Six new dactylogyrid species (Platyhelminthes, Monogenea) from the gills of cichlids (Teleostei, Cichliformes) from the Lower Congo Basin

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Received 29 May 2018, Accepted 4 November 2018, Published online 7 December 2018

Abstract – The Lower Congo Basin is characterized by a mangrove-lined estuary at its mouth and, further upstream, by many hydrogeographical barriers such as rapids and narrow gorges. Five localities in the mangroves and four from (upstream) left bank tributaries or pools were sampled. On the gills of Coptodon tholloni, Coptodon rendalli, Hemichromis elongatus, Hemichromis stellifer and Tylochromis praecox, 17 species of parasites (Dactylogyridae & Gyrodactylidae, Monogenea) were found, eight of which are new to science. Six of these are herein described: Cichlidogyrus bixlerzavalai n. sp. and Cichlidogyrus omari n. sp. from T. praecox, Cichlidogyrus calycinus n. sp. and Cichlidogyrus polyenso n. sp. from H. elongatus, Cichlidogyrus kmentovae n. sp. from H. stellifer and onchobdella ximenae n. sp. from both species of Hemichromis. On Cichlidogyrus reversati a ridge on the accessory piece was discovered that connects to the basal bulb of the penis. We report a putative spillback effect of the native parasites Cichlidogyrus berradae, Cichlidogyrus cubitus and Cichlidogyrus flexicpolpos from C. tholloni to the introduced C. rendalli. From our results, we note that the parasite fauna of Lower Congo has a higher affinity with the fauna of West African and nearby freshwater ecoregions than it has with fauna of other regions of the Congo Basin and Central Africa.

Key words: Parasitology, biodiversity, biogeography, Cichlidogyrus, Cichlidae.

Résumé – Six espèces nouvelles de Dactylogyridae (Platyhelminthes, Monogenea) parasites des branches de cichlids (Teleostei, Cichliformes) du bassin du Bas Congo. Le cours du Bas Congo est caractérisé par un estuaire bordé de mangroves et, plus en amont, par de nombreuses barrières hydro-géographiques formées de rapides ou de gorges étroites. Nous avons échantillonné dans cinq localités au niveau des mangroves et dans quatre autres en amont sur la rive gauche du fleuve, dans des affluents ou des étangs. Nous avons trouvé, sur les branches de Coptodon tholloni, Coptodon rendalli, Hemichromis elongatus, Hemichromis stellifer et Tylochromis praecox, 17 espèces de parasites (Dactylogyridae et Gyrodactylidae, Monogenea), dont huit sont nouvelles pour la science. Six d’entre elles sont décrites ici : Cichlidogyrus bixlerzavalai n. sp. et Cichlidogyrus omari n. sp. sur T. praecox, Cichlidogyrus calycinus n. sp. et Cichlidogyrus polyenso n. sp. sur H. elongatus, Cichlidogyrus kmentovae n. sp. sur H. stellifer et onchobdella ximenae n. sp. sur les deux espèces d’Hemichromis. Nous décrivons, chez Cichlidogyrus reversati, une arête sur la pièce accessoire qui la connecte avec l’ampoule basale du pénis. Nous notons un probable transfert latéral des espèces autochtones Cichlidogyrus berradae, Cichlidogyrus cubitus et Cichlidogyrus flexicpolpos de C. tholloni vers l’espèce introduite C. rendalli. Nos résultats montrent que la faune parasitaire du Bas Congo présente plus d’affinités avec les faunes d’Afrique de l’Ouest ou des écorégions d’eau douce voisines, qu’avec celles des autres parties du bassin du Congo ou de l’Afrique Centrale.
Introduction

The Lower Congo River (LCR) is 350 km long and extends from the Kintambo Rapids at the outlet of Pool Malebo to the Atlantic Ocean [2]. With its tributaries, the LCR forms the Lower Congo Basin, which contains the Lower Congo and the Lower Congo Rapids ecoregions. The Lower Congo ecoregion covers the LCR from its mouth to Matadi and the left-bank tributaries, the largest of which is the Inkisi River. At the mouth, a mangrove-lined estuary is found with euryhaline fishes and freshwater representatives of marine families. The Lower Congo Rapids ecoregion spans the LCR from Matadi to the Kintambo Rapids and the right-bank tributaries (see Fig. 1) [1]. The Lower Congo Rapids ecoregion is characterized by large rapids and canyons that are up to 200 m deep [24, 41]. This makes it the most hydrologically and spatially complex of the two ecoregions. Because of this complexity, there is a high habitat heterogeneity through numerous dispersal barriers. This and the downstream location in the Congo basin lead to the LCR having a hyperdiverse ichthyofauna with high levels of species endemism [15, 16]. Of the over 320 fish species, 84 are documented endemics for the LCR [15]. The families Mochokidæ, Cyprinidæ and Cichlidae are the most species-rich in the area [1]. The focus of this study is the taxonomic exploration of monogenean gill parasites (Platyhelminthes) of Cichlidae (Teleostei) in the Lower Congo Basin. More specifically, representatives of Cichlidogyrus Paperna, 1960 (Dactylorhynchidae), Onchobdella Paperna, 1968 (Dactylorhynchidae) and Gyrodactylus Von Nordmann, 1832 (Gyrodactylidae) are likely to be observed, because they are known to infect African cichlids [34, 48]. Of these, Cichlidogyrus, with over 100 species described, is the most species-rich genus occurring on cichlids throughout Africa and the Middle East [14, 34, 39, 40]. Species of Onchobdella are known from species of Hemichromis Peters, 1857, from Pelmatochromis buettikofleri (Steindacher, 1894) and Chromidotilapia guntheri (Sauvage, 1882) [31]. Onchobdella comprises eight species [4, 26, 30]. They occur mostly in West Africa, but have also been found in Cameroon [34]. Gyrodactylus includes 17 species known from African cichlids. This genus, however, is much larger, as over 450 species have been described and representatives are known to infect most fish orders [12, 48]. The members of Onchobdella, Cichlidogyrus and Gyrodactylus are most easily distinguished through the morphology of the haptor, the caudal attachment organ, which includes sclerotized hooks and transverse bars. The haptor of species of Cichlidogyrus consists of seven pairs of hooks (I–VII), one pair of dorsal and one pair of ventral anchors associated with dorsal and ventral transverse bars. Hooks of pair II are always short and associated with the ventral anchors. Pairs I and III–VII can be short or elongated [32, 34, 46, 47]. The haptor of species of Onchobdella contains five to six pairs of short hooks, a pair of large dorsal anchors that are arranged distal-laterally, one pair of small ventral anchors associated with two ventral bars and one large horseshoe-shaped or straight dorsal bar [26, 34]. The hard parts in the haptor of species of Gyrodactylus comprise 16 marginal hooks and a pair of anchors that are connected by a superficial and deep ventral bar [38]. Species within these genera can be distinguished based on morphological differences between sclerotized structures, which are the male copulatory organ (MCO), the vagina (when sclerotized), and the haptoral sclerites. These parasite genera have not been thoroughly studied in the Lower Congo Basin, but parasites from the neighbouring Ogooué-Nyanga-Kouilou-Niari freshwater ecoregion (see Fig. 1) [1] were explored [30, 33]. These include Cichlidogyrus reversati Pariselle & Euzet, 2003 and C. lemoalae Pariselle & Euzet, 2003 from the mouth of the Lower Kouilou River (Republic of Congo, ROC), C. berradae Pariselle & Euzet, 2003 from Lake Cayo and Loufoualéba, and C. legendrei Pariselle & Euzet, 2003 and Scutogyrus chikhii Pariselle & Euzet, 1995 from Lake Cayo. These parasites were collected from Pelmatolapia cabræ (Boulenger, 1899), except for Scutogyrus chikhi, which was described from the introduced Oreochromis mossambicus (Peters, 1852). In addition, Cichlidogyrus microscutus Pariselle & Euzet, 1996 was found on Coptodon guineensis (Günther, 1862) from Lake Loufoualéba [see [32]]. From the Congo River itself, Cichlido- gyrus flexicolpos Pariselle & Euzet, 1995 was described from Coptodon guineensis [29]. This study serves as a first exploration of the gill monogeneans of Coptodon tholloni (Poll & Thys van den Audenaerde, 1960), Hemichromis elongatus (Guichenot, 1861), Hemichromis stellifer Loislle, 1979 and Tylochromis praecox Stiasny, 1989. Parasites from C. rendalli have already been studied from the Bangwuelu-Mweru ecoregion [14, 46] and from Lake Kariba [7].

Materials and methods

During a field expedition to the Lower Congo region in June 2015, fish were collected from nine localities (see Fig. 1 and caption for the coordinates). Fish were caught using gill nets and euthanized with an overdose of MS222. All specimens were diagnosed in the field and later verified in the lab, except for the specimen of T. praecox, which was verified in the lab with a picture of the specimen, because it came from an existing collection from the Institut Supérieur Pédagogique de Mbanza-Ngungu and was not transported to the RMCA, Royal Museum for Central Africa. From each fish, the right gill arches were removed, stored on ethanol and used for parasitological screening. The storage fluid was also exhaustively screened. Parasites were identified using an entomological needle under a WILD M5 stereomicroscope (Wild, Heerbrugg, Switzerland), mounted on a glass slide and fixed with Malmberg’s solution (in the field) or Hoyer’s medium (in the lab). Coverslips were sealed with Glyceel [3], D-pep or nail polish. Parasites were identified through a Leitz Dialux 22 microscope (Leitz, Wetzlar, Germany) with differential interference contrast and measured with Auto-montage software (Imaging & Microscopy, Weinheim, Germany). Images were taken with an optical camera on a Leica DM2500 microscope with Leica Application suite software VX (Leica, Wetzlar, Germany). Illustrations were drawn using a drawing tube and finalized with GIMP V2.8 (www.gimp.org). The accessory piece and heel of the MCO, and one large horseshoe-shaped or straight dorsal bar [26, 34]. The hard parts in the haptor of species of Gyrodactylus comprise 16 marginal hooks and a pair of anchors that are connected by a superficial and deep ventral bar [38].
measured (minimum value / maximum value). The standard deviation is only represented when $n \geq 30$. Numbering of the hooks follows Pariselle & Euzet [33, 35]. Cichlids were deposited in the ichthyology collection of the RMCA in collections 2015–29 under accession numbers AB54005942, AB53952197 and AB54006866 and 2015–30 under RMCA_Vert_2015.030.P.0009–0022. Individual accession numbers are represented in addendum 1. Whole-mounted parasites were deposited in the collections of the RMCA (M.T.38280–38375), the Natural History Museum (London, United Kingdom, NHMUK 2018.1.31.1–6), the Iziko South African Museum (Cape Town, South Africa, SAMC-A090065–69) and the Finnish Museum of Natural History (Helsinki, Finland, MZH, KN10043–10057). The MZH specimens can be consulted online through https://laji.fi/en/view?uri=luomus:KN.10043 and onwards. More hyperlinks and all accession numbers of parasites are given in Addendum 2.

