International Journal for Parasitology: Parasites and Wildlife 15 (2021) 87–94

Contents lists available at ScienceDirect

International Journal for Parasitology: Parasites and Wildlife

journal homepage: www.elsevier.com/locate/ijppaw

Gyrodactylus molweni sp. n. (Monogenea: Gyrodactylidae) from *Chelon richardsonii* (Smith, 1846) (Mugilidae) from Table Bay, South Africa

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ARTICLE INFO

Keywords:
Marine
Intertidal fish
South African mullet
Grey mullet

ABSTRACT

Gyrodactylus molweni sp. n. is described from the body surface and fins of the South African mullet, *Chelon richardsonii* (Smith, 1846) collected from Table Bay Harbour, Cape Town and is compared to five other *Gyrodactylus* species described from grey mullets globally namely *G. zhukovi* Ling, 1963 and *G. mugili* Zhukov, 1970 from *Planiliza haematocheila* (Temminck and Schlegel, 1845); *G. mugelus* Rawson, 1973 from *Mugil cephalus* L.; *G. curemae* Conroy and Conroy, 1985 from *Mugil curema* Valenciennes, 1836 and *G. xiamenensis* Zang,Yang and Liu, 2001 from *Planiliza macrolepis* (Smith, 1846). Morphologically, *G. molweni* sp. n. has prominent ventral bar processes that near cover the hamulus roots, marginal sickles with large rhomboid heels, slender shafts and fine points that extend beyond the sickle toes. *Gyrodactylus molweni* sp. n. can, however, be readily differentiated: *G. mugili* and *G. xiamenensis* have ventral bars with small ventral processes; *G. zhukovi* has marginal hooks sickles with slender shafts and proportionately short points and open-faced blades; *G. mugelus* possesses marginal hook sickles with deep, rounded heels, forward slanting shafts and an angular, square line to the inner face of the blades. Although the length of the marginal hooks of *G. curemae* are similar to *G. molweni* sp. n., their hamuli are double the size. A GenBank BlastN search with the 931 bp sequence covering ITS1, 5.8S and ITS2 gave no close hits; the nearest species for which sequences are available is *G. nipponensis* Ogawa and Egusa, 1978 (identity 96.56%, 899/931 bp). The proposal of *G. molweni* sp. n. as a new species, therefore, is well supported by both the molecular and morphological analyses presented herein. This *Gyrodactylus* species is the first to be described from *C. richardsonii* and only the second *Gyrodactylus* species to be described from the marine environment off the African continent.

1. Introduction

The grey mullets (Mugilidae) are a cosmopolitan family of teleost fishes and are widely distributed in fresh, brackish, and coastal marine waters of the tropical and temperate regions of the world (Smith and Heemstra, 1995). In South Africa, there are thirteen species in this family that are well represented in estuaries from all the South African coastal bioregions (James et al., 2016).

The South African mullet, *Chelon richardsonii* (Smith, 1846), is an endemic grey mullet to southern Africa with a restricted distribution range from Angola on the west coast of southern Africa to the subtropical waters of KwaZulu Natal on the east coast of South Africa (Lasiak, 1983; Horton et al., 2019). *Chelon richardsonii* is considered an important fishery species off Namibia and the south and west coastal regions of South Africa, where it is the primary target species of the inshore net fishery and yields approximately 6,000 t per annum (Hutchings and Lamberth, 2002; Griffiths et al., 2010; Reed, 2015; Horton et al., 2019), much of which is sold salted and dried and known locally as "*bokkoms*". This grey mullet is also an important exhibit species in public aquaria in South Africa and is often included in displays in large shoals, or in smaller numbers together with various intertidal species, or in artificial lagoon systems.

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https://doi.org/10.1016/j.ijppaw.2021.02.011
Received 30 December 2020; Received in revised form 14 February 2021; Accepted 14 February 2021
Available online 7 April 2021

Despite their commercial importance and relatively high abundance both in terms of number and biomass throughout their distribution range (James et al., 2016), little is known regarding the parasite fauna infecting *C. richardsonii* (see Schramm, 1991; Paperna, 1996; Grobler et al., 2002; Smit et al., 2005; Utevsky, 2007). Only one monogenean, a species of *Ligophorus* Euzet and Suriano, 1977, has been reported from this host (Dmitrieva et al., 2007). No species of *Gyrodactylus* von Nordmann, 1832 have been reported from *C. richardsonii* to date.

