


An annotated list and molecular data on larvae of gryporhynchid tapeworms (Cestoda: Cyclophyllidea) from freshwater fishes in Africa

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Received: 20 October 2017 / Accepted: 20 March 2018 / Published online: 16 May 2018
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Abstract An annotated list of larvae (metacestodes) of gryporhynchid tapeworms (Cestoda: Cyclophyllidea) from freshwater fishes in Africa is provided with numerous new host and geographical records. Newly collected materials from Burundi, Democratic Republic of the Congo, Kenya, Madagascar, Namibia, Senegal, South Africa, Sudan and Zimbabwe practically double the total number of species reported from African fish so far. We confirm the occurrence of 16 species (five unidentified to the species level and most likely representing new taxa) belonging to the genera *Amirthingamia* Bray, 1974 (1 species), *Cycluster* Fuhrmann, 1901 (2 species), *Dendrouterina*

Fuhrmann, 1912 (1 species), *Neogryporhynchus* Baer & Bona, 1960 (1 species), *Paradilepis* Hsü, 1935 (4 species), *Parvitaenia* Burt, 1940 (5 species), and *Valipora* Linton, 1927 (2 species). Additionally, metacestodes of four unidentified species of *Paradilepis* and *Parvitaenia* are reported from fish for the first time. Rostellar hooks of all species are illustrated and their measurements are provided together with a host-parasite list. The molecular phylogenetic analysis based on partial LSU rDNA sequences offers the first insight into the internal phylogenetic relationships within the family. Together with the morphological observations, the present study provides a taxonomic baseline for future studies on this largely neglected, but widely distributed and relatively frequent, group of parasites of African fishes, including economically important cichlids like tilapias and cyprinids.

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This article is part of the Topical Collection Cestoda.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s11230-018-9796-y>) contains supplementary material, which is available to authorized users.

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Introduction

Freshwaters of the African continent are inhabited by an extraordinarily rich fauna of teleost fishes, hosts of numerous groups of parasites including helminths (Khalil & Polling, 1997). Some helminths of African fishes have been studied relatively intensively, especially monogeneans of cichlids, including the economically important tilapias (e.g. Vanhove et al., 2016 and references therein). In contrast, some groups of metazoan fish parasites remain completely neglected, such as the larvae (metacestodes) of gryporhynchid tapeworms (Cestoda: Cyclophyllidea).

Adult tapeworms of the family Gryporhynchidae Spassky & Spasskaya, 1973 are intestinal parasites of fish-eating birds, especially herons, storks, cormorants and ibises (Baer & Bona, 1960). They were previously placed in the Dilepididae (see Bona, 1975, 1994), but are currently recognised as a separate family within the Cyclophyllidea (see Cairra & Jensen, 2017; Mari-aux et al., 2017).

The systematics and diversity of gryporhynchids parasitising fish-eating birds of the Order Ciconiiformes were reviewed by Bona (1975), who reported adults of 19 species to occur in Africa, but did not provide any data on gryporhynchid larvae in African fishes. The first record of metacestodes of gryporhynchids from African fishes was published by Bray (1974), who found larvae of *Amirthingamia macracantha* (Joyeux & Baer, 1935) in *Oreochromis niloticus* (L.). Khalil & Polling (1997) reported larvae of only two species of gryporhynchids identified to the species level, i.e. *A. macracantha* and *Paradilepis delachauxi* (Fuhrmann, 1909). In addition, larvae of an unidentified species of *Anomotaenia* Cohn, 1900 and ‘dilepidid’ larvae were reported from tilapias (Khalil & Polling, 1997).

In a review of gryporhynchid metacestodes in fishes, Scholz et al. (2004) listed only two species from Africa, namely *A. macracantha* and *Cyclustera magna* (Baer, 1959). Later, Scholz et al. (2008) reported *Parvitaenia samfyia* Mettrick, 1967 and *Cyclustera* sp. from the common carp, *Cyprinus carpio* L., a non-native fish introduced to Africa for aquaculture. Most

recently, Truter et al. (2016) reported, but did not characterise morphologically, the following four species from the cichlid *Pseudocrenilabrus philander* (Weber) in South Africa: *Paradilepis scolecina* (Rudolphi, 1819); *P. maleki* Khalil, 1961; *Neogryporhynchus lasiopeius* Baer & Bona, 1960; and *Valipora campylancristrota* (Wedl, 1855). Therefore, a total of eight species of six genera were known, but not characterised in detail, from African freshwater fishes before the present study.

The main goal of the present account is to provide a robust taxonomic baseline necessary for future research on this almost completely neglected, but relatively frequently occurring group of fish parasites. The present study also appeals to fish parasitologists and veterinarians for much more attention to be paid to gryporhynchid larvae, which are relatively common in several African fishes such as cichlids, including the economically important tilapias, but whose biology, species diversity, distribution and associations with their fish hosts remain poorly known.

Materials and methods

The present review is based on taxonomic evaluation of extensive material of gryporhynchid larvae (metacestodes) recently collected by the authors and their collaborators from a range of fish species throughout Africa (Burundi, Kenya, Madagascar, Namibia, Senegal, South Africa, Sudan and Zimbabwe; see Supplementary file for a list of material studied). To better observe the hooks, some specimens were flattened under a coverslip and fixed in glycerine ammonium picrate solution (GAP) following the method of Malmberg (1957) and Ergens (1969) used for studies of sclerotised parts of monogeneans. Because of large number of larvae in some fish, other larvae were fixed in 70% or 96% ethanol. Some of the former specimens were stained with Mayer’s carmine, dehydrated and mounted as permanent preparations.

Samples fixed in 99% molecular-grade ethanol were used for DNA extraction and sequencing of the partial (domain D1–D3) nuclear large subunit of the ribosomal RNA gene (LSU rDNA). The molecular dataset was generated within the scope of the BSc thesis of one of the authors (LU) following the methodology described in Brabec et al. (2012). Individual Sanger reads were assembled and checked

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for errors in Geneious 8.1.7. (Kearse et al., 2012). Contiguous sequences were aligned using the E-INS-i algorithm of the program MAFFT (Kato & Standley, 2013); ambiguously aligned positions were manually excluded and phylogenetic analyses run under the maximum likelihood criterion using the program PHYML (Guindon et al., 2010); all within the Geneious program environment. The best tree search employed the GTR+I+ Γ model of nucleotide evolution and subtree pruning and regrafting branch swapping.

In addition, search of the literary data published since 2004, i.e., after the review by Scholz et al. (2004), was carried out. Voucher specimens of larvae studied were deposited in the Helminthological Collection of the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic (IPCAS); Collection of Platyhelminthes at the Natural History Museum, Geneva, Switzerland (MHNG-PLAT); Parasite Collection of the Natural History Museum, London, UK (acronym NHMUK); the Royal Museum of Central Africa, Tervuren, Belgium (RMCA); and the South African Museum, Cape Town, South Africa (SAMC).

Measurements of the larvae are in micrometres unless otherwise stated. Whenever possible, the number of infected/examined fish from a given country is provided in the list of fish hosts but since several metacestodes occurred in high intensities and simultaneously with other gryporhynchid species, it was not possible to identify every metacestode to the species level (this concerns mainly small-sized larvae of the species of *Neogryporhynchus* Baer & Bona, 1960 and *Parvitaenia* Burt, 1940). Thus, information on the intensity of infection cannot be provided. New hosts and geographical records (at the country level) are marked by asterisks. The nomenclature of fish hosts follows Froese & Pauly (2017), that of bird hosts follows del Hoyo et al. (1992).

A survey of larvae of gryporhynchid cestodes in African fishes

Amirthaligamia macracantha (Joyeux & Baer, 1935) Bray, 1974

Syns *Dilepis delachauxi* Joyeux & Baer, 1930, *nec* Fuhrmann, 1909; *Paradilepis macracantha* Joyeux & Baer, 1935; *Amirthaligamia* sp. of Aloo (2002)

Type-host: *Microcarbo africanus* (Gmelin) (syn. *Phalacrocorax africanus*) (Suliformes: Phalacrocoracidae), long-tailed cormorant.

Type-locality: Mali.

Fish hosts: *Coptodon zillii* (Gervais), **Pharyngochromis acuticeps* (Steindachner) (1 of 2 fish from Zimbabwe infected), **Pseudocrenilabrus philander* (2/8; Zimbabwe), **Tilapia sparrmanii* Smith (1/6; Zimbabwe) (all Perciformes: Cichlidae); ‘catfish’ (Siluriformes).

Site in host: Liver, body cavity, intestinal wall.

Geographical distribution of larvae: *Democratic Republic of the Congo, Kenya, *Zimbabwe; adults were found in Mali and the Sudan.

Voucher specimens: IPCAS C-292/1–3; NHMUK 1985.1.7.24.

Representative DNA sequences: Sequences from specimens ex *P. philander* (MH062173; Lake Chivero, Zimbabwe; length of 1,543 bp) and *T. sparrmanii* (MH062172; Lake Chivero, Zimbabwe; length of 1,515 bp) were submitted to the GenBank database; these differed by a single nucleotide.

References: Bray (1974); Aloo (2002); Scholz et al. (2004); present study.

Description (Fig. 1A, B)

[Based on Scholz et al. (2004) and new material from Zimbabwe (n = 3).] Larvae large-sized (up to 17 mm long), with body transversely striated except for posterior, bladder-like part 3.54 mm long, 1.23 mm wide. Scolex subspherical to almost triangular, 1.05–1.10 × 1.23–1.30 mm, bearing subspherical suckers 280–390 × 270–380. Rostellum subspherical, length of its cavity 430–480, width 450–500, armed with 20 hooks of 3 different shapes (see figure 1A in Scholz et al., 2004) and sizes: 4 largest hooks 448–480 long (blade 272–296; handle 240–296; blade/handle ratio 1.00–1.16); 6 slightly smaller hooks 390–450 long (blade 140–280; handle 224–256; blade/handle ratio 1.00–1.18); 10 smallest hooks 240–290 long (blade 157–184; handle 144–160; blade/handle ratio 0.98–1.11).