Results

Seventeen species of monogeneans, eight of which are new to science, were found on five hosts (Table 1). For five described parasite species, this is their first record from the Lower Congo region, and for all of them, new host records were found. Six new species are described in the present study. In addition, morphological remarks are given for $C$. reversati, because the specimens in this study varied slightly from the original description. Additionally, more details on the connection of the accessory piece with the basal bulb of the penis in $C$. reversati were observed and mentioned under remarks.

\begin{table}[ht]
\centering
\begin{tabular}{|c|c|c|c|}
\hline
Species & Hosts & Number & Remarks \\
\hline
\end{tabular}
\caption{List of described parasite species from the Lower Congo region.}
\end{table}

\textbf{Cichlidogyrus bixlerzavalai} Jorissen, Pariselle & Vanhove n. sp.

urn:lsid:zoobank.org:act:3E7C4017-8E0E-4DE3-A3BD-6CD67D806601

Type host: \textit{Tylochromis praecox} Stiassny, 1989.

Infection site: Gills.

Type locality: Muila Kaku, mangroves near Lower Congo River 05°59′33″S 12°35′03.2″E.

Material: Four whole-mounted specimens in Malmberg’s solution.

Holotype: M.T.38339
Paratypes: M.T.38340–41, KN10053

Etymology: The species epithet is a homage to singer Cedric Bixler-Zavala of bands At the drive-in, The Mars Volta and Antemasque and is a noun (name) in the genitive case.

Authorship: Note that the authors of the new taxon are different from the authors of this paper; Article 50.1 and
Recommendation 50A of International Code of Zoological Nomenclature [13].

Description (Table 3, Figs. 3, 4a–4c)

Dorsal anchors with guard length 4 to 5 times the shaft length. U-shaped indentation at the base. Point short and curved ($e = 11 \mu m$). Ventral anchors 10 $\mu m$ smaller than dorsal ones. Blade equally long as in dorsal anchors, but base of the ventral anchors shorter, with deeper V-shaped indentation. Hooks pair I long (>1.7 times the length of hooks pair II [35]), with rectangular-shaped shaft, slightly broader than the anterior, larval part. Hooks pair III–VII short (<2 times the length of hooks pair II [35]). Ventral transverse bar large ($X = 53 \mu m$) and broad ($W = 9 \mu m$) with lateral extension on each arm. Extension long, covers around 70% of the length of each arm, except for the proximal and distal ends. Dorsal transverse bar with short auricles ($h = 12 \mu m$), with usual morphology for species of Cichlidogyrus infecting species of Tylochromis (i.e. auricles in continuity with dorsal bar anterior face [23, 28]). Penis, thick-walled, tubular with a sinuous curve most proximally, followed by a 360° loop. At the distal end, the penis curves approximately 60°. Basal bulb granulated. Heel absent. Accessory piece not directly connected to the basal bulb. It starts at the height of the loop, where it is club-shaped and ridged. Further distally, it narrows until it is thinner than the penis.

Remarks

Species of Cichlidogyrus that infect species of Tylochromis have reduced auricles on the dorsal transverse bar. The accessory piece does not connect to the basal bulb of the penis [23, 28]. However, a thin, filamentous connection was described for C. sigmocirrus Pariselle, Bitja Nyom, Bilong Bilong, 2014 and C. chrysopiformis Pariselle, Bitja Nyom, Bilong Bilong, 2014 [36], but with uncertainty. Both species were described from Tylochromis sudanensis Daget, 1954 from the Cross River in Cameroon [36]. Furthermore, all species have a tubular curved penis, referred to as a spirally-winding penis [23]. Cichlidogyrus bixlerzavalai n. sp. resembles C. muzumanii Muterezi Bukiinga, Vanhove, Van Steenberge & Pariselle, 2012 the most, as both species have large anchors with a long guard, elongated hooks pair I and a curved tubular

Figure 2. Schematic representation of the measurements taken of the hard parts of specimens of Cichlidogyrus and Onchobdella. Structures from top left to bottom right: anchor, ventral transverse bar, MCO, dorsal transverse bar, vagina and hook. Abbreviations: I–VII, hook length; a, total anchor length; Ap, length of accessory piece; b, blade length; c, shaft length; d, guard length, e, point length; h, auricle length; He, Heel length; l, vagina width; L, vagina length; Pe, penis length; W, maximum width of ventral transverse bar; w, maximum width of dorsal transverse bar; X, branch length of ventral transverse bar; x, total length of dorsal transverse bar; y, distance between auricles.
penis with an accessory piece at the distal end of the penis that runs to almost half of the length of the penis. The major difference between these species is that in *C. muzumani*, the accessory piece engulfs the penis partially, while in *C. bixlerzavalai* n. sp., the accessory piece lies separate from the penis. This has never been observed for species of *Cichlidogyrus*. It remains unclear if and where the accessory piece attaches to the penis in *C. bixlerzavalai* n. sp. However, it is certain that the accessory piece does not connect to the basal bulb proximally and that the accessory piece does not engulf the distal end of the penis. One specimen has a bulge-shaped extension at the distal end of the penis, but this is probably an artefact, because it is an open structure, clearly observable and absent on other specimens. Additionally, the specimen with the extension is also the only one of which the distal end of the penis is oriented towards the accessory piece. It is observed on this specimen that at the 360°/C176 loop the penis turns in the other direction. However, this directional change is likely the result of the flattening of the MCO. On one specimen, ridges at the proximal end of the accessory piece were not observed.

**Table 1.** Occurrence of parasite species on their respective hosts, marked by an “x” and abundance of host and parasite, respectively.

| Host species | C. tholloni | C. rendalli | H. elongatus | H. stellifer | T. praecox | N (171) |
|--------------|-------------|-------------|--------------|-------------|-----------|--------|
| C. tholloni  | 5           | 3           | 4            | 1           | 1         | 8      |
| C. berradae* |             |             | H            |             |           | 3      |
| C. bixlerzavalai n. sp.* |             |             |              |             |           | 9      |
| C. calycinus n. sp.* | H          |             |             |             |           | 36     |
| C. sp.1*     |             |             | H            |             |           | 3      |
| C. sp.2*     |             |             | H            |             |           | 9      |
| C. cubitus*  | H           | H           | H            |             |           | 371    |
| C. falcifer  |             |             | H            |             |           | 11     |
| C. flexicolpos |             | H           |             |             |           | 5      |
| C. polyenso n. sp.* |             |             | H           |             |           | 16     |
| C. kmentovae n. sp.* |             |             | H           |             |           | 8      |
| C. longicirrus |             |             |             |           | H         | 5      |
| C. omari n. sp.* |             |             | H           |             |           | 1      |
| C. reversati |             |             | H            |             |           | 4      |
| C. tilapia*  |             |             |             |             |           | 4      |
| C. sp.       |             |             |             |             | x         | 4      |
| G. chitandiri* | H           |             | H           |             |           | 21     |
| O. aframae   |             |             | H            |             |           | 3      |
| O. ximenae n. sp.* |             |             | H           |             |           | 25     |
| O. sp.       |             |             |             |             | x         | 1      |

* Represents the first record of this species in Lower Congo. An “H” represents a new host record. “N” represents the number of hosts (2nd row) or parasites (last column).

**Table 2.** Number of parasite species per locality and infection intensity. Localities correspond to those in Figure 1. See Addenda 1 and 2 for the individual voucher and accession numbers.

| Host species         | Parasite species     | Locality | Infection intensity/no. infected hosts |
|----------------------|----------------------|----------|----------------------------------------|
| Coptodon tholloni    | C. sp.1              | 9        | 3/1                                    |
|                      | C. sp.2              | 9        | 9/1                                    |
|                      | C. cubitus           | 4        | 1/1                                    |
|                      | C. reversati         | 8        | 8/1                                    |
|                      | C. tilapia           | 3        | 4/1                                    |
|                      | G. chitandiri        | 5        | 21/1                                   |
| Coptodon rendalli    | C. berradae          | 1        | 1–4/3                                  |
|                      | C. cubitus           | 1        | 7–14/3                                 |
|                      | C. flexicolpos       | 1        | 5/1                                    |
| Hemichromis elongatus| C. calycinus n. sp.  | 4        | 3–6/3                                  |
|                      | C. falcifer          | 6        | 2/1                                    |
|                      | C. polyenso n. sp.   | 4        | 2–3/3                                  |
|                      | C. longicirrus       | 4        | 1/1                                    |
|                      | O. aframae           | 4        | 4/1                                    |
|                      | O. ximenae n. sp.    | 4        | 1–8/1                                  |
| Hemichromis stellifer| C. kmentovae n. sp.  | 7        | 5/1                                    |
| Tylochromis praecox  | O. ximenae n. sp.    | 7        | 1/1                                    |
|                      | C. bixlerzavalai n. sp. | 2        | 4/1                                    |
|                      | C. omari n. sp.      | 2        | 1/1                                    |

penis with an accessory piece at the distal end of the penis that runs to almost half of the length of the penis. The major difference between these species is that in *C. muzumani*, the accessory piece engulfs the penis partially, while in *C. bixlerzavalai* n. sp., the accessory piece lies separate from the penis. This has never been observed for species of *Cichlidogyrus*. It remains unclear if and where the accessory piece attaches to the penis in *C. bixlerzavalai* n. sp. However, it is certain that the accessory piece does not connect to the basal bulb proximally and that the accessory piece does not engulf the distal end of the penis. One specimen has a bulge-shaped extension at the distal end of the penis, but this is probably an artefact, because it is an open structure, clearly observable and absent on other specimens. Additionally, the specimen with the extension is also the only one of which the distal end of the penis is oriented towards the accessory piece. It is observed on this specimen that at the 360° loop the penis turns in the other direction. However, this directional change is likely the result of the flattening of the MCO. On one specimen, ridges at the proximal end of the accessory piece were not observed.