Five species of *Gyrodactylus,* however, have been described from grey mullets globally, namely *Gyrodactylus zhukovi* Ling, 1963 and *G. mugili* Zhukov, 1970 from the So-iuy mullet, *Planiliza haematocheila* (Temminck and Schlegel, 1845) [syn. *Mugil haematocheila*], *G. mugelus* Rawson, 1973 from the flathead grey mullet, *Mugil cephalus* L.*; G. curemae* Conroy and Conroy, 1985 from the white mullet, *Mugil curema* Valenciennes, 1836 and, *G. xiamenensis* Zhang, Yang and Liu, 2001 from the largescale mullet, *Planiliza macrolepis* (Smith, 1846) [syn. *Chelon macrolepis*]; see Table 1 for host species associations and distribution records. In addition to these, there are several additional *Gyrodactylus* species that were originally reported from non-mugilid hosts and have subsequently been reported from a mugilid host or have a broad host range including grey mullets. Of these, *G. alviga* Dmitrieva and Gerasev, 2000 with a broad host range that includes marine representatives from both the Chondrichthyes and Osteichthyes, from the golden grey mullet, *Chelon auratus* (Risso, 1810) [syn. *Liza aurata*] is perhaps the most tenuous. This species, recognised as a valid species in Harris et al. (2004), was originally described in Dmitrieva and Gerasev (1997) as "*Gyrodactylus* sp. 1" with measurements and drawings of a full complement of haptoral elements. The account, however, does not include photographs nor does it allude to the submission of prepared specimens to a museum collection for re-evaluation. The authors list 15 hosts for *Gyrodactylus* sp. 1 but indicate that *Merlangius merlangus* (L.) [syn. *Odontogadus merlangus euxinus*] is most likely the main host. The authors measured 80 specimens from seven hosts, but this did not include specimens collected from *C. aurata*. The species was subsequently named, without additional details, in Dmitrieva and Gerasev (2000). As Dmitrieva and Gerasev (1997) do not present measurements or images of the *Gyrodactylus* specimens collected specifically from *C. aurata*, the record of *G. alviga* on this host is not recognised until more material for re-evaluation is forthcoming. Additional records of *Gyrodactylus* species originally reported from non-mugilid hosts include *G. anguillae* Ergens, 1960*,* which had previously only been reported from three species of *Anguilla* (Anguillidae), from *P. haematocheila* [syn. *Mugil soiuy*]. *Gyrodactylus baicalensis* Bogolepova, 1950*, G. elegans* von Nordmann, 1832*, G. menschikowi* Gvosdev, 1950 and *G. vicinus* Bychowsky, 1957 have all been recorded from the Abu mullet, *Planiliza abu* (Heckel, 1843) [syn. *Liza abu*] from Iran (Mhaisen and Abdul-Ameer, 2013). Furthermore, seven additional records exist for *Gyrodactylus* species from grey mullets that were either not identified to the species level or there was insufficient material available to permit a formal description. These latter species and records are also listed in Table 1.

In 2006, routine sampling of marine fishes for exhibition at Two Oceans Aquarium in Cape Town, South Africa revealed the presence of an unknown species of *Gyrodactylus* von Nordmann, 1832. The first species of *Gyrodactylus* to be described from species destined for exhibit within the public aquarium was *Gyrodactylus eyipayipi* Vaughan, Christison, Hansen and Shinn, 2010 and was described from the skin, fins, gills, flute and male brood pouch of the greater pipefish, *Syngnathus acus* L. (see Vaughan et al., 2010). The current study presents the description of the first species of *Gyrodactylus* collected from the skin and fins of the South African mullet, *C. richardsonii*, and its comparison to morphologically similar and phylogenetically related species of *Gyrodactylus*, as well as to *Gyrodactylus* species recorded from grey mullets globally.

Table 1
Species of *Gyrodactylus* von Nordmann, 1832 recorded from grey mullets (Mugilidae) in marine waters.

Gyrodactylus species	Host Species	Locality	Reference
Gyrodactylus alviga Dmitrieva and Gerasev, 2000[a]	*Chelon auratus*[b]	Azov Sea, Black Sea	Dmitrieva and Gaevskaya (2001)
Gyrodactylus anguillae Ergens, 1960 [c]	*Planiliza haematocheila*[d]	Azov Sea, Black Sea	Dmitrieva and Gaevskaya (2001)
Gyrodactylus baicalensis Bogolepova, 1950	*Planiliza abu*[e]	Iraq	Mhaisen and Abdul-Ameer (2013)
Gyrodactylus curemae Conroy and COnroy, 1985	*Mugil curema*	Patanemo Cove, Venezuela	Conroy and Conroy (1985); Kohn and Cohen (1998)
Gyrodactylus elegans Nordmann, 1832	*Planiliza abu*[e]	Iraq	Mhaisen and Abdul-Ameer (2013)
Gyrodactylus menschikowi Gvosdev, 1950	*Planiliza abu*[e]	Iraq	Al-Zubaidy (2007); Mhaisen and Abdul-Ameer (2013)
Gyrodactylus mugelus Rawson, 1973	*Mugil cephalus*	Big Hole Creek, Sapelo Island, Georgia, USA	Rawson (1973)
Gyrodactylus mugili Zhukov, 1970	*Planiliza haematocheila*[d]	Zarubino, Sea of Japan, Japan	Zhukov (1970)
	Planiliza haematocheila[d], *Mugil cephalus*	Azov Sea	Miroshnichenko and Maltsev (1998)
	Planiliza haematocheila[d]	Sea of Japan, Azov-Black Sea	Sarabeev (2015); Sarabeev et al. (2018)
	Planiliza haematocheila[d]	Azov-Black Sea, Western North Pacific	Kostadinova (2008)
	Planiliza subviridis[f], *Valamugil speigleri*	Iraq	Mhaisen and Abdul-Ameer (2013); Kritsky et al. (2013)
Gyrodactylus vicinus Bychowsky, 1957	*Planiliza abu*[e]	Iraq	Mhaisen and Abdul-Ameer (2013)
Gyrodactylus xiamenensis Zhang, Yang and Liu, 2001	*Planiliza macrolepis*[g]	Xiamen, Fuijan	Zhang et al. (2001)
Gyrodactylus zhukovi Ling, 1963	*Planiliza haematocheila* [d]	Liao Ho River, China	Ling (1963)
	Planiliza haematocheila[d]	Sea of Japan, Azov-Black Sea	Sarabeev (2015); Sarabeev et al. (2018)
	Planiliza haematocheila[d]	Azov-Black Sea, Western North Pacific	Kostadinova (2008)
	Planiliza haematocheila[d]	Azov Sea Basin	Miroshnichenko and Maltsev (1998)
Gyrodactylus sp. 1	Grey mullets (Mugilidae)	Bardawil Lagoon, Egypt	Paperna (1975); Paperna and Lahav (1975)
Gyrodactylus sp. 2	*Chelon auratus*[b]	Black Sea	Dmitrieva and Gerasev (1997)
Gyrodactylus sp. 3	*Mugil liza*[h]	Uruguay	Carnevia and Speranza (2003)
Gyrodactylus sp. 4	*Chelon ramada*	Italy	Paladini et al. (2011)
Gyrodactylus sp. 5	*Planiliza abu*	Iraq	Mhaisen and Abdul-Ameer (2013)
Gyrodactylus sp. 6	*Planiliza subviridis*	Iraq	Mhaisen and Abdul-Ameer (2013)
Gyrodactylus sp. 7	*Chelon auratus*[b]	Turkey	Öztürk (2013)
Gyrodactylus sp. 8	*Mugil liza*	Brazil	Mentz et al. (2016)