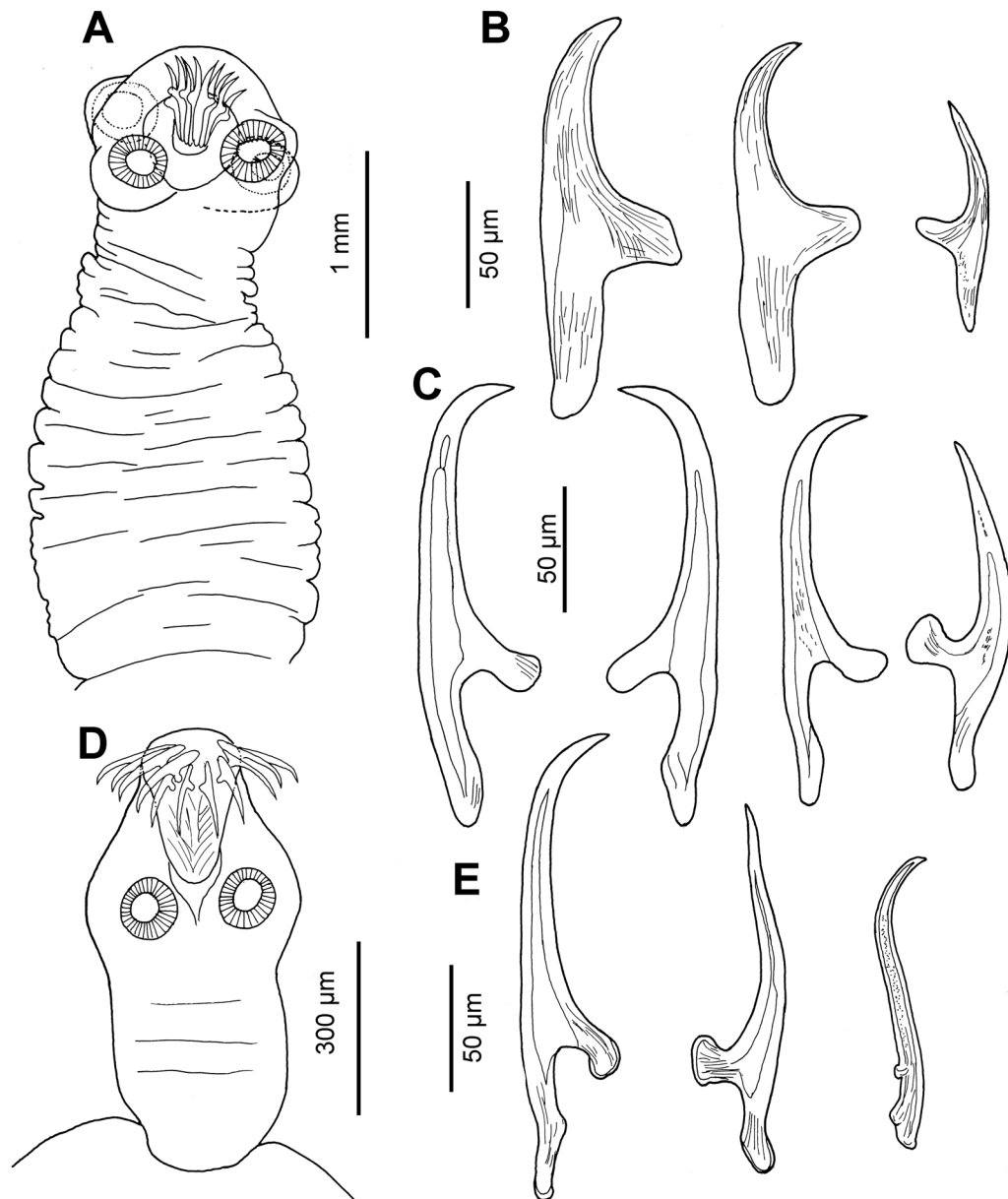


Fig. 1 Metacestodes of gryporhynchids from African fishes. A, B, *Amirthalingamia macracantha* (Joyeux & Baer, 1935). A, Anterior part of larva ex *Pseudocrenilabrus philander*, Zimbabwe (IPCAS C-292/2); B, Rostellar hooks of larva ex intestinal wall of *Tilapia zillii*, Kenya (IPCAS C-292/1; redrawn after Scholz et al., 2004). C, D, *Cyclustera magna* (Baer, 1959). C, Rostellar hooks (two largest, one medium and one smallest) of larva ex liver of *O. niloticus*, Kenya (first three hooks; IPCAS C-293/2) and *Sarotherodon galilaeus*, Turkana Lake, Kenya (smallest hook; IPCAS C-293/3); D, Scolex of larva ex *Oreochromis niloticus*, Sudan (NHMUK 1974.7.9.100–106). E, *Cyclustera* sp. ex liver of *Cyprinus carpio*, River Limpopo, Mozambique (large and small hooks, sclerite-like hooklet; IPCAS C-476/1; redrawn after Scholz et al., 2008)

Remarks

Amirthalingamia macracantha is a specific parasite of cormorants in Africa, reported from *M. africanus* (type-host) in Mali and *Phalacrocorax carbo* L. in the

Sudan (Joyeux & Baer, 1935; Bray, 1974). Its larvae are large-sized (length of the whole body up to 17 mm) and their scolex bears 20 massive hooks of three different sizes (4 and 6 large-sized hooks 390–480 µm

long of similar shape except for the guard (see figure 1A in Scholz et al., 2004; and 10 smaller hooks, 240–290 µm long, see Scholz et al., 2004). The cichlids *P. acuticeps*, *P. philander* and *T. sparrmanii* are new fish hosts of the parasite, which is reported from the Democratic Republic of the Congo and Zimbabwe for the first time.

***Cyclustera magna* (Baer, 1959) Bona, 1975**

Syns *Parvitaenia magna* Baer, 1959; *Cyclustera* sp. of Aloo (2002)

Type-host: *Mycteria ibis* (L.) (Ciconiiformes: Ciconiidae), yellow-billed stork.

Type-locality: Zaire (now the Democratic Republic of the Congo).

Fish hosts: *Coptodon zillii*, **Oreochromis niloticus*, **Sarotherodon galilaeus* (L.) (all Perciformes: Cichlidae); **Labeo horie* Heckel (Cypriniformes: Cyprinidae).

Site in host: Liver, intestinal wall, mesenteries.

Geographical distribution of larvae: Kenya, *Sudan.

Voucher specimens: IPCAS C-293/1–4; MHNG-PLAT 120506; NHMUK 1974.7.9.100–106, 2017.12.6.4–5; RMCA 38276, 38277; SAMC A089973.

References: Baer (1959); Bona (1975); Aloo (2002); Scholz et al. (2004, 2008).

Description (Fig. 1C, D)

[Measurements of larvae from different hosts pooled together; for measurements from individual host species see Supplementary Table S1; measurements from Scholz et al. (2004) in brackets.] Larvae 1.93–2.12 mm [0.90–1.48 mm] × 1.15–1.41 mm [0.50–0.74 mm]. Scolex 364–625 × 378–800. Suckers subspherical, 160–175 × 160. Rostellum 340–400 × 160–230, armed with 28 massive hooks; 14 larger (distal) hooks of same shape but two different sizes: 4 largest hooks 177–207 [179–198] long (blade 112–137 [109–141]; handle 67–75 [67–96]; blade/handle ratio 1.60–1.83 [1.14–1.96]); 10 smaller hooks 155–164 [154–163] long (blade 90–107 [93–109]; handle 60–70 [64–70]; blade/handle ratio 1.28–1.78 [1.43–1.70]); 14 smallest (proximal) hooks 127–137 [138–147] long (blade 77–87 [90–102]; handle 45–60 [61–70]; blade/handle ratio 1.37–1.77 [1.33–1.67]); semilunar, hook-like sclerites as in *Cyclustera* sp. (see below) absent.

Remarks

Baer (1959) described the species as *Parvitaenia magna* from the intestine of the yellow-billed stork, *M. ibis*, in Zaire (now the Democratic Republic of the Congo). Adults of *C. magna* have never been found since the original description of the species (Gibson et al., 2005), but metacestodes may occur relatively frequently in cichlids from eastern Africa; they may also occur in cyprinids. Three fish species are reported as intermediate hosts of *C. magna* for the first time. A metacestode on one of the slides identified as “dilepidid larva (*Parvitaenia*)” from *O. niloticus* in the Sudan collected by C. Amirthalingam (BMNH 1974.7.9.100–106) belongs to *C. magna*. Metacestodes are typified by the presence of 28 massive hooks of three different sizes, with the largest ones up to 208 µm long (see Supplementary Table S1).

***Cyclustera* sp.**

Fish host: *Cyprinus carpio* (2/21) (Cypriniformes: Cyprinidae).

Site in host: Liver.

Geographical distribution of larvae: Mozambique.

Voucher specimens: IPCAS C-476/1; NHMUK 2007.9.5.10.

Reference: Scholz et al. (2008).

Description (Fig. 1E)

[Data after Scholz et al. (2008).] Larvae 2.1 × 0.67 mm. Scolex 378 × 364. Rostellum armed with 28 hooks of 2 sizes; 14 larger (distal) hooks 171–187 long (blade 108–122; handle 60–72; blade/handle ratio 1.59–2.00); 14 smaller (proximal) hooks 139–149 (blade 94–103; handle 54–57; blade/handle ratio 1.69–1.89). In addition, 2 semilunar, hook-like sclerites 76–115 long present on rostellum.

Remarks

Metacestodes of *Cyclustera* sp. were found only in the common carp from Mozambique (Scholz et al., 2008). They could not be identified to the species level and may represent a new species. In hook morphology, they differ from the larva of *C. magna* in the shape of the hooks, with the blade more slender and less curved (larger hooks) and relatively longer blade (smaller

hooks), i.e. larger blade/handle ratio (1.69–1.89 in *Cyclustera* sp. vs 1.33–1.67 in *C. magna*). In addition, the rostellum of metacestodes of *Cyclustera* sp. possesses two semilunar sclerites (Fig. 1E), which are absent in *C. magna* (see Scholz et al., 2008).

Dendrouterina herodiae Fuhrmann, 1912

Type-host: *Egretta garzetta* (L.) (Ciconiiformes: Ardeidae), little egret.

Type-locality: Sudan.

Fish host: **Schilbe intermedius* Rüppell (1/4) (Siluriformes: Schilbeidae).

Site in host: Gall-bladder.

Geographical distribution of larvae: Africa: *Senegal; adults were found in Italy, Sudan and Zambia (Bona, 1975).

Voucher specimen: IPCAS C-780/1.

Reference: Present study.

Description (Fig. 2A, D)

[Based on one stained larva.] Larva 0.20 × 0.13 mm. Scolex 135 × 98. Rostellum armed with 20 hooks of 2 sizes; 10 larger (distal) hooks 40–42 long (blade 18; handle 26–27; blade/handle ratio 0.67–0.69); 10 smaller (proximal) hooks 22.5–23 long (blade 7–8; handle 15–17; blade/handle ratio 0.41–0.53).

Remarks

Only a single, unflattened larva from the gall-bladder of the silver catfish, *Schilbe intermedius*, from Senegal was available. Even though the rostellar hooks were difficult to properly observe and measure, the larva was identified as *D. herodiae* because of the shape and size of relatively slender hooks, especially larger ones (Fig. 2A). This species was described by Fuhrmann (1912) from the little egret in the Sudan and then reported also from Zambia and Italy (Bona, 1975).

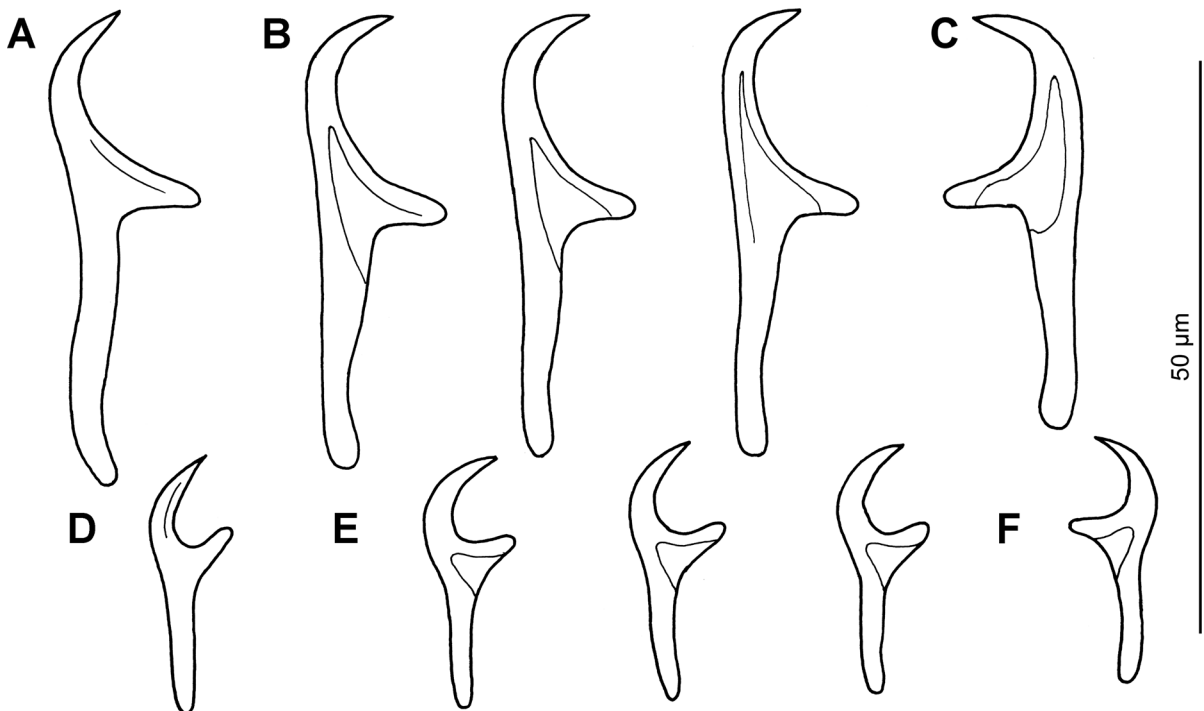


Fig. 2 Metacestodes of *Dendrouterina herodiae* Fuhrmann, 1912 from the gall-bladder of *Schilbe* sp., Senegal (IPCAS C-780/1) (A, D) and *Valipora minuta* (Coil, 1950) from the gall-bladder of *Chetia flaviventris*, South Africa (IPCAS C-240/4) (B, E) and *Ptychochromis grandidieri*, Madagascar (C, F). A–C, Larger hooks; D–F, Smaller hooks

Rostellar hooks of adults are 42–43 μm long (38–39 μm according to Metrick, 1967; blade 18–20 μm ; handle 24–26 μm) and 25–28 μm (blade 10–11 μm ; handle 16.5–18.5 μm) long, respectively (Bona, 1975). Metacestodes of *D. herodiae* are reported for the first time and Senegal is the third African country with the occurrence of this species.

