

Ancyrocephalidae (Monogenea) of Lake Tanganyika: Does the *Cichlidogyrus* parasite fauna of *Interchromis loocki* (Teleostei, Cichlidae) reflect its host's phylogenetic affinities?

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Abstract

The faunal diversity of Lake Tanganyika, with its fish species flocks and its importance as a cradle and reservoir of ancient fish lineages seeding other radiations, has generated a considerable scientific interest in the fields of evolution and biodiversity. The Tropheini, an endemic Tanganyikan cichlid tribe, fills a peculiar phylogenetic position, being closely related to the haplochromine radiations of Lakes Malawi and Victoria. Several problems remain regarding their genus-level classification. For example, the monotypic genus *Interchromis* is phylogenetically nested within *Petrochromis*; its only representative, *I. loocki*, has often been reclassified. As monogenean flatworms are useful markers for fish phylogeny and taxonomy, the monogenean fauna of *Interchromis loocki* was examined and compared to that of other tropheine cichlids. Three new monogenean species belonging to *Cichlidogyrus* are described from *Interchromis loocki*: *Cichlidogyrus buescheri* Pariselle and Vanhove, sp. nov., *Cichlidogyrus schreyenbrichardorum* Pariselle and Vanhove, sp. nov. and *Cichlidogyrus vealli* Pariselle and Vanhove, sp. nov. Their haptor anchors remind more of congeners infecting species of *Petrochromis* than of all *Cichlidogyrus* spp. hitherto described from other tropheine cichlids. Attachment organ morphology has been proven to mirror the phylogenetic affinities of *Cichlidogyrus* lineages. Therefore the monogenean parasite fauna of *I. loocki* reflects this host's position within *Petrochromis*. Moreover, *I. loocki* differs in habitat choice from *Petrochromis* spp. This study hence confirms that host range and host-specificity in *Cichlidogyrus* spp. parasitizing tropheines is determined by the host's phylogenetic position, rather than by a shared ecological niche.

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Introduction

Lake Tanganyika is, with an estimated age of 9-12 million years (Cohen *et al.*, 1997), the oldest of the East African Great Lakes. Although less species-rich than Lakes Victoria and Malawi, its 250 endemic cichlids form the morphologically, behaviourally and phylogenetically most diverse lacustrine cichlid fauna (Snoeks, 2000) which acted as an evolutionary reservoir from which other lineages evolved (Salzburger *et al.*, 2005). The lake's cichlids are grouped into 14 to 17 tribes (Poll, 1986; Takahashi, 2003; Koblmüller *et al.*, 2008). One of these tribes, the Tropheini, is nested within the haplochromines, which contains the mega-diverse cichlid flocks of Lake Malawi and Lake Victoria (Salzburger *et al.*, 2005). In comparison to these radiations, tropheines are relatively species-poor, as they currently only comprise

24 species classified in nine genera (Poll, 1986; Takahashi, 2003; Takahashi and Koblmüller, 2014).

Traditionally, generic definitions of Lake Tanganyika cichlids are largely based on oral tooth morphology (Poll, 1986). For many tribes, this has proven to be an oversimplification (Sturmbauer et al., 2010). Yet, in tropheine cichlids, phylogenetic reconstructions to a large extent support the grouping of species based on similarities in oral morphology (Koblmüller et al. 2010; Van Steenberge, 2014). One tropheine species, *Interchromis loocki* (Poll, 1949), has, however, been particularly difficult to classify and its generic placement has changed frequently.

Interchromis loocki was described based on 13 specimens collected at Kigoma (Tanzania) (type locality) and Kalemie (Democratic Republic of Congo). Poll (1949) originally described the species as belonging to *Limnotilapia* Regan, 1920, which he considered to represent a ‘limnetic’ form of *Tilapia* Smith 1840. The species was later transferred to *Simochromis* Boulenger, 1898 when Greenwood (1978) synonymised *Limnotilapia* with *Simochromis*. This decision was motivated in a subsequent paper in which Greenwood (1979) stated that, although the type species of both genera, *S. diagramma* (Günther, 1894) and *L. dardennii* (Boulenger, 1899), differ greatly in osteological characters, *I. loocki* is intermediate between the two. Poll (1986) resurrected *Limnotilapia*; yet, as he did not refute Greenwood’s (1979) observations, *I. loocki* remained in *Simochromis*. This was justified as Poll (1986) considered *I. loocki* closer to *Simochromis* than to *Limnotilapia*. Moreover, he claimed that the osteological similarities between both genera were also shared with other representatives of the Tropheini (Poll, 1986).

Interchromis Yamaoka, Hori and Kuwamura, 1998 was erected by Yamaoka et al. (1998) as a monotypic genus to harbour *I. loocki*. The reason for describing the genus was based on the morphological and ecological similarities between *I. loocki* and species of *Petrochromis* Boulenger, 1898 (Yamaoka et al., 1998) and the differences between *I. loocki* and species of *Simochromis*. Yamaoka et al. (1998) argued that, whereas members of *Tropheus* Boulenger, 1898, *Simochromis*, *Pseudosimochromis* Nelissen, 1977 and *Limnotilapia* are browsers that use their firmly set teeth to cut of strands of filamentous algae, *Interchromis* and *Petrochromis* spp. are grazers, or ‘combers’ (Yamaoka, 1997), which collect unicellular algae (mostly diatoms) using their loosely set teeth. Poll (1949) also mentioned the loosely fit teeth in his original description of *I. loocki*. However, he did not use it as a distinguishing character.

The main difference between *Interchromis* and *Petrochromis* is that the outer oral teeth of *I. loocki* are bicuspid, whereas species belonging to the latter genus have tricuspid outer teeth. The similarity in diet between *I. loocki* and *Petrochromis* spp. was also observed after stomach analyses (Muschick et al. 2012). Konings (1998) observed that juvenile *I. loocki* collect algae from plants, just as *Petrochromis* species collect these from rocks. *Interchromis* and *Petrochromis* were also shown to be closely related in a nuclear phylogeny of Tropheini (Koblmüller et al. 2010). Here, *I. loocki* rendered *Petrochromis* paraphyletic as it was sister to two *Petrochromis* species: *P. orthognathus* Matthes, 1959 and *P. fasciolatus* Boulenger, 1914. This is in agreement with Yamaoka (1997), who described the feeding behaviour of different *Petrochromis* species and who noticed the similarity between these two *Petrochromis* species and *I. loocki*.

