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Diversity of *Quadriacanthus* (Monogenea: Dactylogyridae) in the Upper Congo Basin: new geographical records and description of five new species from the gills of *Clarias ngamensis* (Siluriformes: Clariidae)

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ABSTRACT. Monogenean parasites belonging to *Quadriacanthus* have never been reported from *Clarias ngamensis*, but are commonly found on congeners. In view of the specificity of monogeneans, the genetic proximity and the co-occurrence of *C. ngamensis* and *C. gariepinus* in Africa, it is hypothesised that a parasitological survey of *C. ngamensis* will yield several species of *Quadriacanthus* as its congeneric host *C. gariepinus* harbours these parasites. The present study aims to explore the monogenean parasites from the gills of *C. ngamensis* in the Upper Congo Basin by (i) inventorying their diversity and providing their morphological characterisation, and (ii) analysing their infection parameters. Monogeneans were isolated from the gills, and identified based on morphological analysis of genital and haptoral sclerotized parts. Seven parasite species belonging to *Quadriacanthus* were found. Among them, two species, *Q. aegypticus* and *Q. allobychowskiella,* are both newly reported in the Upper Congo Basin and newly recorded on *C. ngamensis*. *Quadriacanthus amakaliae* sp. nov., *Q. halajiani* sp. nov., *Q. domatanai* sp. nov., *Q. lubandaensis* sp. nov., and *Q. curvicirrus* sp. nov. are new to science and described herein. The most prevalent parasite species was *Q. curvicirrus* sp. nov. in the Luapula River (prevalence = 66.7%) with mean infection intensity of 6.3 ± 5.8. *Quadriacanthus allobychowskiella* and *Q. aegypticus* are known parasites from *C. gariepinus* and their presence on *C. ngamensis* is probably the result of lateral transfers. The discovery of five new species from *C. ngamensis* highlights the parasite diversity still to be explored in the region.

KEY WORDS. Bangweulu-Mweru ecoregion, Haut-Katanga, Lake Lubanda, Luapula River, Lufira River.

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INTRODUCTION

African clariids are known to harbour monogenean gill parasites belonging to four genera: *Birgiellus* Bilong Bilong, Nack & Euzet, 2007, *Gyrodactylus* von Nordmann, 1832, *Macrogyrodactylus* Malmberg, 1957 and *Quadriacanthus* Paperna, 1961 (Paperna 1979, Bilong Bilong et al. 2007). Members from the latter genus have a wide host and geographical distribution (infesting African and Asian fish); it is the most species rich on these hosts with currently 39 known species (Řehulková et al. 2018, Truter 2022, Truter et al. 2023). Thirty-seven of 39 *Quadriacanthus* species were recorded on the following African fish species: Clariidae: *Clarias gariepinus* (Burchell, 1822) synonym: *C. lazera*; *C. jaensis* Boulenger, 1909; *C. ebriensis* Pellegrin, 1920; *C. pachynema* Boulenger, 1903; *C. camerunensis* Lönnberg, 1895; *C. maclareni* Trewavas, 1962; *C. submarginatus* Peter, 1882; *Heterobranchus longifilis* Valenciennes, 1840; *H. isopterus* Bleeker, 1863; *H. bidorsalis* Geoffroy Saint-Hilaire, 1809 (N'Douba et al. 1999, Lim et al. 2001, Bahanak et al. 2016, 2022, Francová et al. 2017, Řehulková et al. 2018, Bouah et al. 2021); Bagridae: *Bagrus docmak* (Forsskål, 1775); *B. bajad* (Forsskål, 1775); *B. orientalis* Boulenger, 1902 (Paperna 1979, Lim et al. 2001, Francová et al. 2017, Řehulková et al. 2018); Notopteridae: *Papyrocranus afer* (Günther, 1868) (Nack et al. 2016); Claroteidae: *Anaspidoglanis macrostoma* Pellegrin, 1909 (Akoumba et al. 2017, Řehulková et al. 2018) and Cichlidae: *Oreochromis esculentus* (Graham, 1928) (Paperna 1979, Řehulková et al. 2018). In the latter case, the validity of the parasite species, *Q. tilapiae* Paperna, 1973, is doubtful as its presence on the cichlid host could be considered as an accidental infection (Paperna 1979, Kritsky and Kulo 1988, Pariselle and Euzet 2009, Řehulková et al. 2018).

According to the "host diversity begets parasite diversity" hypothesis, increasing host genetic, taxonomic, and functional richness increases parasite species richness, through both ecological and co-evolutionary processes (Hechinger and Lafferty 2005). Then it can be assumed that ecologically, increasing host diversity increases the variety of niches for parasites, facilitating colonisation by diverse parasite species or isolation of populations followed by allopatric speciation, on the one hand (Krasnov et al. 2004, Wood and Johnson 2016).

On the other hand, evolutionarily, increasing host speciation rates can drive co-speciation for associated parasites (Vas et al. 2012, Wood and Johnson 2016). From this interaction (relationship) between parasites and their hosts, in Monogenea, it is recognised that speciation may occur in allopatry, that is on two distinct ecologically and geographically differentiated host species, or in sympatry, either on distinct host species by a host switch or in the same host species by duplication, or cospeciation where parasite phylogeny mirrors host phylogeny (Tripathi et al. 2007, Vanhove et al. 2016).

Despite the number of parasitologically screened members of *Clarias*, there are still *Clarias* spp. that have never been studied for their monogenean fauna, such as the blunt-toothed African catfish *C. ngamensis* Castelnau, 1861 (Scholz et al. 2018). This is a tropical African freshwater fish, reported from the Quanza, Cunene, Okavango, Chobe, Lake Ngami, Zambezi (upstream Victoria Falls), Kafue, Lake Malawi, Upper Lualaba, Luapula, Lake Moeru and Bangweulu, Pungue, Buzi, Save, Limpopo, Incomati and lower Pongolo basins (Teugels 1986, 2003, Froese and Pauly 2023). *Clarias ngamensis* is an omnivorous fish, with carnivorous tendencies like *C. gariepinus* which it lives in sympatry with (Teugels 1986, Van Steenberge et al. 2020, Froese and Pauly 2023). It prefers to reside in grassy habitats, permanent marshes, muddy bottoms and calm waters. It has the IUCN conservation status of Least Concern (not threatened or rare species) (Konings et al. 2018).

This study aims to record the diversity of the monogenean parasite fauna belonging to *Quadriacanthus* of *C. ngamensis* in the Upper Congo Basin. *Clarias ngamensis* is selected for the study, given its economic value in aquaculture and fishing in the natural environment (fished for human consumption). *Clarias ngamensis* plays also an important role in the environment (regulation of population of mosquitoes, snails, small fish, algae, insect larvae and nymphs, molluscs, etc.), being a species on top of the trophic chain (Willoughby and Tweddle 1978).

In view of the high biodiversity of potential clariid host species in the tropics and the often narrow specificity of species of *Quadriacanthus* (Birgi 1988, Bahanak et al. 2016, Akoumba et al. 2017), it can be expected that parasitological surveys of *C. ngamensis* lead to the record of many parasite species, including species new to science (Whittington 1998). Objectives include: (i) inventorying the diversity, and providing descriptions of potential new species, of gill monogeneans of *Quadriacanthus*, and (ii) analysing infection parameters of these monogenean parasites.

MATERIAL AND METHODS

This study was conducted in two localities in the Upper Congo Basin (Fig. 1), in the North-East of the Haut-Katanga province (in the south of the former Katanga province), on the Kasenga road (National #5), Democratic Republic of Congo.

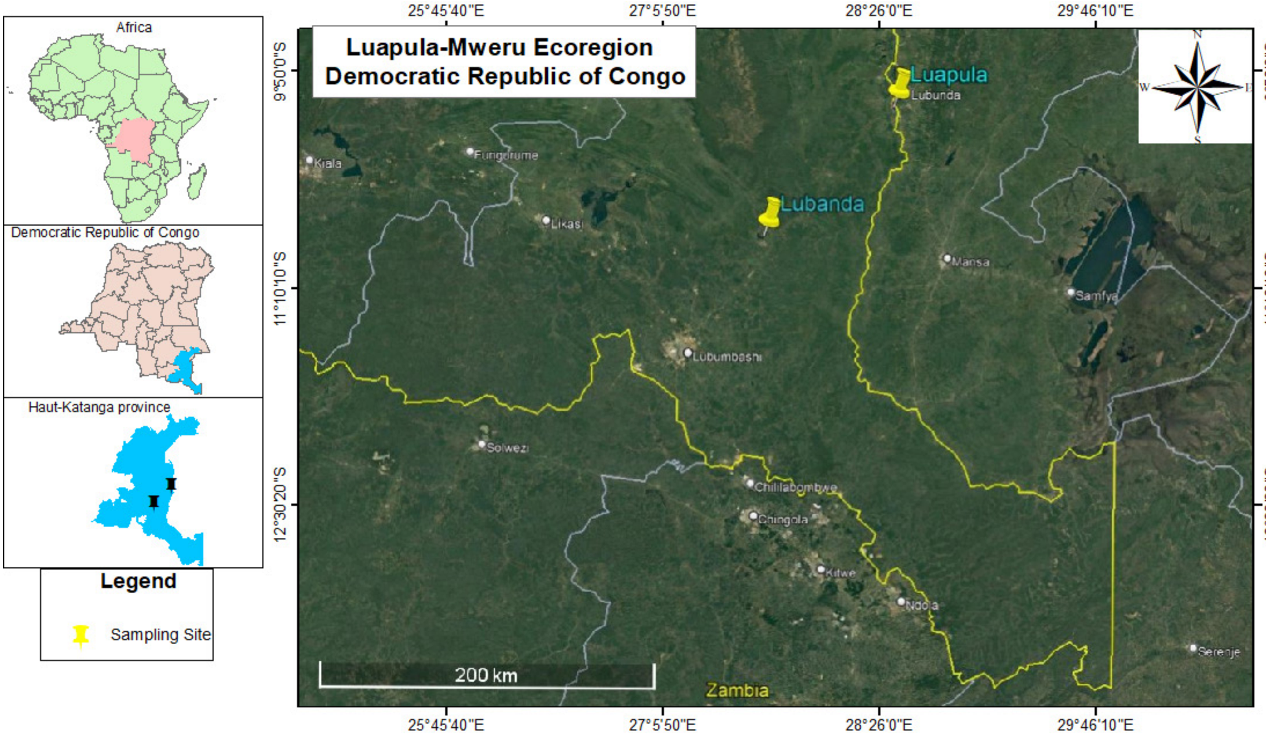

Figure 1. Map of sampling sites in the Upper Congo Basin: Lake Lubanda (11°04'57.3"S; 027°55'43.7"E); Luapula River (10°24'1.01"S; 028°37'16.57"E).

