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Louizi, H; VANHOVE, Maarten; Rahmouni, I; Rkhami, OB; Benhoussa, A; VAN STEENBERGE, Maarten & Pariselle, A (2023) Species depauperate communities and low abundances of monogenean gill parasites at the edge of the natural distribution range of their cichlid hosts in northern Africa. In: HYDROBIOLOGIA, 850 , p. 2461-2471.

DOI: 10.1007/s10750-022-05031-3

Handle: <http://hdl.handle.net/1942/40381>

1 **Species depauperate communities and low abundances of monogenean gill parasites at**
2 **the edge of the natural distribution range of their cichlid hosts in northern Africa**

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16

17 **Abstract**

18 In Morocco, no work has been carried out on parasitic monogeneans of cichlid fish. An examination of the gills
19 of 375 fish from three native species of Cichlidae: *Oreochromis aureus*, *Coptodon zillii* and *Coptodon guineensis*
20 from different localities, revealed the presence of two monogenean species (1328 monogenean specimens were
21 recovered from 56 fish specimens) belonging to the family Dactylogyridae and to the genus *Cichlidogyrus*: three
22 morphotypes of *C. cirratus* were identified from *O. aureus* and *C. zillii*; and *C. cubitus* was identified from *C.*
23 *guineensis*. This is the first time that these monogeneans were collected and identified in Morocco. In addition, *O.*
24 *aureus* was revealed as a new host for *C. cirratus*. The low parasite species richness and intensity, appear to support
25 the enemy release hypothesis, and have probably promoted the lateral transfer of parasites in natural populations
26 between *O. aureus* and *C. zillii*, and the synxenic diversification of *C. cirratus*.

27

28 **Keywords**: Morocco, enemy release hypothesis, lateral transfer, morphotypes, synxenic diversification.

29

30 Introduction

31 The diversification of continental aquatic organisms is the result of different events linked on the one hand to
32 the evolutionary potential of the species, and on the other hand to the duration of hydrographic isolations, to the
33 size of the watersheds and also to the diversity of aquatic habitats. Currently, ichthyologists distinguish the
34 existence of several large main ichthyological provinces in Africa; Morocco being between the Maghreb province
35 and a Saharan zone (Lévêque et al., 1997).

36 These two zones, located between the African and European tectonic plates, are characterized by a very poor
37 fish fauna, of which Cyprinidae Rafinesque, 1815 is the most widespread family. In the Maghreb province cyprinid
38 fishes have the highest species diversity (70.7%) (Doadrio, 1994), with 20 valid species in Morocco alone
39 (Rahmouni, 2020).

40 Another family, with a mostly tropical distribution, is also present: Cichlidae Heckel, 1840 (Doadrio, 1994;
41 Lévêque & Paugy, 2006). This family represents one of the most species-rich fish, with conservative estimates
42 citing about 3000 extant species on earth (Takahashi & Koblmüller, 2011). Cichlids are widely distributed in
43 Africa, Central and South America, the Middle East and parts of South Asia, while fossils have been found in
44 Europe (Italy) (Nelson, 1994). In Morocco, cichlids are tropical relics from the last glacial episodes (Lévêque,
45 1990); they are represented by small isolated populations (Louizi et al., 2019). They are naturally represented by
46 only two genera: *Coptodon* Gervais, 1848 and *Oreochromis* Günther, 1889, with three native species: *Coptodon*
47 *zillii* (Gervais, 1848), *C. guineensis* (Günther, 1862), and *Oreochromis aureus* (Steindachner, 1864). A fourth
48 species, *O. niloticus* (L, 1758), has been introduced into northern Morocco for aquaculture purposes (Louizi et al.,
49 2019; Ainou et al., 2021).

50 To date, African cichlid fishes are known to be parasitized by members of six genera of monogenean parasites
51 (Platyhelminthes): the representatives of two of them are mesoparasites (*sensu* Euzet, 1989) living in a natural
52 cavity of the host (*Enterogyrus* Paperna, 1963 in the stomach; *Urogyrus* Bilong Bilong, Birgi and Euzet, 1994 in
53 the urinary bladder) and four are ectoparasites (Pariselle et al., 2011). The members of three of these are found on
54 the gills and belong to Dactylogyridae: *Cichlidogyrus* Paperna, 1960, *Onchobdella* Paperna, 1968 and *Scutogyrus*
55 Pariselle & Euzet, 1995 (Pariselle et al., 2011) while one genus, mainly found on the skin and on the fins, belongs
56 to Gyrodactylidae: *Gyrodactylus* von Nordmann, 1832. Among these, *Cichlidogyrus* is the most species-rich,
57 including 138 described species in Africa and Middle East (Cruz-Laufer et al., 2021).