In this study, we explore another perspective with regard to the question of the relationships of *I. loocki*. To this end, we investigate the monogenean gill parasite fauna infecting this species. Monogenean flatworms exhibit considerable potential for improving our understanding of their hosts’ biogeography, phylogeny and taxonomy (Guégan and Lambert, 1990, Paugy et al., 1990; Pariselle, 1996; Boeger and Kritsky, 2003; Barson et al., 2010; Pariselle et al., 2011; Vanhove, 2012; Vanhove et al., 2013, 2014). Given their simple single-host lifecycle, high species diversity and relatively high host-specificity, these flatworms are good markers for studying biodiversity and speciation in groups of closely related fishes (Pariselle et al., 2003b). The most species-rich genus on African cichlids is *Cichlidogyrus* Paperna, 1960 (Pariselle and Euzet, 2009). This genus is usually considered a member of the Ancyrocephalidae, although studies have suggested the group to be non-monophyletic. In that case its representatives should be considered to belong to the Dactylogyridae (Kritsky and Boeger, 1989; Šimková et al., 2003, 2006; Plaisance et al., 2005). *Cichlidogyrus* spp. are common parasites of Tanganyikan cichlids (Vanhove et al., 2011a; Raeymaekers et al., 2013); thirteen new species have recently been described from Lake Tanganyika (Vanhove et al., 2011b; Gillardin et al., 2012; Muterezi Bukinga et al., 2012; Pariselle et al., 2014).

By characterising the morphological affinities of *Cichlidogyrus* species infecting *I. loocki* as a source of information on its phylogenetic position, we also aim to add to our understanding of what determines host range and host-specificity in the parasite fauna of littoral cichlids in Lake Tanganyika. In the phylogeny of

the Tropheini, major clades are separated according to habitat preferences (Koblmüller *et al.*, 2010). Therefore the evolution of tropheine cichlids can be explained by the general model of cichlid evolution as proposed by Danley and Kocher (2001). It describes how intra-lacustrine differentiation occurs at first by habitat segregation, then by specialisation to a certain trophic niche and finally by the emergence of differences in colour pattern. Although the original model (Danley and Kocher, 2001) describes a split between sand- and rock-dwelling lineages, a similar split between rock- and sediment-dwelling clades is observed in the phylogeny of the Tropheini (Koblmüller *et al.* 2010). However the phylogenetic position of *I. loocki* does not fit into this framework. *Interochromis loocki* occurs amongst macrophytes and in sediment-rich and muddy habitats (Yamaoka, 1997; Konings, 1998). Hence, it has the same habitat requirements as the ‘sediment dwellers’ (*sensu* Koblmüller *et al.*, 2010), including representatives of the tropheine genera *Simochromis*, *Limnotilapia*, *Pseudosimochromis* and ‘*Ctenochromis*’ *horei* Günther, 1894 and ‘*Gnathochromis*’ *pfefferi* Boulenger, 1898. Nevertheless, *I. loocki* is nested within *Petrochromis* (Koblmüller *et al.*, 2010). All representatives of *Petrochromis* feed on epilithic algae, which restricts them to Lake Tanganyika’s rocky shores although *P. orthognathus* and *P. fasciolatus* have a larger tolerance to sediment (Konings, 1998). By comparing the *Cichlidogyrus* fauna infesting *I. loocki* with those of other Lake Tanganyika cichlids, we test whether the high host-specificity hitherto recorded in *Cichlidogyrus* spp. infecting littoral Tanganyikan cichlids, notably tropheines (Vanhove, 2012), is related to the habitat requirements of the host or to its phylogenetic affinities. In the first case, we expect *I. loocki* to harbour a parasite fauna similar to that of the sediment dwellers (Gillardin *et al.*, 2012; Van Steenberge, 2014). In the latter scenario, we anticipate similarities between *Cichlidogyrus* spp. infecting *I. loocki* and those found on species of *Petrochromis*.

Material and methods

A specimen of *Interochromis loocki* (Fig. 1) was collected with a gill net off Kalambo Lodge (8°37’19” S; 31°12’00” E), along the Zambian shoreline of Lake Tanganyika (Fig. 2) in April 2008. It was fixed in pure ethanol and identified to the species level *ex situ*. Its gills were inspected for monogenean parasites using a stereomicroscope. Monogeneans were removed with a dissection needle. They were mounted on a slide under a

cover-slip using ammonium picrate glycerine (Malmberg, 1957) or Hoyer’s medium (see Humason, 1979). Monogeneans observed from *I. loocki* were compared with parasites reported from other Lake Tanganyikan hosts (Vanhove *et al.*, 2011b; Gillardin *et al.*, 2012; Muterezi Bukinga *et al.*, 2012; Grégoir *et al.*, 2014; Pariselle *et al.*, 2014; Van Steenberge, 2014) and with specimens belonging to hitherto undescribed species, retrieved from tropheines (notably *Petrochromis* species) from the collections of the Royal Museum for Central Africa (RMCA).

Micrographs and measurements of the hardparts of haptor and male apparatus (MA) (also known as male copulatory organ) were taken based on Gussev (1962) using a Leica DM2500 microscope at a magnification of $\times 1000$ (oil immersion, $\times 10$ ocular) with the software LAS v.3.6 and a DFC 425 Leica camera. The numbering of the haptoral hardparts was adopted from ICOPA IV (Euzet and Prost, 1981); the terminology follows Pariselle and Euzet (1995) (*i.e.*, ‘uncinuli’ for marginal hooks); and the metrics taken are shown in Fig. 3. Host taxon names and authorities follow Eschmeyer (2014).

Results

Three monogenean species were retrieved from the gills of *Interochromis loocki*, all belonging to *Cichlidogyrus* Paperna, 1960 *sensu* Paperna (1960) and Pariselle *et al.* (2003a). All three species are new to science; they are described in the Appendix, chiefly based on the morphology of the hardparts of the posterior attachment organ (haptor) and of the MA. Measurements on the newly described species are shown in Table 1. Type material was deposited in the invertebrate collection of the RMCA (Tervuren, Belgium), in the Muséum national d’Histoire naturelle (MNHN) (Paris, France) and in the Iziko South African Museum (SAMCTA) (Cape Town, Republic of South Africa). The symbiotype (Frey *et al.*, 1992) was deposited in the RMCA.