**Cichlidogyrus calycinus** Kusters, Jorissen, Pariselle & Vanhove n. sp.

* Represents the first record of this species in Lower Congo. An “H” represents a new host record. “N” represents the number of hosts (2nd row) or parasites (last column).
Table 3. Measurements of Cichlidogyrus bixlerzavalai n. sp., C. omari n. sp. and C. reversati. Note the size difference in dorsal bar length, x between the two groups of C. reversati. All measurements in µm as the average ± standard deviation, count and range (in parentheses).

| Species               | C. bixlerzavalai n. sp. | T. praecox | C. omari n. sp. | C. tholloni | C. reversati | C. reversati | P. cabrae |
|-----------------------|--------------------------|------------|----------------|-------------|-------------|-------------|----------|
| **Host**              | T. praecox               | T. praecox | T. praecox     | T. praecox  | T. praecox  | T. praecox  | T. praecox |
| **Locality**          | Present study            | Present study | Present study | Present study | Present study | Present study | Present study |
| **Reference**         |                          |             |               |             |             |             |           |
| **Number of specimens** |                          |             |               |             |             |             |           |
| **Ventral anchor**    |                          |             |               |             |             |             |           |
| Total length, a       | 40, 3 (39–41)            | 32          | 43, 8 (41–45)  | 44 ± 2 (40–49) |
| Blade length, b       | 39, 3 (35–41)            | 26          | 42, 8 (40–44)  | 44 ± 1.6 (40–46) |
| Shaft length, c       | 2, 3 (1–3)               | 4           | 4, 8 (3–7)     | 3 ± 1.3 (1–9) |
| Guard length, d       | 13, 3 (11–14)            | 12          | 16, 8 (13–17)  | 11 ± 1.5 (6–16) |
| Point length, e       | 11, 3 (9–12)             | 7           | 17, 8 (16–19)  | 16 ± 1.3 (13–19) |
| **Dorsal anchor**     |                          |             |               |             |             |             |           |
| Total length, a       | 50, 3 (49–51)            | 31          | 57, 8 (55–60)  | 59 ± 1.9 (53–63) |
| Blade length, b       | 38, 3 (37–39)            | 22          | 40, 8 (37–43)  | 42 ± 1.8 (36–45) |
| Shaft length, c       | 4, 3 (3–5)               | 6           | 4, 8 (2–6)     | 4 ± 1.8 (2–14) |
| Guard length, d       | 22, 3 (18–24)            | 15          | 28, 8 (25–30)  | 21 ± 1.7 (17–28) |
| Point length, e       | 11, 3 (10–11)            | 8           | 14, 8 (13–16)  | 14 ± 1.1 (11–16) |
| **Unciniuli**         |                          |             |               |             |             |             |           |
| Length, I             | 24, 3 (21–26)            | 14          | 25, 7 (23–29)  | 25 ± 1.5 (22–28) |
| Length, II            | 12, 3 (10–13)            | 10          | 12, 5 (11–13)  | 12 ± 0.8 (9–14) |
| Length, III           | 19, 3 (17–21)            | 14          | 20, 8 (15–22)  | 18 ± 0.8 (17–21) |
| Length, IV            | 21, 3 (21–22)            | 19          | 23, 8 (20–27)  | 22 ± 0.9 (20–25) |
| Length, V             | 21, 3 (21–22)            | 23          | 25, 8 (23–28)  | 24 ± 1.3 (20–27) |
| Length, VI            | 21, 3 (20–22)            | 18          | 22, 7 (20–24)  | 21 ± 0.8 (20–23) |
| Length, VII           | 19, 3 (16–22)            | 17          | 19, 6 (18–23)  | 19 ± 0.9 (15–20) |
| **Ventral bar**       |                          |             |               |             |             |             |           |
| Branch length, X      | 53, 3 (48–57)            | 39          | 48, 7 (35–55)  | 45 ± 3.2 (37–50) |
| Maximum width, W      | 9, 3 (8–10)              | 5           | 8, 7 (7–11)    | 9 ± 1.4 (6–13) |
| **Dorsal bar**        |                          |             |               |             |             |             |           |
| Total length, x       | 59, 3 (57–61)            | 62          | 57, 7 (53–64)  | 46 ± 2.3 (42–51) |
| Maximum width, w      | 9, 3 (8–10)              | 6           | 10, 7 (8–12)   | 11 ± 1.4 (9–15) |
| Distance between auricles, y | 17, 3 (15–18) | 8          | 20, 7 (13–24)  | 15 ± 2.4 (12–24) |
| Auricle length, h     | 12, 3 (9–15)             | 11          | 20, 7 (17–23)  | 18 ± 2.2 (14–24) |
| **MCO**               |                          |             |               |             |             |             |           |
| Penis length, Pe      | 65, 3 (61–70)            | 48          | 27, 8 (24–31)  | 33 ± 1.4 (31–36) |
| Length of accessory piece, AP | 26, 2 (22–32) | 58          | 32, 8 (28–34)  | /            |
| Heel length, He       | N.A.                     | 2           | N.A.           | N.A.        |
| Length of accessory piece straight, Aps | 21, 3 (16–26) | 20 ± 1.5 (17–23) |
| Total body length     | 449, 3 (424–488)         | 460         | 364, 8 (312–429) | 713 ± 106 (545–1011) |

Other localities: Mvuazi River (Lower Congo) 5°19’S 15°7’E.

Material: Fifteen whole-mounted specimens of which six are fixed in Hoyer’s medium (including the holotype), the other nine in Malmberg’s solution.

Holotype: M.T. 38316.

Paratypes: M.T. 38312–13, 38317–18, 38321, 38326, 38329, 38331, 38333, 38335, KN10046–47, https://laji.fi/en/view?uri=luomus:KN.10046 and https://laji.fi/en/view?uri=luomus:KN.10047, SAMC-A090066, NHMUK 2018.1.31.1.

Symbiotype: RMCA_Vert_2015.030.P0020.

Paratype host vouchers: RMCA_Vert_2015.030.P0019, RMCA_Vert_2015.030.P0021, RMCA_Vert_2015.030.P0022.

Etymology: The species epithet in Latin refers to the cup-shaped distal end of the vagina (calyx, Latin: cup) and is an adjective.

Authorship: Note that the authors of the new taxon are different from the authors of this paper; Article 50.1 and Recommendation 50A of International Code of Zoological Nomenclature [13].

Description (Table 4, Figs. 4d–4f, 5)

Dorsal anchors, with long guard (d = 17 µm), which is more than twice the shaft length (d = 7 µm). Blade long and curved. Ventral anchors on average 4 µm smaller than dorsal anchors, but with longer point. Hooks I and V long. Hooks III–IV and VII–VII sometimes long, sometimes short. Ventral transverse bar with small extension at distal third of each arm. Dorsal transverse bar slightly concave, with developed, but rather short auricles (h = 15 µm). Penis long, thin, tubular and makes a long turn of almost 360° after leaving the basal bulb and ends near the middle of the distal plate of the accessory piece. Heel oval. Accessory piece proximally broader than penis and with bean-shaped extension at one sixth of the length, where accessory piece and penis meet. Further distally,
Table 4. Measurements of *Cichlidogyrus calycinus* n. sp., *C. teugelsi*, *C. polyenso* n. sp., *C. euzeti*, *C. kmentovae* n. sp., *C. cf. bychowskii* and *C. dracolemma*. All measurements in μm as the average ± standard deviation, count and range (in parentheses).

