

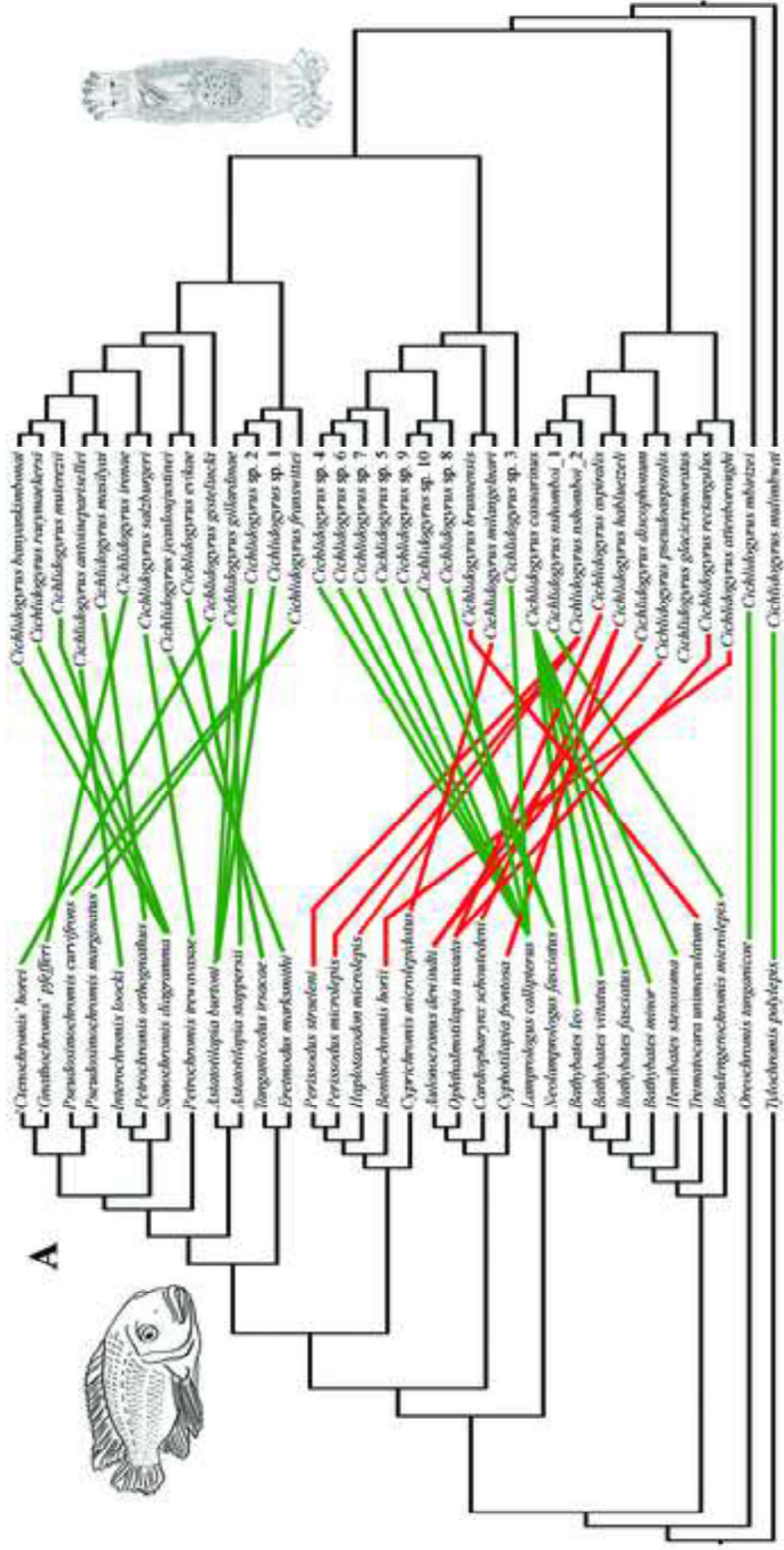
Molecular phylogeny and speciation patterns in host-specific monogeneans (Cichlidogyrus, Dactylogyridae) parasitizing cichlid fishes (Cichliformes, Cichlidae) in Lake Tanganyika

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Highlights

- *Cichlidogyrus* species from most East African cichlids are monophyletic.
- Host switching followed by duplications as the most frequent coevolutionary event.
- Strict specialist species of *Cichlidogyrus* possess primitive character states.

1 **Molecular phylogeny and speciation patterns in host specific monogeneans**
2 **(*Cichlidogyrus*, Dactylogyridae) parasitizing cichlid fishes (Cichliformes, Cichlidae) in**
3 **Lake Tanganyika**

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14

15 **Abstract**

16 *Cichlidogyrus* (including *Scutogyrus*) is the most speciose dactylogyridean monogenean genus known
17 from African and Levantine cichlid fishes (Cichlidae). While its taxonomy is well established, little is known about
18 the phylogenetic relationships and evolutionary history of this ectoparasite, especially from hosts belonging to one
19 of the most impressive vertebrate radiations, the cichlid fishes from the East African Great Lakes and surrounding
20 hydrological systems. Phylogenetic inference based on DNA sequences of the nuclear 18S, ITS1 and 28S rDNA
21 genes revealed that *Cichlidogyrus* parasitizing mainly West African cichlid tribes is paraphyletic with respect to
22 species parasitizing hosts belonging to the East African cichlid radiation, which constitute a well-supported
23 monophylum. Members of *Cichlidogyrus* from tylochromine and oreochromine hosts that colonised Lake
24 Tanganyika (LT) only recently, cluster with their non-LT relatives, indicating that they colonized LT with their
25 current host species, and did not jump over from any of the many cichlid species already present in the lake. The
26 diversification of *Cichlidogyrus* in LT seems to be driven by failure to diverge in old lineages of cichlids,
27 cospeciation in more recently evolved ones, and host switching followed by parasite duplication at the level of the
28 various host tribes. Evaluation of host specificity and structural evolution of haptor and reproductive organs in
29 LT *Cichlidogyrus* revealed that strict specialist species with larval hook size represent the ancestral state of haptor
30 configuration, suggesting that members of *Cichlidogyrus* in this system evolved from a very simple form to a more
31 complex one like their West African congeners. Generalist species among *Cichlidogyrus* with a sclerotized vagina
32 parasitizing ancient LT lineages seem to have developed a different hook configuration, most probably to ensure
33 successful colonization of new, phylogenetically unrelated hosts.

34 **Keywords** African Great Lakes, Cichlidae, Monogenea, vagina, haptor, hooks, cophylogeny, host range.

35 **Introduction**

36 Parasites and their hosts may show intimate ecological interactions due to their common evolutionary
37 histories over long time spans (Klassen, 1992). Parasites do not randomly infect hosts, as they have to synchronize
38 their life cycle with that of their hosts to ensure optimal individual growth, survival and fecundity. Thus, they are
39 expected to coevolve with their hosts to achieve maximal fitness in the [ir](#) new environment (Garamszegi, 2009).
40 The continuous evolution of parasites over time, gaining and/or losing hosts, considerably shapes the
41 evolutionary trajectories of both host and parasite lineages (Nylin et al., 2018).

42 Monogenean flatworms are well suited for evaluating host-parasite coevolutionary relationships for
43 several reasons. These parasites are highly diverse in terms of [species number](#) (Řehulková et al., 2018),
44 morphology (forms of attachment organs), and ecology (mainly gill and fin ectoparasites exhibiting host and
45 microhabitat specificity) ([Rohde, 1989; Euzet and Combes, 1998; Šimková et al., 2006; Woo, 2006](#)). The
46 evolutionary success of monogeneans is presumed to be related to the diversity of their attachment organ (haptor),
47 and their adaptation to hosts and infection sites (Whittington and Chisholm, 2008). With a direct life cycle,
48 monogeneans further show a strong colonization ability, through either physical contacts between hosts or by the
49 ciliated infectious stage (oncomiracidium) (Cable and Harris, 2002). Monogenean species are known to parasitize
50 either a single host species (strict specialists), a narrow group of congeneric host species (intermediate specialists),
51 phylogenetically closely related non-congeneric hosts (intermediate generalists), or phylogenetically unrelated
52 host species (generalists) ([Desdevises et al., 2002; Šimková et al., 2006; Thatcher, 2006; Franceschini et al., 2018;](#)
53 [Kuchta et al., 2020](#)).

54 From an evolutionary perspective, perfect cospeciation at the macroevolutionary level seems to be rare in
55 parasitic flatworms and was shown to be restricted to higher taxonomical levels due to geographical isolation of
56 particular hosts and parasite lineages (Boeger and Kritsky, 1997). Under cospeciation, a congruence between host
57 and parasite phylogenies is expected ([Stammer, 1957; Brooks and McLennan, 1993](#)). Host switching, parasite
58 duplication and sorting events are coevolutionary events in which parasites fail to respond to host speciation
59 (Johnson et al., 2003; Poulin, 2008), hence host and parasite phylogenies show incongruences (Brooks and
60 McLennan, 1991; Page, 1993). These events were often suggested in scenarios of speciation and diversification of
61 dactylogyridean monogeneans in freshwater fish hosts (Šimková et al. 2004; Mendlová et al., 2012; Šimková et
62 al. 2013; Benovics et al. 2020a). Host switching tends to occur more often between closely related host species
63 (Charleston and Robertson, 2002; De Vienne et al., 2013). Host-parasite associations in marine diplectanids were
64 [inferred](#) to be driven by ecological factors, which facilitated host switching rather than cospeciation (Desdevises

65 et al., 2002). Moreover, sympatric speciation of monogeneans on closely related hosts by host switching was found
66 in marine gyrodactylids (Huyse and Volckaert, 2002; Huyse et al., 2003). In this latter group of viviparous
67 monogeneans, speciation by geographic isolation (allopatric mode), host switching and instant isolation by host
68 specificity were further revealed (Meinilä et al., 2004).

69 African and Levantine cichlid fishes (Cichlidae Bonaparte, 1835) are known to host representatives of six
70 dactylogyridean genera, plus a single gyrodactylid genus. This includes endoparasitic (mesoparasitic) genera found
71 in the stomach and urinary bladder, i.e., *Enterogyryus* Paperna, 1963 and *Urogyryus* Bilong Bilong, Birgi & Euzet,
72 1994, respectively, and ectoparasitic genera found on fish gills: *Onchobdella* Paperna, 1968, *Scutogyryus* Pariselle
73 and Euzet 1995, *Cichlidogyryus* Paperna, 1960, and *Gyrodactylus* von Nordmann, 1832, the latter of which also
74 occurs on fins (Pariselle and Euzet, 2009; Dos Santos et al., 2019). The sixth and final dactylogyridean genus
75 *Insulacleidus* Rakotofiringa and Euzet, 1983 is an ectoparasite genus restricted to Madagascar (Rakotofiringa and
76 Euzet, 1983). Of the above-listed genera, *Cichlidogyryus* is the most speciose and mostly restricted to cichlid fishes.
77 The monophyly of the group *Cichlidogyryus-Scutogyryus* and the paraphyly of *Cichlidogyryus* is well established
78 (Pouyaud et al., 2006; Mendlová et al., 2010, 2012; Messu Mandeng et al., 2015; Caña-Bozada et al., 2021). To
79 date, 130 species of *Cichlidogyryus* have been reported from 112 cichlid species inhabiting Africa and the Levant
80 (Pariselle and Euzet, 2009; Vanhove et al., 2016; Rahmouni et al., 2018; Geraerts et al., 2020). Although rarely, a
81 few representatives of this genus were reported from non-cichlid hosts like the pupfish (Cyprinodontidae Gill,
82 1865 (Birgi and Euzet, 1983)) and leaffish (Nandidae Bleeker, 1852 (Birgi and Lambert, 1986)). To account for
83 this, host switches from cichlid hosts to distant fish families were then suggested, but only a single case was
84 supported by molecular data (Messu Mandeng et al., 2015). Host switching was also recently documented
85 following the introduction of African mainland cichlids to Madagascar, where native Malagasy cichlids and
86 aplocheilids were infected by non-native species of *Cichlidogyryus* (Šimková et al., 2019).

87 *Cichlidogyryus* bear highly characteristic sclerotized structures in their attachment organ and reproductive
88 organs. The haptoral parts are characteristic for major phylogenetic lineages, while the reproductive organs,
89 especially the male copulatory organ (MCO), seem to be important for species-level identification (Pouyaud et al.,
90 2006; Mendlová et al., 2012; Van Steenberge et al., 2015). The MCO consists of two main and highly
91 morphologically diverse parts, the copulatory tube and accessory piece. Similarly, the vagina in *Cichlidogyryus* can
92 be sclerotized or not. The haptor comprises two pairs of anchors (or gripi) (one dorsal and one ventral), two
93 transversal bars (dorsal bar with two typical auricles and a V-shaped ventral bar), and seven pairs of hooks (or
94 uncinuli) (Paperna, 1960; Pariselle and Euzet, 2009). Using molecular data and geomorphometrics of mainly West

95 [African species of *Cichlidogyrus*](#), Vignon et al. (2011) recognized four main haptoral groups [based on the](#)
96 [configuration](#) (size and shape) of hook pairs.