58 Contemporary ecology has widely emphasized the importance of parasites as models for studying the structure
59 and organization of communities (Kmentová et al., 2020). Their assessment represents a simple and inexpensive
60 way of collecting ecological information about their hosts (Williams et al., 1992; Poulin, 2021). Monogeneans
61 present an often high level of host specificity; several studies showed that this specificity may reflect the evolution,
62 phylogeny, historical biogeography and ecology of host species (Pariselle et al., 2003; Vanhove et al., 2016;
63 Pariselle et al., 2011; Boeger et al., 2003; Cruz-Laufer et al., 2022).

64 Parasite species richness varies according to several host- or parasite-dependent factors such as the maximum
65 size (Guégan et al., 1992) and the ethology of the host, the environment in which the host species lives, the
66 geographical distribution of the host (Combes, 2001), the number of parasite species inherited from the ancestral
67 host species, lateral transfers or host switches, evolutionary changes of the host specificity of a parasite that can
68 occur between related host species (Pariselle et al., 2011) or even between phylogenetically distant host species,

69 in natural or artificial conditions (Vanhove & Huyse, 2015), stochastic losses of parasitic species (following
70 bottleneck events experienced by host populations) (Pariselle et al., 2003), etc.

71 The survival of introduced host populations may be favored by the loss of their original parasitic fauna (lower
72 parasitic species richness and relatively lower parasite load) following the enemy release hypothesis (ERH)
73 (Mlynarek et al., 2017). This theory assumes that introduced host species gain permanent or temporary advantage
74 compared to the local fauna by losing their native parasites (Torchin et al., 2003). Introduction of alien populations
75 may also result in three possible effects (Sheath et al., 2015): spillback “occurs when parasites from native hosts
76 transfer to the introduced alien host and there is increase in infection”, dilution “occurs when there is a decrease
77 in the infection of the native hosts as aliens reduce transmission of parasites”, and spillover “might occur when an
78 alien host introduces new parasites which then parasitise novel hosts in the new range” (Truter et al., 2017).

79 In Morocco, cichlid fishes are in the northern limit of their natural distribution area, where they arrived a long
80 time ago from sub-Saharan areas. During this long-distance dispersal process, they probably experienced many
81 bottleneck events, as was the case for present-day anthropogenically introduced populations. The fact that
82 Moroccan cichlid fishes now survive in suboptimal conditions may have been enabled by the enemy release
83 hypothesis. For example the low lethal temperature for *O. aureus* ranges from 8 to 15 °C (Rezk & Kamel, 2011),
84 temperature that are common in Moroccan rivers. They also may have been subject to spillback/over effects.

85 The present study aimed to test these expected scenarios in Morocco on native (non-invasive) species at the
86 edge of the natural distribution range, by studying their gill monogenean fauna diversity using the quantitative
87 descriptors of parasite communities by Bush et al. (1997).

88

89 **Materials and methods**

90 *Fish sampling and identification:*

91 Cichlids, identified following Teugels & Thys van den Audenaerde (1992), were caught in various rivers,
92 gueltas (ponds fed by a source generally corresponding to an oasis), wadis and sebkhas (a type of salted wetland
93 in the hot desert regions of North Africa) of Morocco from 2010 to 2021, by either gillnets (length: 20 m, height:
94 2 m; extended mesh size: 60 and 80 mm) or electrofishing using a portable Samus 725G Fish Shocker Stunner
95 (adjusted according to the physicochemical descriptors of the water) connected to a 12V battery. A total of 66
96 sampling points, in all the watersheds of the North, West, East and South of Morocco (Fig. 1) were sampled using
97 gillnets or electrofishing. Specimens were euthanized by severing their spinal cord, and either dissected in the field
98 immediately after fishing following Justine et al. (2012) or stored in a portable deep freezer (Engel) until
99 examination in the lab.

100

101 *Collection and identification of monogeneans:*

102 For the collection of monogeneans, gill arches were placed in a Petri dish, and thoroughly rinsed using a wash
103 bottle and tap water. Monogeneans observed under a stereomicroscope (Leica ES2) were removed using an
104 entomological needle mounted on a mandrel, and placed between slide and coverslip in Malmberg's medium
105 (glycerin ammonium picrate) (Malmberg, 1957). After 24 hours, the slide was sealed with Glyceel (Bates, 1977).
106 The mounts were then observed under a microscope (Leica DM500) and the identification of the monogeneans
107 followed the identification key of Pariselle & Euzet (2009).

