375	MW580361	MW580384	MW580384	Zambia	Cruz-Laufer et al. (2021b)
<i>Cornudiscoides</i> Kulkarni, 1969							
<i>Cornudiscoides geminus</i> Gusev, 1976	<i>Mystus vittatus</i> (Bloch, 1794)	E07, EMOSS gc	KU358727	KU358728		India	Verma et al. (2017)
<i>Cornudiscoides proximus</i> Gusev, 1976	<i>Mystus vittatus</i>	C08, EMOSS pc	KU358726	KU235550		India	Verma et al. (2017)
<i>Cosmetocleithrum</i> Kritsky, Thatcher & Boeger, 1986							
<i>Cosmetocleithrum bifurcum</i> Mendoza-Franco, Mendoza-Palmero & Scholz, 2016	<i>Hassar orestis</i> (Steindachner, 1875)	Co8H2	KP056216			Peru	Mendoza-Palmero et al. (2015)
<i>Cosmetocleithrum bulbocirrus</i> Kritsky, Thatcher & Boeger, 1986	<i>Pterodoras granulosus</i> (Valenciennes, 1821)		MG001326			Brazil	Acosta et al. (2018)
<i>Cosmetocleithrum trachydorasi</i> (Acosta, Scholz, Blasco-Costa, Alves & da Silva, 2017)	<i>Trachydoras paraguayensis</i> (Eigenmann & Ward, 1907)		MG001323			Brazil	Acosta et al. (2018)
<i>Dactylogyridae</i> gen. sp. 13	<i>Hypophthalmus edentatus</i> Spix & Aggasiz, 1829	Ancy13He2	KP056230			Peru	Mendoza-Palmero et al. (2015)
<i>Dactylogyridae</i> gen. sp. 18	<i>Pseudoplatystoma fasciatum</i> (Linnaeus, 1766)	Ancy18Pf	KP056231			Peru	Mendoza-Palmero et al. (2015)
<i>Dactylogyridae</i> gen. sp. 23	<i>Platysilurus mucosus</i> (Vaillant, 1880)	Ancy23Pm	KP056232			Peru	Mendoza-Palmero et al. (2015)
<i>Dactylogyridae</i> gen. sp. 26	<i>Platynemichthys notatus</i> (Jardine, 1841)	Ancy26Pn	KP056234			Peru	Mendoza-Palmero et al. (2015)
<i>Dactylogyridae</i> gen. sp. 4	<i>Ageneiosus vittatus</i> Steindachner, 1908	Ancy4Av1	KP056218			Peru	Mendoza-Palmero et al. (2015)
<i>Dactylogyridae</i> gen. sp. 9	<i>Platynemichthys notatus</i>	Ancy9Pn5	KP056222			Peru	Mendoza-Palmero et al. (2015)

<i>Dactylogyroides</i> Gusev, 1963						
<i>Dactylogyroides tripathii</i> (Yamaguti, 1963)	<i>Pethia ticto</i> (Hamilton, 1822)		JX993982			India Chiary et al. (2013)
<i>Dactylogyrus</i> Diesing, 1859						
<i>Dactylogyrus bicornis</i> Malevitskaja, 1941	<i>Rhodeus meridionalis</i> Karaman, 1924	ROME Bicornis	KY629345			Greece Šimková et al. (2003)
<i>Dactylogyrus extensus</i> Mueller & Van Cleave, 1932	<i>Cyprinus caprio</i> Linnaeus, 1758		AJ969944	AJ564129	AJ564129	Czech Republic Šimková et al. (2003, 2006)
<i>Dactylogyrus lamellatus</i> Akhmerow, 1952	<i>Ctenopharyngodon idella</i> (Valenciennes, 1844)		AJ969948	AJ564141	AJ564141	Czech Republic Šimková et al. (2006)
<i>Dactylogyrus mascomai</i> El Gharbi, Renaud & Lambert, 1993	<i>Luciobarbus graellsii</i> (Steindachner, 1866)	LUGL Mascomai S13	MN338215	MN365680	MN365680	Spain Benovics et al. (2020a)
<i>Demidospermus</i> Suriano, 1983						
<i>Demidospermus anus</i> Suriano, 1983	<i>Loricariichthys platymetopon</i> Isbrücker & Nijssen, 1979	2	KY766957			Brazil Franceschini et al. (2018)
<i>Demidospermus mortenthaleri</i> Mendoza-Palermo, Scholz, Mendoza-Franco & Kuchta, 2012	<i>Brachyplatystoma juruense</i> (Boulenger, 1898)	DemoBj1	KP056245			Peru Mendoza-Palmero et al. (2015)
<i>Demidospermus prolixus</i> Franceschini, Zago, Müller, Francisco, Takemoto & da Silva, 2017	<i>Loricaria prolixa</i> (Isbrücker & Nijssen, 1978)		KY766955			Brazil Franceschini et al. (2018)
<i>Demidospermus rhinelepisi</i> Acosta, Scholz, Blasco-Costa, Alves & da Silva, 2017	<i>Rhinelepis aspera</i> Spix & Agassiz, 1829		MG001324			Brazil Acosta et al. (2018)
<i>Demidospermus</i> sp. 11	<i>Brachyplatystoma vaillantii</i> (Valenciennes, 1840)	De11Bv	KP056235			Peru Mendoza-Palmero et al. (2015)
<i>Demidospermus</i> sp. 23	<i>Brachyplatystoma vaillantii</i>	De23Bv	KP056236			Peru Mendoza-Palmero et al. (2015)
<i>Diaphorocleidus</i> Jogunoori, Kritsky & Venkatanarasaiah, 2004						

<i>Diaphorocleidus magnus</i> Zago, Franceschini, Abdallah, Müller, Azevedo & da Silva, 2021	<i>Astyanax lacustris</i> (Lütgen, 1875)	1	MZ408903			MZ408253	Brazil	Zago et al. (2021)
<i>Diaphorocleidus neotropicalis</i> Zago, Franceschini, Abdallah, Müller, Azevedo & da Silva, 2021	<i>Astyanax lacustris</i> (Lütgen, 1875)	1	MZ408906			MZ408254	Brazil	Zago et al. (2021)
<i>Dogieli</i> Bychowsky, 1936								
<i>Dogieli</i> <i>catlani</i> (Jain, 1962)	<i>Labeo rohita</i> (Hamilton, 1822)		KC687091				India	Dash et al. (2014)
<i>Enterogyrus</i> Paperna, 1963								
<i>Enterogyrus coronatus</i> Pariselle, Lambert & Euzet, 1991	<i>Tilapia dageti</i> Thys van den Audenaerde, 1967		HQ010030				Senegal	Mendlová et al. (2010)
<i>Enterogyrus malmbergi</i> Bilong Bilong, 1988	<i>Oreochromis niloticus</i>	GZ-ZSDX	MN152976			MN095193	China	Zhang et al. (2019)
<i>Ergenstrema</i> Paperna, 1964								
<i>Ergenstrema mugilis</i> Paperna, 1964	<i>Chelon ramada</i> (Risso, 1827)		JN996800	JN996835	JN996835		Spain	Blasco-Costa et al. (2012)
<i>Euryhaliotrema</i> Kritsky & Boeger, 2002								
<i>Euryhaliotrema johnii</i> Tripathi, 1959	<i>Lutjanus johnii</i> (Bloch, 1792)	ZSU 20060501-1	EU836193	EU836214			China	Sun et al. (2014)
<i>Euryhaliotrema mehen</i> (Solar-Jiménez, García-Gasca & Fajera-Ávila, 2012)	<i>Lutjanus guttatus</i> (Steindachner, 1869)	LSJ-2011	HQ615997				Mexico	Soler-Jiménez et al. (2012)
<i>Euryhaliotrema pirulum</i> (Plaisance & Kritsky, 2004)	<i>Chaetodon lunula</i> (Lacepède, 1802)		AY820618	AY820607			French Polynesia	Plaisance et al. (2005)
<i>Euryhaliotrema spirobifurum</i> (Zhang in Zhang, Yang & Liu, 2001)	<i>Lutjanus stellatus</i> (Akazaki, 1983)		DQ157656	DQ537347			China	Wu et al. (2006, 2007)
<i>Eutrianchoratus</i> Paperna, 1969								
<i>Eutrianchoratus cleithrum</i> Lim, 1989	<i>Belontia hasselti</i> (Cuvier, 1831)		HQ719224				Malaysia	Tan et al. (2011)
<i>Glyphidohaptor</i> Kritsky, Galli & Yang, 2007								