[a] The record of this *Gyrodactylus* species on a mullet is not accepted.
[b] Formerly *Liza aurata*.
[c] Record cannot be verified.
[d] Formerly *Mugil soiuy*.
[e] Formerly *Liza abu*.
[f] Formerly *Chelon subviridis*.
[g] Formerly *Liza macrolepis*.
[h] Senior synonym for *Mugil platanus*.

2. Materials and methods

2.1. Specimen collection and preparation

A small shoal of approximately 400 individual juvenile *C. richardsonii* were seine-netted from the old slipway at the National Sea Rescue Institute (NSRI) at the Victoria and Alfred Waterfront, GPS: -33.905571° S, 18.420845° E, Table Bay Harbour, Cape Town, South Africa in May 2006. The fish destined for public exhibit in the aquarium were caught and landed through commercial fishing activity in Table Bay Harbour. The parasites described in this study were isolated from a subset of 20 fish that were assessed as part of routine health screening procedures of stocks held under quarantine. Although the fish were not subject to an intervention covered by South African legislation involving the use of animals in scientific procedures, the fish were euthanased humanely with 2-phenoxyethanol (1.2 mL/L for 5–10 min), in accordance with national and organisational regulations (See Hutson et al., 2018). Euthanased fish were transferred to individual glass Petri dishes and checked for the presence and location of *Gyrodactylus* species on the body using an Olympus SZ60 dissection microscope. *Gyrodactylus* individuals were removed from the skin and fins of each host using a pair of dissecting needles. Gill tissue was also checked for the presence of *Gyrodactylus* individuals but no specimens were found.

Water quality parameters at the collection site, were measured using a YSI 85 dissolved oxygen, temperature and conductivity meter and a Cyberscan pH 300 series hand-held pH and ORP meter. At the time of collection in May 2006, the seawater in the harbour was 35.8 ppt and the water temperature was 13.8 °C and although the salinity is stable, the annual surf-zone temperature ranges between 9 and 21 °C. Due to upwelling, which is driven by south-easterly summer winds, the surf-zone water temperature can drop to around 13 °C and fluctuate rapidly within relatively short time spans of a few days. By contrast, winter water temperatures seldom vary more than a degree and are typically around 15–16 °C (Quick and Roberts, 1993). The South African mullet frequent these waters all year round.

2.2. Morphometric analysis

Individual parasites were mounted live either in glycerine ammonium picrate (Malmberg, 1970) or in glycerine jelly (Gussev, 1983). From the material collected, several specimens were prepared as whole mounts, as described above, while additional specimens were processed by first removing their attachment organ – the haptor and subsequently processing the hard components for morphometric analysis, while the corresponding body portion of each worm was fixed in absolute ethanol (Sigma-Aldrich®) and stored individually in labelled 1.5 mL graduated microcentrifuge tubes with flat top caps (Quality Scientific Plastics® Cat# 509-GRD) for molecular analysis. The hard parts of the haptor were liberated using both complete and partial proteolytic enzyme digestion (Harris et al., 1999). Point-to-point and angular measurements on the attachment hooks were made on images captured using a Nikon Digital Sight (DS Fi2) camera mounted on a Nikon Eclipse Ni compound microscope and interfacing with a Nikon Digital Sight (DS U3) camera control unit. Images were captured at magnifications ranging from × 20 to × 100 oil immersion. Selected measurements according to Shinn et al. (2004) were obtained using the Nikon Imaging Systems Basic Research (NIS-BR V4.00.01) image analysis software package and are expressed in micrometres and given as the mean ± standard deviation followed by the range and sample size in parentheses. Drawings of the marginal hook sickles were then compared to other relevant species of *Gyrodactylus* as a series of pairwise comparisons, where the outline of each pair of hooks were overlaid and the size of each pair of hooks were adjusted to try and give a best fit to one another as a means of directly comparing their morphologies and in identifying where they might differ from one another.