***Neogryporhynchus lasiopeius* Baer & Bona, 1960**

Type-host: *Ardea purpurea* L. (Pelecaniformes: Ardeidae), purple heron.

Type-locality: Camargue, France.

Fish hosts: **Bathybathes graueri* Steindachner, **Chetia flaviventris* Trewavas, **Coptodon rendalli* (Boulenger), **Oreochromis mossambicus* Peters, **O. niloticus*, **Pseudocrenilabrus philander*, **Tilapia sparrmanii* (all Perciformes: Cichlidae); **Cyprinus carpio* (Cypriniformes: Cyprinidae); **Heterotis niloticus* (Cuvier) (Osteoglossiformes: Arapaimidae).

Site in host: Intestine (wall and lumen).

Geographical distribution of larvae: *Burundi, *Kenya, *Madagascar, Mozambique, South Africa, *Sudan, *Zimbabwe.

Voucher specimens: IPCAS C-773/2–8; NHMUK 1974.7.9.100–106, 2017.12.6.13–14; RMCA 38270, 38271; SAMC A089974, A089975.

Representative DNA sequences: Sequences from specimens ex *C. rendalli* (MH062162; Parc Ankarafantsika, Madagascar; length of 1,299 bp), *P. philander* (MH062163; Lake Chivero, Zimbabwe; length of 1,441 bp; MH062166 and MH062167; Nwanedi Dam Lake, South Africa; length of 1,442 and 1,456 bp, respectively) and *T. sparrmanii* (MH062164 and MH062165; Lake Chivero, Zimbabwe; 1,501 and 1,502 bp, respectively). Sequences of all isolates of *N. lasiopeius* from different hosts and localities (Madagascar, Zimbabwe and South Africa) showed very low intraspecific nucleotide divergence (0–5 bp difference). They formed a monophyletic lineage together with the genus *Parvitaenia* (see below).

References: Truter et al. (2016); present study.

Description (Fig. 3)

[Measurements of larvae from different hosts pooled together; see Supplementary Table S2 for measurements from individual host species.] Larvae small,

0.91–1.37 \times 0.28–0.45 mm. Scolex 154–231 \times 174–343. Suckers 58–73 \times 43–73. Rostellum 64–86 \times 58–73, armed with 20 hooks of 2 sizes; 10 larger (distal) hooks 42–48 long (blade 21–27; handle 21–26; blade/handle ratio 0.95–1.10); 10 smaller (proximal) hooks 24–29 (blade 12–14; handle 14–17; blade/handle ratio 0.74–0.93).

Remarks

This species was described from the purple heron, *A. purpurea*, in southern France by Baer & Bona (1960). Metacestodes were reported for the first time by Truter et al. (2016) from the intestinal lumen of the cichlid *P. philander* from South Africa, but these authors did not provide any morphological or biometrical data, except for a photomicrograph of rostellar hooks (see figure 2c in Truter et al., 2016). In the present paper, the first measurements and drawings of the hooks of metacestodes of *N. lasiopeius* are provided (Supplementary Table S2) and several new host and geographical records are reported. Re-evaluation of metacestodes from the intestinal wall of the common carp *C. carpio* in Mozambique, identified as *Parvitaenia samfyia* Metrick, 1967 by Scholz et al. (2008), has revealed that they actually belong to *N. lasiopeius* based on the shape of their rostellar hooks (see Fig. 3). It seems that *N. lasiopeius* is one of the most widely distributed and abundant species of gryporhynchids in African cichlids, but it was apparently overlooked in previous surveys.

***Paradilepis delachauxi* (Fuhrmann, 1909) Joyeux & Baer, 1935**

Syn. *Oligorchis delachauxi* Fuhrmann, 1909

Type-host: *Microcarbo africanus* (Suliformes: Phalacrocoracidae), reed cormorant.

Type-locality: White Nile in Egypt or the Sudan (not specified).

Fish hosts: **Chetia flaviventris* (4/28; South Africa), **Coptodon rendalli* (1/28; South Africa), **Oreochromis macrochir* (Boulenger), **Pharyngochromis acuticeps* (Steindachner) (1/8; Zimbabwe), **Pseudocrenilabrus philander* (2/35; Zimbabwe) (Perciformes: Cichlidae); **Labeobarbus marequensis* (Smith) (1/25; South Africa) (Cypriniformes: Cyprinidae).

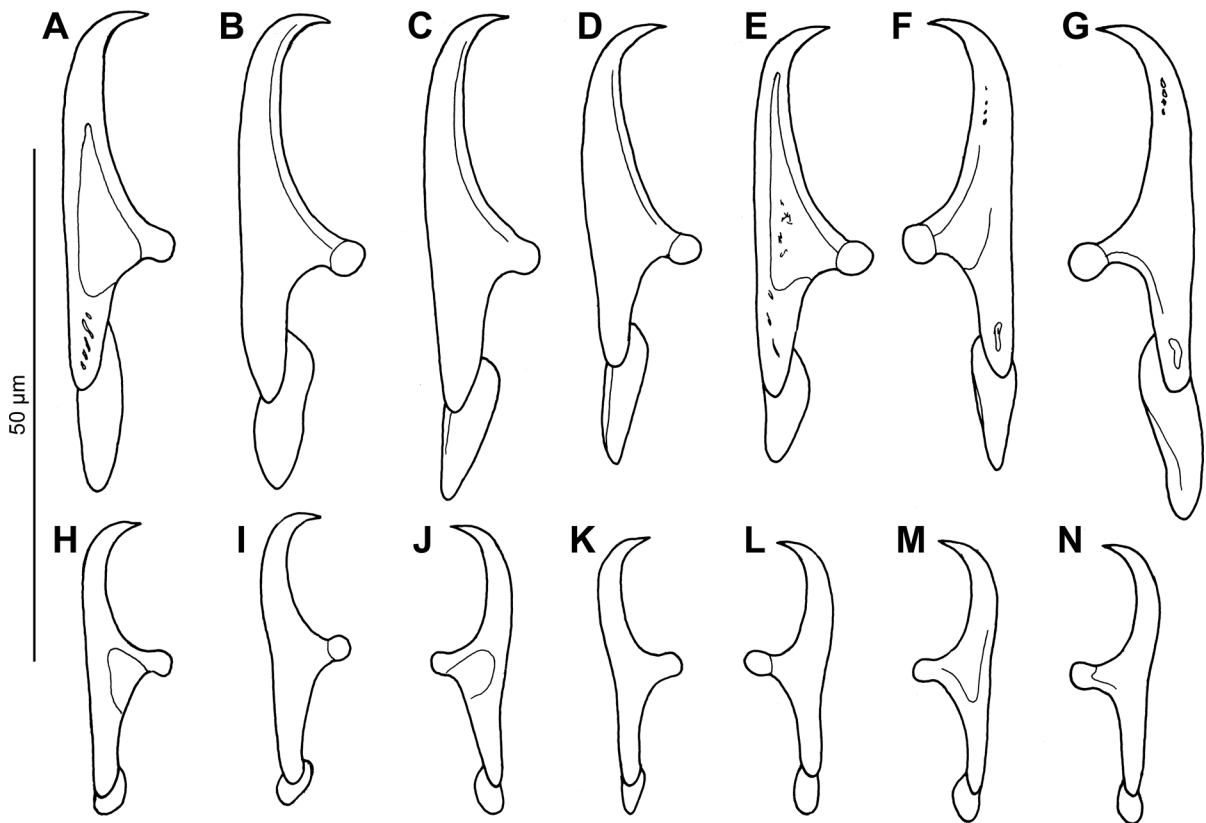


Fig. 3 Metacestodes of *Neogryporhynchus lasiopeius* Baer & Bona, 1960 ex *Oreochromis niloticus*, Kenya (A, H), *Chetia flaviventris*, South Africa (B, I), *O. niloticus*, Sudan (C, J), *Oreochromis mossambicus*, Madagascar (D, K, L), *Pseudocrenilabrus philander* (E), *Cyprinus carpio*, Mozambique (misidentified as *Parvitaenia samfyia* Metrick, 1967 by Scholz et al., 2008) (F, M), and *Oreochromis niloticus*, Sudan (NHMUK 1974.7.9.100–106) (G, N). A–G, Larger hooks; H–N, Smaller hooks

Site in host: Liver, intestinal wall and mesenteries.

Geographical distribution of larvae: *South Africa, Zambia, *Zimbabwe; adults were found in Egypt (or Sudan) and the Democratic Republic of the Congo (Edward Lake).

Voucher specimens: IPCAS C-776/1–3; NHMUK 2017.12.6.6; RMCA 38275; SAMC A089977.

References: Batra (1984); present study.

Description (Fig. 4A, B, E–G)

[Measurements of larvae from different hosts pooled together; see Supplementary Table S3 for measurements from individual host species.] Larvae medium-sized, 1.27×0.83 mm. Scolex 610×444 wide, bearing subspherical suckers $133\text{--}155 \times 136\text{--}159$. Rostellum $217\text{--}264 \times 180\text{--}235$, armed with 20 massive hooks of 2 sizes; 10 larger (distal) hooks $117\text{--}127$ (blade $59\text{--}65$; handle $59\text{--}67$; blade/handle

ratio $0.95\text{--}1.08$); 10 smaller (proximal) hooks $85\text{--}93$ (blade $39\text{--}45$; handle $50\text{--}56$; blade/handle ratio $0.74\text{--}0.89$).

Remarks

Paradilepis delachauxi was described as *Oligorchis delachauxi* within the family Hymenolepinidae (sic!) by Fuhrmann (1909) from *Microcarbo africanus* (Gmelin) (as *Phalacrocorax africanus*) in Egypt or the Sudan. Metacestodes were first found in *O. macrochir* from Zambia by Batra (1984); they are typified by the presence of two types of robust hooks with a short, curved blade and a massive guard (Fig. 4 A, B, E, F). In the present study, we add another three species of cichlids and a cyprinid to the list of fish intermediate hosts. South Africa and Zimbabwe represent new geographical records. Rostellar hooks of metacestodes from fishes are identical with those of

