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Trematode diversity in southern Africa: metacercariae of the Clinostomidae and Cryptogonimidae in intermediate freshwater fish hosts

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Research Paper

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Abstract

The freshwater fish fauna of southern Africa is highly diverse; however, the magnitude of parasitic species they host is unevenly known. The region's documented adult trematode fish fauna is sparse, while the opposite is evident for intermediate trematode stages. Perceived difficulty in identification of underdeveloped stages lead to the exclusion of reporting metacercariae or lack either morphological or molecular data resulting in a depauperate comparative molecular data repository for species of the region and Africa as a whole. In an effort to address the morphological and molecular data void of the parasite fauna of southern African freshwater fishes, we sought to comprehensively investigate and characterise this fauna. Here we report on three metacercarial forms of *Clinostomum* (Clinostomidae) from three fish families (Clariidae, Mochokidae, and Mormyridae), provide the first report of a species of the Cryptogonimidae from a cyprinid host in South Africa, and include molecular data for the partial 28S rDNA, ITS1–2 and COI mtDNA regions of these metacercarial forms. Our clinostomid specimens morphologically and genetically corresponded with *Clinostomum brieni* (e.g., *Clarias gariepinus*) and *Clinostomum* 'morphotype 2' and 'morphotype 3' per Caffara *et al.* (2017) from the mormyrid *Marcusenius pongolensis* and the mochokid catfish *Chiloglanis* sp., respectively. Our cryptogonimid metacercariae did not correspond with any known species or available molecular sequence data; however, the presence of robust circumoral spines on the oral sucker indicated that they are either a species of *Acanthostomum* or *Proctocaecum*. The molecular data we provide are the first for an *Acanthostomum*/*Proctocaecum*-type cryptogonimid from Africa.

Introduction

The freshwater systems of southern Africa hold highly diverse fish communities (Skelton 2024); however, the role of these fishes as intermediate and definitive hosts to trematodes remains poorly studied (Scholz *et al.* 2018). Knowledge is especially depauperate regarding heteroxenous (i.e., with multiple-host life cycles) parasitic species. Freshwater fishes play an essential ecological role in freshwater systems, supporting trophic and ecological diversity and, as such, ensure links within food webs and interactions across trophic levels (Dunne *et al.* 2013; Poulin 2014). These interactions provide an integral platform for life cycle completion for organisms such as digenetic trematodes, of which several representatives utilise molluscs as first intermediate hosts, fishes as second intermediate (or definitive) hosts, and piscivorous birds as definitive hosts. Records of adult trematodes are sparse in southern African freshwater fishes, with only a handful of species known from the region (Beverley-Burton 1962; Bray and Hendrix 2007; Curran *et al.* 2021; Douëllou 1992b; Dumbo *et al.* 2019a; Dumbo *et al.* 2019b; Jansen van Rensburg *et al.* 2013; Kudlai *et al.* 2018; Warren *et al.* 2024). In South Africa, adult trematodes are represented by a mere five species across the families Gorgoderidae (two species), Allocreadiidae, Cephalogonimidae, and Orientocreadiidae (one each) (Boomker 1984; Dos Santos *et al.* 2021; King *et al.* 2018; Prudhoe and Hussey 1977; Truter *et al.* 2023a; Truter *et al.* 2023b). The first species to be reported was *Phyllodistomum vanderwaali* Prudhoe & Hussey, 1977, who described this gorgoderid species from the urinary bladder of North African catfish, *Clarias gariepinus* (Burchell) (Clariidae) from the Olifants River, Transvaal (now Limpopo Province) (Prudhoe and Hussey 1977). Boomker (1984) subsequently described *Phyllodistomum bavuri* Boomker, 1984 from the same fish host collected from the Bangu River, Kruger National Park. King *et al.* (2018) described *Emoleptalea nwanedi* King, Smit, Baker & Luus-Powell, 2018 (Cephalogonimidae) from silver catfish, *Schilbe*

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intermedius Rüppell (Schilbeidae) from the Nwanedi-Luphephe Dam in Limpopo Province, and Dos Santos *et al.* (2021) described *Allocreadium apokryfi* Dos Santos, Gilbert, Avenant-Oldewage & Dumbo, 2021 from smallmouth yellowfish, *Labeobarbus aeneus* (Burchell) (Cyprinidae) from a site downstream of the Vaal Dam, Gauteng Province. Truter *et al.* (2023a) reported a species of *Orientocreadium* Tubangui, 1931 (Orientocreadiidae) from *C. gariepinus* from two dam and river systems in central South Africa. The species was identified as being *Orientocreadium batrachoides* Tubangui, 1931; the status of this species in southern Africa is uncertain, identifications (e.g., by Dumbo *et al.* 2019b) being made based on morphological similarity and in the absence of molecular sequence data from the type-locality (Philippines).

In contrast to this depauperate adult fauna, the richness of intermediate stages (both first-intermediate stages and metacercariae) is highly diverse. Studies on freshwater first intermediate-stage infections have a long and productive history in southern Africa, with key work predating much of that on adult trematodes (e.g., Cawston 1917; Cawston 1920; Faust 1919; Faust 1920; Porter 1938) and continuing to this day (e.g., Mudavanhu *et al.* 2024; Outa and Avenant-Oldewage 2024a; Outa and Avenant-Oldewage 2024b; Outa *et al.* 2024). Foundational work such as that by Porter (1938) has demonstrated that southern African freshwater molluscs harbour a rich fauna of trematode first intermediate stages, though most species have yet to be matched to definitive or other intermediate stages. This knowledge is still deficient in many aspects, with no records of first intermediate stages for highly prevalent families such as clinostomids, cryptogonimids, and diplostomids in the region. Knowledge regarding second intermediate stages in the region is also patchy. To date, records of intermediate stages representing at least 15 putative species across two trematode families (Clinostomidae and Diplostomidae) have been documented from fish hosts in southern Africa (Barson and Avenant-Oldewage 2006; Barson *et al.* 2008; Grobbelaar *et al.* 2014; Hoogendoorn *et al.* 2019; Hoogendoorn *et al.* 2020; Madanire-Moyo and Barson 2010; Madanire-Moyo *et al.* 2010; Madanire-Moyo *et al.* 2012; Moema *et al.* 2013; Moema *et al.* 2019; Olivier *et al.* 2009; Smit *et al.* 2023, see Table 2 for clinostomid records). Most reports of metacercariae from the region lack either morphological or molecular data. Although the use of molecular sequencing to identify and link intermediate stages is increasing in the region (e.g., Hoogendoorn *et al.* 2019; Hoogendoorn *et al.* 2020; Moema *et al.* 2019), its utilisation remains limited. Perceived difficulty in identification of underdeveloped stages, with limitations in reliable morphological characters for taxonomic placement, further hinder the linking of life cycle stages to definitive hosts. This has led to a depauperate comparative molecular data repository for species of the region and Africa as a whole. In an effort to address the morphological and molecular data void of the parasite fauna of southern African freshwater fishes, we sought to comprehensively investigate and characterise this fauna. In the process of our investigations, we encountered several types of metacercariae belonging to four trematode families: the Clinostomidae, Cryptogonimidae, Diplostomidae, and Strigeidae. Findings concerning the latter two families will be reported in a separate publication. We herewith report our observations of the former two families from four freshwater fish families in southern Africa.

Materials and methods

Host collection and parasite fixation

Sampling of *Clarias gariepinus* in Zambia was done in 2019. The present manuscript provides molecular data for *Clinostomum brieni* (Dollfuss, 1950) previously reported in Truter *et al.* (2023a, 2023b). The collection of all other host species, namely *Chiloglanis* sp., *Labeo cylindricus* Peters and *Marcusenius pongolensis* (Fowler) occurred in 2023 as part of a larger aquatic biodiversity project (REFRESH) and parasitological data is reported here for the first time. A list of hosts and sampling localities are presented in Table 1. Methods used for host collection included rod and reel, baited longlines, seine netting, cast netting, and electrofishing. All organs of freshly collected host individuals were screened for trematode infection, including the gills, branchial chambers, eyes, brain, cranial cavity, muscle tissue, and viscera. After removal from the host, free metacercarial stages were rinsed in a 0.9% saline solution, and encysted or encapsulated metacercariae were excysted using fine insect needles and rinsed, and all individuals were heat fixed and stored in 96% molecular grade ethanol.

Morphological and molecular analyses

The general morphology of whole individuals was initially studied to identify different morphotypes using a Nikon Eclipse N*i* (Nikon, Tokyo, Japan) compound microscope equipped with differential interference contrast. Photomicrographs and measurements were obtained using the computerised digital camera system and NIS-Elements BR 4.60© software for image analysis. A selection of individuals representing each morphotype was used to prepare hologenophores (Pleijel *et al.* 2008) and permanent mounts stained with either Mayer's hematoxylin or acetocarmine; permanent mounts were prepared using standard protocols for each respective stain (Georgiev *et al.* 1986; Yong *et al.* 2021). Photomicrographs of all representatives not prepared as hologenophores were used as photohologenophores (Achatz *et al.* 2022) and whole specimens were subsequently molecularly analysed. Hologenophores and other vouchers were deposited in the parasitological collection of the National Museum, Bloemfontein, South Africa (NMB). Photohologenophore records were stored in the electronic parasitological collection of the Water Research Group, North-West University, South Africa. Measurements are given in micrometres (µm) unless stated otherwise, with means following ranges in parentheses.

Genomic DNA from whole specimens (photohologenophores) and hologenophores were extracted using the PCRBIO Rapid

Table 1. Localities where respective hosts were collected from in South Africa and Zambia

Host	n	Locality	Country	Coordinates
Clariidae				
Clarias gariepinus[a]	17	Barotse floodplain	Zambia	15°12′01.59″ S, 22°58′09.27″ E
Cyprinidae				
Labeo cylindricus	3	Letaba River	South Africa	23°38′56.79″ S, 30°39′31.1″ E
Mochokidae				
Chiloglanis sp.	10	Letaba River	South Africa	23°51′1.33″ S, 30°06′21.6″ E
Mormyridae				
Marcusenius pongolensis	3	Tzaneen Dam	South Africa	23°48′55.8″ S, 30°08′31.9″ E
	4	Letaba River		23°38′56.7″ S, 30°39′31.1″ E

[a]Same *C. gariepinus* individuals reported on in Truter *et al.* (2023a, 2023b).

Table 2. List of records of *Clinostomum* species from Africa; *Clinostomatopsis intermedialis* is included as its junior synonym, *Clinostomum phalocrocoracis*, is still widely recognised in literature. Unless otherwise noted, all hosts are fishes bearing metacercariae. Entries marked '*' represent type-records from original descriptions

Species	Synonymised names	Host	Locality	Reference
Clinostomatopsis intermedialis (Lamont, 1920)	*Clinostomum intermedialis* Lamont, 1920 *Clinostomum phalacrocoracis* Dubois, 1931 *Neutraclinostomum intermedialis* (Lamont, 1920) Feizullaev & Mirzoeva, 1983	*Anhinga rufa* (Daudin) (Aves: Anhingidae)	Lake Nungua, Ghana	Ukoli (1966a) Ukoli (1968)
		Ardea cinerea L. (Aves: Ardeidae)	Lepellane Dam, South Africa (experimental infection)	Britz *et al.* (1984)
			Sagana, Kenya	Locke *et al.* (2015)
		Pelecanus onocrotalus (Aves: Pelecanidae)	Lake Edward, Uganda	Peirce and Din (1970)
			Chibuto, Mozambique	Tendeiro *et al.* (1974)
		Pelecanus rufescens (Aves: Pelecanidae)	Lake Edward, Uganda	Peirce and Din (1970)
		Phalacrocorax sp.*,[a] (Aves: Phalacrocoracidae)	Angola	Dubois (1931)
		Clarias gariepinus (Burchell) (Clariidae)	Phalaborwa Barrage, South Africa	Caffara *et al.* (2017)
		Coptodon zillii (Gervais) (Cichlidae)	Giza, Egypt	Mahdy *et al.* (2022)
		Oreochromis mortimeri (Trewavas) (Cichlidae)	Lake Kariba, Zimbabwe	Douëllou (1992a; 1992b)
		Oreochromis mossambicus (Peters) (Cichlidae)	Lepellane Dam, South Africa	Britz *et al.* (1984)
			Tzaneen Dam, South Africa	Grobler *et al.* (1999) Grobler and Mokgalong (2002)
			Nwanedi-Luphephe Dam, South Africa	Grobler and Mokgalong (2002)
			Arabie Dam, South Africa	Grobler and Mokgalong (2002)
			Loskop Dam, South Africa	Caffara *et al.* (2017)
			Matlala Dam, South Africa	Caffara *et al.* (2017)
			Phalaborwa Barrage, South Africa	Caffara *et al.* (2017)
			Rhenosterkop Dam, South Africa	Caffara *et al.* (2017)
		Oreochromis niloticus (L.) (Cichlidae)	Assiut Governorate, Egypt	Taher (2009)
			El-Minia district, Egypt	Ahmed *et al.* (2018)
			Giza, Egypt	Mahdy *et al.* (2021, 2022, 2023) Salem *et al.* (2021)
		Oreochromis sp.	Lac de Retenue de la Lufira, Democratic Republic of Congo (DRC)	Kabunda and Sommerville (1984)
Clinostomum brieni (Dollfus, 1950)	*Clinostomoides brieni* Dollfus, 1950	*Ardea goliath* Cretzschmar (Aves: Ardeidae)*	Kadia, DRC	Dollfus (1950)
		Clarias gariepinus	Lake Upemba, DRC	Prudhoe (1957)
			Lake Kariba, Zimbabwe	Chishawa (1991) Douëllou (1992b) Douëllou and Erlwanger (1993)

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Table 2. (*Continued*)

Species	Synonymised names	Host	Locality	Reference
			Save-Runde floodplain, Zimbabwe	Barson *et al.* (2008)
			Okavango Delta, Botswana	Jansen van Rensburg *et al.* (2013)
			Kiswishi River near Futuka, DRC	Caffara *et al.* (2019)
			Lake Tshangalele, DRC	Caffara *et al.* (2019)
			Phalaborwa barrage, South Africa	Caffara *et al.* (2019)
			Barotse floodplain near Mongu, Zambia	**This study**
		Clarias senegalensis Valenciennes (Clariidae)	Lake Nungua, Ghana	Fischthal and Thomas (1970)
		Clarias sp.	Lake Malawi (unspecified)	Prudhoe (1957)
			Lake Saké, Rwanda	Manter and Pritchard (1969)
Clinostomum chabaudi Vercammen-Grandjean, 1964	*Clinostomum* 'morphotype 4' *sensu* Caffara *et al.* (2017)	*Ptychadena* sp. (Anura: Ptychadenidae)	Lake Kivu, DRC	Vercammen-Grandjean (1960)
		Enteromius trimaculatus (Peters) (Cyprinidae)	Middle Letaba Dam, South Africa	Caffara *et al.* (2017)
		Hyperolius kivuensis Ahl (Anura: Hyperoliidae)	Huye, Rwanda	Sinsch *et al.* (2021a; 2021b)
		Hyperolius viridiflavus (Duméril & Bibron) (Anura: Hyperoliidae)	Huye, Rwanda	Sinsch *et al.* (2021a; 2021b)
Clinostomum complanatum (Rudolphi, 1814)	*Clinostomum chrysichthys* Dubois, 1930 *Clinostomum macrosomum* Jaiswal, 1957 *Clinostomum vanderhorsti* Ortlepp, 1935	*Anhinga rufa*	Middle Letaba Dam, South Africa	Olivier *et al.* (2009)
		Ardea cinerea	Middle Letaba Dam, South Africa Tanzania	Olivier *et al.* (2009) Calhoun *et al.* (2019)[b]
		Ardea ibis L. (Aves: Ardeidae)	Beni-Suef Governorate, Egypt	Aboel Hadid and Lotfy (2007)
		Ardea melanocephala Children & Vigors (Aves: Ardeidae)	Onderstepoort, South Africa (experimental infection; as *Clinostomum vanderhorsti*)	Ortlepp (1935)
			Nwanedi-Luphephe Dam, South Africa	Britz (1983)
		Nycticorax nycticorax (L.) (Aves: Ardeidae)	Middle Letaba Dam, South Africa	Olivier *et al.* (2009)
			Zimbabwe	Calhoun *et al.* (2019)[b]
		Phalacrocorax africanus (Gmelin) (Aves: Phalacrocoracidae)	Middle Letaba Dam, South Africa	Olivier *et al.* (2009)
		Phalacrocorax carbo (L.) (Aves: Phalacrocoracidae)	Qena, Egypt	El-Dakhly *et al.* (2018)
		Phalacrocorax lucidus (Lichtenstein) (Aves: Phalacrocoracidae)	Middle Letaba Dam, South Africa	Olivier *et al.* (2009)
		Auchenoglanis biscutatus (Geoffroy Saint-Hilaire) (Claroteidae)	Niger River, Shagunu, Nigeria	Ukoli (1965)

