

Communication

Monogeneans from catfishes in Lake Tanganyika. II: new infection site, new record, and additional details on the morphology of the male copulatory organ of *Gyrodactylus transvaalensis* Prudhoe and Hussey, 1977

Archimède Mushagalusa Mulega^{1,2,3}, Maarten Van Steenberge^{2,4}, Nikol Kmentová², Fidel Muterezi Bukinga³, Imane Rahmouni¹, Pascal Masilya Mulungula^{3,5}, Abdelaziz Benhoussa¹, Antoine Pariselle^{1,6} and Maarten P.M. Vanhove²

¹ Laboratory Biodiversity, Ecology and Genome, Research Center Plant and Microbial Biotechnology, Biodiversity and Environment, Mohammed V University in Rabat, Morocco

² Hasselt University, Centre for Environmental Sciences, Research Group Zoology: Biodiversity & Toxicology, Diepenbeek, Belgium

³ Département de Biologie, Centre de Recherche en Hydrobiologie, B.P. 73, Uvira, Democratic Republic of the Congo.

⁴ OD Taxonomy and Phylogeny, Royal Belgian Institute for Natural Sciences, Belgium

⁵ Unité d'Enseignement et de Recherche en Hydrobiologie Appliquée, Département de Biologie-Chimie, ISP/Bukavu, Bukavu, Democratic Republic of the Congo

⁶ ISEM, Université de Montpellier, CNRS, IRD, Montpellier, France

* archimedemulega@gmail.com; Tel.: +212 6840298 319

Abstract : The ichthyofauna of Lake Tanganyika consists of 12 families of fish of which five belong to Siluriformes (catfishes). Studies on siluriforms and their parasites in this lake are very fragmentary. The present study was carried out to help fill the knowledge gap on the monogeneans parasitizing the siluriform fishes of Lake Tanganyika in general and more particularly *Clarias gariepinus*. The gills of a specimen of *Clarias gariepinus* (Clariidae) were examined for ectoparasites. We identified the monogenean *Gyrodactylus transvaalensis* (Gyrodactylidae). This is the first time this parasite was found infecting gills. We are the first to observe a large spine in the male copulatory organ of this species, and to provide measurements of its genital spines; this completes the description of the male copulatory organ which is important in standard monogenean identification. This is the first monogenean species reported on *C. gariepinus* at Lake Tanganyika and the third known species on a representative of Siluriformes of this lake. It brings the total number of species of *Gyrodactylus* recorded in Lake Tanganyika to four. Knowing that other locations where this species has been reported are geographically remote from Lake Tanganyika, we propose a "failure to diverge" phenomenon for *G. transvaalensis*.

Keywords: Clariidae, *Clarias gariepinus*, gills, Gyrodactylidae, Monogenea, Parasite, Platyhelminthes, D.R.C, East Africa, failure to diverge

The distribution of the catfishes (Siluriformes) spans every continent except Antarctica. There are now 4,094 recognized species distributed among 497 genera and 39 families in this order. In Africa's freshwaters, Siluriformes is represented by 476 species in 51 genera and nine families [1]. This order contains some of the world's most economically significant freshwater and brackish water fishes. In many nations, they make up a sizeable portion of inland fisheries. Several species are used in aquaculture and have been introduced around the globe. Additionally, many species are valuable to the aquarium industry, where they account for a substantial part of global trade [2]. A typical economically important species is *Clarias gariepinus* (Burchell, 1822) (Clariidae: Siluriformes), a strong, air-breathing catfish from Africa and the Middle East [3]. It is thought to be the freshwater fish species with the greatest natural geographic distribution in Africa. The most common fish species raised in sub-Saharan Africa seem to be African catfish [4] followed by 'tilapia' [5]. Despite the great diversity and economic importance of catfishes, there is a paucity of knowledge about their parasites [6-8].

Lake Tanganyika is the oldest [9,10] of the East African Rift Lakes. It has a unique ichthyofauna that also contains about 34 catfish species [11] belonging to five families: Bagridae, Clariidae, Claroteidae, Malapteruridae, and Mochokidae [12]. The lack of information on Tanganyikan and East African catfish parasites prompted us to study the monogeneans of representatives of Siluriformes in Lake Tanganyika [13].

Monogeneans (Platyhelminthes) are typically ectoparasitic on the gills of fishes or on the exterior surfaces of other cold-blooded vertebrates. Additionally, there are several endoparasitic species. The adults can anchor themselves to the surfaces of their hosts using their conspicuous posterior attachment structure, or haptor. This noticeable organ is equipped with suckers, different types of hooks, or both, and often varies in form between species [14]. Hence monogenean species identification is often based on the morphology of the sclerotized structures of the haptor but also on distal sclerotized sections of the reproductive systems: the male copulatory organ (MCO) and the vagina [15]. This work is part of a series of studies we are conducting on the monogeneans of siluriform representatives in Tanganyika. In particular, this study focuses on the fish *C. gariepinus*.

During a survey, in Lake Tanganyika, at the mouth of the Mutambala River (29°04.4042'E, 04°16.4598'S), in the Democratic Republic of the Congo (DRC) a single individual of *C. gariepinus* (Figure 1) was captured using a gill net. The specimen was killed by severing its spinal cord. Identification was carried out using the key of Fermon et al. [16].