97 [Certain morphotypes within *Cichlidogyrus* appear typical](#) to a certain host lineage across distant
98 freshwater systems. This was repetitively evidenced by monogeneans sharing [characteristic](#) morphological
99 features in a range of host species of Tylochromini ([Pariselle and Euzet, 1994; Muterezi Bukinga et al., 2012](#)).
100 Host specificity of species of *Cichlidogyrus*, contrariwise, [varies](#) considerably across the African continent. In
101 southern and [Central](#) African systems, it ranges from strict specialists, to generalists parasitizing several tilapiine
102 and haplochromine hosts (Geraerts et al., 2020). Likewise, the host specificity in West Africa includes strict
103 specialists [on](#) heterotilapiines (Pariselle and Euzet, 1998), intermediate specialists like those restricted to
104 tylochromines ([Pariselle and Euzet, 1994; Pariselle et al., 2014; Jorissen et al., 2018](#)), and generalists parasitizing
105 a range of cichlid species representing distinct host lineages ([Paperna and Thurston, 1969; Paperna, 1979; Pariselle](#)
106 [et al., 2003; Pouyaud et al., 2006; see also Mendlová and Šimková \(2014\)](#)). Some [species of *Cichlidogyrus*](#) exhibit
107 variability in local host specificity (Mendlová and Šimková, 2014). For example, *C. zambezensis* Douëllou, 1993
108 was reported as [an](#) intermediate specialist restricted to haplochromine hosts in the Bangweulu-Mweru ecoregion
109 (Jorissen et al., 2017), whereas it was reported as generalist in Lake Kariba parasitizing haplochromine and
110 oreochromine hosts (Douëllou, 1993). Mendlová and Šimková (2014) showed that intermediate specialists
111 represent the ancestral state of host specificity for West African species of *Cichlidogyrus*. Their study also showed
112 a weak correlation between morphometry of haptoral sclerites and host specificity in *Cichlidogyrus* and
113 *Scutogyrus*, and a link between host specificity and host phylogeny, whilst host specificity was independent of
114 parasite phylogeny (Mendlová and Šimková, 2014).

115 [The focus of the present study is on Lake Tanganyika \(LT\)](#), the deepest and oldest lake in Africa (Cohen
116 et al., 1997; Lezzar et al., 2002), harbouring a number of different teleost lineages that radiated within the confines
117 of the lake and show very high levels of endemism (Salzburger et al., 2014). Cichlids are the by far most species
118 rich fish family in this lake and well established as model system in evolutionary biology (e.g. Kocher, 2004;
119 Seehausen, 2006). Compared to the other East African rift lakes, the cichlid assemblages in LT are genetically,
120 morphologically, ecologically and behaviourally the most diverse (Snoeks, 2000; Koblmüller et al., 2008).
121 Roughly 240 cichlid species belonging to 16 tribes occur in the lake (Ronco et al. 2020). While some lineages are
122 very species-rich (e.g. Lamprologini), others count a single representative in the lake (Tylochromini and
123 Boulengerochromini) (Koblmüller et al., 2008). Whereas most tribes evolved [in situ](#) within a short period of time;
124 [their rapid initial diversification was](#) likely facilitated by hybridization at the base of the radiation (Irisarri et al.,

125 2018)), single representatives of other tribes like Oreochromini and Tylochromini, have colonized the lake only
126 recently (Klett and Meyer, 2002; Koch et al., 2007). Recent phylogenomic studies have clarified the phylogenetic
127 relationships not only among cichlid tribes, but also among all known (valid plus yet undescribed) species from
128 Lake Tanganyika ([Takahashi and Sota, 2016](#); [Irisarri et al., 2018](#); [Ronco et al., 2021](#)), and thus provided an
129 invaluable resource for comparative follow-up studies on this system.

130 Mirroring the cichlid diversity in LT, various lineages of *Cichlidogyrus* inhabit this freshwater system.
131 To date, 39 species are known from a total of 36 cichlid species of [12](#) distinct tribes (Rahmouni et al., 2018). In
132 LT, the study of species of *Cichlidogyrus* parasitizing [tropheine cichlids](#) revealed phylogenetic congruence
133 between parasites and hosts, and geographically-dependent diversification (Vanhove et al., 2015). Moreover, it
134 was hypothesized that representatives of *Cichlidogyrus* infecting species belonging to Ectodini and Tropheini
135 evolved either by intrahost speciation or by host switching ([Vanhove et al., 2011](#); Pariselle et al., 2015). However,
136 [so far](#), there is no phylogenetic study inferring the origin and relationships of host-specific *Cichlidogyrus* species
137 parasitizing cichlids representing LT tribes other than Tropheini. The phylogenetic relationship between West
138 African species of *Cichlidogyrus* and their congeners parasitizing East African cichlids (including the LT
139 radiation), and the evolution of haptor and reproductive organ morphologies in species of *Cichlidogyrus*
140 parasitizing LT cichlids, are still unknown. Concerning host specificity, Kmentová et al. (2016**[b](#)**) provided an
141 overview on host specificity of *Cichlidogyrus* in [LT](#) cichlids, [which](#) included host representatives of only few LT
142 cichlid tribes. [Lake Tanganyika](#) species of *Cichlidogyrus* include strict or intermediate specialists [parasitizing](#)
143 members of Tropheini (Vanhove et al., 2015), intermediate generalists parasitizing a wide range of deep-water
144 bathybatines ([Kmentová et al., 2016b, 2021](#)), or true generalists parasitizing species of unrelated cichlid
145 lineages Ectodini and Cyphotilapiini (Rahmouni et al., 2018).

146 [This](#) study aimed at (i) investigating the phylogenetic position of species of *Cichlidogyrus* parasitizing
147 East African cichlid lineages inhabiting one of the main biodiversity hotspots in Africa (LT), in relation to
148 congeners outside of the lake, (ii) assessing whether the phylogeny of *Cichlidogyrus* from LT follows their cichlid
149 host phylogeny at tribal level, (iii) identifying the role of coevolutionary processes in the diversification of
150 *Cichlidogyrus* parasitizing LT cichlids, (iv) investigating whether there is a relationship between parasite
151 phylogeny and morphological adaptation based on attachment (hook pairs) and reproductive organs (sclerotization
152 in the vagina), and (v) discussing local host specificity in *Cichlidogyrus* in the Tanganyika system and its potential
153 link to [specific](#) morphological characters in monogeneans.

154

155 **Material and methods**

156 **Fish and parasite collection**

157 In total, 185 cichlid individuals belonging to 23 species representing the majority of LT tribes were
158 sampled across the northern part of Lakes Tanganyika (Burundi and the Democratic Republic of the Congo
159 (DRC)), Cohoha (Burundi) and Kivu (DRC) between 2008 and 2016, and from Chitili and Kalambo Falls River
160 (Zambia) in 2015 (Table 1). The fish were obtained by local fishermen, caught using gill nets or during snorkelling
161 or diving. Cichlids were identified [on site by ichthyologists based on available keys/literature](#) and dissected using
162 standard methods described by Ergens and Lom (1970). Protocols used for isolating and fixing gill-infecting
163 monogeneans follow Rahmouni et al. (2017a, 2018a). Parasite determination was performed on the basis of
164 morphology and size of the sclerotized parts of haptor and reproductive organs [following original descriptions](#).
165 Some individuals of each collected monogenean species were cut into half using fine needles [using](#) a dissecting
166 microscope during the [collection](#). The anterior part of the worm, which contains the sclerotized parts of the
167 reproductive organs, was fixed on microscopic slides using a mixture of glycerine and ammonium picrate (GAP)
168 (Malmberg, 1957), whereas the remaining half of the body was placed in 96% ethanol for DNA extraction.

169 **DNA extraction, amplification and sequencing**

170 The conspecificity of parasites infecting the respective host species was confirmed using whole
171 individuals mounted on slides based on their hard parts, and fragments of the small and large subunits of ribosomal
172 DNA (18S and 28S rDNA), plus the entire first internal transcribed spacer (ITS1). Parasite individuals were
173 removed from ethanol and dried using an Eppendorf 5301 concentrator under vacuum conditions at 30 °C.
174 Genomic DNA was extracted using the DNeasy™ [blood and tissue](#) Kit (QIAGEN) following the manufacturer's
175 instructions. The partial 28S fragment (D1–D2) was amplified using forward primer C1 ([5'-ACCCGCTGAATT](#)
176 [TAAGCAT-3'](#)) and reverse D2 ([5'-TGGTCCGTGTTTCAAGAC-3'](#)) (Hassouna et al., 1984), or alternatively
177 using forward [ANCY55 \(5'-GAGATTAGCCCATCACCGAAG-3'\)](#) (Plaisance et al., 2005) and reverse D2 [if the](#)
178 [first primer combination was unsuccessful](#). The partial 18S rRNA gene and the entire ITS1 region were amplified
179 using the forward primer S1 ([5'-ATT CCGATAACGAACGAGACT-3'](#)) (Sinnappah et al., 2001) and reverse
180 primer IR8 ([5'-GCTAGCTGCGTTCATCGA-3'](#)) (Šimková et al., 2003), or alternatively using forward S1
181 and reverse LIG5.8 ([5'-GATACTCGAGCCGAGTGATCC-3'](#)) primers (Blasco-Costa et al., 2012) if unsuccessful
182 with the first combination of primers. [Because of its utility in previously published multi-marker phylogenetic](#)
183 [trees of representatives of Cichlidogyrus \(Vanhove et al., 2015; Cruz-Laufer et al., 2021\)](#) we also included a
184 fragment of the mitochondrial cytochrome *c* oxidase subunit 1 (COI) gene. The partial COI gene was amplified

185 for selected samples using forward ASmit1 (5'-TTTTTGGGCATCCTGAGGTTTAT-3') (Littlewood et al.,
186 1997) and Schisto3 (5'-TAATGCATMGGAAAAACA-3') (Lockyer et al., 2003), with reverse ASmit2 (5'-
187 TAA AGA AAG AAC ATA ATG AAA ATG-3') (Littlewood et al., 1997) as internal primer for the nested PCR.
188 For DNA amplification, we followed the protocols published by Plaisance et al. (2008), Mendlová et al. (2012),
189 and Benovics et al. (2020). The PCR products were electrophoresed using a 1% agarose gel and then purified by
190 either the High Pure PCR product purification kit™ (Roche, Mannheim, Germany), or treated with ExoSAP-IT
191 (EcoI, Bratislava, SK) according to the manufacturer's instructions. Bi-directional sequencing of PCR amplicons
192 using the BigDye® Terminator v. 3.1 Cycle Sequencing Kit (Applied Biosystems by Thermo Fisher Scientific,
193 Prague, Czech Republic) and the PCR primers was performed. After purification of sequencing products with the
194 BigDye XTerminator® Purification Kit (Applied Biosystems by Thermo Fisher Scientific, Prague, Czech
195 Republic), sequences were visualised on an ABI 3130 Genetic Analyzer (Applied Biosystems).

196 **Alignment and phylogenetic analyses**

197 Raw sequences were edited using the Sequencher® software v. 5.0 (Gene Codes Corporation, Ann Arbor,
198 MI USA) and aligned with ClustalW (Thompson et al., 1994) as implemented in MEGA X (Kumar et al., 2018).
199 In addition, previously published sequences of species of *Cichlidogyrus* and *Scutogyrus* (Pouyaud et al., 2006; Wu
200 et al., 2007; Mendlová et al., 2010, 2012; Messu Mandeng et al., 2015; Kmentová et al., 2016a, b, 2018; Šimková
201 et al., 2019) (Table 2), were downloaded from GenBank and included in the analyses to determine the position of
202 *Cichlidogyrus* from LT cichlids in relation to *Cichlidogyrus* and *Scutogyrus* from the rest of Africa. Of West
203 African monogeneans, a few sequences downloaded from GenBank correspond to species of *Cichlidogyrus*
204 sampled from introduced cichlids in Asia and Madagascar, and a single species, *C. amieti* Pariselle & Euzet, 1995,
205 known from *Aphyosemion* spp. (Nothobranchiidae). Sequences representing *C. mbirizei* Muterezi Bukinga,
206 Vanhove, Van Steenberge & Pariselle, 2012 described from the LT species *Oreochromis tanganicae*
207 (Günther, 1894) were obtained from introduced cichlids in Asia (see Table 2 and below). GBlocks v. 0.91b
208 (Talavera and Castresana, 2007) was applied to remove unreliably aligned sequences (gaps and ambiguously
209 aligned regions) using less stringent parameters under the following criteria (i) smaller final blocks, (ii) gap
210 positions within the final blocks, and (iii) less strict flanking positions. Final alignment length (after trimming)
211 was 585 bp for 28S rDNA (raw sequences of ~775 bp), 389 bp for 18S rDNA and 301 bp for ITS1 (raw sequences
212 of ~820 bp for these two adjacent regions). All newly obtained sequences were deposited in GenBank (see Table
213 1 for accession numbers). Phylogenetic relationships were inferred using Maximum Likelihood (ML) and
214 Bayesian Inference (BI). For each locus, the best fitting model of molecular evolution was inferred based on the