108

109 *Ecological analysis:*

110 In this study, we use the quantitative descriptors of parasites proposed by Bush et al. (1997):

111 - Prevalence (P%).

112 - Mean Intensity (MI).

113 - Parasitic abundance (A).

114 Parasites were classified as dominant if ($P > 50\%$), satellite if ($10 \leq P \leq 50\%$) or rare if ($P < 10\%$) according
115 to Valtonen et al. (1997). For the Mean Intensity (MI), they were classified according to Bilong Bilong & Njiné
116 (1998), namely: $MI > 100$ (high); $50 < MI \leq 100$ (average); $10 < MI \leq 50$ (low); $MI < 10$ (very low).

117

118 *Statistical analysis:*

119 The Chi square (χ^2) test was used to compare the Prevalences. The one-way ANOVA was used to compare the
120 Abundances and Mean Intensities of the different localities. The differences were considered significant at the 5%
121 level. These tests were performed using STATISTICA 10.0 software.

122

123 **Results**

124 A total of 375 fish specimens were collected and identified as *Coptodon zillii* [$n = 80$, $TL = 10.87 \pm 1.56$ (7.5–
125 14.7)], *C. guineensis* [$n = 240$, $TL = 14.27 \pm 3.79$ (8.2–23)] and *Oreochromis aureus* [$n = 55$, $TL = 16.55 \pm 3.15$
126 (9.8–22.5)]. *Coptodon zillii* and *O. aureus* were found in the Draa basin in sympatry (W. Draa, Mrimima and G.
127 Zerga), except for localities W. El Maleh where only *C. zillii* and G. Kehla where only *O. aureus* were sampled.
128 *Coptodon guineensis* was found in the Canal de Nador (W. Drader), Chebika Basin (W. Chebika and W. Aabar),
129 and in the Sebkhla Imlili (Fig. 1, Table 1).

130 A total of 1328 monogenean specimens were recovered: *Cichlidogyrus cubitus* Dossou, 1982 ($n = 149$) from
131 *C. guineensis*, and three morphotypes of *C. cirratus* Paperna, 1964 (here referred under the working names *C.*
132 *cirratus* s.s., *C.* “cirratus 1” and *C.* “cirratus 2”) from both *O. aureus* ($n = 1150$), and *C. zillii* ($n = 29$). The
133 morphotypes were identified (Fig. 2 A) by their male copulatory organ (MCO).

134 *Cichlidogyrus* “cirratus 1” (Fig. 2 B) differs from *C. cirratus* s.s. (Fig. 2 A) by the shape of the extremity of
135 the accessory piece: two smooth and rounded ends of almost equal size vs one end hook-shaped, respectively. This
136 particular morphology of the accessory piece is found only in *C. mbirizei* Muterezi (Bukinga et al., 2012) described
137 from *Oreochromis tanganyicae* (Günther, 1894) in Lake Tanganyika (East Africa). *Cichlidogyrus mbirizei* is
138 distinguished by a spirally coiled vagina while it is sinuous in *C.* “cirratus 1” (and *C. cirratus* s.s. and *C.* “cirratus
139 2”).

140 The morphotype *C.* “cirratus 2” (Fig. 2 C) is very similar to *C.* “cirratus 1” with regard to the morphology of
141 its haptor, MCO and vagina. Nevertheless, it differs by the shape of the accessory piece termination which presents
142 two ends, one is a short rounded outgrowth and the other, longer, has a hook-shape vs two rounded ends in *C.*
143 “cirratus 2” (and one hook-shaped in *C. cirratus* s.s.) and by the direction of the heel which rises posteriorly in *C.*
144 *mbirizei* (and *C. cirratus* s.s.) and anteriorly in *C.* “cirratus 2” (and *C.* “cirratus 1”).

145 *Cichlidogyrus cubitus* (Fig. 2 D) has a thin open C-shaped MCO with a developed basal ampulla. The sharply
146 angled accessory piece is attached to the basal ampulla of the MCO, the end is bifid, one of the points is twice as
147 long as the other, and the heel is reduced.

148 The values of the quantitative descriptors of parasite from *O. aureus*, *C. zillii* and *C. guineensis* are presented
149 in Table 2, which shows that the infection parameters of *C. cirratus* (3 morphs) and *C. cubitus* varied between
150 localities.

