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Diversity and host-specificity of monogenean gill parasites (Platyhelminthes) of cichlid fishes in the Bangweulu-Mweru ecoregion

Michiel W. P. Jorissen[1,2*], Antoine Pariselle[3], Tine Huyse[1,4], Emmanuel J. Vreven[1], Jos Snoeks[1,4], Filip A. M. Volckaert[4], Auguste Chocha Manda[5], Gyrhaiss Kapepula Kasembele[5], Tom Artois[2], Maarten P. M. Vanhove[1,2,4,6,7]

[1]Department of Biology, Royal Museum for Central Africa, Leuvensesteenweg 13, BE-3080 Tervuren, Belgium.

[2]Research Group Zoology: Biodiversity & Toxicology, Centre for Environmental Sciences, Hasselt University, BE-3590 Diepenbeek, Belgium.

[3]Institut des Sciences de l'Evolution, IRD, B.P. 1857, Yaoundé, Cameroon.

[4]Laboratory of Biodiversity and Evolutionary Genomics, Department of Biology, University of Leuven, Ch. Deberiotstraat 32, BE-3000 Leuven, Belgium.

[5]Unité de recherche en Biodiversité et Exploitation durable des Zones Humides (BEZHU), Faculté des Sciences Agronomiques, Université de Lubumbashi, Haut-Katanga, R.D. Congo.

[6]Capacities for Biodiversity and Sustainable Development, Royal Belgian Institute of Natural Sciences, Brussels, Belgium.

[7]Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic.

*Corresponding author: michiel.jorissen@uhasselt.be

Running title: gill parasites of cichlids in the Bangweulu-Mweru ecoregion

Abstract

This study represents the first exploration of the parasite fauna of cichlid fishes in the Mweru-Luapula subregion (Central Africa). Twelve species of cichlids and 14 species of Monogenea from three genera (*Cichlidogyrus*, *Gyrodactylus* and *Scutogyrus*) were collected. We present a first record of the gill parasite fauna of eight host species, *Oreochromis mweruensis*, *Orthochromis* sp. 'Mambilima', *Sargochromis mellandi*, *Serranochromis angusticeps*, *S. stappersii*, *S. thumbergi* and *Tylochromis mylodon*. The host range of 10 parasite species was expanded. The study further includes the description of *Cichlidogyrus consobrini* sp.n. from *S. mellandi* and *Orthochromis* sp. 'Mambilima'. A new morphotype of *C. halli* is characterized and three species, *C. papernastrema*, *C. quaestio* and *C. zambezensis* are redescribed. Furthermore, the biodiversity and host-specificity of these parasites are compared with cichlid parasites from Lake Kariba and Cameroon. Two species, including *C. consobrini* sp.n. and a new morphotype of *C. halli*, are putative endemics. Additionally, the parasite fauna is highly similar in species composition to Lake Kariba, but in Bangweulu-Mweru the same parasite species are more host-specific, probably because of hydrogeographical differences between the two regions.

Keywords: Africa, Biogeography, Dactylogyridae, Gyrodactylidae, Congo, Zambezi

Introduction

The Bangweulu-Mweru ecoregion is part of the Congo basin and covers the Southeastern part of the Democratic Republic of Congo (DRC) and the Northeastern part of Zambia (Thieme *et al.*, 2005; FEOW, 2016). It lies just north of the Zambezi-Congo watershed, but parts of the ecoregion drained into the Zambezi basin from the late Tertiary (Moore & Larkin, 2001) up to the Holocene (Lévêque, 1997; Key *et al.*, 2004; Katongo *et al.*, 2007; Koblmüller *et al.*, 2008). These historical connections are also reflected in the freshwater fish fauna, which is highly similar in both basins (Van Steenberge *et al.*, 2014). The freshwater fish fauna has the highest similarity with the Upper Congo, to which it currently drains (Van Steenberge *et al.*, 2014). The Bangweulu-Mweru region is relatively speciose and exhibits a high degree of endemicity relative to other freshwater ecoregions (Thieme *et al.*, 2005). The Biological Distinctiveness Index of the ecoregion is globally outstanding and the Conservation Status Index lists it as a first priority area (Thieme *et al.*, 2005; FEOW, 2016). Bangwuelu-Mweru harbours 138 fish species belonging to 58 genera and 18 families (Van Steenberge *et al.*, 2014). Within the ecoregion, the Mweru-Luapula subregion is the most diverse, harbouring 135 freshwater fish species of which 35 are endemic, with Lake Mweru and the Lower Luapula being the most speciose (Van Steenberge *et al.*, 2014). In contrast, the Bangweulu-Chambeshi subregion is species-poor relative to Mweru-Luapula with 93 species and a single endemic species (Van Steenberge *et al.*, 2014).

The Cichlidae (Teleostei: Cichliformes) have the highest number of endemic species (Thieme *et al.*, 2005) and, after the Cyprinidae, constitute the second most speciose family (Lévêque, 1997) within Bangweulu-Mweru. A typical species for the Mweru-Luapula subregion is *Oreochromis mweruensis* Trewavas, 1983, occurring in the Lualaba, Luvua, Lake Mweru and the Lower Luapula (Schwanck, 1994). It is closely related and morphologically similar to *O. macrochir* (Boulenger, 1912) (Trewavas, 1983; Schwanck, 1994). Both species have an allopatric distribution, with *O. macrochir* occurring in the Upper Luapula, Lake Bangwuelu, Chambeshi, Kafue, Kalomo, Upper Zambezi, Okavango, Cunene, Buzi and Luembe Rivers (Schwanck 1994). In 1945, a few pairs of *O. mweruensis* from Mweru-Luapula were introduced in the vicinity of Lubumbashi for farming purposes (Thys van den Audenaerde, 1988). Also *O. macrochir* was introduced in Bangweulu-Mweru (Kipopo) (De Vos *et al.* 2001). Both species hybridise, as discovered by Thys van den Audenaerde (1964), but were classified as subspecies at the time.

Other common species in the region, such as *Tilapia sparrmanii* Smith, 1840 and *Coptodon rendalli* (Boulenger, 1857), have a wider distribution. They occur in both the Congo and

Zambezi Basins, and as far south as the Limpopo Basin (Skelton, 2001; Schwarzer *et al.*, 2009; Zengeya *et al.*, 2011). The serranochromine cichlids have several representatives in Bangweulu-Mweru and are speciose throughout Southern Africa (Van Steenberge *et al.*, 2014). They also have a complex evolutionary history (Joyce *et al.*, 2005; Katongo *et al.*, 2007; Koblmüller *et al.*, 2008). The Serranochromine cichlids probably migrated from the Congo Basin to paleolake Makgadikgadi where they experienced an explosive radiation (Joyce *et al.*, 2005). When the lake dried up, several species persisted in the Southern African rivers and dispersed from there (Joyce *et al.*, 2005) into the Congo Basin (Katongo et al., 2007) through a recent link between the basins (Lévêque, 1997; Key *et al.*, 2004).

In complex biogeographical situations, e.g. the dispersal of serranochromine cichlids across the Zambezi-Congo watershed, hydrology and molecular markers are used as biogeographical tools (Joyce *et al.*, 2005; Katongo *et al.*, 2007; Koblmüller *et al.*, 2008). Additionally, fossil evidence is used for studies on a larger geographical scale and on higher taxonomical levels (Murray, 2001; Sparks & Smith, 2005; Friedman *et al.*, 2013). Parasites can also function as biogeographical tools for freshwater fish biogeography (Pérez-Ponce de Léon & Choudhury, 2005; Barson *et al.*, 2010; Pariselle *et al.*, 2011). Although not often used in biogeographical research, monogeneans are an ideal choice as taxonomic marker. They have limited dispersal capability because they are aquatic, strictly parasitic and have a direct lifecycle, thus linking them strongly to the host species. Furthermore, monogeneans are the most host-specific of fish parasites and very host-specific in general (Whittington *et al.*, 2000; Cribb *et al.* 2002). Consequently, host species are often infected by a characteristic set of monogenean species, thus providing a distinguishable feature between them.

The most speciose monogenean genus on African cichlids is *Cichlidogyrus* Paperna, 1960 (Dactylogyridae), with about 120 valid species described. It occurs solely on the gills of African and Levantine cichlids, with the exception of *C. nandidae* Birgi & Lambert, 1986, *C. inconsultans* Birgi & Lambert, 1986 and *C. amieti* Birgi & Euzet, 1983 (Pariselle & Euzet, 2009). The former two are found on *Polycentropsis abreviata* Boulenger, 1901 (Nandidae) and the latter on representatives of Nothobranchidae. Species of *Scutogyrus* Pariselle & Euzet, 1995, a closely related genus, co-occur with representatives of *Cichlidogyrus* on the gills of African cichlids and comprise seven described species (Pariselle & Euzet, 2009; Pariselle et al., 2013). Representatives of both genera differ in haptor morphology. Representatives of *Scutogyrus* have a winged dorsal transversal bar with two very long auricles. They also have a thin oval-shaped plate associated with the ventral transverse bar (Pariselle & Euzet, 2005; 2009; Pariselle *et al.*, 2013). In representatives of *Cichlidogyrus* the plate and wings are absent and the auricles are shorter (Pariselle & Euzet, 2009). A single exception to this is an undescribed *Cichlidogyrus* representative from *Limnochromis auritus* (Boulenger, 1901) collected in the Burundese part of Lake Tanganyika; it has even longer auricles than those found on *Scutogyrus* representatives (Kmentová *et al.,* 2016a). Phylogenetically, *Scutogyrus* forms a monophyletic clade within *Cichlidogyrus,* making the latter paraphyletic, but a formal re-classification has not been carried out (Pouyaud *et al.*, 2006; Wu *et al.*, 2007; Mendlová *et al.*, 2010; Mendlová & Šimková, 2014). The host range of species of *Scutogyrus* was limited to mouth-brooding cichlids, specifically Oreochromini, but one recently-discovered species was found on *Coptodon mariae* (Boulenger, 1899) (Coptodini) in Cameroon, possibly the result of a host switch (Pariselle *et al.*, 2013). Another genus known to infect the gills of African cichlids, *Gyrodactylus* Von Nordmann, 1832 (Gyrodactylidae), infects most fish orders on most continents and comprises over 450 valid species (Shinn *et al.*, 2011; Zahradníčková *et al.*, 2016). Of these species only 17 are found on African cichlids (Zahradníčková *et al.*, 2016). They differ substantially from representatives of Dactylogyridae, e.g. they have 16 small hooks, two large hooks with two ventral bars holding them together, and a unique lifecycle that is a combination of parthenogenesis and hyperviviparity (Bakke *et al.*, 2007).

Little is known of cichlid gill monogeneans in Bangweulu-Mweru and knowledge is limited to a small-scale study in the Bangweulu wetlands, Zambia from the Bangwuelu-Chambeshi subregion (Vanhove *et al.*, 2013). In the rest of the Congo Basin, the majority of recent reports are from Lake Tanganyika (Kmentová *et al.*, 2016b). Studies on Zambezian cichlid monogeneans are limited to Douëllou (1993) and Zahradníčková *et al.* (2016). The current study serves as the first report on cichlid gill monogeneans (Platyhelminthes) from the Mweru-Luapula subregion (see Fig. 1 for sample sites).

To date, over 140 African cichlid monogenean species have been described reported from over 100 species of cichlids (Vanhove *et al.*, 2016). Over 1100 valid African cichlid species have been described (Froese & Pauly, 2016) and the species richness of monogenean gill parasites is estimated higher than that of cichlids. In general it is estimated that 75,000–300,000 helminth species parasitize the approximately 45,000 vertebrate species on earth (Poulin & Morand, 2004). We assume that the known African cichlid monogenean species only represent a small fraction of the diversity. Given that the Luapula-Mweru subregion has not yet been explored for cichlid monogeneans, we hypothesize, that multiple new monogenean species remain to be discovered in the region. Furthermore, it is known that the ancestral character of host-specificity for representatives of *Cichlidogyrus*/*Scutogyrus* is intermediate specialism (Mendlová & Šimková, 2014). Therefore, we hypothesize that within the studied parasite fauna the host range for a single species of *Cichlidogyrus*/*Scutogyrus* is limited to a single cichlid genus.

Material and methods

Sample collection

Host fish were caught with gillnets during a field expedition in the DRC from 26th August to 11th September, 2014. They were killed with an overdose of MS222. Fish were collected from five sampling localities in the Upper Congo Basin (Fig. 1), which included riverine, small lacustrine and aquaculture environments. For *Cichlidogyrus zambezensis* Douëllou, 1993 fresh material from the type locality and type host *Serranochromis macrocephalus* (Boulenger, 1899) was collected because the original materials (holotype 138HF Tg7 and vouchers 161HF Tg30 and 162HF Tg31 from the Muséum national d'Histoire naturelle, MNHN, Paris, France) had lost their transparency and were inadequate for morphological analysis. Therefore, fresh specimens from the type locality, Lake Kariba, were used as a reference to diagnose the specimens from Bangwuelu-Mweru.

Sample preparation and conservation

Hosts were fixed in formaldehyde and deposited in the ichthyology collection of the Royal Museum for Central Africa (Tervuren, Belgium; RMCA; MRAC is the French translation and is used as abbreviation for the collections), stored in denatured ethanol (70%). They were identified to species level by E.J. Vreven (RMCA) and U. Schliewen (Bavarian State Collection of Zoology). Before fixation of the host specimens, gills (only from the right gill chamber) were dissected *in situ* and stored in 100% ethanol or investigated in the field. From the gills, parasites were collected exhaustively with an entomological needle under Optika ST-30-2 and WILD M5 stereomicroscopes in the field and lab, respectively. Parasites were mounted on slides with water and fixed under a coverslip with Hoyer's medium. The coverslips were sealed with glyceel (Bates, 1997) or D-Pex. Type material was deposited in the invertebrate collection of the RMCA (MRAC), the MNHN and the Iziko South African museum (Cape Town, South Africa; SAMC). Voucher specimens of *Cichlidogyrus* spp. were deposited under accession numbers 37980–38171, *Scutogyrus* spp. 38714–38722 and *Gyrodactylus* spp. 38723–38740 in the invertebrate collection of the RMCA. Symbiotype and host vouchers were deposited in the ichthyology collection of the RMCA under collection

2016-15-P. Note that the authors of the new taxon are different from the authors of this paper; see article 50.1, recommendation 50A and 51E of the International Code of Zoological Nomenclature (ICZN, 1999: Article 50.1, recommendation 50A and 51E).