| Species | C. calycinus n. sp. | C. teugelsi | C. polyenso n. sp. | C. euzeti | C. kmentovae n. sp. | C. cf. bychowskii | C. dracolemma |
|---------|---------------------|-------------|-------------------|-----------|---------------------|------------------|-------------|
| Host    | H. elongatus        | H. fasciatus| H. elongatus      | H. fasciatus| H. stellifer        | H. bimaculatus   | H. letourneuxi |
| Locality| 4 & 6               | 4           | 4                 | Benin & Cameroon | 7               | Congo River at Bokalaka, DRC | Nikiolo Koba |
| Reference| Present study       | Present study| Present study     | Dossou and Birgi  | Present study     | Messu Mandeng et al. [22] | R̆ehulková et al. |
| Number of specimens | 15             | 30          | 6                 | 30         | 6                  | 5                | 1 (Holotype) |
| Ventral anchor | Total length, a  | 35, 7 (30–38) | 36 ± 1.1 (33–38) | 40, 4 (37–43) | 40–45             | 32, 4 (30–35) | 34 (31–37) |
|         | Blade length, b    | 30, 7 (26–33) | 31 ± 1.4 (29–34) | 38, 4 (37–39) | 30–35             | 27, 3 (24–29) | 28 (26–31) |
|         | Shaft length, c    | 7, 7 (4–12)   | 5 ± 1 (3–7)       | 4, 4 (2–5)   | 8–10              | 4, 4 (2–5) | 5 (4–9) |
|         | Guard length, d    | 11, 7 (9–14)  | 11 ± 1.5 (8–14)   | 15, 4 (14–16) | 10–12             | 13, 4 (12–15) | 10 (9–14) |
|         | Point length, e    | 13, 7 (9–17)  | 15 ± 1.2 (12–17)  | 15, 4 (13–19) | 10–12             | 12, 4 (10–15) | 12 (10–13) |
| Dorsal anchor | Total length, a   | 39, 7 (33–43) | 41 ± 1.6 (35–45) | 46, 4 (43–47) | 40–50             | 32, 5 (31–34) | 33 (31–35) |
|         | Blade length, b    | 26, 7 (22–28) | 27 ± 1.2 (25–31) | 31, 4 (29–33) | 28–30             | 22, 5 (19–23) | 23 (21–25) |
|         | Shaft length, c    | 7, 6 (5–10)   | 5 ± 0.9 (3–7)     | 5, 4 (2–7)   | 8–10              | 3, 5 (2–4) | 5 (4–7) |
|         | Guard length, d    | 17, 6 (15–20) | 17 ± 1.7 (12-20)  | 22, 4 (20–23) | 20–25             | 16, 5 (15–18) | 13 (10–15) |
|         | Point length, e    | 10, 7 (9–12)  | 11 ± 0.7 (10–13)  | 9, 4 (7–10)  | 8–10              | 9, 5 (9–10) | 9 (6–10) |
| Uncinuli | Length, I          | 32, 7 (22-42) | 31 ± 1.6 (28–37) | 43, 4 (38–47) | 35–40             | 32, 4 (29–34) | 34 (33–37) |
|         | Length, II         | 9, 2 (8–9)    | 10 ± 0.5 (9–12)   | 10, 3 (9–11) | 10                | 10, 4 (10–11) | 11 (11–11) |
|         | Length, III        | 17, 5 (13–21)| 18 ± 1.2 (17–23) | 21, 4 (19–22) | 15–20             | 20, 4 (19–22) | 21 (19–22) |
|         | Length, IV         | 19, 5 (15–23)| 20 ± 1.5 (18–25) | 22, 4 (20–23) | 15–20             | 23, 4 (22–26) | 22 (20–23) |
|         | Length, V          | 25, 6 (21–31)| 24 ± 1.2 (21–29) | 24, 4 (22–27) | 15–20             | 25, 4 (21–27) | 23 (23–27) |
|         | Length, VI         | 20, 6 (16–23)| 21 ± 1.1 (19–23) | 25, 4 (20–28) | 15–20             | 21, 4 (18–23) | 24 (22–25) |
|         | Length, VII        | 17, 6 (13–21)| 18 ± 0.8 (16–20) | 22, 4 (21–25) | 15–20             | 20, 4 (19–22) | 22 (20–23) |
| Ventral bar | Branch length, X   | 34, 6 (26–38)| 34 ± 2.7 (31–39) | 46, 3 (40–54) | 40                | 31, 4 (28–34) | 31 (29–36) |
|         | Maximum width, W   | 5, 6 (3–6)    | 6 ± 0.5 (4–7)     | 6, 4 (5–7)   | /                | 5, 4 (5–5) | 4 (3–5) |
| Dorsal bar | Total length, x    | 40, 6 (31–55)| 35 ± 1.7 (32–38) | 50, 3 (41–58) | 45                | 37, 5 (34–43) | 36 (31–40) |
|         | Maximum width, w   | 7, 6 (5–9)    | 8 ± 0.9 (7–10)    | 8, 4 (6–11)  | /                | 7, 5 (6–8) | 7 (6–8) |
|         | Distance between auricles, y | 15, 6 (12–25) | 12 ± 1 (10–13)   | 23, 3 (20–27) | 20                | 12, 5 (11–16) | 12 (9–14) |
|         | Auricle length, h  | 10, 6 (9–15)  | 11 ± 1.2 (8–14)   | 12, 4 (11–13) | 10–12             | 9, 5 (8–11) | 9 (8–11) |
| MCO     | Penis length, Pe   | 104, 6 (77–119)| 99 ± 4.3 (90–111)| 256, 5 (225–284)| 375–390             | 137, 5 (103–187)| 185 (108–203) |
|         | Length of accessory piece, AP | 52, 7 (36–63) | 74 ± 3.9 (69–87) | 127, 5 (112–163)| 130                | 77, 4 (65–88) | 185 (108–203) |
|         | Heel length, He    | 14, 5 (4–24)  | /                | 4, 5 (3–5)   | 3 (2–4)         | 3 (2–5)         |
| Vagina  | Vagina length, L  | 85, 7 (67–105)| 72 ± 7.2 (61–88) | 129             | /                | 29              | N.A.         |
|         | vagina width, l    | 4, 7 (3–6)    | 3 ± 0.3 (3–4)    | /              | /                | /              |
| Total body length | /              | 528 ± 55.9 (403–605) | 497, 5 (436–583) | 600–700         | /                | /              |
the accessory piece narrows to the width of the penis and follows its trajectory, but ends further distally. Accessory piece ends distally in an irregularly-shaped plate. Distal plate with separate elongated structure in the middle. The plate itself is twice as long as it is broad and with rounded edges. Elongated structure longer than plate and reaches further proximally than plate. Proximal from where the elongation overshoots the plate, it touches the penis and narrow part of the accessory piece. Vagina large and tubular. Distally, the vagina has a forceps-shaped structure, engulfed by a semi-hollow structure, which resembles the cup of a flower. More proximally, the forceps-like structure thickens after which it narrows into a long and narrow tube. At the proximal end, the vagina makes a loop and broadens slightly.

Remarks

In general, the morphology of the haptor of species of Cichlidogyrus that infect species of Hemichromis hardly varies [22, 34]. Thus, the morphology and measurements of the haptoral sclerites of C. calycinus n. sp. are nearly identical to that of C. teugelsi Pariselle & Euzet, 2004. The main distinction in these structures is that the dorsal bar of C. calycinus n. sp. is larger (x = 40 μm, 31–55 μm, n = 15) than that of C. teugelsi (x = 35 μm, 32–38 μm, n = 30). The major morphological differences between the two are found on the MCO and vagina. Both have a long tubular penis that almost makes a 360° turn and an accessory piece with a bean-shaped extension at 1/6 of its length. Both species differ at the distal end of the accessory piece. In C. teugelsi, at the distal end the accessory piece makes a loop, while in C. calycinus n. sp. it forms an irregularly-shaped plate with an elongated structure attached to it. Furthermore, the narrow part of the accessory piece in C. calycinus n. sp. reaches further distally than that in C. teugelsi, which broadens and forms the loop structure at 5/6 of the length of the penis. Also, the accessory piece is on average 22 μm longer in C. teugelsi than in C. calycinus n. sp., while the penes differ 5 μm in length, with C. calycinus n. sp. having the longer one (Pe = 104 μm). The heel of C. teugelsi is irregularly shaped, whilst that of C. calycinus n. sp. is oval shaped. In some specimens of C. calycinus n. sp., the heel seemed longer. The vaginas of both species are also similar in morphology and size as they are long, tubular structures that make a loop at their proximal end. However, the distal ends are different. In C. teugelsi the distal end is a slightly sclerotized plate, while in C. calycinus n. sp. there is a forceps-like structure and an overall cup shape.

Cichlidogyrus polyenso Jorissen, Pariselle & Vanhove n. sp.

urn:lsid:zoobank.org:act:C1165346-CFFB-45C7-951E-0D3E094084B9

Type host: Hemichromis elongatus (Guichenot, 1861).
Infection site: Gill.
Type locality: Pond near Kila Kindinga 5°29′7″S 14°53′3.8″E.
Material: four whole-mounted specimens in Malmberg’s solution (including the holotype) and two in Hoyer’s medium.
Holotype: M.T. 38330.
Paratypes: M.T. 38314–15, 38332, NHMUK 2018.1.31.3, KN10050 https://laji.fi/en/view?uri=luomus:KN.10050.
Symbiotype: RMCA_Vert_2015.030.P.0021.
Paratype host vouchers: RMCA_Vert_2015.030.P.0019, RMCA_Vert_2015.030.P.0020.

Etymology: Species epithet is derived from Zen Buddhism and the Japanese language where an *enso* is a hand-drawn circle. This refers to the shape of the penis, as it is coiled. Species epithet consists of a prefix and a noun.

Authorship: Note that the authors of the new taxon are different from the authors of this paper; Article 50.1 and

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**Figure 4.** Compound micrographs of (a–c) *Cichlidogyrus bixlerzavalai* n. sp. from *Tylochromis praecox*: haptor of holotype (a), MCO of holotype (b) and MCO of paratype (c); of (d–f) *Cichlidogyrus calycinus* n. sp. from *Hemichromis elongatus*: haptor of holotype (d), MCO of holotype (e), vagina of holotype (f); of (g–h) *Cichlidogyrus polyenso* n. sp. from *Hemichromis elongatus*: haptor (g), MCO (h). Scale bar 20 μm, except for (g) 50 μm.
Recommendation 50A of International Code of Zoological Nomenclature [13].

Description (Table 4, Figs. 4g–4h, 6)

Dorsal anchors with guard length four to five times the shaft length. Guard elongated and narrow. Point short (e = 9 μm). Ventral anchors 6 μm smaller than dorsal ones. Base with shallow, but wide indentation. Point long (e = 15 μm). Hooks pair I elongated. Secondary shaft (see [35]) widens gradually and ends rounded. Hooks III-VII short. Dorsal transverse bar slightly concave with narrow auricles that are far apart (y = 23 μm). Ventral transverse bar V-shaped with small extension at 1/3 of the distal ends of each arm. MCO with long tubular penis, which is spirally coiled and makes two to three loops. Distally from the loops, the penis makes a 90° turn and continues straight before ending. Short, rectangular heel with rounded edges (He = 4 μm). Accessory piece attaches to basal bulb, proximally broad but narrows distally of the basal bulb. Accessory piece makes two to three loops within the loops of the penis. Distally from the loops, the accessory piece leaves the space within the loops of the penis, turns 120°, meets the penis again and forms a plate resembling the tail of cetaceans, but with asymmetrical lateral ends and sides. At the proximal side, closest to the basal bulb, the plate is convex and results in a sharp point. The distal side is partially concave and partially convex and ends in a hook-like structure. The penis overshoots the plate and ends further distally. The vagina is large, tubular. Most proximally it corkscrews once, after which it makes a short loop. Soon after this it turns 180° to stack two loops of tube after which it ends distally, shortly after leaving the coil.

Remarks

Cichlidogyrus polyenso n. sp. has multiple characteristics in common with C. euzeti Dossou & Birgi, 1984. Similarities are that both species have elongated hooks pair I, short hooks pairs III-VII, dorsal anchors with a long guard and short point, ventral anchors with a long point, a spirally-coiled penis, accessory piece and vagina. The major difference with C. euzeti is that the penis of C. polyenso n. sp. has fewer coils, two to three, rather than the four to five in C. euzeti, and is shorter in length. Moreover, the accessory piece is less coiled.
Additionally, the vagina in *C. polyenso* n. sp. is more compacted, because it coils, while the vagina of *C. euzeti* is a long tube that winds, but never coils. Also, *C. polyenso* n. sp. has slightly larger ventral anchors (*b* = 38 μm, *e* = 15 μm) and hooks (*I* = 43 μm, *V* = 24 μm) than does *C. euzeti* (*b* = 30–35 μm, *e* = 10–12 μm, *I* = 35–40 μm, *V* = 15–20 μm). *Cichlidogyrus euzeti* is reported from Benin and Cameroon [6, 22] and the ROC [35]. Other species that have a similar sclerite morphology are *C. longicirrus* Paperna, 1965 and *C. sanseoi* Pariselle & Euzet, 2004, both from *H. fasciatus* Peters, 1858 and the former from *Chromidotilapia guentheri* (Sauvage, 1882) as well, but both parasites have a longer MCO with more coils than do *C. polyenso* n. sp. and *C. euzeti*.