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Table 2. (*Continued*)

Species	Synonymised names	Host	Locality	Reference
		Chrysichthys auratus (Geoffroy Saint-Hilaire) (Claroteidae)	Angola (as *Clinostomum chrysichthys*)[c]	Dubois (1930)
		Chrysichthys nigrodigitatus (Lacépède) (Claroteidae)	Niger River, Shagunu, Nigeria	Ukoli (1965)
			Warri River, Nigeria	Ejere *et al.* (2014)
			Okpokwu River, Nigeria	Omeji *et al.* (2022b)
		Clarias gariepinus	Niger River, Shagunu, Nigeria	Ukoli (1965)
			Lake Kariba, Zimbabwe	Douëllou and Erlwanger (1993)
			Save-Runde floodplain, Zimbabwe	Barson *et al.* (2008)
			Owena, Nigeria	Afolabi *et al.* (2020)
			Igbokoda, Nigeria	Afolabi *et al.* (2020)
			Yola, Nigeria	Idowu *et al.* (2023)
		Clarotes laticeps (Rüppell) (Claroteidae)	Niger River, Shagunu, Nigeria	Ukoli (1965)
		Coptodon guineensis (Günther) (Cichlidae)	Opi Lake, Nigeria	Echi *et al.* (2009b)
		Coptodon zillii	Sudan (unspecified)	Khalil (1969)
			Opi Lake, Nigeria	Echi *et al.* (2012)
		Enteromius trimaculatus	Middle Letaba Dam, South Africa	Olivier *et al.* (2009)
		Enteromius unitaeniatus (Günther) (Cyprinidae)	Middle Letaba Dam, South Africa	Olivier *et al.* (2009)
		Labeobarbus marequensis (Smith) (Cyprinidae)	Middle Letaba Dam, South Africa	Olivier *et al.* (2009)
		Marcusenius pongolensis (Peters) (Mormyridae)	University of Witwatersrand, South Africa (captive specimens; as *C. vanderhorsti*)	Ortlepp (1935)
			Transvaal, South Africa (unspecified) (as *C. vanderhorsti*)	Lombard (1968)
			Tzaneen Dam, South Africa	Grobler *et al.* (1999)
		Oreochromis mossambicus	Save-Runde floodplain, Zimbabwe	Barson *et al.* (2008)
		Oreochromis niloticus	Sudan (unspecified)	Khalil (1969)
			Lake Mugesera, Rwanda (as *Clinostomum macrosomum*)	Manter and Pritchard (1969)
			Oyo state, Nigeria (as *C. tilapiae*)	Agbede *et al.* (2004)
			Giza, Egypt	Mahdy *et al.* (2021, 2023) Salem *et al.* (2021)
		Pseudocrenilabrus philander (Weber) (Cyprinidae)	Middle Letaba Dam, South Africa	Olivier *et al.* (2009)
		Sarotherodon galilaeus (L.) (Cichlidae)	Sudan (unspecified)	Khalil (1969)
		Sarotherodon melanotheron Rüppell (Cichlidae)	Opi Lake, Nigeria	Echi *et al.* (2009a)

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Table 2. (*Continued*)

Species	Synonymised names	Host	Locality	Reference
		Schilbe depressirostris Rüppell (Schilbeidae)	Nortá Transvaal (unspecified) (as *C. vanderhorsti*)	Paperna (1980)
		Synodontis budgetti Boulenger (Mochokidae)	Niger River, Shagunu, Nigeria	Ukoli (1965)
			Okpokwu River, Nigeria	Omeji *et al.* (2022b)
		Synodontis membranaceus (Geoffroy Saint-Hilaire) (Mochokidae)	Niger River, Shagunu, Nigeria	Ukoli (1965)
		Synodontis nigrita Valenciennes (Mochokidae)	Niger River, Shagunu, Nigeria	Ukoli (1965)
		Synodontis ocellifer Boulenger (Mochokidae)	Niger River, Shagunu, Nigeria	Ukoli (1965)
		Synodontis schall (Bloch & Schneider) (Mochokidae)	Niger River, Shagunu, Nigeria	Ukoli (1965)
Clinostomum cutaneum Paperna, 1964		*Ardea cinerea*	Sagana, Kenya	Locke *et al.* (2015)
			Kirinyaga County, Kenya	Murugami *et al.* (2018)
		Ardea goliath	Sagana, Kenya	Gustinelli *et al.* (2010)
		Oreochromis niloticus	Sagana, Kenya	Gustinelli *et al.* (2010) Locke *et al.* (2015)
		Sarotherodon galilaeus	Lake Kompienga, Burkina Faso	Coulibaly *et al.* (1995)
Clinostomum falsatum Ortlepp, 1963		*Felis catus* L. (Mammalia: Felidae)	Lydenburg, South Africa	Ortlepp (1963)
Clinostomum hylaranae Fischthal & Thomas, 1968		*Hylarana albolabris* (Hallowell) (Anura: Ranidae)	Kade, Ghana	Fischthal and Thomas (1968a)
Clinostomum marginatum (Rudolphi, 1819)		*Oreochromis niloticus*	Epe, Nigeria	Ashade *et al.* (2013)
			Ikorodu, Nigeria	Ashade *et al.* (2013)
		Protopterus annectens (Owen) (Protopteridae)	Edo State, Nigeria	Osimen and Anagha (2020)
Clinostomum tilapiae Ukoli, 1966		*Bubulcus ibis* (L.) (Aves: Ardeidae)*	Ghana (as experimental infection)	Ukoli (1966a; 1966b)
		Anhinga rufa	Nungua Lake, Ghana	Ukoli (1968)
		Ardea goliath	Kisale, Kikondja & Kadia Lakes, DRC	Dollfus (1950) Manter and Pritchard (1969)[d]
		Chromidotilapia guntheri (Sauvage) (Cichlidae)	Osse River, Nigeria	Okaka and Akhigbe (1999)
			Owa Stream, Nigeria	Olurin and Somorin (2006)
			Agulu Lake, Nigeria	Okoye *et al.* (2014)
		Coptodon rendalli	Ebrié Lagoon at Attoutou, Cote d'Ivoire	Dollfus (1950)
		Coptodon zillii	Niger River, Shagunu, Nigeria	Ukoli (1965)
			Nungua Lake, Ghana	Ukoli (1966a; 1966b) Fischthal and Thomas (1970)
			Jos Plateau, Nigeria	Onwuliri and Mgbemena (1987)
			Opi Lake, Nigeria	Echi *et al.* (2012)

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Table 2. (*Continued*)

Species	Synonymised names	Host	Locality	Reference
			Oshun River, Nigeria	Olurin *et al.* (2012)
			Agulu Lake, Nigeria	Okoye *et al.* (2014)
			Asa Dam, Nigeria	Amaechi (2015)
			Eleyele Dam, Nigeria	Simon-Oke (2017)
		Cyprinus carpio L. (Cyprinidae)	Chuáli Lagoon, Mozambique	Boane *et al.* (2008)
			Limpopo River, Mozambique	Boane *et al.* (2008)
		Hemichromis fasciatus (Peters) (Cichlidae)	Owa Stream, Nigeria	Olurin and Somorin (2006)
			Ooka Lake, Nigeria	Enize and Alfred-Ockiya (2024)
		Oreochromis aureus (Steindachner) (Cichlidae	Niger River, Shagunu, Nigeria	Ukoli (1965)
		Oreochromis niloticus	Niger River, Shagunu, Nigeria	Ukoli (1965)
			Jos Plateau, Nigeria	Onwuliri and Mgbemena (1987)
			Oyo State, Nigeria	Agbede *et al.* (2004)
			Assiut Governorate, Egypt	Taher (2009)
			Eleyele Dam, Nigeria	Omeje *et al.* (2011) Simon-Oke (2017)
			Kesses Dam, Kenya	Ochieng *et al.* (2012)
			Asa Dam, Nigeria	Amaechi (2015)
		Pelmatolapia mariae (Boulenger)	Owa Stream, Nigeria	Olurin and Somorin (2006)
		Sarotherodon galilaeus	Niger River, Shagunu, Nigeria	Ukoli (1965)
			Nungua Lake, Ghana	Ukoli (1966a; 1966b) Fischthal and Thomas (1970)
			Oshun River, Nigeria	Olurin *et al.* (2012)
			Oba Reservoir, Nigeria	Ajala and Fawole (2015)
			Eleyele Dam, Nigeria	Simon-Oke (2017)
		Sarotherodon melanotheron Rüppell (Cichlidae)	Nungua Lake, Ghana	Ukoli (1966a; 1966b) Fischthal ans Thomas (1970)
			Opi Lake, Nigeria	Echi *et al.* (2009a)
			Eleyele Dam, Nigeria	Simon-Oke (2017)
		Synodontis batensoda Rüppell (Mochokidae)	Anambra River basin, Nigeria	Caffara *et al.* (2017)
Clinostomum ukolii Caffara, Locke, Echi, Halajian, Luus-Powell, Benini, Tedesco & Fioravanti, 2020		*Schilbe depressirostris*	Nandoni Dam, South Africa	Caffara *et al.* (2017)
			Nwanedi-Luphephe dams, South Africa	Caffara *et al.* (2017)
			Flag Boshielo Dam, South Africa	Caffara *et al.* (2017)
		Synodontis batensoda Rüppell (Mochokidae)*	Anambra River basin, Nigeria	Caffara *et al.* (2017)

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Table 2. (*Continued*)

Species	Synonymised names	Host	Locality	Reference
Clinostomum sp.		*Psammophis sibilans* (L.) (Serpentes: Psammophiidae)	Labé, Fouta Djallon, Guinea	Dollfus (1950)
	Clinostomum 'morphotype 3' *sensu* Caffara *et al.* (2017)	*Anoplopterus* sp. 'southern stargazer' (Amphiliidae)	Lydenburg, South Africa	Caffara *et al.* (2017)
	Clinostomum 'morphotype 3' *sensu* Caffara *et al.* (2017)	*Auchenoglanis* sp. (Claroteidae)	Venda, South Africa	Caffara *et al.* (2017)
			Makokou, Gabon	Manter and Pritchard (1969)
		Bagrus bajad (Forsskål) (Bagridae)	Upper Benue River at Mutum Biu, Nigeria	Omeji *et al.* (2022c)
		Chrysichthys nigrodigitatus	Nangue Ntongolo, Gabon	Manter and Pritchard (1969)
		Chrysichthys walkeri Günther (Claroteidae)	Lake Ezanga, Gabon	Manter and Pritchard (1969)
		Citharinus citharus (Geoffroy Saint-Hilaire) (Citharinidae)	Osse River, Nigeria	Okaka and Akhigbe (1999)
			Niger River, Illushi, Nigeria	Onyedineke *et al.* (2010)
	Clinostomum 'morphotype 3' *sensu* Caffara *et al.* (2017)	*Chiloglanis pretoriae* van der Horst (Mochokidae)	Dzindi, South Africa	Caffara *et al.* (2017)
			Lydenburg, South Africa	Caffara *et al.* (2017)
	Clinostomum 'morphotype 3' *sensu* Caffara *et al.* (2017)	***Chiloglanis* sp.**	**Letaba River, South Africa**	**This study**
		Clarias alluaudi Boulenger (Clariidae)	Lake Victoria, Tanzania	Mwita (2014)
		Clarias gariepinus	Transvaal, South Africa (unspecified)	Lombard (1968)
			Lake Awassa, Ethiopia	Tedla and Tadesse (1979)
			Lake Ziway, Ethiopia	Yimer (2000)
			Koka Reservoir, Ethiopia	Gulelat *et al.* (2013)
			Lake Victoria, Tanzania	Mwita (2014) Mwita and Nkwengulila (2004)
			Haramaya district, Ethiopia	Tesfaye *et al.* (2023)
		Clarotes laticeps (Rüppell) (Claroteidae)	Benue River, Nigeria	Omeji *et al.* (2014)
		Coptodon rendalli	Lusaka, Zambia	Batra (1984)
			Lake Kariba, Zimbabwe	Douëllou (1992a; 1992b) Douëllou and Erlwanger (1993) Magadza (1991)
		Coptodon zillii	Kainji Reservoir, Nigeria	Awachie (1965)
			Khartoum, Sudan	Khalil (1969)
			Osse River, Nigeria	Okaka and Akhigbe (1999)
			Lake Ziway, Ethiopia	Yimer (2000)
			Lake Naivasha, Kenya	Aloo (2002)
			Lake Tiga, Nigeria	Bichi and Ibrahim (2009)
			Niger River, Illushi, Nigeria	Onyedineke *et al.* (2010)
		Ctenopoma kingsleyae Günther (Anabantidae)	Osse River, Nigeria	Okaka and Akhigbe (1999)

(*Continued*)

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Table 2. (*Continued*)

Species	Synonymised names	Host	Locality	Reference
			Niger River, Illushi, Nigeria	Onyedineke *et al.* (2010)
		Cyprinus carpio	Lake Hashengie, Ethiopia	Adugna *et al.* (2013)
		Enteromius eutaenia (Boulenger) (Cyprinidae)	Mohlapitse River, South Africa	Mashego (1982)
			Nwanedi-Luphephe Dam/Nwanedi River, South Africa	Mashego (1982)
		Enteromius rapax (Steindachner) (Cyprinidae)	Mohlapitse River, South Africa	Mashego (1982)
			Olifants River, South Africa	Mashego (1982)
			Piet Gouws Dam, South Africa	Mashego (1982)
		Enteromius paludinosus (Peters) (Cyprinidae)	Mohlapitse River, South Africa	Mashego (1982)
			Nwanedi-Luphephe Dam/Nwanedi River, South Africa	Mashego (1982)
			Olifants River, South Africa	Mashego (1982)
			Piet Gouws Dam, South Africa	Mashego (1982)
		Enteromius radiatus (Peters) (Cyprinidae)	Nwanedi-Luphephe Dam/Nwanedi River, South Africa	Mashego (1982)
	Clinostomum 'morphotype 4' *sensu* Caffara *et al.* (2017)	*Enteromius trimaculatus*	Mohlapitse River, South Africa	Mashego (1982)
			Middle Letaba Dam, South Africa	Caffara *et al.* (2017)
			Nwanedi-Luphephe Dam/Nwanedi River, South Africa	Mashego (1982)
			Olifants River, South Africa	Mashego (1982)
			Piet Gouws Dam, South Africa	Mashego (1982)
		Enteromius inermis (Peters)	Nwanedi-Luphephe Dam/Nwanedi River, South Africa	Mashego (1982)
		Epiplatys sexfasciatus Gill (Nothobranchiidae)	Freetown, Sierra Leone	Williams and Chaytor (1966)
		Epiplatys spilargyreius (Duméril) (Nothobranchiidae)	Freetown, Sierra Leone	Williams and Chaytor (1966)
		Haplochromis obliquidens (Hilgendorf) (Cichlidae)	Lake Victoria, Uganda	Khalil and Thurston (1973)
		Hemichromis fasciatus	Lake Kompienga, Burkina Faso	Coulibaly *et al.* (1995)
		Labeo coubie Rüppell (Cyprinidae)	Cross River, Nigeria	Ayotunde *et al.* (2007)
		Labeobarbus intermedius (Rüppell) (Cyprinidae)	Koka Reservoir, Ethiopia	Gulelat *et al.* (2013)
	Clinostomum 'morphotype 2' *sensu* Caffara *et al.* (2017)	*Marcusenius macrolepidotus*	Bubiana River, Zimbabwe	Caffara *et al.* (2017)
	Clinostomum 'morphotype 2' *sensu* Caffara *et al.* (2017)	*Marcusenius krameri*	Latonyanda River, South Africa	Caffara *et al.* (2017)