The first sampling locality is Lake Lubanda: Lubanda Village, located at about 97 km from Lubumbashi, on the Kafila River, a right affluent of the Middle Lufira River, Upper Lualaba Ecoregion sensu Thieme et al. (2005); and the second locality is the Luapula River: Kasenga Village, located at about 200 km from Lubumbashi, on the Luapula River System, Bangweulu-Mueru Ecoregion sensu Thieme et al. (2005).

Fish sampling

A total of 30 fish specimens were bought from fishermen along the shores of Lake Lubanda (15) and the Luapula River (15) (Fig. 1) in November 2021. Fish were bought alive and kept in an aerated tank containing water from the lake or the river, and transported to a field laboratory. Fish were identified to species level following the keys proposed by Teugels (1986). They were killed by severing the spinal cord just posterior to the cranium, immediately prior to examination, following Olivier et al. (2009).

Parasite sampling

Fish were dissected and right gill arches removed by dorso-ventral section. These were placed in a petri-dish containing water for examination using a stereomicroscope Optika 4.0.0 (Optika Microscopes Italy). Fresh parasites were dislodged from the gill filaments using entomological needles and fixed between slide and cover slip into a drop of ammonium picrate-glycerin, according to Malmberg (1957) and Nack et al. (2016). Twenty-four hours later, coverslips were sealed using nail varnish. Parasites were deposited in the collection of the Research Group Zoology: Biodiversity & Toxicology, at Hasselt University (Diepenbeek, Belgium) under accession numbers HU n°888 – HU #1004 type material & XXII.3.04 – XXII.3.44 reference material.

Monogenean xenocommunity composition and infection parameters

Parasite identification was based on the morphology and the size of sclerotized parts of the genital structures and the haptor (Nack et al. 2016, Bahanak et al. 2022). The measurements were carried out according to Gussev (1962) and modifications by N'Douba et al. (1999) (Fig. 2) with the aid of a Leica DM 2500 microscope, LAS software (3.8), and drawings of the sclerotized parts of the genital structures and haptor were made with the aid of Corel Draw Graphics

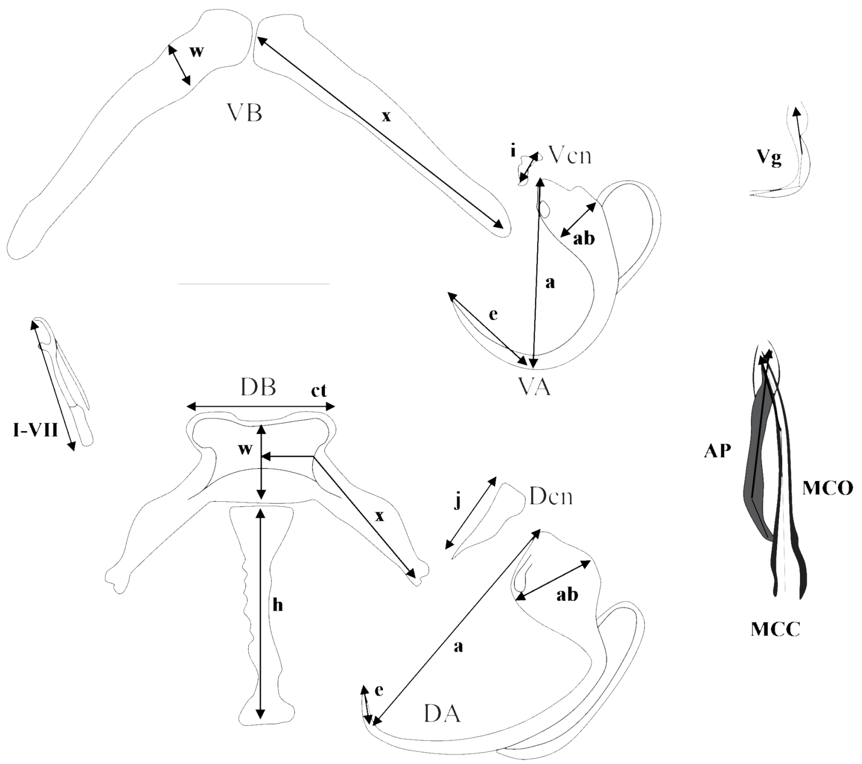

Figure 2. Morphometrics of *Quadriacanthus* spp. used in this study are based on Gussev (1962) with modifications by N'Douba et al. (1999). MCO: male copulatory organ length; AP: accessory piece length; MCC: male copulatory complex (MCO and AP combined); I-VII: length of hooks; DB: dorsal bar: (x) length, (w) width, (h) median process length, (ct) centre length; DA: dorsal anchor: (a) length, (ab) base diameter or width, (e) point length; DCn: dorsal cuneus (j) length; VB: ventral bar: (x) length, (w) width; VA: ventral anchor: (a) length, (ab) base diameter or width, (e) point length; VCn: ventral cuneus (i) length; Vg: vagina length. Scale bar: 20 µm.

Suite X8 software. Measurements, in micrometers (µm) are presented as follows: mean (minimum-maximum). To comply with the regulations set out in article 8.5 of the amended 2012 version of the International Code of Zoological Nomenclature (ICZN 2012), details of the new species have been submitted to ZooBank.

Parasite diversity is summarised by the species richness; infection parameters: prevalence (P) and mean intensity (MI) are provided following definitions given by Margolis et al. (1982) and Bush et al. (1997) and categorised following Valtonen et al. (1997).

TAXONOMY

The investigation of gill filaments of *C. ngamensis* resulted in the record of seven dactylogyrid species, with anatomy corresponding to the diagnosis of *Quadriacanthus* given by Paperna (1961) and amendments by Kritsky and Kulo (1988). Two of them (*Q. aegypticus* and *Q. allobychowskiella*) are known species, and five are newly described. The characterization of each monogenean species is given below. Measurements of sclerotized structures taken from flattened specimens are shown in Table 1.

Monogenea Van Beneden, 1858

Dactylogyridea Bychowsky, 1937

Dactylogyridae Bychowsky, 1933

Quadriacanthus Paperna, 1961

Quadriacanthus aegypticus El-Naggar & Serag, 1986

Type-host and locality: *Clarias gariepinus*; Lake Manzala and the Demietta branch of the Nile River, Dakahlia Governorate, Egypt (El-Naggar and Serag 1986).

Other localities: Ammar drainage canal, Bahr Mouis, Damroo drainage canal, Mansoura drainage canal, Nawasa

Table 1. Average measurements (in micrometers) of sclerotized parts of specimens of *Quadriacanthus* species, with range in parentheses. Legend: MCO: Male copulatory organ length; AP: Accessory piece length; I-VII: Hooks length; DB: Dorsal bar: (x) length, (w) width, (h) median process length, (ct) center length; DA: Dorsal anchor): (a) length, (ab) base diameter or width, (e) point length; DCn: Dorsal cuneus length; VB: Ventral bar: (x) length, (w) width; VA: Ventral anchor: (a) length, (ab) base diameter, (e) point length; VCn: Ventral cuneus length. Number of flattened specimens on which measurements of sclerotized pieces were taken: (n).