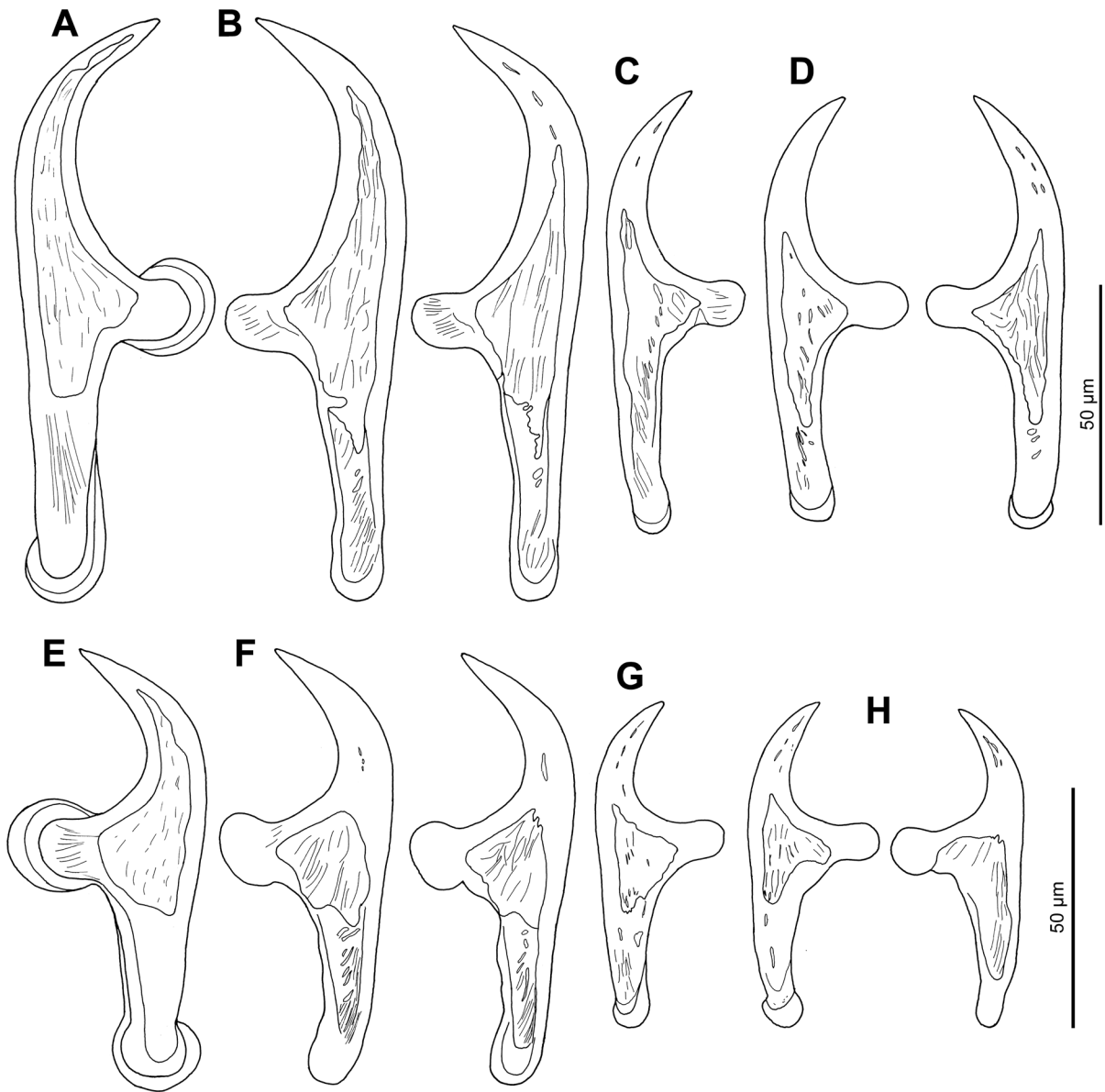


Fig. 4 *Paradilepis delachauxi* (Fuhrmann, 1909) (A, B, E, F) and *Paradilepis* sp. (C, D, G, H). A–D, Larger hooks; E–H, Smaller hooks. A, E, Adults from *Microcarbo africanus*, Democratic Republic of the Congo; B, F, Larvae from *Chetia flaviventris*, South Africa (IPCAS C-776/1); C, H, Larvae from *Oreochromis mossambicus*, South Africa; D, G, Larvae from *Tilapia rendalli*, South Africa

adults worms from cormorants, except for the presence of a thick hyaline layer on the surface of the base of the handle and on the guard (Fig. 4A, E).

***Paradilepis maleki* Khalil, 1961**

Type-host: *Threskiornis aethiopicus* (Latham) (Pelecaniformes: Threskiornithidae), African sacred ibis.

Type-locality: Sudan.

Fish hosts: **Benthochromis horii* Takahashi (1/1), *Pseudocrenilabrus philander* (5/18) (Perciformes: Cichlidae).

Site in host: Liver, intestinal wall.

Geographical distribution of larvae: *Burundi, South Africa.

Voucher specimens: IPCAS C-777/1, 2; NHMUK 2017.12.6.7; RMCA 38272; SAMC A089978.

Representative DNA sequences: Sequences from three larvae ex *Pseudocrenilabrus philander* (MH062159–MH062161; Barberspan, South Africa) were submitted to the GenBank database (length of 1,359, 1,543 and 1,584 bp); these differed by 1–6 nucleotides.

Phylogenetic analysis supported the monophyletic status of the genus *Paradilepis*, with *Paradilepis maleki* forming a clade with *P. scolecina* and *Paradilepis* sp. (see below).

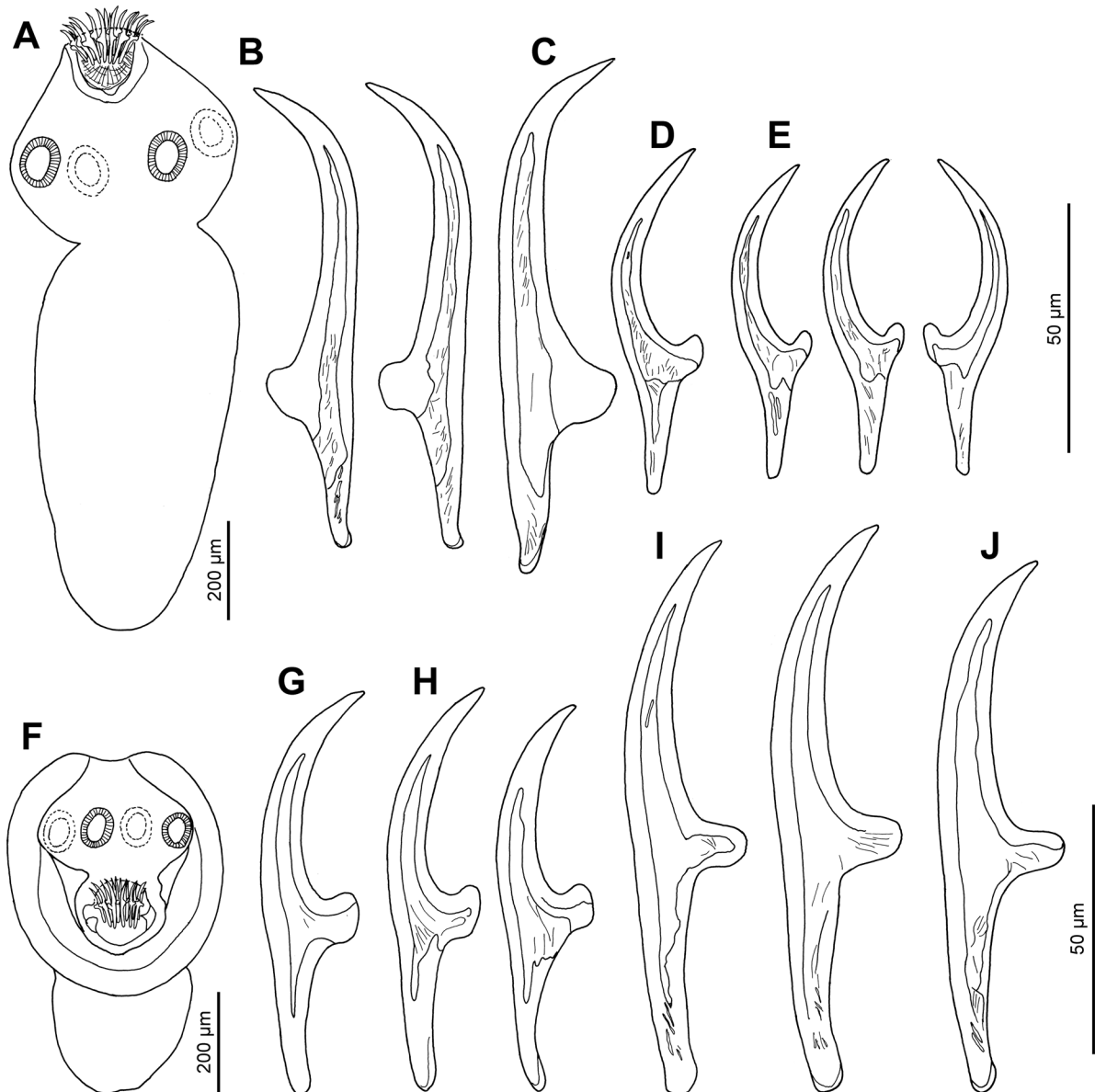


Fig. 5 Metacestodes of *Paradilepis scolecina* (Rudolphi, 1819) (A, F–J) and *Paradilepis maleki* Khalil, 1961 (B–E). A, F, Total view of larva with everted (A) and invaginated (F) scolex; B, C, I, J, Larger hooks; D, E, G, H, Smaller hooks. A, F, Larvae from mesenteries of *Enteromius trimaculatus*, South Africa; B, E, Larvae from the intestinal wall of *Benthochromis horii*, Burundi (IPCAS C-777/1); C, D, Larvae from the liver of *Pseudocrenilabrus philander*, South Africa (IPCAS C-777/2); G, I, Larvae from the liver of *Oreochromis mossambicus*, South Africa; H, J, Larvae from mesenteries of *E. trimaculatus*, South Africa

Description (Fig. 5B–E)

[Based on 6 specimens.] Larvae small, $0.62\text{--}0.76 \times 0.34\text{--}0.62$. Scolex $200\text{--}295 \times 355\text{--}512$, with subspherical to oval suckers $83\text{--}117 \times 65\text{--}103$, and rostellum $129\text{--}175 \times 96\text{--}167$, armed with 20 hooks of 2 sizes; 10 larger (distal) hooks $94\text{--}99$ long (blade $59\text{--}66$; handle $31\text{--}37$; blade/handle ratio $1.61\text{--}1.77$); 10 smaller (proximal) hooks $63\text{--}70$ (blade $34\text{--}41$; handle $28\text{--}31$; blade/handle ratio $1.06\text{--}1.33$).

References: Truter et al. (2016); present study.

Remarks

The species was described by Khalil (1961) from the African sacred ibis. Its larvae (metacestodes) were reported from fish for the first time by Truter et al. (2016), who found them in the cichlid *P. philander* from South Africa. However, no measurements or illustrations of the hooks were provided. The present report of the parasite from *B. horii* in Burundi is a new host and geographical record. The species is typified by its rostellar hooks, especially larger ones, which possess a long, slightly curved blade, thus making blade/handle ratio much higher compared to congeneric species ($1.61\text{--}1.77$).

***Paradilepis scolecina* (Rudolphi, 1819) Hsü, 1935**

Syns *Taenia scolecina* Rudolphi; *Dilepis scolecina* (Rudolphi, 1819) Fuhrmann, 1908; *Cysticercus dilepidis* Dogiel & Bychowsky, 1934; *Paradilepis duboisi* Hsü, 1935; *Paradilepis brevis* Burt, 1940

Type-host: *Phalacrocorax carbo carbo* (L.) (as *Pelecani carbonis*) (Suliformes: Phalacrocoracidae), great black cormorant.

Type-locality: Europe (not specified).

Fish hosts (only in Africa): **Coptodon rendalli* (2/28; South Africa), **Oreochromis mossambicus* (1/8; Namibia; 8/117; South Africa), *Pseudocrenilabrus philander* (all Perciformes: Cichlidae); **Enteromius paludinosus* (Peters) (6/92; Namibia), **E. trimaculatus* (Peters) (11/37; South Africa), **E. unitaeniatus* (Günther) (3/13; South Africa), **Labeobarbus kimberleyensis* (Gilchrist & Thompson) (3/9; Namibia) (all Cypriniformes: Cyprinidae).

Site in host: Liver, intestinal wall, mesenteries, gall-bladder.

Geographical distribution of larvae: *Namibia; South Africa; Palaearctic Region (see Scholz et al., 2004 for more detailed data); adults are widely distributed in the Palaearctic and Ethiopian regions (Gibson et al., 2005).

Voucher specimens: IPCAS C-127/13–19; NHMUK 2017.12.6.1–2, 2017.12.6.3; RMCA 38273, 38274; SAMC A089978–A089980.

Representative DNA sequences: Sequences from two specimens ex *P. philander* (MH062155, MH062156; Barbespan, South Africa; length of 1,732 and 1,706 bp) differing by a single nucleotide were submitted to the GenBank database. *Paradilepis scolecina* formed a monophyletic clade together with the remaining species of the genus *Paradilepis* included in the current phylogenetic analysis (see below).

References: Truter et al. (2016); present study.

Description (Fig. 5A, F–J)

[Measurements of larvae from different hosts in Africa pooled together; see Supplementary Table S4 for measurements from individual host species.] Larvae medium-sized, $0.63\text{--}0.83 \times 0.36\text{--}0.48$ mm. Scolex $239\text{--}270 \times 322\text{--}442$. Suckers subspherical, $80\text{--}108 \times 64\text{--}94$. Rostellum $142\text{--}170 \times 134\text{--}158$, armed with 20 hooks of 2 sizes; 10 larger (distal) hooks $106\text{--}115$ long (blade $56\text{--}64$; handle $49\text{--}55$; blade/handle ratio $1.03\text{--}1.22$); 10 smaller (proximal) hooks $74\text{--}80$ long (blade $39\text{--}45$; handle $36\text{--}40$; blade/handle ratio $1.03\text{--}1.25$).