215 corrected Akaike Information Criterion (AICc) ([Sugiura, 1978; Hurvich and Tsai, 1989](#)) in jModelTest v. 2.1.10
216 ([Guindon et al., 2010; Darriba et al., 2012](#)): TVM +I+ Γ for 28S rDNA with a gamma shape parameter of 0.91,
217 K80+I for 18S rDNA, and TPM2uf+ Γ for ITS1 with a gamma shape parameter of 0.64. To assess the phylogenetic
218 content of the dataset, likelihood mapping based on quartet puzzling (Strimmer and Von Haeseler, 1997)
219 implemented in TREE-PUZZLE v. 5.2 (Schmidt et al., 2002) was used. Since the combined alignment showed
220 relatively high phylogenetic content (96.2% fully resolved, 2.4% partly resolved and 1.2% unresolved quartets), a
221 concatenated dataset (1275 bp) containing a total of 65 sequences from species of *Cichlidogyrus* was generated
222 using SeaView v. 5.0.4 (Gouy et al., 2010) and used for [phylogenetic](#) tree inference. *Cichlidogyrus pouyaudi*
223 Pariselle & Euzet, 1994 parasitizing *Tylochromis intermedius* (Boulenger, 1916) from West Africa and *C.*
224 *mulimbwai* Muterezi Bukinga, Vanhove, Van Steenberge and Pariselle, 2012, from the Lake Tanganyika species
225 *Tylochromis polylepis* (Boulenger, 1900) (Tylochromini) were used as outgroup following Mendlová et al. (2012)
226 and references therein. ML trees were inferred using IQ-TREE v. 1.5.5 (Nguyen et al., 2015), employing the best
227 fit substitution model for each alignment (see above) and a SPR branch-swapping algorithm. The branch support
228 (bootstrap support, BS) was estimated using ultrafast bootstrap approximation (Minh et al., 2013) with 1 000
229 replicates. Selected models which are not implemented in MrBayes were substituted by the closest over-
230 parameterized model (Huelsenbeck and Rannala, 2004). The analysis was performed using MrBayes v. 3.2.1
231 (Ronquist et al., 2012) with two independent Markov Chain Monte Carlo (MCMC) simulations (6 chains, 2×10^6
232 generations, sampling frequency 100, 25% burn-in). Chain stationarity and parameter convergence were assessed
233 in TRACER v. 1.7.1 (Rambaut et al., 2018), with effective samples sizes (ESS) always > 200 for all parameters,
234 and via the average standard deviation of split frequencies (always well below 0.01), and post burn-in trees were
235 summarized in a 50% majority rule consensus tree. The ML and BI trees were visualized in FigTree v. 1.4.4
236 (Rambaut, 2009). It should be noted that as the incongruence length difference (ILD) test performed in the
237 WinClada program (Farris, 1995) with 1000 replicates revealed heterogenous gene fragments ($p=0.004$),
238 sequences of the COI gene were not included in the phylogenetic and cophylogenetic analyses [for lack of sufficient](#)
239 [DNA data \(sequencing not successful for all species\)](#). [Recent study by Jorissen et al. \(2021\), however, indicated](#)
240 [the utility of COI sequences in barcoding and species delineation within *Cichlidogyrus*, hence these sequence data](#)
241 [are a valuable resource for future research on representatives of this genus](#). Sequences were deposited in GenBank
242 (see Table 1 for accession numbers).

243 **Cophylogenetic analyses**

244 To study the coevolutionary associations between species of *Cichlidogyrus* and their LT cichlid hosts, the
245 ML tree topology was used. For the cichlid hosts, the recently published phylogenomic tree by Ronco et al. (2021)
246 was downloaded from <https://datadryad.org/stash/dataset/doi:10.5061/dryad.9w0vt4bbf>. The outgroup taxa were
247 removed with TreeGraph v. 2.15 (Müller and Müller, 2004) and the host tree was rooted using *T. polylepis* as the
248 representative of the earliest diverging tribe in LT ([see for instance Dunz and Schlieven \(2013\)](#)). We investigated
249 whether the phylogeny of species of *Cichlidogyrus* follows the tribal level classification of LT cichlids using
250 Mesquite v. 3.61 (Maddison and Maddison, 2019). Prior to the mapping, the ML tree of *Cichlidogyrus* was reduced
251 with TreeGraph to include only LT species, with *C. mulimbwai* as an outgroup. The tanglegram illustrating host-
252 parasite associations was **inferred** using TreeMap v. 3.0b (Charleston, 2012). Two different methods were
253 employed to assess the level of cophylogenetic signal in host-parasite associations. The distance-based method
254 ParaFit (Legendre et al., 2002) implemented in CopyCat (Meier-Kolthoff et al., 2007) was used with 9999
255 permutations to assess the statistical significance of global fit and individual coevolutionary links. Jane v. 4.0
256 (Conow et al., 2010) was applied to analyse host-parasite associations using an event-based approach. This method
257 compares two tree topologies (considering branch lengths) and optimally fits the parasite tree onto the host tree by
258 mixing different coevolutionary events with predefined costs. Costs were attributed for the five coevolutionary
259 events that can be inferred in this software package: (i) cospeciation (joint parasite and host speciation); (ii)
260 duplication (multiple parasites diversify within the same host species); (iii) duplication with host switch (parasites
261 diverge and then transfer from one host species to another); (iv) losses (loss of parasite); and (v) failure to diverge.
262 The latter event occurs when parasite speciation misses host speciation, resulting in the presence of the same
263 parasite species on new host species. A cost is attributed to each type of event, and the algorithm searches the
264 reconstruction with the lowest global cost. Eleven models with different cost schemes were applied for the
265 cophylogenetic analyses performed using 500 generations and a population size of 100 as parameters of the genetic
266 algorithm to assess the influence of each evolutionary event. Following Deng et al. (2013), the Jane default model,
267 TreeMap default model (Charleston, 1998) and TreeFitter default model (Ronquist, 1995) were included in our
268 analyses. Each of these default models states that cospeciation has the lowest cost, which corresponds to the most
269 common evolutionary event. Seven additional models were incorporated in the cophylogenetic analyses, of which
270 TreeFitter models adjusted for codivergence and host switch, respectively, with equal weights for coevolutionary
271 events following Mendlová et al. (2012). Five other models, where each event is alternatively extremely penalized
272 (cost of specific event set to 10 and all others to 1, following Deng et al. (2013) and Benovics et al. (2020b)), were
273 further used. Statistical tests were computed using 500 randomizations with random parasite trees (Table 3).

274 **Mapping of morphological characters onto the phylogeny of *Cichlidogyrus***

275 The ML tree including only species of *Cichlidogyrus* parasitizing LT cichlid hosts was used to evaluate
276 the structural evolution of haptoral and reproductive organs in this system. Unambiguous morphological character
277 states exhibited by species of *Cichlidogyrus* were mapped onto the parasite phylogeny. The mapping was
278 performed using maximum parsimony ancestral state reconstruction in Mesquite. The following morphological
279 characters were evaluated: (i) hook pair configuration: haptoral groups in terms of size of hook pairs, and (ii) the
280 sclerotization in the vagina (present or absent). A previous study of Vignon et al. (2011) and the overview in
281 Rahmouni et al. (2017) mentioned the following haptoral groups, i.e., states for hook pair configuration: group A
282 for species of *Cichlidogyrus* with short hook pairs I-IV, VI and VII (pair V with larval size); group B for species
283 of *Cichlidogyrus* exhibiting long hook pair I (pair V with larval size) and short pairs II-IV, VI and VII; group C
284 for species of *Cichlidogyrus* with short hook pair I (pair V with larval size) and longer pairs II-IV, VI and VII; and
285 group D for species of *Cichlidogyrus* showing long hook pairs I-VII, except larval-sized pair V. The numbering
286 of hook pairs (Roman letters I–VII) is that recommended by Mizelle (1936). Regarding the vagina, we followed
287 the classification elaborated by Pariselle and Euzet (2003) and applied in Rahmouni et al. (2017).

288 **Host specificity in *Cichlidogyrus* from Lake Tanganyika**

289 Host specificity in species of *Cichlidogyrus* from LT cichlids investigated herein was recorded. We
290 considered host specificity for 35 species of *Cichlidogyrus* based on previous records from LT cichlids (Kmentová
291 et al., 2016b) and our data. With regard to the index of host specificity (IS), the classification of species of
292 *Cichlidogyrus* follows that of Šimková et al. (2006) and applied by Kmentová et al. (2016b) for *Cichlidogyrus*: (i)
293 strict specialists parasitizing a single cichlid host species, (ii) intermediate specialists parasitizing two or more
294 congeneric cichlid species, (iii) intermediate generalists parasitizing heterogeneric cichlid species from the same
295 tribe, and (iv) true generalists parasitizing cichlid species belonging to different tribes. Host range was expressed
296 as the total number of LT cichlid species parasitized by a given species of *Cichlidogyrus*.

297 **RESULTS**

298 **Monogenean phylogeny**

299 The phylogenetic tree (Fig. 1) based on concatenated nuclear genes (18S, ITS1 and 28S rDNA) included
300 a total of 63 species of *Cichlidogyrus* and three *Scutogyrus* spp.: 29 species of *Cichlidogyrus* and *Scutogyrus*
301 parasitizing West African cichlid hosts, plus a single species from a South African haplochromine, and 36 species
302 of *Cichlidogyrus* from LT itself. The alignment comprised sequences of ten undescribed species of *Cichlidogyrus*
303 from Haplochromini (*Cichlidogyrus* sp. 1 and *Cichlidogyrus* sp. 2) inhabiting East African freshwater systems

304 outside of LT (see Table 1), and from LT lamprologines (*Cichlidogyrus* sp. 3 to *Cichlidogyrus* sp. 10). Maximum
305 Likelihood (Fig. 1) and BI trees showed identical topologies when considering the well-supported nodes.
306 *Cichlidogyrus amphoratus* Pariselle & Euzet, 1996 and *C. sclerosus* Paperna & Thurston, 1969 constituted the
307 sister group of a well-supported LT cluster of *Cichlidogyrus* including three main clades (3, 4 and 5 in Fig. 1).
308 However, two species of *Cichlidogyrus* from LT, *C. mbirizei* and *C. mulimbwai* parasitizing oreochromine and
309 tylochromine cichlids, respectively, belonged to lineages branching off earlier than the clade including species of
310 *Cichlidogyrus* from the East African radiation (Fig. 1). A weakly supported clade 1, formed by species of
311 *Scutogyrus*, plus *C. falcifer* Dossou & Birgi, 1984, *C. longicirrus* Paperna, 1965 and *C. dracolemma* Řehulková,
312 Mendlová & Šimková, 2013 parasitizing West African *Hemichromis* spp., and *C. amieti* from *Aphyosemion*
313 *cameronense* (Boulenger, 1903), was sister to the group including *Cichlidogyrus* from coptodonine, hemichromine
314 and oreochromine host lineages with high support (BS = 81, PP = 0.98). Within clade 2, the phylogenetic position
315 of *C. philander* Douéllou, 1993 parasitizing the Southern African haplochromine *Pseudocrenilabrus philander*
316 (Weber, 1897) was weakly supported only by BS. The Lake Tanganyika species *C. mbirizei* from *O. tanganyicae*
317 was sister to West African *C. cirratus* Paperna, 1964 from *Oreochromis niloticus* (Linnaeus, 1758), and both
318 species together with *C. njinei* Pariselle, Bilong Bilong & Euzet, 2003 from *Sarotherodon galilaeus*
319 (Linnaeus, 1758) formed a moderately supported group (only by BS). With high to low support values (BS = 98,
320 PP = 0.71), clade 2 also included a group of *C. nageus* Řehulková, Mendlová & Šimková, 2013, *C. acerbus*
321 Dossou, 1982, and *C. halli* Price & Kirk, 1967 from *S. galilaeus* and *O. niloticus*, in addition to a well-supported
322 subclade (BS = 91, PP = 1) clustering species of *Cichlidogyrus* restricted to coptodonines, from African *Coptodon*
323 *guineensis* (Günther, 1862) and *C. rendalli* (Boulenger, 1897) introduced to Madagascar, but including also *C.*
324 *douellouae* Pariselle, Bilong Bilong & Euzet, 2003 from the oreochromine *S. galilaeus*. Within *Cichlidogyrus*
325 from LT, three clades (3 to 5) were recognized. Clade 3 (BS = 81 and PP = 0.76) represented the earliest diverging
326 lineage, including species of *Cichlidogyrus* from the six LT cichlid tribes Bathybatini, Benthochromini,
327 Boulengerochromini, Cyphotilapiini, Ectodini and Perissodini (Fig. 2). The group of species of *Cichlidogyrus*
328 from *Ophthalmotilapia nasuta* (Poll & Matthes, 1962) (Ectodini), *C. aspiralis*, *C. glaciemoratus* and *C.*
329 *rectangulus* Rahmouni, Vanhove & Šimková, 2017, was paraphyletic, just like *C. nshombi* Muterezi Bukinga et
330 al., 2012 (from *Boulengerochromis microlepis* (Boulenger, 1899), Boulengerochromini, plus *Perissodus*
331 *microlepis* Boulenger, 1898, and *P. straeleni* Poll, 1948, both Perissodini), whereas *C. pseudoaspiralis* and *C.*
332 *discophonum* Rahmouni, Vanhove & Šimková, 2017 from *Aulonocranus dewindti* (Boulenger, 1899) (Ectodini)
333 formed a monophyletic group (Fig. 1, 2). With high support values (BS = 98 and PP = 0.95), the first subclade