Sclerotized pieces	*Q. aegypticus* (n=3)	*Q. allobychowskiella* (n=7)	*Q. amakaliae* sp. nov. (n=13)	*Q. halajiani* sp. nov. (n=9)	*Q. domatanai* sp. nov. (n=13)	*Q. lubandaensis* sp. nov. (n=7)	*Q. curvicirrus* sp. nov. (n=12)
MCO	37.4 (36.4–38.7)	36.4 (34.6–37.5)	36 (34–37.9)	31.2 (28.3–34.8)	65.3 (58.2–68.7)	24.1 (21.6–26.7)	53.1 (49–55.1)
AP	40.6 (34.4–44.4)	44.2 (41.4–46)	31 (29–33)	34.2 (31.7–35.7)	67.9 (63.1–70.8)	25.6 (23.5–28.5)	59.3 (56.2–63.4)
I	16.5 (16.5–16.5)	14.5 (13.8–15.1)	11.6 (10.1–13.7)	15.4 (13.8–18.7)	15.2 (13.4–17.4)	15.7 (13.7–20.5)	14.3 (12.8–16.2)
II	12.2 (12–12.4)	12 (10.9–13.1)	11.6 (10.6–12.3)	11.1 (10.2–12)	11.9 (11.3–12.7)	12.1 (11.6–12.8)	13 (10.8–16.1)
III	16.6 (14.4–17.9)	16.8 (16.5–17.1)	12.3 (10.6–13.5)	17.9 (16.3–20	16.8 (12.5–18.1)	15.6 (13–17.6)	14.4 (13.3–15.4)
IV	28.4 (27.2–29.5)	25.1 (23.8–27.9)	18 (16.5–20.1)	30.7 (28.9–33.7)	30.8 (28.9–32.8)	29.3 (24.5–36.4)	21.5 (19.6–23.2)
V	12.2 (12.1–12.2)	12.7 (11.5–13.2)	12.1 (10.6–13.4)	12.7 (11.7–13.3)	12.2 (10.7–13.1)	13.1 (12.3–14)	12.9 (11.2–14.2)
VI	12.4 (12.2–12.8)	13.2 (12.2–14.1)	12.6 (12–13.4)	12.8 (12.2–13.4)	12.6 (11.6–13.7)	13.3 (12.3–14.5)	13.4 (12.4–14.7)
VII	12.9 (12.7–13.4)	12.5 (11.7–13.5)	12.1 (9.9–13.5)	12.7 (11.9–13.4)	12.4 (12.1–13.1)	13.1 (12.7–13.5)	13 (11.9–14.4)
DBx	30.4 (27.7–32.8)	31.6 (29.2–33.9)	27.1 (25.4–29.2)	31.3 (28.9–34.8)	32.2 (29.2–35.2)	36.8 (34.3–40.1)	36.6 (34.2–39.6)
DBw	16 (13.4–18.6)	16.9 (14.4–21.4)	10.4 (8.4–12)	16.5 (13.4–18.8)	17.9 (15.3–21.7)	15 (11.2–17.7)	10.4 (7.8–14.9)
DBh	16.4 (14.4–19.5)	13.2 (12.2–14.2)	24.5 (22.3–29.8)	14.3 (13.1–15.7)	13.7 (11.7–15.9)	13.8 (11.9–15.8)	44.8 (41.1–50.2)
DBct	25.4 (24.2–27.4)	22.8 (21.7–24.7)	20 (18.3–22.1)	27.3 (24.4–30.2)	27.3 (22.5–32.8)	28.2 (24.7–31.5)	27.8 (22.4–36.9)
DAa	36.8 (36.4–37.3)	36.8 (35.1–37.9)	33.9 (33.1–34.6)	37.9 (35.7–43.7)	41.3 (38.3–43.7)	38.9 (23.6–43.8)	34.3 (32.1–38.2)
DAab	12.8 (12.1–13.3)	13.4 (12.5–14.1)	11.2 (10.7–11.7)	12.8 (8.6–14.7)	14 (12.9–15.7)	12.4 (9.7–14.3)	14.4 (13.2–15.4)
DAe	3.7 (3.6–3.8)	4 (3.3–5)	3.8 (3.4–4.5)	3.5 (3–4)	5.7 (5.1–6.2)	7.4 (5–11.6)	4.6 (3.6–5.4)
DCn	12.1 (9.1–17.1)	27.8 (24.5–34.2)	11.7 (10.5–13.5)	23.8 (22–28)	17.6 (15.6–19.6)	13.1 (9.2–16.7)	14.5 (13.7–15.6)
VBx	40.3 (40–40.9)	39.5 (36.3–41.5)	43.3 (41.6–45.8)	40.7 (38.2–44.7)	43.9 (34.6–48.6)	50.1 (44.5–53.2)	52.3 (49.7–59.5)
VBw	8.78 (7.1–9.6)	6.8 (6.3–8)	6.4 (4.9–8.6)	8.3 (7.3–9.8)	12.5 (10.6–16.1)	9.4 (8–11)	9.8 (8.5–11.5)
VAa	27.3 (26.1–28.4)	23.4 (21.9–24.6)	24 (23.2–24.6)	31.1 (28.5–34.3)	36.3 (34.7–37.2)	27 (25.3–29)	30.1 (29.2–31.2)
VAab	8.3 (7.9–8.8)	6.8 (6.1–7.5)	7.3 (6.5–10.1)	8.2 (7.8–9.1)	10.2 (9.3–11.3)	7.5 (7.2–7.6)	10.5 (9.8–11.9)
VAe	14.1 (12.8–16.3)	10.5 (9.2–11.5)	13.7 (9.5–15.4)	11.5 (7.5–14.1)	13.7 (12.3–14.8)	15.7 (13.8–18)	27.5 (23.2–29.8)
VCn	10.1 (9.5–10.6)	11.2 (10.3–13.3)	6.2 (5.5–7.1)	11.6 (10–14)	9.8 (8–11.6)	7.4 (5.8–8.7)	9.8 (7.5–12.5)

El-Gheit drainage canal, Telbanah drainage canal (Egypt), Blue Nile, White Nile (Sudan), Krugerdrift Dam, Gariep Dam, Lake Tzaneen, Middle Letaba Dam, Nwanedi-Luphephe Dams, Phalaborwa Barrage, Vaal Dam (South Africa), Lake Tana (Ethiopia), Lake Turkana (Kenya) and Lake Kariba (Zimbabwe) (Truter 2022, Truter et al. 2023).

New host: *Clarias ngamensis*.

New localities: Lake Lubanda, Luapula River.

Prevalence: P = 6.7% (Lake Lubanda); P = 40% (Luapula River).

Mean intensity: MI = 1 ± 1 (Lake Lubanda); MI = 2.7 ± 3.3 (Luapula River).

Voucher specimens: 17 Voucher specimens XXII.3."06; 15; 18; 23; 25; 26; 28; 29; 31; 35; 37–43" are deposited in the collection of the Research Group Zoology: Biodiversity & Toxicology, at Hasselt University (Diepenbeek, Belgium).

Diagnosis: Tubular and straight male copulatory organ (MCO), widest at base and narrowing towards distal extremity. Accessory piece ends in two distinctive lateral, club-shaped outgrowths projecting from its posterior half. Vagina partly sclerotized tube. Dorsal anchor without shaft nor guard, with broad base and short point. Dorsal bar with rectangular centre, funnel-like median process posteriorly directed and two lateral expansions. Large dorsal cuneus triangular. Ventral anchor without shaft nor guard, with regularly curved blade. Ventral bar with two lateral branches. Y-shaped ventral cuneus. Seven pairs of hooks: pairs IV, III, I (decreasing size) larger than pairs II, V, VI and VII, latter pairs almost equal (Fig. 3).

Remarks: The specimens are reminiscent of the morphological characters of the MCO of the original description of *Q. aegypticus* by El-Naggar and Serag (1986) (base of copulatory tube wider, anterior end pointed; accessory piece terminates in two hooks and possesses two distinctive, lateral club-shaped outgrowths, projecting from the posterior half) as well as the drawings/measurements provided by El-Naggar and Serag (1986), Kritsky and Kulo (1988), Douëllou and Chishawa (1995) and Francová et al. (2017). We consider

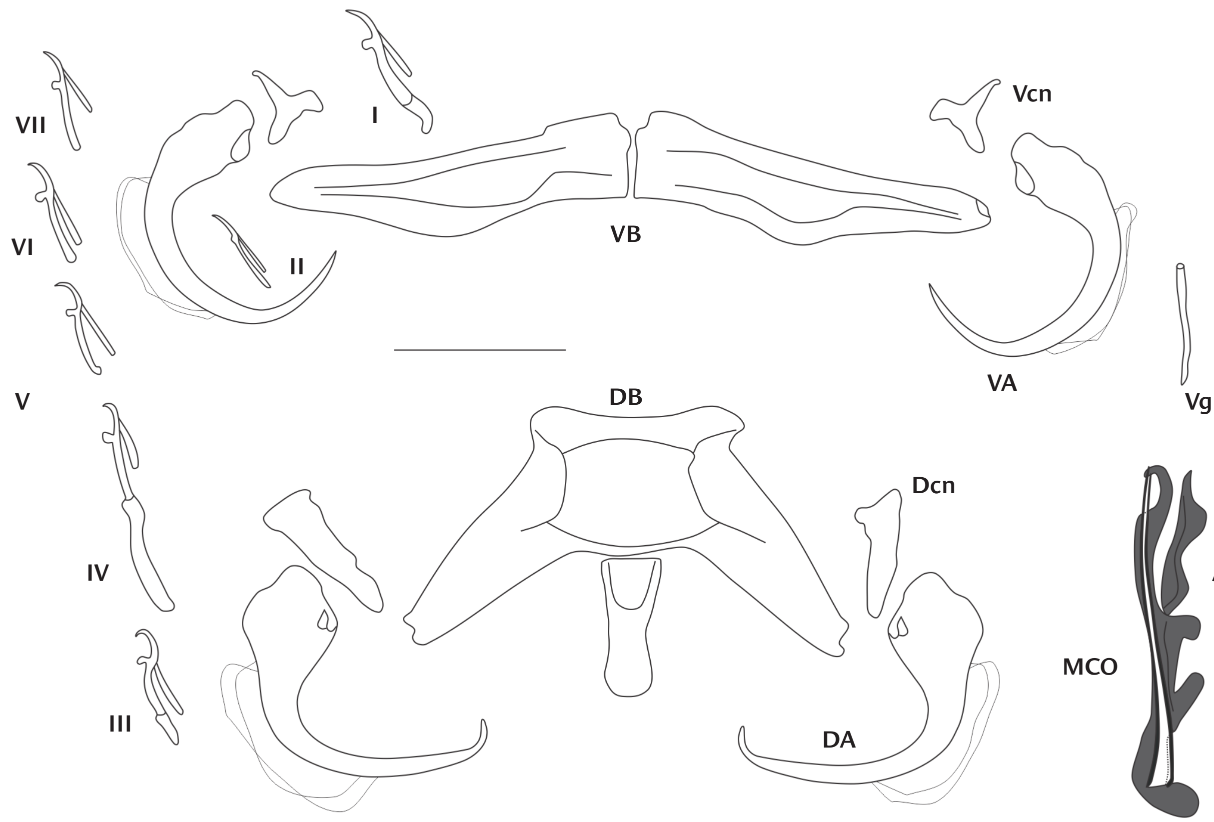

Figure 3. Sclerotized parts of the genitals and haptor of *Quadriacanthus aegypticus*. With the male copulatory organ (MCO), accessory piece (AP), vagina (Vg), ventral bar (VB), ventral anchor (VA), ventral cuneus (Vcn), dorsal bar (DB), dorsal anchor (DA), dorsal cuneus (Dcn), (I-VII) hooks. Scale bar: 20 µm.

them conspecific, as the morphometrical characteristics of the sclerotized structures correspond to those reported for *Q. aegypticus*, i.e., AP (34–44) in this study vs (33–49), (36–44), (39–44) Kritsky and Kulo (1988), Douëllou and Chishawa (1995) and Francová et al. (2017) respectively; MCO (36–39) in this study vs (34–40), (36–40) following Douëllou and Chishawa (1995) and Francová et al. (2017). However the shafts of the ventral and dorsal anchors deviate from the original description outlined in El-Naggar and Serag (1986).

Quadriacanthus allobychowskiella Paperna, 1979

Type-host and locality: *C. gariepinus*; Uganda, Lake George (Paperna 1979).

Other localities: Nile River basin: Ammar drainage canal, Damietta branch, Lake Manzala, Mansoura drainage canal, Nawasa El-Gheit drainage canal, Nile River barrage, Telbanah drainage canal (Egypt), and Middle Letaba Dam (South Africa) (Truter 2022, Truter et al. 2023).

New host: *Clarias ngamensis*.

New localities: Lake Lubanda; Luapula River.

Prevalence: P = 40% (Lake Lubanda); P = 60% (Luapula River).

Mean intensity: MI = 1.5 ± 1.9 (Lake Lubanda); MI= 1.7 ± 1.1 (Luapula River).