Remarks

Adults of *Paradilepis scolecina* originally described by Rudolphi (1819) as *Taenia scolecina*, are specific parasites of cormorants, with high prevalence and intensity of infection in these hosts (Moravec & Scholz, 2016). Metacestodes of this species are found frequently in a wide spectrum of phylogenetically not closely related fishes throughout the Palaearctic Region, with cyprinids representing the most suitable hosts (Scholz et al., 2004). Truter et al. (2016) reported larvae of *P. scolecina* in African fish for the first time. We report as many as six new fish hosts and one new geographical record (Namibia). Metacestodes possess massive rostellar hooks that differ in their size and shape from congeneric taxa including *P. maleki* (Fig. 5G–J versus Figs. 4A–H and 5B–E).

***Paradilepis* sp.**

Fish hosts: **Chetia flaviventris*, **Coptodon rendalli*, **Oreochromis mossambicus*, **Pharyngochromis acuticeps*, **Pseudocrenilabrus philander* (all Perciformes: Cichlidae).

Site in host: Liver, mesenteries, intestinal wall.

Geographical distribution of larvae: *South Africa, *Zimbabwe.

Voucher specimens: IPCAS C-775/1–4; NHMUK 2017.12.6.8–9; RMCA 38278, 38279; SAMC A089981, A089982.

Representative DNA sequences: Sequences from two larvae ex *P. acuticeps* (MH062157; Lake Chivero; ex *P. philander* MH062158; South Africa) were submitted to the GenBank database (sequence lengths of 1,659 and 1,680 bp); these formed a monophyletic lineage together with the isolates of *P. scolecina* and *P. maleki* (see below).

Reference: Present study.

Description (Fig. 4C, D, G, H)

[Measurements of larvae from different hosts pooled together; see Supplementary Table S5 for measurements from individual host species.] Larvae medium-sized, 1.06–1.48 × 0.57–1.19 mm. Scolex 469–587 × 643–763, bearing oval to subspherical suckers 174–195 × 157–190. Rostellum 218–290 × 172–216, armed with 20 hooks of 2 sizes: 10 larger (distal) hooks 87–94 long (blade 42–48; handle 47–54; blade/handle ratio 0.80–1.00); 10 smaller (proximal) hooks 64–73 long (blade 28–34; handle 40–49; blade/handle ratio 0.62–0.82).

Remarks

Metacestodes of *Paradilepis* sp. possess rostellar hooks somewhat similar in their shape to those of *P. delachauxi* (Fig. 4A, B, E, F versus Fig. 4C, D, G, H), but they are much smaller (total length of hooks 89–95 and 68–70 µm in *Paradilepis* sp. vs 117–127 and 85–93 µm in *P. delachauxi*, i.e. only about 3/4 of the length of the hooks of the latter species) and more robust, considering their smaller size (Fig. 4C, D, G, H). It is possible that larvae from African cichlids belong to a new species of *Paradilepis*. Scholz & Salgado-Maldonado (2001) and Scholz et al. (2002) found one larva of unidentified species of *Paradilepis*

in the liver of the atheriniform fish *Chirostoma jordani* (Atheriniformes: Atherinopsidae) from Guanajuato, Mexico and corresponding adults from the cormorant *Phalacrocorax brasilianus* (Gmelin) (as *P. olivaceus*) in Veracruz, Mexico. Even though both species have robust rostellar hooks, those of the African larvae are conspicuously different in their shape and slightly smaller (larger hooks 87–94 vs 101–103 µm and 64–73 vs 71–75 µm).

***Parvitaenia macropeos* (Wedl, 1855) Baer & Bona, 1960**

Syns *Taenia macropeos* Wedl, 1855; *Anomotaenia nycticoracis* Yamaguti, 1935; *Parvitaenia echinatia* Mettrick, 1967

Type-host: *Nycticorax nycticorax* (L.) (Pelecaniformes: Ardeidae), night heron.

Type-locality: Hungary, Europe.

Fish hosts: **Coptodon rendalli*, **Hemichromis letourneuxi* Sauvage, **Oreochromis mossambicus*, **O. niloticus* (Perciformes: Cichlidae).

Site in host: Intestinal wall.

Geographical distribution of larvae: *Madagascar, *Senegal; North America: Mexico; adults have been found in Africa (Zambia), Asia (Japan) and Europe (Hungary, Italy) (Bona, 1975).

Voucher specimens: IPCAS C-283/2–5; NHMUK 2017.12.6.10–12; RMCA 38267–38269.

References: Scholz & Salgado-Maldonado (2002); present study.

Description (Fig. 6G–M)

[Based on 7 specimens.] Larvae small, 0.56–0.90 × 0.22–0.40 mm. Scolex 125–181 × 118–150, with subspherical suckers 44–60 × 37–64 and rostellum 49–70 × 44–57, armed with 20 hooks of 2 sizes; 10 larger (distal) hooks 41.5–47 long (blade 22.5–26; handle 19.5–23; blade/handle ratio 0.97–1.17); 10 smaller (proximal) hooks 26–29 (blade 11.5–14; handle 14–16.5; blade/handle ratio 0.79–0.96).

Remarks

This species was described as *Taenia macropeos* by Wedl (1855) and redescribed by Baer & Bona (1960), who transferred the species to *Parvitaenia*. It is a specific parasite of *Nycticorax nycticorax* with a

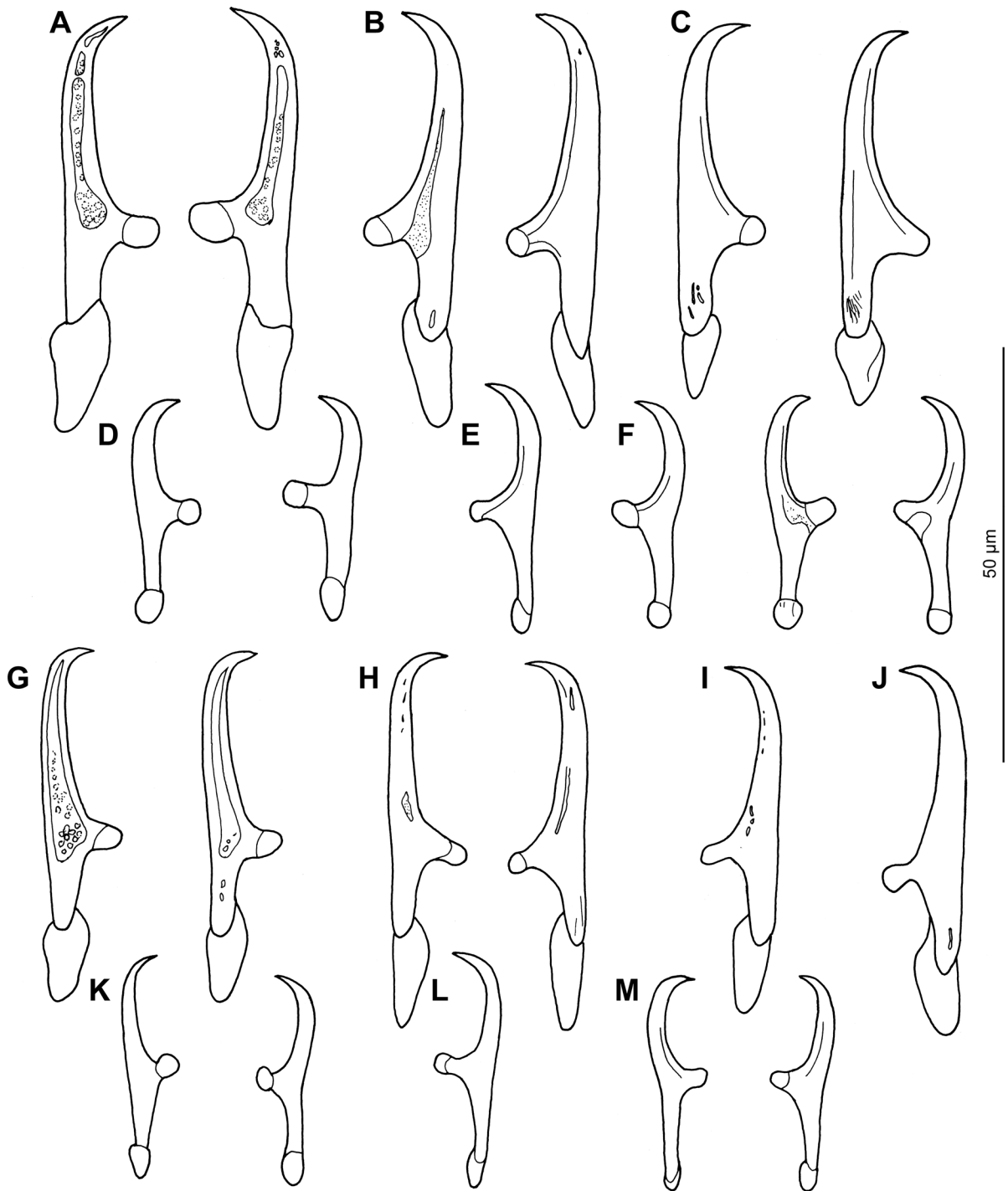


Fig. 6 *Parvitaenia samfyia* Metrick, 1967 (A–F) and *Parvitaenia macropeos* (Wedl, 1855) (G–M). A–C, G–J, Larger hooks; D–F, K–M, Smaller hooks. A, D, Adults from *Ardea purpurea*, Zambia (holotype; RMCA 33.613); B, E, Larvae from *Tilapia* sp., Zimbabwe; C, F, Larvae from *Pseudocrenilabrus philander*, South Africa; G, K, Adults of *Parvitaenia echinatia* Metrick, 1967 (syn. of *P. macropeos*) from *Nycticorax nycticorax*, Zambia (holotype; RMCA 33612/1); H, L, Larvae from *Oreochromis mossambicus*, Madagascar; I, M, Larvae from *Coptodon rendalli*, Madagascar; J, Larva from *Oreochromis niloticus*, Madagascar

worldwide distribution (Bona, 1975), but metacestodes were previously found only in the cichlid *Cichlasoma istlanum* (Jordan & Snyder) from Mexico (Scholz & Salgado-Maldonado, 2001). Rostellar hooks of the metacestodes from Madagascar and Senegal correspond in their shape (Fig. 6H, I, L, M) and size to those of *P. macropeos* including the holotype of *Parvitaenia echinatia* Mettrick, 1967 (syn. of *P. macropeos*) from *N. nycticorax* (RMCA 33612/1) (larger hooks 39–43 µm, smaller hooks 24–28 µm) and those of metacestodes from Mexican fishes (see Scholz & Salgado-Maldonado, 2002; larger hooks 43–46 µm, smaller hooks 26–30 µm). Metacestodes of *P. macropeos* are reported from Africa for the first time and all fishes represent new host records.

Parvitaenia samfyia Mettrick, 1967

Type-host: *Ardea purpurea* (Pelecaniiformes: Ardeidae), purple heron.

Type-locality: Zambia.

Fish hosts: **Pseudocrenilabrus philander*, **Tilapia* sp. (1/1; Zimbabwe) (all Perciformes: Cichlidae).

Site in host: Intestinal wall.

Geographical distribution of larvae: *South Africa, *Zimbabwe.

Voucher specimens: IPCAS C-469/1, 2.

References: Mettrick (1967); present study.

Description (Fig. 6A–F)

[Based on 10 specimens.] Larvae 1.06–1.65 × 0.27–0.47 mm. Scolex 168–289 × 161–420, with subspherical to oval suckers 82–112 × 65–92, and rostellum 67 × 61, armed with 20 hooks of 2 sizes; 10 larger (distal) hooks 45.5–50 long (blade 24.5–27; handle 20.5–25.5; blade/handle ratio 1.09–1.25); 10 smaller (proximal) hooks 27–30 (blade 13–15; handle 16; blade/handle ratio 0.79–0.92).

Remarks

Metacestodes described above correspond in their hook morphology including size to that of the holotype of *P. samfyia* (length of the hooks 46–48 and 25.5–27.5 µm, respectively; see Fig. 6A, D). The species was described by Mettrick (1967) from *A. purpurea* (type-host) and *Ardeola ralloides* (Scopoli)

in Zambia and redescribed by Bona (1975). Adults have never been found since the original description. Hooks of the metacestodes from African fishes are rather similar to those of *P. macropeos* (see above), but are more robust (Fig. 6B, C, E, F) and slightly larger. Scholz et al. (2008) misidentified larvae of *N. lasiopeius* from *C. carpio* in Mozambique as *P. samfyia* (see above); the latter species seems to be a rare parasite of African fishes.