Microscopy and illustration

The mounted specimens were diagnosed through a Leitz Dialux 22 microscope with differential interference contrast and measured with Auto-montage software. Images were taken with an optical camera on a Leica DM2500 microscope with Leica Application Suite software, unless noted otherwise. Specimens were measured following the methods by Douëllou (1993) and Fannes *et al.* (2017). The total length of the animal, 23 haptoral characters, the heel, penis, accessory piece of the male copulatory organ (MCO) and the vagina were measured. Illustrations were drawn freehand using a drawing tube and finalized with GIMP V2.8. Filaments associated with uncinuli and anchors are not represented.

Results

Twelve species species of cichlids, 104 individuals and 14 species of Monogenea, 552 individuals, were collected. Eight host species, *O. mweruensis*, *Orthochromis* sp. 'Mambilima' (see Schedel *et al.*, 2014), *Sargochromis mellandi* (Boulenger, 1905), *Serranochromis angusticeps* (Boulenger, 1907), *S. stappersii* Trewavas, 1964, *S. thumbergi* (Castelnau, 1861) and *Tylochromis mylodon* Regan, 1920, received their first gill parasite screening (Table 1). For 10 parasite species the host range was expanded, most notably, *Cichlidogyrus papernastrema* Price, Peebles and Bamford 1969 which is now found on *C. rendalli*, *O. mweruensis* in addition to *T. sparrmanii*, making it a generalist species following the terminology of Mendlová & Šimková (2014). Another generalist is *Gyrodactylus nyanzae* Paperna, 1973, which was found on *C. rendalli* and *O. mweruensis*. This parasite was previously collected from *C. rendalli* and *O. niloticus* from the Zambezi Basin (Zahradníčková *et al.*, 2016), Zimbabwe and from *O. variabilis* (Boulenger, 1906) from the Ugandese part of Lake Victoria (Paperna, 1973). Eleven of the collected parasite species are either intermediate generalists or generalists (Table 1). Regarding host species, *O. mweruensis* has the most diverse parasite fauna, with nine parasite species from three genera, while *Pseudocrenilabrus philander* (Weber, 1897) is infected by a single species, *C. philander* Douëllou, 1993 (Table 2). Our results further include one new parasite species, three new cases of intraspecific variation and three redescriptions.

Taxonomic account

Cichlidogyrus consobrini *Jorissen, Pariselle and Vanhove* sp.n. (Fig. 2; 3a,b).

Type host. S. mellandi.

Additional host. Orthochromis. sp. 'Mambilima'.

Infection site. Gills.

Type locality. Kipopo INERA aquaculture station (INERA = Institut National pour l'Etude et la Recherche Agronomiques) (11°34'S 27°21"E).

Other localities. Kiswishi River near Futuka Farm on *S. mellandi* and *Orthochromis.* sp. 'Mambilima' (11°29'S 27°39'E); Luapula River off Kashobwe on *S. mellandi* (09°40'S 28°37'E) (Table 2).

Material studied. 11 specimens.

Type material. Holotype: MRAC 37980 *paratypes*: six in the RMCA 37980–379082, 37993, 38001–38002, two in the MNHN xxxx and two in the SAMC under A088908.

Symbiotype. MRAC 2016-15-P tag 2661.

Etymology. The species epithet is derived from the Latin "consobrinus" (cousin) and is a noun in apposition of the second declension in the plural form of the nominative. It honours 'Neveneffecten', a cabaret quartet with members who are all relatives, and in particular Lieven Scheire for his efforts towards popularizing science.

Description. Monogenean on average 575 µm long. Dorsal and ventral anchors small (a<40 µm) and in several specimens, fenestrated. Dorsal anchors strongly asymmetrical as the guard length is 3–4 times the shaft length. Dorsal anchors with V-shaped indentation in the base. Blade curved and short as the distal tip does not surpass the guard laterally. Dorsal transverse bar slightly concave with developed auricles. Ventral anchors 1–5 µm larger than dorsal ones, with a more symmetrical base and a longer, more pronouncedly-curved blade that surpasses the guard laterally. Indentation U shaped. Ventral transverse bar V shaped and simple. Uncinuli short (<1.7 times the length of uncinuli pair II *sensu* Pariselle & Euzet, 2009). Penis is a simple, thick-walled, slightly-curved tube with a rounded basal bulb. A rectangular heel is attached to the side of the basal bulb. The accessory piece crosses the penis and is attached to it at the distal side of the basal bulb. It is a slightly curved tubular structure with at the distal end a broad sickle-shaped hook. At the base of this hook there is a knob-shaped structure with a groove in the middle. This structure protrudes and continues as a secondary tube within the accessory tube (Fig. 2, 3b).

Remarks. The general shape of the MCO is reminiscent of *C. haplochromii* Paperna and Thurston, 1969. Following Vignon *et al.* (2011) both species belong to group A in the genus, because they possess seven pairs of small uncinuli. Furthermore, in the redescription of *C. haplochromii*, Douëllou (1993) mentioned that the accessory piece ends in a massive hook beyond the end of the copulatory tube, as is the case in *C. consobrini* sp.n. However, there are differences between both species. *Cichlidogyrus haplochromii* is mostly known from species of *Haplochromis*, but has never been recorded on *Sargochromis* (Pariselle & Euzet, 2009). Morphologically, *C. haplochromii* possesses less asymmetrical and less deeply indented anchors than *C. consobrini* sp.n. and *C. haplochromii* lacks a heel, while *C. consobrini* sp.n. does possess one. Furthermore, the ventral transversal bar of *C. consobrini* sp.n. is twice as long and thick as in *C. haplochromii* (56 vs. 27µm), the auricles of the dorsal bar are over twice as long (22 vs. 8µm), and the dorsal transversal bar is also a lot longer (48 vs. 26µm) (Douëllou, 1993). Based on these differences we consider *C. consobrini* sp.n. a different species from *C. haplochromii*. Douëllou (1993) mentioned that *C. haplochromii* is probably a species complex based on variations in the ventral transverse bar, but did not specify the variations.

Cichlidogyrus halli Price & Kirk, 1967 species complex (Fig. 3c,d; 4).

*Type host. Tilapia shirana (*Boulenger, 1897) (now *Oreochromis shiranus* Boulenger, 1897).
Infection site. Gills.
Type locality. Fort Johnston, Upper Shire River, Malawi.
Other localities. Luapula River off Kashobwe (09°40'S 28°37'E) on *O. mweruensis* (this study); Kipopo INERA aquaculture station, (11°34'S 27°21''E) on *O. mweruensis* (Table 2; this study). Ouémé and Couffo, Benin on *Sarotherodon melanotheron* Rüppel, 1852 (Pariselle & Euzet, 2009); Lake Albert, Lake Edward, Lake George and Kajansi fish ponds, Uganda on *O. niloticus* (Linnaeus, 1758) (Pariselle & Euzet, 2009); Lake Victoria, Entebbe and Jinja, Uganda on *O. variabilis* (Boulenger, 1906) (Pariselle & Euzet, 2009); Lake Kariba, Zimbabwe on *O. mortimeri* (Trewavas, 1966) and *S. macrocephalus* (Pariselle & Euzet, 2009); Guinea and Sierra Leone on *Sarotherodon occidentalis* (Daget, 1962) (Pariselle & Euzet, 2009); Lake Albert, Uganda, Lake Volta and lower Volta River, Ghana on *S. galilaeus* (Linnaeus, 1758) (Pariselle & Euzet, 2009); Lake Albert and Lake George, Uganda (Pariselle & Euzet, 2009) and Lake Naivasha, Kenya on *O. leucostictus* (Trewavas, 1933) (Mogoi

Rindoria *et al.*, 2016); Nwanedi-Luphephe dams, Limpopo River, South-Africa on *O. mossambicus* (Peters, 1852) (Madanire-Moyo *et al.*, 2012); Lake Tana, Ethiopia on *O. niloticus tana* (Beletew *et al.*, 2016); Kalemie, Lake Tanganyika, DRC on *O. tanganicae* (Gunther, 1894) (Muterezi Bukinga *et al.*, 2012); Nyangara wetlands, DRC on *O. niloticus* (Muterezi Bukinga *et al.*, 2012) and introduced on onther continents e.g. Perak, Malaysia on *O. niloticus* and *Oreochromis* spp. 'red hybrid tilapia' (Lim *et al.*, 2016); Água Vermelha Reservoir, Southeastern Brazil on *O. niloticus* (Zago et al., 2014).

Material studied. Seven specimens from Kipopo INERA aquaculture station and five specimens from the Luapula River (Table 2).

Remarks. From *O. mweruensis* two morphotypes of *C. halli* were collected. The first corresponds well with the original description (Price & Kirk, 1967) and is present in the INERA aquaculture station. Morphotype 2 was only found in the Lower Luapula River and differs in haptoral morphology compared with the other specimens. The dorsal anchors are on average 12 µm smaller than the ventral ones, while in other representatives of *C. halli* both pairs of anchors are of comparable size. Furthermore, the ventral bar is much longer (79 vs. 66 µm). Lastly, the uncinuli of pair I are smaller (15 vs. 19 µm; Table 3). All other sclerotized elements of the specimens from the Luapula River match with the description of *C. halli*. We observe that *C. halli* is a morphologically variable species; subspecies have been defined in the past (Paperna, 1979), but have since been synonymized by Pariselle & Euzet (2009). However, more work on this species complex needs to be done with special attention paid to identifying possible cryptic species backed by genetic data. Preliminary studies have confirmed that *C. halli* consists of different genetic strains. However, species have not been formally delineated (Pouyaud *et al.*, 2006; Mendlová & Šimková, 2012). Therefore, we refrain from officially describing this morphotype as a separate species until this is supported by genetic data. Our decision is also based on the fact that no representative of *Cichlidogyrus* has been described solely based on morphological differences in haptoral structure, while no morphological differences are apparent on the MCOs of the two morphotypes.

C. papernastrema (Fig. 5;6a,b,c).

Type host. T. sparrmanii.

Infection site. Gills.

Type locality. Ingwauana, Natal, Republic of South Africa.

Other localities. Futuka Farm on *T. sparrmanii* (11°29'S 27°39'E) (this study); Luapula River off Kashobwe on *T. sparrmanii* (09°40'S 28°37'E) (this study); Kipopo INERA aquaculture station on *C. rendalli*, *O. mweruensis* and *T. sparrmanii* (11°34'S 27°21"E) (this study); Lake Kipopo on *C. rendalli* and *T. sparrmanii* (11°34'S 27°21"E) (this study); Lubumbashi Zoo on *T. sparrmanii* (11°39'S 27°28'E) (this study); Bumaki Farm on *T. sparrmanii* (11°34"S 27°30'E) (Table 2, this study).

Material studied. Seventy mounted specimens from fresh material and one holotype.

Type material. Holotype: USNM 1366817 (Parasite collection, Smithsonian Institute) *Paratypes:* Six in personal collection of original authors.

Redescription. Small to medium-sized representative of *Cichlidogyrus*, on average 351 µm long. Dorsal anchors arched with a strongly-asymmetrical base. Guard length approximately thrice the shaft length. Indentation of the base deep, sharp and asymmetrical with one long, curved side towards the guard and one short, straight side to the shaft. Ventral anchors about the same size as the dorsal ones, but with shallower V-shaped indentation and more symmetrical at the base: guard about twice as long as the shaft. Dorsal transverse bar with well-developed auricles. Ventral transverse bar simple, V-shaped, slightly thickened at mid-length of each arm. Uncinuli pair I elongated and thick. Uncinuli pairs III-VII short. MCO consists of a penis with a heel and an accessory piece that is longer than the penis itself. Latero-proximally at the basal bulb a heel is attached, which is shaped like a bulge, sometimes also broadened. The penis narrows slightly at the distal end of the basal bulb, after which it broadens again to the same width as the basal bulb. The penis then again narrows and curves towards a sharp end. The accessory piece is attached to the distal end of the basal bulb and starts as a narrow tube under the penis. Where the penis curves, the accessory piece broadens. More distally, the accessory piece turns towards the penis and ends in a hook. The vagina is not sclerotized.

Remarks. Since the original description of *C. papernastrema* in 1969, there have been no new records of this parasite. The newly-collected specimens differed in some parts from the holotype (Price *et al.*, 1969). The accessory piece does not connect to the basal bulb in the holotype, while all collected specimens do have this connection. Probably, the accessory piece was detached from the basal bulb due to the flattening of the holotype during mounting. In turn this has moved the accessory piece and flattened the penis, giving it a broader appearance. Secondly, in the original description the presence of a heel was not mentioned. Detailed examination of the holotype, did however, reveal the presence of such a heel. The placement of the heel on the basal bulb was consistent among specimens and also on the holotype. This heel is connected to a proximally closed basal bulb, which is depicted as open on the proximal side in the figures of the original description. Because the morphology, measurements (Table 4) and host species of our collected specimens coincide with the holotype, we consider them conspecific. Among recent specimens a slight variation in measurements between individuals from different host species was observed. Specimens from *O. mweruensis* were consistently smaller in total length, size of anchors and bars, while one specimen from *C. rendalli* was much larger than all other collected specimens in total length, size of anchors and bars. Possibly, this is intraspecific variation influenced by host species. The only further difference we noticed was that the shaft of the ventral anchors is slightly shorter in our collected specimens than in the holotype (Table 4).