2.3. Molecular analyses

Four of the *Gyrodactylus* bodies stored in absolute ethanol were subjected to molecular analysis targeting part of the RNA array spanning the ribosomal internal transcribed spacers 1 and 2 (ITS1 and 2) and 5.8S. The ITS fragment is the most common species barcode in the genus *Gyrodactylus* (see Gelnar et al., 2003; Ziętara and Lumme, 2003; Bakke et al., 2007). DNA was extracted from individual specimens using the QIAamp DNA Mini kit (Qiagen) in accordance with the manufacturer's instructions. The primer pairs ITS1A and ITS2 (Matějusová et al., 2001) were used to amplify the specified fragment. All PCR reactions were performed with puRe taq Ready-to-Go PCR beads (Amersham Biosciences) in a GeneAmp PCR System 9700 (Applied Biosystems) using the following protocol: 4 min at 95 °C, followed by 35 cycles of 1 min at 95 °C, 1 min at 50 °C and 2 min at 72 °C. Following PCR, the positive products were then sequenced on a MEGABACE 1000 (GE Healthcare) using DyeET-terminator mix (GE-Healthcare) according to standard protocols. Both PCR primers and internal primers (ITS1R, ITS2F, ITS18R, ITS28F – see Ziętara and Lumme, 2003) were used for sequencing. Proofread sequences were compared with those from available *Gyrodactylus* species via a GenBank BlastN search (http://www.ncbi.nlm.nih.gov/) (Zhang et al., 2000). Both the whole fragment (excluding partial 28S and partial 18S) and the ITS2 separately were subjected to a BlastN search.

The reference sequence for *G. molweni* sp. n. (GenBank accession number **FJ040182**) has already been included in a comprehensive phylogenetic analysis based on an alignment of the 5.8S+ITS2 segment of the ribosomal DNA with selected sequences published in GenBank (see Ziętara et al., 2012). The analysis is not repeated here. Furthermore, ITS, and especially ITS1, is generally difficult to align reliably due to high variation in the sequence length between different species (Ziętara and Lumme, 2004), and while it serves as a good marker for species differentiation, it is not the most suitable for deeper phylogenetic analyses.

2.4. ZooBank

To comply with the regulations set out in Article 8.5 of the amended 2012 version of the International Code of Zoological Nomenclature (ICZN, 2012), details of all taxonomic treatments herein have been submitted to ZooBank.

3. Results

3.1. Gyrodactylus molweni sp. n.

Type-host: Chelon richardsonii (Smith, 1846)
Site of infection: Skin and fins.
Type locality: Victoria and Alfred Waterfront, Table Bay Harbour, Cape Town, South Africa
(-33.905571° S, 18.420845° E)
Environmental parameters on collection: Dissolved oxygen = 75.9%,/ 6.3 mg/L, temperature = 13.8 °C, salinity = 35.8‰, and pH = 7.97.
DNA reference sequences: A 985 bp DNA reference sequence covering the 18S (12 bp), ITS 1 (381 bp), 5.8S (157 bp), ITS 2 (393 bp) and partial 28S (42bp) are deposited in GenBank under accession number **FJ040182**.

Type material: The holotype (NHMUK 2021.4.15.1) and two paratypes (NHMUK 2021.4.15.2-3) are deposited in the Parasitic Worms collection of the Natural History Museum, London. Further paratypes are deposited in the South African Museum, Cape Town, South Africa (SAMCT A093740-44) and in the Helminthological collection of the Institute of Parasitology, České Budějovice Czech Republic (IPCAS M-757).

ZooBank registration: The Life Science identifier for *Gyrodactylus molweni* sp. n. is urn:lsid:zoobank.org:act:2DCFE189-46BD-4E74-8A81-59532D4422C1.

Etymology: Named for the general greeting '*molo*' (single person), '*molweni*' or '*molweni nonke*' (multiple people) in the local African Xhosa language. The name is proposed as a salutation to the parasites found on this commercially important native species of fish.

Description (Figs. 1–3)

Coverslip-flattened specimens 257.2 ± 19.1 (227–282, n = 25) long, 72.3 ± 8.00 (63–86, n = 25) wide at the level of the uterus. Intestinal crura extend to the posterior end of uterus when the uterus is occupied with a well-developed embryo; when the uterus is empty, the crura extend as far as the testis. Haptor approximately circular 52.9 ± 3.6 (48–61, n = 25) long, 47.5 ± 5.3 (39–59, n = 25) wide. The pharyngeal bulb measures 21.6 ± 5.5 (15–30, n = 12) long × 25.5 ± 4.8 (19–33, n = 12) wide across the anterior bulb; 22.2 ± 3.8 (18–28, n = 12) long × 25.3 ± 6.5 (18–32, n = 12) wide across the posterior bulb. Male copulatory organ (MCO) spherical positioned posterior to the posterior pharyngeal bulb. MCO bulb diameter 11.7 ± 0.4 (11–12, n = 4). MCO armature consists of one principal spine and four smaller spines arranged in a single row, the outer two larger than the central pair. Hamulus total length 45.3 ± 2.1 (42–48, n = 24); hamulus shaft length 31.7 ± 2.5 (27–38, n = 24); proximal shaft width 7.6 ± 1.5 (5–11, n = 24); point length 22.4 ± 1.4 (19–24, n = 24). Hamulus aperture 16.0 ± 1.4 (13–19, n = 24); outer aperture angle 33.3 ± 2.2° (29–37°, n = 24);