Parvitaenia sp. 1

Fish hosts: **Enteromius treurensis* (Groenewald) (1/4), **E. trimaculatus* (3/37) (Cypriniformes: Cyprinidae).

Site in host: Intestine; intestinal wall.

Geographical distribution of larvae: *South Africa.

Voucher specimens: IPCAS C-778/1, 2.

Representative DNA sequences: A sequence (length of 1,473 bp) from a larva ex *E. trimaculatus* (MH062171) was submitted to the GenBank database. In the present unrooted phylogenetic tree, *Parvitaenia* sp. 1 formed a monophyletic lineage (even though only weakly supported) together with the isolates of *Parvitaenia* sp. 3 from *P. philander* in South Africa (see below).

Reference: Present study.

Description (Fig. 7A, E)

[Measurements of larvae from *E. treurensis* and *E. trimaculatus*; see Supplementary Table S6 for measurements of larvae from different hosts.] Larvae small, 0.50–0.71 × 0.29–0.46 mm. Scolex 213–337 × 300–400, with four subspherical suckers 91–102 × 77–95. Rostellum 83–124 × 65–129, armed with 20 hooks of 2 sizes; 10 larger (distal) hooks 61–73 long (blade 40–49; handle 21–24; blade/handle ratio 1.7–2.1); 10 smaller (proximal) hooks 43–50 (blade 23–29; handle 19–22; blade/handle ratio 1.09–1.39).

Reference: Present study.

Remark

Based on the shape of the hooks, the larvae from two species of barbels (*Enteromius* spp.) are assigned to *Parvitaenia* Burt, 1940, but they could not be identified to the species level.

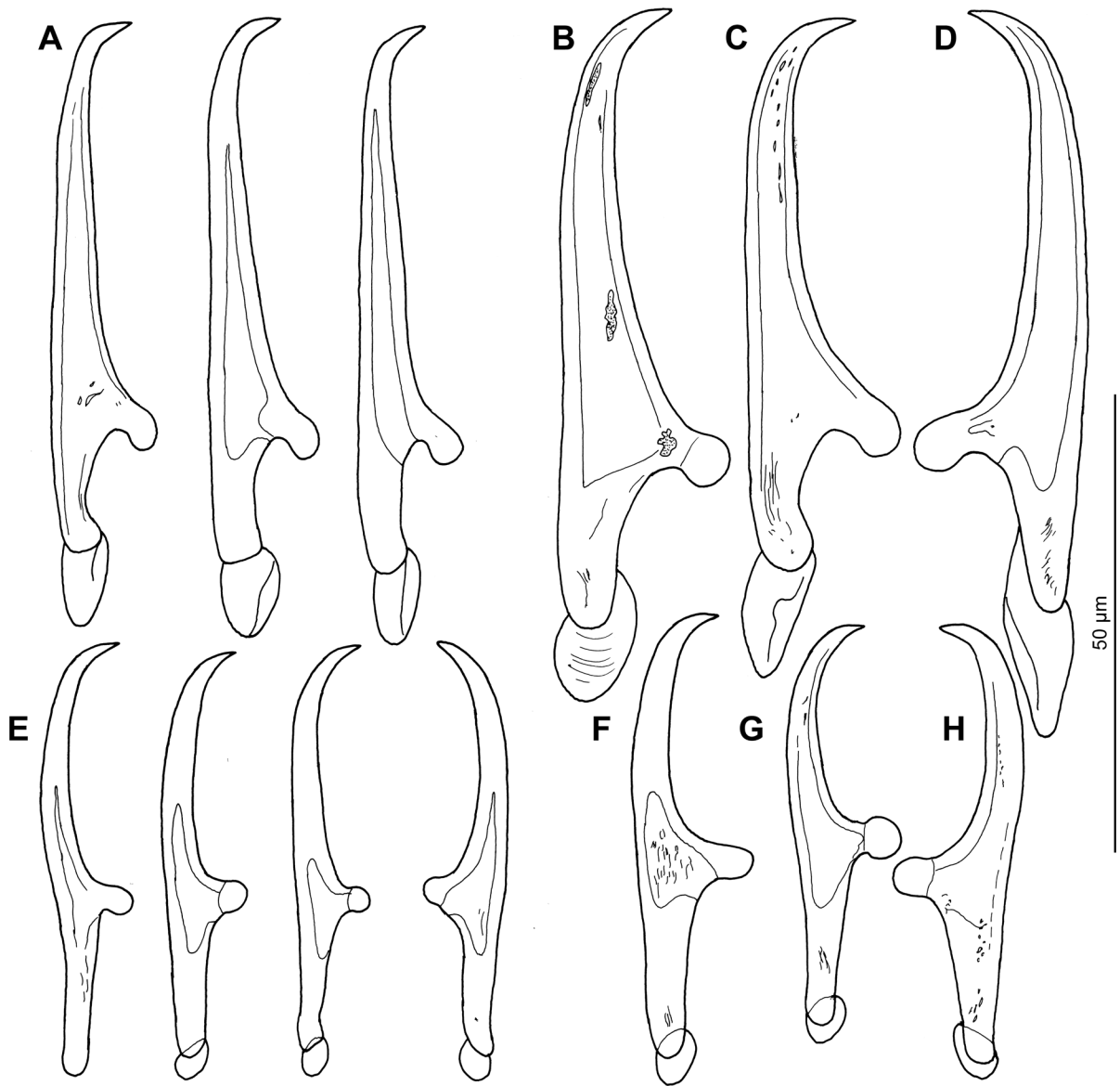


Fig. 7 Rostellar hooks of metacestodes of unidentified species of *Parvitaenia* Burt, 1940. *Parvitaenia* sp. 1 from the intestinal wall of *Enteromius trimaculatus*, South Africa (A, E) and *Parvitaenia* sp. 2 from *Enteromius macrops* (B, H), '*Barbus*' sp. (C, G; NHMUK 1981.1.2.1–20) and *E. trimaculatus* (D, F), all from South Africa. A–D, Large hooks; E–H, Small hooks

Parvitaenia sp. 2

Fish hosts: *'*Barbus*' sp., **Enteromius macrops* (Boulenger), **E. trimaculatus* (1/37) (Cypriniformes: Cyprinidae).

Site in host: Liver, mesenteries and stomach wall.

Geographical distribution of larvae: *Senegal, *South Africa.

Voucher specimens: IPCAS C-779/1, 2; NHMUK 1981.1.2.1–20.

Reference: Present study.

Description (Fig. 7B–D, F–H)

[Based on 4 specimens.] Larvae small, 0.46–0.52 mm × 0.24–0.30 mm (strongly flattened larva from *E. trimaculatus* 0.97 × 0.53 mm). Scolex 141–211 ×

184–246 (395–528), with subspherical suckers 64–104 × 56–91 (116–126 × 88–102), and rostellum 80–82 × 56–59 (98 × 75), armed with 20 hooks of 2 sizes; 10 larger (distal) hooks 70–79 long (blade 45–49; handle 28.5–34.5; blade/handle ratio 1.39–1.59); 10 smaller (proximal) hooks 46–51 (blade 23–27; handle 23.5–26; blade/handle ratio 0.97–1.11).

Remark

These larvae from three species of cyprinids are also assigned to *Parvitaenia*, because of the shape of their rostellar hooks. They are rather similar to those of *Parvitaenia* sp. 1, but their hooks are more robust, with blades more curved and the guard almost perpendicular (Fig. 7B–D, F–H), whereas the hook guard of larvae of *Parvitaenia* sp. 1 is directed more posteriorly (Fig. 7A, E).

Parvitaenia sp. 3

Fish host: *Pseudocrenilabrus philander* (3/28) (Perciformes: Cichlidae).

Site in host: Intestinal lumen.

Geographical distribution of larvae: *South Africa.

Voucher specimens: none.

Representative DNA sequences: Sequences of all three ethanol-fixed specimens from *P. philander* in Barberspan wetland, South Africa (lengths of 1,428, 1,468 and 1,504 bp) were submitted to the GenBank database (MH062168–MH062170). The sequences were either identical or differed by a single nucleotide and grouped with the representative of *Parvitaenia* sp. 1 from South Africa, which possesses rostellar hooks of a similar shape, but conspicuously longer (see above).

Reference: Present study.

Description (Fig. 8)

[Based on 3 specimens.] Larvae small. Scolex with rostellum armed with 20 hooks of 2 sizes; 10 larger (distal) hooks 52–58 long (blade 33–37; handle 20–22; blade/handle ratio 1.64–1.85); 10 smaller (proximal) hooks 36–40 (blade 20–23; handle 17–19; blade/handle ratio 1.16–1.35).

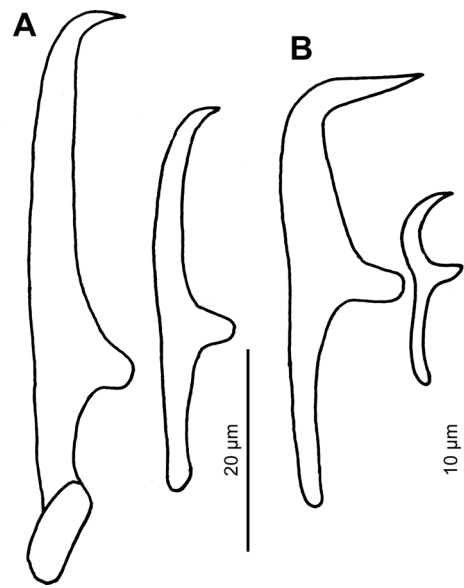


Fig. 8 Rostellar hooks of *Parvitaenia* sp. 3 from the intestinal lumen of *Pseudocrenilabrus philander*, South Africa (A) and *Valipora campylancristrota* (Wedl, 1855) from the gall-bladder of *P. philander*, South Africa

Remark

These unidentified larvae of *Parvitaenia* differ from those designated as *Parvitaenia* sp. 1 and *Parvitaenia* sp. 2 in a smaller size of rostellar hooks, especially larger ones.

Valipora campylancristrota (Wedl, 1855)

Syn. *Taenia campylancristrota* Wedl, 1855

Type-host: *Ardea cinerea* L. (Pelecaniformes: Ardeidae), grey heron.

Type-locality: Hungary, Europe.

Fish hosts (only in Africa): **Enteromius paludinosus* (1/92) (Cypriniformes: Cyprinidae); *Pseudocrenilabrus philander* (2/28) (Perciformes: Cichlidae).

Site in host: Gall-bladder.

Geographical distribution of larvae (in Africa): *Namibia, *South Africa.

Voucher specimens: None.

Representative DNA sequences: A sequence from one larva ex *P. philander* was submitted to the GenBank database (MH062174; length of 1,465 bp); this sequence formed a monophyletic lineage with the only representative of *Valipora minuta* (see below).

Reference: Truter et al. (2016); present study.

Description

[Based on one larva from *E. paludinosus*.] Larva small. Scolex with rostellum armed with 20 hooks of 2 sizes; 26–28 long (blade 11–12; handle 14–15; blade/handle ratio 0.78–0.80); smaller hooks 12–13 (blade 4–5; handle 7–8; blade/handle ratio 0.57–0.62).

Remarks

The species was described as *Taenia campylancristrota* by Wedl (1855) from the grey heron, *Ardea cinerea*, in Hungary. Baer & Bona (1960) and Bona (1975) redescribed the species and clarified its taxonomic position. Metacestodes of *V. campylancristrota* are common parasites of a wide spectrum of freshwater and brackish water fishes, with numerous reports from the Palaearctic Region and Mexico (Scholz & Salgado-Maldonado, 2001; Scholz et al., 2004; Ortega-Olivares et al., 2014). However, metacestodes were reported from African fishes just recently by Truter et al. (2016).

***Valipora minuta* (Coil, 1950) Baer & Bona, 1960**

Syn. *Ophiovalipora minuta* Coil, 1950

Type-host: *Butorides virescens* (L.) (Pelecaniformes: Ardeidae), green heron.

Type-locality: Laffayette, Tippecanoe County, Indiana, USA.