Voucher specimens: 24 voucher specimens XXII.3."04; 05; 07–14; 16; 17; 19–22; 24; 27; 30; 32–34; 36;44" are deposited in the collection of the Research Group Zoology: Biodiversity & Toxicology, at Hasselt University (Diepenbeek, Belgium).

Diagnosis: Tube-shaped MCO wider at its base and gradually shrinking towards distal extremity. Accessory piece possessing two lateral outgrowths arising from outer surface of middle region of sclerite and ending with well-developed hook. Vagina relatively long tube, partly sclerotized duct wide at the basal extremity. Dorsal anchor without shaft nor guard, with broad base and short point. Dorsal bar with rectangular centre, small median process posteriorly directed and two lateral expansions. Large dorsal cuneus with bifid end. Ventral anchor regularly curved without shaft nor guard. Ventral bar

V-shaped with two lateral branches. Y-shaped ventral cuneus. Seven pairs of hooks: pairs IV, III, I (decreasing size), bigger than pairs II, V-VII almost equal (Fig. 4).

Remarks: This species, *Q. allobychowskiella* (synonyms: *Quadriacanthus clariadis allobychowskiella* Paperna, 1979; *Quadriacanthus kearni* El-Naggar & Serag, 1985) could be mixed up with *Q. clariadis* Paperna, 1961 by the morphology of the ventral anchors with a curved shaft and long point, the dorsal anchor with an elongated bent shaft and short point, and the Y-shaped ventral cunei. It is however easily distinguishable as *Q. allobyschowskiella* by possessing a large dorsal cuneus with a bifid end vs a triangular one for *Q. clariadis* (Kritsky and Kulo 1988, Francová et al. 2017, Truter 2022, Truter et al. 2023).

Quadriacanthus amakaliae Kasembele, Bahanak & Vanhove, sp. nov.

https://zoobank.org/83453616-133F-4558-84E3-0EC86C687CC3

Type-host and locality: *C. ngamensis*; DR Congo, Haut-Katanga, Lubanda village, Lake Lubanda 11°04'S, 27°55'E, November 2021, G.K. Kasembele leg.

Other locality: Luapula River.

Prevalence: P = 6.7% (Lake Lubanda); P = 6.7% (Luapula River).

Mean intensity: Lake Lubanda: 3 ± 0; Luapula River: 1 ± 0.

Type-material: The holotype HU #888 and three paratypes HU #889; 890; 987 are deposited in the collection of the Research Group Zoology: Biodiversity & Toxicology, at Hasselt University (Diepenbeek, Belgium).

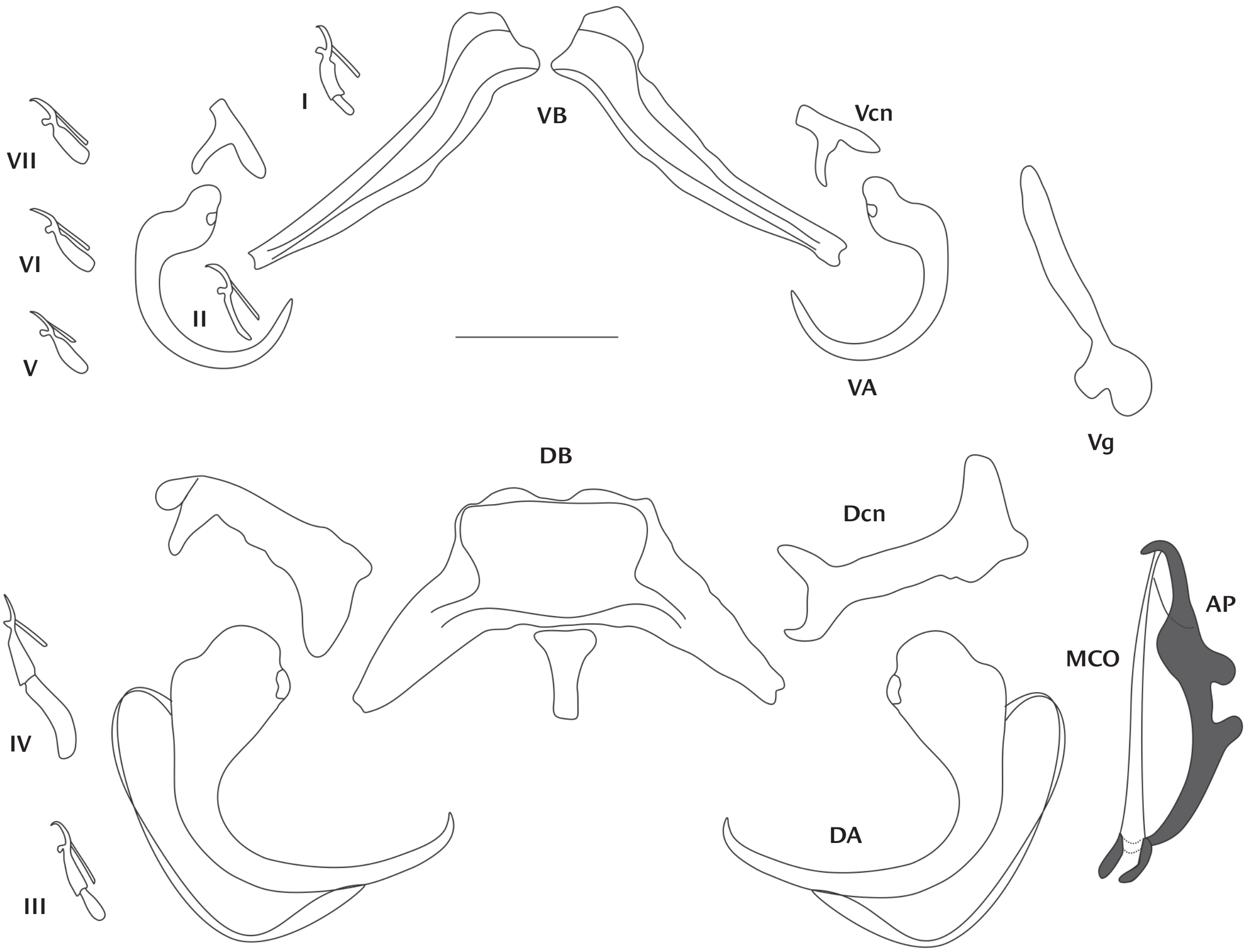

Figure 4. Sclerotized parts of the genitals and haptor of *Quadriacanthus allobychowskiella*. With the male copulatory organ (MCO), accessory piece (AP), vagina (Vg), ventral bar (VB), ventral anchor (VA), ventral cuneus (Vcn), dorsal bar (DB), dorsal anchor (DA), dorsal cuneus (Dcn), (I-VII) hooks. Scale bar: 20 µm.

Etymology: This species is named in honour of Annette Megameno Amakali, MSc, of the National Marine Information and Research Centre (NatMIRC), Ministry of Fisheries and Marine Resources, Swakopmund, Namibia, for her contribution in lab work.

Description: Tube-shaped MCO (thick-walled) wide at its base and gradually shrinking towards the distal extremity. Accessory piece articulating with MCO, ending in point and having two filaments on either side of the terminal point. Funnel shaped tubular vagina. Dorsal bar with rectangular centre, median process posteriorly directed and two lateral expansions. Dorsal anchor without shaft nor guard, with broad base, shaft sharply curved, ending with short point. Dorsal cuneus triangular. Ventral bar V-shaped with two lateral branches. Ventral anchor without shaft nor guard, with base smaller than that of dorsal anchor, and curved blade. Ventral cuneus smaller than dorsal one. Seven pairs of hooks: pair IV bigger than the rest which are almost equal in length (Fig. 5).

Remarks: *Quadriacanthus amakaliae* sp. nov. is comparable to *Q. barombiensis* Bahanak, Nack & Pariselle, 2022, *Q. levequei* Birgi, 1988 and *Q. anaspidoglanii* Akoumba, Pariselle & Tombi, 2017, described in Cameroon from *C. maclareni*, *C. pachynema* and *Anaspidoglanis macrostoma*, respectively, by the shape of the dorsal bar median process, the tubular shape of the MCO which is enlarged at the basal zone and tapered at the distal end, and the shape of the accessory piece ending in a point. However, some differences differentiate them, namely: (i) the dorsal bar postero-median process without filaments at its end vs two filaments present in *Q. barombiensis* and *Q. levequei*; (ii) the morphology of the distal extremity of the accessory piece with one small hook surrounded by two filaments vs simply one small hook in *Q. barombiensis* and *Q. anaspidoglanii* and two small hooks in *Q. levequei*; (iii) the difference in the size of the following sclerotized parts for *Q. amakaliae* sp. nov. vs *Q. barombiensis*: MCO (34–37.9) vs (25–29), AP (29–33) vs (20–26).

Quadriacanthus halajiani Kasembele, Bahanak & Vanhove, sp. nov.

https://zoobank.org/C86AAF04-FA01-49CD-B24E-1B3BFCB39FA5

Type-host and locality: *C. ngamensis*; DR Congo, Haut-Katanga, Lubanda village, Lake Lubanda 11°04'S, 27°55'E, November 2021, G.K. Kasembele leg.

Other locality: Luapula River.

Prevalence: P = 46.7% (Lake Lubanda); P = 40% (Luapula River).

Mean intensity: Lake Lubanda: 1.9 ± 1.8; Luapula River: 2.7 ± 2.3

Type-material: The holotype HU #985 and 27 paratypes HU #891; 894; 896–899; 902; 903; 906–909; 918; 919; 923; 9388–940; 950; 951; 960; 967; 973; 986; 988; 992; 999 are deposited in the collection of the Research Group Zoology: Biodiversity & Toxicology, at Hasselt University (Diepenbeek, Belgium).

Etymology: This species is named in honour of Dr. Ali Halajian for his valuable and kind contribution during field work and practice in fish parasitology in South Africa (University of Limpopo).

Description: Tube-shaped MCO. Accessory piece simple, thicker in its distal part and with bulge and depression respectively on the external and internal sides of its median part and ending in well-developed point. Vagina not observed. Dorsal anchor without shaft nor guard, with broad base and short point. Dorsal bar with rectangular centre, medium median process posteriorly directed and two lateral expansions. Dorsal cuneus big and triangular. Ventral anchor without shaft nor guard, with regularly curved blade. Ventral bar V-shaped with two lateral branches. Y-shaped ventral cuneus. Seven pairs of hooks: pairs IV, III, I (decreasing size) larger than pairs II, V-VII almost equal (Fig. 6).