**Cichlidogyrus kmentovae** Jorissen, Pariselle & Vanhove n. sp.

urn:lsid:zoobank.org:act:8A9E340B-2B30-428E-B994-AB9E296F5DEC

Type host: *Hemichromis stellifer* Loiselle, 1979.
Infection site: Gills.

Type locality: Mbola River near Tshianya Village 05°52’09.8”S 12°39’52.6”E.

Material: Six whole-mounted specimens in Malmberg’s solution.

Holotype: M.T. 38338.
Paratypes: M.T. 38336–37, NHMUK 2018.1.31.5, SAMC-A090068.

Symbiotype: AB53952197.

Etymology: Species epithet refers to biologist Nikol Kmentová (Czech Republic), an enthusiastic researcher on the monogenean fauna of Lake Tanganyika and is a noun (name) in the genitive case.

Authorship: Note that the authors of the new taxon are different from the authors of this paper; Article 50.1 and Recommendation 50A of International Code of Zoological Nomenclature [13].

**Description (Table 4, Figs. 7, 8a–8b)**

Dorsal anchors with elongated guard that is four to five times the shaft length. Indentation, smooth, convex up to the
shaft. Short point \((e = 9 \mu m)\). Ventral anchors of same size \((a = 32 \mu m)\) but with a more robust blade and base. Guard shorter \((d = 13 \mu m)\). Indentation at the base less convex than in dorsal anchors. Hooks pair I large with broad primary shaft and even broader secondary shafts. Hooks pair IV–V long. Hooks pair VII short. Hooks VI of variable size, some long, some short. Pair III short and sometimes differs less than 0.2 \(\mu m\) from twice the length of II. Dorsal transverse bar slightly concave with short extensions. Auricles developed, but short \((h = 9 \mu m)\). Ventral transverse bar small \((X = 31 \mu m)\) and narrow \((W = 5 \mu m)\) with extension that starts halfway along the course of each arm and reaches almost to the distal tip. MCO large with a long, thin, tubular penis \((Pe = 137 \mu m)\), which gradually narrows over its course and makes a large turn of 270° at about the middle of its length. More distally, the penis turns 90° and meets the accessory piece. Basal bulb with small rectangular heel with rounded edges \((He = 3 \mu m)\). Accessory piece departs from the basal bulb and makes a short 180° turn after which it broadens and meets the penis. At the distal end, the accessory piece connects to a semi-circular plate with seven discernible grooves on its surface. At the junction between the semi-circular plate and the rest, two small, sharp extensions protrude towards the semi-circular plate. Vagina consists of a thick-walled bulbous structure connected to a tube.

**Remarks**

*Cichlidogyrus kmentovae* n. sp. closely resembles *C. amieti* Doussou & Birgi, 1983; *C. bychowskii sensu* Paperna, 1965 and *C. dracolemma* Řehulková, Mendlová & Šimková, 2013. *Cichlidogyrus bychowskii* was originally described by Markevitch, 1934 [17] as *Ancyrocephalus bychowskii* from the Leningrad aquarium from *Hemichromis bimaculatus* Gill, 1862. No type material was deposited and a drawing of the MCO and vagina was lacking [17]. However, the penis was described as a long tube that was coiled many times [17]. A redescription of *C. bychowskii* on new material from Southern Ghana from the same host species followed in 1965 by Paperna [25], this time with a drawing of all sclerotized structures. However, the penis was represented as a long tube that makes one large loop instead of multiple coils. Paperna did not address the difference in morphology of the penis and based his diagnosis on the total length of the animal and the morphology of some haptoral sclerites [25, 41]. Therefore, Messu Mandeng et al., Řehulková et al. [22, 41] and the present authors suspect that Paperna misidentified his specimens, which are different from *C. bychowskii* and represent a new species. Furthermore, because the description of Markevitch [17] is not sufficient to recognize the animal and fails to illustrate its
Figure 8. DIC micrographs of (a–b) *Cichlidogyrus kmentovae* n. sp. from *Hemichromis stellifer*: haptor (a), MCO (b); of (c–d) *Cichlidogyrus omari* n. sp. from *Tylochromis praecox*: haptor of holotype (c), MCO of holotype (d); compound micrographs of (e–f) *Onchobdella ximenae* n. sp. from *Hemichromis elongatus*: haptor (e), MCO (f). Scale bar 20 μm, except for (e) 50 μm.
key characteristics, *Cichlidogyrus bychowskii* is considered a nomen dubium. It was previously considered a nomen nudum [22], but the term was misused. In Messu Mandeng et al. [22] specimens were found that resembled the species of Paperna, 1965 and were considered as *C. cf. bychowskii*. The present authors will use *C. cf. bychowskii* for the specimens described by Paperna, 1965 and collected by Messu Mandeng et al. [22] and stress that the species would need a new name in time, preferably, based on a description of new material. No voucher material was deposited by Paperna [25]. The difference between *C. kmentovae* n. sp. (*L* = 29 μm) and *C. amieti* is that the vagina of *C. amieti* is longer (*L* = 65–70 μm from [5]) and the distal plate of the accessory piece is absent. *Cichlidogyrus dracolemma* and *C. cf. bychowskii* both have a distal plate, but the vagina of *C. dracolemma* is longer (*L* = 46 μm) and thicker than in *C. kmentovae* n. sp. (*L* = 29 μm). Both *C. dracolemma* and *C. cf. bychowskii* also have a broadened, irregularly-shaped distal plate with a large hook. In *C. kmentovae* n. sp. the distal plate is semi-circular and has grooves. *Cichlidogyrus cf. bychowskii* and *C. kmentovae* n. sp. both have a vagina with a circular, broadened proximal part, from which a thin, tubular structure extends to the genital pore, but in *C. cf. bychowskii*, this tube makes a 360° loop. With regard to the length of the hooks, there was a categorical size difference in length between pairs III–VII, which is not mentioned in the descriptions of other species. However, the average length of pairs III and VI were short, whilst pairs IV–VI were long for *C. cf. bychowskii* [22]. In *C. kmentovae* n. sp., some measurements of hook pair III differed less than 0.2 μm from twice the length of pair II. It is, therefore, not always straightforward to categorize the length of the hooks. Our sample size was limited, and thus a larger dataset of measurements should further clarify the discrepancy in hook lengths.

*Cichlidogyrus omari* Jorissen, Pariselle & Vanhove n. sp.

[urn:lsid:zoobank.org:act:73B533F8-2E50-4A01-BF82-80DF705281CB](urn:lsid:zoobank.org:act:73B533F8-2E50-4A01-BF82-80DF705281CB)

Type host: *Tylochromis praecox* Stiassny, 1989.

Infection site: Gill.

Type locality: Muila Kaku, mangroves near Lower Congo River 05°59'33"S 12°35'03.2"E.

Material: One whole-mounted specimen fixed in Malmberg’s solution.

Holotype: M.T. 38342.

Etymology: The species epithet is a homage to lead guitarist Omar Rodriguez-Lpez from bands At the drive-in, The Mars Volta, Antemasque, The Omar Rodriguez-Lopez group and Bosnian Rainbows and is a noun (name) in the genitive case.

Authorship: Note that the authors of the new taxon are different from the authors of this paper; Article 50.1 and Recommendation 50A of International Code of Zoological Nomenclature [13].

Description (Table 3, Figs. 8c–8d, 9)

Dorsal anchors small (*a* = 31 μm) with a short point (*e* = 7 μm). Ventral anchors of similar size (*a* = 32 μm) with
a slightly longer point (e = 8 µm) and a slightly bulkier base. All hooks are small. Ventral transverse bar small (X = 39 µm), thin (W = 5 µm) and V-shaped. Extension absent. Dorsal transverse bar with short, stubby auricles (h = 11 µm). Penis has a rectangular basal bulb with rounded edges and a small rectangular heel with rounded edges. Penis is thin, tubular and curved. Accessory piece lies distally of the penis and consists of two parts, the most proximal one being a mantle-like structure that engulfs the penis at the height of the curvature and further distally from there. This mantle-like structure ends proximally in a point. Distally, it is connected to a second part, which is an elongated, blunt structure with rounded edges.

Remarks

_Cichlidogyrus omari_ n. sp. has a small, rectangular heel, an accessory piece divided into two parts, and small transversal bars, anchors and hooks. These features have not been seen until now for species of _Cichlidogyrus_ infecting _Tylochromis_ spp. However, the accessory piece is large, mantle-shaped and partially engulfs the penis, which is also seen in _C. kothiasi_ Pariselle & Euzet, 1994; _C. djietoi_ Pariselle, Bitja Nyom & Bilong Bilong, 2014; _C. chrysopiformis_ and _C. mulimbwai_ Muterezi Bokinga, Vanhove, Van Steenberge and Pariselle, 2012. _Cichlidogyrus bixlerzavalai_ n. sp. and _C. omari_ n. sp. are easily distinguishable by the size difference in ventral transversal bar, anchors and hooks pair I. Furthermore, _C. omari_ n. sp. has a penis that is curved once and it has a large accessory piece that partially engulfs the penis, whilst _C. bixlerzavalai_ n. sp. has a penis that makes one loop and has a smaller accessory piece with three indentations at the distal end. It is not common practice for species of _Cichlidogyrus_ to be described based on a single specimen (see _Cichlidogyrus_ sp. “T. polylepis 3” in [36]), but on the specimen of _C. omari_ n. sp. all characters are discernible and are clearly different from already described species.

_Cichlidogyrus reversati_ Pariselle & Euzet, 2003

Type host: _Tilapia cabrae_ Boulenger, 1899 (now _Pelmato- lapia cabrae_).

Other hosts: _Coptodon tholloni_ (Poll & Thys van den Audenaerde, 1960).

Infection site: Gills.

Type locality: Mouth of Bas Kouilou River, Congo.
Other localities: Congo River at Nganda Flash station 06°02′01.8″S 12°31′48.2″E.

Material: Eight whole-mounted specimens in Malmberg’s solution.

Vouchers: M.T. 38308–09, KN10043–45 https://laji.fi/en/view?uri=luomus:KN.10043, https://laji.fi/en/view?uri=luomus:KN.10044, https://laji.fi/en/view?uri=luomus:KN.10045.