The haptoral hardparts of the three *Cichlidogyrus* species found on *I. loocki* show considerable similarity with those of currently undescribed species of this genus infecting *Petrochromis* spp. (Fig. 4). This is particularly apparent in the point of the anchors, which is separated quite sharply from the rest of the anchor (whereas the blade is aligned less towards the guard in congeners from ‘sediment dwellers’: see Gillardin *et al.*, 2012) and in the weak incision between the guard and shaft of the ventral anchor.



Fig. 1. The symbiotype (*Interochromis loocki* MRAC B3-36-P-1) of *Cichlidogyrus buescheri* sp. nov., *C. schreyenbrichardorum* sp. nov. and *C. vealli* sp. nov. from Kalambo Lodge, Zambia.

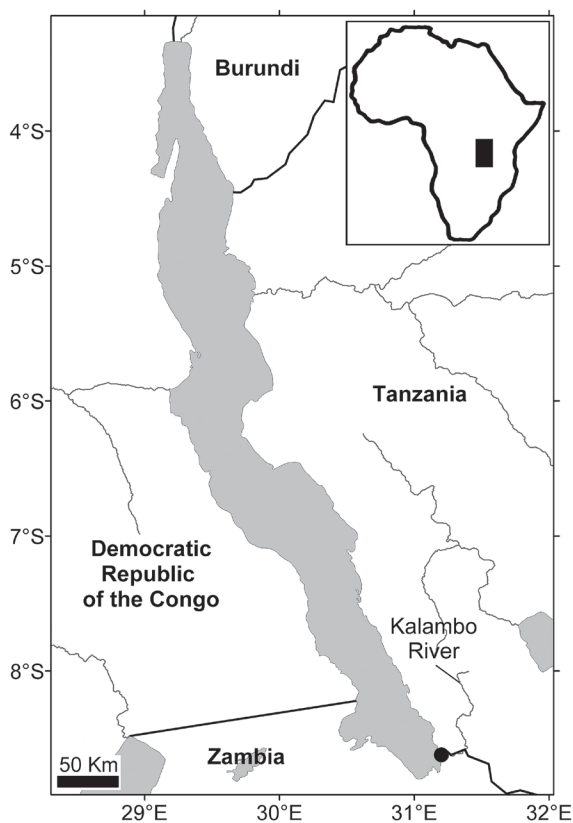


Fig. 2. Map indicating Kalambo Lodge, Zambia (black dot), the type locality of the three newly described *Cichlidogyrus* species.

Discussion

The diverse ichthyofauna of Lake Tanganyika, and specifically its cichlid assemblage, provides an ideal model system for investigating the influence of history and ecology on host-range and speciation mechanisms in parasites (e.g. Pariselle et al., 2014). In littoral cichlids, such as the endemic Tropheini, monogeneans of the genus *Cichlidogyrus* are relatively host-specific, i.e. restricted to a single host species, or a limited number of closely related ones (Vanhove, 2012). However, it is unclear whether their host choice is mainly a result of the ecological or rather the phylogenetic situation of the host species and, hence, whether the affinities of the *Cichlidogyrus* fauna can always provide information on the cichlids' phylogeny. We address this question by studying the monogenean fauna of *Interochromis loocki*, a tropheine cichlid phylogenetically nested within *Petrochromis* but ecologically more similar to 'sediment-dwelling' species classified as, e.g. *Limnotilapia*, *Pseudosimochromis* or *Simochromis*.

Three parasite species were retrieved from *I. loocki* and are described as *Cichlidogyrus buescheri* Pariselle and Vanhove, sp. nov., *C. schreyenbrichardorum* Pariselle and Vanhove, sp. nov. and *C. vealli* Pariselle and Vanhove, sp. nov. (see Appendix). These three new species possess anchors in which the blade point is clearly separated from the 'roots', and in which the ventral

anchor shaft and guard are poorly incised. Such characteristics have not been observed in *Cichlidogyrus* species previously reported from tropheines (Gillardin *et al.*, 2012; Van Steenberge, 2014). Conversely, these features are found in numerous undescribed congeners infecting a range of *Petrochromis* species, related to a greater or lesser extent to *I. loocki* (Fig. 4). It has been shown previously that haptoral elements are valuable for inferring phylogenetic relationships in the lineages of *Cichlidogyrus* spp. (Pouyaud *et al.*, 2006; Vignon *et al.*, 2011). Genetic data have also suggested that the *Cichlidogyrus* fauna of *I. loocki* and *Petrochromis* spp. are closely related (Vanhove, 2012). This similarity between the *Cichlidogyrus* fauna infecting *I. loocki* and the one found on *Petrochromis* species reflects the affinity between *I. loocki* and members of the former genus, despite their ecological differences. This can hence not be an artefact of parasite transmission in a shared habitat and indicates an important influence of host phylogeny on host range in the *Cichlidogyrus* assemblage of the Tropheini. Furthermore, it may provide an extra line of evidence supporting the observations of Yamaoka *et al.* (1998) that, despite its bicuspid frontal teeth, *I. loocki* is not a member of *Simochromis* but more closely affiliated to *Petrochromis*.

Although *I. loocki* can be easily distinguished from species of *Petrochromis* by its outer oral dentition (bicuspid versus tricuspid), the phylogenetic position of *I. loocki* renders *Petrochromis* a paraphyletic genus (Koblmüller *et al.*, 2010). Whether paraphyletic genera are acceptable is currently under debate (Hörandl, 2006; Ebach *et al.* 2006; Hörandl and Stuessy, 2010). Nevertheless, it could be argued that there is no need to maintain *Interochromis* as distinct from *Petrochromis*. When synonymised, species of *Petrochromis* would then be defined as tropheine cichlids with a loosely set oral dentition.