Figure 1. Examined specimen of *Clarias gariepinus* from Lake Tanganyika (Uvira, DRC), picture by Fidel Muterezi Bukinga.

To enable the study of its parasites, the gills of the specimen were stored in 96% ethanol. These gills were examined under a Wild Heerbrugg® M8 binocular. We noted the presence of a single monogenean individual. The parasite specimen was recovered using an entomological needle and mounted on a slide in a drop of Hoyer's medium [17]. The slide was covered with a coverslip to flatten the specimen. It was left for 24 hours in a horizontal position before sealing the coverslip with glyceel [18]. Identification was done using a Leica® DM 2500 microscope equipped with a digital camera (Leica DMC 4500). Based on Příkladová et al. [19] the specimen was identified as belonging to *Gyrodactylus transvaalensis* Prudhoe & Hussey, 1977 (Figure 2). The slide was deposited at the Royal Museum for Central Africa, Tervuren, Belgium (number RMCA_VERMES_43681).



Figure 2. Photomicrograph of the haptoral hard parts of *Gyrodactylus transvaalensis* from the gills of *Clarias gariepinus* captured in Lake Tanganyika off the mouth of Mutambala River, D.R.C. (RMCA_VERMES_43681).

The measurements performed on the sclerified parts (Figure 3) of this monogenean follow [20] and are as follows (distances in μm): Hamulus total length (HTL) = 44.9; Hamulus root length (HRL) = 14.7; hamulus aperture distance (HAD) = 17.1; hamulus proximal shaft width (HPSW) = 6.9; hamulus point length (HPL) = 21.1; hamulus distal shaft width (HDSW) = 2.8; hamulus shaft length (HSL) = 27.9; hamulus inner curve length (HICL) = 1.5; the angle θ between the hamulus point tip through its base and the lower edge of the ventral bar articulation point on the hamulus $\theta = 44.0^\circ$; the angle between the hamulus point tip, its blade and the vector describing its length and base $\alpha = 5.6^\circ$; the angle λ between the hamulus point tip through the vector describing its length to the inner curve of the hamulus and the lower edge of the ventral bar articulation point on the hamulus $\lambda = 50.3^\circ$; marginal hook total length (MHTL) = 21.5; marginal hook shaft length (MHSL) = 18.2; marginal hook sickle length (MHSL) = 3.7; marginal hook sickle proximal width (MHSPW) = 4.4; marginal hook toe length (MHSTL) = 3.0; marginal hook sickle distal width (MHSDW) = 3.7; marginal hook aperture (MHAD) = 5.6; marginal hook instep/arch height (MHH) = 0.5. These measurements are within (or close to) the ranges reported by [19]; these authors also re-examined paratype specimens. Probably because of the fixation in Hoyer's medium, the morphology of the haptoral dorsal and ventral bars was not discernible. The MCO has a diameter of 13.1 with at least 6 spines (visible) of average length 4.0 (3.6-5.0) arranged in a single row, and a single large one that is 6.2 long. While [19] mentioned a similar MCO diameter (14.5), they found the genital hardparts to be indiscernible on the studied specimen. Conversely, Prudhoe & Hussey [21] did not provide measurements regarding the MCO; they observed a single row with eight spines but saw no large spine. It is important to remember that the number of MCO spines in *Gyrodactylus* may vary within the same species [22,23]. We here provide the first report on the size of the MCO spines of *G. transvaalensis*, and on the presence of a large spine in this species' MCO.

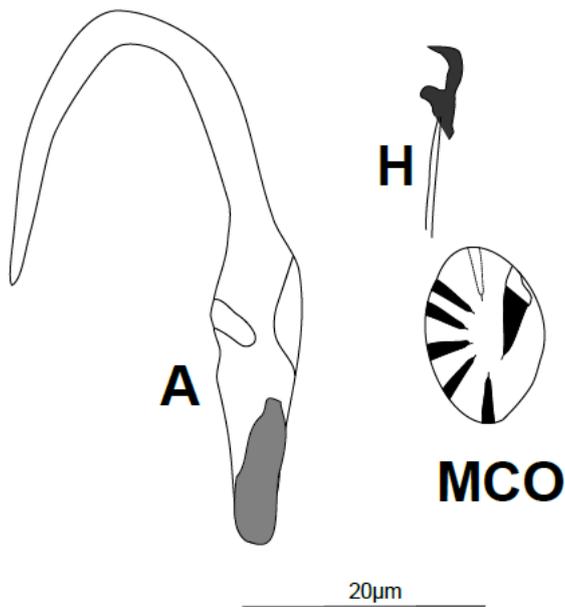


Figure 3. Line drawings of haptoral hard parts of *Gyrodactylus transvaalensis* (RMCA_VERMES_ 43681) (A = hamulus, H= marginal hook, MCO = male copulatory organ).