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Table 2. (*Continued*)

Species	Synonymised names	Host	Locality	Reference
			Nwanedi-Luphephe Dam, South Africa	Caffara *et al.* (2017)
			Letaba River, South Africa	**This study**
	Clinostomum 'morphotype 2' *sensu* Caffara *et al.* (2017)	*Marcusenius pongolensis* (Fowler) (Mormyridae)	Xihlakati, South Africa	Caffara *et al.* (2017)
		Oreochromis leucostictus (Trewavas) (Cichlidae)	Lake Naivasha, Kenya	Aloo (2002)
		Oreochromis mortimeri	Lake Kariba, Zimbabwe	Douëllou (1992a; 1992b) Douëllou and Erlwanger (1993)
		Oreochromis mossambicus	Transvaal, South Africa (unspecified)	Lombard (1968)
			Lake Kariba, Zimbabwe	Magadza (1991)
			Limpopo/Olifants Rivers, South Africa	Madanire-Moyo *et al.* (2012)
			Mashoko Dam, Zimbabwe	Mutengu and Mhlanga (2018)
		Oreochromis niloticus	Kainji Reservoir, Nigeria	Awachie (1965)
			Khartoum, Sudan	Khalil (1969)
			Lake Awassa, Ethiopia	Tedla and Tadesse (1979) Zekarias and Yimer (2007)
			Lake Nasser, Egypt	Saoud and Wannas (1984)
			Lake Kompienga, Burkina Faso	Coulibaly *et al.* (1995)
			Lake Chamo, Ethiopia	Yimer *et al.* (1999)
			Lake Ziway, Ethiopia	Bihonegn and Tilahun (2017) Yimer (2000)
			Assiut Governorate, Egypt	Marwan and Mohammed (2003)
			Lake Tana, Ethiopia	Yimer and Enyew (2003)
			Lake Hashengie, Ethiopia	Adugna *et al.* (2013)
			Koka Reservoir, Ethiopia	Gulelat *et al.* (2013)
			Lake Lugo, Ethiopia	Amare *et al.* (2014)
			Lake Small Abaya, Ethiopia	Reshid *et al.* (2015)
			Loumbila & Ziga Reservoirs, Burkina Faso	Sinaré *et al.* (2016)
			Lake Koftu, Ethiopia	Mitiku *et al.* (2018)
			Makurdi, Nigeria	Omeji *et al.* (2022a)
			Haramaya district, Ethiopia	Tesfaye *et al.* (2023)
			Midmar Reservoir, Ethiopia	Tesfay *et al.* (2024)
		Oreochromis shiranus Boulenger (Cichlidae)	Bunda Reservoir, Tanzania	Maguza-Tembo and Mfitilodze (2008)
		Pharyngochromis acuticeps (Steindachner) (Cichlidae)	Lake Kariba, Zimbabwe	Douëllou (1992b)
		Sargochromis codringtonii (Boulenger) (Cichlidae)	Lake Kariba, Zimbabwe	Douëllou (1992b) Douëllou and Erlwanger (1993)

(*Continued*)

Table 2. (*Continued*)

Species	Synonymised names	Host	Locality	Reference
		Sarotherodon galilaeus	Kainji Reservoir, Nigeria	Awachie (1965)
			Khartoum, Sudan	Khalil (1969)
			Lake Nasser, Egypt	Saoud and Wannas (1984)
			Lake Kompienga, Burkina Faso	Coulibaly *et al.* (1995)
		Serranochromis macrocephalus (Boulenger) (Cichlidae)	Lake Kariba, Zimbabwe	Douëllou (1992b) Douëllou and Erlwanger (1993)
		Schilbe intermedius	Osse River, Nigeria	Okaka and Akhigbe (1999)
		Schilbe depressirostris	Nwanedi-Luphephe Dam, South Africa	Caffara *et al.* (2017) Smit and Luus-Powell (2012)
		Synodontis eupterus Boulenger (Mochokidae)	Niger River, Illushi, Nigeria	Onyedineke *et al.* (2010)
		Synodontis nigrita	Lower Ouémé Valley, Benin	Dougnon *et al.* (2012)
		Synodontis schall	Lower Ouémé Valley, Benin	Dougnon *et al.* (2012)
		Synodontis zambezensis Peters (Mochokidae)	Lake Kariba, Zimbabwe	Chishawa (1991) Douëllou (1992b) Douëllou and Erlwanger (1993)

Notes:
[a]Dubois (1931) gives the host as *Phalacrocorax levaillanti*, a name that does not exist. We cite the host as *Phalacrocorax* sp.
[b]Calhoun *et al.* (2019), in their supplementary table, ascribe these records to Echi *et al.* (2009b), but that paper does not contain any mention of them.
[c]Skrjabin (1947) gives the location of discovery as Angola; this is not mentioned in Dubois (1930), who only gives the location as 'Africa'.
[d]Dollfus (1950) noted these specimens, collected by P. Brien, but did not describe them; Manter and Pritchard (1969) subsequently identified these as *Clinostomum tilapiae* on the basis of two of Brien's specimens.

Extract PCR Kit (PCRBiosystems, Analytical Solutions, Randburg, South Africa). Buffer volume adjustments were as follows for the extraction reaction: 10 µl 5× PCRBIO Rapid Extract Buffer A, 5 µl 10× PCRBIO Rapid Extract Buffer B, and 70 µl of PCR grade water to a final volume of 85 µl. Final reaction dilution after incubation, as per manufacturer instruction, was done with 200 µl PCR grade water instead of 900 µl to obtain DNA at a higher concentration. The Polymerase Chain Reactions (PCR) for all three gene regions, 28S rDNA, ITS1-5.8S-ITS2 (ITS1–2), and cytochrome oxidase I (COI) mtDNA were adapted in volume and in the thermal cycling profiles compared to the reference literature and are provided below. The PCR reactions for the partial 28S rDNA and ITS1–2 regions were made in a final volume of 25 µl, consisting of 12.5 µl DreamTaq PCR Master Mix (2×) (Thermo Fisher Scientific, Waltham, Massachusetts, USA), 1.25 µl of each primer (10 µM), 7–8 µl PCR grade water, and 2 µl and 3 µl of DNA supernatant, respectively. While the final reaction volume for the COI region was performed at a final volume of 20 µl with 4 µl of DNA supernatant. Amplification of the 28S rDNA region was performed using the primer set Digl2 (5'- AAG CAT ATC ACT AAG CGG -3') (Tkach *et al.* 2001) and 1500R (5'- GCT ATC CTG AGG GAA ACT TCG -3') (Snyder and Tkach 2001). The thermal cycling profile was as follows: initial denaturation 95°C for 5 min, 40 cycles of amplification at 95°C for 30 sec, 55°C for 30 sec, 72°C for 2 min and final extension at 72°C for 7 min. Primers D1F (5'- AGG AAT TCC TGG TAA GTG CAA G -3') and D2R (5'- CGT TAC TGA GG GAA TCC TGG T -3') (Galazzo *et al.* 2002) were used for the ITS1–2 rDNA region. Thermal cycling conditions were as follows: initial denaturation 95°C for 3 min, 40 cycles of amplification at 94°C for 1 min, 56°C for 1 min, 72°C for 2 min, and final extension at 72°C for 5 min. The following primer sets were used for the COI mtDNA region: Dice1F (5'- ATT AAC CCT CAC TAA ATT WCN TTR GAT CAT AAG -3') and Dice14R (5'- TAA TAC GAC TCA CTA TAC CHA CMR TAA ACA TAT GAT G -3') (Van Steenkiste *et al.* 2015), or MPlatCOX1dF (5'- TGT AAA ACG ACG GCC AGT TTW CIT TRG ATC ATA AG -3') and MPlatCOX1dR (5'- CAG GAA ACA GCT ATG ACT GAA AYA AYA IIG GAT CIC CAC C -3') (Moszczynska *et al.* 2009). Amplification of COI mtDNA region was done using one of the following thermal cycling conditions: initial denaturation of 95°C for 2 min, 40 cycles of amplification at 94°C for 30 sec, 50°C for 30 sec, 72°C for 1 min, and final extension at 72°C for 10 min, or alternatively, an initial denaturation at 94°C for 4 min, 40 cycles at 94°C for 40 sec, 51°C for 40 sec, 72°C for 1 min, and final extension at 72°C for 10 min was used. PCR products were visualised on 1% agarose gel using SafeView™ Classic (Applied Biological Materials Inc, Richmond, Canada). The 28S PCR products were sequenced using the amplification primer set (Digl2 and 1500R) and internal primers 300F (5'- CAA GTA CCG TGA GGG AAA GTT G -3') (Littlewood *et al.* 2000) and ECD2 (5'- CTT GGT CCG TGT TTC AAG ACG GG -3') (Tkach *et al.* 2003), while the ITS1–2 and COI gene regions were sequenced with the same primers used in the PCR reaction. PCR amplicons were sent to Inqaba Biotechnical Industries (Pty) Ltd, Pretoria, South Africa for purification and sequencing.

Phylogenetic analyses

Novel sequences of the partial 28S and ITS1–2 rDNA and COI mtDNA gene regions were generated for all clinostomid specimens. For the cryptogonimid specimens, only partial 28S rDNA sequences

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were generated and analysed; COI mtDNA sequence data were generated but not analysed due to a lack of public data with which to compare for the family from the region. Newly generated sequences were visually inspected, and consensus sequences assembled using Geneious® 2025.0.3 (Kearse *et al.* 2012). All sequences were subjected to a BLAST search to identify congeners for inclusion in the subsequent phylogenetic analyses (Supplementary Tables 1–4). Sequences of clinostomid and cryptogonimid metacercariae were aligned with those of their respective families available on GenBank. Alignments were performed under default parameters using MAFFT version 7.490 (Katoh and Standley 2013). Each alignment was visually inspected, and final trimming was done using GBlocks v0.91b under the least stringent criteria (Castresana 2000; Dereeper *et al.* 2008). For partial 28S and ITS1–2 rDNA alignments of the Clinostomidae, analyses were focused on the genus *Clinostomum* Leidy, 1856, with species of *Ithyoclinostomum* Witenberg, 1925 and *Odhneriotrema* Travassos, 1928 designated as outgroup taxa and *Euclinostomum* Travassos, 1928 as ingroup taxa. Selected species of Diplostomidae (*Bolbophorus* sp.) were designated as outgroup taxa for the COI mtDNA analyses of the Clinostomidae. Selected species of Heterophyidae and Opisthorchiidae were used as outgroup taxa in the partial 28S rDNA analyses of the Cryptogonimidae. Optimal phylogenetic model selection for all alignments was determined in jModeltest version 2.1.10 (Darriba *et al.* 2012; Guindon and Gascuel 2003). Based on the Akaike Information Criterion (AIC), the generalised time-reversible model GTR+I+Γ was selected. Each alignment was subjected to a Bayesian Inference (BI) and Maximum Likelihood (ML) analyses using MrBayes v3.2.7a (Ronquist *et al.* 2012) and RAxML 8.2.12 (Stamatakis 2014) implemented in the CIPRES portal (Miller *et al.* 2010). Each BI analysis was run (ngen = 10 ,000,000), two chains with four MCMC chains with a sample frequency of 1,000 and sample burnin of 30%. For each dataset, 100 bootstrap pseudoreplicates were run. Uncorrected *p*-distances for each alignment were generated using MEGA X (Kumara *et al.* 2018) and numbers of base-pair differences were determined in Geneious® 2025.0.3.

Results

Clinostomid and cryptogonimid metacercariae were recovered from four host species collected during the present study (Table 1). Metacercariae were found in various organs of the fish hosts. All representatives of the Clinostomidae corresponded with the genus *Clinostomum* (Figures 1a–c) and were free in the branchial chambers of *C. gariepinus* or encysted in the body cavities of suckermouth catfishes, *Chiloglanis* sp. (Mochokidae), and the mormyrid *Marcusenius pongolensis* (Peters). Cryptogonimid metacercariae (Figure 6) were encysted in the muscle tissue and fin rays of Redeye labeo, *Labeo cylindricus* Peters (Cyprinidae). Specimens recovered in the present study correspond to one described and two undescribed species of the genus *Clinostomum* which have been previously recorded from South Africa and elsewhere on the African continent, while that of the Cryptogonimidae do not correspond to any known taxa with available molecular data. Final alignment lengths were 1,240 bp and 840 bp for the partial 28S rDNA region of the Clinostomidae and Cryptogonimidae, respectively, and 996 bp and 529 bp for the ITS1–2 rDNA and COI mtDNA regions respectively for the Clinostomidae. Sequence data for the partial 28S and ITS1–2 rDNA and COI mtDNA gene regions (Figures 2–4) were obtained for the species of Clinostomidae found during the present study. Tree topologies for BI and ML analyses of the partial 28S rDNA region were identical, but not so for the ITS1–2 rDNA and COI mtDNA regions (see Figures 3a–b and Figures 4a–b). Tree topologies for the partial 28S rDNA gene region (Figure 5) of the Cryptogonimidae were 100% congruent.

Taxonomy

Superfamily Schistosomatoidea Stiles & Hassall, 1898
Family Clinostomidae Lühe, 1901
Genus: *Clinostomum* Leidy, 1856
Clinostomum brieni (Dollfus, 1950) (Figure 1a)
Host: *Clarias gariepinus* (Burchell) (Siluriformes: Clariidae).
Locality: Barotse floodplain, Southwestern Province, Zambia (15° 12′ 1" S, 22° 58′ 9" E).
Prevalence: Three out of 17 fishes (18%) infected by 1–2 metacercariae.
Site of infection: Free in branchial chambers.
Voucher material: One hologenophore (NMB P 1070), five voucher specimens, all slides mounted (NMB P 1071–1075).
Representative DNA sequence data: 28S rDNA – one sequence of 1,229 bp length (GenBank PV547526); ITS1–2 – one sequence of 1,222 bp length (GenBank PV547524); COI – one sequence of 539 bp length (GenBank PV548073).

Morphology

With features of species. Body 4,589–9,582 (6,865) long, maximal breadth 908–1,681 (1,297), 5.0–5.7 (5.3) times longer than broad. Oral sucker 175–408 × 136–336 (296 × 233), 1.2–1.4 (1.3) times longer than broad. Ventral sucker 518–758 × 512–822 (641 × 642), 0.9–1.1 (1.0) times longer than broad, anterior edge 472–806 (650) from posterior edge of oral sucker. Forebody (pre-ventral sucker portion of body) 759–1,187 (982) or 12.4–17.1% (14.6%) of total body length. Hindbody 3,217–7,637 (5,237) or 70.1–79.7% (75.6%) of total body length. Caeca distinctly diverticulated, extend to near posterior extremity. Nascent testes, ovary, and cirrus-sac form genital complex in posterior hindbody, 5,455–8,026 (6,622) or 83.8–84.9% (84.3%) of total body length from anterior extremity, 381–543 (480) or 5.7–6.5% (6.1%) of total body length from posterior extremity. Testis anlages distinctly lobed, tandem, anterior testis 180–348 (281) from posterior testis. Anterior testis 61–151 × 277–618 (119 × 426), posterior testis 49–151 × 206–416 (94 × 338). Ovary anlage reniform, dextral in genital complex, between and slightly overlapping testes, 106–271 × 53–167 (192 × 87), 1.6–4.1 (2.5) times longer than broad. Cirrus-sac anlage reniform, dextral in genital complex, overlaps ovary and testicular margins, 139–268 × 105–190 (181 × 134), 0.9–2.0 (1.4) times longer than broad.