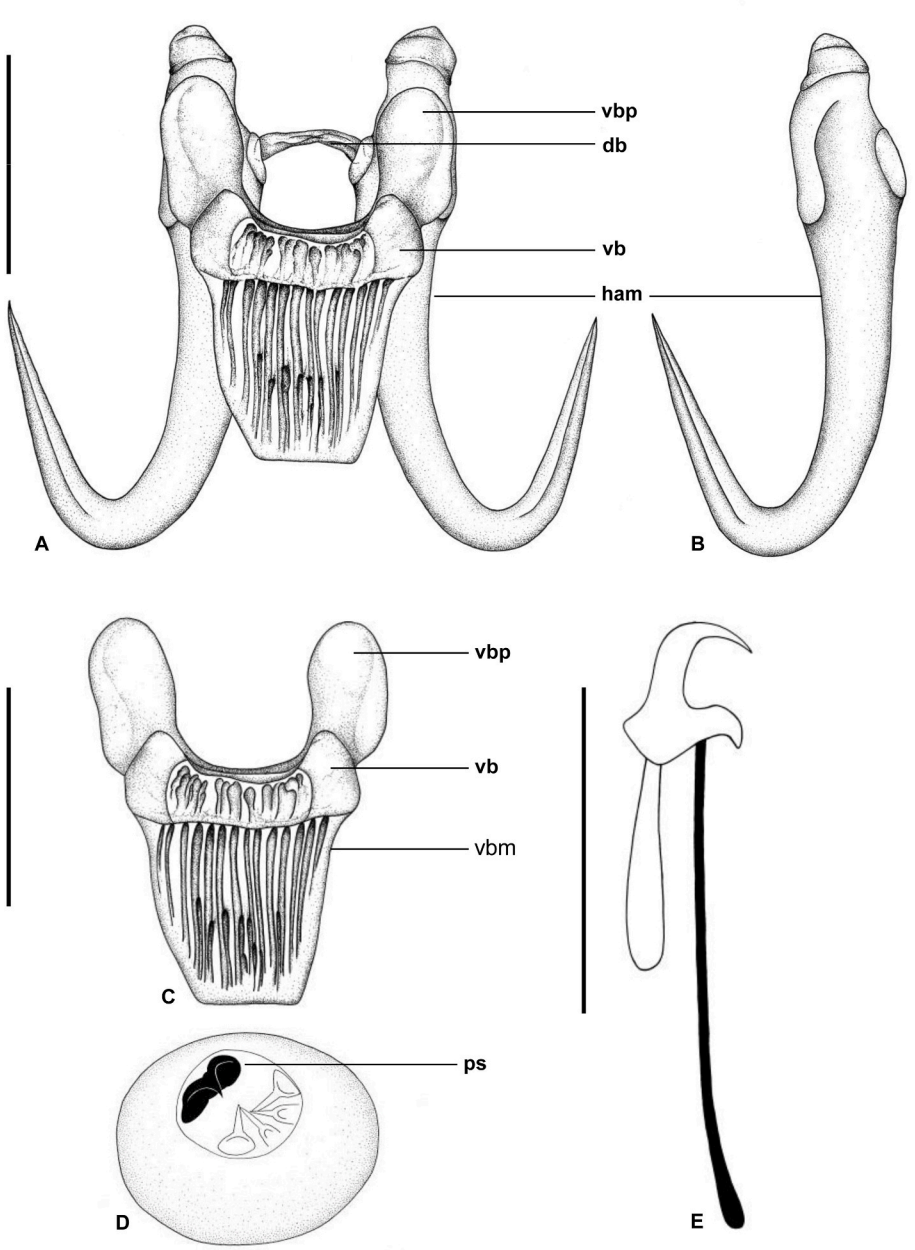

Fig. 1. *Gyrodactylus molweni* sp. n. A. The haptoral central hook complex of hamuli (ham), dorsal (db) and ventral (vb) bars. B. Hamulus. C. Ventral bar (vb) which for this species bears large ventral bar processes (vbp) and a rhomboid-shaped ventral bar membrane (vbm). D. Male copulatory organ bearing a single principal spine (ps) and then a single row of four small spines, the outer two larger than the central pair. E. Marginal hook. Scale Bars = 10 μm.