Remarks: Based on the comparative morphology of the ventral and dorsal bars, ventral and dorsal cunei, *Q. halajiani* sp. nov. is comparable to *Q. agnebiensis* N'Douba, Lambert & Euzet, 1999 and *Q. longifilisi* N'Douba, Lambert & Euzet, 1999 described from *Heterobranchus isopterus* and *H. longifilis*, in Ivory Coast. The new species differs from the latter two species by the shape and size of the MCO, slightly curved vs straight tube in *Q. longifilisi* (28.3–34.8) vs (35–42), the AP, ending in a point and possessing a bulge at its external side vs two points at the distal part of the AP of *Q. agnebiensis*, with two bulges at its external side (31.7–35.7) vs (38–43), and the vagina, non-sclerotized vs sclerotized in the two other species. *Quadriacanthus halajiani* sp. nov. also differs in the length of the dorsal cuneus (22–28) vs (7–10) and (7–17) from *Q. agnebiensis* and *Q. longifilisi* respectively.

Quadriacanthus domatanai Kasembele, Bahanak & Vanhove, sp. nov.

https://zoobank.org/7F290D48-6835-4D0F-9E05-7BE97306AFF2

Type-host and locality: *C. ngamensis*; DR Congo, Haut-Katanga, Lubanda village, Lake Lubanda 11°04'S, 27°55'E, November 2021, G.K. Kasembele leg.

Other locality: Luapula River

Prevalence: P = 13.3% (Lake Lubanda); P = 20% (Luapula River).

Mean intensity: Lake Lubanda: 1.5 ± 1.6; Luapula River: 2 ± 2.1

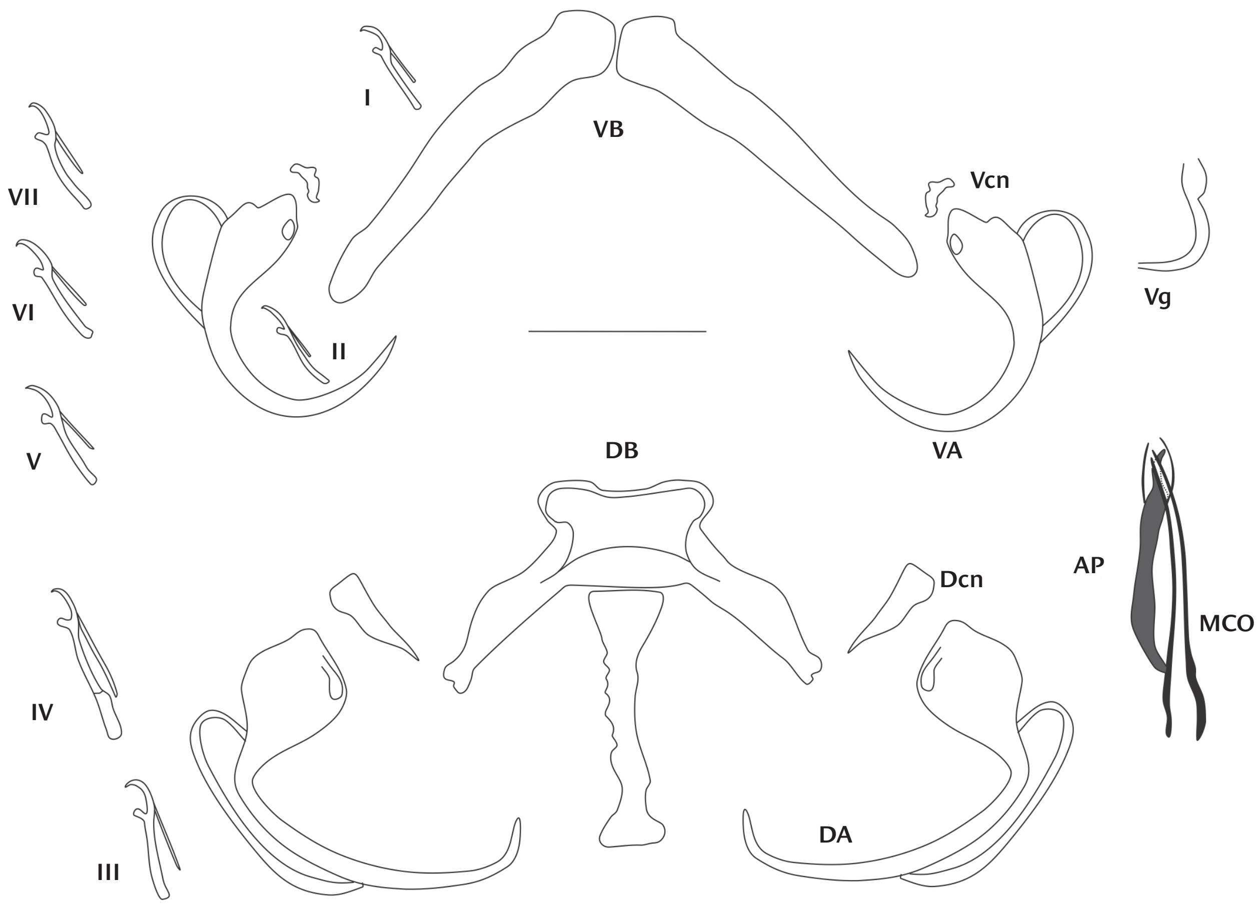

Figure 5. Sclerotized parts of the genitals and haptor of *Quadriacanthus amakaliae* sp. nov. With the male copulatory organ (MCO), accessory piece (AP), vagina (Vg), ventral bar (VB), ventral anchor (VA), ventral cuneus (Vcn), dorsal bar (DB), dorsal anchor (DA), dorsal cuneus (Dcn), (I-VII) hooks. Scale bar: 20 µm.

Type-material: The holotype HU n° 892 and seven paratypes HU #900; 901; 928–930; 1001; 1004 are deposited in the collection of the Research Group Zoology: Biodiversity & Toxicology, at Hasselt University (Diepenbeek, Belgium).

Etymology: This species is named in honour to Doma Tana Anicet, MSc, of the Unité de Recherche en Biodiversité et Exploitation durable des Zones Humides, Faculté des Sciences agronomiques, Université de Lubumbashi, DR Congo, for his valuable and kind assistance during our field campaigns.

Description: MCO long, wide at proximal end and tapered at distal extremity. Accessory piece long, robust and thickening in its median part, and with bulge on the external and internal faces and ending in hook. Vagina not observed. Dorsal anchor without shaft nor guard, but with curved blade ending with short point. Dorsal bar with rectangular centre, one small median process posteriorly directed and two lateral expansions. Dorsal cuneus triangular. Ventral anchor without shaft nor guard, with thin and regularly curved blade. Ventral bar V-shaped with two lateral branches. Y-shaped ventral cuneus. Seven pairs of hooks: pairs IV, III, I (decreasing size) larger than pairs II, V, VI and VII, latter pairs almost equal in length (Fig. 7).

Remarks: This species is similar to *Q. ndoubai* Bahanak, Pariselle & Bilong Bilong, 2017 and *Q. macrocirrus* N'Douba, Lambert & Euzet, 1999, described respectively on *H. longifilis* and *H. isopterus*, considering the morphology of their haptoral structures (the robust shape of the ventral and dorsal bars). However, they can be distinguished by the shape of the MCO (large and slightly curved vs large and straight in *Q. macrocirrus*), and the shape of the AP (large, robust, thickening in its median part and ending in a point vs simple, long and tapered in *Q. macrocirrus*, and ending in a fork in *Q. ndoubai*).