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

<i>Haliotrematoides plectridium</i> Kritsky & Mendoza-Franco, 2009	<i>Lutjanus guttatus</i>		HQ615994				Mexico	García-Vásquez et al. (2015)
<i>Haliotrematoides spinatus</i> Kritsky & Mendoza-Franco, 2009	<i>Lutjanus guttatus</i>		HQ615995	JN054404			Mexico	Soler-Jiménez et al. (2012)
<i>Hamatopeduncularia</i> Yamaguti, 1953								
<i>Hamatopeduncularia arii</i> Yaamaguti, 1953	<i>Arius jella</i> Day, 1877			KT252895			Mexico	Illa et al. (2019)
<i>Hamatopeduncularia bagre</i> Hargis, 1955	<i>Bagre marinus</i> (Mitchill, 1815)	5	MG586871				Mexico	Mendoza-Franco et al. (2018)
<i>Hamatopeduncularia</i> <i>isosimplex</i> Lim, 1996	<i>Arius maculatus</i> (Thunberg, 1792)	Hi1	MN108167	MN105018			Malaysia	Soo and Tan (2021)
<i>Hamatopeduncularia</i> <i>petalumvaginata</i> Soo & Tan, 2021	<i>Nemapteryx caelata</i> (Valenciennes, 1840)	Hp1	MN108164	MN105015			Malaysia	Soo and Tan (2021)
<i>Heteronchocleidus</i> Bychowsky, 1957								
<i>Heteronchocleidus buschkieli</i> Bychowsky, 1957	<i>Macropodus opercularis</i> (Linnaeus, 1758)		AY841876				China	Tan et al. (2011)
<i>Heteropriapul</i> Kritsky, 2007								
<i>Heteropriapul heterotylus</i> (Jogunoori, Kritsky & Venkatanarasaiah, 2004)	<i>Pterygoplichthys</i> <i>ambrosettii</i> (Holmberg, 1893)		MF116370				Brazil	Acosta et al. (2017)
<i>Heteropriapul simplex</i> Li & Huang, 2012	<i>Pterygoplichthys</i> <i>ambrosettii</i>		MF116372				Brazil	Acosta et al. (2017)
<i>Kapentagyris</i> Kmentová, Gelnar & Vanhove 2018								
<i>Kapentagyris limnotrissae</i> (Paperna, 1973)	<i>Limnotrissa miodon</i> (Boulenger, 1906)	LI14	MH071782	MH071808	MH071808	MK598084	Dem. Rep. of the Congo	Kmentová et al. (2018, 2020b)
<i>Kapentagyris tanganicanus</i> Kmentová, Gelnar & Vanhove 2018	<i>Stolothrissa tanganicae</i> Regan, 1907	LI8	MH071783	MH071807	MH071807	MK598180	Dem. Rep. of the Congo	Kmentová et al. (2018, 2020b)
<i>Lethrinotrema</i> Lim & Justine, 2011								
<i>Lethrinotrema</i> <i>grossecurvitubum</i> (Li & Chen, 2005)	<i>Lethrinus nebulosus</i> (Forsskål, 1775)	ZSU 20060522-1	EU836204	EU836225			China	Sun et al. (2014)

<i>Lethrinus nebulosus</i> Sun, Li & Yang, 2014	<i>Lethrinus nebulosus</i>	ZSU 20060524-1	EU836203	EU836224		China	Sun et al. (2014)
<i>Ligictaluridus</i> Beverley-Burton, 1984							
<i>Ligictaluridus pricei</i> (Mueller, 1936)	<i>Ameiurus nebulosus</i> (Lesueur, 1819)		AJ969939	AJ490168	AJ490168	Czech Republic	Šimková et al. (2003, 2006)
<i>Ligophorus</i> Euzet & Suriano, 1977							
<i>Ligophorus imitans</i> Euzet & Suriano, 1977	<i>Chelon ramada</i> (Risso, 1827)		JN996813	JN996849	JN996849	Spain	Blasco-Costa et al. (2012)
<i>Ligophorus leporinus</i> (Zhang & Ji, 1981)	<i>Mugil cephalus</i> Linnaeus, 1758		DQ537380			China	Wu et al. (2007)
<i>Ligophorus vanbenedenii</i> (Parona & Perugia, 1890)	<i>Chelon auratus</i> (Risso, 1810)		JN996801	JN996836	JN996836	Spain	Blasco-Costa et al. (2012)
<i>Metahaliotrema</i> Yamaguti, 1953							
<i>Metahaliotrema digyroides</i> (Zhang in Zhang, Yang & Liu, 2001)	<i>Gerres macrosoma</i> Cuvier, 1830		DQ537377	DQ537349		China	Wu et al. (2007)
<i>Metahaliotrema scatophagi</i> Yamaguti, 1953	<i>Scatophagus argus</i> (Linnaeus, 1766)		DQ157646	DQ537352		China	Wu et al. (2006, 2007)
<i>Metahaliotrema subancistroides</i> (Zhang in Zhang, Yang & Liu, 2001)	<i>Gerres decacanthus</i> (Bleeker, 1864)	ZSU 20050917B-1	EU836210	EU836231		China	Sun et al. (2014)
<i>Mexicana</i> Caballero & Bravo-Hollis, 1959							
<i>Mexicana rubra</i> Camargo, Luque & Santos, 2017	<i>Orthopristis ruber</i> (Cuvier, 1830)	E514	KY553147	KY553146		Brazil	Camargo et al. (2017)
<i>Mymarothecium</i> Kritsky, Boeger & Jégu, 1998							
<i>Mymarothecium viatorum</i> Boeger, Piasecki & Sobecka, 2002	<i>Piaractus mesopotamicus</i> (Holmberg, 1887)	PR84	MH843723			Brazil	Moreira et al. (2019b)
<i>Nanayella</i> Acosta, Mendoza-Palmero, da Silva & Scholz, 2019							
<i>Nanayella aculeatrium</i> Acosta, Mendoza-Palmero, da Silva & Scholz, 2019	<i>Sorubim lima</i> (Bloch & Schneider, 1801)	Ancy12SI	KP056228			Peru	Mendoza-Palmero et al. (2015)
<i>Nanayella amplofalcis</i> Acosta, Mendoza-Palmero, da Silva & Scholz, 2019	<i>Hemisorubim platyrhynchos</i> (Valenciennes, 1840)		MG001325			Brazil	Acosta et al. (2018)