Remarks

Clinostomum brieni was described by Dollfus (1950) (as *Clinostomoides brieni*) from an adult infecting a Goliath Heron, *Ardea goliath* Cretzschmar (Aves: Ardeidae) from Kadia, Belgian Congo [now the southern Democratic Republic of the Congo (DRC)]. This species is among the most frequently recorded of the African clinostomids, having been reported multiple times from localities across the continent, including Botswana, the DRC, Ghana, Rwanda, and Zimbabwe (Table 2). Most recently, Caffara *et al.* (2019) reported this species from localities in the greater Lubumbashi region, DRC, and from Phalaborwa, South Africa. With the exception of the type-description, all subsequent records are of metacercariae recovered from catfishes of the genus *Clarias* Scapoli. Despite these numerous records, the latter study is the only one to

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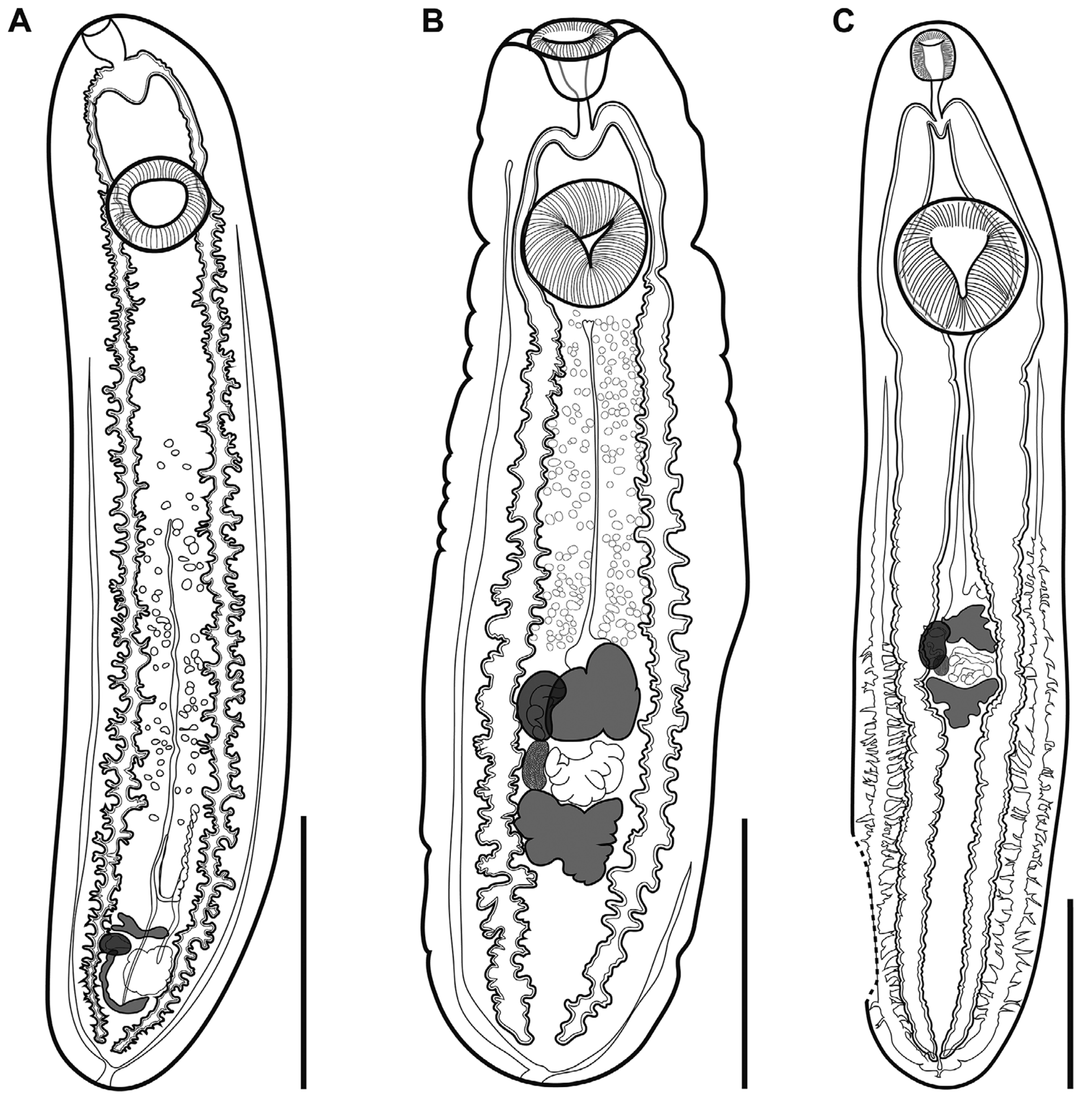

Figure 1. (A), *Clinostomum brieni* from the branchial chambers of *Clarias gariepinus* from the Barotse floodplain, Zambia (NMB P 1071); (B), *Clinostomum* sp. 'morphotype 2' *sensu* Caffara *et al*. (2017) encysted in the body cavity of *Marcusenius macrolepidotus* from the Letaba River, South Africa (NMB P 1077); (C), *Clinostomum* sp. 'morphotype 3' *sensu* Caffara *et al*. (2017) encysted in the body cavity of *Chiloglanis* sp. from the Letaba River, South Africa (NMB P 1078). Scale bars: 2 mm (A, B); 1 mm (C).

be supported by complementary molecular sequence data, the only other such data coming from specimens putatively ascribed to this species from Manipur, northeast India (Athokpam *et al.* 2016). The record from Zambia is the first of this species from this country and is broadly morphologically consistent with all previous reports.

Analyses of the partial 28S, ITS1–2 rDNA and COI mtDNA datasets for the Clinostomidae support the morphological identification of the specimen as being *C. brieni* (Figures 2–4). In both the ITS1–2 rDNA and COI mtDNA analyses, the sequence from the specimen in this study formed a clade with others of *C. brieni* from South Africa and DRC, with no differences in ITS1–2 rDNA and only 1–2 bp differences in the COI mtDNA region (Supplementary Tables 5–7). Caffara *et al.* (2019), who provided most of the available COI mtDNA sequences with which to compare, also generated one sequence of *C. brieni* which fell distant to all other conspecifics, instead forming a clade with *Clinostomum* 'morphotype 3' of Caffara *et al.* (2017) and explained this as most likely due to hybridisation. The same topology was observed in the present analyses.

The partial 28S rDNA sequence for this taxon was not comparable with others from Africa, as no other study had generated sequence data for this gene region from the continent. The sequence

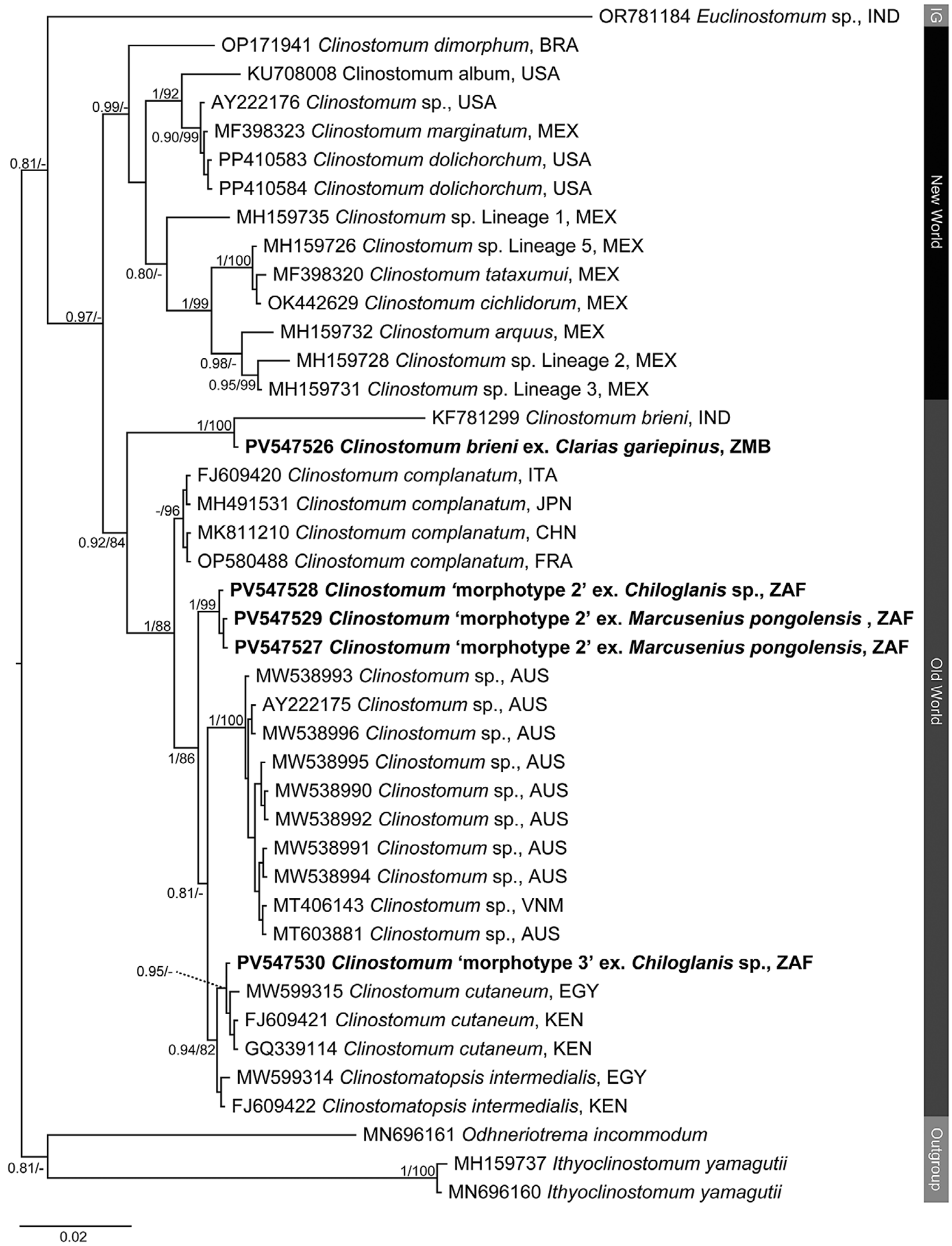

Figure 2. Phylogenetic tree based on the 1,240 bp alignment of the 28S rDNA gene region of the Clinostomidae, with our species analysed against available sequence data from Old World and New World taxa. Tree topology presented based on the Bayesian Inference (BI) analysis. Nodal support values indicate posterior probabilities from the BI and bootstrap values from the ML analyses. Dashes indicate values below 75. Species from the present study presented in bold. IG = ingroup; BRA = Brazil; CHN = China; EGY = Egypt; FRA = France; IND = India; ITA = Italy; JPN = Japan; KEN = Kenya; MEX = Mexico; USA = United States of America; VNM = Vietnam; ZAF = South Africa.

generated in the present study formed a clade with the only sequence on GenBank identified as belonging to *C. brieni*, a sequence obtained from a specimen infecting the clariid catfish *Heteropneustes fossilis* (Bloch) from India (Athokpam and Tandon 2016). The genetic difference between the specimen from this study and the one from India (23 bp difference and a *p*-distance of 1.9%), in combination with the lack of divergence in the other analysed gene regions between our sequence and others from Africa, strongly suggest that the taxon from India is not *C. brieni* and is instead a closely related but new species. Analysis of 18S rDNA sequence data of the latter taxon by Caffara *et al.* (2019), wherein it also forms a clade with *C. brieni* from Africa, further supports this inference.

Clinostomum sp. 'morphotype 2' (*sensu* Caffara *et al.* 2017) (Figure 1b)
Hosts: *Chiloglanis* sp. (Siluriformes: Mochokidae); *Marcusenius pongolensis* (Peters, 1852) (Osteoglossiformes: Mormyridae)

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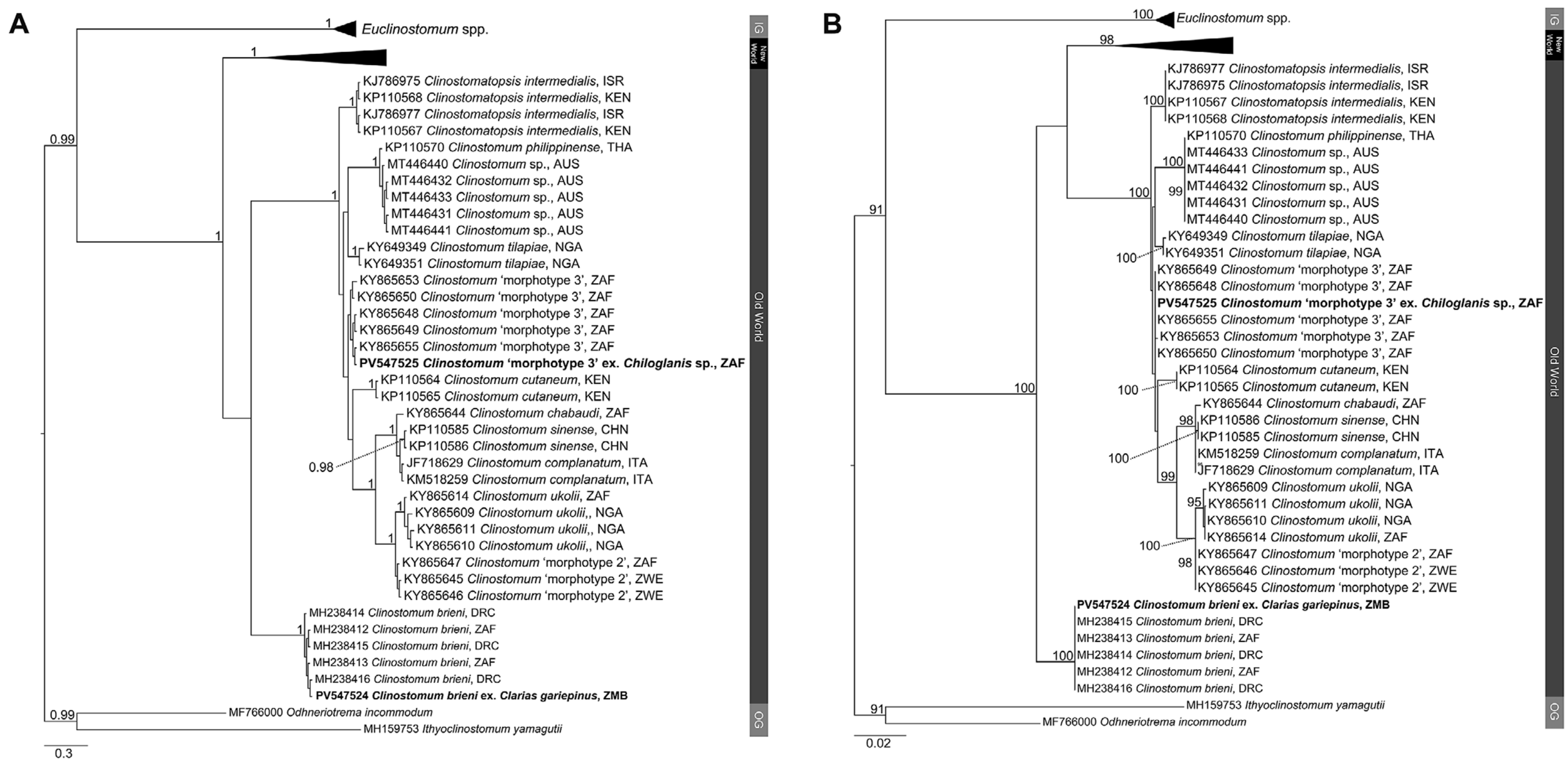

Figure 3. Phylogenetic trees based on the 996 bp alignment of the ITS1–2 rDNA gene region of the Clinostomidae, with our species analysed against available sequence data from Old World and New World taxa. Tree topologies presented based on (A), Bayesian Inference (BI) and (B), Maximum likelihood (ML) analysis. Nodal support values indicate posterior probabilities from the BI and bootstrap values from the ML analyses. Species from the present study presented in bold. OG = Outgroup; BOL = Bolivia; BRA = Brazil; CAN = Canada; DRC = Democratic Republic of the Congo; CHN = China; ISR = Israel; ITA = Italy; MEX = Mexico; NGA = Nigeria; KEN = Kenya; THA = Thailand; PER = Peru; USA = United States of America; ZAF = South Africa; ZMB = Zambia; ZWE = Zimbabwe.