Remarks (Table 3, Fig. 10)

The eight recorded specimens of C. reversati from the Congo River had a dorsal bar length that was 9 μm longer on average and a total length of half the size compared with the specimens from the type locality. In the original drawing (see [33]), the accessory piece connected with the heel through a thin filament. However, this connection was not observed in the specimens from Lower Congo. In three specimens, an extension of the heel in another focal plane was observed and could correspond with the thin filamentous connection of the original description. Additionally, in three specimens, the distal ends of the accessory piece and the penis did not meet. Also, in all specimens, it was observed that the accessory piece has a ridge, which separates the distal hook from the C-shaped part. This ridge continues towards the basal bulb as a filament. Most proximally, it forms a separate structure that attaches separately to the basal bulb. This ridge was also observed on one paratype of C. reversati on the slide RMCA37.402. However, the paratypes lost transparency due to the fixation in Malmberg’s solution.

Type locality: Pond Near Kila Kindinga 5°29′7″S 14°53′3.8″E.

Other localities: Mvuazi River on H. elongatus 5°19′S; 15°7″E; Mbola River near Tshianya village on H. stellifer 05°52′09.8″S 12°39′52.6″E.

Material: Three whole-mounted specimens in Hoyer’s medium, including the holotype and 13 in Malmberg’s solution.

Holotype: M.T. 38311.

Paratypes: M.T. 38319–20, 38324–25, 38327–28, 38334NHUK 2018.1.31.2 and 2018.1.31.4, KN10049 https://laji.fi/en/view?uri=luomus:KN.10049 and 10052 https://laji.fi/en/view?uri=luomus:KN.10052, SAMC-372 A090065, A090067.

Symbiotype: RMCA_Vert_2015.030.P0020.

Paratype host vouchers: RMCA_Vert_2015.030.P0019, RMCA_Vert_2015.030.P0021, RMCA_Vert_2015.030.P0022, AB53952197.

**O. ximenae**

*Onchobdella ximenae* Jorissen, Pariselle, from the Muséum national d’Histoire naturelle in Paris. The holotype, prepared with the same fixative, was not ordered in Belgium, these structures were not observable. Because of this, the name is not available. Additionally, in three specimens, the distal ends of the accessory piece and the penis did not meet. Also, in all specimens, it was observed that the accessory piece has a ridge, which separates the distal hook from the C-shaped part. This ridge continues towards the basal bulb as a filament. Most proximally, it forms a separate structure that attaches separately to the basal bulb. This ridge was also observed on one paratype of *C. reversati* on the slide RMCA37.402. However, the paratypes lost transparency due to the fixation in Malmberg’s solution.

**Remarks (Table 3, Fig. 10)**

The eight recorded specimens of *C. reversati* from the Congo River had a dorsal bar length that was 9 μm longer on average and a total length of half the size compared with the specimens from the type locality. In the original drawing (see [33]), the accessory piece connected with the heel through a thin filament. However, this connection was not observed in the specimens from Lower Congo. In three specimens, an extension of the heel in another focal plane was observed and could correspond with the thin filamentous connection of the original description. Additionally, in three specimens, the distal ends of the accessory piece and the penis did not meet. Also, in all specimens, it was observed that the accessory piece has a ridge, which separates the distal hook from the C-shaped part. This ridge continues towards the basal bulb as a filament. Most proximally, it forms a separate structure that attaches separately to the basal bulb. This ridge was also observed on one paratype of *C. reversati* on the slide RMCA37.402. However, the paratypes lost transparency due to the fixation in Malmberg’s solution.

Type host: *Hemichromis elongatus* (Guichenot, 1861).

Other hosts: *H. stellifer* Loiselle, 1979.

Infection site: Gills.

**Type locality:** Pond Near Kila Kindinga 5°29′7″S 14°53′3.8″E.

**Other localities:** Mvuazi River on *H. elongatus* 5°19′S; 15°7″E; Mbola River near Tshianya village on *H. stellifer* 05°52′09.8″S 12°39′52.6″E.

Material: Three whole-mounted specimens in Hoyer’s medium, including the holotype and 13 in Malmberg’s solution.

**Holotype:** M.T. 38311.

**Paratypes:** M.T. 38319–20, 38324–25, 38327–28, 38334NHUK 2018.1.31.2 and 2018.1.31.4, KN10049 https://laji.fi/en/view?uri=luomus:KN.10049 and 10052 https://laji.fi/en/view?uri=luomus:KN.10052, SAMC-372 A090065, A090067.

**Symbiotype:** RMCA_Vert_2015.030.P0020.

**Paratype host vouchers:** RMCA_Vert_2015.030.P0019, RMCA_Vert_2015.030.P0021, RMCA_Vert_2015.030.P0022, AB53952197.

**Table 5.** Measurements of *Onchobdella ximenae* n. sp. and *O. voltensis*. All measurements in μm as the average ± standard deviation, count and range (in parentheses).

| Species              | O. ximenae n. sp. | O. voltensis |
|----------------------|------------------|-------------|
| Host                 | H. stellifer, H. elongatus | H. fasciatus, H. bimaculatus |
| Locality             | 4, 6 & 7         | Volta Lake |
| Reference            | Present study    | Paperna [26] |
| Number of specimens  | 12               | 7           |
| Ventral Anchor       |                  |             |
| f                    | 11, 5 (8–12)     | 15–20       |
| Dorsal Anchor        |                  |             |
| a                    | 51, 6 (49–54)    | 60–90       |
| b                    | 43, 6 (40–46)    | /           |
| c                    | 2, 6 (1–3)       | /           |
| d                    | 19, 6 (17–21)    | 10–15       |
| e                    | 22, 6 (21–23)    | /           |
| Uncinuli             |                  |             |
| unciniuli 1          | /                | 10          |
| unciniuli 2          | 13, 2 (12–13)    | /           |
| unciniuli 3          | 13, 3 (12–15)    | /           |
| unciniuli 4          | 13, 3 (12–14)    | /           |
| unciniuli 5          | 13, 4 (11–13)    | /           |
| unciniuli 6          | 13, 6 (11–15)    | /           |
| Ventral Bars         |                  |             |
| x                    | 34, 6 (29–43)    | 20–40       |
| Dorsal Bar           |                  |             |
| x                    | 50, 5 (31–69)    | 70–100      |
| h                    | 33, 5 (29–41)    | /           |
| w                    | 5, 6 (4–6)       | 2–5         |
| MCO                  |                  |             |
| pe                   | 66, 7 (60–70)    | 30–50       |
| ap                   | 22, 6 (19–26)    | 25–30       |
| he                   | 3, 7 (2–5)       | N.A.        |
| Vg                   |                  |             |
| L                    | 33, 2 (21–40)    | N.A.        |
| l                    | 3, 2 (2–3)       | N.A.        |

**Etymology:** The species epithet is a homage to Ximena Sariñana Rivera, a Mexican singer and is a noun (name) in the genitive case.

**Authorship:** Note that the authors of the new taxon are different from the authors of this paper; Article 50.1 and Recommendation 50A of International Code of Zoological Nomenclature [13].

**Description (Table 5, Figs. 8e–8f, 11)**

Dorsal anchors large (a = 51 μm) and orientated distally. Shaft undeveloped and bulbous (c = 2 μm). Guard with rounded edges. Point long with sudden and well-marked thickening on the interior side of the curve. Ventral anchors (f = 11 μm), with T-shaped base with rounded edges and a short, curved point. Dorsal bar slightly bent where both arms meet. Both arms make a 90° turn distally and thicken slightly. Distal tip of each arm bulbously thickened. Two ventral bars, thin, near straight. Six pairs of small hooks of same size. MCO consists of a basal bulb with a long, tubular penis (Pe = 66 μm), which makes one large loop of almost 360° along its...
course. A rounded, irregularly-shaped heel engulfs the basal
bulb, except where the penis transitions into the basal bulb.
Accessory piece consists of two rib-like structures that form
an ellipsoid (resembling a windsurf wishbone), through which
the penis passes. Both rib-like structures come together proxi-
mally, where they form a small bulge and distally, where their
connection is smooth. At the distal end of the penis a leaf-like,
smooth-edged plate is present, and is orientated perpendicular to
the ellipsoid. Vagina, small, with two 90° curves, tubular
(L = 33 μm).

Remarks

Onchobdella ximenae n. sp. resembles O. voltensis Paperna,
1968, described from Lake Volta, Ghana from
H. fasciatus and H. bimaculatus. Both O. ximenae n. sp. and
O. voltensis have ventral bars with solid distal ends instead of
filamentous ends, such as are seen in all other congeners. Fur-
thermore, both species have an accessory piece that forms an
ellipsoid, a penis that passes through it and a smooth, leaf-like
plate at the distal end of the accessory piece. The differences
between these species are that the dorsal anchors in O. ximenae
n. sp. are 10–40 μm smaller (see Table 5) and have an undevel-
oped shaft. The ventral anchors have a T-shaped base, contrary
to the ones in O. voltensis, which have a base that is orientated
proximally and not laterally. The penis of O. voltensis is
J-shaped, whilst in O. ximenae n. sp. it almost makes a loop
and is 16–36 μm longer (see Table 5). Also, the leaf-shaped
plate is orientated perpendicularly on the ellipsoid, while in
O. voltensis it follows the orientation of the ellipsoid. Lastly,
O. voltensis does not have a sclerotized vagina.

Discussion

Seventeen species of monogeneans, eight of which are new
for science, were collected from five host species. Six of these
new parasite species are described. For C. reversati, slight
variations in morphology are mentioned as well as a ridge
on the accessory piece. Two undescribed parasites, C. sp.1
and C. sp.2, were also found in the Middle Congo Basin and
will be described in the report from that expedition.