<i>Nanayella fluctuatrum</i> Acosta, Mendoza-Palmero, da Silva & Scholz, 2019	<i>Sorubim lima</i> (Bloch & Schneider, 1801)		MG001327			Brazil	Acosta et al. (2018)
<i>Onchobdella</i> Paperna, 1968							
<i>Onchobdella aframae</i> Paperna, 1968	<i>Hemichromis fasciatus</i> Peters, 1857		HQ010034				Mendlová et al. (2010)
<i>Onchobdella bopeleti</i> Bilong Bilong & Euzet, 1995	<i>Hemichromis letourneuxi</i> Sauvage, 1880		HQ010033				Mendlová et al. (2010)
<i>Onchocleidus</i> Mueller, 1936							
<i>Onchocleidus similis</i> Mueller, 1936	<i>Lepomis gibbosus</i>		AJ969938	AJ490167	AJ490167	Slovakia	Šimková et al. (2003, 2006)
<i>Paradiplectanotrema</i> Gerashev, Gayevskaya & Kovaleva, 1987							
<i>Paradiplectanotrema klimpeli</i> Theisen, Palm, Stolz, Al-Jufaili & Kleinertz, 2018	<i>Saurida tumbil</i> (Bloch, 1795)	ST-2018	MG763101			Indonesia	Theisen et al. (2018)
<i>Parancyrocephaloides</i> Yamaguti, 1938							
<i>Parancyrocephaloides daicoci</i> Yamaguti, 1938	<i>Dactyloptena peterseni</i> (Nyström, 1887)		LC190513	LC176447	LC176447	Japan	Ogawa and Itoh (2017)
<i>Parasciadicleithrum</i> Mendoza-Palmero, Blasco-Costa, Hernández-Mena & Pérez-Ponce de León, 2017							
<i>Parasciadicleithrum octofasciatum</i> Mendoza-Palmero, Blasco-Costa, Hernández-Mena & Pérez-Ponce de León, 2017	<i>Rocio octofasciata</i> (Regan, 1903)	ExC9 15	KY305885			Mexico	Mendoza-Palmero et al. (2017)
<i>Pavanelliella</i> Kritsky & Boeger, 1998							
<i>Pavanelliella takemotoi</i> Aguiar, Ceccarelli & Luque, 2011	<i>Pimelodus maculatus</i> Lacepède, 1803	298		MF398305	MF398305	Brazil	Aguiar et al. (2017)
<i>Platycephalotrema</i> Kritsky & Nitta, 2019							
<i>Platycephalotrema macassarensis</i> (Yamaguti, 1963)	<i>Ratabulus megacephalus</i> (Tanaka, 1917)	ZSU 20060523-1	EU836207	EU836228		China	Sun et al. (2014)
<i>Platycephalotrema platycephali</i> (Yin & Sproston, 1948)	<i>Platycephalus indicus</i> (Linnaeus, 1758)		DQ157662			China	Wu et al. (2006)
<i>Protogyrodactylus</i> Johnston & Tiegs, 1922							
<i>Protogyrodactylus alienus</i> Bychowsky & Nagibina, 1974	<i>Gerres filamentosus</i> Cuvier, 1829		DQ157650	DQ537355		China	Wu et al. (2006; 2007)

<i>Protygodactylus hainanensis</i> Pan, Ding & Zhang, 1995	<i>Therapon jarbua</i> (Forsskål, 1775)		DQ157653			China	Wu et al. (2006)
<i>Pseudancylodiscoides</i> Yamaguti, 1963							
<i>Pseudancylodiscoides</i> sp. 1	<i>Pseudobagrus fulvidraco</i> (Richardson, 1846)	HSY1	EF100542	EF100564		China	Wu et al. (2008)
<i>Pseudancylodiscoides</i> sp. 2	<i>Pseudobagrus fulvidraco</i>	HSY3	EF100543	EF100565		China	Wu et al. (2008)
<i>Pseudancylodiscoides</i> sp. 3	<i>Pseudobagrus fulvidraco</i>	HSY4	EF100544	EF100566		China	Wu et al. (2008)
<i>Pseudempleurosoma</i> Yamaguti, 1965							
<i>Pseudempleurosoma haywardi</i> Theisen, Palm, Al-Jufaili & Kleinertz, 2017	<i>Johnius amblycephalus</i>	worm 1 2698625 1 D2	MF115715			Indonesia	Theisen et al. (2018)
<i>Pseudodactylogyrus</i> Gusev, 1965							
<i>Pseudodactylogyrus anguillae</i> (Yin & Sproston, 1948)	<i>Anguilla anguilla</i> (Linnaeus, 1758)		AJ969950	AJ490162	AJ490162	Slovakia	Šimková et al. (2003, 2006)
<i>Pseudodactylogyrus bini</i> (Kikuchi, 1929)	<i>Anguilla Anguilla</i>		AJ969949	AJ490163	AJ490163	Austria	Šimková et al. (2003, 2006)
<i>Pseudohaliotrema</i> Yamaguti, 1953							
<i>Pseudohaliotrema</i> <i>sphincteroporos</i> Yamaguti, 1953	<i>Siganus doliatus</i> Guérin- Méneville, 1829-38		AF382058	AJ287568		Australia	Olson and Littlewood (2002)
<i>Quadriacanthus</i> Paperna, 1961							
<i>Quadriacanthus clariadis</i> Paperna, 1961	<i>Clarias gariepinus</i> (Burchell, 1822)		KX685952	KX713994	KX713994	Sudan	Francová et al. (2017)
<i>Quadriacanthus fornicates</i> Francová & Řehulková, 2017	<i>Clarias gariepinus</i>		KX685953	KX713995	KX713995	Sudan	Francová et al. (2017)
<i>Quadriacanthus mandibulatus</i> Francová & Řehulková, 2017	<i>Heterobranchus bidorsalis</i> Geoffroy Saint-Hilaire, 1809		KX685954	KX713996	KX713996	Sudan	Mendoza- Palmero et al. (2015)
<i>Schilbetrema</i> Paperna & Thurston, 1968							
<i>Schilbetrema</i> sp.	<i>Pareutropius debauwi</i> (Boulenger, 1900)	ScPd2	KP056244			West Africa	Mendoza- Palmero et al. (2017)
<i>Sciadicleithrum</i> Kritsky, Thatcher & Boeger, 1989							

<i>Sciadicleithrum bravohollisae</i> Kritsky, Vidal-Martínez & Rodríguez-Canul, 1994	<i>Vieja fenestrata</i> (Günther, 1860)	ExC2 3	KY305879				Mexico	Mendoza- Palmero et al. (2017)
<i>Sciadicleithrum meekii</i> Mendoza-Franco, Scholz & Vidal-Martínez, 1997	<i>Thorichthys meeki</i> Brind, 1918	ExC10 12	KY305889				Mexico	Mendoza- Palmero et al. (2017)
<i>Scutogyrus</i> Pariselle & Euzet, 1995								
<i>Scutogyrus longicornis</i> (Paperna & Thurston, 1969)	<i>Oreochromis niloticus</i>	PC105	HQ010035	HE792800	HE792800	MT447060 <sup>b</sup>	Senegal	Mendlová et al. (2010, 2012); Caña-Bozada et al. 2021
<i>Scutogyrus vanhovei</i> Pariselle, Bitja Nyom & Bilong Bilong, 2013	<i>Pelmatolapia mariae</i> (Boulenger, 1899)	AP385	MW580366				Cameroon	Cruz-Laufer et al. (2021b)
<i>Susanlimocotyle</i> Soares, Domingues & Adriano, 2020								
<i>Susanlimocotyle narina</i> Soares, Domingues & Adriano, 2020	<i>Sciades herzbergii</i> (Bloch, 1794)			MW144824	MW179606			Soares et al. (2021)
<i>Tetrancistrum</i> Goto & Kikuchi, 1917								
<i>Tetrancistrum indicum</i> (Paperna, 1972)	<i>Siganus canaliculatus</i> (Park, 1797)	Ti6	MN179335	MN179330			Oman	Al Jufaili et al. (2020)
<i>Tetrancistrum labyrinthus</i> Al Jufaili & Palm, 2017	<i>Siganus canaliculatus</i>	TI6	MN179332	MN179334			Oman	Al Jufaili et al. (2020)
<i>Tetrancistrum</i> sp.	<i>Siganus fuscescens</i> (Houttuyn, 1782)		AF026114				Australia	Mollaret et al. (1997)
<i>Thaparocleidus</i> Jain, 1952								
<i>Thaparocleidus siluri</i> (Zandt, 1924)	<i>Silurus glanis</i> Linnaeus, 1758		AJ969940	AJ490164	AJ490164		Czech Republic	Šimková et al. (2003, 2006)
<i>Thaparocleidus vistulensis</i> (Sivak, 1932)	<i>Silurus glanis</i>		AJ969941	AJ490165	AJ490165		Czech Republic	Šimková et al. (2003, 2006)
<i>Thylacicleidus</i> Wheeler & Klassen, 1988								
<i>Thylacicleidus</i> sp.	<i>Dichotomyctere fluviatilis</i> (Hamilton, 1822)	Malaysia-AS- 2002		AJ490169	AJ490169		Malaysia	Šimková et al. (2003)
<i>Trianchoratus</i> Price & Berry, 1966								