151 Morphotypes of *C. cirratus* were present on all the sampled populations of *O. aureus* (W. Draa (P = 100%),
152 Mrimima (P = 77.8%) and G. Zerga (P = 57.1%)), except locality G. Kehla. All the morphotypes were found on
153 one specimen of *C. zillii* in locality W. Draa (P = 6.67%), whereas this host carried only *C. cirratus s.s.* in locality
154 Mrimima (P = 3.1%). Monogeneans were absent on this host in localities W. El Maleh and G. Zerga. In contrast,
155 *C. cubitus* was only present on *C. guineensis* at locality W. Aabar (P = 32.8%).

156 The three morphotypes of *C. cirratus* were dominant species (P > 50%) on localities W. Draa (*O. aureus* and
157 *C. zillii*), Mrimima and G. Zerga (*O. aureus* only). *Cichlidogyrus cirratus s.s.* was rare in locality Mrimima on *C.*
158 *zillii*. *Cichlidogyrus cubitus* was a satellite species on *C. guineensis* in locality W. Aabar. Finally, the mean
159 intensity for all parasites (the 3 morphs of *C. cirratus* and *C. cubitus*) varies from low (10 < MI ≤ 50) to very low
160 (< 10) among the localities.

161 The Chi square statistical test carried out on the prevalences according to the hosts (*O. aureus* and *C. zillii*) (χ^2
162 = 3.79, df = 2, $p = 0.14$) and the ANOVA on the mean intensities and the abundances (F = 0.53, dl = 2, $p = 0.59$)
163 showed no significant difference between the localities.

164

165 Discussion

166 North Africa, and in particular Morocco, is part of the Palearctic and more particularly of the Mediterranean
167 biogeographical region. The cichlid species naturally present in Morocco are relict populations of the tropical
168 fauna present during the last glacial episodes when the Sahara was a humid region (Paugy et al., 2011); (Ballouche,
169 2017). The Sahara acts as a barrier to dispersal between the Palearctic and the Afro-tropics. This is why freshwater
170 fish species of Afrotropical origin are poorly represented in North Africa and we therefore encounter a fauna that
171 is mainly of European origin, dominated by the cyprinid species (Doadrio, 1994).

172 The North of the Sahara receives little water and currently only has a few residual permanent aquatic
173 environments: the gueltas, some lakes and some sebkhas. The three species of Cichlidae, present naturally in
174 Morocco, have different ecological requirements. While *C. zillii* and *O. aureus* generally live in the middle course
175 of rivers, *C. guineensis* is found more in estuaries or brackish lagoons (Lévêque et al., 1992). The presence of *C.*
176 *zillii* and *O. aureus* living in sympatry in the lower valley of the Draa watershed is therefore not surprising. The
177 likely absence of *C. guineensis* at the mouth of this Wadi could be due either to a too northern position [which is
178 unlikely since *C. guineensis* has recently been recorded from the Canal de Nador (Ainou et al., 2021)], or to a
179 disappearance of this species over the time as the mouth of the Wadi Draa is very small, often dries up and is
180 subject to substantial seasonal floods. The absence of these same two species (*C. zillii* and *O. aureus*) in the Al
181 Wa'er, Oumma Fatma and Chbika wadies complex could have an opposite explanation: either they never reached
182 this wadies complex over the course of time in view of its isolation, or they disappeared following episodes of
183 drought. On the other hand, *C. guineensis*, the only one present in this watershed, was able, after having arrived
184 from the sea, to move upstream in these wadies in the absence of competition with *C. zillii* and therefore colonize
185 these rivers upstream of their mouth (Louizi et al., 2019). Recently, two specimens of *C. guineensis* were
186 unexpectedly found in the Canal de Nador (Ainou et al., 2021), nearly 1000 km north of the Wadi Aabar, the
187 northernmost locality where this species was previously recorded (Qninba et al., 2012). Probably, this species

188 could have colonized the Canal de Nador via the sea (an ancient (Holocene) or contemporary colonization Ainou
189 et al. (2021)). Cichlid fish are now living at the northern limit of their distribution area, where the populations tend
190 to be more constrained by abiotic factors, to be smaller and more genetically isolated (Sexton et al., 2009).
191 Consequently, their diversity in these watersheds is then logically low (Louizi et al., 2019); (Ainou et al.,2021).