Parasites of Coptodon

From the Tondé estuary (see Fig. 1), the non-native
Coptodon rendalli was captured [10]. Its native range includes
tributaries and parts of the Middle and Upper Congo, the
Zambezi, Cuanza, Catumbela, Okavango and Cunene rivers
[10]. In Lower Congo, Coptodon rendalli was infected by
Cichlidogyrus berradae Pariselle & Euzet, 2003; Cichli-
dogyrus cubitus Dossou, 1982 and Cichlidogyrus flexicolpos
Pariselle & Euzet, 1995 (see Table 1). These species have
not been found on Coptodon rendalli before, but on other rep-
resentatives of Coptodon from Benin, Ivory Coast, Cabinda
and the ROC [35]. Additionally, parasite species known from
Coptodon rendalli from other regions, such as Cichlidogyrus
dossoui Douëllou, 1993; Cichlidogyrus quaestio Douëllou,
1993; Cichlidogyrus papernastrema Price, Peebles & Bamford,
1969 or Cichlidogyrus tiberianus Paperna, 1960 [7, 14, 46]
were not found in Lower Congo. This indicates that Coptodon
rendalli lost its original parasite fauna during or after introd-
uction, supporting the enemy-release hypothesis [38]. When

Figure 11. Haptoral and genital hard parts of Onchobdella ximenae n. sp. from Hemichromis elongatus. Accessory piece of the MCO in
grey, to highlight the plate-like structure of the accessory piece. I-VI, hooks; AP, accessory piece; DA, dorsal anchors; DB, dorsal transverse
bar; MCO, male copulatory organ; Pe, penis; VA, ventral anchors; VB, ventral transverse bars; Vg, vagina. Scale bar: 20 μm, scale bar of the
MCO 10 μm.
comparing the parasite fauna of the native Coptodon tholloni with that of Coptodon rendalli in this study, only C. cubitus is shared between the two hosts. However, our sample size is small and, therefore, it is presumable that more parasite species are shared. Cichlidogyrus cubitus does not occur in the native range of Coptodon rendalli, so it is possible that Coptodon rendalli acquired this parasite through a spillback effect from Coptodon tholloni [11]. The same applies for C. flexicolpos on Coptodon rendalli. However, the reservoir for C. flexicolpos in Lower Congo could also be Coptodon guineensis, since there are no records of C. flexicolpos on Coptodon tholloni. Furthermore, Coptodon guineensis is known to host C. flexicolpos [29] and to occur in the mangroves of Lower Congo [10].

In our study, Gyrodactylus chitandiri Zahradničková, Barson, Luus-Powell and Přikrylová, 2016 infected Coptodon tholloni, which constitutes a new host and geographical record and results in a disjunct distribution for G. chitandiri. The parasite is known from Coptodon rendalli and Pseudocrenilabrus philander (Weber, 1897) from Chirundu, Zambezi River and Lake Kariba [49], whilst it was lacking in Upper Congo on both hosts [14]. Instead, Coptodon rendalli was infected by Gyrodactylus nyzaeae Paperna, 1973 in Upper Congo [14]. The disjunct distribution of G. chitandiri could be biased due to limited sampling in the past. From our observations, species of Gyrodactylus are far less prevalent (occurring on one out of 14 infected cichlid specimens in Lower Congo and on 1 out of 12 in Upper Congo) than species of Cichlidogyrus on gills of African cichlids, so it is easy to miss species of Gyrodactylus during sampling. We hypothesize that G. chitandiri shows a continuous distribution from the Zambezi River to Lower Congo. It should be noted that although their minimum prevalence is lower than that of species of Cichlidogyrus, their infection intensity is often higher (see Table 2 in this study and [14]). One specimen of Coptodon tholloni from the Ndamba Leta ponds, Mbanza-Ngungu (locality 3, Fig. 1) was exclusively infected by Cichlidogyrus tilapiae Paperna, 1960. This parasite is a generalist (see [21]), but has mostly been found on mouth-brooding cichlids (Oreochromini, see [8]) and has a wide native range that spans most of Central and western Africa, and the Levant [14, 27, 35]. Several species of Coptodon have been screened previously for parasites (e.g. Coptodon rendalli from Upper Congo [14, 46]), but of these, C. tilapia has only been found on Coptodon zillii, so far [9]. In the case of the C. tilapia infection on Coptodon zillii, O. niloticus was also present in the area [9], which is also the case in the Ndamba-Leta ponds. Whether the infection of C. tilapia on Coptodon tholloni is natural or a result of spillover (see [45] and references therein) has to be determined in future research. If the infection is the result of spillover, this would support the hypothesis of Jorissen et al. [14], that certain aquatic systems, such as ponds or artificial lakes, stimulate interspecies interactions between cichlid host species and have a higher host density, both of which stimulate parasite host-switching.

Parasites of Hemichromis

The collected representatives of Hemichromis are the native H. elongatus and H. stellifer [10]. On these hosts, we have discovered three new species that are morphologically similar to already described ones: O. ximenae n. sp., which resembles O. voltensis; C. calycinus n. sp., which resembles C. teugelsi and C. polyenso n. sp., which resembles C. euzeti [35]. Furthermore, we can assume from the literature that C. euzeti is sympatric (occurs on the same individual host) with C. longicirrus in Benin, Cameroon and ROC, though not explicitly stated [6, 22, 34], while in Lower Congo, C. longicirrus is sympatric with C. polyenso n. sp. Similarly, O. voltensis and O. aframae are presumably sympatric in Benin, Cameroon, Senegal, Gambia, Mali and Ivory Coast [6, 26, 34], while in Lower Congo O. aframae is sympatric with O. ximenae n. sp. As shown, there are similarities between the parasite faunas of Hemichromis spp. throughout different ecoregions. However, parasites of Hemichromis spp. remain unexplored for large portions of Africa; thus, it is too early to draw conclusions about their biogeography and diversity. Nonetheless, it can be hypothesized that compared with the species discovered in Lower Congo, more morphologically similar species exist in other freshwater ecoregions on other representatives of Hemichromis. Cichlidogyrus kmentoae n. sp. was only found on H. stellifer, but our sample size is too small to verify whether it does not infect H. elongatus as well. Cichlidogyrus falcifer occurs on H. fasciatus [35] as well as on H. elongatus and thus is an intermediate specialist (a parasite occurring on more than one host from the same genus, see [21]).

Parasites of Tylochromis praecox

From Tylochromis praecox, C. bixlerzavalai n. sp. and C. omari n. sp. are described. New species were expected as no monogeneans had yet been described from T. praecox. Furthermore, all dactylogyrids from species of Tylochromis mentioned in the literature are considered strict specialists [14, 23, 35, 36], meaning, they occur on a single host species. In those studies, representatives of Tylochromis were caught in low numbers and restricted to a single host species. In Lower Congo, Tylochromis labrodon Regan, 1920 and Tylochromis lateralis (Boulenger, 1898) occur further upstream and are sympatric, but not with T. praecox [43]. It would be worthwhile to investigate whether C. bixlerzavalai n. sp. and C. omari n. sp. occur on these hosts as well, to see if these parasites are all strict specialists or if they only appear to be so because of biogeographical barriers. The ancestral state for host-specificity within Cichlidogyrus/Scotogyrus is intermediate specialism [21]. Species of Cichlidogyrus that infect species of Tylochromis are shown to be ancestral to all others within Cichlidogyrus/Scotogyrus [19–21, 37, 48], similar to Tylochromis (and Tylochromini) being ancestral to all African cichlids except Heterochromis [8, 43]. We could hence hypothesize that species of Cichlidogyrus that infect species of Tylochromis are intermediate specialists when sympatric host congeners are present in the area. It has to be noted that only Cichlidogyrus poyanadi Parissle & Euzet, 1994 was included as a representative that infects species of Tylochromis in the phylogenies of Cichlidogyrus/Scotogyrus [19–21, 37, 48]. However, we expect species of Cichlidogyrus that infect species of Tylochromis to form a monophyletic clade based
on the morphological similarities between the species [37]. Both new species showed typical morphological characters of their congeners that infect species of Tylochromis, such as less developed auricles on the dorsal transverse bar, an accessory piece that does not connect directly to the basal bulb of the penis, and a spirally-winding penis [23, 28]. Following the phylogeny, we assume these morphological characters to be ancestral to all others within Cichlidogyrus/Scutogyrus [37].

Species richness and comparison with other regions

Half of the parasite species found in this study are new to science, which is high in comparison to the single new species described from the Mweru-Luapula subregion in the Upper Congo Basin [14]. This can partially be explained by the Lower Congo region being more diverse and having many biogeographical barriers that facilitate speciation [15, 16]. In addition, almost all host species in the Lower Congo region were screened for parasites for the first time. Also, most of the cichlid species studied in the Mweru-Luapula subregion had a more widespread distribution than the ones in Lower Congo [10], and thus it was more likely for us to find previously-described parasites [14]. The diversity of monogenean parasites outmatches that of their hosts by more than 3:1 in this study, which is in line with the African average of 3.1 [44]. The parasite fauna reported in this study has more species in common with ecoregions from other basins, such as the nearby Ogooué-Nyanga-Koulou-Niari ecoregion than with the rest of the Congo Basin. A possible explanation for this is that the Lower Congo was not a part of the Congo Basin until the Early Quaternary [42] and has stayed isolated from the rest of the Congo Basin because of the biogeographical barriers that the region is known for [15, 16, 24, 42]. Furthermore, representatives of Tylochromis and Hemichromis have predominantly been screened from Ghana, Benin, Cameroon, Senegal, Gambia, Mali, Guinea and Ivory Coast [6, 25, 26, 28, 34], whilst most parts of the Congo Basin or Central Africa remain unexplored. These genera have their origins in West Africa [18]. Furthermore, the parasite fauna of P. cabrae from the coastal lowlands of the ROC was reported to be highly homogeneous with that of West African cichlid hosts [33], so it is possible that an overlap in monogenean biodiversity between these two regions exists. Our results support this claim.

Note

Michel Jorissen won the prize for the best student presentation at the 8th International Symposium on Monogenea, held on 6–11 August 2017 at Masaryk University, Faculty of Science, Brno, Czech Republic, which was a fee-waiver for a paper in Parasite. The cost of publication of the present paper was thus offered by EDP Sciences.

Conflict of interest

The authors declare that there is no conflict of interest.