Cichlidogyrus quaestio Douëllou, 1993 (Fig. 6 d,e;7).

Type host. Tilapia rendalli Boulenger, 1897 (now *C. rendalli* (Boulenger, 1897)).

Additional hosts. Sargochromis codringtonii (Boulenger, 1908), *S. macrocephalus, T. sparrmanii*.

Infection site. Gills.

Type locality. Lake Kariba, Zimbabwe.

Other localities. Lake Kipopo on *C. rendalli* (11°34'S 27°21’E); Kipopo, INERA aquaculture station on *C. rendalli* (11°34'S 27°21’E) (this study); Futuka Farm on *C. rendalli* and *T. sparrmanii* (11°29'S 27°39'E) (this study); Luapula River off Kashobwe on *C. rendalli* (09°40'S 28°37'E) (Table 2; this study) and Fiwili settlement, Bangweulu Wetlands, Zambia from *C. rendalli* and *T. sparrmanii* (Vanhove *et al.*, 2013).

Material studied. 108 specimens.

Type material. Holotype: MNHN 137 HF.

Redescription. Small dactylogyridean monogenean, on average 300 µm long. Dorsal and ventral anchors of similar size. Ventral anchors on average 4 µm shorter than dorsal ones. Dorsal anchors asymmetrical with a guard length four to five times the shaft length and a V-shaped indentation at the base. Blade curved, but subtly interrupted by an angle in the middle. Dorsal transverse bar simple, slightly concave with well-developed auricles. Ventral anchors more symmetrical, with a shallower V-shaped indentation and broader base than the dorsal anchors. Blade crescent shaped and with longer point than the blade of the dorsal anchors. Ventral transverse bar V-shaped. Arms thickest at mid-length and thinnest where both arms meet. Distal end of each arm rounded and slightly thickened. At 1/3 from the distal end a flattened rim is present. Uncinuli pair I long, III to VII short (*sensu* Pariselle & Euzet 2003; 2009). Penis thin, tubular, slightly curved. The basal bulb is oval shaped but has an indentation opposite to where the penis continues. At the distal part of the basal bulb an elongated rectangular heel is present. The accessory piece connects to the basal bulb, is thin and longer than the penis. At 4/5 of its length the accessory piece abruptly broadens and forms a hook as a tip. Vagina not sclerotized.

Remarks. Because uncinuli pair I are long and pairs III to VII short (*sensu* Pariselle & Euzet 2003; 2009) *C. quaestio* belongs to group B within the genus (*sensu* Vignon *et al.*, 2011). Within this group *C. berradae* Pariselle & Euzet 2003, *C. digitatus* Dossou 1982, *C. quaestio* and *C. yanni* Pariselle & Euzet 1996 have multiple features in common. Firstly, all species occur predominantly on species of *Coptodon* Gervais 1853, but not exclusively, since *C. berradae* can occur on *Pelmatolapia cabrae* (Boulenger, 1899) and *C. digitatus* on "*Tilapia" brevimanus* Boulenger, 1911 as well (Pariselle & Euzet, 2009; host taxonomy taken from Dunz & Schliewen, 2012, representatives of *Tilapia* belonging to Gobiocichlini are under revision and mentioned within quotation marks). Secondly, in all these species the guard and shaft of the dorsal anchors are asymmetrical. Furthermore, the curvature of the dorsal blade is interrupted by an angle, while the ventral anchors are more symmetrical and have a continuous crescent-shaped blade. The dorsal transverse bar is concave and quite thick. The MCOs all have an elongated heel, a slender and simple tubular penis and an accessory piece that is a bit longer than the penis and ends in a long hook. The ventral and dorsal bar, the auricles and uncinuli I of *C. quaestio* are larger than those of *C. berradae*, *C. digitatus* and *C. yanni*, while the penis is shorter. Furthermore, among these four species, *C. quaestio* is the only species that has a straight and rectangular heel. Also, the accessory piece of *C. quaestio* is more slender and the accessory tip is unique because the base of the hook is broadened and gradually narrows in a longer curve than the others. Lastly, the basal bulb of *C. quaestio* is unique in its morphology in that it has an oval-shaped indentation.

The differences with the original description (Douëllou, 1993) are predominantly found on the MCO. Firstly, on the original drawing the attachment of the accessory piece with the basal bulb was not represented and the basal bulb lacked the indentation. Furthermore, the heel is shorter and more rounded in the original description. Lastly, the primary shafts of uncinuli pair I are not as broad as represented on the original drawing.

Cichlidogyrus papernastrema and *C. quaestio* co-occur on *C. rendalli* and *T. sparrmanii* and can be hard to distinguish since both have long uncinuli pair I, short uncinuli pairs III-VII and an MCO in which the accessory piece is longer than the penis. However, the primary shaft (*sensu* Pariselle & Euzet, 2003) of uncinuli pair I is thicker and larger in *C. quaestio* than in *C. papernastrema*. Furthermore, the shape of the basal bulb of *C. quaestio* is sufficiently characteristic to differentiate it from *C. papernastrema*. The basal buld of *C. papernastrema* lacks the indentation that is present in the basal bulb of *C. quaestio*. Also, the position of the heel is different as in *C. quaestio* it is at the distal end of the basal bulb and in *C. papernastrema* it is located more laterally. Lastly, the blades of the ventral anchors in *C. quaestio* are more pronounced and have a longer crescent-shaped point than do those of *C. papernastrema*.

Cichlidogyrus zambezensis Douëllou, 1993 (Fig. 8; 9a,b).

Type host. S. macrocephalus.

Additional hosts. O. mortimeri; *Serranochromis robustus jallae* (Günther, 1864); *S. mellandi; S. stappersii*; *S. thumbergi*; *S. angusticeps.*

Infection site. Gills.

Type locality. Lake Kariba, Zimbabwe.

Other localities. Lake Kipopo on *S. macrocephalus* (11°34'S 27°21’E) (this study); Kipopo, INERA aquaculture station on *S. mellandi* and *S. thumbergi* (11°34'S 27°21’E) (this study); Futuka Farm on *S. mellandi* (11°29'S 27°39'E) (this study); Kiswishi River near Futuka on *S. mellandi* (11°29'S 27°39'E) (this study); Luapula River off Kashobwe on *S. mellandi*, *S. angusticeps*, *S. macrocephalus* and *S. stappersii* (09°40'S 28°37'E) (Table 2; this study); Fiwili settlement, Bangweulu Wetlands, Zambia from *S. robustus jallae* (Vanhove *et al.*, 2013).

Material studied. 92 fresh specimens from Bangweulu-Mweru, 1 holotype and 42 vouchers from Lake Kariba (MNHN 138HF,161HF, 162HF), 5 vouchers of a 2010 expedition in

Bangweulu Wetlands, Zambia (MT.37714) and 32 freshly collected specimens from Lake Kariba.

Type material. Holotype. MNHN 138 HF.

Redescription. Monogenean between 300–600 μm long. Ventral anchors more slender root than dorsal ones with a slightly asymmetrical indentation. Blade continuous. Dorsal anchors strongly asymmetrical with a guard double to quadruple the length of the shaft. Blade bent more than the ventral anchors' blade. Dorsal transverse bent with long auricles. Ventral transverse bar simple, V-shaped with an extension at 1/3 from where both arms meet. Uncinuli pairs I–VII short (*sensu* Pariselle & Euzet 2003; 2009). The MCO consists of a thick-walled penis with a well-developed swollen portion, a small basal bulb, and a narrow S-shaped distal end. A heel engulfs the basal bulb and is irregular in shape, broad and short. The accessory piece is often larger than the penis and is a curved tubular structure with a fingerlike extension at the distal end. Proximally the accessory piece crosses the penis after which it connects to the basal bulb. The sclerotized vagina is small, thick walled, triangular, funnel shaped.

Remarks. Douëllou described this species in 1993 from Lake Kariba from *S. macrocephalus* and *O. mortimeri*. Additional specimens from *S. robustus jallae* were collected from Fiwili settlement, Bangweulu Wetlands, Zambia in 2010 (Vanhove *et al.*, 2013). Both articles report morphological variation, which was considered intraspecific by the authors, and a possible broad geographical and host range. However, freshly collected specimens from Bangweulu-Mweru and from the type locality, Lake Kariba, differed from the original drawing and measurements.

The major difference from the original drawing is that in all but a single specimen (from Lake Kariba) the swollen portion of the penis is much larger than originally drawn. Furthermore, Douëllou (1993) states that *C. papernastrema* and *C. zambezensis* are the only representatives of *Cichlidogyrus* with an accessory piece that is not connected to the basal bulb. However, (see remarks on *C. papernastrema* above) we have observed this connection in both species. In some specimens, the accessory piece appears to be segregated from the basal bulb but in others it is clearly continuous. Furthermore, in specimens where the accessory piece is split off, a very thin connection between the piece and the bulb is still visible, and also a part of the basal bulb points towards the distal end of the accessory piece. The accessory piece is connected to the basal bulb and does not articulate with the penis as stated in Douëllou (1993). Also, uncinuli I appear with a slightly longer shaft than originally drawn; the ventral anchors are a bit more slender and the dorsal anchors do not always have such a pronouncedly asymmetrical guard as on the original drawing.

A few differences in measurements between the freshly collected specimens from Bangweulu-Mweru and Lake Kariba were observed. Firstly, both the ventral and dorsal transverse bars as well as the auricles are larger in specimens from Bangweulu-Mweru. The accessory piece is smaller in specimens from Lake Kariba (Table 6). These differences between the two localities can be explained by stochastic effects, geographical variation or host adaptation. However, the measurements of these specimens from *S. macrocephalus* from both regions correspond with each other, which may point to differences in the size of sclerotized elements due to adaptation to the host.

Lastly, *C. zambezensis* is a species similar in morphology to all congeners typically infecting representatives of Haplochromini: it has a simple MCO, short uncinuli, an asymmetry between dorsal and ventral anchors and well-developed but normal-sized auricles (Pouyaud *et al.*, 2006; Gillardin *et al.*, 2012; Muterezi Bukinga *et al.*, 2012). Other haplochromine-infecting species are e.g. *C. gillardinae* Muterezi Bukinga, Vanhove, Van Steenberge and Pariselle, *C. irenae* Gillardin, Vanhove, Pariselle, Huyse and Volckaert, 2012 and *C. karibae* Douëllou, 1993; the latter two also have a swollen penis. However, *C. zambezensis* is the only species in this group with a sclerotized vagina and thus is distinct from the others.

Cichlidogyrus sp. (Fig. 6f).

Host. T. mylodon.

Infection site. Gills.

Locality. Luapula River off Kashobwe (09°40'S 28°37'E).

Material studied. 3 mounted specimens.

Remarks. From *T. mylodon,* three parasites were collected whith a haptoral morphology that corresponds with species of *Cichlidogyrus* infecting representatives of *Tylochromis* (see Pariselle *et al.*, 2014b). The ventral transversal bar is simple and V-shaped while the dorsal transversal bar has reduced auricles, similar to *C. berrebii* Pariselle & Euzet 1994. Furthermore uncinuli pairs III-VII are short. Because species of *Cichlidogyrus* from *T. mylodon* have not been studied yet it is possible that the specimens found here belong to an undescribed species. However, this cannot be assessed with the material available. Because in none of the three specimens the MCO was visible, they could not be identified to species level.

Discussion

Diversity

During our study, 14 monogenean species were recovered from a total of 12 host species. The cichlid species with the highest monogenean species richness was *O. mweruensis*; nine species of monogeneans were found. Representatives of *Oreochromis* tend to have a high number of monogenean species on their gills, e.g. *O. niloticus* and *O. mortimeri* with seven and eight species respectively (Douëllou, 1993; Pariselle & Euzet, 2009). Several representatives of *Cichlidogyrus* and all but one species of *Scutogyrus* infect multiple species of *Oreochromis* and *Sarotherodon* exclusively (Pariselle & Euzet, 2009), which are two closely related mouth-brooding cichlid genera, belonging to Oreochromini (Schwarzer *et al.*, 2009; Dunz & Schlieuwen, 2012). Hence, one might refer to a monogenean gill fauna typical of Oreochromini. In our study, the parasite fauna of *O. mweruensis* comprised of typical parasite species of Oreochromini such as *C. sclerosus* Paperna & Thurston, 1969, *C. cirratus* Paperna, 1964, *C. tilapiae* Paperna, 1960, *C. halli* and *S. gravivaginus* (Paperna & Thurston, 1969). Other typical species are all representatives of *Scutogyrus*, except for *S. vanhovei* Pariselle, Bitja Nyom & Bilong Bilong, 2013. In addition, the generalist *C. papernastrema* was also found on *O. mweruensis*. In contrast to the diverse gill parasite fauna of *O. mweruensis*, the gills of the four representatives of *Serranochromis* were infected by a single monogenean species, *C. zambezensis*. One of these representatives, *S. macrocephalus* is known to host five parasite species in Lake Kariba, all of which are also found in the Mweru-Luapula area. These are *C. dossoui*, *C. quaestio*, *C. zambezensis*, *C. sclerosus* and *C. halli*, the latter two of which occur only occasionally on representatives of *Serranochromis* (Douëllou, 1993). However, in Bangwuelu-Mweru only *C. zambezensis* was found to infect this fish (Vanhove *et al.*, 2013; *nobis*). This is likely the result of sampling bias. For *C. rendalli* and *T. sparrmanii* the same gill parasite fauna was observed in both Mweru-Luapula and Bangwuelu-Chambeshi (Vanhove *et al.*, 2013). The only difference was that *C. tiberianus* was not found on *T. sparrmanii* in the Mweru-Luapula area. However, we suspect that *C. tiberianus* does occur here on *T. sparrmanii*, but was not found due to sampling bias. Furthermore, no species of *Gyrodactylus* were found on representatives of *Serranochromis*, which corresponds with the results from Zahradníčková *et al.* (2016). In our study, *G. nyanzae* was the only representative of *Gyrodactylus* on *C. rendalli*, while in the study of

Zahradníčková *et al*. (2016) the fauna of *C. rendalli* was dominated by *G. chitandiri* Zahradníčková, Barson, Luus-Powell & Přikrylová, 2016. The Bangweulu-Mweru region is situated in-between the other known localities where *G. nyanzae* occurs. It possibly has a continuous distribution from central to southern Africa living on *C. rendalli* and representatives of *Oreochromis* within this range.