Alternatively, *Interochromis* could be enlarged to include *P. orthognathus* and *P. fasciolatus*. These two species are sister to *I. loocki* in a nuclear phylogeny (Koblmüller *et al.*, 2010). *Petrochromis orthognathus* and *P. fasciolatus* differ from their congeners by their relatively small number of oral teeth (Yamaoka, 1997) and rapid jaw movement while feeding. These traits are shared with *I. loocki* (Yamaoka *et al.*, 1998). By including *P. orthognathus* and *P. fasciolatus* in *Interochromis*, not all systematic issues in *Petrochromis* would be solved as three clades are observed in the genus (Koblmüller *et al.*, 2010). The first contains *I. loocki*, *P. orthognathus* and *P. fasciolatus* and the second is made up of the ‘large’ species: *P. polyodon* Boulenger, 1898, *P.*

trewavasae trewavasae Poll, 1948, *P. macrognathus* Yamaoka, 1983, *P. trewavasae ephippium* Brichard, 1989 and *P. horii* Takahashi and Koblmüller, 2014 as well as several undescribed species (Konings, 1998; Koblmüller *et al.*, 2010). A third clade, containing only *P. famula* Matthes and Trewavas, 1960 was resolved as sister to the first, although this position has not been supported (Koblmüller *et al.*, 2010). Morphologically, *P. famula* is intermediate between representatives of both clades, as it has many teeth, just like the ‘large’ *Petrochromis* species, but it also displays a fast feeding behaviour similar to representatives of the second clade (Yamaoka, 1997). The intermediate position of *P. famula* is further illustrated by its similarity in general body shape to representatives of the first clade, whereas it clusters with those of the second clade when comparing pharyngeal jaw morphology (Muschick *et al.*, 2012).

The strong host-specificity of these *Cichlidogyrus* spp. (Vanhove, 2012) can often render these parasites useful markers of their hosts’ phylogenetic position. Indeed, the similarity of the *Cichlidogyrus* fauna infecting species of *Interochromis* and *Petrochromis* also reflects the evolutionary affinity between these host genera. It also shows that the host choice of these Tanganyikan *Cichlidogyrus* spp. can reflect host phylogeny independent of the host’s preferred habitat. We therefore propose the use of distribution patterns of gill parasites of the genus *Cichlidogyrus* to support the (sub-)generic classification of the *Petrochromis-Interochromis* complex. A similar approach was followed in the ‘sediment dwelling’ Tropheini (*sensu* Koblmüller *et al.* 2010), where the distribution patterns of *Cichlidogyrus* species and morphotypes provided an extra line of evidence used to re-define the genera *Simochromis* and *Pseudosimochromis* (Van Steenberge, 2014).

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Appendix

Family Ancyrocephalidae Bychowsky, 1937
 Genus *Cichlidogyrus* Paperna, 1960
Cichlidogyrus buescheri Pariselle and Vanhove sp. nov.
 (Figs 4, 8a, b, 9c).

Type host. *Interochromis loocki* (Poll, 1949) (symbio-
 type: MRAC B3-36-P-1).

Infection site. Gills.

Type locality. Kalambo Lodge, Zambia (08°37' S; 31°12' E).

Material studied. 10 individuals.

Type material. Holotype: MRAC 37745; paratypes: MRAC 37744, MNHN HEL418, SAMCTA 61809.

Etymology. The specific epithet is given for Heinz Büscher (Germany/ Switzerland), aquarist and collector

of Lake Tanganyika cichlids, in gratitude for his selfless contributions to the community of cichlid researchers.

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

Description. Pharynx ovoid. Striated tegument. Dorsal anchor short, with poorly marked shaft (fenestration sometimes present between shaft and guard); blade arched in distal third. Dorsal transverse bar arched with well-developed auricles. Ventral anchor similar to dorsal anchor in shape and size. Ventral transverse bar simple, V-shaped. Uncinuli I short (relative to uncinuli II, pair retaining their larval length: see Pariselle and Euzet,

Table 1. Comparison of body, haptor and genital measurements (in micrometres, average with range and number of observations *n* in parentheses) of *Cichlidogyrus buescheri* sp. nov., *C. schreyenbrichardorum* sp. nov. and *C. vealli* sp. nov. When *n* > 30, average ± standard deviation is presented.