334 within clade 3 (Fig. 1, 2) harboured *C. attenboroughi* Kmentová et al., 2016 from the benthochromine
335 *Benthochromis horii* Takahashi, 2008 as sister species to *C. glacicremoratus* and *C. rectangulus* Rahmouni,
336 Vanhove & Šimková, 2017, both from ectodines (see above). The second subgroup was represented by seven
337 species, *C. discophonum* and *C. pseudoaspiralis* as sister species parasitizing *A. dewindti* (BS = 100 and PP = 1),
338 and a monophyletic group including *C. spiralis* from the ectodine *O. nasuta*, *C. habluetzeli* Rahmouni, Vanhove
339 & Šimková, 2018 from *Cyphotilapia frontosa* (Boulenger, 1906) and *Cardiopharynx schoutedeni* Poll, 1942, *C.*
340 *nshomboi*, and *C. casuarinus* Pariselle, Muterezi Bukinga & Vanhove, 2015 parasitizing members of Bathybatini.
341 Clade 4 (BS = 99 and PP = 1) grouped undescribed species parasitizing lamprologines, *C. brunensis* Kmentová
342 et al., 2016 from *Trematocara unimaculatum* Boulenger, 1901 (Trematocarini), and *C. milangelnari* Rahmouni,
343 Vanhove & Šimková, 2017 from *Cyprichromis microlepidotus* (Poll, 1956) (Cyprichromini) (Fig. 1, 2). Clade 5
344 (BS = 100 and PP = 1) included mainly two subclades grouping *Cichlidogyrus* from Eretmodini, Haplochromini
345 and Tropheini. Three species of *Cichlidogyrus* from haplochromine hosts including two undescribed ones formed
346 a monophyletic group with high support (BS = 100 and PP = 1), while species from tropheine hosts were
347 paraphyletic, with *C. franswittei* Pariselle & Vanhove, 2015 as sister group to *Cichlidogyrus* from the non-
348 tropheine haplochromines (BS = 86 and PP = 0.97) (Fig. 1, 2). Two monogenean species, *C. jeanloujustinei*
349 Rahmouni, Vanhove & Šimková, 2017 from *Eretmodus marksmithi* Burgess, 2012 and *C. evikae* Rahmouni,
350 Vanhove & Šimková, 2017 from *Tanganicodus irsacae* Poll, 1950, both from Eretmodini, formed a highly
351 supported lineage within species infecting members of Tropheini (BS = 86 and PP = 0.99). Concerning
352 monogenean species of members of Tropheini, species of *Cichlidogyrus* from *Simochromis diagramma*
353 (Günther, 1894) formed a highly supported monophyletic group (BS = 100 and PP = 1), while species of
354 *Cichlidogyrus* from congeneric *Petrochromis* spp. were polyphyletic; *C. antoineparisellei* Rahmouni, Vanhove &
355 Šimková, 2018 from *Interochromis loocki* (Poll, 1949) and *C. masilyai* Rahmouni, Vanhove & Šimková, 2018
356 from *P. orthognathus* Matthes, 1959 were sister to *Cichlidogyrus* from *S. diagramma*, with a polytomy of species
357 formed by *C. salzburgeri* Rahmouni, Vanhove & Šimková, 2018 from *P. trewavasae* Poll, 1948 and *C. irenae*
358 Gillardin et al., 2012 from '*Gnathochromis*' *pfefferi* (Boulenger, 1898) (Fig. 1, 2).

359 Mapping the cichlid host tribes (lineages) from LT onto the ML tree (Fig. 2) again showed that
360 Tylochromini is the host group for the earliest diverging lineage of *Cichlidogyrus*, followed by Oreochromini.
361 *Cichlidogyrus* from six LT cichlid tribes are included in a single lineage (clade 3 in Fig. 1), just like *Cichlidogyrus*
362 from Lamprologini, Cyprichromini and Trematocarini (clade 4 in Fig. 1), and monogenean species from members

363 of Haplochromini, Eretmodini and Tropheini (clade 5 in Fig. 1). *Cichlidogyrus* from the latter tribe represents the
364 most derived lineage in LT.

365 **Cophylogenetic analyses of cichlids and *Cichlidogyrus* in Lake Tanganyika**

366 The tanglegram indicating associations between species of *Cichlidogyrus* and their cichlid fish hosts is
367 shown in Fig. 3A. A global test calculated in ParaFit revealed a highly significant overall cophylogenetic structure
368 (ParaFitGlobal = 886.05494, $p < 0.001$ for 9999 permutations). The ParaFitLink test showed that 31 host-parasite
369 links out of a total of 45 significantly contributed to the overall phylogenetic congruence. Significant host-parasite
370 links were inferred for species of *Cichlidogyrus* parasitizing cichlids belonging to Boulengerochromini,
371 Bathybatini, Eretmodini, Haplochromini, Lamprologini, Tropheini and Tylochromini. Species of *Cichlidogyrus*
372 parasitizing cichlid species belonging to the remaining tribes Benthochromini, Cyphotilapiini, Cyprichromini,
373 Ectodini, Perissodini and Trematocarini revealed statistically non-significant links.

374 The event-based method of Jane also recovered a global signal of congruence across the whole dataset (p
375 < 0.001) (Table 3). The lowest total cost (27) was produced by the host switch- adjusted TreeFitter model,
376 corresponding to six cospeciation events, 12 duplications, 17 duplications followed by host switch, nine failures
377 to diverge and a single loss event (Fig. 3B). The scenarios with the highest total costs were presented by the FTD
378 prohibitive, and the host switch prohibited models.

379 **Mapping of morphological characters onto the phylogeny of *Cichlidogyrus***

380 Mapping of morphological characters of species of *Cichlidogyrus* in terms of hook pair configuration
381 (Fig. 4A) showed that short pairs I-IV, VI and VII (group A) represent the ancestral state in LT, and the acquisition
382 of thickness and/or length in the hooks represent derived character states that are not common in species of
383 *Cichlidogyrus* in LT. Derived hook configurations were mostly found in species of *Cichlidogyrus* of clade 3 and
384 only *C. salzburgeri* from clade 5. Mapping of sclerotization in the vagina (Fig. 4B) showed that sclerotization or
385 loss of this organ evolved multiple times during diversification of *Cichlidogyrus* in LT (i.e., this character state is
386 present in *C. mbirizei* from Oreochromini and some species within clades 3, 4 and 5). When considering both
387 morphological characters, the represented LT species of *Cichlidogyrus* belonging to haptoral group D of Vignon
388 et al. (2011) seem to have acquired or retained sclerotization in their vagina.

389 **Host specificity in Lake Tanganyika *Cichlidogyrus***

390 The host range of species of *Cichlidogyrus* from LT varied from a single host species to five host species
391 (*Cichlidogyrus casuarinus* parasitizing 7 cichlid species of Bathybatini (Supplementary Table S1)). Strict
392 specialism is apparently the ancestral state of host specificity (but note that less than 15% of LT's cichlid species

393 were included in this study), and other forms of host specificity (that were rarely reported) are derived. Lower host
394 specificity was found in some species of *Cichlidogyrus* belonging to the clades 3 and 5. When considering
395 morphological characters investigated herein, the haptoral group D was found in [the](#) true generalists *C. nshomboi*
396 [and](#) *C. habluetzeli*, and in the intermediate generalist *C. casuarinus*. These species possess long hook pairs I-VII,
397 except [for](#) pair V which retained its larval size, and a sclerotized vagina (Fig. 4A, B).

398

399 **Discussion**

400 The present study was focused on monogeneans of *Cichlidogyrus* parasitizing cichlid hosts inhabiting
401 LT, one of the main biodiversity hotspots in Africa. This system harbours various lineages of *Cichlidogyrus* in
402 terms of morphology and genetics.

403 **Phylogeny of *Cichlidogyrus***

404 First, we focussed on the phylogenetic relationships between *Cichlidogyrus* from LT and its members
405 outside of the lake. *Cichlidogyrus* outside of LT was represented mostly by West African species sampled from
406 three cichlid tribes, the coptodonines, hemichromines and oreochromines, and by a single species sampled from
407 each of a Southern African haplochromine and a nothobranchiid host (Mendlová et al., 2012; Mendlová and
408 Šimková, 2014; Messu Mandeng et al., 2015; Šimková et al., 2019). *Cichlidogyrus pouyaudi* parasitizing West
409 African tylochromines was previously recognized as an early diverging species of *Cichlidogyrus* in West Africa
410 by Mendlová et al. (2012). In line with their study, we showed that *C. mulimbwai* found solely on *T. polylepis*
411 (Tylochromini) [which occurs](#) LT and its tributaries (Stiassny, 1991, 1990) belongs to the same early diverging
412 lineage as *C. pouyaudi*, consistent with the phylogenetic placement of *T. polylepis*, and the tylochromines as a
413 whole, among African cichlids (Irisarri et al. 2018; Ronco et al. 2021). We also demonstrated that species of
414 *Cichlidogyrus* parasitizing West African hemichromines, coptodonines and oreochromines, together with *C.*
415 *mbirzei* from LT, were sister to the rest of the assemblage of *Cichlidogyrus* [including its representatives](#) from the
416 lake itself, consistent with the phylogenetic relationships among the hosts ([Schwarzer et al., 2009; Irisarri et al.,](#)
417 [2018](#)). The position of *C. amieti* from a non-cichlid host within the monogenean species of hemichromines is as
418 previously shown by Messu Mandeng et al. (2015). Our results showed that, unlike *Scutogyrus*, *Cichlidogyrus* in
419 West Africa is not monophyletic, in accordance with results by Mendlová et al. (2012). A clade of *C. amphoratus*
420 and *C. sclerosus* collected from coptodonine and oreochromine cichlid hosts was sister to the well supported large
421 LT clade of *Cichlidogyrus*.

422 **Phylogenetic position of *Cichlidogyrus* parasitizing Lake Tanganyika cichlids**

423 In the present phylogenetic study, 35 species of *Cichlidogyrus* parasitizing 32 LT cichlids belonging to
424 14 endemic tribes of a total of 16 (Ronco et al., 2020) were included. This includes some species, such as
425 *Cichlidogyrus* sp. 1 and *Cichlidogyrus* sp. 2, sampled also from haplochromines inhabiting other East African
426 freshwater habitats. Our study provides the first molecular evidence for a polyphyletic assemblage of
427 *Cichlidogyrus* in LT, as *C. mulimbwai* infecting *T. polylepis* and *C. mbirizei* from *O. tanganyicae*, both from LT,
428 were sister to *C. pouyaudi* from West African *Tylochromis* species, and a few species from oreochromine hosts,
429 respectively, both quite divergent from the rest of the LT species of *Cichlidogyrus* (Fig. 1). The centre of diversity
430 of *Tylochromis* Regan, 1920 and *Oreochromis* Günther, 1889 lies in West Africa and the Congo River system
431 (Stiassny, 1990, 1991; Agnèse et al., 1997), and both *T. polylepis* and *O. tanganyicae* colonized LT only fairly
432 recently (Klett and Meyer, 2002; Koch et al., 2007). Three well-supported clades of *Cichlidogyrus* (3 to 5)
433 parasitizing distinct cichlid tribes from LT were found. Clades 3 and 4 appear to be restricted to species of
434 *Cichlidogyrus* parasitizing representatives of cichlid tribes occupying particular ecological niches – semi-pelagic
435 (Cyprichromini and some members of Ectodini and Lamprologini), and deep and benthopelagic habitats
436 (Bathybatini, Benthochromini, Boulengerochromini, Cyphotilapiini, a few species of Perissodini, and
437 Trematocarini) (Konings, 2019). Clade 5 is restricted to species of *Cichlidogyrus* from Eretmodini, Haplochromini
438 (both from within and outside of LT) and Tropheini, consistent with the close phylogenetic relationships of the
439 host tribes (Takahashi and Sota, 2016; Irisarri et al., 2018; Ronco et al., 2021), but also indicating host switches
440 across tribes.

441 **Speciation and diversification of *Cichlidogyrus* on Lake Tanganyika cichlids**

442 Considering the inferred phylogenetic relationships between species of *Cichlidogyrus* from LT and their
443 West African congeners, we can infer that cospeciation has a low contribution to the diversity of this genus. As
444 already mentioned, host switching of *Cichlidogyrus* between phylogenetically distant cichlid hosts in African
445 freshwater habitats is far from unusual and can be considered as a main coevolutionary event shaping the
446 diversification within this genus.

447 The evolutionary associations between species of *Cichlidogyrus* and their LT cichlid hosts were
448 investigated using both distance-based and event-based methods. The analyses confirmed significant global
449 cophylogenetic structure in this system. Overall, our analyses indicated that host switching followed by
450 duplications is the most frequent coevolutionary event in most of the models (except for host switch prohibited
451 models with highest penalization of host switch and TreeFitter default with higher penalization of host switch
452 when compared to other events and zero costs for cospeciation and duplication). Most models revealed only one

453 [loss event. All models produced the same number of instances of failure to diverge.](#) Few species of *Cichlidogyrus*
454 from early diverging lineages showed to have failed to diverge, while most species of *Cichlidogyrus* from LT
455 tribes have diversified either by host switching and/or duplications, like *Cichlidogyrus* from lamprologines for
456 instance, or by cospeciation as evidenced for [a few species parasitizing ectodines](#), both monogenean species from
457 eretmodines and most species from tropheines. For the latter host tribe, a similar scenario was reported by
458 Vanhove et al., (2015) (see below). Based on previous studies by Pariselle et al. (2015a) and Kmentová et al.
459 (2016b), we can assume a failure to diverge for the intermediate generalist *C. casuarinus* parasitizing a wide range
460 of bathybatines. Herein, a similar scenario was attributed to monogeneans parasitizing unrelated host lineages, *C.*
461 *habluetzeli* from Ectodini and Cyphotilapiini (Rahmouni et al., 2018), *C. nshombi* from the bouleengerochromine
462 *B. microlepis* and heterogeneric perissodines (Muterezi Bukinga et al. 2012; Rahmouni, 2021), and to a lesser
463 degree to species of *Cichlidogyrus* from congeneric or closely related hosts, *C. gillardinae* [Muterezi Bukinga et](#)
464 [al., 2012](#) and *C. franswittei* [from Haplochromini](#); and Tropheini (Van Steenberge et al. 2015 and reference herein),
465 respectively. At the same time, we find host switching of *Cichlidogyrus* from tropheine to haplochromine hosts
466 (Fig. 3B). Several factors could have promoted to keeping gill ectoparasites behind the course of their cichlid hosts
467 diversification. Johnson et al. (2003) stated that a given parasite species most likely fails to speciate when gene
468 flow among diverging host populations is maintained. For *C. casuarinus*, most bathybatine hosts are good
469 dispersers with lake-wide distribution in deep-water habitats (Koblmüller et al. 2005; 2019). It is well known that
470 physical proximity can facilitate gene flow among populations, and that long-distance dispersal offers the
471 opportunity for long-distance gene flow, and thus high levels of gene flow among populations (Mitton, 2013).
472 Further, high gene flow limits interpopulation differentiation (Woodruff, 2001).