<i>Trianchoratus gussevi</i> Lim, 1986	<i>Anabas testudieus</i> (Bloch, 1792)		AY841875		China	Tan et al. (2011)
<i>Trinigyrrus</i> Hanek, Molnár & Fernando, 1974						
<i>Trinigyrrus anthus</i> Franceschini, Acosta, Zago, Müller & da Silva, 2020	<i>Hypostomus regani</i> (Ihering, 1905)		MN947622	MN916719	Brazil	Franceschini et al. (2020)
<i>Trinigyrrus carvalhoi</i> Franceschini, Acosta, Zago, Müller & da Silva, 2020	<i>Hypostomus ancistroides</i> (Ihering, 1911)		MN947608	MN922321	Brazil	Franceschini et al. (2020)
<i>Trinigyrrus peregrinus</i> Nitta & Nagasawa, 2016	<i>Pterygoplychthys ambrosettii</i> (Holmberg, 1893)		MN944890	MN913212	Brazil	Franceschini et al. (2020)
<i>Unibarra</i> Suriano & Incorvaia, 1995						
<i>Unibarra paranoplatensis</i> Suriano & Incorvaia, 1995	<i>Aguarunichthys torosus</i> Stewart, 1986	UnpaAt1	KP056219		Peru	Mendoza-Palmero et al. (2015)
<i>Unilatus</i> Mizelle & Kritsky, 1967						
<i>Unilatus unilatus</i> Mizelle & Kritsky, 1967	<i>Pterygoplychthys ambrosettii</i>	Unilatus unilatus P ambrosettii 5 Jan/15	MF102106		Brazil	Acosta et al. (2017)
<i>Urocleidoides</i> Mizelle & Price, 1964						
<i>Urocleidoides digitabulum</i> Zago, Yamada, De Oliveira Fadel Yamada, Franceschini, Bongiovani & da Silva, 2020	<i>Leporinus friderici</i> (Bloch, 1794)	d ACZ-2020	MT556796	MT594400	Brazil	Zago et al. (2020)
<i>Urocleidoides tenuis</i> Zago, Yamada, De Oliveira Fadel Yamada, Franceschini, Bongiovani & da Silva, 2020	<i>Apareiodon</i> sp.	1	MT556797		Brazil	Zago et al. (2020)
<i>Urocleidoides uncinus</i> Zago, Yamada, De Oliveira Fadel Yamada, Franceschini, Bongiovani & da Silva, 2020	<i>Gymnotus sylvius</i> Albert & Fernandes-Matioli, 1999	u ACZ-2020	MT556798	MT594473	Brazil	Zago et al. (2020)
<i>Vancleaveus</i> Kritsky, Thatcher & Boeger, 1986						

<i>Vancleaveus janauacaensis</i> Kritsky, Thatcher & Boeger, 1986	<i>Pterodoras granulosus</i> (Valenciennes, 1821)	VajaPg1	KP056247					Peru	Mendoza- Palmero et al. (2015)
<i>Xenoligophoroides</i> Dmitrieva, Sanna, Piras, Garippa & Merella, 2018									
<i>Xenoligophoroides cobitis</i> (Ergens, 1963)	<i>Gobius cobitis</i> Pallas, 1814	B9	MG194744					Russia	Dmitrieva et al. (2018)
<b>Outgroup: Diplectanidae Monticelli, 1903</b>									
<i>Dolicirroplectanum lacustre</i> Kmentová, Gelnar & Vanhove, 2021	<i>Lates niloticus</i> (Linnaeus, 1758)	LN1	MK937579	MK937576	MK937576	MK908186		Uganda	Kmentová et al. (2021)
<i>Paradiplectanum sillagonum</i> (Tripathi, 1959)	<i>Sillago sihama</i> (Forsskål, 1775)		AY553626	AY553617				China	Wu et al. (2005)
<i>Pseudorhabdosynochus</i> <i>grouperi</i> (Bu, Leong, Wong, Woo & Foo, 1999)	<i>Epinephelus coioides</i> (Hamilton, 1822)		AY553628	AY553618				China	Francová et al. (2017)

<sup>a</sup> 28S and COI sequences with different isolate numbers but same author list, <sup>b</sup> 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 + $\Gamma$ 4	GTR + F + R6
18S rDNA: part 1 + part 2	1320 + 496	SYM + I + $\Gamma$ 4	TIM3e + R3
ITS1 rDNA	238	GTR + F + $\Gamma$ 4	TVM + F + R2
COI mtDNA: 1st codon	828/3	GTR + F + I + $\Gamma$ 4	TN + F + $\Gamma$ 4
COI mtDNA: 2nd codon	828/3	GTR + F + $\Gamma$ 4	GTR + F + $\Gamma$ 4
COI mtDNA: 3rd codon	828/3	HKY + F + I + $\Gamma$ 4	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	
<i>Metahaliotrema</i> (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	
<i>Protygodactylus</i> (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	
<i>Parasciadicleithrum</i> (Mendoza-Palmero et al., 2017)	A2	a	d		c	b	a	b		a		a	a	a	a	a	a	a	d	a		b	a	
<i>Gussevia</i> (Kritsky et al., 1986)	A2	a			c		a	b	a	a	d	a	a	a	a	b	a	b	d	b		b	a	
<i>Ligophorus</i> (Sarabeev et al., 2013)	A3	a	d	c	c		a	c	b	a		a		a	a	b	a	a	d	b	b	b	a	
<i>Xenoligophoroides</i> (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	
<i>Ergenstrema</i> (Paperna, 1964)	A3	a			c			d	b	a		a		a	b		a	a	d	b		b	a	
<i>Cichlidogyrus</i> (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	
<i>Scutogyrus</i> (Pariselle and Euzet, 2009)	A4				c		a	b	b	a	b	a	b	b	a	a	a	a	d	b	b	b	a	
<i>Euryhaliotrema</i> (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	
<i>Sciadicleithrum</i> (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	
<i>Haliotrematoides</i> (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	
<i>Mexicana</i> (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	
<i>Pseudempleurosoma</i> (Yamaguti, 1965)	A7				c		a	a		a		b	b	b	a	b	a	a	d	b	a	b	a	
<i>Paradiplectanotrema</i> (Theisen et al., 2018)	A7				c		a	a		a	b	a	b	a	a	b	a	a	d	b	a	b	a	
<i>Enterogyrus</i> (Pariselle and Euzet, 2009)	A7	b			c		a	a	a	a	b	a	b	a	b		a	b	d	b	b	b	a	
<i>Onchobdella</i> (Paperna, 1968)	A8	a	a		d		a	a			c	a	b	b	a	b	a	a	d	b		b	a	
<i>Caballeria</i> (Lim, 1995)	A8	a			c		a	a	a	b	b	b		a	a	b	a	b	d	a		b	a	
<i>Bravohollisia</i> (Lim, 1995)	A8	b			c		a	a	a	b	b	b		a	a	b	a	b	d	a		b	a	
<i>Platycephalotrema</i> (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	
<i>Lethrinitrema</i> (Lim and Justine, 2011)	A8				c	b	a	a	a	a	c	c		a	a	b	a	b	d	a		b	a	
<i>Haliotrema</i> (Adapted form Young, 1968)	A8				c		a	a	a	a	b	c		a	a	b	a	a	d	b		b	a	
<i>Thylacicleidus</i> (Wheeler and Klassen, 1988)	A8	b	a		c		a	a				a		b	a	b	a	b	d	a		b	a	
<i>Parancyrocephaloides</i> (Ogawa and Itoh, 2017)	A8				c		a	a	a	a	c	b	b	a	a	a	a	b	d	a		b	a	
<i>Tetrancistrum</i> (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	
<i>Glyphidohaptor</i> (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	
<i>Pseudohaliotrema</i> (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	
<i>Gobioecetes</i> (Ogawa and Itoh, 2017)	A9	a	a		c	b	a	a	a	a	c	a	b	a	b		a	b	d	a		b	a	
<i>Heteronchocleidus</i> (Bychowsky, 1957)	A9				c		a	a				a			a	b	a	b	c	b		b	a	
<i>Eutrianchoratus</i> (Paperna, 1969)	A9				c		a	a			c	a			a	a	b	b		c	b		b	a