This is the first time that this monogenean species is reported from this infection site. Indeed, *G. transvaalensis* was described in 1977 by Prudhoe and Hussey [21] on the skin of *C. gariepinus* captured at the confluence of the Elands and Olifants Rivers, about 17 km north of Marble Hall in the central Transvaal (24°48'45.94''S; 29°21'28.94''E), currently the Limpopo province, Republic of South Africa. The second report of this species originates from West Africa, where it was found on the fins of *Clarias anguillaris* (Linnaeus, 1758) at Mare Simenti, Niokolo Koba National Park (13°01.79 N, 13°17.6' W), Senegal [19] (Figure 4).

This study increases the number of species of monogenean flatworms known from representatives of Siluriformes in Lake Tanganyika from two [13] to three and the number of species belonging to *Gyrodactylus* in the lake from three [24] to four. In general, endemicity in Lake Tanganyika is high for a variety of taxa [25, 26] including monogenean parasites [27, 28]. Currently, 48 monogenean species are known from Lake Tanganyika (see Table 1), including two species of *Bagrobdella* Paperna, 1969, 39 of *Cichlidogyrus* Paperna, 1960, one of *Dolicirroplectanum* Kmentová, Gelnar and Vanhove, 2018, four of *Gyrodactylus* von Nordmann, 1832 and two of *Kapentagyryrus* Kmentová, Gelnar and Vanhove, 2018.

Table 1. Alphabetical list of monogenean species reported in Lake Tanganyika. The "Reference" column indicates the publication in which the species is reported from Lake Tanganyika, except for those marked by *, which indicates the publications that reported the same species outside of Lake Tanganyika. Species not endemic to Lake Tanganyika are listed in bold.

Species	Authors of species	Reference
<i>Bagrobdella vanhovei</i>	Mushagalusa Mulega & Pariselle, 2022	[13]
<i>Bagrobdella vansteenbergei</i>	Mushagalusa Mulega & Pariselle, 2022	[13]
<i>Cichlidogyrus adkoningsi</i>	Rahmouni, Vanhove & Šimková, 2018	[29]
<i>Cichlidogyrus antoineparisellei</i>	Rahmouni, Vanhove & Šimková, 2018	[29]
<i>Cichlidogyrus aspiralis</i>	Rahmouni, Vanhove & Šimková, 2017	[30]
<i>Cichlidogyrus attenboroughi</i>	Kmentová et al., 2016	[31]
<i>Cichlidogyrus banyankimbonai</i>	Pariselle & Vanhove, 2015	[32]
<i>Cichlidogyrus brunnensis</i>	Gelnar, Koblmüller & Vanhove, 2016	[31]
<i>Cichlidogyrus buescheri</i>	Pariselle & Vanhove, 2015	[28]
<i>Cichlidogyrus casuarinus</i>	Pariselle, Muterezi Bukinga & Vanhove, 2015	[33]
<i>Cichlidogyrus centesimus</i>	Vanhove, Volckaert & Pariselle, 2011	[34]
<i>Cichlidogyrus discophonum</i>	Rahmouni, Vanhove & Šimková, 2017	[30]
<i>Cichlidogyrus evikae</i>	Rahmouni, Vanhove & Šimková, 2017	[30]
<i>Cichlidogyrus frankwillemsi</i>	Pariselle & Vanhove, 2015	[32]
<i>Cichlidogyrus franswittei</i>	Pariselle & Vanhove, 2015	[32]
<i>Cichlidogyrus georgesmertensi</i>	Pariselle & Vanhove, 2015	[32]
<i>Cichlidogyrus gillardinae</i>	Muterezi Bukinga et al., 2012	[27]
<i>Cichlidogyrus gistelincki</i>	Gillardin et al., 2012	[35]
<i>Cichlidogyrus glacicremoratus</i>	Rahmouni, Vanhove & Šimková, 2017	[30]
<i>Cichlidogyrus habluetzeli</i>	Rahmouni, Vanhove & Šimková, 2018	[29]
<i>Cichlidogyrus irenae</i>	Gillardin et al., 2012	[35]
<i>Cichlidogyrus jeanloujustinei</i>	Rahmouni, Vanhove & Šimková, 2017	[30]
<i>Cichlidogyrus koblmülleri</i>	Rahmouni, Vanhove & Šimková, 2018	[29]
<i>Cichlidogyrus makasai</i>	Vanhove, Volckaert & Pariselle, 2011	[34]
<i>Cichlidogyrus masilyai</i>	Rahmouni, Vanhove & Šimková, 2018	[29]
<i>Cichlidogyrus mbirizei</i>	Muterezi Bukinga et al., 2012	[27]
		* [36]
		* [37]
		* [38]
<i>Cichlidogyrus milangelnari</i>	Rahmouni, Vanhove & Šimková, 2017	[30]
<i>Cichlidogyrus mulimbwai</i>	Muterezi Bukinga et al., 2012	[27]
<i>Cichlidogyrus muterezii</i>	Pariselle & Vanhove, 2015	[32]
<i>Cichlidogyrus muzumanii</i>	Muterezi Bukinga et al., 2012	[27]
<i>Cichlidogyrus nshomboi</i>	Muterezi Bukinga et al., 2012	[27]
<i>Cichlidogyrus pseudoaspiralis</i>	Rahmouni, Vanhove & Šimková, 2017	[30]
<i>Cichlidogyrus raeymaekersi</i>	Pariselle & Vanhove, 2015	[32]