	<i>C. buescheri</i> sp. nov.	<i>C. schreyenbrichardorum</i> sp. nov.	<i>C. vealli</i> sp. nov.
Total body length	373 (307-430, <i>n</i> = 7)	401 (281-515, <i>n</i> = 10)	490 (412-659, <i>n</i> = 16)
Body width at mid-body	146 (100-224, <i>n</i> = 9)	158 (108-211, <i>n</i> = 11)	178 (128-246, <i>n</i> = 16)
Pharynx maximal width	47 (42-58, <i>n</i> = 6)	34 (31-43, <i>n</i> = 7)	38 (32-47, <i>n</i> = 11)
Dorsal anchor total length (a DA)	28 (25-31, <i>n</i> = 12)	47 (43-51, <i>n</i> = 18)	34 (30-37, <i>n</i> = 27)
Dorsal anchor blade length (b DA)	24 (23-27, <i>n</i> = 12)	34 (32-37, <i>n</i> = 18)	25 (22-27, <i>n</i> = 27)
Dorsal anchor shaft length (c DA)	2 (1-2, <i>n</i> = 12)	4 (2-10, <i>n</i> = 19)	3 (2-5, <i>n</i> = 27)
Dorsal anchor guard length (d DA)	9 (5-13, <i>n</i> = 12)	15 (13-17, <i>n</i> = 18)	13 (10-15, <i>n</i> = 27)
Dorsal anchor point length (e DA)	10 (9-12, <i>n</i> = 12)	11 (8-12, <i>n</i> = 18)	9 (7-10, <i>n</i> = 27)
Length of dorsal bar auricle (h DB)	17 (15-20, <i>n</i> = 14)	17 (14-21, <i>n</i> = 20)	15 ± 1.8 (11-19, <i>n</i> = 31)
Dorsal bar maximum width (w DB)	6 (5-8, <i>n</i> = 7)	9 (8-11, <i>n</i> = 11)	8 (7-9, <i>n</i> = 16)
Dorsal bar total length (x DB)	37 (31-47, <i>n</i> = 7)	54 (46-63, <i>n</i> = 11)	39 (33-48, <i>n</i> = 16)
Distance between dorsal bar auricles (y DB)	9 (7-13, <i>n</i> = 7)	18 (15-24, <i>n</i> = 11)	15 (13-18, <i>n</i> = 16)
Ventral anchor total length (a VA)	29 (28-33, <i>n</i> = 10)	37 (35-41, <i>n</i> = 19)	29 ± 1.3 (28-33, <i>n</i> = 32)
Ventral anchor blade length (b VA)	27 (24-28, <i>n</i> = 11)	37 (33-40, <i>n</i> = 19)	29 ± 1.1 (26-32, <i>n</i> = 32)
Ventral anchor shaft length (c VA)	2 (1-3, <i>n</i> = 11)	4 (2-5, <i>n</i> = 20)	3 ± 0.7 (1-5, <i>n</i> = 32)
Ventral anchor guard length (d VA)	9 (7-11, <i>n</i> = 10)	7 (5-10, <i>n</i> = 19)	8 ± 1.1 (5-10, <i>n</i> = 32)
Ventral anchor point length (e VA)	11 (9-13, <i>n</i> = 11)	12 (10-13, <i>n</i> = 19)	11 ± 0.8 (9-13, <i>n</i> = 32)
Ventral bar maximum width (w VB)	5 (5-6, <i>n</i> = 7)	7 (6-8, <i>n</i> = 11)	6 (5-7, <i>n</i> = 16)
Length of one ventral bar branch (x VB)	33 (27-37, <i>n</i> = 14)	49 (42-55, <i>n</i> = 21)	42 ± 2.5 (38-48, <i>n</i> = 31)
Length of first pair of uncinuli (UI)	12 (11-13, <i>n</i> = 14)	15 (14-16, <i>n</i> = 22)	14 ± 0.7 (12-15, <i>n</i> = 32)
Length of second pair of uncinuli (UII)	12 (11-13, <i>n</i> = 8)	12 (11-13, <i>n</i> = 13)	12 ± 0.6 (10-13, <i>n</i> = 31)
Length of third pair of uncinuli (UIII)	17 (14-19, <i>n</i> = 12)	17 (16-19, <i>n</i> = 22)	18 (14-20, <i>n</i> = 22)
Length of fourth pair of uncinuli (UIV)	19 (16-21, <i>n</i> = 12)	22 (20-24, <i>n</i> = 21)	22 (20-24, <i>n</i> = 24)
Length of fifth pair of uncinuli (UV)	20 (17-23, <i>n</i> = 12)	24 (21-26, <i>n</i> = 22)	25 (23-27, <i>n</i> = 26)
Length of sixth pair of uncinuli (UVI)	18 (15-20, <i>n</i> = 13)	21 (18-23, <i>n</i> = 22)	22 (20-24, <i>n</i> = 25)
Length of seventh pair of uncinuli (UVII)	16 (14-18, <i>n</i> = 11)	18 (16-20, <i>n</i> = 22)	18 (16-19, <i>n</i> = 26)
Accessory piece length (AP)	38 (31-52, <i>n</i> = 9)	49 (44-54, <i>n</i> = 12)	52 (41-64, <i>n</i> = 16)
Penis total length (Pe)	53 (49-58, <i>n</i> = 9)	61 (58-65, <i>n</i> = 12)	50 (45-56, <i>n</i> = 16)
Heel length (He)	8 (6-11, <i>n</i> = 10)	5 (4-8, <i>n</i> = 12)	5 (4-6, <i>n</i> = 16)

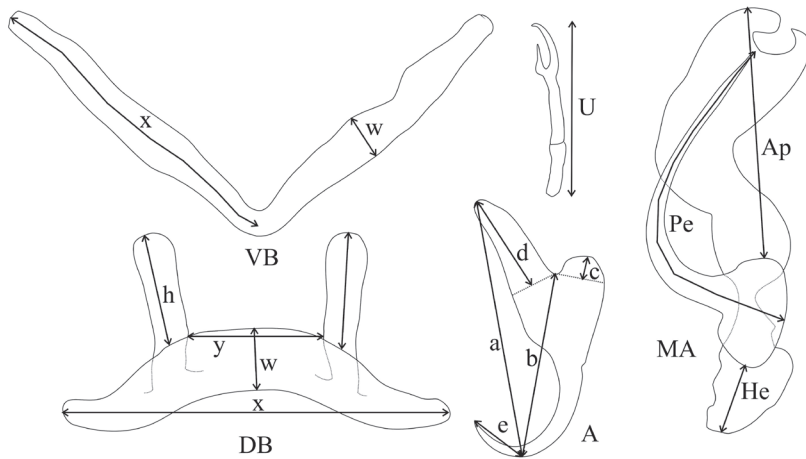


Fig. 3. Measurements used. A, anchor: a, anchor total length; b, anchor blade length; c, anchor shaft length; d, anchor guard length; e, anchor point length. DB, dorsal transverse bar: h, length of dorsal bar auricle; w, dorsal bar maximum width; x, dorsal bar total length; y, distance between auricles. VB, ventral transverse bar: w, ventral bar maximum width; x, length of one ventral bar branch. MA, male apparatus: Ap, accessory piece straight length; Pe, penis total curved length; He, heel straight length. U, uncinuli length.