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



<i>Mymarothecium</i> (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	
<i>Diaphorocleidus</i> (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	
<i>Pavanelliella</i> (Kritsky and Mendoza-Franco, 2003)	B6	a			c	c	a	b	a	a	b	a		a	b		b		a		b	b	a
<i>Characithecium</i> (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
<i>Pseudorhabdosynochus</i> (Neifar and Euzet, 2007)	outgroup	c			c	b	b		b	a	b	b		a	a	a	a	b	d	b		c	b
<i>Dolicirroplectanum</i> (Kmentová et al., 2021)	outgroup	a			c		b		b	a	b	b		a	a	a	a	b	d	b		a	b
<i>Paradiplectanum</i> (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)

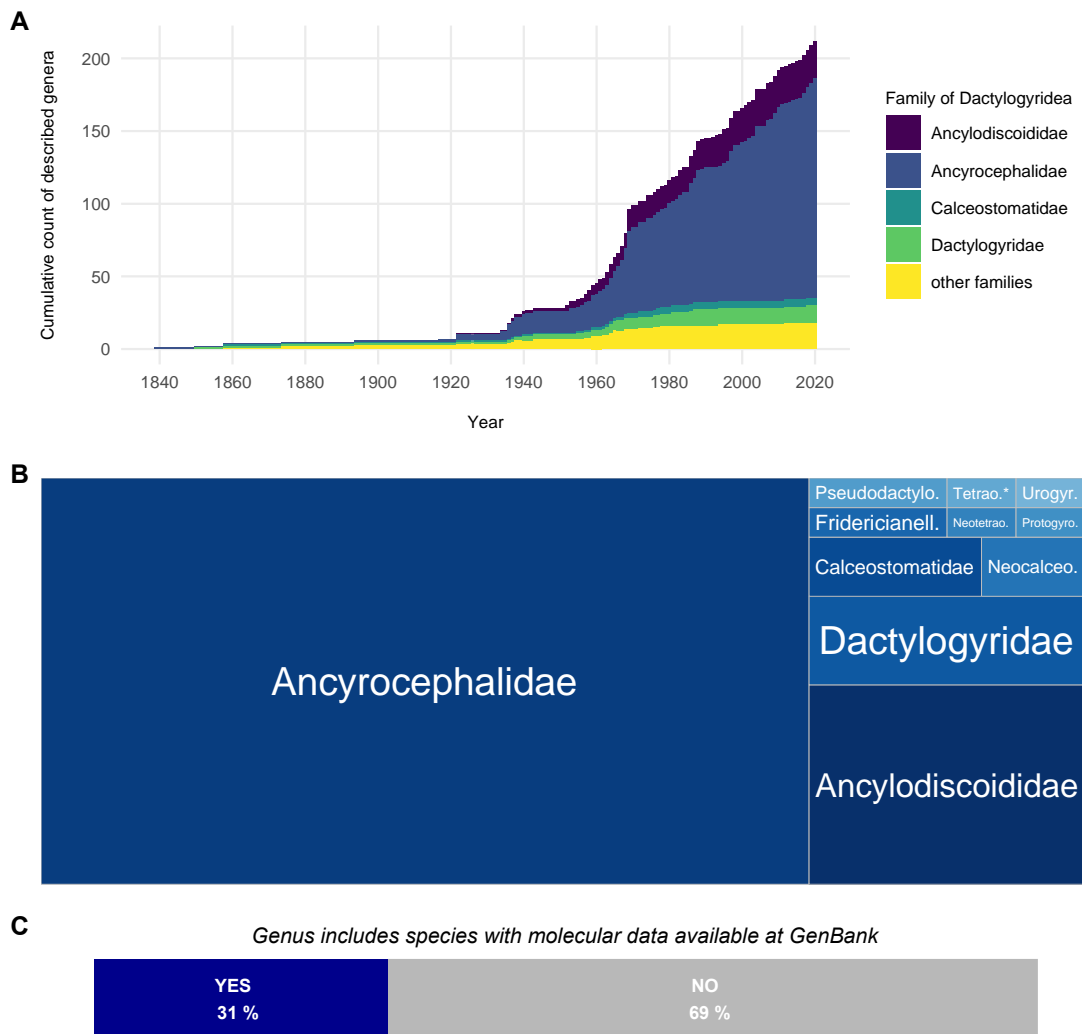
**Table 4.** Information reported in the literature for clades inferred through phylogenetic analyses including infection site, habitat, hosts repertoires, potential synapomorphies, and phylogenetic relationships as well as synapomorphies inferred from character maps in Fig. 5 and Fig. 6.

#	Clade name	Node support	Genera/species included	Site of infection	Habitat	Ecoregions	Host repertoire	Synapomorphies	Results of previous phylogenetic studies
A1	<i>Metahaliotrema</i> – <i>Protogyrodactylus</i>	100/100/100/*	<i>Metahaliotrema</i> <i>Protogyrodactylus</i>	gills	marine	Central Indo-Pacific	Centrarchiformes Gerreiformes Scatophagidae	-	Wu et al. (2006): <i>Metahaliotrema</i> and <i>Protogyrodactylus</i> reported as sister taxa.
A2	<i>Gussevia</i> – <i>Parasciadicleithrum</i>	99/95/100/*	<i>Gussevia</i> <i>Parasciadicleithrum</i>	gills	fresh-water	Neotropical	Cichliformes	Preovarian position of testis (present study), coiled copulatory tube (Kritsky et al., 1986; Mendoza-Palmero et al., 2017)	-
A3	' <i>Ligophorus</i> '-like	95/87/98/*	<i>Ligophorus</i> <i>Ergenstrema</i> <i>Xenoligophoroides</i>	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): <i>Ergenstrema</i> and <i>Ligophorus</i> closely related but relationship with <i>X. cobitis</i> unresolved
A4	' <i>Cichlidogyrus</i> '-like	100/100/100/100	<i>Cichlidogyrus</i> <i>Scutogyrus</i>	gills	fresh-water	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): <i>Scutogyrus</i> nested in <i>Cichlidogyrus</i>
A5	<i>Euryhaliotrema</i> – <i>Sciadicleithrum</i>	100/96/100/*	<i>Euryhaliotrema</i> <i>Sciadicleithrum</i>	gills	marine and fresh-water	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): <i>Sciadicleithrum</i> nested in a clade of species now considered members of <i>Euryhaliotrema</i>