<i>Cichlidogyrus rectangulus</i>	Rahmouni, Vanhove & Šimková, 2017	[30]
<i>Cichlidogyrus salzburgeri</i>	Rahmouni, Vanhove & Šimková, 2018	[29]
<i>Cichlidogyrus schreyenbrichardorum</i>	Pariselle & Vanhove, 2015	[28]
<i>Cichlidogyrus sergemorandi</i>	Rahmouni, Vanhove & Šimková, 2018	[29]
<i>Cichlidogyrus steenbergei</i>	Gillardin et al., 2012	[35]
<i>Cichlidogyrus sturmbaueri</i>	Vanhove, Volckaert & Pariselle, 2011	[34]
<i>Cichlidogyrus vandekerkhovei</i>	Vanhove, Volckaert & Pariselle, 2011	[34]
<i>Cichlidogyrus vealli</i>	Pariselle & Vanhove, 2015	[28]
<i>Dolicirroplectanum lacustre</i>	(Thurston & Paperna, 1969)	[39]
<i>Gyrodactylus sturmbaueri</i>	Vanhove, Snoeks, Volckaert & Huyse, 2011	[24]
		* [40]
<i>Gyrodactylus thysi</i>	Vanhove, Snoeks, Volckaert & Huyse, 2011	[24]
<i>Gyrodactylus transvaalensis</i>	Prudhoe & Hussey, 1977	* [21]
		* [19]
		Present study
<i>Gyrodactylus zimbae</i>	Vanhove, Snoeks, Volckaert & Huyse, 2011	[24]
<i>Kapentagyris limnotrissae</i>	(Paperna, 1973)	[41]
		[42]
		* [43]
<i>Kapentagyris tanganicanus</i>	Kmentová et al., 2018	[42]

About 90% of monogenean species (43/48) are endemic to Lake Tanganyika. Non-endemic species include *Kapentagyris limnotrissae* (Paperna, 1973), which was, together with its host artificially introduced into Lake Kariba [43]. This species was first described by Paperna in 1973 in Lake Tanganyika, on *Limnothrissa miodon* (Boulenger, 1906), as *Ancyrocephalus limnotrissae*. Kmentová, Gelnar & Vanhove subsequently redescribed it as *Kapentagyris limnotrissae* (Paperna, 1974) which is specific to *L. miodon* [42]. *Gyrodactylus sturmbaueri* Vanhove, Snoeks, Volckaert & Huyse, 2011 infects cichlids. It has been described from Lake Tanganyika on the gills (probably present on the fins and skin as well) of *Simochromis diagramma* (Günther, 1894) [24], but was subsequently reported on the gills of *Pseudocrenilabrus philander* (Weber, 1897) in South Africa and Zimbabwe [40]. *Dolicirroplectanum lacustre* (Thurston & Paperna, 1969) is a parasite of latid fishes throughout Africa [39]. *Cichlidogyrus mbirizei* has been described from the gills of *Oreochromis tanganicae* from Lake Tanganyika [27], but was later reported in Thailand [36], Malaysia [37], and China [38].

Eight species of monogeneans belonging to *Gyrodactylus* are known from African populations of *C. gariepinus* [44]. These are: *G. alberti* Paperna, 1973, *G. alekosi* Příkladová, Blažek, & Vanhove, 2012, *G. clarii* Paperna, 1973, *G. gelnari* Příkladová, Blažek & Vanhove, 2012, *G. groschafti* Ergens, 1973, *G. rysavyi* Ergens, 1973, *G. transvaalensis* Prudhoe & Hussey, 1977 and *G. turkanaensis* Příkladová, Blažek & Vanhove, 2012.