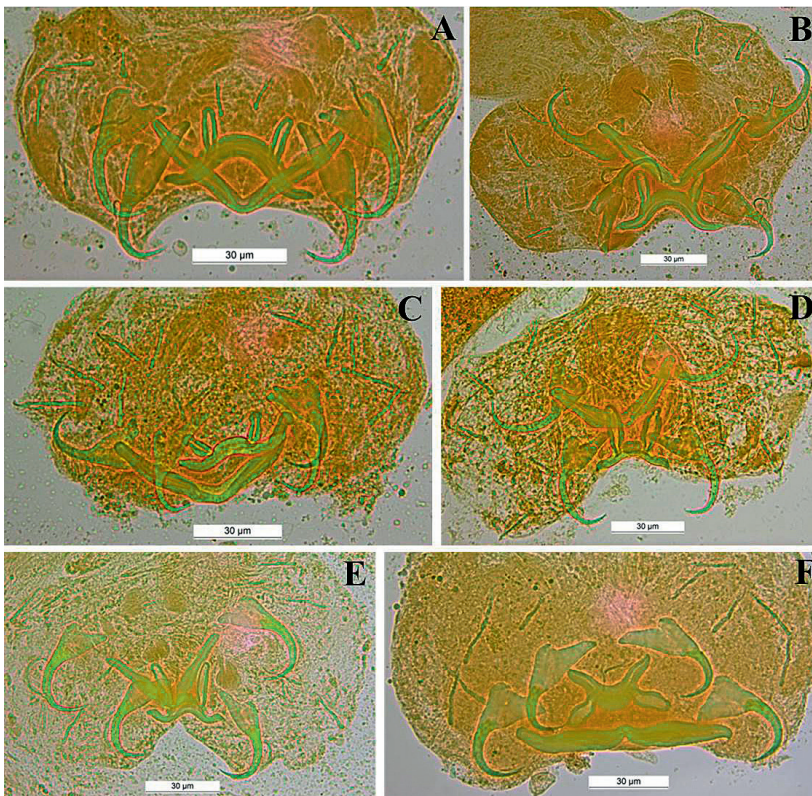


Fig. 4. Haptoral hardparts of *Cichlidogyrus* infecting *Petrochromis*. Micrographs (400×) of the haptor of parasites, fixed in glycerine ammonium picrate, infecting: A, B, *P. fasciolatus* (MRAC B0-12-P-861) (phylogenetically close to *Interchromis loocki*); C, D, *P. famula* (MRAC B0-12-P-866) (intermediate between the *Petrochromis/Interchromis* clade and the 'large' *Petrochromis* clade); E, F, *P. trewasvae ephippium* (MRAC B0-12-P-867) (a 'large' *Petrochromis*). Note the kink marking the beginning of the anchor blade points and the little incision between ventral anchor shaft and guard.

2003, 2009); III to VII short (*sensu* Pariselle and Euzet, 2003, 2009). Penis a curved tube with narrow extremity, beginning in large flattened bulb with large heel of irregular shape. Accessory piece wide, with its distal end pincer-like, directly attached to basal bulb. No sclerotized vagina observed.

Comments. *Cichlidogyrus buescheri* sp. nov. belongs to the group with short uncinuli I and III to VII (see Vignon et al., 2011). The distinct shape of its accessory piece (with a pincer-like distal end) is reminiscent of *C. bifurcatus* Paperna, 1960, *C. fontanai* Pariselle and Euzet, 1997 and *C. makasai* Vanhove, Volckaert and Pariselle,

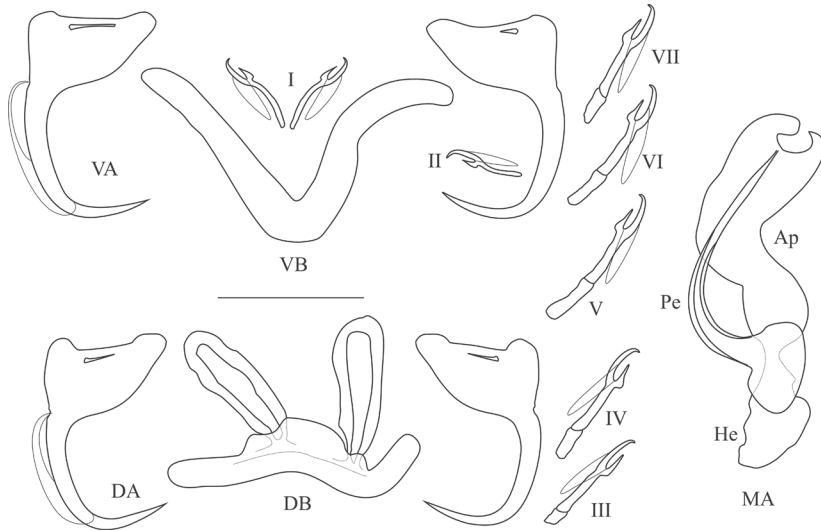


Fig. 5. Haptor and genital hardparts of *Cichlidogyrus buescheri* sp. nov. Ap, accessory piece; DB, dorsal transverse bar; DA, dorsal anchor; He, heel; MA, male apparatus; Pe, penis; VB, ventral transverse bar; VA, ventral anchor; I to VII, uncinuli. Scale bar = 20 μ m.

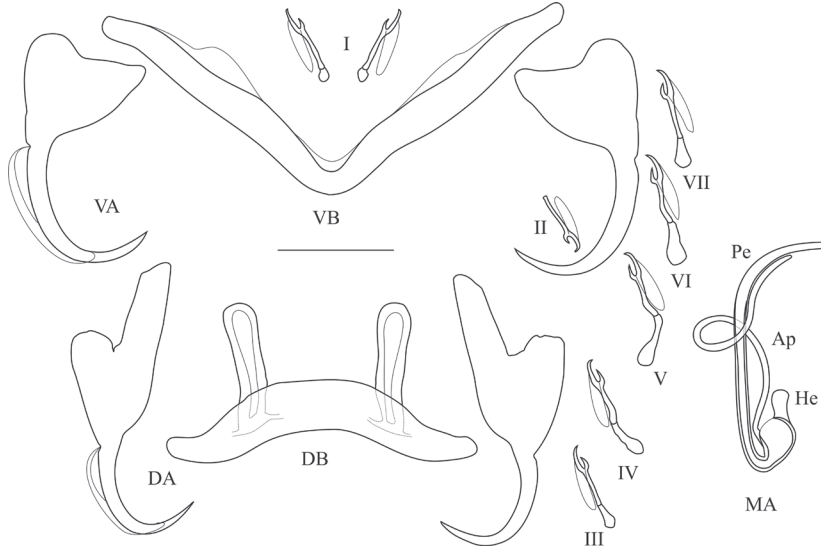


Fig. 6. Haptor and genital hardparts of *Cichlidogyrus schreyenbrichardorum* sp. nov. Ap, accessory piece; DB, dorsal transverse bar; DA, dorsal anchor; He, heel; MA, male apparatus; Pe, penis; VB, ventral transverse bar; VA, ventral anchor; I to VII, uncinuli. Scale bar = 20 μ m.