Of the 14 parasite species, *C. consobrini* sp.n. was described; one new morphotype of *C. halli* was characterised and three cases of intraspecific morphological variation were discussed. Furthermore, one *Cichlidogyrus* species living on the gills of *T. mylodon* was not identified to species level due to the insufficient quality of the collected specimens; it possibly represented an undescribed species as this host species has not been sampled for parasites before. All other recorded species were already known. This study reported a relatively low number of new species for a sampling of an almost unexplored ecoregion. Most of the parasites found have already been described from Lake Kariba, Zambezi Basin (Douëllou, 1993). This outcome reflects the hydrological history of the ecoregion with frequent connections between the Congo and Zambezi rivers (Lévêque, 1997; Moore & Larkin, 2001; Key *et al.*, 2004; Katongo *et al.*, 2007; Koblmüller *et al.*, 2008). However, more sampling in the Lower Luapula River and Lake Mweru would be interesting, since more endemic cichlid species are present there (Van Steenberge *et al.*, 2014) and have not previously been screened for parasites. Additionally, investigation in the Bangwuelu-Mweru ecoregion may be useful to determine to what extent the parasite fauna is a reflection of the distribution of its hosts.

Host-specificity and biogeography

The parasites found in Bangweulu-Mweru range from strict specialists to generalists (following Mendlová & Šimková, 2014) (Table 1). Only one strict specialist, *C. philander*, was found in this study; occurring on *P. philander* (Pariselle & Euzet, 2009). A species for which the reported host range was remarkedly increased is *C. papernastrema*, which was previously known as a strict specialist, but is now found to be a generalist. This illustrates how understudied some of these parasite species are. However, in general the host range of these parasite species in Bangweulu-Mweru is found to be narrower compared with Lake Kariba. This trend is most distinct for parasites from *O. mortimeri* and *S. macrocephalus*. In Lake Kariba, these hosts are both infected by *C. dossoui*, *C. halli*, *C. sclerosus* and *C. zambezensis* (Douëllou, 1993). All four of these parasite species also occur in Bangweulu-Mweru but none were found on representatives of both *Oreochromis* and *Serranochromis*.

Cichlidogyrus dossoui and *C. tiberianus* typically infect representatives of *Coptodon*, but are also found on other host genera. *Cichlidogyrus halli* and *C. zambezensis* are typical of, respectively, representatives of *Oreochromis* and *Serranochromis*. Although Lake Kariba is highly similar to Bangwuelu-Mweru in parasite and host fauna, the two systems are hydrographically and ecologically very different. Lake Kariba is a man-made lake created as a result of the construction of a hydroelectric dam. This dam transformed the previously riverine environment into a lake system, thereby impacting the ethology/ecology of host species. Such transition creates an environment where new host-parasite encounters can occur (Combes, 1990). In other words, the transition from a river to a lake system may favour a broader host range for parasites and a higher tendency for host switching through more or new encounters between host species. In Lake Ossa, Cameroon, a broader host range for several parasites was also observed following host switching. *Scutogyrus vanhovei* Pariselle, Bitja Nyom & Bilong Bilong, 2013 occurs on *Coptodon mariae* (Boulenger, 1899) instead of on a mouth-brooding host (Pariselle & Euzet, 2009). Also, *Quadriacanthus euzeti* Nack, Pariselle & Bilong Bilong, 2015 occurs in Lake Ossa on *Papyrocranus afer* (Günther, 1868) (Osteoglossiformes) instead of on a host belonging to the Siluriformes (Pariselle *et al.*, 2013; Nack *et al.*, 2015). Other noteworthy examples of host switching within *Cichlidogyrus* are *C. amieti*, *C. nandidae* and *C. inconsultans* from small forest streams in South Cameroon, as these species infect non-cichlids (Pariselle & Euzet, 2009; Messu Mandeng *et al.*, 2015). The extended host range in South Cameroon is probably the result of a host switch away from cichlids (Messu Mandeng *et al.*, 2015). The pattern observed in the Mweru-Luapula subregion is that the fauna is determined by the host taxon up to the level of host genus in most cases, because the parasite species found behave as intermediate specialists to intermediate generalists (coinciding with the ancestral state for host specificity for *Cichlidogyrus*/*Scutogyrus*, see Mendlová & Šimková, 2014). However, our results may demonstrate that the host range of a parasite species may differ between regions. For example *C. zambezensis* is a generalist in Lake Kariba because it occurs on the distantly related hosts *O. mortimeri* and *S. macrocephalus* (Douëllou, 1993), but in Bangweulu-Mweru it is limited to *Serranochromis* spp., thus being an intermediate specialist there. *Cichlidogyrus zambezensis* was not found on the local *O. mweruensis* in Mweru-Luapula of which a sufficient number of hosts were investigated. We propose that there is a geographic pattern to host-specificity (Krasnov *et al.*, 2004 and Korallo-Vinarskaya *et al.*, 2009) and host-parasite dynamics (Valois & Poulin, 2015) in species of *Cichlidogyrus*/*Scutogyrus*, which implies that distribution and host-specificity are not only taxon bound but also determined by ecology and geography. However, a formal statistical analysis is in order to further investigate this. A thorough parasitological screening of Luapula-Mweru and other regions with a highly similar cichlid species composition (Upper Zambezi, Upper Congo, Lualaba River and the Bangwuelu-Chambeshi subregion) (Van Steenberge *et al.*, 2014) has not yet been done; and would be of great interest in further unravelling a geographic pattern to host-specificity and host-parasite dynamics. Also, this would help to answer the question posed in Vanhove *et al*. (2013) as to whether the biogeographical pattern of species of *Cichlidogyrus*/*Scutogyrus* mirrors the host biogeography, or whether parasite assemblages are basin specific.

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Table 1 Overview of the occurrence of monogenean gill parasites of the studied cichlid species in Bangweulu-Mweru. An ‘x’ represents the occurrence of the species on the corresponding host, while a ‘H’ represents a new host record for this parasite. A ‘*’ represents the first time this parasite was found in the ecoregion. The host-specificity is divided in strict specialists (SS), intermediate specialists (IS), intermediate generalists (IG) and generalists (G) (Mendlová & Šimková, 2014). Host range data based on Pariselle & Euzet (2009); Vanhove *et al.* (2013) and supplemented with our own findings.

		Host-specificity	***C. rendalli***	***O. mortimeri***	***O. mweruensis***	***Orthochromis*. sp. ‘Mambilima’**	***P. philander***	***S. mellandi***	***Serranochromis*. spp.**	***T. sparrmanii***	***T. mylodo***
N (104)			16	1	31	5	11	7	9	15	10
C. cirratus	*	IG			H						
C. consobrini sp.n.	*	IG				H		H			
C. dossoui		G	x		H					x	
C. halli	*	G			H						
C. papernastrema	*	G	H		H					x	
C. philander	*	SS					x				
C. quaestio		G	x							x	
C. sclerosus	*	IS			H						
Cichlidogyrus. sp.	*	N.A.									H
C. tiberianus		G	x		H						

C. tilapiae	*	G		x	H				
C. zambezensis		G						H	H
G. nyanzae	*	G	H		H				
S. gravivaginus	*	IG			H				

Table 2 Number of host species studied and infected per locality in addition to the infection intensity from a certain locality.

Host species	Parasite species	Locality	#host specimens studied/#host specimens infected	Infection intensity
C. rendalli	*C. dossoui*	Futuka Farm	5/3	1–2
		Kipopo	8/4	1–29
		Luapula River off Kashobwe	3/3	1–9
	C. papernastrema	Kipopo	8/1	3
	C. quaestio	Futuka Farm	5/2	1–2
		Kipopo	8/4	1–20
		Luapula River off Kashobwe	3/2	1–8
	C. tiberianus	Futuka Farm	6/2	1–3
		Kipopo	8/3	1–7
		Luapula River off Kashobwe	3/2	2–5
	G. nyanzae	Kipopo	8/2	2–4
O. mortimeri	*C. tilapiae*	Futuka Farm	1/1	1
O. mweruensis	*C. cirratus*	Futuka Farm	6/3	1–7

		Kipopo	16/3	2–21
	C. dossoui	Futuka Farm	6/1	1
		Kipopo	16/4	1–2
		Luapula River off Kashobwe	7/4	1
	C. halli	Bumaki Farm	2/1	1
		Kipopo	16/2	1–4
		Luapula River off Kashobwe	7/2	3
	C. papernastrema	Kipopo	16/1	2
	C. sclerosus	Bumaki Farm	2/1	3
		Luapula River off Kashobwe	7/1	1
	C. tiberianus	Kipopo	16/1	2
	C. tilapiae	Kipopo	16/1	1
		Futuka Farm	6/1	1
	G. nyanzae	Kipopo	16/2	2–37
		Luapula River off Kashobwe	7/1	2
	S. gravivaginus	Futuka Farm	6/2	2
		Kipopo	16/2	1
		Luapula River off Kashobwe	7/4	1–3
Orthochromis sp. 'Mambilima'	*C. consobrini* sp.n.	Futuka Farm	2/1	1
		Kipopo	3/1	1
P. philander	*C. philander*	Kipopo	1/1	6
		Lubumbashi Zoo	10/7	1–10
S. mellandi	*C. consobrini* sp.n.	Kipopo	6/2	1–8
		Luapula River off Kashobwe	1/1	2
	C. zambezensis	Kipopo	6/3	2–64

		Luapula River off Kashobwe	1/1	9
Serranochromis spp.	*C. zambezensis*	Futuka Farm	4/0	0
		Kipopo	2/2	1–21
		Luapula River off Kashobwe	2/1	1
T. sparrmanii	*C. dossoui*	Bumaki Farm	2/1	1
		Futuka Farm	6/3	2–5
		Kipopo	5/2	1–2
		Luapula River off Kashobwe	1/1	7
	C. papernastrema	Bumaki Farm	2/1	2
		Futuka Farm	6/6	1–10
		Kipopo	5/2	2–9
		Luapula River off Kashobwe	1/1	22
		Lubumbashi Zoo	1/1	3
	C. quaestio	Futuka Farm	5/1	1
T. mylodon	*Cichlidogyrus* sp.	Luapula River off Kashobwe	9/1	3

Table 3 Measurements of *C. consobrini* sp.n. and two morphotypes of *C. halli*. Note the size difference in dorsal anchor and ventral bar between the two morphotypes. Measurements are represented in µm as the average ± standard deviation, count and the range (in brackets).

Species	*C. consobrini* sp.n.	*C. halli* morphotype 1	*C. halli* morphotype 2
Host	*S. mellandi*, *Orthochromis.* sp. 'Mambilima'	*O. mweruensis*	*O. mweruensis*
Locality	Bangweulu-Mweru	Bumaki, Kipopo	Luapula River off Kashobwe
Reference	Present study	Present study	Present study

Number of specimens	n = 11	n=7	n=5
Ventral anchor			
Total length, a	31 ± 1.5, 7 (29–33)	46 ± 2.5, 5 (43–49)	42 ± 0.1, 2 (42–42)
Blade length, b	27 ± 1, 7 (25–28)	37 ± 1, 5 (37–39)	36 ± 2.1, 2 (34–37)
Shaft length, c	4 ± 0.9, 7 (3–5)	6 ± 1.4, 5 (4–8)	5 ± 1.7, 2 (4–6)
Guard length, d	11 ± 1.6, 7 (8–12)	22 ± 1.9, 5 (21–25)	20 ± 1.4, 2 (19–21)
Point length, e	11 ± 1.3, 7 (9–13)	15 ± 1.5, 5 (13–17)	15 ± 0.4, 2 (15–16)
Dorsal anchor			
Total length, a	34 ± 2.5, 5 (31–38)	42 ± 2.9, 3 (39–45)	29 ± 0.7, 2 (29–30)
Blade length, b	24 ± 2.8, 5 (20–28)	29 ± 1.8, 3 (27–31)	23 ± 5.4, 2 (19–27)
Shaft length, c	4 ± 1.4, 5 (3–7)	8 ± 2.6, 3 (5–10)	7 ± 4.7, 2 (3–10)
Guard length, d	15 ± 5, 5 (6–19)	23 ± 3.7, 3 (20–27)	16 ± 3.5, 2 (14–19)
Point length, e	9 ± 1, 5 (8–11)	14 ± 2.3, 3 (11–15)	10 ± 0.5, 2 (9–10)
Ventral bar			
Branch length, X	56 ± 3.5, 7 (52–63)	66 ± 12.6, 6 (44–78)	79 ± 1.8, 2 (78–80)
Maximum width, W	8 ± 1, 7 (7–9)	12 ± 1.9, 6 (8–14)	12 ± 0.9, 2 (12–13)
Dorsal bar			
Total, length, x	48 ± 4.4, 6 (41–52)	78 ± 16.9, 6 (45–93)	73 ± 0.9, 2 (72–73)
Maximum widith, w	8 ± 1, 5 (6–9)	13 ± 3.2, 6 (10–18)	17 ± 2.3, 2 (16–19)
Distance between auricles, y	13 ± 2.1, 5 (11–16)	26 ± 4, 6 (18–29)	30 ± 0.3, 2 (30–30)
Auricle length, h	22 ± 2.7, 5 (18–25)	23 ± 6.2, 5 (13–29)	20 ± 1.4, 2 (19–21)
Uncinuli			
Length, I	13 ± 0, 1	19 ± 1.1, 3 (18–20)	15 ± 0.7, 2 (15–16)
Length, II	12 ± 0.4, 2 (12–12)	15 ± 0, 1	14 ± 0.8, 2 (13–14)
Length, III	15 ± 0, 1	33 ± 4.7, 5 (27–40)	32 ± 0.8, 2 (31–32)
Length, IV	25 ± 0, 1	37 ± 2.5, 5 (34–40)	33 ± 4.5, 2 (30–37)
Length, V	24 ± 0, 1	36 ± 4.6, 5 (30–41)	38 ± 2.6, 2 (36–40)
Length, VI	22 ± 0, 1	33 ± 6.3, 5 (24–39)	36 ± 5.3, 2 (32–40)
Length, VII	21 ± 3.8, 2	42 ± 16, 6 (32–75)	35 ± 0.4, 2 (34–35)

MCO			
Penis length, Pe	38 ± 3.5, 7 (32–42)	65 ± 4.5, 6 (57–69)	69 ± 4.9, 5 (64–71)
Length of accessory piece, AP	47 ± 2.6, 3 (44-50)	58 ± 8.1, 6 (46-65)	63 ± 6.3, 5 (58-74)
Heel length, He		6 ± 1.8, 6 (4-8)	6 ± 1.1, 3 (6-8)
Total body length	681 ± 115, 6 (534-886)	745 ± 162, 5 (587-965)	681 ± 306, 2 (465-898)

Table 4 Measurements of *C. papernastrema* (in µm). Measurements are represented as the average ± standard deviation, count and the range (in brackets).