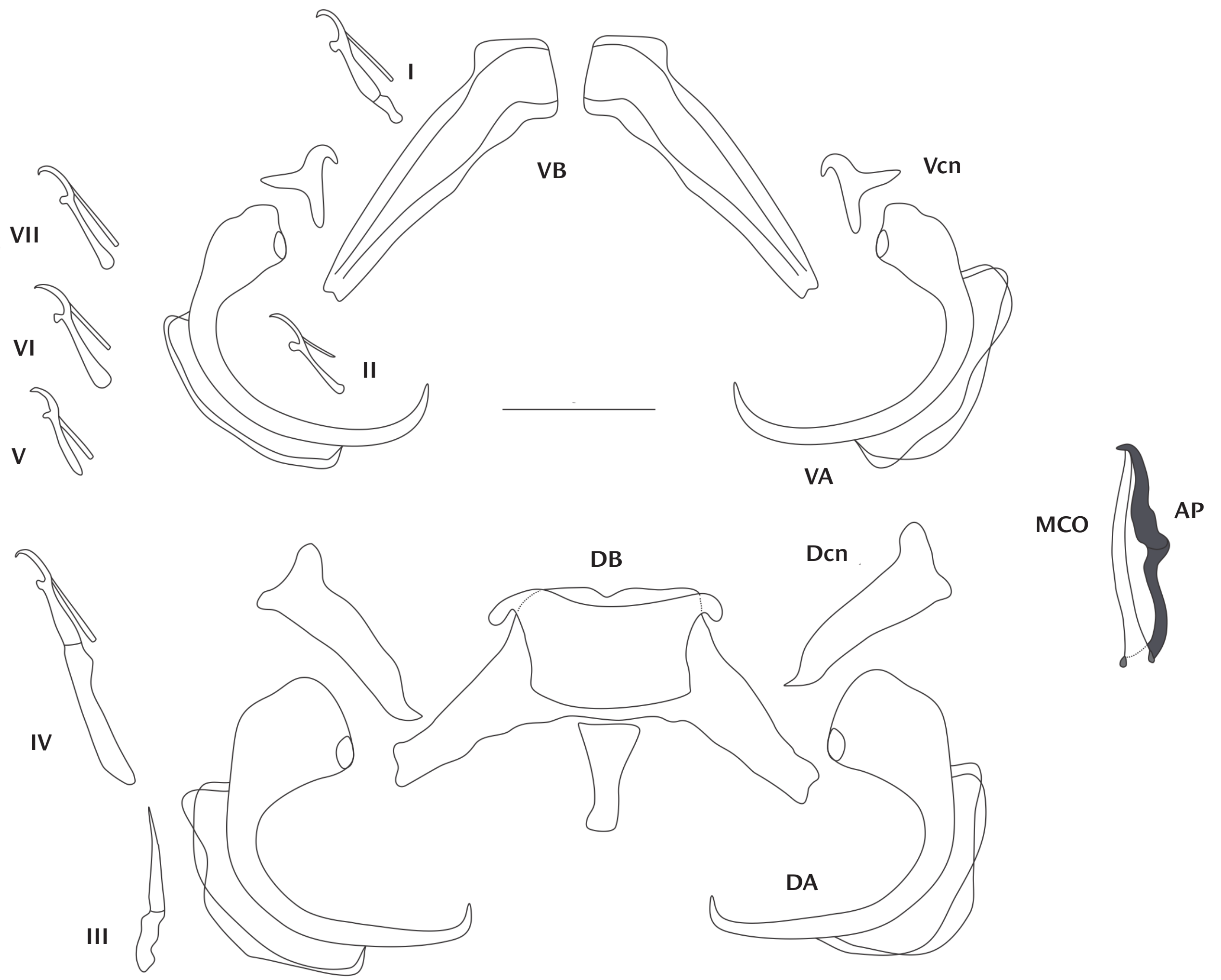

Figure 6. Sclerotized parts of the genitals and haptor of *Quadriacanthus halajiani* sp. nov. With the male copulatory organ (MCO), accessory piece (AP), ventral bar (VB), ventral anchor (VA), ventral cuneus (Vcn), dorsal bar (DB), dorsal anchor (DA), dorsal cuneus (Dcn), (I-VII) hooks. Scale bar: 20 µm.

Quadriacanthus lubandaensis Kasembele, Bahanak & Vanhove, sp. nov.

https://zoobank.org/F914590C-3987-466B-8FB0-470B7C280F7D

Type-host and locality: *Clarias ngamensis*; DR Congo, Haut-Katanga, Lubanda village, Lake Lubanda 11°04'S, 27°55'E, November 2021, G.K. Kasembele leg.

Other locality: Luapula River.

Prevalence: P = 26.7% (Lake Lubanda); P = 33.3% (Luapula River).

Mean intensity: Lake Lubanda: 1 ± 0.8; Luapula River: 1.8 ± 1.4.

Type-material: The holotype HU #954 and 12 paratypes HU #893; 895; 904; 905; 914; 920; 934; 956; 972; 978; 990; 991 are deposited in the collection of the Research Group Zoology: Biodiversity & Toxicology, at Hasselt University (Diepenbeek, Belgium).

Etymology: The epithet *lubandaensis* refers to the type locality.

Description: MCO simple and straight tube. Accessory piece articulating with copulatory tube, with hook-like ending. Vagina not observed. Dorsal anchor without shaft nor guard, with broad base, curved shaft, medium point lenght. Dorsal bar with rectangular centre, medium median process posteriorly directed and two lateral expansions. Dorsal cuneus triangular. Ventral anchor without shaft nor guard, with regular curved blade. Ventral bar V-shaped

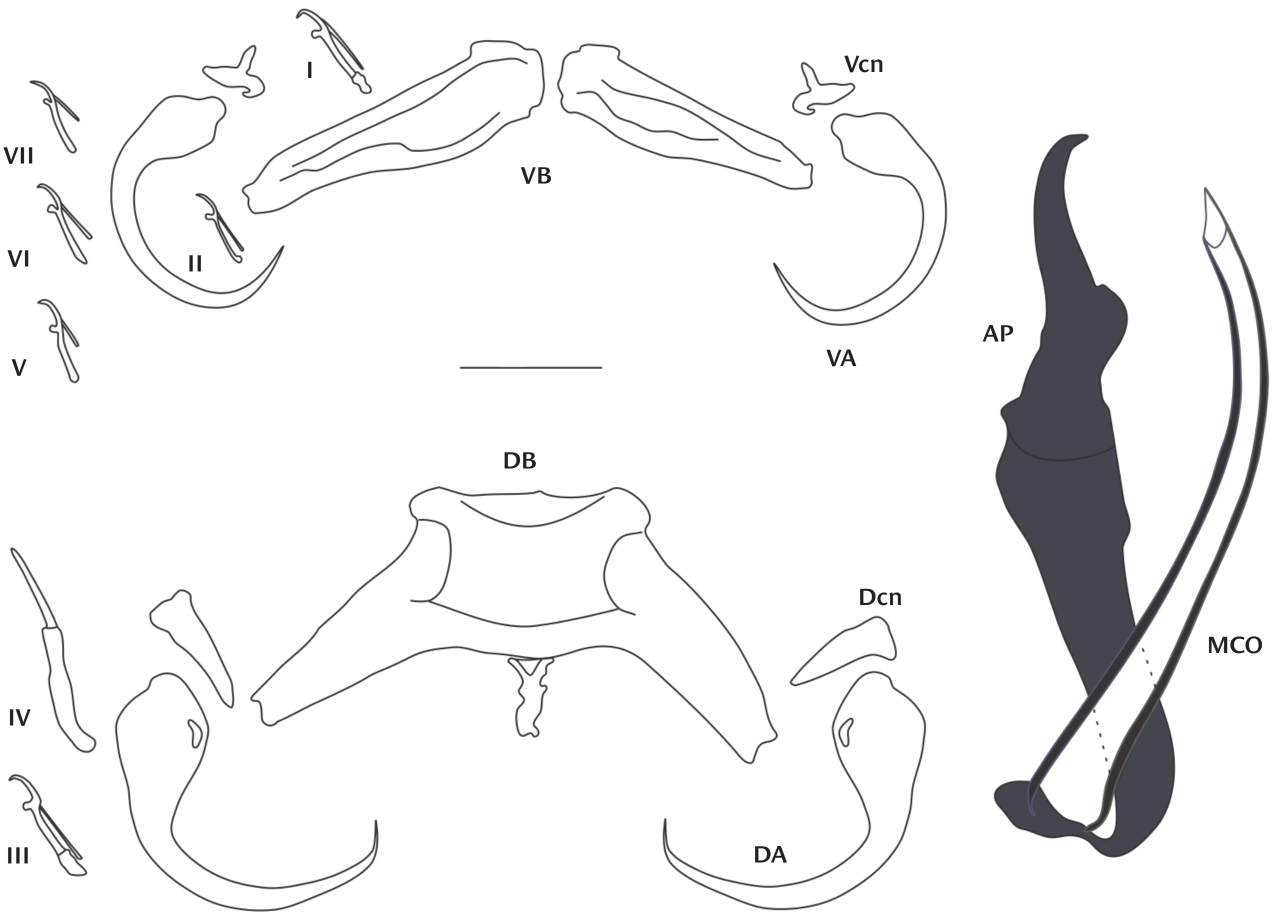

Figure 7. Sclerotized parts of the genitals and haptor of *Quadriacanthus domatanai* sp. nov. With the male copulatory organ (MCO), accessory piece (AP), ventral bar (VB), ventral anchor (VA), ventral cuneus (Vcn), dorsal bar (DB), dorsal anchor (DA), dorsal cuneus (Dcn), (I-VII) hooks. Scale bar: 20 µm.

with two lateral branches. Y-shaped ventral cuneus. Seven pairs of hooks: pairs IV, I, III (decreasing size) larger than pairs II, V, VI and VII. Four latter pairs are almost equal in length (Fig. 8).

Remarks: This species is comparable to *Q. fornicatus* Francová & Řehulková, 2017, described from *C. gariepinus* from Sudan (Francová et al. 2017) by the morphology of the ventral bar, the ventral anchors, the ventral and dorsal cunei, and the MCO (straight tube, base simple). However, these species are different in the morphology of the dorsal anchors (with long points in *Q. fornicatus* 12–13 vs 5–11 in *Q. lubandaensis* sp. nov.), the MCO (with a thickened wall) and the AP (with a well developed hook at the distal end) in *Q. fornicatus* vs the MCO (with thin margin) and the AP (hook-like, not well developed, less curved) in *Q. lubandaensis* sp. nov.

Quadriacanthus curvicirrus Kasembele, Bahanak & Vanhove, sp. nov.

https://zoobank.org/8DCFEA56-C3A9-426F-94E4-B620B0DE2F5B

Type-host and locality: *Clarias ngamensis*; DR Congo, Haut-Katanga, Kasenga, Luapula River 10°24'S, 28°37'E, November 2021, G.K. Kasembele leg.

Prevalence: P = 66.7% (Luapula River).

Mean intensity: Luapula River: 6.3 ± 5.8.

Type-material: The holotype HU n° 984 and 62 paratypes HU n° 910–913; 915–917; 921; 922; 924–927; 931–933; 935–937; 941–949; 952; 953; 955; 957 –959; 961–966; 968–971; 974–976; 979–984; 989; 993–998; 1000; 1002; 1003 are deposited in the collection of the Research Group Zoology: Biodiversity & Toxicology, at Hasselt University (Diepenbeek, Belgium).

Etymology: the epithet *curvicirrus* refers to the curved form of the male copulatory tube.