473 Our results partially correspond to the findings of Vanhove et al. (2015) who found significant congruence
474 between the phylogeny of Tropheini and their species of *Cichlidogyrus*, potentially suggesting divergence with
475 the initial radiation of this tribe, whereas host switching was rare. Generally speaking, cospeciation is encouraged
476 either by little interspecific contacts (Paterson et al., 2000) or by predominantly vertical transmission (Clark et al.,
477 2000), which is not the case of dactylogyrideans parasitizing modern LT tribes investigated herein. The tropheine
478 *S. diagramma* sampled off the north-eastern lakeshore showed to host the same monogenean community as
479 reported by Van Steenberge et al. (2015) from opposite locations in north-eastern and southern parts of LT. In the
480 case of Haplochromini, *A. burtoni* [\(Günther, 1894\)](#) from LT was previously shown to be parasitized by *C.*
481 *gillardinae*, whereas the gills of this host inhabiting distinct East African freshwater systems (see material and
482 methods [section and Table 1](#)) harboured two different (undescribed) species of *Cichlidogyrus* (sequenced in this

483 study). [It should be noted that the presence of *C. gillardinae* on *A. stappersii* \(Poll, 1943\) is reported herein for the](#)
484 [first time.](#)

485 **Structural evolution and host specificity in *Cichlidogyrus***

486 Using the morphological delimitation of Vignon et al. (2011), based on Pariselle and Euzet (2003), for
487 species outside of LT, most- species of *Cichlidogyrus* [from](#) LT belonged to the haptoral group A characterized by
488 the presence of larval (short) hooks, whilst species of *Cichlidogyrus* representing the remaining haptoral groups
489 were rarely reported. With regard to the vagina, most studied LT species of *Cichlidogyrus* exhibited a non-
490 sclerotized one (Fig. 4B). Mendlová et al. (2012) examined the evolution of haptoral morphology in West African
491 species of *Cichlidogyrus* and, in accordance with our findings, they found that larval hook size represents the
492 ancestral character state of the haptoral hooks. In the LT system, multiple transitions from this configuration to
493 derived ones seem to have occurred. Mapping of morphological characters onto the phylogeny of West African
494 *Cichlidogyrus* also indicated a clade-specific morphology, which is not, however, the case [for *Cichlidogyrus* from](#)
495 LT. This discrepancy may be related [to](#) a potentially different age of *Cichlidogyrus* in West African riverine and
496 East African lake systems. It should be noted that the West African species *C. amphoratus* and *C. sclerosus*, the
497 sister group of the species from the East African cichlid radiation, show short hook pairs but both possess a
498 sclerotized vagina ([Paperna and Thurston, 1969; Pariselle and Euzet, 1996; Mendlová et al., 2012](#)). Generally
499 speaking, the acquisition of thickness/length in the hooks seems to be the result of adaptation to specific hosts.
500 Indeed, it is well known that to successfully parasitize large hosts, stronger (larger) haptoral sclerites are necessary.
501 This was already [shown for](#) dactylogyrean monogeneans (Šimková et al., 2006), and recently observed in
502 specimens of *C. nshomboi* parasitizing the world's biggest cichlid, *B. microlepis*, in LT. The specimens of *C.*
503 *nshomboi* on this cichlid have larger and differently shaped anchors when compared to specimens parasitizing
504 smaller-sized perissodines (Rahmouni, 2021). Sclerotization in the vagina seems to have evolved [or been lost](#)
505 multiple times.

506 The different levels of host specificity of species of *Cichlidogyrus* occurring in West African cichlids and
507 the high species richness on some cichlid species provided the motivation to investigate the processes that have
508 contributed to diversification in *Cichlidogyrus* ([Pouyaud et al., 2006; Mendlová and Šimková, 2014](#)). A narrow
509 host specificity (strict specialism) was previously attributed to LT species of *Cichlidogyrus*, whilst generalist
510 species were rare, [with](#) only *C. casuarinus* [reported as](#) an intermediate generalist ([Kmentová et al., 2016b](#)). In our
511 study, host specificity was evaluated for 35 species of *Cichlidogyrus* parasitizing LT cichlids. The strict specialist
512 lifestyle seems to constitute the ancestral state of host specificity in *Cichlidogyrus* from LT cichlid hosts, and

513 changes towards lower host specificity were rare, recorded in few species of the clades 3 and 5 only (Muterezi
514 Bukinga et al. 2012; Kmentová et al. 2016b; Rahmouni et al. 2018; Rahmouni et al. unpublished). This corresponds
515 to findings for West African systems (Vignon et al. 2011; Mendlová and Šimková, 2014). The degree of host
516 specificity at global scale was shown, indeed, to differ from that at local levels in *Dactylogyrus* Diesing, 1850
517 parasitizing European cyprinids (Šimková et al., 2006), and *Cichlidogyrus* parasitizing West African cichlids. Such
518 differences could potentially be explained by isolation of monogenean populations (Mendlová and Šimková,
519 2014). Reduced host specificity reported by Kmentová et al. (2016b) in deep-water monogeneans of LT
520 Bathybatini seems to also occur in *C. nshomboi* and *C. habluetzeli* parasitizing benthopelagic hosts – *B. microlepis*
521 occurring down to the limit of the oxygenated layer (~ 50–200 m), while *C. frontosa* and *C. schoutedeni* are
522 commonly found in coastal water along rocks, and in shallow sandy habitats, respectively (~ 30–50 m) (Konings,
523 2019). In marine *Lamellodiscus* Johnston & Tiegs, 1922 (Desdevises et al., 2002) and freshwater *Dactylogyrus*
524 (Šimková et al., 2006), strict specialism represents the ancestral state of host specificity. This may indicate that
525 specificity is not an evolutionary ‘dead-end’ as previously suggested by Simpson (1953).

526 When summarizing the output of our mapping of morphology onto the parasite phylogeny and
527 considering our assumptions regarding host specificity in the LT system, we can deduce that strict specialists with
528 larval hook size (group A) represent character states of the ancestral *Cichlidogyrus* in LT, indicating that
529 decreasing host specificity could be at least in some species related to the evolution of complex parasite
530 morphology (increased thickness and/or elongation of hooks). We can support this observation by a few examples
531 of species of *Cichlidogyrus* with typical morphology and low host specificity. This is the case, for instance, for the
532 type-species *C. arthracanthus* Paperna, 1960 described from Levantine *C. zillii* (Gervais, 1848) (Paperna, 1960).
533 At the global level, this species is recognized as a true generalist in view of its occurrence on genetically and
534 geographically distant cichlid hosts, i.e., oreochromines native to the Levantine region (Paperna, 1960),
535 coptodonines and tilapiines native to West Africa (Paperna, 1960; Pariselle and Euzet, 2009, 1996; Pouyaud et al.,
536 2006). In terms of haptor morphology, *C. arthracanthus* displays a unique hooks organization with massive hook
537 pairs I and VI compared to larval-shaped pair V (see Pariselle and Euzet 2003; Vignon et al. 2011). Overall, it is
538 still too premature to attribute an adaptive meaning to the morphological variations in the hooks and vagina, in
539 association to the decrease of host specificity in *Cichlidogyrus*.

540 **Conclusion**

541 The application of molecular phylogenetics provided the first data on the phylogenetic position of LT
542 species of *Cichlidogyrus* in relation to their relatives inhabiting freshwater habitats elsewhere in Africa, and also

543 [on the relationships among LT species](#). The phylogenetic tree mirrored the evolutionary history of LT cichlid
544 tribes, on the one hand, and provided support for previous morphological observations reflecting phylogenetic
545 relatedness among species of *Cichlidogyrus*. Various speciation mechanisms, ranging from failure to diverge to
546 cospeciation, with host switches and duplications observed at host tribal level, were revealed to have been involved
547 in the diversification of this ectoparasite genus. Further research is, however, needed to determine the exact
548 evolutionary meaning of morphological features of the haptor and reproductive organs, in relation to parasite
549 specialization.

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574 **Author contributions**

575 CR, MPMV and AŠ designed the study. AŠ and MPMV supervised the work. MPMV and SK co-organised the
576 fieldtrips, parasite collection, preparation of specimens and provided scientific background in the field. SK
577 identified the host specimens and provided scientific background on the system and the analyses. CR performed
578 the lab work and data analysis, CR, MPMV, SK and AŠ wrote and corrected the manuscript. All authors read and
579 approved the final manuscript.

580 **Ethics declarations**

581 **Conflict of interest**

582 The authors declare no conflict of interest.

583 **Data availability**

584 Genetic sequence data is available from the NCBI database (see Table 1 for accession numbers) or from the authors
585 upon request. [Data associated with this manuscript is provided online as electronic supplementary material at:](http://dx.doi.org/10.17632/fwpczwwsbs)
586 [http://dx.doi.org/10.17632/fwpczwwsbs.](http://dx.doi.org/10.17632/fwpczwwsbs)

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910

911 **Figure captions**

912 **Fig. 1** Maximum Likelihood (ML) phylogram of species of *Cichlidogyrus* and *Scutogyrus* parasitizing Lake
913 Tanganyika cichlid hosts and lineages from the rest of Africa based on analysis of the [18S, ITS1 and 28S rDNA](#)
914 sequences. Species of *Cichlidogyrus* from tylochromine hosts were selected to root the tree following Mendlová
915 et al. (2012). Values above branches indicate bootstrap values (BS) from ML and posterior probabilities (BP) from
916 BI analyses. Values below 50 (ML) and 0.80 (BI) are shown as dashes. [Clade numbers](#) 1–5 refer to different
917 *Cichlidogyrus* lineages (including *Scutogyrus*). Clades in black cluster West African cichlid lineages of
918 *Cichlidogyrus*, while those in red are for species parasitizing LT hosts. Branch lengths correspond to the expected
919 number of substitutions per site.

920 **Fig. 2** Mapping of cichlid host lineages onto the ML tree of *Cichlidogyrus* from Lake Tanganyika.

921 **Fig. 3** (A) Tanglegram of phylogenies of Lake Tanganyika cichlid hosts (left) and associated *species of*
922 *Cichlidogyrus* (right) obtained using ML tree inference for species of *Cichlidogyrus* and the cichlid tree topology
923 from Ronco et al. (2021). Green lines indicate statistically significant host-parasite links ($p < .05$) and red lines
924 indicate non-statistically significant links. (B) One of the possible cophylogenetic scenarios between cichlid hosts
925 and their specific *Cichlidogyrus* obtained using Jane software, with the lowest cost produced by the host switch-
926 adjusted TreeFitter model (6 cospeciation events (hollow coloured circle), 12 duplications (solid coloured circle),
927 17 duplications followed by host switch (duplication with an arrow following the trajectory of the switching
928 species), nine failures to diverge (jagged line) and 1 loss event (dashed line)). Black branches represent the cichlid
929 phylogeny and blue branches represent the phylogeny of *Cichlidogyrus*.

930 **Fig. 4** Mapping of (A) haptoral groups in term of hooks configuration and (B) sclerotization in the vagina onto
931 the ML phylogenetic tree of species of *Cichlidogyrus* from Lake Tanganyika cichlid hosts. The haptoral groups
932 A-D are represented by hook pairs of *C. milangelnari*, *C. aspiralis*, *C. rectangulus* and *C. nshomboi*. The
933 represented vagina is that exhibited by *C. salzburgeri*.

934

Supplementary Table S1 List of species of *Cichlidogyrus* from Lake Tanganyika investigated in this study with their cichlid hosts classified by tribes, host range, local index of specificity (IS) and information regarding the presence of a sclerotized vagina and their haptor groups in terms of size of hook pairs. Host range is expressed as the total number of Tanganyikan cichlid host species parasitized by a given species of *Cichlidogyrus*. The index of specificity (IS) follows that of Kmentová et al. (2016): (i) strict specialists parasitizing a single cichlid host species, (ii) intermediate specialists parasitizing two or more congeneric host species, (iii) intermediate generalists from heterogeneric host species from the same tribe, and (iv) true generalists from phylogenetically unrelated cichlid species. This classification was adopted for mapping the host specificity of species of *Cichlidogyrus* from Tanganyikan cichlids onto their phylogenetic tree. Based on Pariselle and Euzet (2003), Vignon et al. (2011) and Rahmouni et al. (2017), group A clusters species of *Cichlidogyrus* with short hook pairs I-IV, VI and VII, group B for species exhibiting long hook pair I (pair V with larval size) and short pairs II-IV, VI and VII, group C harbors species with shorter hook pair I (pair V with larval size) and longer pairs II-IV, VI and VII, and group D for species with long hook pairs, except larval-shaped pair V.