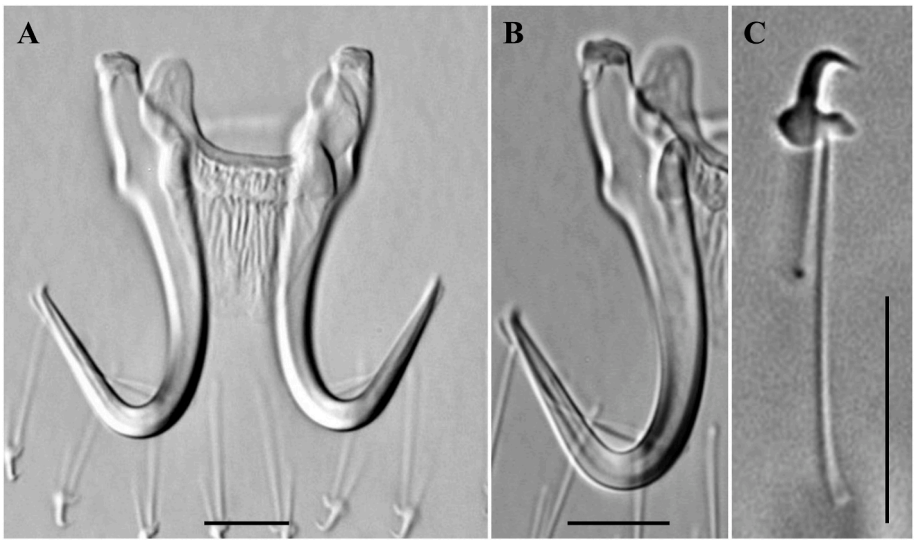

Fig. 2. Light micrographs of the attachment hooks of *Gyrodactylus molweni* sp. n. A. The haptoral central hook complex of hamuli, and ventral bar. B. Hamulus. C. Marginal hook. Scale Bars = 10 μm.

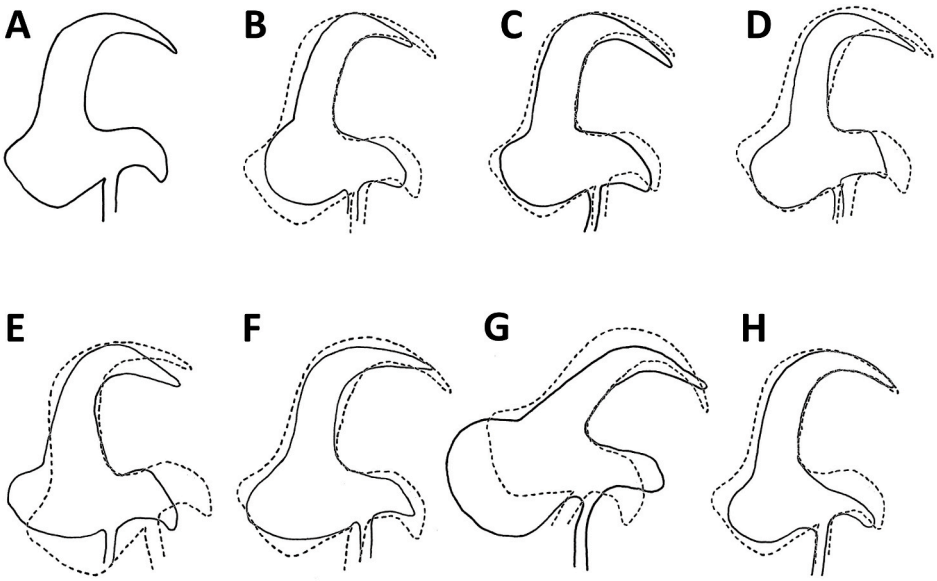

Fig. 3. Comparison of the marginal hook sickle of *Gyrodactylus molweni* sp. n. (dotted outline) with those of *Gyrodactylus* species described from various mullet species and with a number of closely related species. Each pair of marginal hook sickles are aligned by their inner curved faces. A. *G. molweni* sp. n.; B. *G. arcuatus* Bychowsky, 1933 (drawn from a scanning electron micrograph of liberated hooks from specimens parasitizing *Gasterosteus aculeatus* L.); C. *G. arcuatoides Huyse, Malmberg and Volckaert, 2004* (redrawn from Huyse et al., 2004); D. *G. branchialis* Huyse, Malmberg and Volckaert, 2004 (redrawn from Huyse et al., 2004); E. *G. flavescensis* Huyse, Malmberg and Volckaert, 2004 (redrawn from Huyse et al., 2004); F. *G. gondae* Huyse, Malmberg and Volckaert, 2004 (redrawn from Huyse et al., 2004); G. *G. mugelus* Rawson, 1973 (redrawn from Rawson, 1973); and, H. *G. zhukovi* Ling, 1963 (redrawn from Miroshnichenko and Maltsev, 1998).

inner aperture angle 38.9 ± 3.1° (33–44°, n = 24). Hamulus distal shaft width 3.8 ± 0.5 (3–5, n = 24); root length 13.8 ± 2.4 (10–19, n = 24). Dorsal bar simple, 1.9 ± 0.3 (1–3, n = 16) wide by 17.5 ± 2.2 (14–21, n = 16) long. Ventral bar with conspicuous bilateral processes 33.4 ± 2.6 (29–39, n = 23) long, 25.2 ± 1.5 (22–28, n = 24) wide; ventral bar process to mid-length 11.4 ± 0.6 (10–13, n = 24); ventral bar median length 5.7 ± 0.4 (5–7, n = 25); ventral bar processes 8.5 ± 1.0 (6–10, n = 24) long; ventral bar membrane rhomboid, 16.1 ± 1.5 (13–20, n = 23) long. Total length of marginal hooks 20.1 ± 1.3 (17–22, n = 16); marginal hook shaft 16.0 ± 1.2 (13–18, n = 16) long; marginal hook sickle proper 4.6 ± 0.3 (4–5, n = 21) long with sickle proximal width 3.8 ± 0.3 (3–4, n = 21); toe length 1.4 ± 0.3 (1–2, n = 21); sickle distal width 2.7 ± 0.3 (2–3, n = 21); sickle aperture 3.6 ± 0.4 (3–5, n = 21); instep/arch height 0.6 ± 0.1 (0.4–0.8, n = 18).