Fish hosts: **Chetia flaviventris* (2/28), **Ophthalmotilapia nasuta* (Poll & Matthes), **Pseudocrenilabrus philander*, **Ptychochromis grandidieri* Sauvage (all Perciformes: Cichlidae).

Site in host: Gall-bladder.

Geographical distribution of larvae: *Burundi, *Madagascar, *South Africa; Mexico.

Voucher specimens: IPCAS C-240/4, 6.

Representative DNA sequences: A sequence from one specimen ex *P. philander* (C11/14; Nwanedi Dam Lake, South Africa; length of 1,585 bp) was submitted to the GenBank database (MH062175); this formed a monophyletic lineage with *V. campylancristrota*.

References: Coil (1950); Bona (1975); Scholz & Salgado-Maldonado (2001); present study.

Description (Fig. 2B, C, E, F)

[Based on 5 specimens.] Larvae small, 0.42 mm × 0.26 mm. Scolex 243 wide, with oval suckers 75 × 46–50, and rostellum armed with 20 hooks of 2 sizes: larger hooks 37–41 long (blade 17.5–20; handle 23–24.5; blade/handle ratio 0.74–0.83); smaller hooks 21.5–23 (blade 7–9; handle 14–16; blade/handle ratio 0.57–0.60).

Remarks

Metacestodes found in the gall-bladder of three species of cichlids (all new fish hosts) from Burundi, Madagascar and South Africa (all new geographical records) are identified as *V. minuta* because their rostellar hooks best correspond in their size and shape to those of *V. minuta* from Mexico (larger hooks 36–40 µm long and smaller hooks 18–21.5 µm long; see Scholz & Salgado-Maldonado 2001, 2004), and to adults from *Butorides virescens* (larger hooks 35–40 µm long, smaller hooks 17–20 µm long). The species was described by Coil (1950) from *B. virescens* in Indiana, USA. Bona (1975) redescribed the species based on a study of Coil's material. In Mexico, Ortega-Olivares et al. (2008, 2014) reported adults from the type-host (*B. virescens*) and the little blue heron *Egretta caerulea* (L.), whereas Scholz & Salgado-Maldonado (2001) reported metacestodes of *V. minuta* from the cichlid *Cichlasoma istlanum*.

Molecular data

Here we obtained LSU rDNA sequences for nine species of gyporhynchid metacestodes belonging to the genera *Amirhalingamia*, *Neogyporhynchus*, *Paradilepis*, *Parvitaenia* and *Valipora* (Table 1). All genera represented by more than one species (i.e. *Paradilepis*, *Parvitaenia* and *Valipora*) formed monophyletic lineages in our phylogenetic estimate, thus supporting the monophyletic status of these genera, monophyly of *Paradilepis* and *Valipora* receiving absolute nodal support in nonparametric bootstrap analysis. Since we failed to find a suitable cestode representative among the available LSU rDNA sequences for cyclophyllidean cestodes to use as an outgroup, the phylogenetic estimate published here (Fig. 9) is an unrooted tree and as such does not allow

Table 1 List of larvae of gryporhynchid cestodes sequenced, with data on their fish hosts, localities and GenBank accession numbers

Cestode species	Host species	Locality	GenBank ID
<i>Amirthalingamia macracantha</i> (Joyeux & Baer, 1935)	<i>Pseudocrenilabrus philander</i> (Weber)	Lake Chivero, Zimbabwe	MH062173
<i>Amirthalingamia macracantha</i>	<i>Tilapia sparrmanii</i> Smith	Lake Chivero, Zimbabwe	MH062172
<i>Neogryporhynchus lasiopeius</i> Baer & Bona, 1960	<i>Tilapia sparrmanii</i>	Lake Chivero, Zimbabwe	MH062164
<i>Neogryporhynchus lasiopeius</i>	<i>Tilapia sparrmanii</i>	Lake Chivero, Zimbabwe	MH062165
<i>Neogryporhynchus lasiopeius</i>	<i>Pseudocrenilabrus philander</i>	Lake Chivero, Zimbabwe	MH062163
<i>Neogryporhynchus lasiopeius</i>	<i>Coptodon rendalli</i> (Boulenger)	Parc Ankarafantsika, Madagascar	MH062162
<i>Neogryporhynchus lasiopeius</i>	<i>Pseudocrenilabrus philander</i>	Nwanedi, South Africa	MH062167
<i>Neogryporhynchus lasiopeius</i>	<i>Pseudocrenilabrus philander</i>	Nwanedi, South Africa	MH062166
<i>Paradilepis maleki</i> Khalil, 1961	<i>Pseudocrenilabrus philander</i>	Barberspan, South Africa	MH062159
<i>Paradilepis maleki</i>	<i>Pseudocrenilabrus philander</i>	Barberspan, South Africa	MH062161
<i>Paradilepis maleki</i>	<i>Pseudocrenilabrus philander</i>	Barberspan, South Africa	MH062160
<i>Paradilepis scolecina</i> (Rudolphi, 1819)	<i>Pseudocrenilabrus philander</i>	Barberspan, South Africa	MH062155
<i>Paradilepis scolecina</i>	<i>Pseudocrenilabrus philander</i>	Barberspan, South Africa	MH062156
<i>Paradilepis</i> sp.	<i>Pharyngochromis acuticeps</i> (Steindachner)	Lake Chivero, Zimbabwe	MH062157
<i>Paradilepis</i> sp.	<i>Pseudocrenilabrus philander</i>	South Africa	MH062158
<i>Parvitaenia</i> sp. 1	<i>Enteromius trimaculatus</i> (Peters)	South Africa	MH062171
<i>Parvitaenia</i> sp. 3	<i>Pseudocrenilabrus philander</i>	Nwanedi, South Africa	MH062168
<i>Parvitaenia</i> sp. 3	<i>Pseudocrenilabrus philander</i>	Nwanedi, South Africa	MH062170
<i>Parvitaenia</i> sp. 3	<i>Pseudocrenilabrus philander</i>	Nwanedi, South Africa	MH062169
<i>Valipora campylancristrota</i> (Wedl, 1855)	<i>Pseudocrenilabrus philander</i>	Barberspan, South Africa	MH062174
<i>Valipora minuta</i> (Coil, 1950)	<i>Pseudocrenilabrus philander</i>	Nwanedi, South Africa	MH062175

assessing the direction of cladogenesis within the group.

Discussion

The present study has revealed the occurrence of 16 species of gryporhynchid metacestodes in African fishes, but only 11 species could be identified to the species level based on the number, shape and size of their rostellar hooks. Five morphotypes could be assigned only to a genus, because they did not match any of the known species of gryporhynchids. Compared to the Palearctic Region, in which only four species of four genera are known to occur in freshwater fishes (Scholz et al., 2004; Sokolov et al., 2015), the African fauna of gryporhynchid metacestodes is much more diverse and species-rich. However, the present

number of taxa is apparently an underestimation of the actual species diversity, considering a little attention that has been paid to these tiny parasites of fish. Until now, the richest fauna of gryporhynchids is known from Mexico, with as many as 25 reported species, including metacestodes of 18 species found in fishes (Ortega-Olivares et al., 2014). In Africa, adults of 19 species of eight gryporhynchid genera have been found (Bona, 1975; Schmidt, 1986).

Gryporhynchid larvae are apparently not as rare in African fishes as one could assume from scarce literary data (see Khalil & Polling, 1997). Recent research on fish parasites in several African countries, especially South Africa (Truter et al., 2016; present study), resulted in the collection of an extensive material of gryporhynchid metacestodes, thus indicating that these larvae may be relatively frequent and abundant, especially in cichlids including

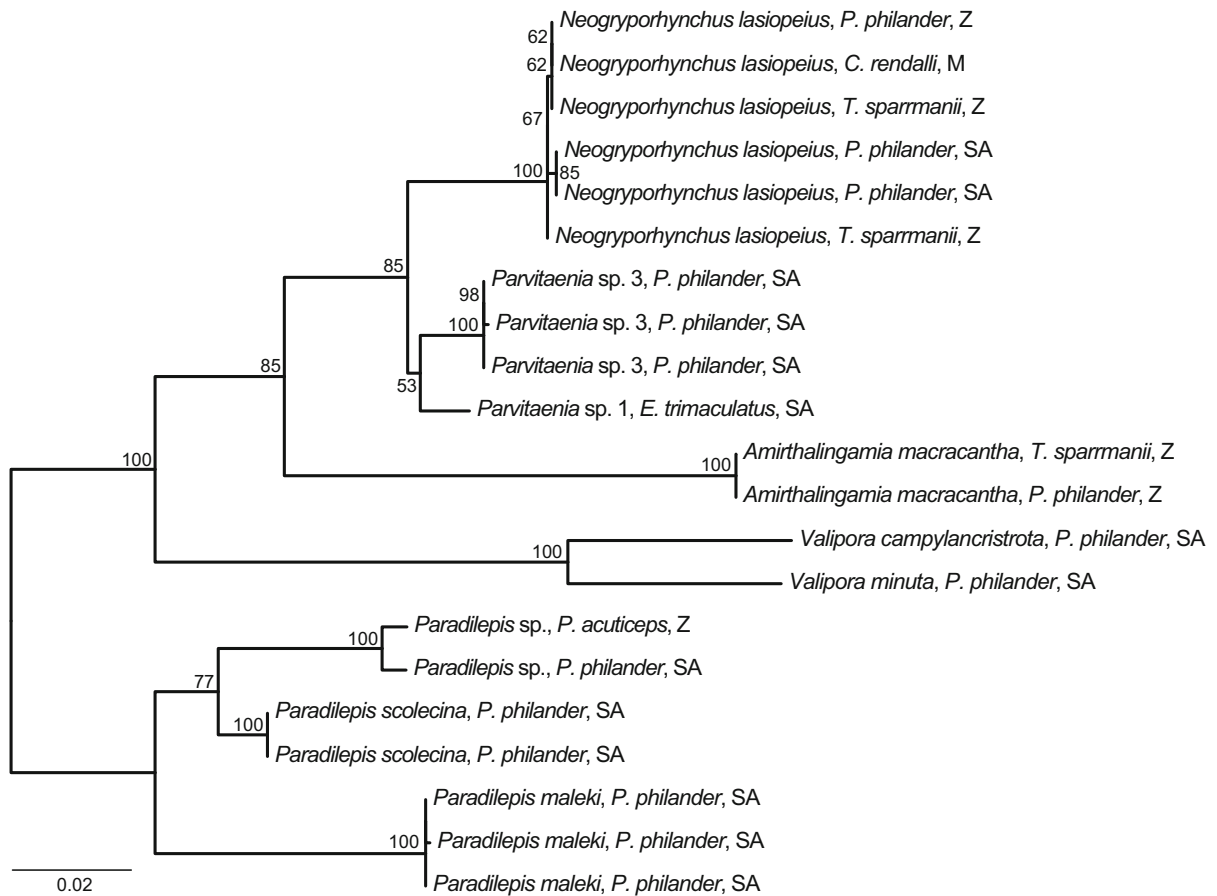


Fig. 9 Maximum likelihood phylogenetic tree based on the partial (domains D1–D3) sequences of LSU rDNA. Values at nodes depict bootstrap support values estimated over 100 repetitions in PHYML. Unrooted phylogram. Branch length scale-bar indicates the number of substitutions per site

economically important tilapias. Several factors may stand behind the fact that these tiny parasites were practically overlooked in the previous surveys on fish parasites in Africa (and elsewhere, see Scholz et al., 2004): (i) they are usually small-sized, especially species of *Dendrouterina*, *Neogryporhynchus*, *Paradilepis* and *Valipora*; (ii) they are encysted; (iii) they occur in parenteral sites of infection (gall-bladder, intestinal wall, mesenteries, liver); (iv) their proper processing is difficult and time-consuming; and (v) their identification requires good-quality optics, best with Nomarski differential contrast. Correct evaluation of hook morphology also requires flattening of the scolex with rostellar hooks positioned in one layer to correctly describe their size and shape; Berlese's fluid can also be used to spread the hooks

properly. Both methods can be laborious and time-consuming, especially in the field.