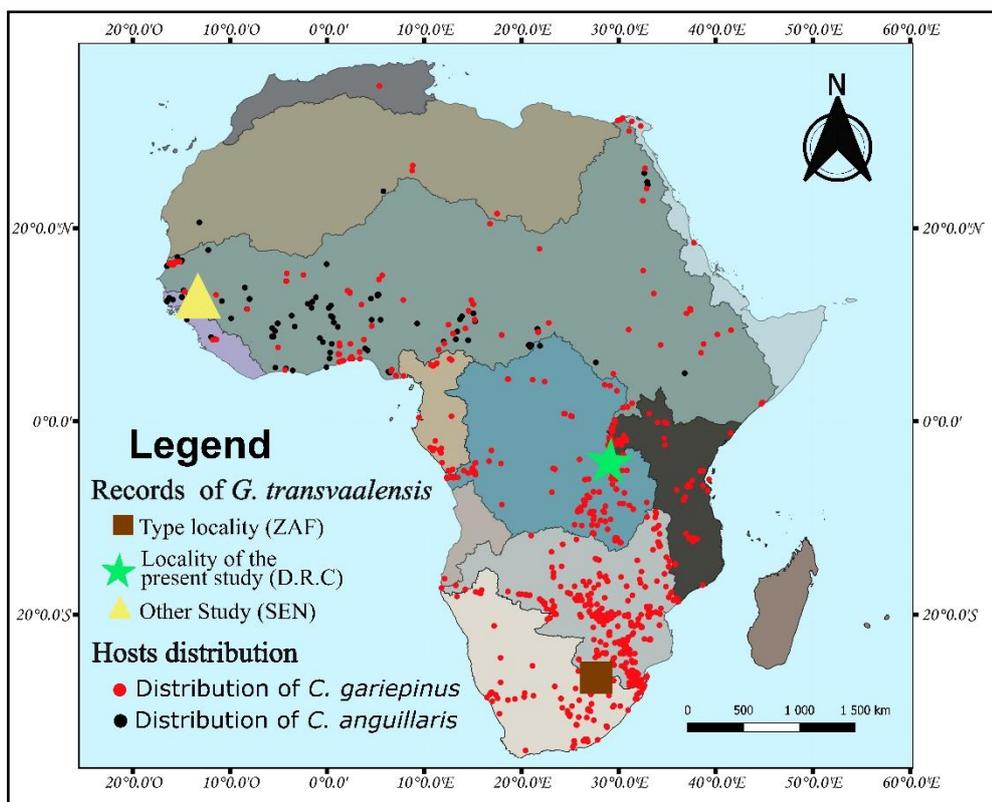


Figure 4. Records of *G. transvaalensis* and distribution range of its hosts. ZAF = South Africa, D.R.C = Democratic Republic of the Congo, and SEN = Senegal. The map was made with QGIS 3.16. Distribution data of *C. gariepinus* and *C. anguillaris* were downloaded from Fishbase (<https://www.fishbase.se/map/OccurrenceMapList.php?genus=Clarias&species=gariepinus> and <https://www.fishbase.se/map/OccurrenceMapList.php?genus=Clarias&species=anguillaris>). Colours denote ichthyofaunal provinces as in [45] (1. Maghreb, 2. Nilo-Sudan, 3. Upper Guinea, 4. Lower Guinea, 5. Congo, 6. Quanza, 7. Zambezi, 8. Southern Province, 9. East Coast, 10. Madagascar).

Molecular and morphological data indicate a large amount of variation in *C. gariepinus*, possibly hinting at unrecognized taxic diversity. Additionally, the species, as currently defined is paraphyletic with respect to *C. anguillaris* and the species of *Bathyclarias* Jackson, 1959 [46-48]. Because of their often-high species specificity, monogenean parasites can be valuable markers to solve problems in fish systematics [48]. Hence, we point out that three of the aforementioned parasite species: *G. gelnari*, *G. rysavyi* and *G. transvaalensis*, are shared between *C. gariepinus* and *C. anguillaris* and that, apart from these three, no other species of *Gyrodactylus* are known in *C. anguillaris* [44]. Hence, a potential explanation of *G. transvaalensis* (as well as the other two species of *Gyrodactylus* mentioned above) being present on both *C. anguillaris* and *C. gariepinus* is that the fish host speciated and the parasite did not. This is labeled “failure to diverge” [49]. This was also suggested for *D. lacustre* [39], a monogenean infecting a widespread African freshwater fish and the species rendering it paraphyletic [50]. A further sampling of parasites of *C. gariepinus* and closely related

species across their natural range should be undertaken. Combined with molecular studies on these parasites, this may, in view of their marker potential, help resolve uncertainties in the taxonomy and evolutionary history of these clariids.

Author Contributions: Conceptualization, A.M.M., M.V.S. and M.P.M.V.; Methodology: A.M.M., F.M.B., P.M.M and A.P.; Investigation: M.P.M.V, N.K and M.V.S.; Data Curation, A.M.M. and A.P.; Writing – original, A.M.M, Data Preparation, A.M.M.; Writing-Review & Editing: A.M.M., M.V.S., N.K., F.M.B., I.R., P.M.M., A.B., A.P. and M.P.M.V. Supervision, M.V.S. and M.P.M.V. All authors have read and agreed to the published version of the manuscript.

Funding: A.M.M. (BOF22BL08) and N.K. (BOF21PD01) are funded by the Special Research Fund of Hasselt University, and M.P.M.V. by the Special Research Fund of Hasselt University (BOF20TT06, BOF21INCENT09) and by research grant 1513419N of the Research Foundation – Flanders (FWO-Vlaanderen).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data availability statement: The voucher specimen was deposited in the Royal Museum for Central Africa (Tervuren, Belgium) under accession number RMCA_VERMES_43681. The observations here reported were posted on iNaturalist under <https://www.inaturalist.org/observations/139872031> (host) and <https://www.inaturalist.org/observations/139872032> (parasite).