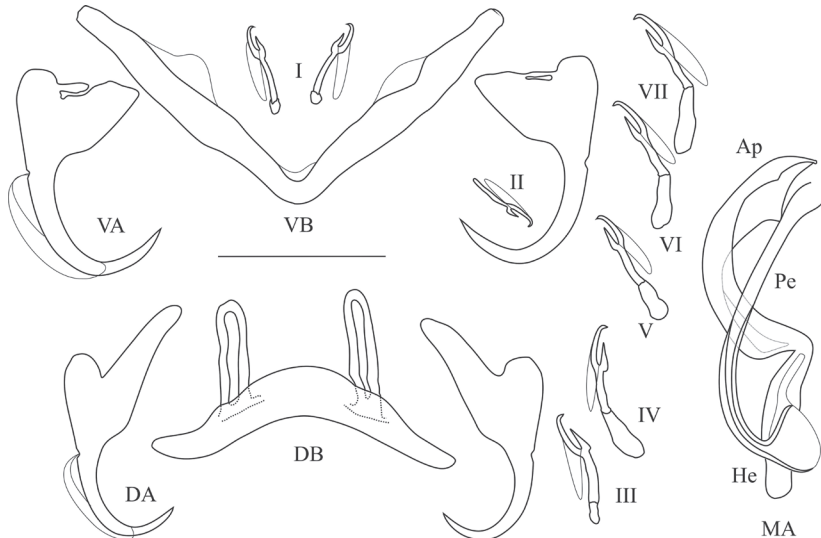


Fig. 7. Haptor and genital hardparts of *Cichlidogyrus vealli* sp. nov. Ap, accessory piece; DB, dorsal transverse bar; DA, dorsal anchor; He, heel; MA, male apparatus; Pe, penis; VB, ventral transverse bar; VA, ventral anchor; I to VII, uncinuli. Scale bar = 20 μ m.

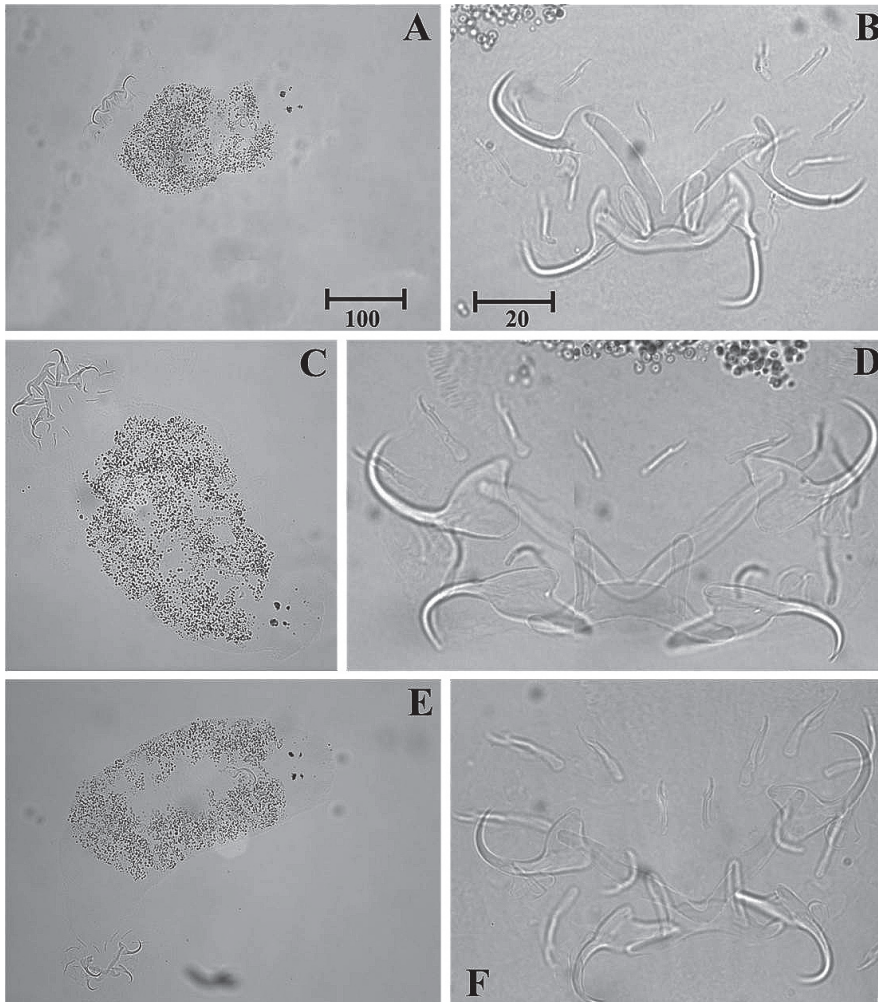


Fig. 8. Whole mount (left) and haptor (right) of the newly described *Cichlidogyrus* species parasitizing *Interochromis loocki*. A, B, *C. buescheri* sp. nov.; C, D, *C. schreyenbrichardorum* sp. nov.; E, F, *C. vealli* sp. nov. Micrographs, of specimens fixed in Hoyer's medium, depicted to scale.