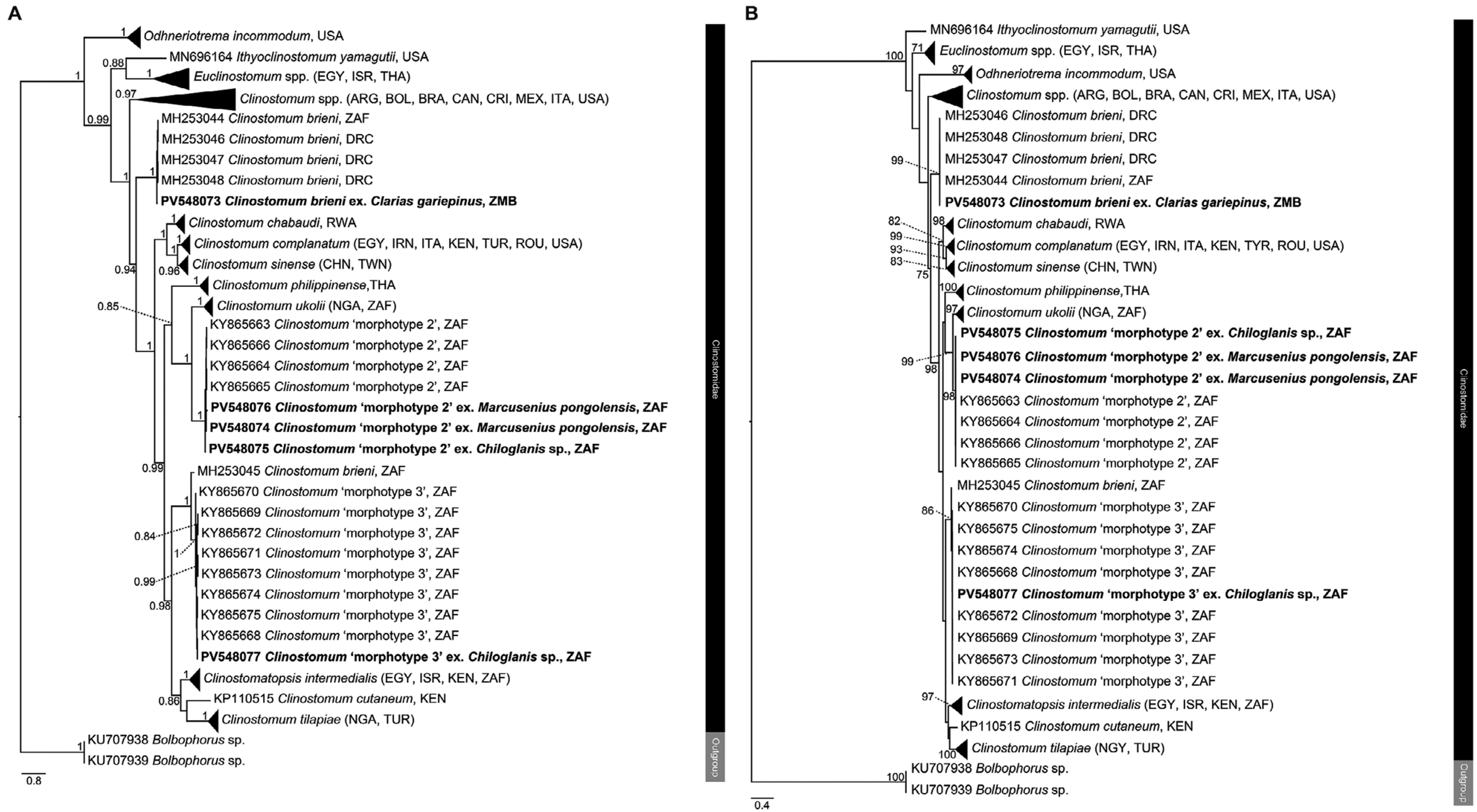

Figure 4. Phylogenetic trees based on the 529 bp alignment of the COI mitochondrial region of the Clinostomidae, with our species analysed against available sequence data from Old World and New World taxa. Tree topology presented based on (A), Bayesian Inference (BI) and (B), Maximum likelihood (ML) analysis. Nodal support values indicate posterior probabilities from the BI and bootstrap values from the ML analyses. Dashes indicate values below 75. Species from the present study presented in bold. ARG = Argentina; BOL = Bolivia; BRA = Brazil; CAN = Canada; DRC = Democratic Republic of the Congo; CRI = Costa Rica; CHN = China; EGY = Egypt; IRN = Iran; ISR = Israel; ITA = Italy; MEX = Mexico; NGA = Nigeria; KEN = Kenya; THA = Thailand; TUR = Turkey; TWN = Taiwan; ROU = Romania; USA = United States of America; ZAF = South Africa; ZMB = Zambia.

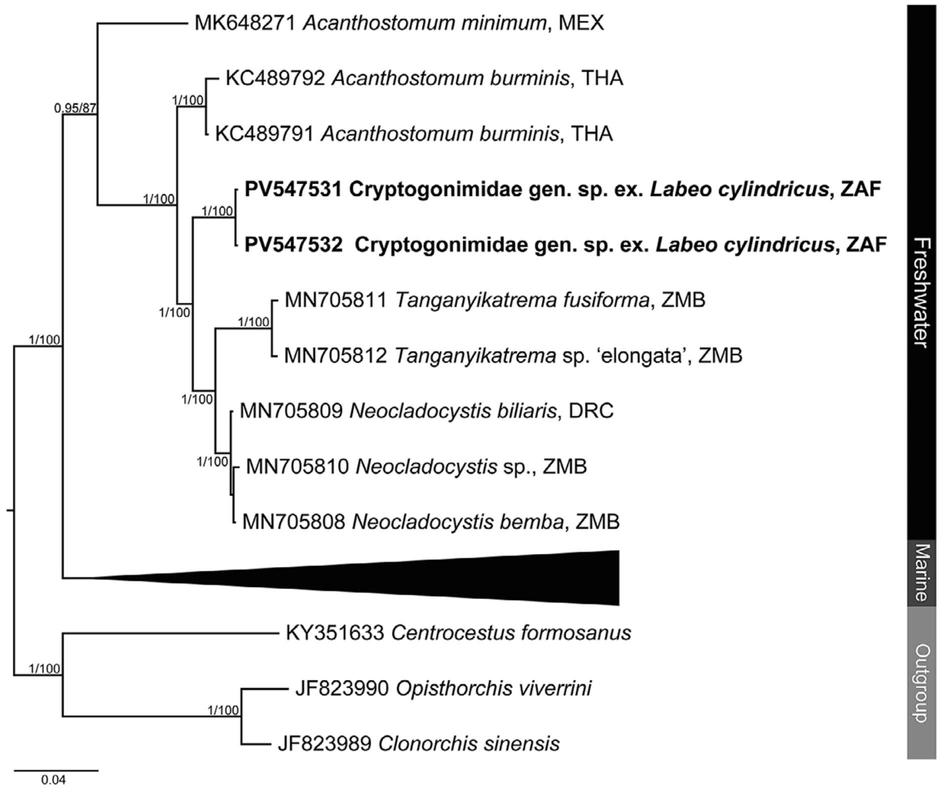

Figure 5. Phylogenetic tree based on the 840 bp alignment of the 28S rDNA region of the Cryptogonimidae. Tree topology presented based on the Bayesian inference analysis. Nodal support values indicate posterior probabilities from the BI and bootstrap values from the ML analyses. Dashes indicate values below 75. DRC = Democratic Republic of the Congo; MEX = Mexico; THA = Thailand; ZAF = South Africa; ZMB = Zambia.

Localities: Tzaneen Dam, Limpopo, South Africa (23° 48′ 55′′ S, 30° 08′ 31′′ E) – *M. pongolensis*; Letaba River, Limpopo, South Africa (23° 51′ 1′′ S, 30° 06′ 21′′ E) – *Chiloglanis* sp.
Prevalence: 67% (2/3), IF = 1 – *M. pongolensis*; 10% (1/10), IF = 1 – *Chiloglanis* sp.
Site of infection: Encysted in body cavity.
Voucher material: Two hologenophores, mounted, NMB P 1076–1077.
Representative DNA sequence data: 28S rDNA – one sequence of 1,237 bp length ex. *Chiloglanis* sp. (GenBank PV547527); two identical sequences ex. *Marcusenius pongolensis*, 1,199 and 1,266 bp length submitted to GenBank (GenBank PV547528, PV547529); COI – one sequences of 668 bp length ex. *Chiloglanis* sp.; 671 and 703 bp ex. *M. pongolensis* (GenBank PV548074, PV548075)

Morphology

With features of taxon. Body 7,981 long, maximal breadth 2,130, 3.7 times longer than broad. Oral sucker 545 × 683, 0.8 times longer than broad. Ventral sucker 994 × 971, 1.0 times longer than broad, anterior edge 649 from posterior edge of oral sucker. Forebody 1,211 or 15.2% of total body length. Hindbody 5,885 or 73.7% of total body length. Caeca distinctly diverticulated, extend to near posterior extremity. Nascent testes, ovary, and cirrus-sac form genital complex in mid-hindbody, 4,837 or 60.6% of total body length from anterior extremity, 1,497 or 18.8% of total body length from posterior extremity. Testis anlages distinctly lobed, anterior much less so than posterior; tandem, anterior testis 367 from posterior testis. Anterior testis 866 × 728, posterior testis 638 × 824. Ovary anlage reniform, dextral in genital complex, between testes, 385 × 183, 2.1 times longer than broad. Cirrus-sac anlage reniform, dextral in genital complex, overlaps ovary and anterior testicular margins, 547 × 242, 2.3 times longer than broad.

Remarks

Attempts to generate ITS1–2 rDNA sequence data for these specimens was unsuccessful. The COI mtDNA sequences, however, showed that three specimens, from the mormyrid *Marcusenius pongolensis* and the mochokid catfish *Chiloglanis* sp., were nearly or 100% identical to those referred to by Caffara *et al.* (2017) as *Clinostomum* 'morphotype 2' (Figures 3a–b). One specimen from *M. pongolensis* was genetically identical to those from the same host from northeastern South Africa, while the other two specimens differed from those of Caffara *et al.* (2017) by 1–2 bp (0.2%), showing intraspecific variation of 2–4 bp (0.3–0.6%) (Supplementary Tables 5 and 7). Caffara *et al.* (2017) did not generate 28S rDNA sequence data for this taxon. The partial 28S rDNA analyses inferred in the present study indicate sequences obtained in the present study formed a clade basal to that containing species of *Clinostomum* from elsewhere in Africa (Egypt and Kenya), Vietnam, and Australia. Caffara *et al.* (2017) obtained specimens of this taxon from two species of *Marcusenius* Gill (Mormyridae) from Zimbabwe and far northeastern South Africa. The record from *Chiloglanis* sp. constitutes a new host record for this taxon. The specimens from the present study do not strongly resemble those of Caffara *et al.* (2017) in terms of genital complex morphology, lacking the strong digitate lobulation of the testes and with the cirrus pouch overlapping the anterior testis (Figure 1b). In those regards, the newly obtained specimens more closely resemble those of *Clinostomum* 'morphotype 1', which has

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since been described as *Clinostomum ukolii* Caffara, Locke, Echi, Halajian, Luus-Powell, Benini, Tedesco & Fioravanti, 2020 (Caffara *et al.* 2020).

Clinostomum sp. 'morphotype 3' (*sensu* Caffara *et al.* 2017) (Figure 1c)
Host: *Chiloglanis* sp. (Siluriformes: Mochokidae)
Locality: Letaba River, Limpopo, South Africa (23° 51' 1" S, 30° 06' 21" E)
Prevalence: One out of 10 fishes (10%) infected with two metacercariae.
Site of infection: Encysted in body cavity.
Voucher material: One hologenophore, mounted (NMB P 1078).
Representative DNA sequence data: 28S rDNA – one sequence of 1,204 bp length (GenBank PV547530); ITS1–2 rDNA – one sequence of 1,161 bp length (GenBank PV547525); COI mtDNA– one sequence of 587 bp length (GenBank PV548077).

Morphology

With features of taxon. Body 3,673–6,162 (4,918) long, maximal breadth 1,113–1,155 (1,134), 3.3–5.3 (4.3) times longer than broad. Oral sucker 249–254 × 240–245 (252 × 243), 1.0–1.1 times longer than broad. Ventral sucker 688–770 × 665–764 (729 × 715), 1.0 times longer than broad, anterior edge 489–689 (589) from posterior edge of oral sucker. Forebody 788–1,020 (904) or 16.6–21.5% (19.0%) of total body length. Hindbody 2,207–3,262 (2,735) or 52.9–60.1% (56.5%) of total body length. Caeca not distinctly diverticulated, extend to near posterior extremity. Nascent testes, ovary, and cirrus-sac form genital complex in mid-hindbody, 2,216–3,478 (2,847) or 56.4–60.3% (58.4%) of total body length from anterior extremity, 630–2,176 (1,403) or 17.2–35.3% (26.2%) of total body length from posterior extremity. Testis anlages distinctly lobed, tandem, anterior testis 167–293 (230) from posterior testis. Anterior testis 191–268 × 313–336 (230 × 325), posterior testis 191–276 × 335–414 (234 × 375). Ovary anlage reniform, dextral in genital complex, between testes, 118–126 × 74–153 (122 × 114), 0.8–1.6 (1.2) times longer than broad. Cirrus-sac anlage reniform, dextral in genital complex, overlaps ovary and anterior testicular margins, 278–282 × 130–160 (280 × 145), 1.8–2.1 (2.0) times longer than broad.

Remarks

Both the ITS1–2 rDNA and COI mtDNA analyses indicated that specimens recovered from *Chiloglanis* sp. from Letaba River, South Africa conformed with *Clinostomum* 'morphotype 3' of Caffara *et al.* (2017). This taxon was recovered by Caffara *et al.* (2017) from catfishes of the same genus (specifically *Chiloglanis pretoriae* van der Horst) as well as the amphiliid catfish *Anoplopterus* sp. 'southern stargazer' from rivers in northeast South Africa. In both analyses, specimens from the present study were within the range of intraspecific variation obtained by Caffara *et al.* (2017) (0–1 bp difference in ITS1–2 rDNA, 0–4 bp difference in COI mtDNA). As with *Clinostomum* 'morphotype 2' (see above), novel partial 28S rDNA sequence data was produced for this taxon. Analyses of each respective gene region produced conflicting topologies with respect to the molecular phylogenetic position of *Clinostomum* 'morphotype 3'. In analyses of the partial 28S rDNA dataset, *Clinostomum* 'morphotype 3' formed a clade with sequences of *Clinostomum cutaneum* Paperna, 1964 from Kenya and Egypt, sister to *Clinostomatopsis intermedialis* (Lamont, 1920) (Gustinelli *et al.* 2010; Hamouda and Younis 2021) (Figure 2). [As an aside, *Clinostomatopsis intermedialis* has been extensively reported in literature as *Clinostomum phalacrocoracis* Dubois, 1931; the synonymy of this species with *Neutraclinostomum intermedialis* (Lamont, 1920) by Feizullaev and Mirzoeva (1983) and subsequent reclassification as a species of *Clinostomatopsis* (after the synonymising of the two genera by Kanev *et al.* 2002) does not appear to be widely accepted]. Our COI mtDNA analyses produced a similar topology, with sequences of *Clinostomum* 'morphotype 3' from the present study and Caffara *et al.* (2017) forming a clade with an anomalous sequence of *Clinostomum brieni* (see section for *C. brieni* above), sister to [*C. intermedialis* (*C. cutaneum* + *C. tilapiae*)], with strong support at all nodes (Figure 4). This topology conflicts strongly with that produced by the ITS1–2 rDNA analyses, which placed *Clinostomum* 'morphotype 3' distant to *Cl. intermedialis* and *C. tilapiae*, instead forming a clade sister to one that included several other African and Asian *Clinostomum* species, but with poor nodal resolution (Figure 3). Morphologically, the specimen from the present study conforms reasonably well with those described by Caffara *et al.* (2017) but with some minor variation. The anterior testis depicted in that paper seems markedly less lobed than that of the newly obtained specimen but is likely within the continuum of variation for this taxon. Caffara *et al.* (2017) described the caeca of morphotype 3 as digitated; the specimen from the present study shows very slight digitation (Figure 1c).

Superfamily Plagiorchioidea Looss, 1899
Family Cryptogonimidae Ward, 1917
Cryptogonimidae gen. sp. (Figure 6a–d)
Host: *Labeo cylindricus* Peters, 1852 (Cypriniformes: Cyprinidae)
Locality: Letaba River, Limpopo, South Africa (23°38'56.79" S, 30° 39'31.1" E)
Site of infection: Encysted in fin rays.
Prevalence: Three out of three individuals (100%), IF = 68–167.
Voucher material: Photohologenophore (Figure 6a–d)
Representative DNA sequence data: 28S rDNA – two identical sequences, 1,158 and 1,235 bp in length, (GenBank PV547531 and PV547532); COI – two sequences 695 and 770 bp in length (GenBank PV548078 and PV548079).