<b>A6</b>	<i>Haliotrematoides</i> – <i>Mexicana</i>	100/100/100/77	<i>Haliotrematoides</i> <i>Mexicana</i>	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)	-	
<b>A7</b>	Mesoparasitic dactylogyrids	100/100/100/87	<i>Enterogyrus</i> <i>Paradipectanotrema</i> <i>Pseudempleurosoma</i>	oesophagus pharynx stomach rarely gills	marine and fresh- water	Afrotropical Central Indo- Pacific	Aulopiformes Cichliformes Scianidae	-	-	
<b>A8</b>	' <i>Haliotrema</i> '-like	100/100/100/74	<i>Haliotrema</i> <i>Bravohollisia</i> <i>Caballeria</i> <i>Glyphidohaptor</i> <i>Lethrinitrema</i> <i>Parancyrocephaloides</i> <i>Platycephalotrema</i> <i>Pseudohaliotrema</i> <i>Tetrancistrum</i> <i>Thylacicleidus</i>	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 ' <i>Haliotrema</i> ' group [without species now considered as members of <i>Euryhaliotrema</i> (Kritsky, 2012), <i>Haliotrematoides</i> (García- Vásquez et al., 2015), <i>Ligophorus</i> (Euzet and Suriano, 1977), and <i>Metahaliotrema</i> (Kritsky et al., 2016)] supported by Dang et al. (2010), Soo (2019), and Al Jufaili et al. (2020)
<b>A9</b>	'pseudodactylogyrids' – 'heteronchocleidids'	99/99/100/39	<i>Heteronchocleidus</i> ' <i>Ancyrocephalus</i> ' <i>mogurndae</i> <i>Eutrianchoratus</i> <i>Gobioecetes</i> <i>Trianchoratus</i> <i>Pseudodactylogyrus</i>	gills	fresh- water	Indo-Malayan Palaeartic	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.
<b>A10</b>	dactylogyrids	100/100/100/*	<i>Dactylogyrus</i> <i>Dactylogyroides</i> <i>Dogielius</i>	gills	fresh- water	Indo-Malayan Palaeartic	Cypriniformes	Two prostatic reservoirs and single pair of anchors	-	
<b>B1</b>	Parasites of siluriforms I: Pimelodidae	100/100/100/*	<i>Boegeriella</i> ' <i>Demidospermus</i> ' <i>mortenthaleri</i> <i>Nanayella</i>	gills	fresh- water	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).
<b>B2</b>	Parasites of siluriforms II: Doradidae and Locariidae	97/86/96/*	<i>Cosmetocleithrum</i> <i>Demidospermus</i>	gills	fresh- water	Neotropical	Siluriformes (Doradidae and Locariidae)	-		Acosta et al. (2019), Mendoza- Palmero et al. (2019): clade reported as monophyletic.

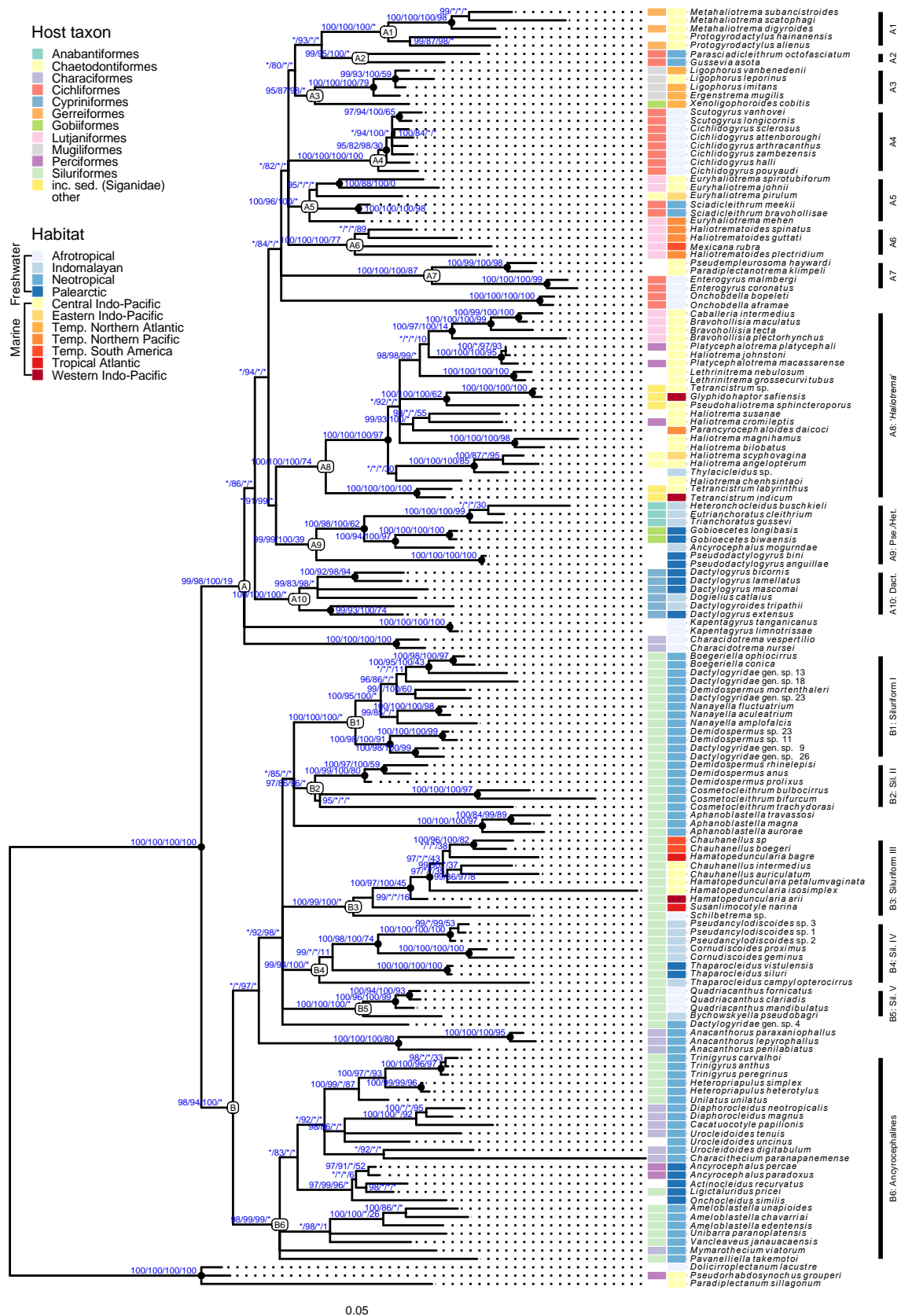
<b>B3</b>	Parasites of siluriforms III: Ariidae, Bagridae, and Schilbeidae	100/99/100/*	<i>Chauhanellus</i> <i>Hamatopeduncularia</i> <i>Schilbetrema</i> <i>Susanlimocotyle</i>	gills	marine and fresh-water	Afrotropical Central Indo-Pacific Temperate South America Tropical Atlantic Western Indo-Pacific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