944

<i>Cichlidogyrus</i> spp.	Cichlid host	Cichlid tribe	Host range	Index of specificity (IS)	Sclerotization in the Vagina	Haptor groups (hooks configuration)
<i>Cichlidogyrus antioineparisellei</i>	<i>Interochromis loocki</i>	Tropheini	1	Strict specialist	Yes	Group A
<i>Cichlidogyrus spiralis</i>	<i>Ophthalmotilapia nasuta</i>	Ectodini	1	Strict specialist	Yes	Group B
<i>Cichlidogyrus attenboronghi</i>	<i>Benthochromis horii</i>	Benthochromini	1	Strict specialist	No	Group A
<i>Cichlidogyrus banyankimbongi</i>	<i>Simochromis diagramma</i>	Tropheini	1	Strict specialist	No	Group A
<i>Cichlidogyrus brunneus</i>	<i>Trematocara unimaculatum</i>	Trematocarini	1	Strict specialist	No	Group A
<i>Cichlidogyrus casuarinus</i>	<i>Bathybates fasciatus</i>	Bathybatini	7	Intermediate generalist	Yes	Group D
	<i>Bathybates graneri</i>					
	<i>Bathybates hornii</i>					
	<i>Bathybates leo</i>					
	<i>Bathybates minor</i>					
	<i>Bathybates vittatus</i>					
	<i>Hemibates stenosoma</i>					
<i>Cichlidogyrus discophonum</i>	<i>Aulonocranus devindti</i>	Ectodini	1	Strict specialist	No	Group A
<i>Cichlidogyrus evitae</i>	<i>Tanganicodus irsacae</i>	Eretmodini	1	Strict specialist	No	Group A
<i>Cichlidogyrus franswiitzi</i>	<i>Pseudosimochromis curvifrons</i>	Tropheini	2	Intermediate specialist	No	Group A
	<i>Pseudosimochromis marginatus</i>					
<i>Cichlidogyrus gillardinae</i>	<i>Astatotilapia burtoni</i>	Haplochromini	2	Intermediate specialist	No	Group A
	<i>Astatotilapia stappersii</i>					
<i>Cichlidogyrus gistelinki</i>	<i>'Ctenochromis' horei</i>	Tropheini	1	Strict specialist	No	Group A

<i>Cichlidogyrus glaciemoratus</i>	<i>Ophthalmotilapia nasuta</i>	Ectodini	1	Strict specialist	No	Group A
<i>Cichlidogyrus hablueteli</i>	<i>Cyphotilapia frontosa</i>	Cyphotilapini	2	True generalist	Yes	Group D
	<i>Cardiopharynx schoutedeni</i>	Ectodini				
<i>Cichlidogyrus irenae</i>	<i>Gnathochromis' pfefferi</i>	Tropheini	1	Strict specialist	No	Group A
<i>Cichlidogyrus jeanolujustini</i>	<i>Eretmodus marksmithi</i>	Eretmodini	1	Strict specialist	No	Group A
<i>Cichlidogyrus masiyai</i>	<i>Petrochromis orthognathus</i>	Tropheini	1	Strict specialist	No	Group A
<i>Cichlidogyrus mbrizei</i>	<i>Oreochromis tanganicæ</i>	Oreochromini	1	Strict specialist	Yes	Group A
<i>Cichlidogyrus milangehnari</i>	<i>Cyprichromis microlepidotus</i>	Cyprichromini	1	Strict specialist	No	Group A
<i>Cichlidogyrus multimbwai</i>	<i>Tylochromis polytepis</i>	Tylochromini	1	Strict specialist	No	Group A
<i>Cichlidogyrus muterezi</i>	<i>Simochromis diagramma</i>	Tropheini	1	Strict specialist	No	Group A
<i>Cichlidogyrus nshomboi</i>	<i>Boulengerochromis microlepis</i>	Boulengerochromini	4	True generalist	Yes	Group D
	<i>Perissodus microlepis</i>	Perissodini				
	<i>Perissodus straeleni</i>					
	<i>Haplotaxodon microlepis</i>					
<i>Cichlidogyrus pseudoaspiralis</i>	<i>Aulonocramis dewindti</i>	Ectodini	1	Strict specialist	No	Group B
<i>Cichlidogyrus raeymaekersi</i>	<i>Simochromis diagramma</i>	Tropheini	1	Strict specialist	No	Group A
<i>Cichlidogyrus rectangularis</i>	<i>Ophthalmotilapia nasuta</i>	Ectodini	1	Strict specialist	No	Group C
<i>Cichlidogyrus salzburgeri</i>	<i>Petrochromis trewavasæ</i>	Tropheini	1	Strict specialist	No	Group C
<i>Cichlidogyrus</i> sp. 1	<i>Astatotilapia burtoni</i>	Haplochromini	1	Strict specialist	No	Group A
<i>Cichlidogyrus</i> sp. 2	<i>Astatotilapia burtoni</i>	Haplochromini	1	Strict specialist	No	Group A
<i>Cichlidogyrus</i> sp. 3	<i>Lamprologus callipterus</i>	Lamprologini	1	Strict specialist	Yes	Group A
<i>Cichlidogyrus</i> sp. 4			1	Strict specialist	No	Group A
<i>Cichlidogyrus</i> sp. 5			1	Strict specialist	No	Group A
<i>Cichlidogyrus</i> sp. 6			1	Strict specialist	No	Group A
<i>Cichlidogyrus</i> sp. 7			1	Strict specialist	No	Group A
<i>Cichlidogyrus</i> sp. 8			1	Strict specialist	Yes	Group A
<i>Cichlidogyrus</i> sp. 9	<i>Neolamprologus fasciatus</i>	Lamprologini	1	Strict specialist	No	Group A
<i>Cichlidogyrus</i> sp. 10			1	Strict specialist	No	Group A

Table 1 Cichlid hosts (classified into tribes) sampled along the Lake Tanganyika shoreline and in neighbouring freshwater habitats, with the number of specimens sampled, date and locality of sampling, the species of *Cichlidogyrus* associated with them, and GenBank accession numbers for [18S rDNA](#), [28S rDNA](#) and [COI mtDNA](#) for the parasites obtained in the present study (see material and methods).

Cichlid Tribe	Cichlid host species	n	Date of sampling	Sampling locality	Country	GPS coordinates	<i>Cichlidogyrus</i> species	18S-ITS1 rDNA	28S rDNA	COI
Boulengerochromini Takahashi, 2003	<i>Boulengerochromis microlepis</i> (Boulenger, 1899)	2	05/09/2013	Bujumbura fish market	Burundi	3°23'S, 29°22'E	<i>C. nshomboi_1</i> Muterezi Bukinga, Vanhove, Van Steenberghe and Pariselle, 2012	OL675317	OL675266	OL704757
Cyphotilapini Salzburger, Meyer, Baric, Verheyen and Sturmhuber, 2002	<i>Cyphotilapia frontosa</i> (Boulenger, 1906)	2	07/08/2016	Makabola village	DRC	3°32'S, 29°9'E	<i>C. adkoningsi</i> Rahmoumi, Vanhove and Šimková, 2018	-	-	-
Cyprichromini Poll, 1986	<i>Cyprichromis microlepidotus</i> (Poll, 1956)	3	23/09/2013	Nyaruhongoka	Burundi	3°41'S, 29°20'E	<i>C. habluetzelii</i> Rahmoumi, Vanhove and Šimková, 2018 <i>C. milangehni</i> Rahmoumi, Vanhove and Šimková, 2017	OL675312 OL675315	OL675271 OL675263	OL704742 OL704754
Ectodini Poll, 1986	<i>Ophthalmotilapia nasuta</i> (Poll and Matthes, 1962)	4	07-09/09/2013	Magara	Burundi	3°44'S, 29°19'E	<i>C. spiralis</i> Rahmoumi, Vanhove and Šimková, 2017 <i>C. glaciorenoratus</i> Rahmoumi, Vanhove and Šimková, 2017 <i>C. rectangularis</i> Rahmoumi, Vanhove and Šimková, 2017	OL675305 OL675311 OL675321	OL675254 OL675262 OL675270	- OL704753 OL704746
Eretmodini Poll, 1986	<i>Aulonocranus dewindti</i> (Boulenger, 1899)	3	04-07/09/2013	Nyaruhongoka	Burundi	3°41'S, 29°20'E	<i>C. discophorum</i> Rahmoumi, Vanhove and Šimková, 2017 <i>C. pseudoaspiralis</i> Rahmoumi, Vanhove and Šimková, 2017	OL675307 OL675319	OL675257 OL675268	OL704745 -
Eretmodini Poll, 1986	<i>Cardiopharynx schoutedeni</i> Poll, 1942	6	07/08/2016	Mulongwe fish market	DRC	3°22'S, 29°6'E	<i>C. koblmuetleri</i> Rahmoumi, Vanhove and Šimková, 2018 <i>C. habluetzelii</i> Rahmoumi, Vanhove and Šimková, 2017	- OL675333	- OL675286	- -
Eretmodini Poll, 1986	<i>Eretmodus markemithi</i> Burgess, 2012	10	03/09/2013	Magara	Burundi	3°44'S, 29°19'E	<i>C. jeanoloustineti</i> Rahmoumi, Vanhove and Šimková, 2017	OL675313	OL675256	OL704747
Haplochromini Trewavas, 1983	<i>Tanganicodus irsacae</i> Poll, 1950	12	04/09/2013	Nyaruhongoka	Burundi	3°41'S, 29°20'E	<i>C. evikae</i> Rahmoumi, Vanhove and Šimková, 2017	OL675308	OL675258	OL704752
Haplochromini Trewavas, 1983	<i>Astatotilapia burtoni</i> (Günther, 1893)	13	23/09/2013	Mukuruka	Burundi	4°14'S, 29°33'E	<i>Cichlidogyrus</i> sp. 1 (undescribed)	OL675322	OL675275	-
Haplochromini Trewavas, 1983	<i>Astatotilapia burtoni</i> (Günther, 1893)	7	20/09/2013	Mukuruka	Burundi	4°14'S, 29°33'E	<i>Cichlidogyrus</i> sp. 1 (undescribed)	OL675309	OL675261	OL704748
Haplochromini Trewavas, 1983	<i>Astatotilapia burtoni</i> (Günther, 1893)	9	25/09/2013	Lake Cohoha	Burundi	-	<i>Cichlidogyrus</i> sp. 1 (undescribed)	OL675309	OL675261	OL704748
Haplochromini Trewavas, 1983	<i>Astatotilapia burtoni</i> (Günther, 1893)	1	25/09/2013	Bujumbura fish market	Burundi	3°23'S, 29°22'E	<i>C. gillardiinae</i> Muterezi Bukinga, Vanhove, Van Steenberghe and Pariselle, 2012	OL675309	OL675261	OL704748
Haplochromini Trewavas, 1983	<i>Astatotilapia burtoni</i> (Günther, 1893)	2	09/09/2013	Mulongwe fish market	DRC	3°22'S, 29°6'E	<i>Cichlidogyrus</i> sp. 2 (undescribed)	OL675324	OL675276	-
Haplochromini Trewavas, 1983	<i>Astatotilapia burtoni</i> (Günther, 1893)	11	16/09/2013	Kilomoni beach	DRC	3°20'S, 29°10'E	<i>C. gillardiinae</i>	OL675334	OL675288	OL753688
Haplochromini Trewavas, 1983	<i>Astatotilapia burtoni</i> (Günther, 1893)	07/08/2016	07/08/2016	Chitili	Zambia	8°36'S, 31°11'E	<i>Cichlidogyrus</i> sp. 2 (undescribed)	OL675324	OL675276	-
Haplochromini Trewavas, 1983	<i>Astatotilapia burtoni</i> (Günther, 1893)	1	16/09/2013	Kilomoni beach	DRC	3°20'S, 29°10'E	<i>C. gillardiinae</i>	OL675334	OL675288	OL753688
Lamprologini Poll, 1986	<i>Lamprologus callipterus</i> Boulenger, 1906	6	06-10/09/2013	Nyaruhongoka	Burundi	3°41'S, 29°20'E	<i>Cichlidogyrus</i> sp. 3 (undescribed)	OL675325	OL675284	-