Morphology

Measurements based on three excysted specimens. Body 347–397 (372) long, maximal breadth 83–90 (87), 4.2–4.4 (4.3) times longer than broad. Oral sucker robust, subtriangular to infundibuliform, 77–115 × 67–88 (100 × 77), 1.1–1.3 times longer than broad, bearing 22–23 (23) circumoral spines. Spines robust, straight, undivided, 18–27 (23) long. Ventral sucker subspherical, 45–51 × 48–54 (49 × 51), 0.9–1.0 (1.0) times longer than broad. Ventrogenital sac not apparent. Forebody 242–253 (248) or 64–70% (67%) of total body length. Hindbody 100–130 (115) or 25–37% (31%) of total body length. Digestive tract not traceable, though hints of pharynx and caecal bifurcation observed pre-ventral sucker. Genital anlages not visible in any specimens.

Remarks

Analyses of the partial 28S rDNA region for species of Cryptogonimidae places the newly obtained sequence data within a clade formed by other African freshwater species of cryptogonimids (Figure 5 and Supplementary Table 8) of the genera *Neocladocystis* Manter & Pritchard, 1969 and *Tanganyikatrema* Kmentová, Georgieva & Bray in Kmentová, Bray, Koblmüller, Artois, De Keyzer,

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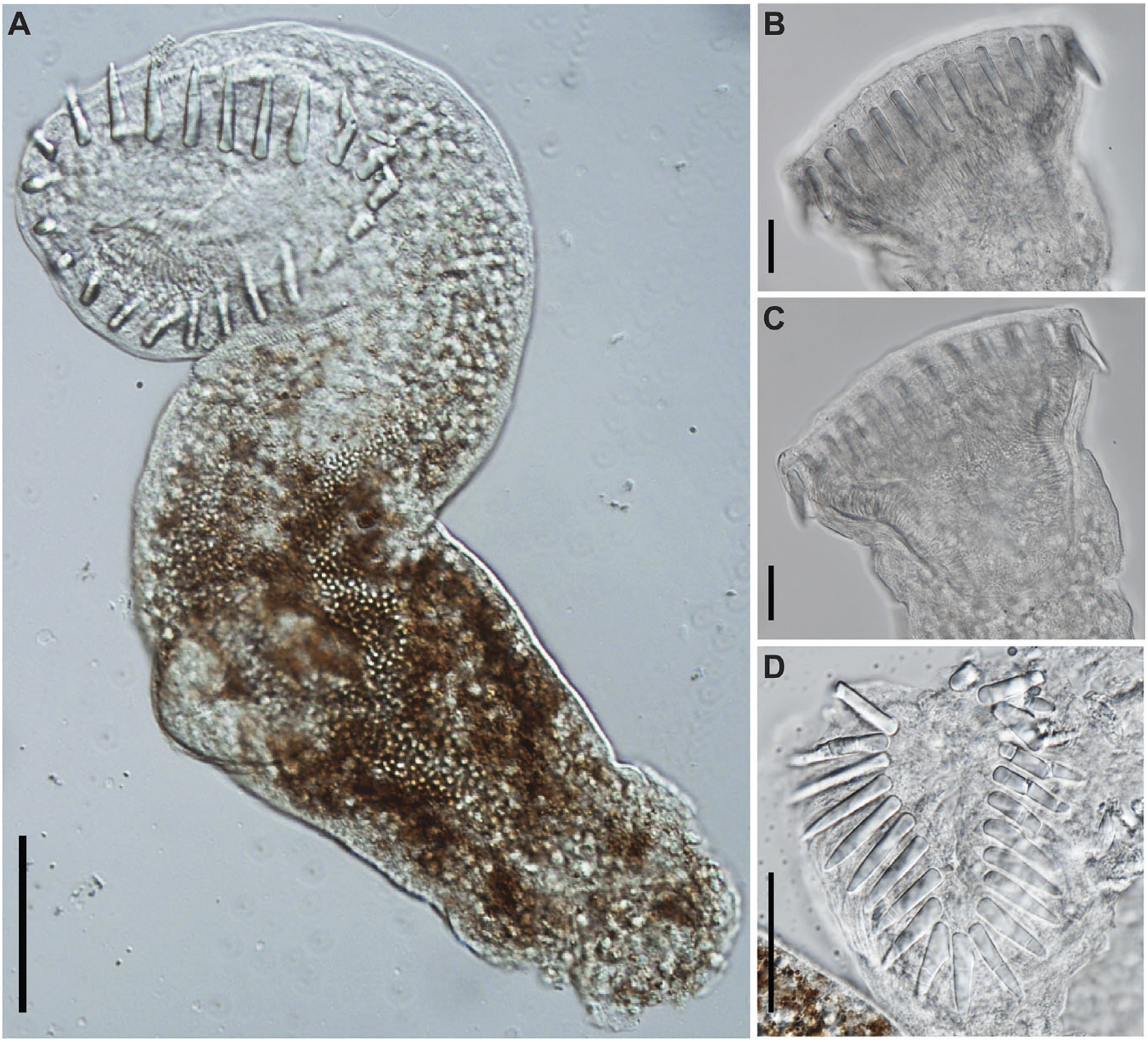

Figure 6. Photomicrographs of Cryptogonimidae gen. sp. found encysted on the fin rays of *Labeo cylindricus* from the Letaba River, South Africa (photohologenophore; GenBank PV547531). (A), Whole body, ventral view; circumoral spines, lateral view; (B), subtriangular oral sucker (C), and apical view (D). Scale bars: 50 µm (A); 20 µm (B, C, D).

Gelnar, Vanhove & Georgieva, 2020, but also including a taxon identified by Jayawardena *et al.* (2013) as *Acanthostomum burminis* (Bhalerao, 1926), a species which infects anuran amphibians as metacercariae and natricine snakes as adults. The stout oral spines of the metacercariae from the present study (Figure 6a–b, d), are more in common with species of *Acanthostomum* Looss, 1899 and *Proctocaecum* Baugh, 1957 than any of the other freshwater African cryptogonimid species, therefore it is highly likely that it corresponds to a species of one of these two genera. The genus *Acanthostomum* was recovered as polyphyletic in the 28S rDNA analysis. This is perhaps illustrative of the fact that defining this and other acanthostomine genera has long been problematic. Both *Acanthostomum* and *Proctocaecum* have had complex histories, with species of many genera (including the latter) previously being classified in the former (Brooks 1980; Lamothe-Argumedo and Ponciano-Rodriguez 1986). A lack of molecular sequence data for the type-species of the *Acanthostomum* and for any species of *Proctocaecum* compounds the difficulties in delineating the genera. Both genera include species which infect fishes and semi-aquatic reptiles; those which infect the latter are known to infect amphibians as metacercariae (see Jayawardena *et al.* 2013). The newly obtained metacercarial specimens possess 22–23 oral spines (Figure 6a, d), a feature of several species of *Proctocaecum*: *P. absconditum*, *P. productum* (Odhner, 1902), and *P. vicinum*. The fact that the metacercaria was found in a fish means it is perhaps more likely to be a fish (specifically a catfish) rather than reptile-infecting species, but the lack of knowledge regarding the freshwater cryptogonimid fauna of the region precludes any firm conclusions.

Discussion

Surveys in southern Africa recovered three distinct clinostomid morphotypes, all represented by metacercariae found in fishes.

Molecular sequence data generated for all three morphotypes validated the presence of three disparate taxa, all with affinities to the genus *Clinostomum*. The first of these, from the clariid catfish *Clarias gariepinus* from Zambia, is ascribed to *Clinostomum brieni* and the first partial 28S rDNA sequence data is provided for this species from this region. The other two putative species match to two as-yet undescribed *Clinostomum* species, known as *Clinostomum* 'morphotype 2' and 'morphotype 3', respectively, first reported by Caffara *et al.* (2017). A first general morphological account and the first partial 28S rDNA sequence data are provided for these. These taxa were collected from the same hosts and general region (Limpopo and Mpumalanga provinces in northeastern South Africa) as Caffara *et al.* (2017); however, the discovery of *Clinostomum* 'morphotype 2', hitherto only known from mormyrid fishes, from a mochokid catfish (a species of *Chiloglanis*) represents a new host record for this taxon. Despite the very low infection rates of clinostomid specimens found in this study, the few specimens obtained provided ample material to illustrate their morphological distinctness and generate comparative molecular data. A novelty to the freshwater fauna in South Africa is the first account of cryptogonimid metacercariae from a cyprinid and this record is accompanied by sequence data of the 28S rDNA and COI mtDNA gene regions.

Clinostomidae

The family Clinostomidae (often inaccurately iterated Clinostomatidae) is a small one, comprising 89 species in six genera; of these, most species are of the genus *Clinostomum* Leidy, 1856 (60 species plus three of uncertain status) and *Euclinostomum* Travassos, 1928 (20 species) (WoRMS; accessed 03/2025). Species of *Clinostomum* and *Euclinostomum*, along with *Nephrocephalus* Odhner, 1902, have been recorded from Africa (Scholz *et al.* 2018). An additional genus, *Clinostomoides* Dollfus, 1950, was proposed by Dollfus (1950) to accommodate *Clinostomoides brieni* Dollfus, 1950, described from an adult infecting a Goliath Heron, *Ardea goliath* Cretzschmar (Aves: Ardeidae) from southern region of the DRC. Species of this genus, including *C. brieni*, have since been reclassified as species of *Clinostomum* on the basis of molecular work by Caffara *et al.* (2019).

Clinostomid taxonomy has undergone several major shifts which have done little to resolve much of the confusion surrounding the family. Most notably, several genera were synonymised with the largest clinostomid genus, *Clinostomum*, and several authors (Feizullaev and Mirzoeva 1983; Ukoli 1966a) performed mass-synonymisations of multiple taxa with just one [*Clinostomum complanatum* (Rudolphi, 1814)] in attempts to resolve the issue of tenuous descriptions. Subsequent studies, however, have shown that many such efforts were over-reaching. On one hand, several species formerly synonymised with *C. complanatum* have since been revalidated (Caffara *et al.* 2014; Dzikowski *et al.* 2004; Matthews and Cribb 1998). For example, Dzikowski *et al.* (2004) demonstrated using 18S rDNA data that *Clinostomum marginatum* (Rudolphi, 1819), which was synonymised with *C. complanatum* by Baer (1933), was actually a separate species. On the other hand, other studies have also validated some of these synonymies. Species of *Clinostomoides* and *Ithyoclinostomum* Witenberg, 1926, for example, have been demonstrated to be, in fact, species of *Clinostomum* (Caffara *et al.* 2019; Simões *et al.* 2022).

Several issues surround the identification of species of *Clinostomum* in Africa, chief among them being the fact that many authors have made tenuous identifications, often based on nothing more than superficial gross morphology. Manter and Pritchard (1969), for example, identified metacercariae collected from *Oreochromis niloticus* (Linnaeus) in Rwanda as *Clinostomum macrosomum* Jaiswal, 1957, a species hitherto only known from India, entirely on the basis of its 'very large size'; *C. macrosomum* was described from metacercariae (Jaiswal 1957) and has never been encountered since.

Eight studies have incorporated molecular sequencing as part of an integrated approach in verifying species identification and systematics of clinostomids in Africa (Caffara *et al.* 2017; Caffara *et al.* 2019; Caffara *et al.* 2020; Hamouda and Younis 2021; Locke *et al.* 2015; Mahdy *et al.* 2021; Mahdy *et al.* 2023; Salem *et al.* 2021) and only 16 out of 103 published studies incorporated or generated samples from definitive hosts. In the absence of molecular sequencing, the ambiguous and highly variable morphology of many species has further complicated efforts to resolve clinostomid taxonomy, and many species have been confused with one another. For instance, in Africa, specimens of *Clinostomatopsis intermedialis* (formerly *Neutraclinostomum intermedialis* and *Clinostomum phalacrocoracis*) have been confused with *Clinostomum tilapiae* (Grobler *et al.* 1999). This disparity between depth of knowledge of *Clinostomum* intermediate stages and that of definitive stages is reflected across the wider world, with the majority of records being made from intermediate stages and, in some cases, species described from them in total absence of knowledge of the adult (see Caffara *et al.* 2020 for example). Although such an approach is traditionally problematic, it has been defended by the likes of Caffara *et al.* (2020), who point out that morphological features characteristic of adult stages, such as egg size/distribution and vitellaria, are not taxonomically discriminatory for clinostomids, that ontogenetic development of other organs minimally impacts their interpretation, that molecular phylogenetics support morphological interpretations of species delineations, and that, contextually, all indications are that the African clinostomid fauna is rather limited and has minimal overlap with the rest of the world. We largely agree with these arguments, though we are still of the opinion that matching known intermediate stages with adults should still be a key goal. We do, however, acknowledge that lack of access to definitive hosts (birds and reptiles) due to ethical and other constraints hampers the attainment of this goal.

The twin issues of historic overly conservative systematic interpretations and lack of molecular sequence data means many species identifications for clinostomids in Africa remain untested. For example, conservatively interpreting many records as being those of *C. complanatum* may well have concealed as-yet uncharacterised richness (Caffara *et al.* 2020). A handful of studies have molecularly validated the presence of this species in north Africa (Egypt) (Mahdy *et al.* 2021, Salem *et al.* 2021), but until parasitological assessments more broadly incorporate molecular sequencing protocols to aid identification, the status of '*C. complanatum*' in Africa, particularly sub-Saharan Africa, remains uncertain.

Cryptogonimidae

Of the 80 recognised cryptogonimid genera, 30 are partly or wholly represented in freshwater fishes. Freshwater fish-infecting cryptogonimids have most strongly radiated in the Americas, with species of 17 genera so far recorded from that region. Species of seven genera have been reported from African freshwater systems: *Acanthostomum* Looss, 1899; *Brientrema* Dollfus, 1950; *Grandifundilamena* Bray, Kmentová & Georgieva in Kmentová, Bray, Koblmüller, Artois, De Keyzer, Gelnar, Vanhove & Georgieva, 2020; *Gymnatrema* Morozov, 1955; *Neocladocystis* Manter & Pritchard, 1969; *Proctocaecum* Baugh, 1957; and *Tanganyikatrema* Kmentová, Georgieva & Bray in Kmentová, Bray, Koblmüller, Artois, De Keyzer, Gelnar, Vanhove & Georgieva, 2020 (Table 3; Figure 7a–d). The genus *Neocladocystis* is the only one of these also represented outside Africa, with *Neocladocystis intestinalis* (Vaz, 1932) Manter & Pritchard, 1969 being found in South America. Other species, of the predominantly marine genera *Siphodera*

Table 3. List of records of freshwater cryptogonimid species from Africa. Hosts are fishes unless otherwise noted. Entries marked '*' represent type-records from original descriptions