Conflicts of interest: the authors declare no conflict of interest

References

1. Fricke, R.; Eschmeyer, W.N; Fong, D.J. Catalog of fishes. Available online: <https://researcharchive.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.ap> (accessed 15 June 2022).
2. Teugels, G.G. Taxonomy, phylogeny and biogeography of catfishes (Ostariophysi, Siluroidei): an overview. *Aquat. Living Resour.* **1996**, *9*, 9-34.
3. Bruton, M.N. The food and feeding behavior of *Clarias gariepinus* (Pisces: Clariidae) in Lake Sibaya, South Africa with emphasis on its role as a predator of cichlids. *Trans. Zool. Soc. Lond.* **1979**, *35*, 47–114.
4. Pouomogne, V. Cultured Aquatic Species Information Programme. *Clarias gariepinus*. Food and Agriculture Organization of the United Nations Fisheries and Aquaculture Department, Rome. https://www.fao.org/fishery/en/culturedspecies/Clarias_gariepinus/en (accessed on 27 September 2022).
5. Jorissen, M.W.P.; Huyse, T.; Pariselle, A.; Wamuini Lunkayilakio, S.; Muterezi Bukinga F.; Chocha Manda, A ; Kapepula Kasembele, G.; Vreven, E. J.; Snoeks, J.; Decru E.; Artois, T; Vanhove, M.P.M. Historical museum collections help detect parasite species jumps after tilapia introductions in the Congo Basin. *Biol. Invasions* **2020**, *22*, 2825–2844.
6. Mendoza-Palmero, C.A.; Blasco-Costa, I.; Scholz, T. Molecular phylogeny of neotropical monogeneans (Platyhelminthes: Monogenea) from catfishes (Siluriformes). *Parasites Vectors* **2015**, *8*, 164.
7. de Chambrier, A.; Kuchta, R.; Scholz, T. Tapeworms (Cestoda: Proteocephalidea) of teleost fishes from the Amazon River in Peru: additional records as an evidence of unexplored species diversity. *Rev. Suisse Zool.* **2020**, *122*, 149–163.

8. Acosta, A. A.; Smit, N. J.; da Silva, R. J. Diversity of helminth parasites of eight siluriform fishes from the Aguapeí River, upper Paraná basin, São Paulo state, Brazil. *Int. J. Parasitol.* **2020**, *11*, 120–128.
9. Cohen, A. S.; Soreghan, M. J.; Scholz, C. A. Estimating the age of formation of lakes: An example from Lake Tanganyika, East African Rift system. *Geology* **1993**, *21*, 511–514.
10. Alin, S.; Cohen, A. Lake-level history of Lake Tanganyika, East Africa, for the past 2500 years based on ostracode-inferred water-depth reconstruction. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2003**, *199*, 31–49.
11. Peart, C.R. Detecting a signature of adaptive radiation: diversification in Lake Tanganyika catfishes, PhD Thesis, University College London, London, September 2014.
12. Coulter, G.W. *Lake Tanganyika and its Life*. Oxford University Press: Oxford, United Kingdom, 1991.
13. Mushagalusa Mulega, A.; Muterezi Bukinga, F.; Akoumba, J.F.; Masilya M.P.; Pariselle, A. Monogeneans from catfishes in Lake Tanganyika. I: Two new species of *Bagrobdella* (Dactylogyridae) from *Auchenoglanis occidentalis* (Siluriformes: Claroteidae). *Zoologia* **2022**, *in press*.
14. Loker, E.S.; Hofkin, B.V. *Parasitology – a conceptual approach*. Garland Science, Taylor & Francis Group, LLC: New York, USA, 2015; pp. 1–560.
15. Řehulková, E.; Seifertová, M.; Přikrylová, I.; Francová, K. Monogenea. In *A Guide to the Parasites of African Freshwater Fishes*. Scholz, T., Vanhove, M.P.M, Smit, N., Jayasundera, Z., Gelnar, M., Eds. CEBioS, Royal Belgian Institute of Natural Sciences: Brussels, Belgium, **2018**; *Abc Taxa* Volume 18, pp. 185–243.
16. Fermon, Y.; Nshombo, M.V.; Muzumani, R.D.; Jonas, B. Lac Tanganyika Guide de la faune des poissons de la côte congolaise, d'Ubwari à la Ruzizi. Aimara, France, 2012. pp. 1–238.
17. Anderson, L.E. Hoyer's solution as a rapid permanent mounting medium for bryophytes. *The Bryologist* **1954**, *57*, 242–244.
18. Bates, J.W. The Slide-Sealing Compound "Glyceel". *J. Nematol.* **1997**, *29*, 565–566.
19. Přikrylová, I.; Blažek, R.; Vanhove, M.P.M. An overview of the *Gyrodactylus* (Monogenea: Gyrodactylidae) species parasitizing African catfishes, and their morphological and molecular diversity. *Parasitol. Res.* **2012**, *110*, 1185–1200.
20. Shinn, A.P.; Hansen, H.; Olstad, K.; Bechmann, L.; Bakke, T.A. The use of morphometric characters to discriminate specimens of laboratory-reared and wild population of *Gyrodactylus salaris* and *G. thymalli* (Monogenea). *Folia Parasitol.* **2004**, *51*, 239–252.
21. Prudhoe, S.; Hussey, C.G. Some parasitic worms in freshwater fishes and fish-predators from the Transvaal, South Africa. *Zoologica Africana* **1977**, *12*, 113–147.
22. King, D.S.; Bentzen, P.; Cone, D.K. *Gyrodactylus patersoni* n.sp. (Monogenean: Gyrodactylidae) infecting Atlantic Silverside (*Menidia menidia*) from Nova Scotia, Canada. *Comp. Parasitol.* **2014**, *81*, 27–32.
23. Kvach, Y.; Ondračková, M.; Seifertová, M.; Hulak, B. *Gyrodactylus ginestrae* n.sp. (Monogenea: Gyrodactylidae), a parasite of the big-scale sand smelt, *Atherina boyeri* Risso, 1810 (Actinopterygii: Atherinidae) from the Black Sea. *Parasitol. Res.* **2019**, *118*, 3315–3325. (<https://doi.org/10.1007/s00436-019-06483-8>)
24. Vanhove, M.P.M.; Snoeks, J.; Volckaert, F.A.M.; Huyse, T. First description of monogenean parasites in Lake Tanganyika: the cichlid *Simochromis diagramma* (Teleostei, Cichlidae) harbours a high diversity of *Gyrodactylus* species (Platyhelminthes, Monogenea). *Parasitology* **2011**, *138*, 364–380.
25. Salzburger, W.; Van Bocxlaer, B.; Cohen, A.S. Ecology and evolution of the African Great Lakes and their faunas. *Annu. Rev. Ecol. Evol. Syst.* **2014**, *45*, 519–545.
26. Wilson, A.B.; Glaubrecht, M.; Meyer, A. Ancient lakes as evolutionary reservoirs: evidence from the thalassoid gastropods of Lake Tanganyika. *Proc. R. Soc. London.* **2004**, *271*, 529–536.
27. Muterezi Bukinga, F.; Vanhove, M.P.M.; Van Steenberge, M.; Pariselle, A. Ancyrocephalidae (Monogenea) of Lake Tanganyika: III: *Cichlidogyrus* infecting the world's biggest cichlid and the non-endemic tribes Haplochromi, Oreochromini and Tylochromini (Teleostei, Cichlidae). *Parasitol. Res.* **2012**, *111*, 2049–2061.