Host	*T. sparrmanii*	All	*C. rendalli*	*O. mweruensis*	*T. sparrmanii*
Locality	Ingwauana, Natal, South Africa (holotype)	Mweru-Luapula	Mweru-Luapula	Mweru-Luapula	Mweru-Luapula
Number of specimens	N=1	N=20	N=5	N=5	N=10
Reference	Price, Peebles & Bamford 1969	Present study	Present study	Present study	Present study
Ventral anchor					
Total length, a	33	30 ± 2.8, 9 (25–34)	31 ± 2.1, 4 (29–34)	26 ± 1.4, 2 (25–27)	32 ± 0.5, 3 (31–32)
Blade length, b	29	25 ± 2.6, 9 (21–30)	26 ± 2, 4 (24–28)	23 ± 2.2, 2 (21–24)	27 ± 2.9, 3 (24–30)
Shaft length, c	8	5 ± 1.1, 8 (3–6)	6 ± 0.9, 3 (5–6)	3 ± 0, 2 (3–3)	5 ± 0.7, 3 (4–6)
Guard length, d	13	11 ± 2.5, 9 (7–14)	13 ± 1.1, 4 (12–14)	7 ± 0.2, 2 (7–7)	12 ± 0.6, 3 (12–13)
Point length, e	10	11 ± 1.8, 9 (8–13)	11 ± 2.6, 4 (8–13)	10 ± 0.9, 2 (9–10)	12 ± 0.8, 3 (11–12)
Dorsal anchor					
Total length, a	38	35 ± 5.9, 8 (28–44)	37 ± 4.2, 4 (31–40)	28 ± 0.3, 2 (28–28)	38 ± 7.2, 2 (33–44)
Blade length, b	25	23 ± 5.1, 8 (19–29)	25 ± 1.6, 4 (24–28)	16 ± 3.9, 2 (13–19)	24 ± 6.6, 2 (20–29)
Shaft length, c	7	6 ± 1.2, 8 (3–7)	6 ± 0.3, 4 (6–7)	5 ± 2.3, 2 (3–6)	6 ± 1.3, 2 (5–7)
Guard length, d	17	17 ± 2.6, 8 (12–	17 ± 1.5, 4 (15–	14 ± 3, 2 (12–	18 ± 3, 2 (16–

		20)	19)	16)	20)
Point length, e	8	9 ± 1.9, 6 (7–12)	10 ± 3.1, 2 (8–12)	8 ± 2, 2 (7–10)	9 ± 0.8, 2 (9–10)
Ventral bar					
Branch length, X	45	39 ± 7.1, 10 (28–51)	39 ± 8, 3 (30–45)	30 ± 2.9, 2 (28–32)	42 ± 5.2, 5 (37–51)
Maximum width, W	6	6 ± 1.6, 10 (4–8)	6 ± 1.9, 3 (4–8)	4 ± 0.5, 2 (4–4)	6 ± 1.3, 5 (4–7)
Dorsal bar					
Total, length, x	32	39 ± 7.9, 12 (26–52)	43 ± 3.8, 6 (38–48)	26 ± 0.3, 2 (26–26)	41 ± 7.7, 4 (35–52)
Maximum width, w	7	8 ± 1.2, 12 (7–10)	7 ± 0.7, 6 (7–8)	7 ± 2.8, 2 (5–9)	8 ± 1, 4 (7–10)
Distance between auricles, y	11	14 ± 3.2, 13 (9–18)	15 ± 2.3, 6 (12–18)	9 ± 1.1, 3 (9–10)	15 ± 2.3, 4 (13–18)
Auricle length, h	18	15 ± 3.3, 11 (10–20)	17 ± 2.3, 5 (16–20)	11 ± 2.5, 2 (10–13)	16 ± 3.5, 4 (12–19)
Uncinuli					
Length, I	28	28 ± 4.5, 12 (22–36)	28 ± 5.5, 5 (22–33)	24 ± 0.7, 2 (24–25)	30 ± 3.6, 5 (27–36)
Length, II	12	11 ± 1.5, 3 (10–13)	10 ± , 1	13 ± 0, 1	11 ± 0, 1
Length, III	21	18 ± 1.7, 7 (15–20)	17 ± 0.2, 3 (17–17)	19 ± 0.9, 2 (19–20)	17 ± 2.8, 2 (15–19)
Length, IV	21	22 ± 2.3, 7 (19–25)	23 ± 1.9, 4 (21–25)	19 ± 0, 1	23 ± 3, 2 (21–25)
Length, V	23	24 ± 4.5, 8 (17–30)	23 ± 4.6, 4 (17–28)	20 ± 2,3, 2 (19–22)	29 ± 1.9, 2 (27–30)
Length, VI	20	24 ± 5.6, 6 (19–33)	24 ± 7.2, 2 (19–29)	20 ± 0.8, 2 (20–32)	28 ± 6.2, 2 (24–33)
Length, VII	16	21 ± 3.9, 8 (14–27)	19 ± 3.5, 4 (14–22)	18 ± 0.1, 2 (18–19)	25 ± 2.3, 2 (24–27)
MCO					
Penis length, Pe	32	31 ± 4.6, 18 (26–44)	32 ± 4.7, 10 (26–44)	30 ± 3.8, 5 (28–36)	26 ± 3.5, 3 (23–30)
Length of accessory piece,	37	39 ± 7.1, 17	42 ± 6, 10 (33–	37 ± 3.2, 4 (33–	30 ± 8.5, 3 (24–

AP		(24–52)	47)	41)	40)
Heel length, He	1	2 ± 0.6, 15 (1–4)	2 ± 0.6, 9 (1–3)	2 ± 0.2, 4 (2–2)	3 ± 0.4, 2 (3–4)
Total body length	273	351 ± 114, 16 (190–631)	381 ± 94.9, 7 (190–473)	254 ± 15.2, 4 (240–272)	385 ± 148,8, 5 (270–631)

Table 5 Measurements of *C. quaestio*, *C. berradae, C. digitatus and C. yanni*. Measurements are represented in µm as the average ± standard deviation, count and the range (in brackets).

Species	*C. quaestio*	*C. berradae*	*C. digitatus*	*C. yanni*
Host	*T. sparrmanii* & *C. rendalli*	*T. cabrae* & *C. guineensis*	*C. zillii* ,*C. guineensis*, *C. dageti, C. louka* & *T. brevimanus*	*C. zillii*
Locality	Mweru–Luapula	Lake Cayo, Cabinda	Benin (type loc), Côte D'Ivoire, Guinee, Ghana, Senegal, Congo, Mali, Gambia	Kogon river, Guinea
Reference	Present study	Pariselle & Euzet 2003	Pariselle & Euzet 1996	Pariselle & Euzet 1996
Maximum count	N=17	N=15	N=30	N=30
Ventral anchor				
Total length, a	37 ± 2.2, 11 (33–41)	39 ± 1.4 (35–42)	36 ± 1.4 (32–38)	34 ± 2.6 (29–39)
Blade length, b	36 ± 2.1, 11 (32–40)	37 ± 1.4 (33–40)	34 ± 1.5 (31–38)	33 ± 2.3 (27–36)
Shaft length, c	4 ± 1.2, 10 (3–7)	4 ± 0.9 (2–6)	3 ± 0.7 (2–5)	3 ± 0.9 (2–5)
Guard length, d	14 ± 2.2, 11 (10–18)	10 ± 1.1 (7–13)	8 ± 1.3 (4–11)	9 ± 1.6 (6–13)
Point length, e	15 ± 2, 11 (11–18)	16 ± 1.1 (13–18)	15 ± 1 (13–17)	14 ± 1.4 (12–18)
Dorsal anchor				
Total length, a	41 ± 1.2, 12 (39–44)	44 ± 1.8 (40–48)	41 ± 1.7 (38–45)	39 ± 2.5 (33–43)
Blade length, b	32 ± 1.4, 12 (30–34)	33 ± 1.3 (28–36)	30 ± 1.5 (27–34)	28 ± 2.2 (23–32)
Shaft length, c	4 ± 0.6, 11 (3–5)	4 ± 1 (1–6)	4 ± 0.9 (2–7)	4 ± 0.8 (2–6)
Guard length, d	17 ± 1, 12 (15–19)	16 ± 0.8 (14–18)	15 ± 1.2 (12–18)	14 ± 1.4 (11–17)
Point length, e	13 ± 1.4, 11 (11–15)	16 ± 0.8 (14–18)	12 ± 0.9 (10–14)	11 ± 1.1 (9–14)
Ventral bar				

Branch length, X	49 ± 2.7, 12 (43–53)	40 ± 1.7 (37–45)	37 ± 2.2 (32–44)	36 ± 3.3 (31–45)
Maximum width, W	7 ± 0.4, 12 (6–7)	5 ± 0.6 (4–6)	6 ± 0.7 (4–7)	5 ± 0.6 (4–7)
Dorsal bar				
Total, length, x	40 ± 2, 6 (37–43)	35 ± 2 (35–40)	33 ± 2.2 (29–37)	31 ± 2.3 (26–36)
Maximum widith, w	9 ± 1.6, 9 (7–11)	7 ± 0.6 (6–9)	8 ± 1.1 (6–10)	7 ± 1.4 (6–11)
Distance between auricles, y	13 ± 1.7, 11 (10–16)	13 ± 1.9 (10–19)	10 ± 1.1 (8–11)	11 ± 2 (8–15)
Auricle length, h	18 ± 1.7, 11 (15–21)	15 ± 1.2 (13–18)	14 ± 1.3 (12–17)	14 ± 2 (9–20)
Uncinuli				
Length, I	29 ± 1.9, 11 (26–32)	26 ± 1 (24–28)	24 ± 0.9 (22–27)	24 ± 1.8 (20–28)
Length, II	13 ± 0.8, 4 (12–14)	11 ± 0.5 (10–13)	12 ± 0.5 (10–13)	12 ± 0.6 (10–13)
Length, III	19 ± 2.2, 5 (16–22)	19 ± 0.8 (20–23)	19 ± 1 (16–22)	18 ± 1.3 (15–21)
Length, IV	23 ± 1.8, 5 (20–25)	21 ± 0.7 (20–23)	21 ± 0.8 (20–24)	21 ± 1.8 (17–25)
Length, V	25 ± 1.2, 12 (22–27)	23 ± 0.7 (21–24)	22 ± 1.2 (19–25)	22 ± 1.8 (18–26)
Length, VI	24 ± 2.9, 11 (17–27)	21 ± 0.7 (20–23)	21 ± 1.3 (15–23)	21 ± 1.8 (17–25)
Length, VII	22 ± 2.6, 11 (16–25)	19 ± 0.9 (17–21)	19 ± 0.8 (17–21)	19 ± 17 (15–24)
MCO				
Penis length, Pe	28 ± 2.3, 13 (24–31)	36 ± 1.3 (33–37)	35 ± 1.9 (32–37)	31 ± 1.7 (29–37)
Length of accessory piece, AP	35 ± 3.2, 10 (31–41)	38 ± 4.4 (28–47)	31 ± 3.1 (24–36)	28 ± 2.4 (23–33)
Heel length, He	7 ± 0.7, 16 (5–8)	8 ± 0.6 (5–9)		
Total body length	316 ± 59.1, 13 (219–413)	569 ± 72 (381–678)	534 ± 84.3 (394–692)	550 ± 70.1 (454–764)

Table 6 Measurements of *C. zambezensis* from four *Serranochromis* species. Measurements are represented in µm as the average ± standard deviation, count and the range (in brackets).