	2	04/09/2013	Magara	Burundi	3°44'S, 29°19'E	<i>Cichlidogyrus</i> sp. 4 (undescribed)	OL675326	OL675277	-
	6	17-19/09/2013	Mukuruka	Burundi	4°14'S, 29°33'E	<i>Cichlidogyrus</i> sp. 5 (undescribed)	OL675327	OL675278	-
	4	20/09/2013	Mvugo	Burundi	4°15'S, 29°34'E	<i>Cichlidogyrus</i> sp. 6 (undescribed)	OL675328	OL675279	-
				Burundi		<i>Cichlidogyrus</i> sp. 7 (undescribed)	OL675329	OL675280	-
	3	23/08/2011	Wonzye Point	Burundi	8°43'S, 31°08'E	<i>Cichlidogyrus</i> sp. 8 (undescribed)	OL675330	OL675281	-
<i>Neolamprologus fasciatus</i> (Boulenger, 1898)	-	18/04/2008	Kalambo Lodge	Zambia	8°37'S, 31°12'E	<i>Cichlidogyrus</i> sp. 9 (undescribed)	OL675331	OL675282	-
<i>Perissodus microlepis</i> Boulenger, 1898	3	09/09/2013	Magara	Burundi	3°44'S, 29°19'E	<i>Cichlidogyrus</i> sp. 10 (undescribed)	OL675323	OL675283	-
	5	09/09/2013	Nyaruhongoka	Burundi	3°41'S, 29°20'E	<i>C. nshomboi_2</i> Muterezi Bukinga, Vanhove, Van Steenberge and Pariselle, 2012	OL675318	OL675267	OL704756
	2	08/08/2016	Pemba	DRC	3°37'S, 29°9'E				
<i>Perissodus sraeleni</i> Poll, 1948	7	14/05/2010	Mukumba	DRC	6°56'S, 29°42'E	<i>C. nshomboi_2</i>	OL675332	OL675285	-
	2	15/04/2010	Mtoto	DRC	6°58'S, 29°43'E				
	1	-	Mtosi	Zambia	7°35'S, 30°38'E				
<i>Haplotaxodon microlepis</i> Boulenger, 1906	3	1957	Luhanga	DRC	3°31'S, 29°08'E	<i>C. nshomboi_2</i>	-	-	-
		24/04/2010	Murega	DRC	5°38'S, 29°23'E				
		1997	Makumba	DRC	6°56'S, 29°42'E				
Tropheini Poll, 1986	7	6-7/09/2013	Nyaruhongoka	Burundi	3°41'S, 29°20'E	<i>C. gistelinki</i> Gillardin, Vanhove, Pariselle, Huyse and Volckaert, 2011	OL675310	OL675260	OL704759
	1	17/09/2013	Mukuruka	Burundi	4°14'S, 29°33'E				
	1	26/09/2013	Bujumbura fish market	Burundi	3°23'S, 29°22'E				
	4	06/09/2013	Magara	Burundi	3°44'S, 29°19'E				
	5	25/09/2013	Mvugo	Burundi	4°15'S, 29°34'E				
<i>Interochromis loocki</i> (Poll, 1949)	9	08/08/2016	Pemba	DRC	3°37'S, 29°9'E	<i>C. antoineparisellei</i> Rahmouni, Vanhove and Šimková, 2018	OL675304	OL675272	-
<i>Petrochromis orthognathus</i> Matthes, 1959	4	08/08/2016	Pemba	DRC	3°37'S, 29°9'E	<i>C. masihai</i> Rahmouni, Vanhove and Šimková, 2018	OL675314	OL675273	OL704749
<i>Petrochromis trewavasae</i> Poll, 1948	1	08/08/2016	Pemba	DRC	3°37'S, 29°9'E	<i>C. salzburgeri</i> Rahmouni, Vanhove and Šimková, 2018	-	OL675274	-
<i>Pseudosinochromis curvifrons</i> Poll, 1942	1	08/08/2016	Pemba	DRC	3°37'S, 29°9'E	<i>C. franswitzei</i> Pariselle and Vanhove, 2015	-	OL675259	-
						<i>C. frankwillemsi</i> Pariselle and Vanhove, 2015	-	-	OL704750
<i>Sinochromis diagramma</i> (Günther, 1893)	10	05/09/2013	Magara	Burundi	3°44'S, 29°19'E	<i>C. banyankimbongi</i> Pariselle and Vanhove, 2015	OL675306	OL675255	OL704760
	10	05-06/09/2013	Nyaruhongoka	Burundi	3°41'S, 29°20'E	<i>C. muterezi</i> Pariselle and Vanhove, 2015	OL675316	OL675265	OL704758

Tylochromini Poll, 1986	<i>Pseudosimochromis marginatus</i> (Poll, 1956)	1	08/08/2016	Pemba		3°37'S, 29°9'E	<i>C. raeymaekersi</i> Pariselle and Vanhove, 2015	OL675320	OL675269	OL704755
	<i>Tylochromis polylepis</i> (Boulenger, 1900)	1	09/09/2013	Mulongwe fish market	DRC	3°22'S, 29°6'E	<i>C. franswitzer</i> Pariselle and Vanhove, 2015	-	OL675287	-
							<i>C. mulimbwai</i> Muterezi Bukinga, Vanhove, Van Steenberge and Pariselle, 2012	-	OL675264	OL704743
							<i>C. muzumani</i> Muterezi Bukinga, Vanhove, Van Steenberge and Pariselle, 2012	-	-	OL704744
							<i>C. sergemorandi</i> Rahmouni, Vanhove and Simková, 2018	-	-	OL704751

Table 2 List of [previously published](#) *Cichlidogyrus* spp. parasitizing West African and LT cichlids included in the present study, with cichlid host species, [cichlid lineage/tribe](#), and GenBank accessions numbers for 18S, ITS1 and 28S rDNA sequences data.

<i>Cichlidogyrus</i> spp.	Cichlid host species	Cichlid lineage	18S rDNA-ITS1	28S rDNA
<i>Cichlidogyrus acerbus</i> Dossou, 1982	<i>Sarotherodon galilaeus</i> (Linnaeus, 1758)	Oreochromini Dunz and Schliewen, 2013	HE792780 ¹	HQ010036 ²
<i>Cichlidogyrus aegypticus</i> Ergens, 1981	<i>Coptodon guineensis</i> (Günther, 1862)	Coptodonini Dunz and Schliewen, 2013	HE792781 ¹	HQ010021 ²
<i>Cichlidogyrus agnesi</i> Pariselle & Euzet, 1995	<i>Coptodon guineensis</i> (Günther, 1862)	Coptodonini	AJ920286 ³	-
<i>Cichlidogyrus amieti</i> Birgi & Euzet, 1983	<i>Aphyosemion cameronense</i> (Boulenger, 1903)	Non-cichlid	-	KT945076 ⁴
<i>Cichlidogyrus amphoratus</i> Pariselle & Euzet, 1996	<i>Coptodon guineensis</i> (Günther, 1862)	Coptodonini	HE792782 ¹	HE792772 ¹
<i>Cichlidogyrus arthracanthus</i> Paperna, 1960	<i>Coptodon guineensis</i> (Günther, 1862)	Coptodonini	HE792783 ¹	HQ010022 ²
<i>Cichlidogyrus attenboroughi</i> Kmentová et al., 2016	<i>Benthochromis horii</i> Takahashi, 2008	Benthochromini Takahashi, 2003	MH708153 ⁵	MH708146 ⁵
<i>Cichlidogyrus bilongi</i> Pariselle & Euzet, 1995	<i>Coptodon guineensis</i> (Günther, 1862)	Coptodonini	AJ920287 ³	-
<i>Cichlidogyrus brunnenis</i> Kmentová et al., 2016	<i>Trematocara unimaculatum</i> Boulenger, 1901	Trematocarini Poll, 1986	MH708152 ⁵	MH708144 ⁵
<i>Cichlidogyrus casuarinus</i> Pariselle, Muterezi Bukinga & Vanhove, 2015	<i>Bathybates minor</i> Boulenger, 1906	Bathybatini Poll, 1986	KX007795 ⁶	KX007822 ⁶
<i>Cichlidogyrus cirratus</i> Paperna, 1964	<i>Oreochromis niloticus</i> (Linnaeus, 1758)	Oreochromini	HE792784 ¹	HE792773 ¹
<i>Cichlidogyrus cubitus</i> Dossou, 1982	<i>Coptodon guineensis</i> (Günther, 1862)	Coptodonini	HE792785 ¹	HQ010037 ²
<i>Cichlidogyrus digitatus</i> Dossou, 1982	<i>Coptodon guineensis</i> (Günther, 1862)	Coptodonini	HE792786 ¹	HQ010023 ²
<i>Cichlidogyrus douellouae</i> Pariselle, Bilong Bilong & Euzet, 2003	<i>Sarotherodon galilaeus</i> (Linnaeus, 1758)	Oreochromini	HE792787 ¹	HE792774 ¹
<i>Cichlidogyrus dracolemma</i> Řehulková, Mendlová & Šimková, 2013	<i>Hemichromis letourneuxi</i> Sauvage, 1880	Hemichromini Dunz and Schliewen, 2013	HE792794 ¹	HQ010027 ²
<i>Cichlidogyrus ergensi</i> Dossou, 1982	<i>Coptodon guineensis</i> (Günther, 1862)	Coptodonini	HE792788 ¹	HQ010038 ²
<i>Cichlidogyrus falcifer</i> Dossou & Birgi, 1984	<i>Hemichromis fasciatus</i> Peters, 1857	Hemichromini	HE792789 ¹	HQ010024 ²
<i>Cichlidogyrus philander</i> Douëllou, 1993	<i>Pseudocrenilabrus philander</i> (Weber, 1897)	Haplochromini	MG250207*	MG279698*
<i>Cichlidogyrus flexicolpos</i> Pariselle & Euzet, 1995	<i>Coptodon guineensis</i> (Günther, 1862)	Coptodonini	AJ920283 ³	-
<i>Cichlidogyrus gallus</i> Pariselle & Euzet, 1995	<i>Coptodon guineensis</i> (Günther, 1862)	Coptodonini	AJ920285 ³	-
<i>Cichlidogyrus halli</i> 1 (Price & Kirk, 1967)	<i>Sarotherodon galilaeus</i> (Linnaeus, 1758)	Oreochromini	HE792790 ¹	HQ010025 ²
<i>Cichlidogyrus halli</i> 2 (Price & Kirk, 1967)	<i>Oreochromis niloticus</i> (Linnaeus, 1758)	Oreochromini	AJ920272 ³	-
<i>Cichlidogyrus irenae</i> Gillardin et al., 2012	<i>'Gnathochromis' pfefferi</i> (Boulenger, 1898)	Tropheini Poll, 1986	KT692939 ⁷	MH708145 ⁷
<i>Cichlidogyrus longicirrus</i>	<i>Hemichromis fasciatus</i>	Hemichromini	HE792791 ¹	HQ010026 ²

Paperna, 1965	Peters, 1857			
<i>Cichlidogyrus mbirizezi</i>	<i>Oreochromis tanganicae</i>	Oreochromini	MG030376*	MG030378*
Muterezi Bukinga et al., 2012	(Günther, 1894)			
<i>Cichlidogyrus nageus</i>	<i>Sarotherodon galilaeus</i>	Oreochromini	HE792795 ¹	HQ010028 ²
Řehulková, Mendlová & Šimková, 2013	(Linnaeus, 1758)			
<i>Cichlidogyrus njinei</i>	<i>Sarotherodon galilaeus</i>	Oreochromini	HE792792 ¹	HE792775 ¹
Pariselle, Bilong Bilong & Euzet, 2003	(Linnaeus, 1758)			
<i>Cichlidogyrus pouyaudi</i>	<i>Tylochromis intermedius</i>	Tylochromini	HE792793 ¹	HQ010039 ²
Pariselle & Euzet, 1994	(Boulenger, 1916)	Poll, 1986		
<i>Cichlidogyrus sclerosus</i>	<i>Oreochromis niloticus</i>	Oreochromini	DQ537359 ⁸	DQ157660 ⁸
Paperna & Thurston, 1969	(Linnaeus, 1758)			
<i>Cichlidogyrus thurstonae</i>	<i>Coptodon rendalli</i>	Coptodonini	AJ920274 ³	MH767406 ⁹
Ergens, 1981	(Boulenger, 1897)			
<i>Cichlidogyrus tiberianus</i>	<i>Coptodon rendalli</i>	Coptodonini	MH767404 ⁹	HE792796 ¹
Paperna, 1960	(Boulenger, 1897)			
<i>Cichlidogyrus tilapiae</i>	<i>Hemichromis fasciatus</i>	Hemichromini	HE792797 ¹	HQ010029 ²
Paperna, 1960	Peters, 1857			
<i>Cichlidogyrus yanni</i>	<i>Coptodon guineensis</i>	Coptodonini	HE792798 ¹	HE792777 ¹
Pariselle & Euzet, 1996	(Günther, 1862)			
<i>Scutogyrus bailloni</i>	<i>Sarotherodon galilaeus</i>	Oreochromini	HE792799 ¹	HE792778 ¹
Pariselle & Euzet, 1995	(Linnaeus, 1758)			
<i>Scutogyrus longicornis</i>	<i>Oreochromis niloticus</i>	Oreochromini	HE792800 ¹	HQ010035 ²
(Paperna & Thurston, 1969)	(Linnaeus, 1758)			
<i>Scutogyrus minus</i>	<i>Sarotherodon melanotheron</i>	Oreochromini	HE792801 ¹	HE792779 ¹
(Dossou, 1982)	Rüppell, 1852			

References: ¹Mendlová et al. (2012); ²Mendlová et al. (2010); ³Pouyaud et al. (2006), ⁴Messu Mandeng et al. (2015); ⁵Kmentová et al. (2018); ⁶Kmentová et al. (2016a); ⁷Kmentová et al. (2016b); ⁸Wu et al. (2007); ⁹Šimková et al. (2019) and . No references are available for sequences indicated by “*”.