Acknowledgements. This research was supported by the Belgian Federal Science Policy Office (BRAIN-be Pioneer Project (BR/132/P/TILAPIA), OCA type II project S1_RDC_TILAPIA and the Mbisa Congo project, the latter two being framework agreement projects of the RMCA with the Belgian Development Cooperation. MWPJ is supported by a BOF Reserve Fellowship from Hasselt University. The research leading to results presented in this publication was carried out with infrastructure funded by EMRBC Belgium – FWO project GOH3817N. Fieldwork was carried out under mission statements AC/075/2015/L.S.P./MBNGU/AUT.AC and AC/076/2015/L.S.P./MBNGU/AUT.AC. We cordially thank Marcel Collet, Paul N’Lemvo (Institut Congolais pour la Conservation de la Nature), Dieudonné Kufulu-ne-Kongo (école Mulu Kiwanga), L’or Matondo Mbela (Université Kongo), Prosper Nguziani Bimbundi, Boble Boki Fukiakanda and general director father Pierre Ntiaa Nsiiku (Institut Supérieur Pedagogique de Mbanza-Ngungu) and Placide Nziaila Mahinga (Institut National pour l’Étude et la Recherche Agronomiques – Mvuazi/Institut Supérieur d’études agronomiques – Mvuazi) for administrative, field and lab support, making this study possible. MPMV received support from the Belgian Directorate-General for Development Cooperation and Humanitarian Aid (CEBioS programme at the Royal Belgian Institute of Natural Sciences) and the Czech Science Foundation (P505/12/G112 (ECIP)). We would like to thank Eileen Harris, Timo Pajunen, Christophe Allard and Albé Bosman for their curatorial services. We would like to thank Nikki Watson for her grammatical input concerning this manuscript. Lastly, we would like to thank the two anonymous reviewers and Jean-Lou Justine (Editor-in-chief) for their constructive remarks.

References

1. Abell R, Thieme M, Revenga C, Bryer M, Kottelat M, Bogutskaya N, Coad B, Mandrik N, Contreras-Balders S, Bussing W, Stassny MLJ, Skelton P, Allen GR, Unnack P, Naseka A, Ng R, Sindorf N, Robertson J, Armijo E, Higgins J, Heibel TJ, Wikramanayake E, Olson D, Lopez HL, Reis RE, Lundberg JG, Sabaj Perez MH, Petry P. 2008. Freshwater Ecoregions of the World: a new map of biogeographic units for freshwater biodiversity conservation. Bioscience, 58, 403–414.
2. Alter SE, Brown B, Stassny ML. 2015. Molecular phylogenetics reveals convergent evolution in lower Congo River spiny eels. BMC Evolutionary Biology, 15, 224.
3. Bates J. 1997. The scaling compound: Glyceel. Journal of Nematology, 29(4), 565–566.
4. Bilong Bilong CF, Euzet L. 1995. Onchobodella bopeleti n. sp. (Monogenea, Ancyrocephalidae) parasite branchial de Hemichromis fasciatus (Peters, 1857) (Cichlidae). Journal of African Zoology, 109(5), 253–258.
5. Birgi E, Euzet L. 1983. Monogènes parasites des poissons des eaux douces du Cameroun. Présence des genres Cichlidogyrus et Dactylogyrhus chez Aphyosemion (Cyprinodontidae). Bulletin de la Société Zoologique de France, 108(1), 101–106.
6. Dossou C, Birgi E. 1984. Monogènes parasites d’Hemichromis fasciatus Peters, 1857 (Teleostei, Cichlididae). Annales des Sciences Naturelles, Zoologie, Paris, 6(2), 101–109.
7. Douéllou L. 1993. Monogeneans of the genus Cichlidogyrus Paperna, 1960 (Dactylogyridae, Ancyrocephalinae) from cichlid fishes of Lake Kariba (Zimbabwe), with descriptions of five new species. Systematic Parasitology, 25, 159–186.
8. Dunz AR, Schiliewen UK. 2013. Molecular phylogeny and revised classification of the haploptilapine cichlid fishes formerly referred to as “Tilapia”. Molecular Phylogenetics and Evolution, 68(1), 64–80.
26. Paperna I. 1968. Monogenea, Ancyrocephalinae) from Egyptian fish. Folia Parasitologica, 28, 205–214.

27. Paperna I, Thurston JP. 1969. Monogenetic trematodes collected from cichlid fish in Uganda; including the description of five new species of Cichlidogyrus. Revue de Zoologie et de Botanique Africaines, 79(1/2), 15–33.

28. Pariselle A, Euzet L. 1994. Three new species of Cichlidogyrus Paperna, 1960 (Monogenea, Ancyrocephalidae) parasitic on Tylotrocoma jentinki (Steindachner, 1895) (Pisces, Cichlidae) in West Africa. Systematic Parasitology, 29(3), 229–234.

29. Pariselle A, Euzet L. 1995. Gill parasites of the genus Cichlidogyrus Paperna, 1960 (Monogenea, Ancyrocephalidae) from Tilapia guineensis (Bleeker, 1862), with descriptions of six new species. Systematic Parasitology, 30, 187–198.

30. Pariselle A, Euzet L. 1995. Scutogyrus gen. n. (Monogenea: Ancyrocephalidae) for Cichlidogyrus longicornis minus Dosso, 1982, C. l. longicornis, and C. l. gravivaginatus Paperna and Thurston, 1969, with description of three new species parasitic on African cichlids. Journal of the Helminthological Society of America, 62(2), 157–173.

31. Pariselle A, Euzet L. 1995. Trois monogones nouveaux parasites branchiaux de Pelmatochromis buettikoferi (Steindachner, 1895) (Pisces, Cichlidae) en Guinée. Parasite, 2, 203–209.

32. Pariselle A, Euzet L. 1996. Cichlidogyrus Paperna, 1960 (Monogenea: Ancyrocephalidae): gill parasites from West African Cichlidae of the subgenus Coptodon Regan, 1920 (Pisces), with descriptions of six new species. Systematic Parasitology, 34, 109–124.

33. Pariselle A, Euzet L. 2003. Four new species of Cichlidogyrus (Monogenea: Ancyrocephalidae), gill parasites of Tilapia cabrerae (Teleostei: Cichlidae), with discussion on relative length of haptoral sclerites. Folia Parasitologica, 50(3), 195–201.

34. Pariselle A, Euzet L. 2004. Two new species of Cichlidogyrus Paperna, 1960 (Monogenea, Ancyrocephalidae) gill parasites on Hemichromis fasciatus (Pisces, Cichlidae) in Africa, with remarks on parasite geographical distribution. Parasite, 11(4), 359–364.

35. Pariselle A, Euzet L. 2009. Systematic revision of dactylogyrine parasites (Monogenea) from cichlid fishes in Africa, the Levant and Madagascar. Zoosystema, 31(4), 849–898.

36. Pariselle A, Bitja Nyom AR, Bilong Bilong CF. 2014. Four new species of Cichlidogyrus (Monogenea, Ancyrocephalidae) from Sarotherodon mwgosi and Tylotrocoma sudanceensis (Teleostei, Cichlidae) in Cameroon. Zootaxa, 3881(3), 258–266.

37. Pouyas L, Desmarais E, Deveney M, Pariselle A. 2006. Phylogenetic relationships among monogenean gill parasites (Dactylogyridea, Ancyrocephalidae) infesting tilapiine hosts (Cichlidae); systematic and evolutionary implications. Molecular Phylogenetics and Evolution, 38(1), 241–249.

38. Prenter J, Macneil C, Dick JT, Dunn AM. 2004. Roles of parasites in animal invasions. Trends in Ecology and Evolution, 19(7), 385–390.

39. Pugachev ON, Gerasov PI, Gussev AV, Ergens R, Khotensky I. 2009. Guide to Monogeneida of freshwater fish of Palearctic and Amur regions. Ledizioni Ledipublishing: Milan. 538 p.

40. Rahmiov C, Vanhove MPM, Šimková A. 2017. Underexplored diversity of gill monogeneans in cichlids from Lake Tanganyika: eight new species of Cichlidogyrus Paperna, 1960 (Monogenea: Dactylogyridae) from the northern basin of the lake, with remarks on the vagina and the heel of the male copulatory organ. Parasites and Vectors, 10, 591.

41. Řehulková E, Mendllová M, Šimková A. 2013. Two new species of Cichlidogyrus (Monogenea: Dactylogyridae) parasitizing the gills of African cichlid fishes (Perciformes) from Senegal: morphometric and molecular characterization. Parasitology Research, 112(4), 1399–1410.
42. Stankiewicz J, de Wit MJ. 2006. A proposed drainage evolution model for Central Africa – Did the Congo flow east? Journal of African Earth Sciences, 44(1), 75–84.

43. Stiassny ML. 1989. A taxonomic revision of the African genus Tylochromis (Labroidei: Cichlidae); with notes on anatomy and relationships of the groups. Annalen Zoölogische Wetenschappen, Koninklijk Museum voor Midden-Afrika, 258, 1–161.

44. Vanhove MPM, Hablützel PI, Pariselle A, Šimková A, Huys T, Raeymaekers JAM. 2016. Cichlids: a host of opportunities for evolutionary parasitology. Trends in Parasitology, 32(10), 820–832.

45. Vanhove MPM, Huyse T. 2015. Host specificity and species jumps in fish–parasite systems, in Parasite diversity and diversification. Morand S, Krasnov BR, Littlewood DTJ, Editors. Cambridge University Press: Cambridge. p. 401–419.

46. Vanhove MPM, Van Steenberge M, Dessein S, Volekaert FAM, Snoeks J, Huys T, Pariselle A. 2013. Biogeographical implications of Zambezian Cichlidogyrus species (Platyhelminthes: Monogenea: Ancyrocephalidae) parasitizing Congolian cichlids. Zootaxa, 3608, 398–400.

47. Vignon M, Pariselle A, Vanhove MPM. 2011. Modularity in attachment organs of African Cichlidogyrus (Platyhelminthes: Monogenea: Ancyrocephalidae) reflects phylogeny rather than host specificity or geographic distribution. Biological Journal of the Linnean Society, 102, 694–706.

48. Wu XY, Zhu XQ, Xie MQ, Li AX. 2007. The evaluation for generic-level monophyly of Ancyrocephalinae (Monogenea, Dactylogyridae) using ribosomal DNA sequence data. Molecular Phylogenetics and Evolution, 44, 530–544.

49. Zahradničková P, Barson M, Luus-Powell WJ, Přikrylová I. 2016. Species of Gyrodactylus von Nordmann, 1832 (Platyhelminthes: Monogenea) from cichlids from Zambezi and Limpopo river basins in Zimbabwe and South Africa: evidence for unexplored species richness. Systematic Parasitology, 93(7), 679–700.

Cite this article as: Jorissen MWP, Pariselle A, Huyse T, Vreven EJ, Snoeks J, Decru E, Kusters T, Lunkayilakio SW, Bukiinga FM, Artois T & Vanhove MPM. 2018. Six new dactylogyrid species (Platyhelminthes, Monogenea) from the gills of cichlids (Teleostei, Cichliformes) from the Lower Congo Basin. Parasite 25, 64.