Species	*C. zambezensis*					
Host	*S. mellandi*	*S. thumbergi*	*S.macrocephalus*	*S. robustus jallae*	*S. macrocephalus*	*S. macrocephalus*
Locality	Mweru–Luapula	Mweru–Luapula	Mweru–Luapula	Zambia Bangwuelu wetlands	Lake Kariba	Lake Kariba

Reference	Present study	Present study	Present study	Vanhove et al. 2013	Douëllou 1993	Present study
Maximum count	n = 17	n = 11	n = 4	n = 6	n = 15	n = 17
Ventral anchor						
Total length, a	35 ± 2.6, 13 (32–39)	34 ± 2.9, 6 (28–37)	33 ± 0.7, 4 (33–34)	41 ± 2.9, 3 (38–44)	39 (37–42)	38 ± 3.2, 8 (33–44)
Blade length, b	31 ± 3.3, 13 (23–35)	29 ± 2.5, 6 (24–31)	29 ± 1.1, 4 (28–30)	30 ± 1.3, 3 (29–32)	34 (32–36)	32 ± 3.2, 8 (26–38)
Shaft length, c	5 ± 1, 11 (3–7)	4 ± 1.1, 6 (3–6)	3 ± 1.1, 4 (2–4)	5 ± 2.5, 3 (4–8)	6 (4–7)	5 ± 1.4, 8 (4–7)
Guard length, d	11 ± 2, 13 (9–15)	14 ± 2.2, 6 (11–18)	13 ± 1.1, 4 (12–15)	17 ± 1.8, 3 (15–18)	12 (9–13)	15 ± 1.4, 8 (13–17)
Point length, e	15 ± 1.3, 11 (12–17)	12 ± 1.9, 6 (9–14)	14 ± 0.6, 4 (14–15)	11 ± 1.9, 3 (9–13)	16 (13–17)	15 ± 1.3, 8 (13–17)
Dorsal anchor						
Total length, a	39 ± 2.3, 11 (36–43)	36 ± 2.9, 10 (33–42)	32 ± 1.4, 4 (31–34)	39 ± 2, 3 (38–41)	43 (41–45)	39 ± 1.9, 6 (37–42)
Blade length, b	31 ± 0.8, 9 (30–33)	28 ± 3, 10 (23–32)	27 ± 1.8, 4 (24–29)	33 ± 0.9, 3 (32–34)	32 (29–35)	28 ± 1.6, 6 (26–30)
Shaft length, c	4 ± 1.1, 8 (3–6)	4 ± 1.2, 10 (3–7)	4 ± 0.6, 4 (3–5)	5 ± 0.5, 3 (5–5)	5 (3–8)	4 ± 0.9, 6 (3–6)
Guard length, d	13 ± 2.2, 10 (10–17)	17 ± 2.1, 10 (14–20)	14 ± 0.6, 4 (13–14)	15 ± 1.8, 3 (13–16)	16 (13–18)	16 ± 2.2, 6 (13–19)
Point length, e	12 ± 1.3, 9 (10–14)	12 ± 1.6, 10 (8–13)	12 ± 0.5, 4 (12–13)	14 ± 1, 3 (13–15)	13 (10–14)	12 ± 1.8, 6 (10–15)
Ventral bar						
Branch length, X	52 ± 3.7, 11 (46–58)	53 ± 4.4, 10 (45–60)	47 ± 3.1, 3 (43–49)	41 ± 3.1, 3 (38–44)	37 (34–41)	42 ± 7.1, 13 (29–54)
Maximum width, W	8 ± 0.9, 12 (7–10)	8 ± 1, 10 (6–9)	6 ± 0.6, 3 (6–7)	6 ± 0.5, 3 (6–7)	5 (4–7)	6 ± 1.2, 13 (4–7)
Dorsal bar						
Total, length, x	50 ± 2.3, 11 (47–55)	49 ± 2.6, 7 (46–53)	46 ± 1.9, 3 (43–47)	37 ± 3.4, 4 (32–40)	35 (32–38)	43 ± 5.5, 13 (31–51)
Maximum width, w	11 ± 1.6, 10 (8–15)	9 ± 1.8, 7 (8–13)	8 ± 1.3, 3 (6–9)	7 ± 0.6, 4 (7–8)	8 (8–10)	8 ± 1.6, 13 (5–10)

Distance between auricles, y	15 ± 4.2, 10 (6–22)	17 ± 1.5, 6 (15–19)	18 ± 0.9, 3 (17–19)	12 ± 1.1, 4 (11–13)	13 (11–15)	14 ± 2.2, 13 (10–16)
Auricle length, h	27 ± 3.2, 10 (23–33)	25 ± 1.3, 6 (23–27)	22 ± 1, 3 (21–22)	21 ± 1.4, 4 (19–23)	15 (14–17)	21 ± 2.6, 11 (16–25)
Uncinuli						
Length, I	18 ± 0.9, 10 (16–19)	17 ± 1.3, 3 (16–19)		18 ± 1.4, 3 (16–19)	19 (18–20)	20 ± 2.5, 11 (16–24)
Length, II					13 (12–13)	13 ± 1.1, 2 (12–13)
Length, III	16 ± 2.3, 3 (14–18)	19 ± 0.5, 4 (18–19)	19 ± 1.1, 3 (18–20)	20 ± 0.4, 2 (19–20)	19 (18–20)	20 ± 1.8, 7 (19–23)
Length, IV	24 ± 2.8, 4 (20–27)	23 ± 2.3, 2 (22–25)	26 ± 2.2, 3 (24–28)	24 ± 2.3, 2 (22–26)	24 (23–25)	24 ± 2.5, 9 (19–26)
Length, V	27 ± 2.9, 10 (23–33)	27 ± 1.5, 6 (26–30)	28 ± 1.3, 3 (26–29)	22 ± 0.4, 2 (22–22)	24 (23–27)	27 ± 3.8, 10 (22–32)
Length, VI	26 ± 2, 12 (23–30)	27 ± 2.1, 6 (25–31)	24 ± 2, 3 (22–25)	22 ± 3.1, 2 (20–24)	24 (23–26)	24 ± 2.8, 11 (20–30)
Length, VII	24 ± 2.2, 12 (21–28)	23 ± 1.2, 6 (22–25)	21 ± 3.7, 3 (17–24)	23 ± 1.9, 3 (22–25)	21 (19–23)	21 ± 3, 10 (14–23)
MCO						
Penis length, Pe	62 ± 2.9, 16 (56–66)	63 ± 2.4, 10 (59–67)	57 ± 1.8, 4 (54–58)	62 ± 2.4, 5 (59–65)	62 (60–65)	60 ± 2, 17 (55–63)
Length of accessory piece, AP	68 ± 6.6, 14 (47–76)	75 ± 3.5, 10 (70–80)	63 ± 1.9, 4 (61–65)	57 ± 3.5, 5 (54–62)	48 (46–50)	61 ± 8.6, 17 (44–74)
Heel length, He	10 ± 1.4, 16 (7–13)	9 ± 1.3, 10 (7–11)	9 ± 1.9, 4 (6–11)	13 ± 0.4, 5 (13–14)		10 ± 1.6, 17 (5–12)
Vaginal length, VgL		12 ± 1, 4 (11–13)	11 ± 1.1, 4 (10–12)		18 (12–22)	14 ± 3.2, 3 (12–18)
Vaginal width, Vgl		8 ± 1.2, 4 (7–10)	9 ± 0.8, 3 (8–10)			13 ± 4.3, 3 (9–17)
Vaginal triangle length, Vgtr	7 ± 1.3, 7 (5–9)	5 ± 0.6, 4 (4–6)	7 ± 0.7, 4 (6–7)			6 ± 1.4, 10 (5–9)
Total body length	390 ± 48.9, 10 (315–445)	345 ± 37, 10 (285–416)	380 ± 101.5, 2 (308–451)	451 ± 30.5, 5 (425–499)	776 (560–1080)	415 ± 81.5, 13 (300–613)

Figure captions

Fig. 1 Map of Bangweulu-Mweru and neighbouring ecoregions in underlined, cursive font. Rivers and water bodies in blue, cursive font. Sampling localities in red. The inset shows the location of Bangweulu-Mweru on the African continent. Sampling localities: 1 Luapula River off Kashobwe, 2 Futuka Farm, 3 Bumaki Farm, 4 Lubumbashi Zoo and 5 Kipopo. Scale in km.

Fig. 2 Haptoral and genital hardparts of *C. consobrini* sp.n. Upper MCO drawn from the holotype from *S. mellandi*. Lower MCO displays the MCO from a different angle and from *O.* sp. 'Mambilima' I–VII uncinuli, Ap accessory piece, DB dorsal transverse bar, DH dorsal anchor, He heel, MA male apparatus, Pe penis, VB ventral transverse bar, VH ventral anchor. Scale 20 µm.

Fig. 3 Stacked phasecontrast micrographs of *C. consobrini* sp.n. from *Sargochromis mellandi*. a) haptor b) MCO and of *C. halli* morphotype 2 c) haptor and d) MCO. Scale a,b 20 µm; c,d 50 µm.

Fig. 4 Haptoral and genital hardparts of *C. halli* morphotype 2. I–VII uncinuli, Ap accessory piece, DB dorsal transverse bar, DH dorsal anchor, He heel, MA male apparatus, Pe penis, VB ventral transverse bar, VH ventral anchor. Scale 20 µm.

Fig. 5 Haptoral and genital hardparts of *C. papernastrema* from *T. sparrmanii*. Left dorsal anchor drawn from different individual. I–VII uncinuli, Ap accessory piece, DB dorsal transverse bar, DH dorsal anchor, He heel, MA male apparatus, Pe penis, VB ventral transverse bar, VH ventral anchor. Scale bar 20 µm.

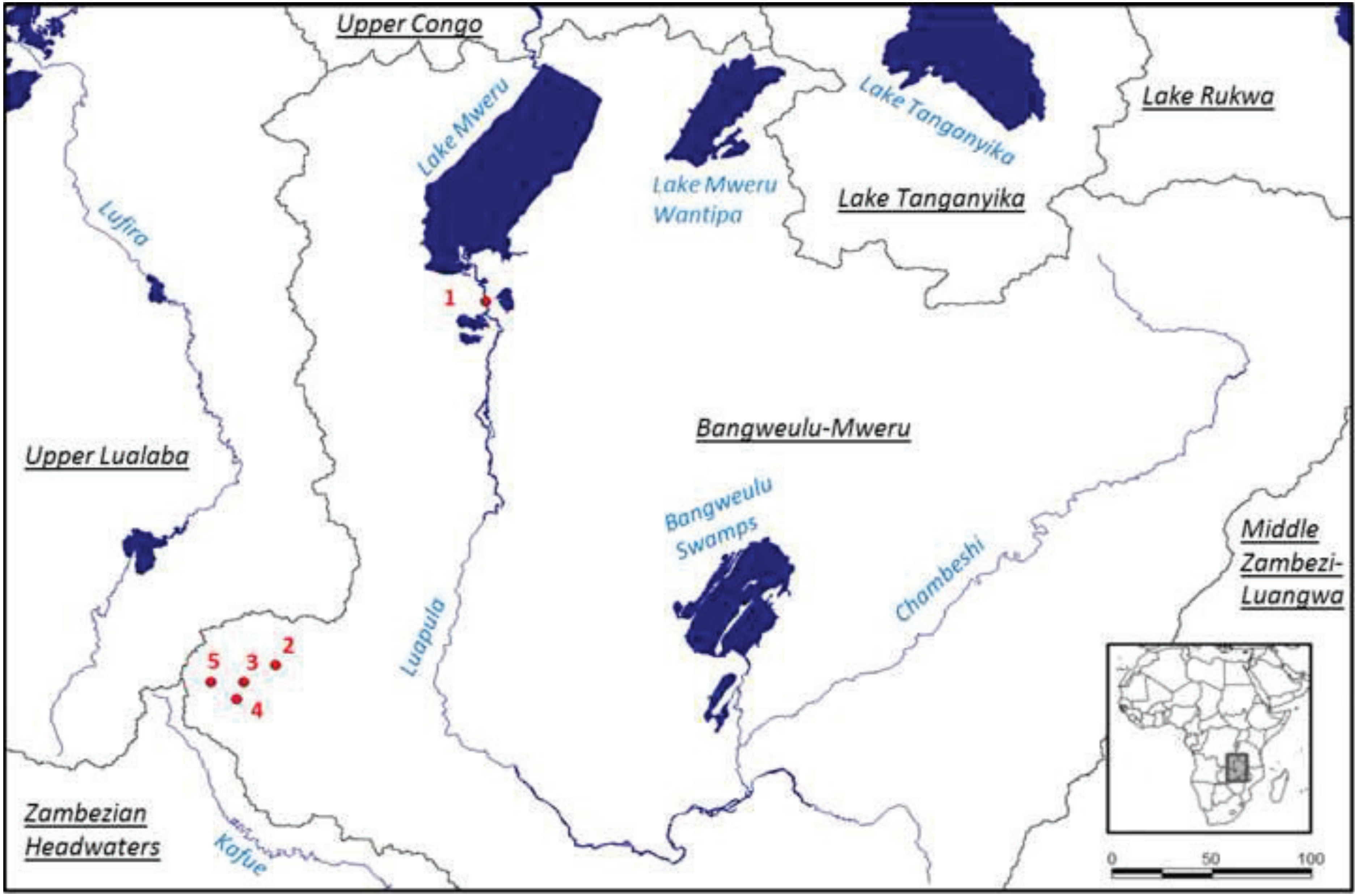
Fig. 6 Stacked phasecontrast micrographs of *C. papernastrema* from *T. sparmanii*: holotype a) haptor, b) MCO and from voucher c) MCO; of *C. quaestio* from *C. rendalli* d) haptor and e) MCO and from *Cichlidogyrus* sp. from *T. mylodon* f) haptor. Scale a,d and f 50 µm; b,c and e 20 µm.

Fig. 7 Haptoral and genital hardparts of *C. quaestio* from *C. rendalli*. I–VII uncinuli, Ap accessory piece, DB dorsal transverse bar, DH dorsal anchor, He heel, MA male apparatus, Pe penis, VB ventral transverse bar, VH ventral anchor. Scale bar 20 µm.

Fig. 8 Haptoral and genital hardparts of *C. zambezensis* from *S. thumbergi*. I–VII uncinuli, Ap accessory piece, DB dorsal transverse bar, DH dorsal Anchor, He heel, MA male apparatus, Pe penis, VB ventral transverse bar, VH ventral anchor. Filaments associated with anchors and uncinuli in grey. Scale bar 20 µm.