Figure 1

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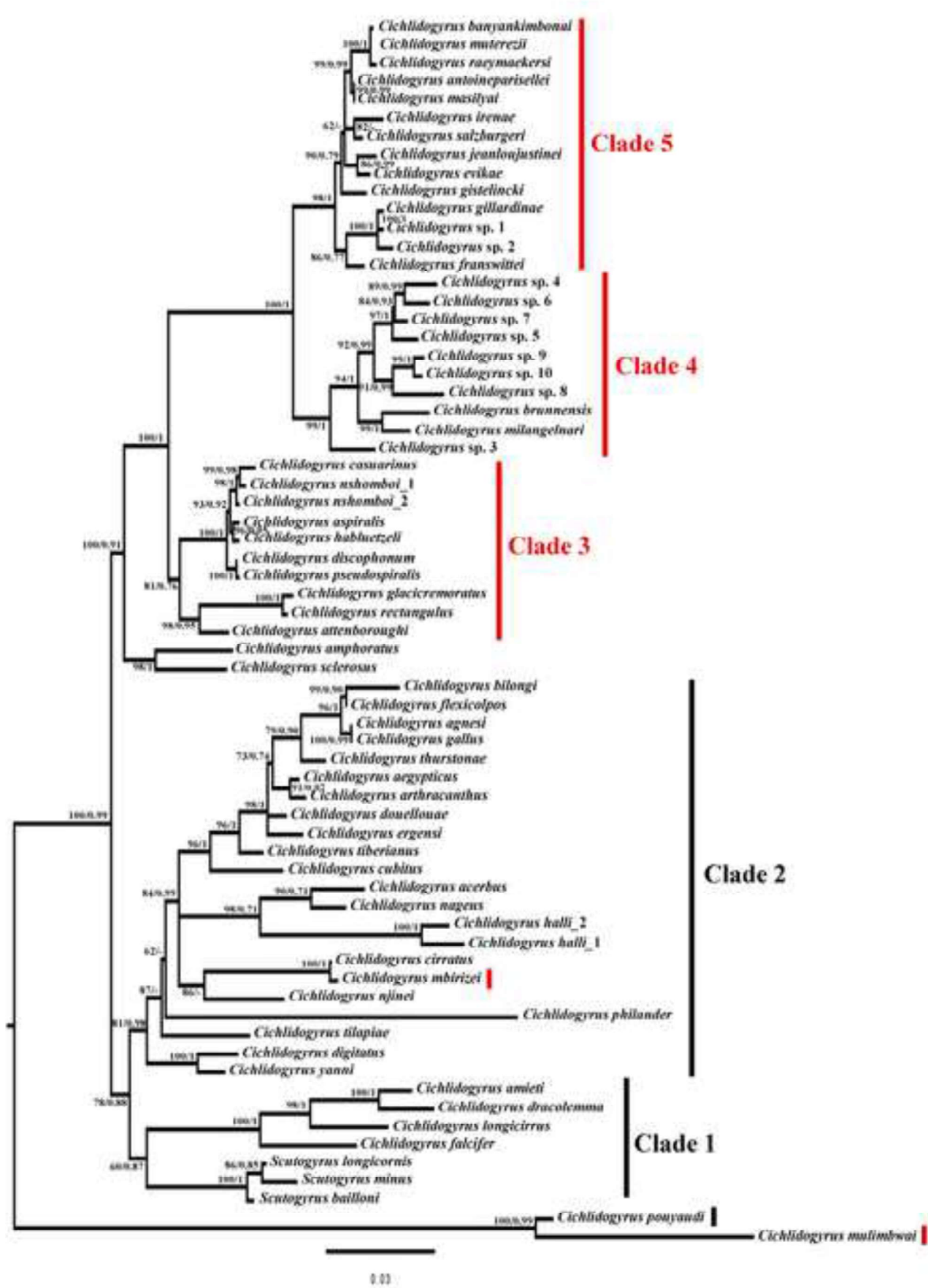


Figure2

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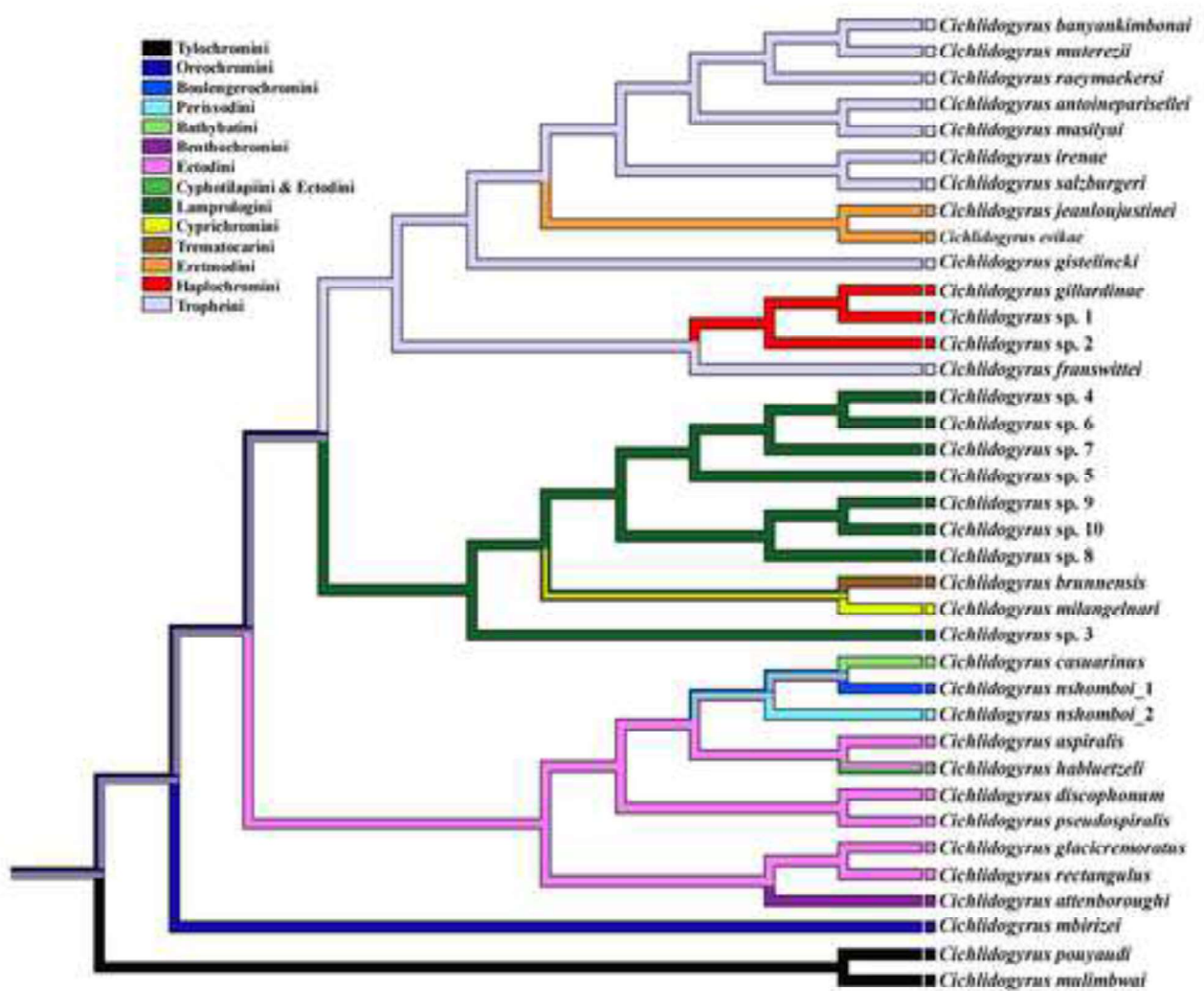


Figure3

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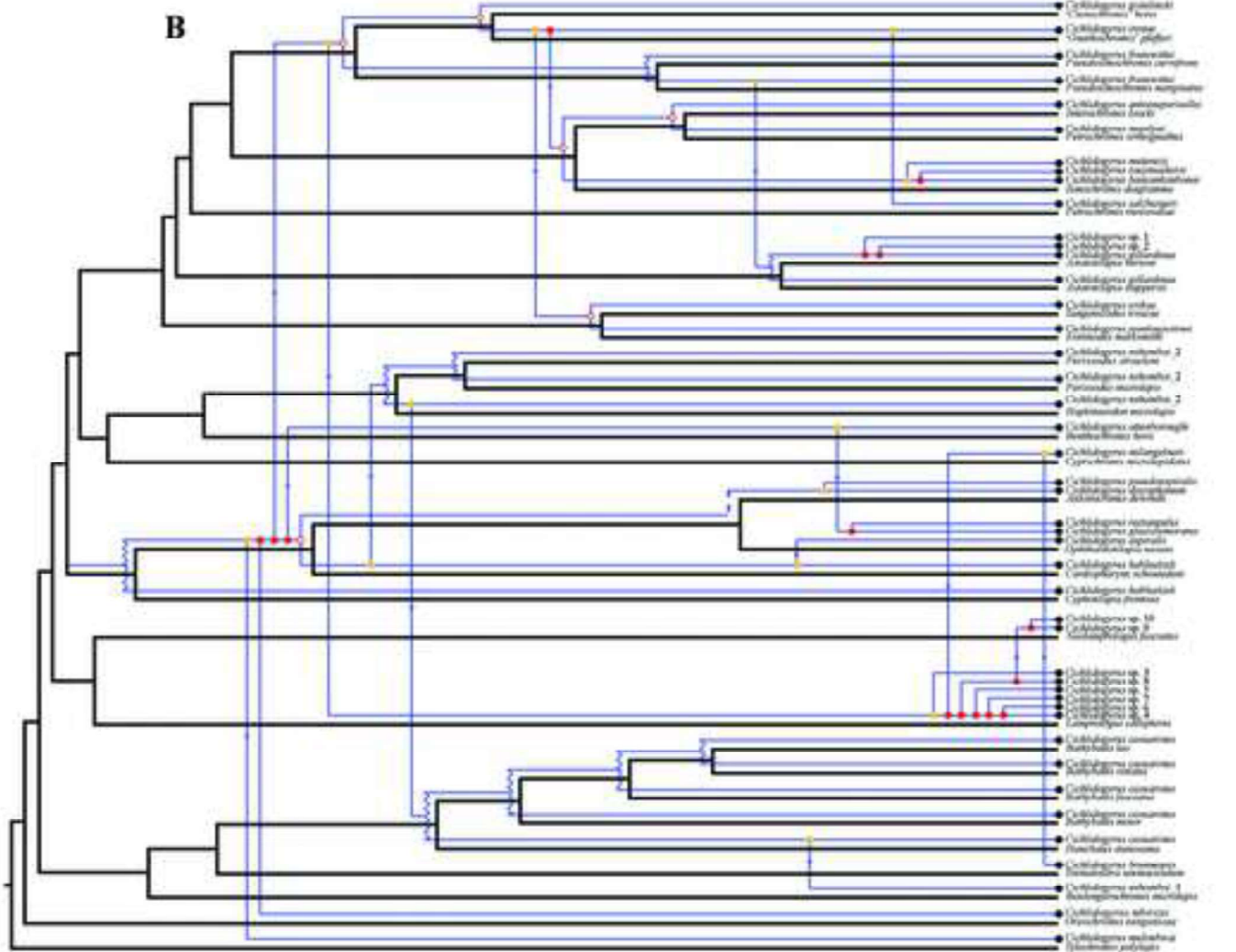
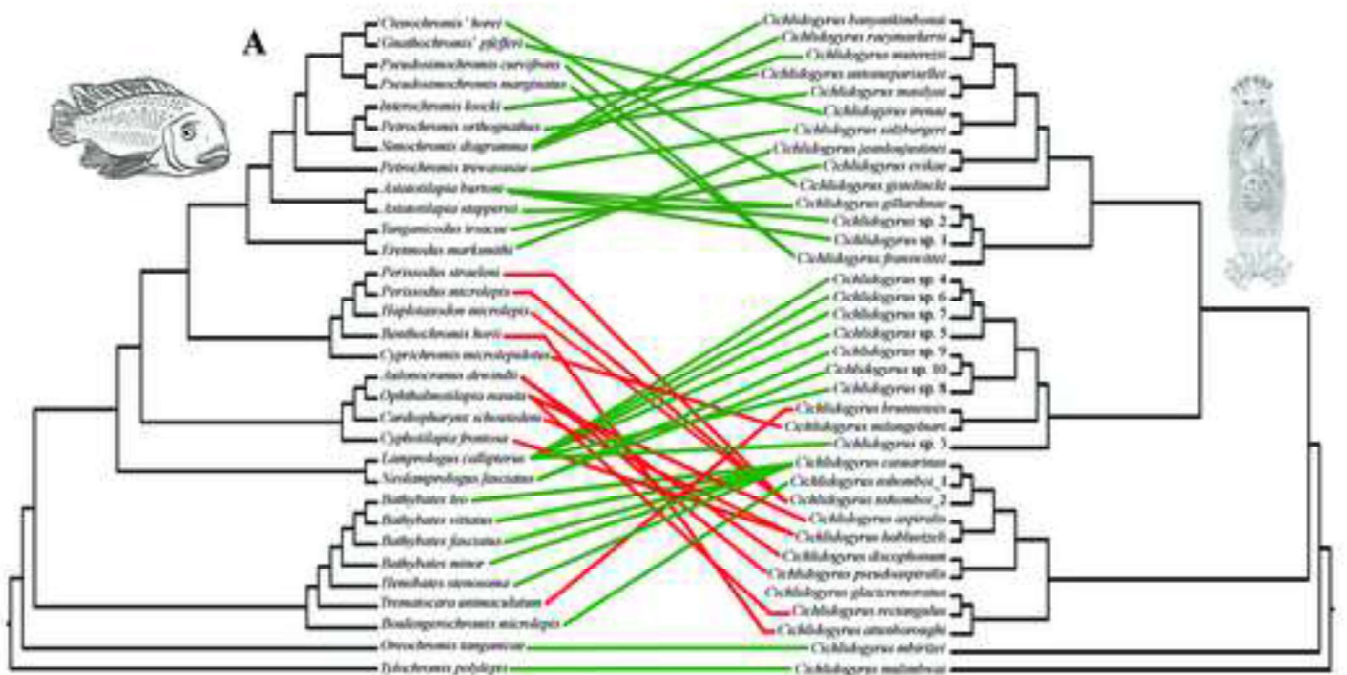


Figure4

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