3.2. Molecular characterisation

A non-variable 985 bp product covering partial 18S (12 bp), ITS1 (381 bp), 5.8S (157 bp), ITS2 (393 bp), and partial 28S (42 bp) was sequenced from three of the four specimens and submitted to GenBank under accession number **FJ040182**. A BlastN search (Zhang et al., 2000) using the 931 bp sequence covering ITS1, 5.8S and ITS2 (excluding the partial 18S and partial 28S) at the time of sequencing (August 2008) revealed no identical or close hits; maximum identity was to *G. nipponensis* Ogawa and Egusa, 1978 (96.56%, 899/931 bp query cover 100%). Other sequences, available for comparison, showed an identity of 94% and lower, showing molecular support for separate species status of *G. molweni* sp. n. A new search in November 2020 gave the same result, however with some additional, but quite genetically distantly related species, e.g., *G. xalapensis* Rubio-Godoy, Paladini, García-Vásquez and Shinn, 2010 and *G. takoke* García-Vásquez, Razo-Mendivil and Rubio-Godoy, 2015, among the top hits. A BlastN search using only the ITS2 fragment gave a similar result with, *G. nipponensis* based on the sequences available, being identified as the most closely related species.

The reference sequence for *G. molweni* sp. n. (GenBank accession

number FJ040182) has already been included in a comprehensive phylogenetic analysis conducted by Ziętara et al. (2012) and thus this is not repeated here.

3.3. Remarks

Of the species of *Gyrodactylus* recorded from mullets (see Table 1), the ventral bar of *G. molweni* sp. n. with its large ventral bar processes can be readily discriminated from those of *G. anguillae*, *G. baicalensis*, *G. elegans*, *G. menschikowi*, *G. mugili*, *G. vicinus* and *G. xiamenensis* where the ventral bar processes are either small or lacking. The remaining species can be discriminated on the morphology of their marginal hook sickles - those of *G. zhukovi* (Fig. 3H) are slender, with proportionately longer sickle shafts giving the marginal hooks sickles a more open face. The marginal hook sickles of *G. molweni* sp. n. and *G. mugelus* can also be readily differentiated from one another. The deep, rounded heel of *G. mugelus* (Fig. 3G) forms over 50% of the sickle base; the marginal hook sickle shaft arises at angle of about 45° to the base which then turns at almost 90° to end in a short tip beyond the toe, giving a square inner line to the sickle blade. The original drawing of the marginal hook sickle for *G. curemae* is small and unclear (drawing not included in this account); what is presented, however, suggests a marginal hook sickle with a short heel and a sickle blade with a circular inner face. *Gyrodactylus curemae* can, however, be discriminated from *G. molweni* sp. n. by the general shape of the ventral bar and the comparatively large size of its hamuli (total length = 75.6–80.4) and marginal hooks (total length 16.2–28.8; sickle proper = 6.0–7.8 long); the size range of the marginal hooks originally reported for this species though is large suggesting either a combination of "adult" and embryonic hooks were measured, that the specimens represent a mix of species or that they possess marginal hooks of differing sizes as seen in some other species, for example *G. heterodactylus* Rogers and Wellborn, 1965 and *G. milleri* Harris and Cable, 2000 (see Rubio-Godoy et al., 2010). The marginal hook sickle of *G. molweni* sp. n. by comparison has a short-hooked toe; a square heel that represents approximately 50% of the width of the sickle base; a proportionately robust shaft to the sickle proper when compared to those of other species with large ventral bar processes, that arises at angle of approximately 80° to the perpendicular and terminates in a gracile point that terminates just beyond the limit of the toe. The MCO of *G. molweni* sp. n. with its four small spines differs from that of *G. mugelus* (five even sized spines) and from *G. zhukovi* (two large spines). The MCO of *G. curemae* is described as having two apical spines and four small spines; the report of the two apical spines is assumed to be an observational error.