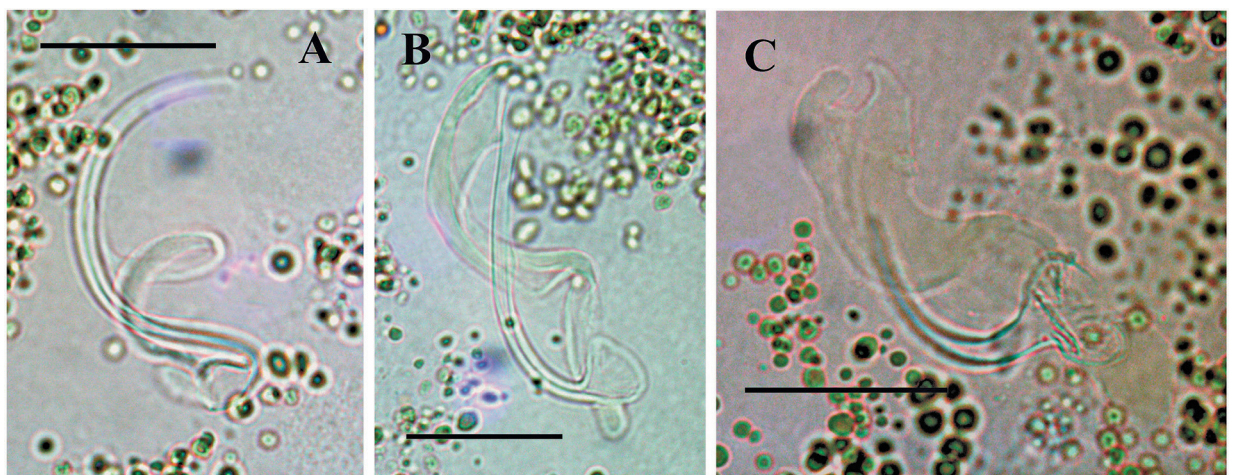


Fig. 9. Comparative morphology of the male apparatus of the newly described *Cichlidogyrus* species parasitizing *Interochromis loocki*. Micrographs, of specimens fixed in Hoyer's medium, depict: A, *C. schreyenbrichardorum* sp. nov.; B, *C. vealli* sp. nov.; C, *C. buescheri* sp. nov. Scale bar = 20 μm.

2011. It can be distinguished from these species as follows: 1) *C. bifurcatus* has a straight penis (*versus* curved in *C. buescheri* sp. nov.) and an asymmetrical dorsal and ventral anchor with a well-marked shaft and guard (*versus* similar anchors and poorly marked shaft in *C. buescheri* sp. nov.); 2) *C. fontanai* has a straight penis and a three-pronged accessory piece (*versus* a curved penis and two-pronged accessory piece in *C. buescheri* sp. nov.); 3) *C. makasai* has a longer penis (73 *versus* 53 μm in *C. buescheri* sp. nov.) and a short dorsal bar (25 μm *versus* 37 μm in *C. buescheri* sp. nov.), resulting in proportionally long auricles (20 *versus* 17 μm in *C. buescheri* sp. nov.).

Cichlidogyrus schreyenbrichardorum Pariselle and Vanhove sp. nov.
(Figs 5, 8c, d, 9a).

Type host. *Interochromis loocki* (Poll, 1949) (symbiotype: MRAC B3-36-P-1).

Infection site. Gills.

Type locality. Kalambo Lodge, Lake Tanganyika, Zambia (08°37' S; 31°12' E).

Material studied. 12 individuals.

Type material. Holotype: MRAC 37741; paratypes: MRAC 37740-1, MNHN HEL416, SAMCTA 61811.

Etymology. the specific epithet is given in honour of the Schreyen-Brichard family (Burundi / Belgium) in recognition of their countless contributions to Lake Tanganyika ichthyology, and their hospitality and active assistance towards African and other researchers active in the region.

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

Description. Pharynx ovoid. Tegument striated. Dorsal anchor large, with marked shaft, long guard and arched blade. Dorsal transverse bar large, arched, with narrow auricles; extremities sometimes bent anteriorly. Ventral anchor with poorly marked guard and shaft, shorter but more robust than dorsal anchor, with blade and total length of same size. Ventral transverse bar V-shaped, large, thick. Uncinuli I short; III to VII short (*sensu* Pariselle and Euzet, 2003, 2009). Penis a thin tube of almost constant diameter, at acute angle with basal bulb; heel relatively small, slender but well developed. Acces-

sory piece simple, thin and coiled (one turn), attached to basal bulb (J-shaped) and curved around penis in middle (rarely straight). No sclerotized vagina observed.

Comments. *Cichlidogyrus schreyenbrichardorum* sp. nov. also has short uncinuli I and III to VII. It is unique in the shape of its penis (J-shaped, with a constant diameter) and associated accessory piece (spirally coiled (1 turn), wound around the penis and attached to the basal bulb). Only *Cichlidogyrus* sp.1 (from Grégoir *et al.*, 2014) and *C. reversati* Pariselle and Euzet, 2003 resemble *C. schreyenbrichardorum* sp. nov. However, *C. reversati* has a large first pair of uncinuli (*versus* short in *C. schreyenbrichardorum* sp. nov.) and the distal end of its penis is folded back (*versus* straight in *C. schreyenbrichardorum* sp. nov.). *Cichlidogyrus* sp.1 (from Grégoir *et al.*, 2014) has a short, wide penis with a bevelled extremity, whereas this organ is J-shaped and straight in *C. schreyenbrichardorum* sp. nov.. Moreover, *C. schreyenbrichardorum* sp. nov. is the only known species of *Cichlidogyrus* with the ventral anchors having a total length and blade length of the same size ($a = b$).

Cichlidogyrus vealli Pariselle and Vanhove sp. nov.
(Figs 6, 8e, f, 9b)

Type host. *Interochromis loocki* (Poll, 1949) (symbiotype: MRAC B3-36-P-1).

Infection site. Gills.

Type locality. Kalambo Lodge, Lake Tanganyika, Zambia (08°37' S; 31°12' E).

Material studied: 16 individuals.

Type material. Holotype: MRAC 37743; paratypes: MRAC 37742-3, MNHN HEL417, SAMCTA 61810.

Etymology. The specific epithet refers to Toby Veall (Zambia / United Kingdom) in gratitude for his contributions to countless Lake Tanganyika expeditions.

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

Description. Pharynx ovoid. Tegument striated. Dorsal anchor with well-developed and distinct shaft; blade arched in distal third. Dorsal transverse bar arched with narrow auricles. Ventral anchor shorter but more robust than dorsal anchor, with poorly marked guard and shaft (fenestration sometimes present between shaft and

guard); blade length and total length similar. Ventral transverse bar V-shaped. Uncinuli I short; III to VII short (*sensu* Pariselle and Euzet, 2003, 2009). Penis a tube of mostly constant length but with enlarged extremity, begins in distinct bulb with short, stubby but well-developed heel. Accessory piece, attached to basal bulb, gutter-like, sharply bent in proximal third, with three-pronged distal end. No sclerotized vagina observed.

Comments. Like its congeners infecting *Interchromis loocki* or other tropheine cichlids, *Cichlidogyrus vealli* sp. nov. belongs to the *Cichlidogyrus* morphotype with short uncinuli I and III to VII. It can be distinguished from other members of the group by the shape of its penis (tube of generally constant width but with an enlarged extremity) and of the associated accessory piece (a gutter-like structure).