28. Pariselle, A.; Van Steenberge, M.; Snoeks, J.; Volckaert, F.A.M.; Huyse, T.; Vanhove, M.P.M. Ancyrocephalidae (Monogenea) of Lake Tanganyika: Does the *Cichlidogyrus* parasite fauna of *Interochromis loocki* (Teleostei, Cichlidae) reflect its host's phylogenetic affinities? *Contrib. Zool.* **2015**, *84*, 25–38.
29. Rahmouni, C.; Vanhove, M.P.M.; Šimková, A. Seven new species of *Cichlidogyrus* Paperna, 1960 (Monogenea: Dactylogyridae) parasitizing the gills of Congolese cichlids from northern Lake Tanganyika. *PeerJ* **2018**, *6*, e5604.
30. Rahmouni, C.; Vanhove, M.P.M. Šimková, A. Underexplored diversity of gill monogeneans in cichlids from Lake Tanganyika: eight new species of *Cichlidogyrus* Paperna, 1960 (Monogenea: Dactylogyridae) from the northern basin of the lake, with remarks on the vagina and the heel of the male copulatory organ. *Parasites Vectors.* **2017**, *10*, 591.
31. Kmentová, N.; Gelnar, M.; Koblmüller, S.; Vanhove, M.P.M. Deep-water parasite diversity in Lake Tanganyika: description of two new monogenean species from benthopelagic cichlid fishes. *Parasites Vectors.* **2016**, *9*, 426.
32. Van Steenberge, M.; Pariselle, A.; Huyse, T.; Volckaert, F.A.M. Snoeks, J.; Vanhove, M.P.M. Morphology, molecules, and monogenean parasites: an example of an integrative approach to cichlid biodiversity. *PLoS ONE* **2015**, *10*(6), e0129987.
33. Pariselle, A.; Muterezi Bukinga, F.; Van Steenberge, M.; Vanhove, M. Ancyrocephalidae (Monogenea) of Lake Tanganyika: IV: *Cichlidogyrus* parasitizing species of Bathybatini (Teleostei, Cichlidae): reduced host-specificity in the deepwater realm? *Hydrobiologia* **2015**, *748*, 99–119.
34. Vanhove, M.P.M. ; Volckaert, F.A.M.; Pariselle, A. Ancyrocephalidae (Monogenea) of Lake Tanganyika: I: Four new species of *Cichlidogyrus* from *Ophthalmotilapia ventralis* (Teleostei: Cichlidae), the first record of this parasite family in the basin. *Zoologia* **2011**, *28*, 253–263.
35. Gillardin, C.; Vanhove, M.P.M.; Pariselle, A.; Huyse, T.; Volckaert, F.A.M. Ancyrocephalidae (Monogenea) of Lake Tanganyika: II: description of the first *Cichlidogyrus* spp. parasites from Tropheini fish hosts (Teleostei, Cichlidae). *Parasitol. Res.* **2012**, *110*, 305–313.
36. Lerssutthichawal, T.; Maneepitaksanti, W.; Purivirojkul, W. Gill Monogeneans of potentially cultured Tilapias and first record of *Cichlidogyrus mbirizei* Bukinga et al., 2012, in Thailand. *Walailak J. Sci. Technol.* **2016**, *13*, 543–553.
37. Lim S.H.; Ooi, A.L.; Wong, W.L. Gill monogeneans of Nile tilapia (*Oreochromis niloticus*) and red hybrid tilapia (*Oreochromis* spp.) from the wild and fish farms in Perak, Malaysia: infection dynamics and spatial distribution. *SpringerPlus* **2016**, *5*, 1609.
38. Zhang, S.; Zhi, T.; Xu, X.; Zheng, Y.; Bilong Bilong, C.; Pariselle, A.; Yang, T. Monogenean fauna of alien tilapias (Cichlidae) in south China. *Parasite* **2019**, *26*, 1–16.
39. Kmentová, N.; Koblmüller, S.; Van Steenberge, M.; Artois, T.; Muterezi Bukinga, F.; Mulimbwa N'sibula, T.; Muzumani, R.D.; Masilya, P.M.; Gelnar, M.; Vanhove, M.P.M. Failure to diverge in African Great Lakes: The case of *Dolicirroplectanum lacustre* gen. nov. comb. nov. (Monogenea, Diplectanidae) infecting latid hosts. *J. Great Lakes Res.* **2020**, *46*, 1113–1130.
40. Zahradníčková, P.; Barson, M.; Luus-Powell, W.J.; Příkladová, I. Species of *Gyrodactylus* von Nordmann, 1832 (Platyhelminthes: Monogenea) from cichlids from Zambezi and Limpopo river basins in Zimbabwe and South Africa: evidence for unexplored species richness. *Syst. Parasitol.* **2016**, *93*, 679–700.
41. Paperna, I. New species of Monogenea (Vermes) from African freshwater fish. A preliminary report. *Revue de Zoologie et de Botanique africaine* **1973**, *87*: 505–518.
42. Kmentová, N.; Van Steenberge, M.; Raeymaekers, J.A.M.; Koblmüller, S.; Hablützel, P.I.; Muterezi Bukinga, F.; Mulimbwa N'sibula, T.; Masilya, M.P.; Nzigidahera, B.; Ntakimazi, G.; Gelnar, M.; Vanhove, M.P.M. Monogenean parasites of sardines in Lake Tanganyika: diversity, origin and intraspecific variability. *Contrib. Zool.* **2018**, *87*, 105–132.
43. Kmentová, N.; Van Steenberge, M.; Thys van den Audenaerde, D.F.E.; Nhiwatiwa, T.; Muterezi Bukinga, F.; Mulimbwa N'sibula, T.; Masilya Mulungula, P.; Gelnar, M.; Vanhove, M.P.M. Co-introduction success of monogeneans infecting the fisheries target *Limnothrissa miodon* differs between two non-native areas: the potential of parasites as a tag for introduction pathway. *Biol. Invasions* **2019**, *21*, 757–773.