192 Ectoparasitic organisms are at least as sensitive as their hosts to heterogeneous environmental conditions
193 (Wiens, 1989), which may contribute to reducing their species richness (Pariselle et al., 2003). Moreover, they
194 also undergo the bottleneck events experienced by their hosts, on which they are typically overdispersed (Vanhove
195 et al., 2016). Then, it is not surprising that the inventory of branchial monogeneans of cichlids showed a low
196 parasite diversity in Morocco, with only two species (three morphotypes of *C. cirratus*, and *C. cubitus*) recorded,
197 while in West Africa (from where these fish species originate) 17 species of *Cichlidogyrus* were described on *C.*
198 *guineensis*, 10 on *C. zillii* and 4 on *O. aureus* (Pariselle, 2003). Over the 375 fish examined, only 56 were
199 parasitized from 4 localities.

200 *Cichlidogyrus cirratus* was described by Paperna in 1964 on a single specimen from *Sarotherodon galilaeus*
201 (L., 1758) (syn. *Tilapia galilaea*), and was later reported mainly on *O. niloticus*. It was also described under the
202 name *C. nematocirrus* Paperna, 1969 (synonymized with *C. cirratus* by Pariselle & Euzet (2009)) on *O. niloticus*
203 in Lake Volta (Ghana). Our new record of this species on *O. aureus* is not surprising as *O. niloticus* and *O. aureus*
204 are closely related species. Mitochondrial DNA of *O. niloticus* was naturally introgressed by that of *O. aureus* in
205 West Africa (Rognon & Guyomard, 2003); there are natural hybrids of these two species in the wild (Bakhom et
206 al., 2009). Nonetheless, it is a new record for *C. cirratus* on *O. aureus*, and also its northernmost locality.
207 *Oreochromis niloticus* and *O. aureus* are known to share their parasites belonging to *Cichlidogyrus* (except now
208 *C. rognoni* Pariselle, Bilong Bilong & Euzet, 2003 found only on *O. niloticus*) (see Pariselle & Euzet, 2009).

209 Although *C. cirratus* had been recorded from *C. zillii* in Lake Albert (Uganda) by Paperna (1979) (with no
210 mention of infection parameters, so likely only few specimens were recovered, potentially indicating accidental
211 infection), it has never been recovered from this host species in Western Africa (Pariselle & Euzet, 2009) despite
212 a great number of hosts examined (Pariselle, 2003). Therefore, the presence in Morocco of *C. cirratus* on *C. zillii*
213 is most probably the result of a lateral transfer (spill over or spill back, see above) between these two distant host
214 species, made easier by the absence of the original species of *Cichlidogyrus* harbored by *C. zillii* [i.e. *C. aegypticus*
215 Ergens, 1981; *C. anthemocolpos* Dossou, 1982; *C. arthracanthus* Paperna, 1960; *C. cubitus* Dossou, 1982; *C.*
216 *digitatus* Dossou, 1982; *C. ergensi* Dossou, 1982; *C. ornatus* Pariselle & Euzet, 1996; *C. tiberianus* Paperna, 1960;
217 *C. vexus* Pariselle & Euzet, 1995; *C. yanni* Pariselle & Euzet, 1996 (Pariselle, 2003)]. As Gobbin et al. (2021)
218 report that relationships between the number of species of *Cichlidogyrus* were negatively correlated with their
219 abundance, the absence of original monogenean species may considerably reduce interspecific competition and
220 favor colonization by spillover or spillback. Another factor that may also favor this spillover/back effect, is the
221 low density of potential host individuals, which may encourage oncomiracidia (monogenean infectious stages
222 actively infecting a host individual) to infest the first available fish, whether it is the preferred one or not (Pariselle
223 et al., 2015); (Kmentová et al., 2016). The differences in prevalence of *C. cirratus* between the two host species,
224 every time higher on *O. aureus* than on *C. zillii*, is also in favor of the latter not being the original host of this
225 monogenean species (Mladineo & Maršić-Lučić, 2007).