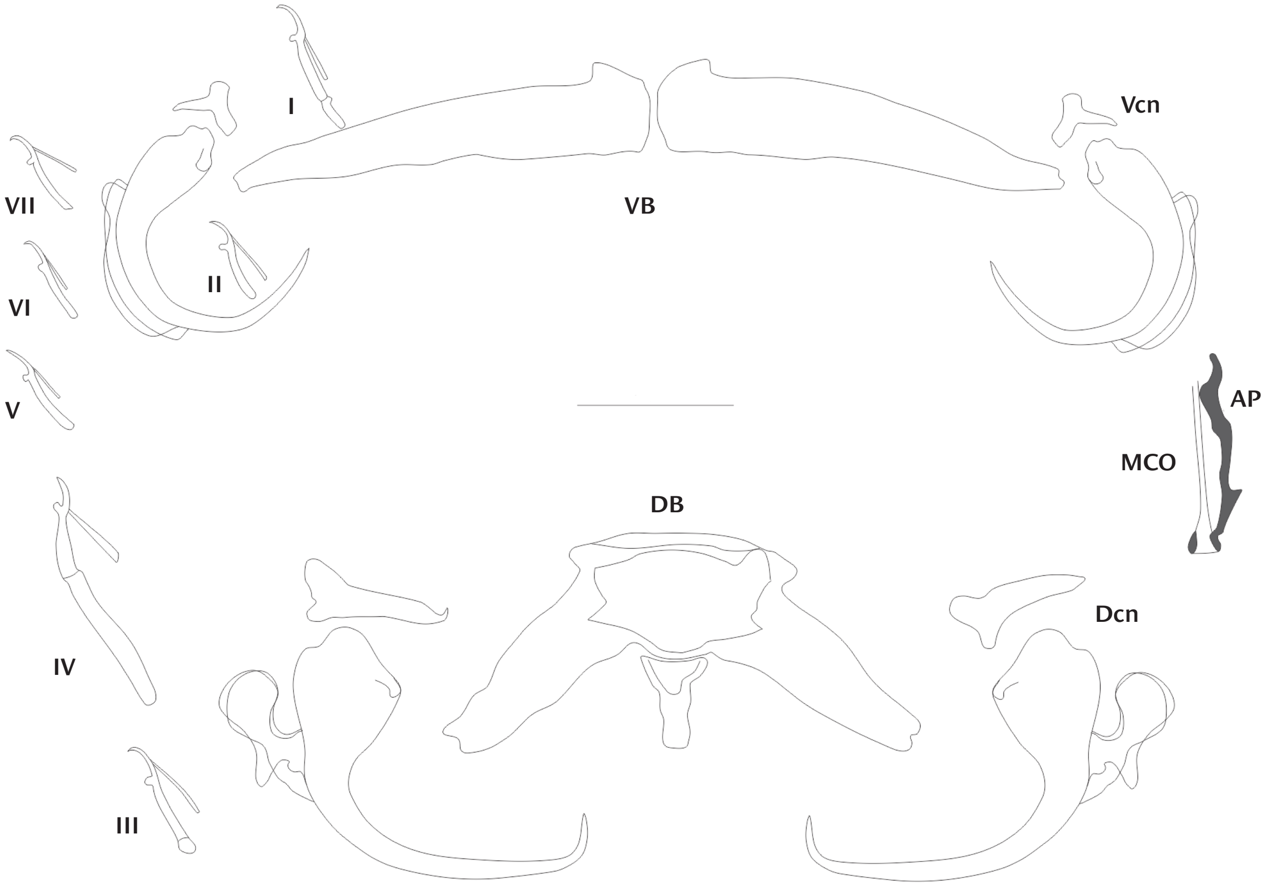

Figure 8. Sclerotized parts of the genitals and haptor of *Quadriacanthus lubandaensis* sp. nov. With the male copulatory organ (MCO), accessory piece (AP), ventral bar (VB), ventral anchor (VA), ventral cuneus (Vcn), dorsal bar (DB), dorsal anchor (DA), dorsal cuneus (Dcn), (I-VII) hooks. Scale bar: 20 µm.

Description: Tubular MCO, with simple base, curved at its distal end, hook shaped, with a swollen portion just before the curvy part. Accessory piece massive with outgrowths posteriorly and anteriorly, with the distal part smaller, ending in a point. Dorsal anchor without shaft nor guard, with broad base, shaft sharply bent, short point. Dorsal bar with rectangular centre, broad and long median process posteriorly directed and two lateral expansions. Dorsal cuneus triangular. Ventral anchor without shaft nor guard, with narrow base and curved blade. Ventral bar V-shaped with two lateral branches. Ventral cuneus triangular. Seven pairs of hooks: pairs IV larger than pairs I, II, III, V, VI and VII. Four latter pairs are almost equal in length (Fig. 9). Vagina not observed.

Remarks: *Quadriacanthus curvicirrus* sp. nov. is similar to *Q. barombiensis* in the shape of the ventral and dorsal anchors and cunei. They can be distinguished by the median process of the dorsal bar without filaments at its end in *Q. curvicirrus* sp. nov. vs with two filaments in *Q. barombiensis*; with respective median process length h= (41.1–50.2) vs (27–32). The MCO of *Q. curvicirrus* sp. nov. is characteristic, tubular, curved at its distal end with a simple base and the accessory piece massive with outgrowths posteriorly and anteriorly directed. This differs from the situation in *Q. barombiensis* with a tubular straight MCO and a simple, slightly S-shaped accessory piece, ending in one small point.

DISCUSSION

This study is the first record of parasites of *Quadriacanthus* as well as of monogeneans in general, from *C. ngamensis*. The report of *Q. aegypticus* and *Q. allobychowskiella* (being a new geographical record in the Congo Basin as well) and

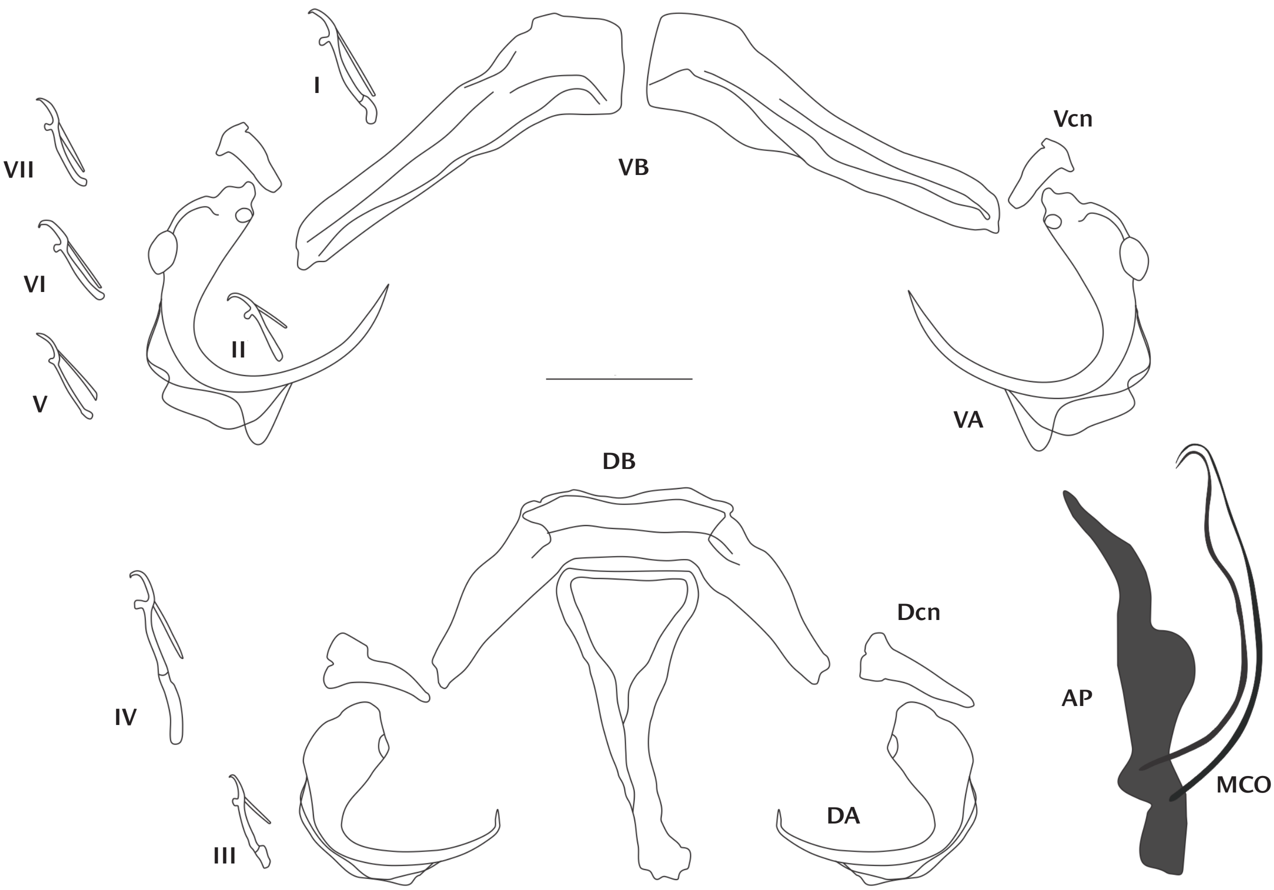

Figure 9. Sclerotized parts of the genitals and haptor of *Quadriacanthus curvicirrus* sp. nov. With the male copulatory organ (MCO), accessory piece (AP), ventral bar (VB), ventral anchor (VA), ventral cuneus (Vcn), dorsal bar (DB), dorsal anchor (DA), dorsal cuneus (Dcn), (I-VII) hooks. Scale bar: 20 µm.

the description of five new species of *Quadriacanthus* (Figs 3–12) on *C. ngamensis* extend the list of known fish species hosting members of *Quadriacanthus* and brings the known number of parasites species in this genus to 44 (Vas et al. 2012, Bouah et al. 2021, Řehulková et al. 2018, Bahanak et al. 2022). So far, *Q. aegypticus* and *Q. allobychowskiella* are known as strictly specific or oioxenous to *C. gariepinus* (Lim et al. 2001, Francová et al. 2017, Řehulková et al. 2018); their record on *C. ngamensis* changes their host-specificity from oioxenous to mesostenoxenous (Jarkovský et al. 2004, Šimková et al. 2006, Řehulková et al. 2013).

As this is the first study on monogeneans of *C. ngamensis*, it cannot be asserted that the number of species recorded is exhaustive. *Clarias ngamensis* being phylogenetically close to *C. gariepinus* (Agnèse and Teugels 2005), and as they co-habit in some lakes and rivers under the same ecological conditions (Teugels 2003), there may be a high probability of lateral transfers of parasites between them. Therefore the presence of these two *Quadriacanthus* species (*Q. allobychowskiella* and *Q. aegypticus*) on *C. ngamensis* could be the result of lateral transfer and could confirm the genetic proximity between these two fish species. To date, *C. gariepinus*, which is a widely distributed fish (Teugels 2003), is known to harbour 11 species of *Quadriacanthus* from different basins/ecoregions or geographic areas (Vas et al. 2012, Řehulková et al. 2018, Truter 2022, Truter et al. 2023). The record of these seven species of *Quadriacanthus* (of which five are new to science) on *C. ngamensis* is consistent with the hypothesis that the potential host diversity in the tropics and the relatively specificity of *Quadriacanthus* spp. could lead to the discovery of several, also new, parasite species (Birgi 1988, Bahanak et al. 2016, Konings et al. 2018).