# Figure captions



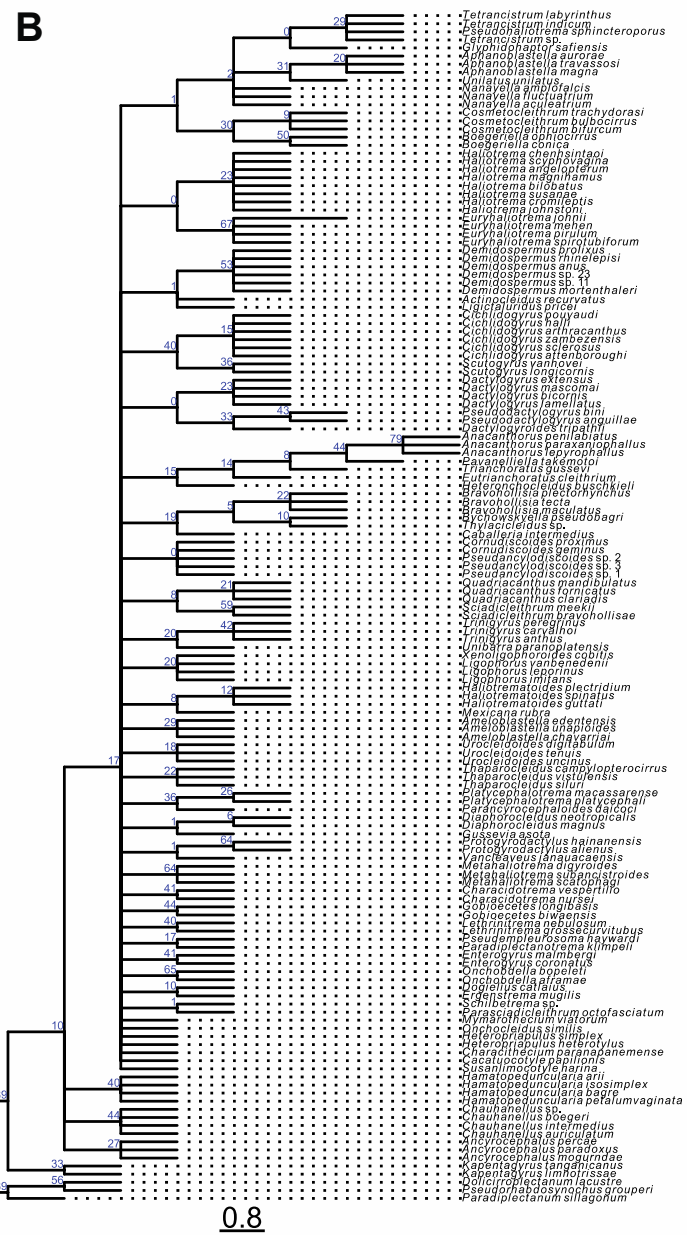
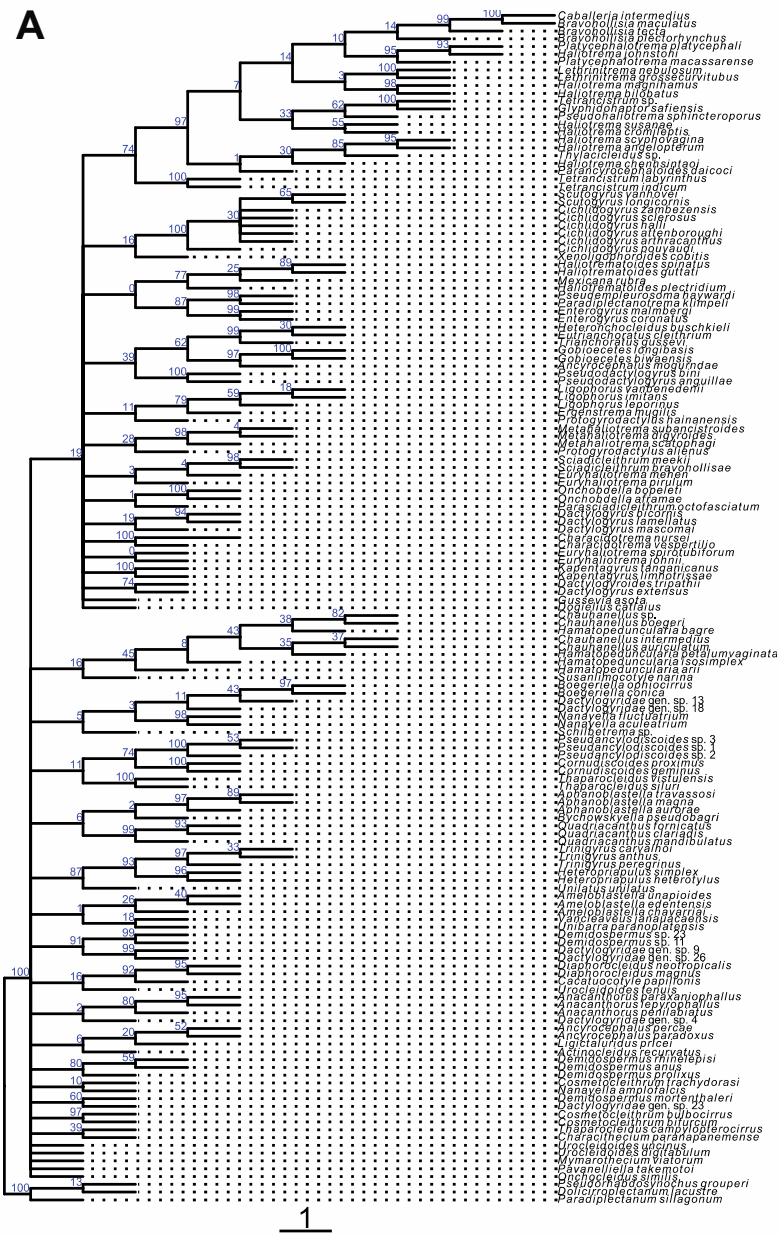
**Figure 1.** Classification system of genera previously included in Dactylogyridea with family affiliations as listed on the WORMS database (Horton et al., 2021): (A) cumulative count of genera described over time, (B) families recognised in WORMS that were previously hypothesised as synonyms of Dactylogyridae 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: Ancyrodiscoididae 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.



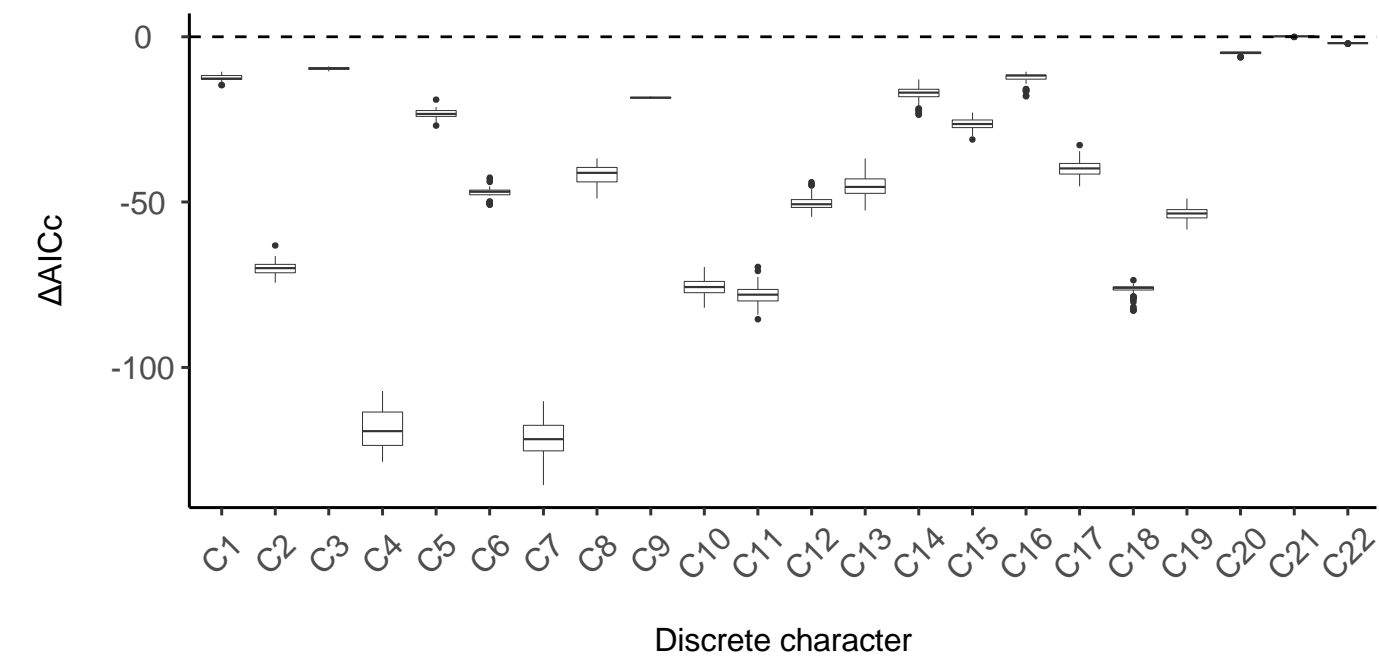
**Figure 2.** Bayesian inference (BI) phylogram of monogenean flatworms belonging to Dactylogyridae (Platyhelminthes: Monogenea) with node support inferred from BI, Maximum Likelihood (ML), and

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 ( $PP < 0.95$ ,  $UBoost < 95$ ,  $SH-aLRT < 80$ ); 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.