Species	Synonymised names	Host	Locality	Reference
Acanthostomum aswaninensis Wannas, 1977[a]		*Bagrus bajad* (Forsskål) (Bagridae)	Lake Nasser, Egypt	Wannas (1977)*
			Lake Timsah, Egypt	Taeleb and Lashien (2013)
Acanthostomum spiniceps (Looss, 1896)	*Distomum spiniceps* Looss, 1896 *Anoiktostoma spiniceps* (Looss, 1896) Stossich, 1899 *Acanthochasmus spiniceps* (Looss, 1896) Looss, 1901 *Proctocaecum spiniceps* (Looss, 1896) Lamothe-Argumedo & Ponciano-Rodriguez, 1986	*Bagrus bajad*	Nile, Cairo, Egypt	Issa and Ebaid (1969a; 1969b) Looss (1896)*
			White & Blue Nile, Khartoum, Sudan	Khalil (1963)
			Giza, Egypt	Fischthal and Kuntz (1963) Moravec (1976)
			Niger River near Shagunu, Nigeria	Ukoli (1965)
			Lake Nasser, Egypt	El-Naffar *et al.* (1983)
			Beni Suef, Egypt	Imam *et al.* (1991)
			Nile, Mansoura, Egypt	Allam *et al.* (2022)
		Bagrus docmak (Forsskål) (Bagridae)	White & Blue Nile, Khartoum, Sudan	Khalil (1963)
			Niger River near Shagunu, Nigeria	Ukoli (1965)
			Giza, Egypt	Moravec (1976)
			Lake Nasser, Egypt	El-Naffar *et al.* (1983)
			Menoufiya Governorate, Egypt	Osman *et al.* (2008)
			Nile, Mansoura, Egypt	Allam *et al.* (2022)
		Bagrus filamentosus Pellegrin (Bagridae)	Lake Débo, Mali	Dollfus (1932)
			Niger River near Shagunu, Nigeria	Ukoli (1965)
		Chrysichthys nigrodigitatus (Lacépède) (Claroteidae)	Lake Débo, Mali	Dollfus (1932)
		Dicentrarchus labrax (L.) (Moronidae)	Lake Idku, Egypt	El-Shahawi and Al-Bassel (1992)
		Lates niloticus (L.) (Latidae)	Nile, Beni Suef, Egypt	Morsy *et al.* (2013)
			Alexandria, Egypt	Abdel-Gaber *et al.* (2018)
Acanthostomum sp.		*Bagrus bajad*	Lake Nasser, Egypt	Saoud and Wannas (1984)
			Lake Wadi al-Rayyan, Egypt	Saoud *et al.* (1990)
		Bagrus docmak	Kainji Reservoir, Nigeria	Awachie (1965)

(*Continued*)

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Table 3. (*Continued*)

Species	Synonymised names	Host	Locality	Reference
			Lake Nasser, Egypt	Saoud and Wannas (1984)
		Lates niloticus	Kainji Reservoir, Nigeria	Awachie (1965)
Brientrema malapteruri Dollfus, 1950		*Malapterurus electricus* (Gmelin) (Malapteruridae)	'Maka', DRC[b]	Dollfus (1950)*
		Distichodus lusosso Schilthuis (Distichodontidae)	'Maka Londo', DRC[b]	Dollfus (1950)
Brientrema pelecani Dollfus, 1950		*Pelecanus rufescens* Gmelin (Aves: Pelecanidae)	'Maka Londo', DRC	Dollfus (1950)*
Grandifundilamena novemtestes Bray, Kmentová & Georgieva in Kmentová, Bray, Koblmüller, Artois, De Keyzer, Gelnar, Vanhove & Georgieva, 2020		*Lates angustifrons* Boulenger (Latidae)	Lake Tanganyika, Zambia	Kmentová *et al.* (2020)*
Gymnatrema gymnarchi (Dollfus, 1950)	*Acanthochasmus gymnarchi* Dollfus, 1950 *Acanthostomum gymnarchi* (Dollfus, 1950) Yamaguti, 1958	*Gymnarchus niloticus* Cuvier (Gymnarchidae)	Nile, Omdurman, Sudan	Dollfus (1950)*
			Khartoum, Sudan	Khalil (1963)
			Kainji Reservoir, Nigeria	Awachie (1965)
			Niger River near Shagunu, Nigeria	Ukoli (1965)
Neocladocystis bemba Georgieva, Kmentová & Bray in Kmentová, Bray, Koblmüller, Artois, De Keyzer, Gelnar, Vanhove & Georgieva, 2020		*Lates angustifrons*	Lake Tanganyika, Zambia	Kmentová *et al.* (2020)*
		Lates microlepis Boulenger (Latidae)	Lake Tanganyika, Zambia	Kmentová *et al.* (2020)
Neocladocystis biliaris Georgieva, Kmentová & Bray in Kmentová, Bray, Koblmüller, Artois, De Keyzer, Gelnar, Vanhove & Georgieva, 2020		*Lates mariae* Steindachner (Latidae)	Lake Tanganyika, DRC	Kmentová *et al.* (2020)*
Neocladocystis congoensis Manter & Pritchard, 1969		*Parauchenoglanis monkei* (Keilhack) (Claroteidae)	Ebogo, Cameroon	Manter and Pritchard (1969)*
Neocladocystis tanganyikae (Prudhoe, 1951)	*Cladocystis tanganyikae* Prudhoe, 1951	Cichlidae or *Lamprichthys tanganicanus* (Boulenger) (Procatopodidae)[c]	Lake Tanganyika, DRC	Prudhoe (1951)*
Neocladocystis sp.		*Lates angustifrons*	Lake Tanganyika, Zambia	Kmentová *et al.* (2020)
Proctocaecum absconditum (Looss, 1901)	*Acanthochasmus absconditus* Looss, 1901 *Acanthostomum absconditum* (Looss, 1901) Gohar, 1934 *Acanthostomum bagri* Thomas, 1958	*Bagrus bajad*	Nile, Cairo, Egypt	Looss (1901)*
			White & Blue Nile, Khartoum, Sudan	Khalil (1963)
			Giza, Egypt	Fischthal and Kuntz (1963) Moravec (1976)
			Lake Albert, Uganda	Khalil and Thurston (1973)
			Lake Nasser, Egypt	El-Naffar *et al.* (1983)

(*Continued*)

Table 3. (*Continued*)

Species	Synonymised names	Host	Locality	Reference
			Beni Suef, Egypt	Imam *et al.* (1991)
			Nile, Mansoura, Egypt	Allam *et al.* (2022) Mansour *et al.* (2003)
			Nile, Minya, Egypt	Gamal and Ibraheem (2019)
		Bagrus docmak	Nile, Cairo, Egypt	Looss (1901)
			Lawra, Ghana	Thomas (1958)
			White & Blue Nile, Khartoum, Sudan	Khalil (1963)
			Lake Nasser, Egypt	El-Naffar *et al.* (1983)
			Nile, Mansoura, Egypt	Allam *et al.* (2022) Mansour *et al.* (2003)
			Menoufiya Governorate, Egypt	Osman *et al.* (2008)
Proctocaecum gonotyl (Dollfus, 1950)	*Acanthochasmus gonotyl* Dollfus, 1950 *Acanthostomum gonotyl* (Dollfus, 1950) Morozov, 1955	*Crocodylus niloticus* Laurenti (Reptilia: Crocodylidae)	Bukama, DRC	Dollfus (1950)*
			'Maka', DRC	Dollfus (1950)
Proctocaecum knobus (Issa, 1962)	*Acanthostomum spiniceps knobus* Issa, 1962 *Acanthostomum knobus* Issa, 1962	*Lates niloticus*	Nile, Cairo, Egypt	Issa (1962)*
Proctocaecum niloticum (Issa, 1962)	*Acanthostomum niloticum* Issa, 1962	*Lates niloticus*	Nile, Cairo, Egypt	Issa (1962)*
Proctocaecum productum (Odhner, 1902)	*Acanthochasmus productus* Odhner, 1902 *Acanthostomum productum* (Odhner, 1902) Gohar, 1934	*Crocodylus niloticus*	Malakal, South Sudan	Odhner (1902)*
			Sudan (unspecified)	Khalil (1969)
			Olifants River, South Africa	Prudhoe and Hussey (1977)
Proctocaecum vicinum (Odhner, 1902)	*Acanthochasmus vicinus* Odhner, 1902 *Acanthostomum vicinum* (Odhner, 1902) Gohar, 1934	*Crocodylus niloticus*	Malakal, South Sudan	Odhner (1902)*
			Sudan (unspecified)	Khalil (1969)
Siphodera ghanensis Fischthal & Thomas, 1968		*Chrysichthys nigrodigitatus* (Lacépède) (Claroteidae)	Kakum River at Iture, Ghana	Fischthal and Thomas (1968c)*
			Ekotsi, Ghana	Fischthal and Thomas (1968b)
			Lake Ezanga, Gabon	Manter and Pritchard (1969)
			Cross River estuary, Nigeria	Obiekezie *et al.* (1988)
		Hydrocynus brevis (Günther) (Alestidae)	Volta River at Sogakofe, Ghana	Fischthal and Thomas (1972)
Siphoderina ghanensis (Fischthal & Thomas, 1968)	*Paracryptogonimus ghanensis* Fischthal & Thomas, 1968	*Lutjanus goreensis* (Valenciennes) (Lutjanidae)	Kakum River estuary, Ghana	Fischthal and Thomas (1968a)*
		Pomadasys jubelini (Cuvier) (Haemulidae)	Densu River, Ghana	Fischthal and Thomas (1972)
Tanganyikatrema fusiforme Kmentová, Georgieva & Bray in Kmentová, Bray, Koblmüller, Artois, De Keyzer, Gelnar, Vanhove & Georgieva, 2020		*Lates angustifrons*	Lake Tanganyika, Zambia	Kmentová *et al.* (2020)*

(*Continued*)

Table 3. (*Continued*)

Species	Synonymised names	Host	Locality	Reference
		Lates microlepis	Lake Tanganyika, Zambia	Kmentová *et al.* (2020)
Tanganyikatrema sp. 'elongata'		*Lates angustifrons*	Lake Tanganyika, Zambia	Kmentová *et al.* (2020)

Notes:
[a]This species was proposed in a thesis and never formally published. It should therefore be regarded as invalid.
[b]It is unclear where the localities of 'Maka' and 'Maka Lombo' provided by Dollfus (1950) are. They could refer to the town of Kalombo, which is in the vicinity of the lakes of the Upemba Depression, where Brien (the collector of these specimens) was collecting at that time.
[c]Specimens were found in the bottom of jar containing mixed fish species; the type-host is therefore unknown.

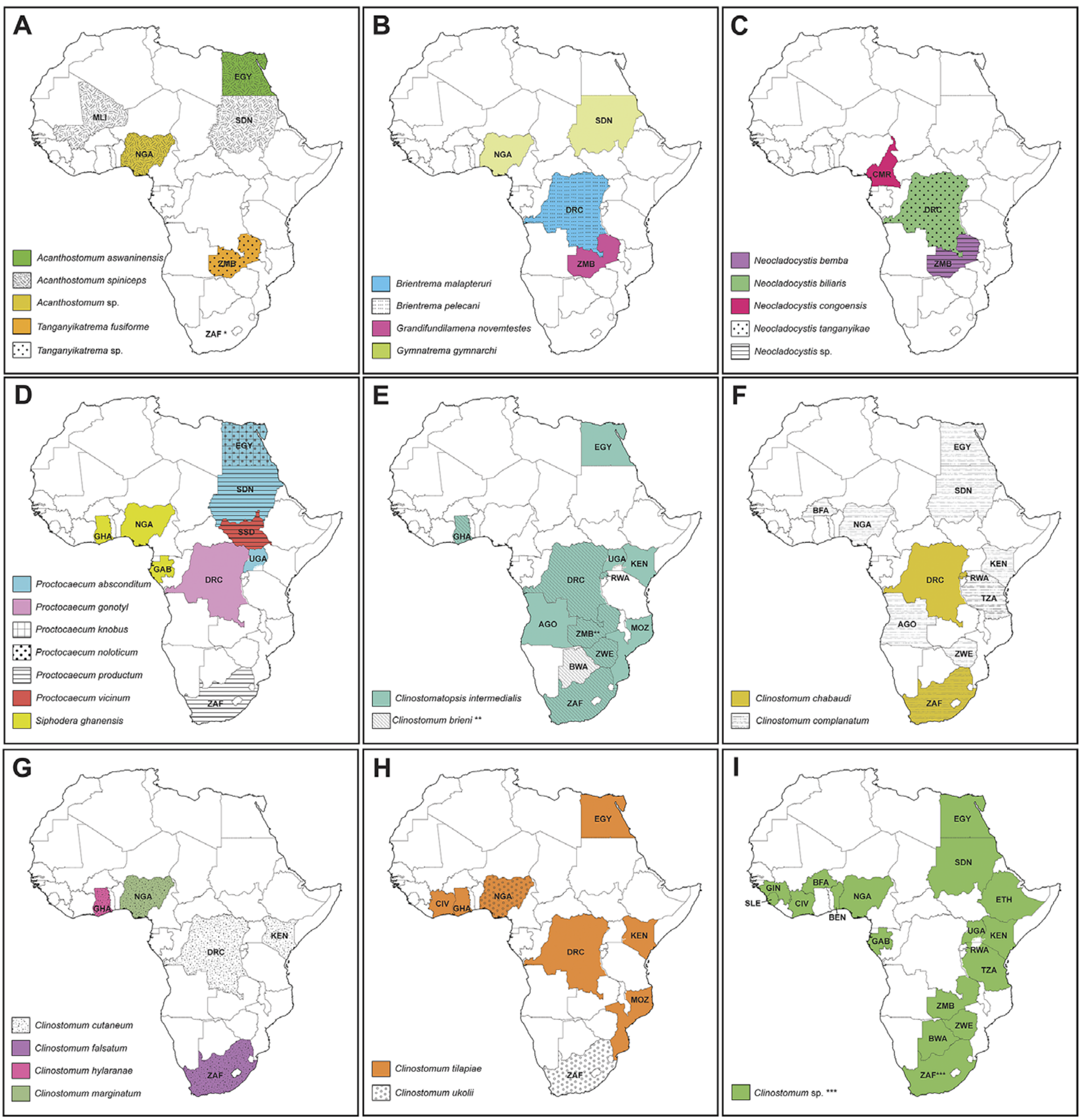

Figure 7. Maps depicting countries with records of species of the Cryptogonimidae (A–D) and Clinostomidae (E–I). Asterisk depicts countries with record data from the current study: * – first record of a species of Cryptogonimidae in South Africa; ** – first report of *Clinostomum brieni* from Zambia; *** – records of *Clinostomum* 'morphotype 2' and *Clinostomum* 'morphotype 3' from South Africa. AGO = Angola; BEN = Benin; BWA = Botswana; BFA = Burkina Faso; CMR = Cameroon; DRC = Democratic Republic of the Congo; EGY = Egypt; Ethiopia; GAB = Gabon; GHA = Ghana; GIN = Guinea; CIV = Ivory Coast; KEN = Kenya; MLI = Mali; MOZ = Mozambique; NGA = Nigeria; RW = Rwanda; SLE = Sierra Leone; ZAF = South Africa; SSD = South Sudan; SDN = Sudan; TZA = Tanzania; UGA = Uganda; ZMB = Zambia; ZWE = Zimbabwe.

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Linton, 1910 and *Siphoderina* Manter, 1934, have occasionally been reported from estuarine or marine-adjacent freshwater systems, and are not considered further.

Two species of *Acanthostomum* have been reported from Africa, including the type-species of the genus, *Acanthostomum spiniceps* (Looss, 1896), which was originally described (as *Distomum spiniceps*) from the bagrid catfish *Bagrus bajad* (Forsskål) (Bagridae) from the Egyptian Nile at Cairo (Looss 1896) and has subsequently been reported from this and other bagrid species from this locality numerous times. This species was subsequently reported from catfishes from elsewhere in Africa: Lake Débo, Mali (Dollfus 1932) and the Sudanese Nile (Khalil 1963), and from *Dicentrarchus labrax* (L.) (Moronidae) from Idku Lake, Egypt (El-Shahawi and Al-Bassel 1992). Multiple authors have also reported it from Nile perch, *Lates niloticus* (L.) (Latidae) from the Egyptian Nile (Abdel-Gaber *et al.* 2018; Al-Ghamdi 2018; Morsy *et al.* 2013;), though one (Al-Ghamdi 2018) appears to heavily plagiarise another (Morsy *et al.* 2013) and should be disregarded. *Acanthostomum spiniceps* is a problematic species, having been redescribed multiple times (Issa 1964; Looss 1901; Moravec 1976; Morsy *et al.* 2013) and also reported from marine localities in Europe and South America (Fernandes *et al.* 2002; Pogoreltseva 1952a; Pogoreltseva 1952b). The species is quite morphologically variable (Moravec 1976), and despite its apparent familiarity, has never been molecularly sequenced. Hassan *et al.* (1990) described *Acanthostomum saoudi* Hassan, Khidr & Samak, 1990 from *D. labrax* from off the Egyptian coast. A further species, *Acanthostomum aswaninensis* Wannas, 1977 was described by Wannas (1977) in a master's dissertation and, as far as we are aware, was never formally published. Occasionally, studies have recognised this taxon (Lashien 1993; Taeleb and Lashein 2013) but we regard it as invalid.