From the phylogenetic analysis in Ziętara et al. (2012), *G. molweni* sp. n. (shown as *G.* sp. **FJ040182** S. AFRICA in Fig. 1 in that paper), groups with high bootstrap support (100%) with *G. nipponensis* – a species which has a ventral bar with small processes. These two species group together within a highly supported (100%) larger phylogenetic grouping that consists of two more clusters, one cluster containing *G. arcuatus* Bychowsky, 1933 and *G. stephanus* Mueller, 1937, and then *G. arcuatoides* Huyse, Malmberg and Volckaert, 2004, *G. branchialis* Huyse, Malmberg and Volckaert, 2004, *G. flavescensis*Huyse, Malmberg and Volckaert, 2004, *G. gondae Huyse, Malmberg and Volckaert, 2004* and *G. ostendicus Huyse, Malmberg and Volckaert, 2004* in a neighbouring cluster. All these latter species, except *G. ostendicus*, possess ventral bars with large lateral processes. The morphology of the marginal hook sickles of *G. arcuatus*, *G. arcuatoides*, *G. branchialis*, *G. flavescensis* and *G. gondae* are similar to that of *G. molweni* sp. n. (see Fig. 3A–F). The sickle of *G. stephanus* is poorly presented in Mueller (1937) and in Putz and Hoffman (1963) such that they cannot reliably be used as a basis of discrimination; the MCO of *G. stephanus* though differs in that it possesses eight spines. If the marginal hook sickles of the former five species are overlaid with *G. molweni* sp. n., using flexible sizing, then there are subtle differences between each, perhaps more so in the shape of the heel, which is square in *G. molweni* sp. n. and more rounded in the other species. Of the five species, *G. molweni* sp. n. is arguably closest to *G. gondae* (Fig. 3F). Likewise, if the ventral bar proper is resized so that it matches that of each of the six species with large ventral bar processes, and the ventral bar membrane is ignored, then the overall proportional size (length and width) of the ventral bar processes are considerably larger in *G. molweni* sp. n. than they are in the other six species and differ in the position at which they arise from the ventral bar proper. An overlay of the ventral bars from each species, however, is not presented here, but those of *G. gondae* and *G. molweni* sp. n. are perhaps the closest matched pair.

4. Discussion

More than 470 nominal species of the genus *Gyrodactylus* von Nordmann, 1832 have been described from freshwater, brackish-water, and marine hosts worldwide (Harris et al., 2004; Boeger et al., 2020). Despite an expectation for high species richness within this genus in Africa as a result of high levels of endemicity in sub-Saharan Africa and the divergence and species richness of African fish lineages (Přikrylová et al., 2012a), only 34 valid *Gyrodactylus* species have been described to date from 12 fish families predominately the Cichlidae (n = 17) (Dos Santos et al., 2019) and Clariidae (n = 7) (Přikrylová et al., 2012b); this figure is believed to be a reflection of research effort and the focus of biodiversity programmes under difficult field sampling conditions rather than an actual paucity of species present. Only five *Gyrodactylus* species are currently known from freshwater fish in South Africa, namely *G. cichlidarum* Paperna, 1968; *G. sturmbaueri* Vanhove, Snoeks, Volckaert and Huyse, 2011; *G. thlapi* Christison, Shinn and van As, 2005; *G. transvaalensis* Prudhoe and Hussey, 1977; and *G. ulinganisus* García-Vásquez, Hansen, Christison, Bron and Shinn, 2011 (see Prudhoe and Hussey, 1977; García-Vásquez et al., 2010; 2011; Truter et al., 2016; Zahradníčková et al., 2016). Along with the description of *G. eyipayipi* from the greater pipefish, *Sygnathus acus* (see Vaughan et al., 2010), the description of *G. molweni* sp. n. from the grey mullet, *C. richardsonii* represent the only two *Gyrodactylus* species currently recorded from the marine environment off the African continent to date.

Eleven *Gyrodactylus* species have been reported from grey mullets globally (Table 1); this figure does not include the *Gyrodactylus* spp. recorded from mullet hosts for which there was insufficient material available to permit formal description. The validity of several of these, however, should be treated with some caution. While *G. alviga* is considered to be a valid species, its presence on a mullet host cannot be verified. Likewise, the reports of *G. anguillae* (see Dmitrieva and Gaevskaya, 2001) and *G. elegans* (see Mhaisen and Abdul-Ameer, 2013) are cited within reviews of the literature; unfortunately, the validity of each report cannot be confirmed and most probably represent accidental infections that have been acquired as mullets re-enter freshwater from the marine environment. New species descriptions and comparative analyses are constrained by the numerous omissions in the morphometric data for the named *Gyrodactylus* species reported from grey mullets, many of which require re-description, the unavailability of type specimens or suitable voucher specimens, and the paucity of molecular sequence data.

Gyrodactylus molweni sp. n. is differentiated from other *Gyrodactylus* species infecting mullets by its large ventral bar processes (Fig. 1A and C) and the morphology of the marginal hook sickle (Fig. 3A–H). No molecular sequence data exist for any of the *Gyrodactylus* species populations previously reported from grey mullets (Table 1). Consequently, a BlastN search (Zhang et al., 2000) using the 931 bp sequence covering ITS1, 5.8S and ITS2 clearly discriminated *G. molweni* sp. n. from all other *Gyrodactylus* species for which complimentary sequence data exist in GenBank with closest affinity to *G. nipponensis* (96.56%, 899/931 bp query cover 100%). The description of *G. molweni* sp. n. as a new species is therefore well supported by both the molecular and morphological analyses presented herein.

Declaration of competing interest

I attest that the above mentioned manuscript has not been published elsewhere, accepted for publication elsewhere or under editorial review for publication elsewhere. This manuscript has been read and approved for submission by all authors.

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Acknowledgements

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

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