Considering infection parameters in the current study system, *Q. allobychowskiella* and *Q. curvicirrus* sp. nov. are the

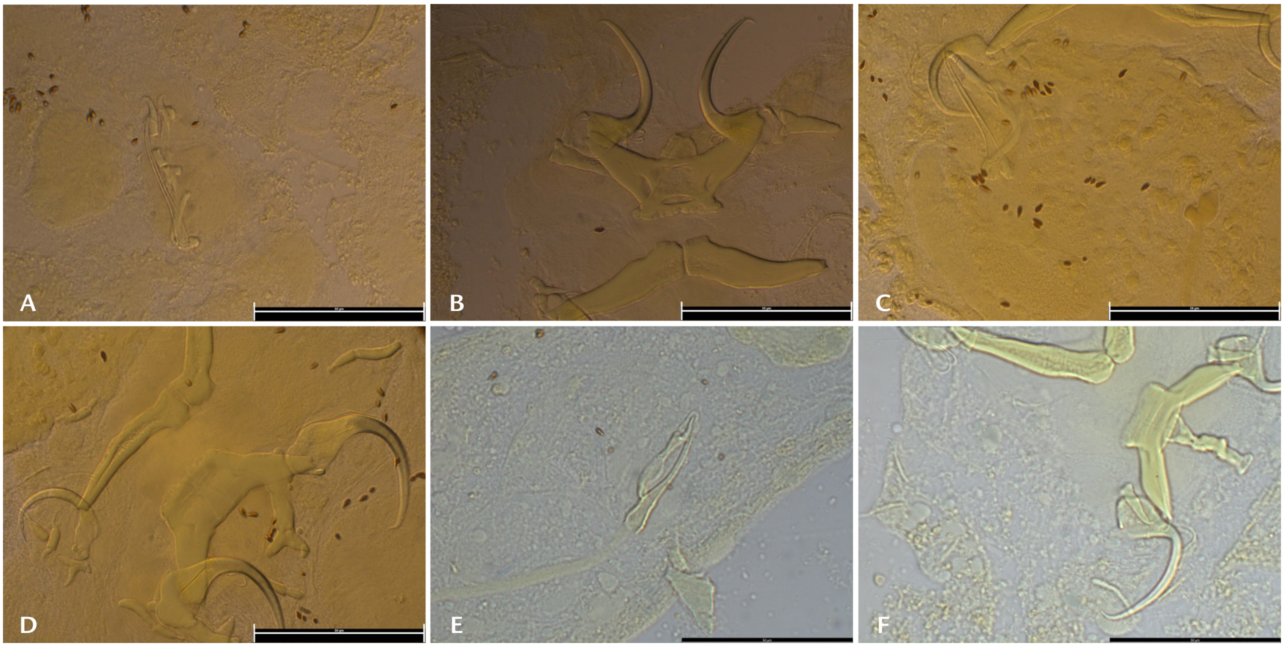

Figure 10. Photomicrographs of the sclerotized structures. (A, B) *Quadriacanthus aegypticus*: (A) genitals, (B) haptor; (C, D) *Quadriacanthus allobychowskiella*: (C) genitals, (D) haptor; (E, F) *Quadriacanthus amakaliae* sp. nov.: (E) genitals, (F) haptor. Scale bars: 50 µm.

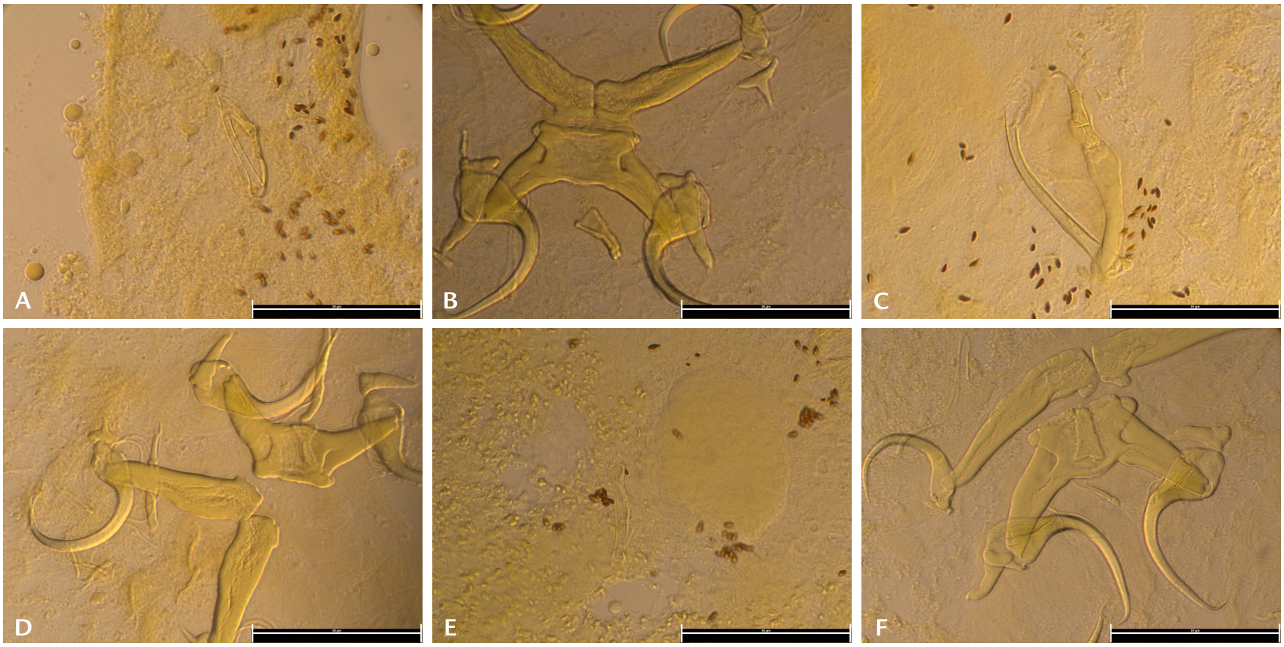

Figure 11. Photomicrographs of the sclerotized structures. (A, B) *Quadriacanthus halajiani* sp. nov.: (A) genitals, (B) haptor; (C, D) *Quadriacanthus domatanai* sp. nov.: (C) genitals, (D) haptor; (E, F) *Quadriacanthus lubandaensis* sp. nov.: (E) genitals, (F) haptor. Scale bars: 50 µm.

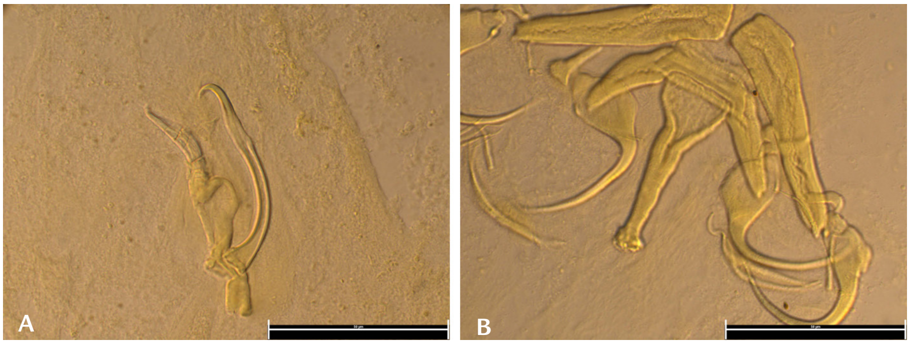

Figure 12. Photomicrographs of the sclerotized structures. (A, B) *Quadriacanthus curvicirrus* sp. nov.: (A) genitals, (B) haptor. Scale bars: 50 µm.

most prevalent species (P = 60% and 66.7% respectively, in the Luapula River) while the prevalence of the other *Quadriacanthus* species is intermediate (P = 10-50%), except for *Q. amakaliae* sp. nov. for both Lake Lubanda and the Luapula River, and *Q. aegypticus* in Lake Lubanda (rare taxa, P < 10%). However, *Q. aegypticus* had already been recorded to reach high prevalences, up to 90.9% on *C. gariepinus* in South Africa (Vaal River System) and Egypt (Nile Delta) (Crafford et al. 2014, Mashaly et al. 2020). On the other hand, all monogenean species recorded in this study have a MI lower than 10 (*Q. curvicirrus* sp. nov., having the highest MI of 6.3, followed by *Q. amakaliae* sp. nov. with MI: 3, *Q. aegypticus* and *Q. halajiani* sp. nov. with MI: 2.7 for both). Therefore, they are classified as of a very low intensity – sensu Valtonen et al. (1997).

Mashaly et al. (2020) reported a MI for *Q. aegypticus* ranging from 3.4 to 8.3 on *C. gariepinus* in Egypt, while Crafford et al. (2014) recorded for the same host and same monogenean species a mean intensity of 18.2 in South Africa. The level of infestation varies with environmental conditions (physico-chemical parameters of water, the degree of pollution, eutrophication), season, and biogeography, but it can also vary according to the sample size and the density of the hosts which can be related to fishing (Wood et al. 2010, Lacerda et al. 2018, Tavares-Dias et al. 2022). In the wild, a low density of hosts reduces transmission efficiency of parasites with a direct transmission mode as hosts are not abundant and not close nor in permanent contact. In such cases, infectious stages of parasites cannot easily locate their hosts after the short free swimming period (Tripathi et al. 2019, Vivanco-Aranda et al. 2019, Salsabilla et al. 2021). Low parasite loads in this study area could be the result of overfishing which reduces the size of host populations, as well as seasonality as parasite species composition and load can vary accordingly (Akoll et al. 2012, Igeh et al. 2020).

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GKK: Conceptualization, Data curation, Investigation, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. MPMV, CFBB, DNDB: Investigation, Validation. MPMV, ACM, MWPJ, WJLP, WJS, CFBB, DNDB: Formal analysis, Writing – review & editing.

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Data Resources

Slides of monogenean parasites are available in the collection of the Research Group Zoology: Biodiversity & Toxicology, at Hasselt University (Diepenbeek, Belgium)

Ethics approval and consent to participate

Fish were bought from fishermen. In the absence of relevant animal welfare regulations in the DRC, we used the guidelines and authorization in accordance with the Unité de Recherche en Biodiversité et Exploitation durable des Zones Humides (BEZHU) of the Université de Lubumbashi.

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