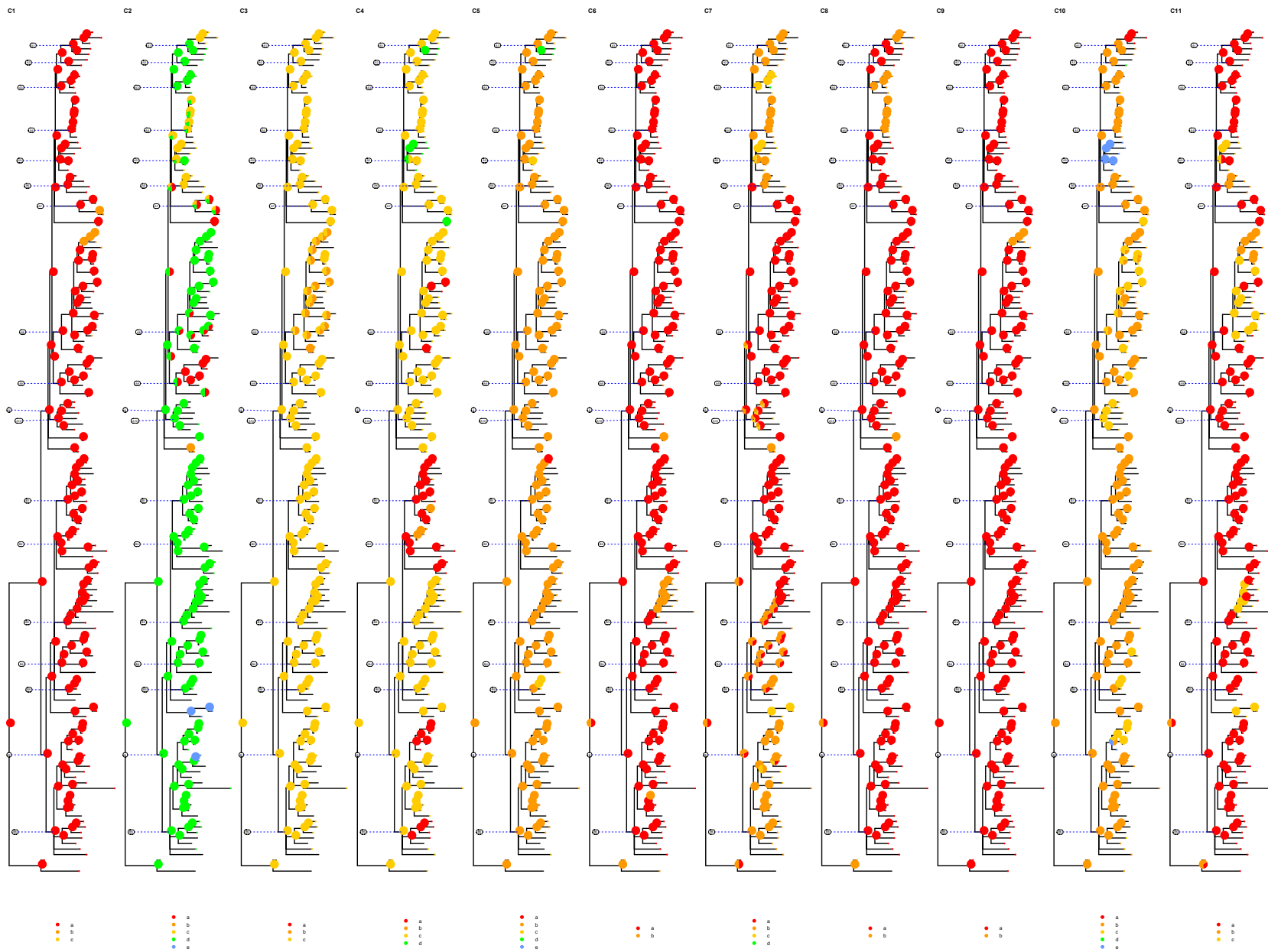




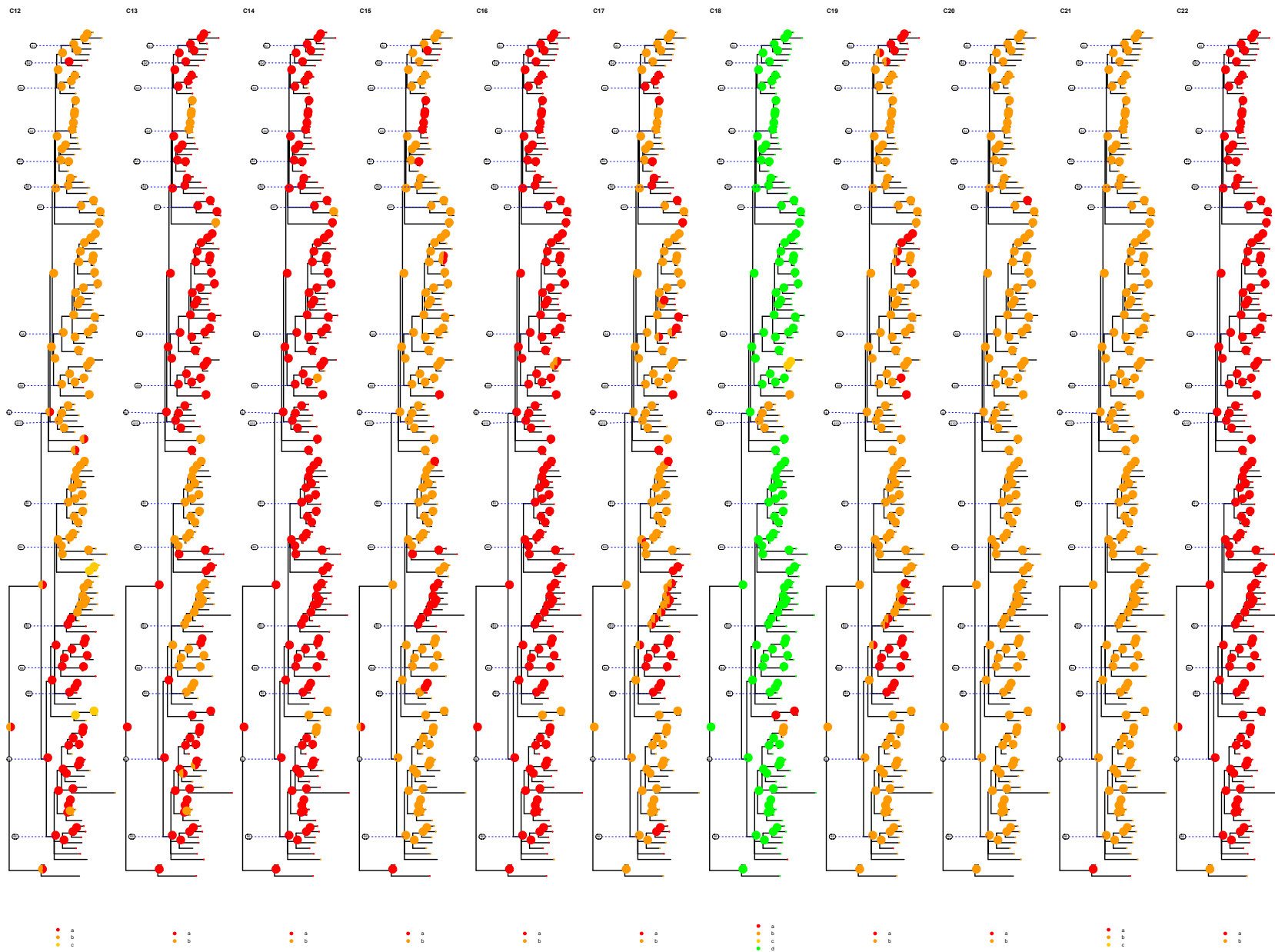
**Figure 3.** Final phylogenetic hypotheses inferred from molecular and morphological data under maximum parsimony. (A) Molecular phylogram inferred from three nuclear DNA portions (18S, 28S, and ITS rDNA) under extended implied weighting. (B) Morphological phylogram based 22 morphological characters (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 ( $\Delta AICc$ ) 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.