226 The appearance/cohabitation of different morphs of *C. cirratus* on the same host(s) was likely promoted
227 following the vacancy of the niches on the gill biotope of *O. aureus*. The loss of almost all the original species of

228 *Cichlidogyrus* contributes to the potential isolation of several populations of *C. cirratus* followed by synxenic
229 drifts (equivalent to sympatric speciation for parasite species) (Euzet & Combes, 1980). Finally, it is not surprising
230 that the only morphological differences between these morphotypes are visible in the copulatory organs, in fact:
231 the morphology of the genitalia seems to be more useful than the haptor morphology for species-level
232 identifications, presumably because of its faster rate of change (Pouyaud et al., 2006). In Morocco, *C. cubitus*,
233 which parasitizes *Coptodon* spp. in different locations in West Africa (e.g. *C. dageti* Thys van den Audenaerde
234 1971; *C. guineensis*; *C. louka* Thys van den Audenaerde, 1969; *C. zillii*) (Pariselle, 2003), is only found on *C.*
235 *guineensis* in Wadi Aabar. Its absence on Moroccan *C. zillii* is also probably due to a local extinction following
236 bottleneck events suffered by the host populations, which also tend to reduce the parasite species richness (see
237 above and (Pariselle et al., 2003)); or to weak sampling effort. This species is also not found in the Sebkh
238 where the salinity of the environment (from 39 to 45 g/L) (Agnès et al., 2018) is probably too high to allow its
239 survival, salt being a common treatment against monogeneans (Schelkle et al., 2011). Following the same
240 spillback/over scenario that we have just sketched for *C. cirratus*, *C. cubitus* was also found in Tunisia on
241 *Haplochromis desfontainii* Lacepède, 1802 (pers. comm. Pr. Lassad Neifar) and it was recorded in Algeria on *C.*
242 *zillii*, a natural host (Attir et al., 2017).

243

244 **Conclusion**

245 Generally, the overall ecological conditions become increasingly difficult and stressful as one moves to the
246 edge of the native range of a species (Gaston, 2003). In Morocco, the studied host species and their parasites are
247 therefore at the limit of their distribution area; they are subject to bottleneck events and are isolated in small gueltas,
248 where abiotic conditions are suboptimal (hydrological stress: strong variations in temperature, salinity and oxygen
249 content) (Louizi et al., 2019). The low parasite diversity and load reported herein thus supports the enemy release
250 hypothesis (Drake, 2003). As monogeneans are often specific to their host species, they are relatively unlikely to
251 change hosts via lateral transfer, so the presence of *C. cirratus* on the gills of two sympatric non-congeneric host
252 species reveals a "host-switching" in natural conditions (spillover or spillback), and the coexistence of 3 morphs
253 shows a likely synxenic speciation in process.

254

255 **Data Availability:** The datasets supporting the discussion and conclusions of this article are included within the
256 current study and its figures and tables.

257

258 **Conflict of interests:** The authors declare that they have no conflict of interests.

259

260 **Authors' contributions:** HL, IR and AP designed and supervised this study. MPMV, MV, OBR, AB contributed
261 to sampling, the collection and identification of fish, and provided scientific background information on the fish.
262 HL, IR, MPMV and AP analysed the data and wrote the paper. All authors critically read and edited the manuscript.

263

264 **Acknowledgements:** We would like to thank the Center for Saharan Studies (CES), which funded part of this
265 work as part of a scientific project entitled "Impact of global climate change on the biodiversity of Saharan
266 wetlands". We also thank the Institute of Research for Development (IRD) in Morocco, which also contributes in
267 the financing of this work. MPMV is funded by the Special Research Fund of Hasselt University (BOF20TT06,

268 BOF21INCENT09). MPMV and MVS were supported for this work under the Global Taxonomy Initiative by the
269 Capacities for Biodiversity and Sustainable Development (CEBioS) programme at the Royal Belgian Institute of
270 Natural Sciences, funded by the Belgian Directorate-General for Development Cooperation and Humanitarian Aid;
271 we gratefully acknowledge Jolien Venneman, Anne-Julie Rochette and Luc Janssens de Bisthoven for facilitating
272 this.

273

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414 **Figure captions**

415 **Figure 1** Map of Morocco indicating the sampling sites, the presence/absence of indigenous cichlid species, and
416 cichlid populations infected by monogeneans. A.O.F & C. Wadies Complex: Al Wa'er, Oumma Fatma & Chbika
417 wadies complex. 1: Canal Nador; 2: Wadi Draa; 3: Wadi El Maleh; 4: Mrimima; 5: Guelta Zerga; 6: Guelta Kehla;
418 7: Wadi Chebika; 8: Wadi Aabar and 9: Sebkha Imlili.

419 **Figure 2** Opisthaptor and genital sclerotized parts of *C. cirratus* s.s; (A): *C. "cirratus 1"*; (B): *C. "cirratus 2"* (C)
420 and *C. cubitus* (D). 1: Haptor. *Scale-bars*: 50 μm ; 2: Vagina and 3: Male copulatory complex. *Scale-bars*: 10 μm .