Fig. 9 Stacked phasecontrast micrographs of *C. zambezensis* from *S. thumbergi* a) haptor, b) MCO. Scale 20 µm.

Figure1



Upper Congo
Lake Mweru
Lake Mweru
Wantipa
Lake Tanganyika
Lake Tanganyika
Lake Rukwa
Lufira
1
Upper Lualaba
Bangweulu-Mweru
Bangweulu
Swamps
Chambeshi
Luapula
Middle
Zambezi-
Luangwa
2
3
5
4
Zambezian
Headwaters
Kafue
0
50
100

Figure2

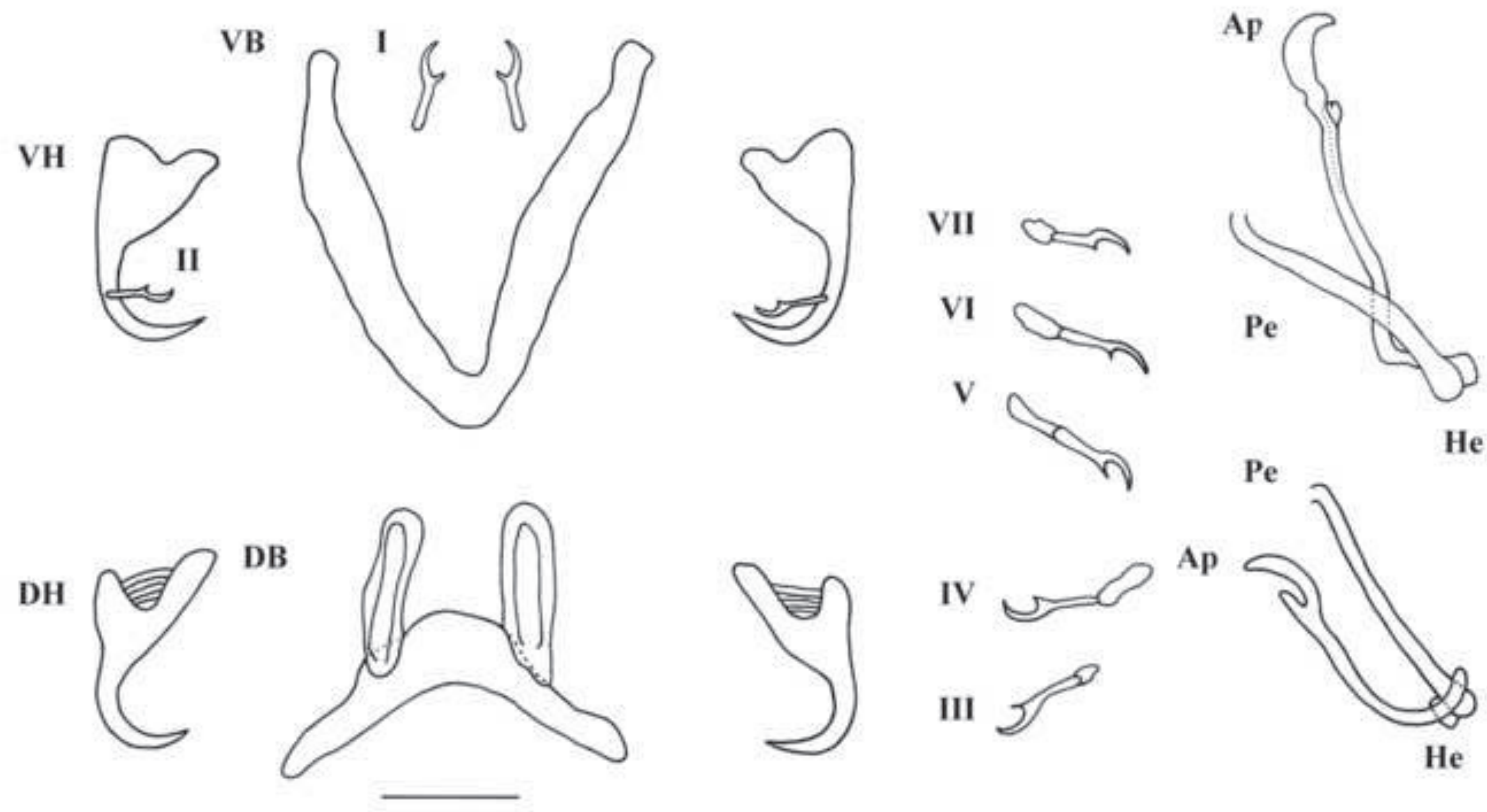


Figure3

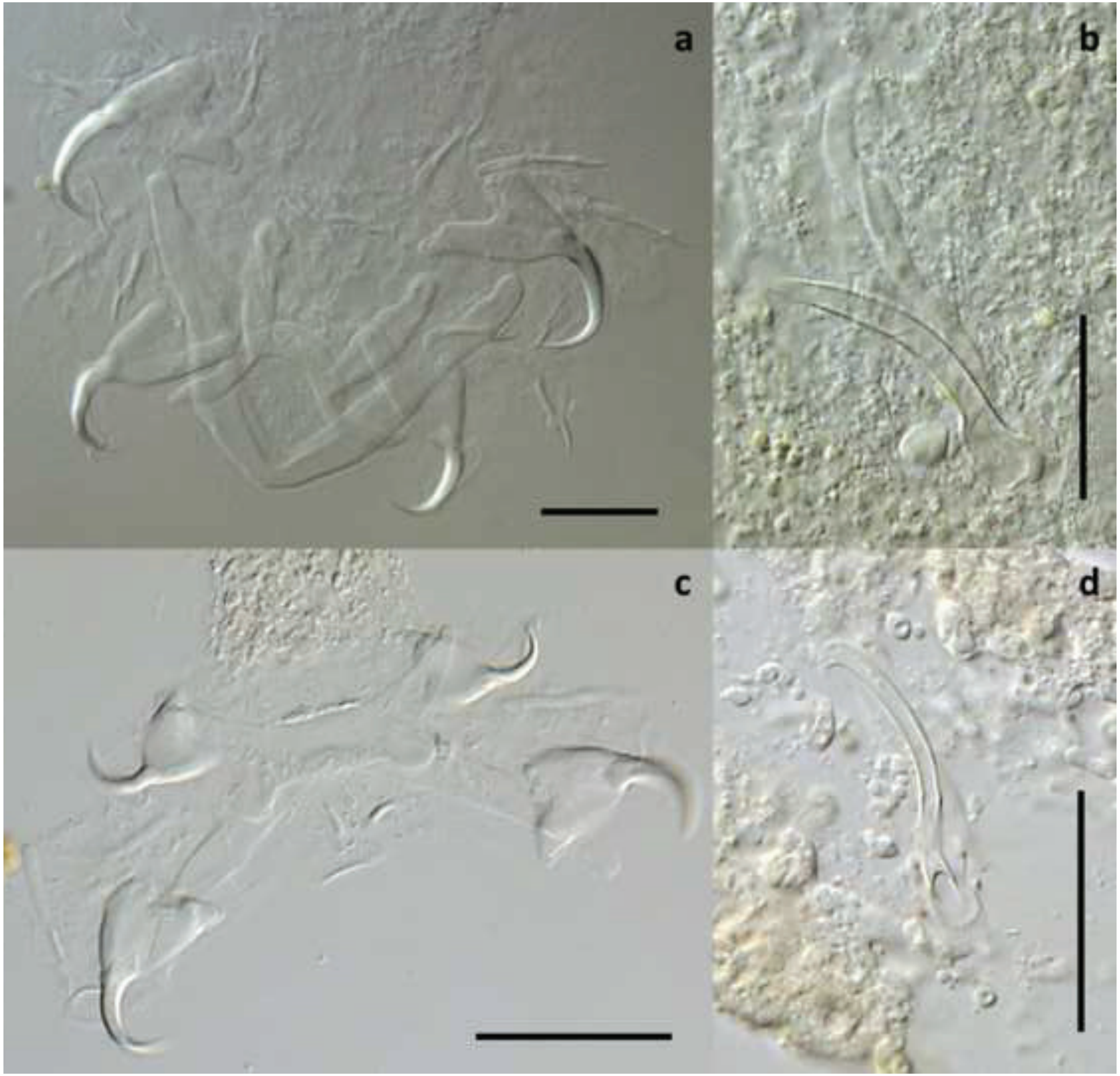


Figure4

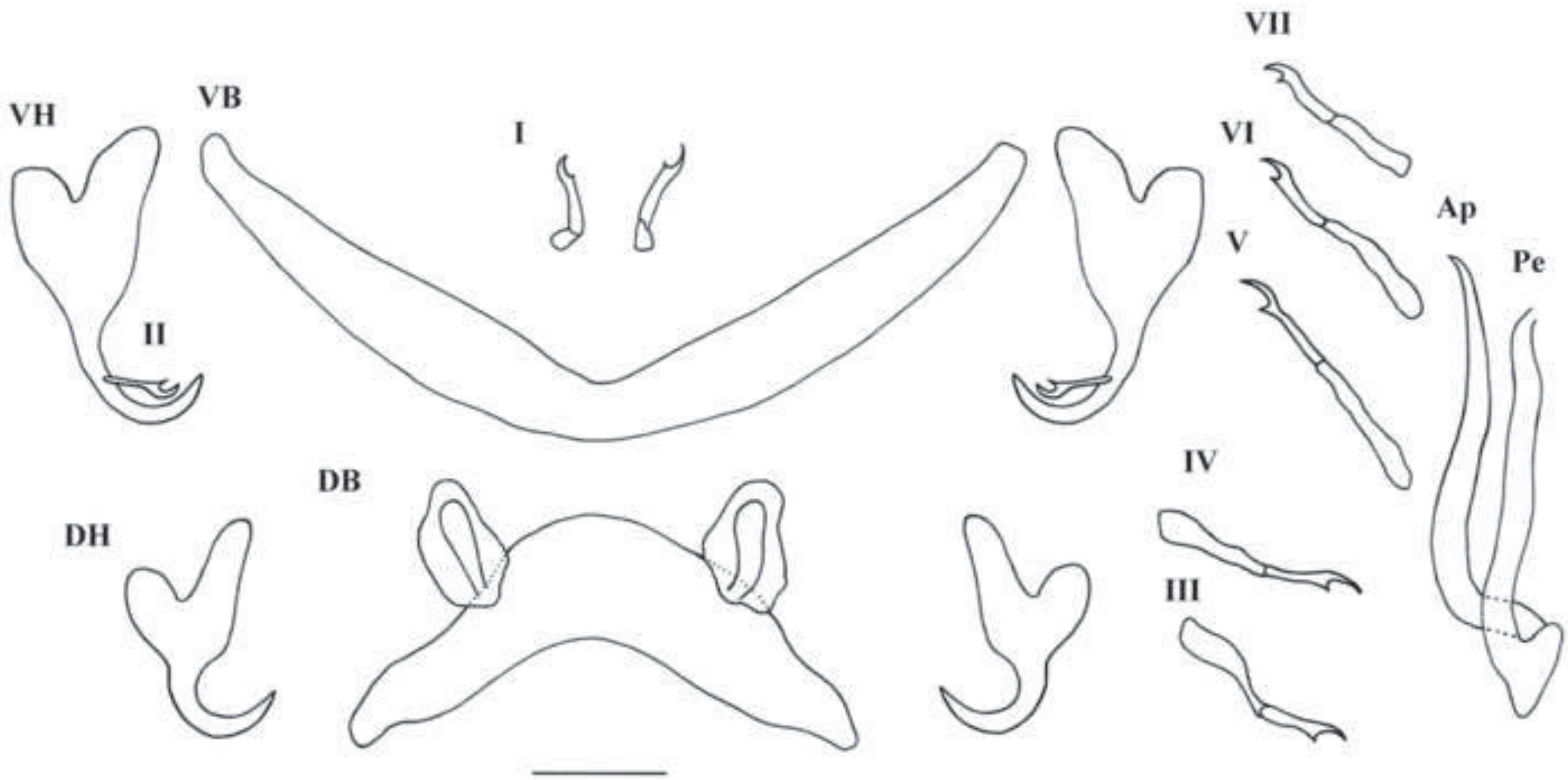


Figure5

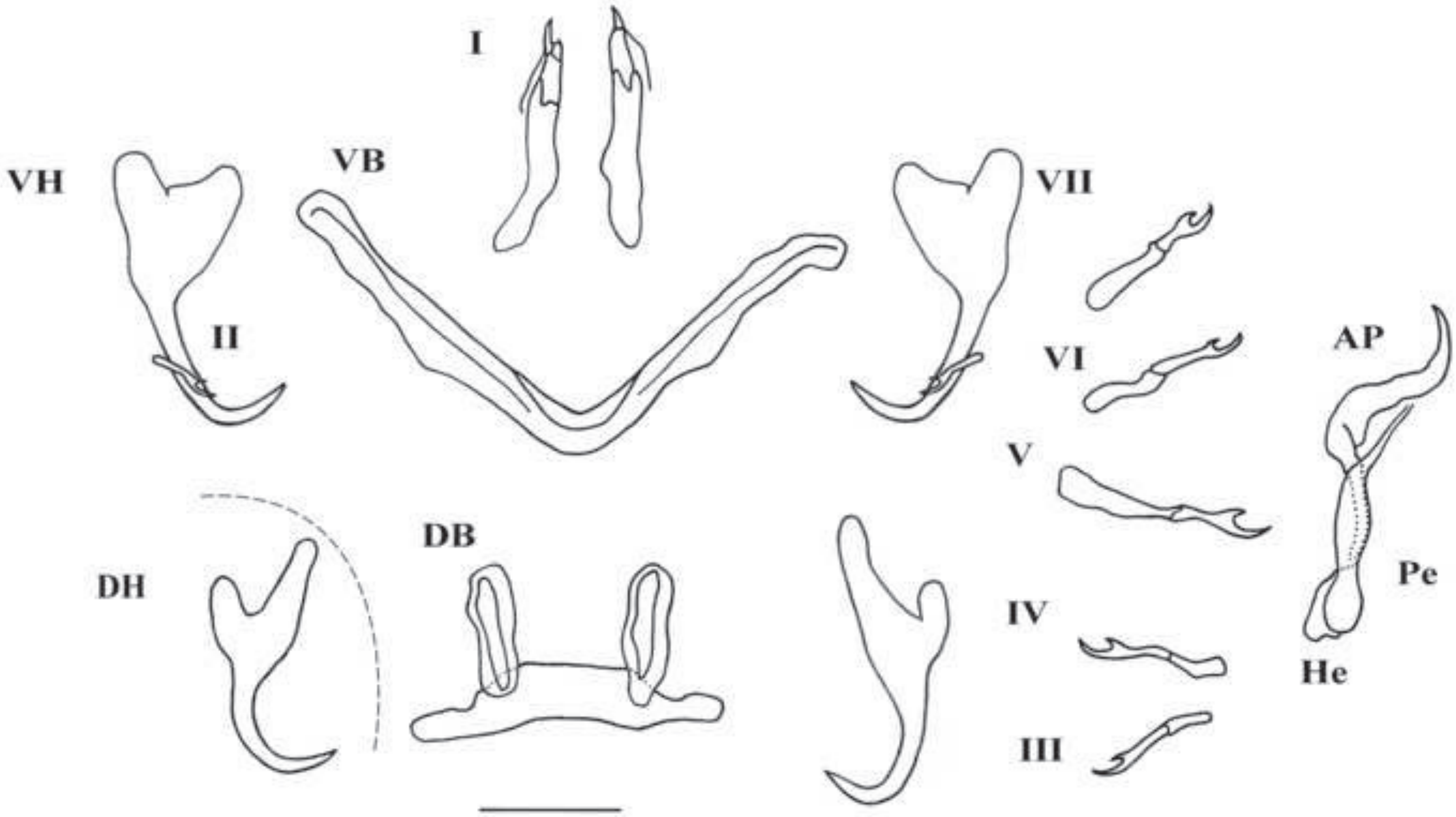


Figure6

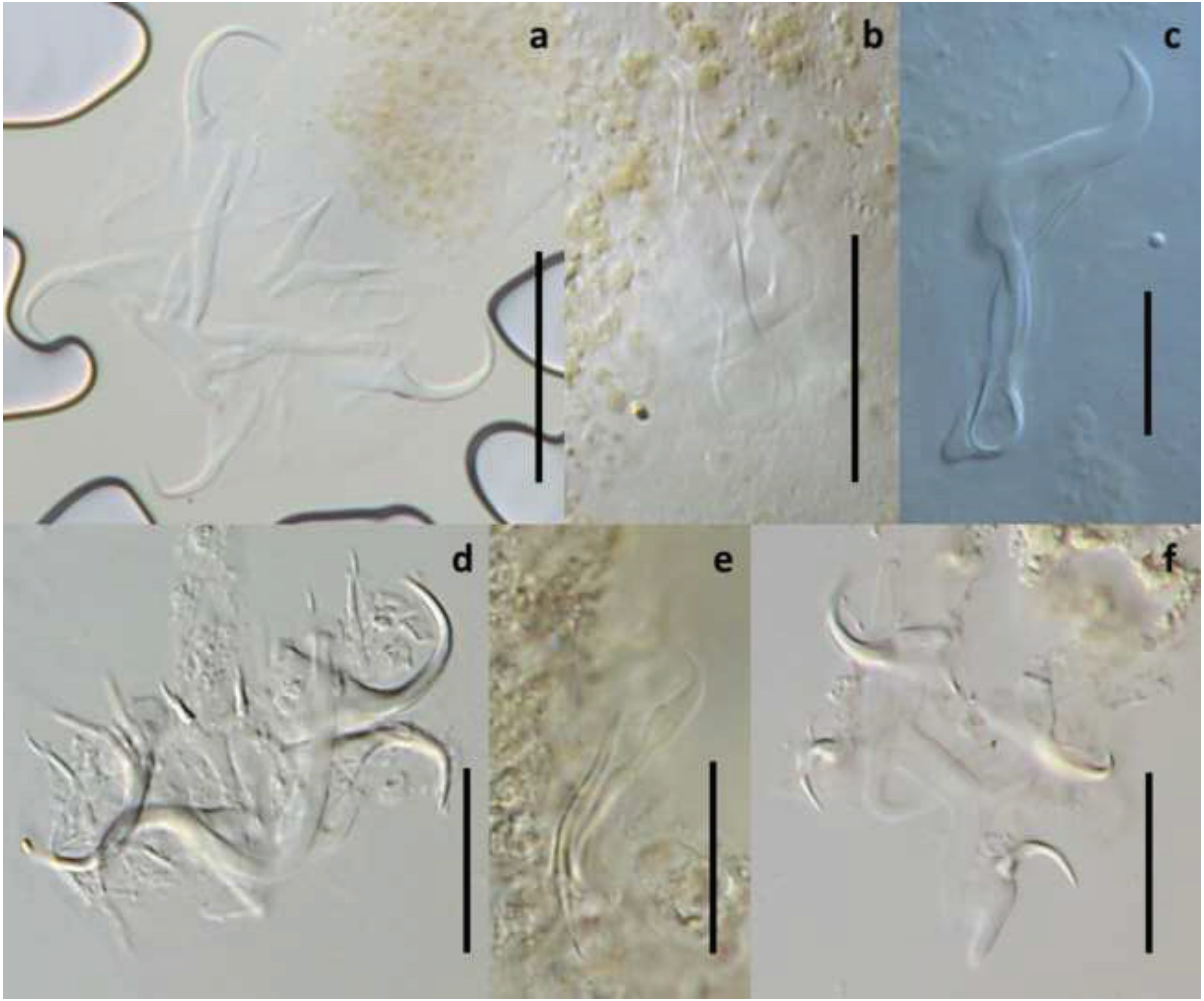
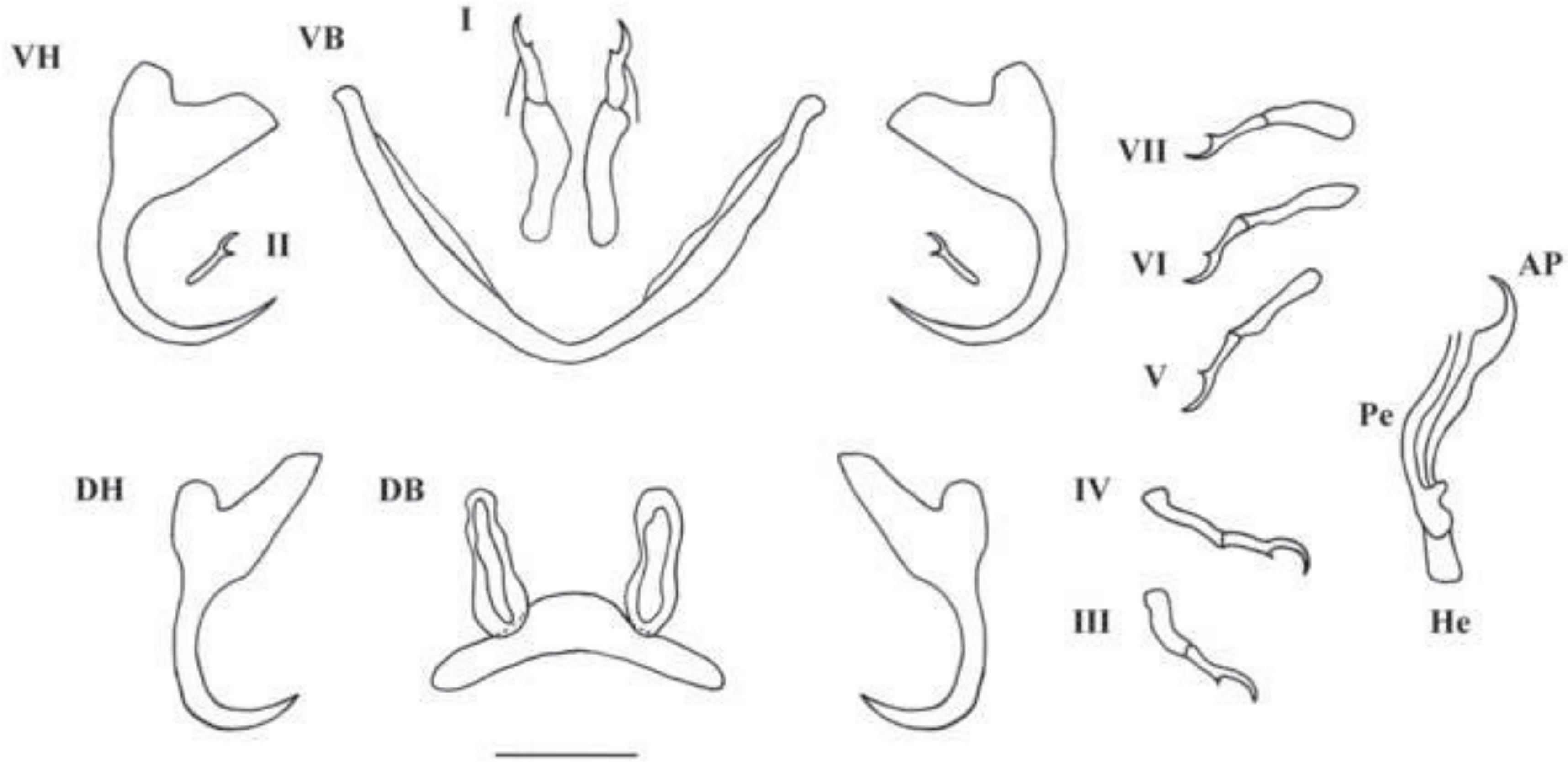


Figure7



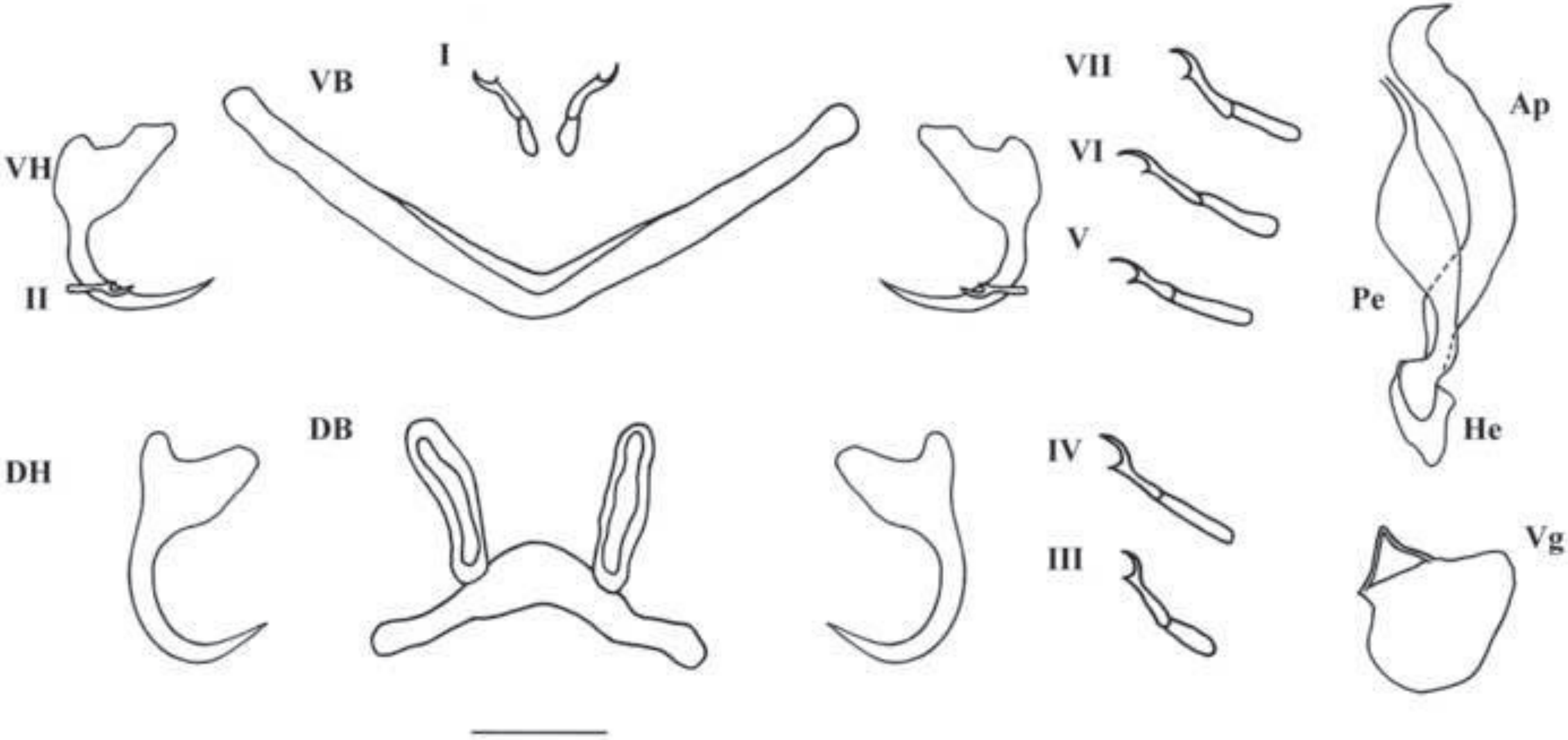

VH
II
VB
I
DH
DB
VII
VI
V
IV
III
Ap
Pe
He
Vg

Figure9