The history of the taxonomy of *Acanthostomum* is inextricably linked to that of the genus *Proctocaecum.* The latter was proposed by Baugh (1957), who transferred three species of *Acanthostomum* whose caeca open as ani close to the posterior extremity to this genus. Brooks (1980) reassigned a further four *Acanthostomum* species to *Proctocaecum* and described one further species. Of the six *Proctocaecum* species recorded from Africa, one, *P. absconditum* (Looss, 1901), infects catfishes (Bagridae: *Bagrus* spp.), two [*P. knobus* (Issa, 1962) and *P. niloticum* (Issa, 1962)] infect Nile perch, and three [*P. gonotyl* (Dollfus, 1950), *P. productum* and *P. vicinum* (Odhner, 1902)] infect Nile crocodiles (*Crocodylus niloticus* Laurenti) as adults (Brooks 1980; Khalil 1963). A listing of *Proctocaecum coronarium* (Cobbold, 1861>) from *Alligator* sp. from Sudan by Gohar (1934) is in error, referring to specimens recovered by Cobbold (1861) from an American alligator [*Alligator mississippiensis* (Duadin) (Reptilia: Alligatoridae)] which died in the London Zoological Society's menagerie (i.e., London Zoo). Only *P. productum* has been recorded from southern Africa; Prudhoe and Hussey (1977) recovered this species from the intestine of *C. niloticus* from the Olifants River in South Africa. The remainder of the species were mostly recorded from north and central Africa in the Nile catchment.

Dollfus (1950), in his studies on trematodes collected from the Belgian Congo (now Democratic Republic of Congo), described the type-species of *Brientrema*, *Brientrema pelecani* Dollfus, 1950, from the Pink-backed Pelican, *Pelecanus rufescens* Gmelin (Aves: Pelecanidae); it has been noted that this was potentially a case of pseudo-parasitism (Miller and Cribb 2008). The other species *Brientrema malapteruri* Dollfus, 1950 was described by the same author from the electric catfish *Malapterurus electricus* (Gmelin) (Malapteruridae) and the longsnout distichodus *Distichodus lusosso* Schilthuis (Distichodontidae) (Dollfus 1950). Dollfus (1950) also described a third cryptogonimid species, *Acanthochasmus gymnarchi* Dollfus, 1950, from the Nile River by Omdurman, Sudan; this species infects the aba, *Gymnarchus niloticus* Cuvier (Gymnarchidae). The genus *Gymnatrema* was proposed by Morozov (1955) to incorporate *A. gymnarchi.* A further species, *Acanthostomum nigeri* Zaidi & Khan, 1977, described from the marine pelagic carangid *Parastromateus niger* (Bloch) from off Karachi, Pakistan was transferred to *Gymnatrema* by Brooks (1980); its status is uncertain, though this classification is almost certainly wrong.

The genus *Neocladocystis* was proposed by Manter and Pritchard (1969) to separate *Cladocystis intestinalis* Vaz, 1932 and *Cladocystis tanganyikae* Prudhoe, 1951 from the then-only other species of that genus, *Cladocystis trifolium* (Braun, 1901), on the basis of possessing tegumental spines, larger oral and ventral suckers, less extensive vitelline follicles, and unbranched arms of the excretory vesicle; this latter species is now recognised as belonging to the family Opisthorchiidae. Prudhoe (1951) described *Neocladocystis tanganyikae* from 'a small bay south of Cape Tembwe' on the Congolese shore of Lake Tanganyika. The two specimens which formed the basis of description were recovered from the residue of a jar containing several species of cichlid fishes mixed with the killifish *Lamprichthys tanganicanus* (Boulenger) (Procatopodidae), making the host species impossible to ascertain. Manter and Pritchard (1969) described *Neocladocystis congoensis* Manter & Pritchard, 1969 from the claroteid catfish *Parauchenoglanis monkei* (Keilhack) [as *Parauchenoglanis guttatus* (Lönnberg)], from Ebogo, Cameroon. Most recently, Kmentová *et al.* (2020) described two species of *Neocladocystis*, *Neocladocystis bemba* Georgieva, Kmentová & Bray in Kmentová, Bray, Koblmüller, Artois, De Keyzer, Gelnar, Vanhove & Georgieva, 2020 and *Neocladocystis biliaris* Georgieva, Kmentová & Bray in Kmentová, Bray, Koblmüller, Artois, De Keyzer, Gelnar, Vanhove & Georgieva, 2020 from three species of *Lates* Cuvier (Latidae) from Lake Tanganyika. A third species of *Neocladocystis* was noted by the same authors from *Lates angustifrons* Boulenger from the same lake on the basis of molecular sequence data, but was not described due to there being only one immature specimen. Kmentová *et al.* (2020) also proposed *Grandifundilamena* and *Tanganyikatrema* for two latid-infecting species from Lake Tanganyika, *Grandifundilamena novemtestes* Bray, Kmentová & Georgieva in Kmentová, Bray, Koblmüller, Artois, De Keyzer, Gelnar, Vanhove & Georgieva, 2020 and *Tanganyikatrema fusiforme* Kmentová, Georgieva & Bray in Kmentová, Bray, Koblmüller, Artois, De Keyzer, Gelnar, Vanhove & Georgieva, 2020. A second species of *Tanganyikatrema* was also reported from *L. angustifrons* from Lake Tanganyika, but again, was not described due to a lack of material.

Biogeography

Information regarding freshwater cryptogonimids in Africa is too sparse to draw any biogeographic inferences; hence the focus of this aspect of discussion is on the clinostomids. We do note with interest the record by Prudhoe and Hussey (1977) of *P. productum* from northeastern South Africa, a species otherwise only known from the Sudanese Nile. It is hoped future studies in these regions will recollect these taxa and generate molecular sequence data.

In accordance with findings on the global clinostomid fauna in previous studies, results from the current study support the separation between clinostomid species of the 'Old World' (Afrotropic,

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Indo-Malayan, and Palearctic realms) and 'New World' (Nearctic and Neotropic realms). This divide is explained by the isolation of avian definitive hosts by oceanic barriers which are rarely crossed by the definitive hosts of clinostomids (see Caffara *et al.* 2014; Caffara *et al.* 2017; Locke *et al.* 2015). Of the Old World clinostomid fauna, affinities between the Afrotropical, Indomalayan, and Palearctic realms are apparent. The definitive hosts of Old World clinostomids are piscivorous birds of the families Anhingidae (darters), Ardeidae (herons), Pelecanidae (pelicans), and Phalacrocoracidae (cormorants). Birds of these families show a range of dispersal abilities, with some species endemic to single continents but able to undertake infra-continental migrations, while others are naturally distributed and move across multiple biogeographic realms (Afrotropic, Indo-Malayan, and Palearctic). This high dispersal ability among piscivorous bird species undoubtedly explains the wide distributions of some clinostomid species. For example, *Cl. intermedialis* has been demonstrated to range across most of Africa (with molecularly verified specimens from South Africa, Kenya, and Egypt), the Middle East (Israel), and southern Europe (Italy), and *C. tilapiae* has been reported (with supporting molecular sequence data) from Nigeria and Turkey. Most dramatically, *C. complanatum* has been reported from throughout the Old World, with records supported by molecular sequence data from Africa (Kenya, Egypt), Europe (France, Italy, Romania), western Asia (Iran, Turkey), and east Asia (China, Japan), as well as North America (USA, Canada). The definitive host of *C. brieni* is the Goliath Heron, *Ardea goliath.* This heron species is widespread and common throughout sub-Saharan Africa and is also found patchily in the Middle East and across the north of the Indian sub-continent (Martínez-Vilalta *et al.* 2020). Although movements in Asia and between continents are unknown, nomadic movements are known within the African populations (Martínez-Vilalta *et al.* 2020). Such movement dynamics are typical of other African bird species which are hosts to *Clinostomum* spp.

It is appropriate to include an additional consideration, that of intermediate host specificity. Several species of *Clinostomum* show stenoxenous host-specificity at the second intermediate stage. For example, *C. brieni* has only ever been reported from clariid catfishes, having been reported from a number of clariids in Africa and, putatively, India. Other clinostomid species, e.g., *C. ukolii* and *Clinostomum* 'morphotype 3' of Caffara *et al.* (2017), infect catfishes across several families; still others, e.g., *C. cutaneum*, infect several species of cichlid fishes; and additional ones, e.g., *Cl. intermedialis* and *C. tilapiae*, infect both catfishes and cichlids but no other fish species. We demonstrated that *Clinostomum* 'morphotype 2', hitherto only known from mormyrid fishes, also infected mochokid catfishes. *Clinostomum chabaudi* Vercammen-Grandjean, 1960 has been demonstrated to have an interesting form of euryxenicity: metacercariae of this species infect both fishes and frogs as second intermediate hosts (Sinsch *et al.* 2021a; Sinsch *et al.* 2021b). Nevertheless, it is predicted that most *Clinostomum* species are stenoxenous, infecting at most two fish families or orders.

The various African freshwater fish lineages showcase a range of particular biogeographic histories, including ancient lineages demonstrating Gondwanan shared ancestry (e.g., lungfishes), radiations which subsequently dispersed to Asia (e.g., knifefishes), and lineages which originated from Asia and subsequently invaded Africa (e.g., synbranchiform air-breathers) (Harrington *et al.* 2023; Inoue *et al.* 2009; Skelton 1988). The circumstances inherent to each lineage relevant to us are too complex to recount in detail here. To cite just one example, the clariid family has radiated widely across the Afrotropical and Indo-Malayan realms, having originated from central Asia ~50 mya and subsequently radiated into southeast Asia and Africa during the Lower Miocene (~15 mya) (Agnese and Teugels 2005; Otero and Gayet 2001). Based on the observed genetic divergences of repeated molecular sequencing analyses (see this study; Briosio-Aguilar *et al.* 2018; Caffara *et al.* 2019), it is most plausible that the Indian record of *C. brieni* instead represents a close relative of *C. brieni* that has allopatrically speciated following the Pangaean and subsequent Gondwanan breakup (Günther 1880; Paugy *et al.* 2017; Skelton 2024), with their common ancestor arising from central Asia and diverging ~15 mya. This hypothesis will require further validation through more comprehensive molecular sequence analyses incorporating more data from the Indian subcontinent, as well as re-assessment of other putative Indo-Asian species hitherto regarded as species of Clinostomoides – *C. baughi* (Pandey, 1988), *C. chauhani* (Pandey, 1971), *C. dollfusi* (Agrawal, 1959), *C. meerutensis* (Pandey & Tyagi, 1986), *C. ophicephali* Tubangui & Masilungan, 1944, *C. pandeyii* (Singh & Sharma, 1994), and *C. rai* (Pandey & Agrawal, 2013). All these species are currently considered *species inquirendae* but share several morphological and ecological features with *C. brieni*, particularly genital complex configuration and affinities to clariid intermediate hosts (Caffara *et al.* 2019; Pandey and Agrawal 2013).

We predict that a combination of highly dispersive definitive hosts and relatively low intermediate host specificity have served to limit speciation among African clinostomid species. Commonalities between African and other fauna may be explained by dispersal of, and linkages (or absence thereof) between, hosts both ancient (e.g., pre- and post-Gondwanan separation of Africa and India ~148 mya) and relatively recent (e.g., invasion of the continent by Asiatic fish lineages such as clariid catfishes ~15 mya). The presence of a clade of Australian *Clinostomum* species nested among African taxa is interesting. No definitive conclusions can be made on definitive or intermediate host specificity; however, it would seem that the two realms share closely related species sharing intermediate hosts across a broad geographic range and at least two definitive hosts spanning four biogeographic realms (Matthews and Cribb 1998; Shamsi *et al.* 2021a; Shamsi *et al.* 2021b).

Other affinities to intermediate hosts are apparent based on available data for *C. cutaneum*, *C. tilapiae*, *Cl. intermedialis* (Cichlidae), *C. ukolii* (Mochokidae) (Table 2) and has been observed at the family level for Nearctic and Neotropical species (see Pérez-Ponce de León *et al.* 2016). Clarity on the diversity, affinities, and geographic distribution of clinostomids in the Afrotropical realm compared to the adjacent and geographically connected Indo-Malayan and Palearctic realms await more intensive sampling across geographic ranges and host taxa.

State of work in Africa and future directions

The preponderance of African freshwater cryptogonimid records are biased towards the north of the continent. Most records have been made and species described from the Nile catchment encompassing Egypt and Sudan, west Africa, and the Great Rift Lakes (Table 3). The only records of freshwater cryptogonimids from central and southern Africa include the handful arising from Dollfus's work in what is now the southeastern DRC (see Dollfus 1950) and a single record of *P. productum* from the Olifants River in South Africa (Prudhoe and Hussey 1977).

The geographical spread of African *Clinostomum* records is more even, with numerous reports from all regions of Africa including southern Africa (southern DRC, Mozambique, South Africa, Zambia, and Zimbabwe) (see Table 2; Figure 7e–i). This is likely due to

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several reasons: first, that clinostomids infect fishes of major subsistence importance in Africa (cichlids such as tilapia, as well as bagrid, clariid, and mochokid catfishes); second, being relatively large, brightly coloured, and often encysting on external surfaces (fins, gills, and lining of the mouth), are easily observed during parasitological assessments; and third, are regarded as being of fisheries significance, as their presence often leads to decline in host condition, as well as rejection of product at market (Kabunda and Sommerville 1984). Species of *Clinostomum* do have some zoonotic potential and have been reported causing infections in humans (Hara *et al.* 2014; Park *et al.* 2009), though these records predominantly originate from regions where eating fresh, raw, freshwater fish is common, a practice that is not prevalent in most of Africa.

The vast majority of clinostomid records in Africa are of second intermediate stages. By comparison, understanding of African clinostomid first intermediate stages is poor; only one first intermediate stage infection, that of *Euclinostomum heterostomum* (Rudolphi, 1809), has ever been reported, from a bulinid snail, *Bulinus globosus* (Morelet) from western Nigeria (Dönges 1974). Knowledge of freshwater cryptogonimid intermediate stages is even poorer. As far as we can tell, our study is the first report of freshwater cryptogonimid metacercariae from Africa. This is likely due to the fact that these metacercariae are very small, encysting within fin rays and membranes, and are hence easily overlooked in cursory parasitological assessments. Furthermore, although several life cycles of freshwater cryptogonimids are fully known elsewhere (e.g., Cribb 1986; Ostrowski de Núñez and Gil de Pertierra 1991; Sulieman *et al.* 2014; Vélez-Sampedro *et al.* 2022), no first intermediate-stage infections have yet been reported from the continent.

In general, the vast majority of freshwater trematode records in Africa are of intermediate stages, many of which are not identified beyond the family or genus level. Most of these records are not substantiable and will never be relatable to adults, as relatively few studies accession specimens in public collections or provide any more than cursory identifications or overviews. The use of molecular sequence data has been invaluable for disentangling the systematic relationships of freshwater trematode species and will continue to be so, particularly in cases where fine-scale morphological differences are ambiguous or elusive. However, the inability to relate metacercarial specimens from many parts of the world with adult specimens, especially those whose definitive hosts are in higher vertebrates, will continue to hinder resolving the identities and systematics of many species. Nevertheless, we are hopeful that the increasing awareness of the value of molecular sequencing for aiding identification and understanding parasite systematics on the African continent will greatly expand our ability to account for freshwater parasite richness.

Supplementary material. The supplementary material for this article can be found at http://doi.org/10.1017/S0022149X2510045X.

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Competing interests. None.

Ethical standard. The authors assert that all procedures contributing to this work comply with the ethical standards of the relevant national and institutional guides on the care and use of laboratory animals. Ethical approval for the use of animal for research purposes and research permits for fish collection was obtained prior to sampling from the North-West University AnimCare Research Ethics Committees [ethics numbers: NWU-00156-18-A5 (MTruter PhD), NWU-00781-22-A5 (REFRESH)]. Permits for the collection of animals for the purpose of research were obtained from the Department of Economic Development, Environment and Tourism (permit no. ZA/LP/116078) and access to Tzaneen Dam was obtained from the Department Water and Sanitation, Limpopo, South Africa. The Ministry of Fisheries and Livestock (Department of Fisheries, Mongu, Zambia) and World Wide Fund for Nature (WWF, Zambia) coordinated research permission in Zambia.

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