Species identification or just generic assignment of some gryporhynchid larvae may be intricate and simultaneous infection of the same organs of the same host by morphologically similar species cannot be excluded. Site of infection and gross morphology of larvae can somewhat help in differentiating genera, because congeneric species often infect similar organs and metacestodes of individual genera may differ in their size. For example, small-sized larvae of species of *Parvitaenia* and *Valipora* are usually unencysted in the gall-bladder or within the intestinal wall, whereas larger larvae such as those of *Amirthingamia*, *Cyclustera* and *Paradilepis* are usually found on the mesenteries or in the liver (Scholz et al., 2004; Ortega-Olivares et al., 2014). However, localisation of

Table 2 List of freshwater fishes in Africa infected with larvae of gryporhynchid cestodes, with country of reports of these parasites

Host	Parasite	Country
Order Cypriniformes		
Family Cyprinidae		
' <i>Barbus</i> ' sp.	<i>Parvitaenia</i> sp. 2	South Africa
<i>Cyprinus carpio</i> Linnaeus	<i>Cyclustera</i> sp.	Mozambique
	<i>Neogryporhynchus lasiopeius</i> Baer & Bona, 1960	Mozambique
<i>Enteromius macrops</i> (Boulenger)	<i>Parvitaenia</i> sp. 2	Senegal
<i>Enteromius paludinosus</i> (Peters)	<i>Paradilepis scolecina</i> (Rudolphi, 1819)	Namibia
	<i>Valipora campylancristrota</i> (Wedl, 1855)	Namibia
<i>Enteromius treurenensis</i> (Groenewald)	<i>Parvitaenia</i> sp. 1	South Africa
<i>Enteromius trimaculatus</i> (Peters)	<i>Paradilepis scolecina</i>	South Africa
	<i>Parvitaenia</i> sp. 1	South Africa
	<i>Parvitaenia</i> sp. 2	South Africa
<i>Enteromius unitaeniatus</i> (Günther)	<i>Paradilepis scolecina</i>	South Africa
<i>Labeo horie</i> Heckel	<i>Cyclustera magna</i> (Baer, 1959)	Kenya
<i>Labeobarbus kimberleyensis</i> (Gilchrist & Thompson)	<i>Paradilepis scolecina</i>	Namibia
<i>Labeobarbus marequensis</i> (Smith)	<i>Paradilepis delachauxi</i> (Fuhrmann, 1909)	South Africa
Order Perciformes		
Family Cichlidae		
<i>Bathybathes graueri</i> Steindachner	<i>Neogryporhynchus lasiopeius</i>	Burundi
<i>Benthochromis horii</i> Takahashi	<i>Paradilepis maleki</i> Khalil, 1961	Burundi
<i>Chetia flaviventris</i> Trewavas	<i>Neogryporhynchus lasiopeius</i>	South Africa
	<i>Paradilepis delachauxi</i>	South Africa
	<i>Paradilepis</i> sp.	South Africa
	<i>Valipora minuta</i> (Coil, 1950)	South Africa
	<i>Neogryporhynchus lasiopeius</i>	Madagascar, South Africa
	<i>Paradilepis delachauxi</i>	South Africa
<i>Coptodon rendalli</i> (Boulenger)	<i>Paradilepis scolecina</i>	South Africa
	<i>Paradilepis</i> sp.	South Africa
	<i>Parvitaenia macropeos</i>	Madagascar
	<i>Amirthalangamia macracantha</i> (Joyeux & Baer, 1935)	Kenya
	<i>Cyclustera magna</i>	Kenya
<i>Hemichromis letourneuxi</i> Sauvage	<i>Parvitaenia macropeos</i> (Wedl, 1855)	Senegal
<i>Ophthalmotilapia nasuta</i> (Poll & Matthes)	<i>Valipora minuta</i>	Burundi
<i>Oreochromis macrochir</i> (Boulenger)	<i>Paradilepis delachauxi</i>	Zambia
<i>Oreochromis mossambicus</i> Peters	<i>Neogryporhynchus lasiopeius</i>	Madagascar, South Africa
	<i>Paradilepis scolecina</i>	South Africa
	<i>Paradilepis</i> sp.	South Africa
	<i>Parvitaenia macropeos</i>	Madagascar, Senegal
	<i>Parvitaenia samfyia</i>	South Africa

Table 2 continued

Host	Parasite	Country
<i>Oreochromis niloticus</i> (Linnaeus)	<i>Cyclustera magna</i>	Kenya, Sudan
	<i>Neogryporhynchus lasiopeius</i>	Kenya, Madagascar, Sudan, Zimbabwe
<i>Pharyngochromis acuticeps</i> (Steindachner)	<i>Parvitaenia macropeos</i>	Madagascar, Senegal
	<i>Amirthalingamia macracantha</i>	Zimbabwe
	<i>Paradilepis delachauxi</i>	Zimbabwe
<i>Pseudocrenilabrus philander</i> (Weber)	<i>Paradilepis</i> sp.	Zimbabwe
	<i>Amirthalingamia macracantha</i>	Zimbabwe
	<i>Neogryporhynchus lasiopeius</i>	Madagascar, South Africa, Zimbabwe
	<i>Paradilepis delachauxi</i>	Zimbabwe
	<i>Paradilepis maleki</i>	South Africa
	<i>Paradilepis scolecina</i>	South Africa
	<i>Paradilepis</i> sp.	South Africa
	<i>Parvitaenia samfyia</i>	South Africa
	<i>Parvitaenia</i> sp. 3	South Africa
	<i>Valipora campylancristrota</i>	South Africa
<i>Ptychochromis grandidieri</i> Sauvage	<i>Valipora minuta</i>	South Africa
	<i>Valipora minuta</i>	Madagascar
<i>Sarotherodon galilaeus</i> (Linnaeus)	<i>Cyclustera magna</i>	Kenya
<i>Tilapia sparrmanii</i> Smith	<i>Amirthalingamia macracantha</i>	Zimbabwe
	<i>Neogryporhynchus lasiopeius</i>	South Africa, Zimbabwe
<i>Tilapia</i> sp.	<i>Parvitaenia samfyia</i>	Zimbabwe
Order Osteoglossiformes		
Family Arapaimidae		
<i>Heterotis niloticus</i> (Cuvier)	<i>Neogryporhynchus lasiopeius</i>	Madagascar
Order Siluriformes		
Family Schilbeidae		
<i>Schilbe intermedius</i> Rüppell	<i>Dendrouterina herodiae</i> Fuhrmann, 1912	Senegal
'Catfish'	<i>Amirthalingamia macracantha</i>	Democratic Republic of the Congo

metacestodes in fish hosts does not enable species identification. As a result, identification of gryporhynchid metacestodes in fishes is almost entirely based on the morphology of rostellar hooks (shape and size of hooks and their number), but the hooks of species of different genera may be difficult to distinguish from each other, e.g. those of *Dendrouterina* and *Valipora*, or some species of *Parvitaenia* from *Neogryporhynchus lasiopeius*.

In African cichlids and other fishes, metacestodes of several small-sized larvae can be found and their identification is difficult or impossible unless the

larvae are properly flattened to make it possible to reliably observe the shape and size of rostellar hooks. This is the case of most small-sized larvae from the gall-bladder and intestine (intestinal wall or lumen) of cichlids and barbels (Cyprinidae), which may be difficult to distinguish from each other (Figs. 2, 3, 6). In addition to differences in the size of the hooks, their shape, especially that of the blade of larger hooks, enabled us to distinguish several morphotypes even in metacestodes unidentified to the species level (three morphotypes of *Parvitaenia*). Larvae of *Parvitaenia samfyia*, *P. macropeos* and all unidentified species of

Parvitaenia were found only in one or two countries and in a few fish hosts, whereas those of *N. lasiopeius* occur in a wider spectrum of fish hosts throughout a large part of Africa.

Identification of larvae should be verified by their comparison with corresponding adults from fish-eating birds, but this is usually impossible due to the absence of reference material (and poor description of rostellar hooks of adults of some species). The ideal option would be to match sequences of commonly used molecular markers such as the LSU rDNA or *cox1* genes of both adults and larvae, thus providing unequivocal evidence of conspecificity of both ontogenetic stages. Unfortunately, molecular data on adult gryporhynchids from Africa are completely lacking.

The present study has revealed that *Parvitaenia* is the most species-rich genus, with five species, but with three species not identified to the species level. *Neogryporhynchus lasiopeius* has been reported from as many as nine species of fish intermediate hosts (Table 2). The principal hosts of gryporhynchids in Africa, at least in its southern part, are apparently cichlids, which host 11 of 16 gryporhynchid species reported in the present study (Table 2). The highest number of gryporhynchids has been found in *Pseudocrenilabrus philander* (9 spp.), *Chetia flaviventris* (5 spp.) and *Coptodon rendalli* (5 spp.). Another group of frequently infected fishes are barbels (Cyprinidae: Barbinae), whereas other cyprinids, catfishes or other fishes are infected with gryporhynchid larvae much less frequently or only sporadically. It is likely that future faunal surveys will reveal new hosts of gryporhynchids from other regions of Africa. The existing data accumulated in the present revision apparently reflect uneven research effort rather than the actual distribution areas of gryporhynchids.

Extensive material of gryporhynchids collected over the two last decades also enabled us to obtain first molecular data for the group. While we are aware that further sequence data for gryporhynchids exist, including the critically important sequences from adult parasite stages, none of these are currently publicly available. For example, M. P. Ortega-Olivares (National Autonomous University of Mexico, Mexico City) obtained sequences of LSU rDNA of several adults of gryporhynchids from fish-eating birds in Mexico (M.P. O.-O.; pers. comm.) and Waeschenbach et al. (2017) made an effort obtaining four genes of several gryporhynchid adults from fish-

eating birds worldwide, including a locality in Gabon; both of these datasets remain to be published.

Based on the present authors' experience, the following recommendations are provided to stimulate future research on gryporhynchids:

- (i) parenteral sites such as mesenteries, gall-bladder, intestinal wall and liver should be examined during fish dissection (and the precise site of infection should be noted);
- (ii) larvae found should be isolated from the host's tissue and excysted;
- (iii) scoleces with rostellar hooks should be flattened to enable proper evaluation of morphology and measurements of rostellar hooks; GAP or Berlese's fluid are recommended to be used for spreading the hooks into a single layer;
- (iv) it is recommended to divide the larvae and fix the posterior part in 99% molecular-grade ethanol for DNA sequencing, whereas the anterior part with the flattened scolex bearing rostellar hooks should serve as a morphological voucher, i.e. hologenophore; in small larvae, a photo of the flattened scolex with hooks can be taken as a photo voucher before placing the whole larva into a vial with 99% molecular-grade ethanol for DNA sequencing;
- (v) representative vouchers should always be deposited in internationally recognised collections to make them available for scrutiny or future examination with new techniques.

Acknowledgements Two anonymous reviewers and the Editor provided helpful suggestions that helped improve the quality of the manuscript. The authors are also indebted to Miloslav Jirků (Institute of Parasitology, BC CAS, České Budějovice, Czech Republic), Božena Koubková (Faculty of Science, Masaryk University, Brno, Czech Republic) and Olena Kudlai (North-West University, Potchefstroom, South Africa) who generously provided us with specimens of gryporhynchids from Kenya, Senegal and South Africa, respectively, Eva Řehulková and Maarten P. M. Vanhove (Faculty of Science, Masaryk University, Brno, Czech Republic; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; KU Leuven, Leuven, Belgium; Hasselt University, Diepenbeek, Belgium) and J. Rasamy Razanabolana (University of Antananarivo, Madagascar), J. R. Rasoloariniaina (Centre National de Recherche sur l'Environnement, Antananarivo) for their assistance with fish dissection and parasite collection from cichlid fish in Madagascar, and Marliese Truter (North-West

University, Potchefstroom, South Africa) for her assistance with dissecting *P. philander* in North-West Province. TS is obliged to staff of the Royal Museum of Central Africa, especially Tine Huyse and Christophe Allard, for help during his short stay in Tervuren.

Funding This study was supported by the Czech Science Foundation (project No. P505/12/G112) and Institute of Parasitology (institutional support RVO 60077344). Some of the results formed part of the BSc thesis of L. Uhrová. Stay of TS in the Royal Museum of Central Africa in Tervuren, Belgium, in February 2016 was funded by the EU-SYNTHESIS Project BE-TAF-5671. This work is also based on the research supported by the South African Research Chairs Initiative (SARChI) of the Department of Science and Technology and National Research Foundation of South Africa (Grant no. 101054). Any opinion, finding and conclusion or recommendation expressed in this material is that of the authors and the funding agencies do not accept any liability in this regard.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional, national and international guidelines for the care and use of animals were followed.

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