-
44. Carvalho Schaeffner, V.C. Host-parasite list. In *A Guide to the Parasites of African Freshwater Fishes*. Scholz, T., Vanhove, M.P.M, Smit, N., Jayasundera, Z., Gelnar, M., Eds.; CEBioS, Royal Belgian Institute of Natural Sciences: Brussels, Belgium, 2018; *Abc Taxa* Volume 18, pp. 185–243.
 45. Snoeks, J.; Getahun, A. African fresh and brackish water fish biodiversity and their distribution: more unknowns than knowns. In Proceedings of the 4th international conference on African fish and fisheries, Addis Ababa, Ethiopia, 22 September 2008 – 26 September 2008; Snoeks, J, Getahun, A., Eds., Royal Museum for Central Africa: Tervuren, Belgium, 2013; pp. 69–76.
 46. Agnèsè, J.F.; Teugels, G.G. The *Bathyclarias*–*Clarias* species flock. *C R Acad Hebd Seances Acad Sci*, **2001**, 324, 683-688.
 47. Rognon, X.; Teugels, G.G. ; Guyomard, R. ; Galbusera, P. ; Andriamanga, M. ; Volckaert, F. ; Agnèsè, J.F. Morphometric and allozyme variation in the African catfishes *Clarias gariepinus* and *C. anguillaris*. *J. Fish Biol.* **1998**, 53, 192-207.
 48. Van Steenberge, M.; Vanhove, M.P.M.; Chocha Manda, A.; Larmuseau, M.H.D.; Swart, B.L.; Khang'Mate, F.; Arndt, A.; Hellemans, B.; Van Houdt, J.; Micha, J.L.; Koblmüller, S.; Roodt-Wilding, R.; Volckaert, F.A.M. Unravelling the evolution of Africa's drainage basins through a widespread freshwater fish, the African sharptooth catfish *Clarias gariepinus*. *J. Biogeogr.* **2020**, 47, 1739–1754.
 49. Brooks, D.R. Testing the context and extent of host-parasite coevolution *Syst. Biol.* **1979**, 28, 299–307.
 50. Koblmüller, S.; Schögl, C. A.; Lorber, C.J.; Van Steenberge, M.; Kmentová, N.; Vanhove, M. P. M.; Zangl, L. African lates perches (Teleostei, Latidae, *Lates*): Paraphyly of Nile perch and recent colonization of Lake Tanganyika. *Mol. Phylogenet. Evol.* **2021**, 160, 107141.