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Bothriocephalidean tapeworms (Cestoda) of freshwater fish in Africa, including erection of *Kirstenella* n. gen. and description of *Tetracampos martinae* n. sp.

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Abstract

A survey of bothriocephalidean tapeworms (Cestoda) parasitizing African freshwater fish is provided. Based on critical evaluation of type specimens and extensive, newly collected material, only the following seven species, instead of 19 taxa listed in the literature, are considered to be valid and their redescriptions are provided: *Bothriocephalus acheilognathi* Yamaguti, 1934 (with 3 synonyms from Africa); *Bothriocephalus claviceps* (Goeze, 1782) (marginally in Africa); *Ichthybothrium ichthybori* Khalil, 1971; *Kirstenella gordoni* (Woodland, 1937) n. comb. (1 synonym); *Polyonchobothrium polypteri* (Leydig, 1853) (4 synonyms); and *Tetracampos ciliotheca* Wedl, 1861 (4 synonyms). In addition, *Tetracampos martinae* Kuchta n. sp. is proposed for tapeworms from the catfish *Bagrus meridionalis* from Lake Malawi. The new species differs from *T. ciliotheca* in a much larger body (19 cm versus 3 cm), dorsoventally flattened strobila and numerous (39 versus 25–35) and longer apical hooks (up to 98 µm versus less than 50 µm). *Kirstenella* Kuchta n. gen. is proposed to accommodate *Senga gordoni* Woodland, 1937 as its type species. The new genus is distinguished from other genera of the Bothriocephalidae by the presence of an apical disc armed with two lateral semicircles of large hooks, cortical vitelline follicles and large-sized cirrus-sac. All but one valid species were recollected. Bothriocephalidean cestodes are widely distributed throughout Africa, but only two species, *B. acheilognathi* and *T. ciliotheca*, occur in other continents. All but one species (*B. acheilognathi*) exhibit narrow host specificity, being limited either to one host species (*K. gordoni* in *Heterobranchus bidorsalis* and *T. martinae* in *Bagrus meridionalis*) or one host genus (*I. ichthybori* in *Ichthyborus* spp., *P. polypteri* in *Polypterus* spp. and *T. ciliotheca* in *Clarias* spp.). Molecular data based on partial sequences of the large subunit rDNA (lsrDNA) show monophyletic position of all African taxa analysed (*B. acheilognathi*, *I. ichthybori*, *K. gordoni*, *P. polypteri* and *T. ciliotheca*).

Key words: Taxonomic revision, morphology, redescriptions, new genus, new species, phylogeny, identification key, zoogeography, host specificity

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Introduction

In Africa, more than 3,000 species of freshwater fish have been recorded, including members of the most ancient groups, such as lungfish (Dipnoi) and bichirs (Polypteriformes) (Lévêque *et al*. 2008; Froese & Pauly 2011). The helminth fauna of African teleosts has been studied since the middle 19th century, when Leydig (1853) and Wedl (1861) described the first tapeworms from bichirs and clariid fish, respectively. Khalil (1971a) published the first checklist of parasites of freshwater fish in Africa and in its updated edition (Khalil & Polling 1997), a total of 359 species of helminths, including 61 species of adult and larval tapeworms (Cestoda), were reported.

Adult tapeworms identified to the species level belong to the orders Amphilinidea (1 species), Caryophyllidea (20 species in 7 genera), Bothriocephalidea (13/3) and Proteocephalidea (19/6). Recently, several taxonomic accounts, which contained critical reviews of tapeworms of two of these orders, Proteocephalidea and Caryophyllidea, have been published (de Chambrier *et al*. 2007, 2008, 2011; Scholz *et al*. 2009, 2011a; Schaeffner *et al*. 2011) and a new genus and species of proteocephalidean cestodes were described (de Chambrier *et al*. 2009).

However, only limited information exists on the actual species composition, host specificity and distribution of members of a newly established order, Bothriocephalidea Kuchta, Scholz, Brabec & Bray, 2008 proposed to accommodate tapeworms with paired bothria on their scoleces, previously placed in the suppressed order Pseudophyllidea (see Kuchta *et al*. 2008a). The new order was revised by Kuchta *et al*. (2008b), who provided amended generic diagnoses, whereas Kuchta & Scholz (2007) proposed numerous synonymies of bothriocephalidean species, including taxa reported from African freshwater fish.

Since publication of the checklist by Khalil & Polling (1997), a number of new host and geographical records from African freshwater fish have been published. However, unsatisfactorily resolved taxonomy of the group, questionable validity of several taxa and continuing use of names of apparently invalid species, such as *Polyonchobothrium clarias* (see Kuchta *et al*. 2008b), make these new records unreliable or confusing. It is thus impossible to use literary data for a reliable assessment of the actual diversity, distribution of individual taxa and their relationships with fish hosts.

Recently, extensive new material was collected by the present authors and their co-workers in several African countries, including type-localities of several taxa (see below). Consequently, bothriocephalidean tapeworms parasitizing freshwater fish in Africa were revised on the basis of morphological and taxonomic evaluation of this new material, supplemented by a study of all available type and voucher specimens and a critical analysis of literary data. Results of this revision are presented herein, including redescriptions of all but one species (*Bothriocephalus acheilognathi*, which is also distributed outside Africa), and data on their fish hosts and distribution. Tapeworms found in *Bagrus meridionalis* Günther from Lake Malawi represents a new, hitherto undescribed species, which is described in this paper. In addition, a new genus is proposed to accommodate *Polyonchobothrium gordoni* Woodland, 1937 from clariid catfish.

Material and methods

Material collected by the present authors and their collaborators was obtained by the examination of more than 2,000 freshwater fish of 120 species of 23 families, carried out from 2006 to 2010 in the Democratic Republic of the Congo, Ethiopia, Gabon, Kenya and the Sudan (A. C., T. S., M. J., M. O.) (Appendix 1). Additional material from the following countries has been provided by co-workers (see sections Material studied): Egypt, Malawi, Senegal and South Africa. Most tapeworms were obtained by dissection of fresh fish.

New material used in this study originates from the following localities. Congo River basin – Democratic Republic of the Congo: Pioka (left bank) 4°54'23''S, 14°23'55''E. Gambia basin – Senegal: Niokolo-Koba National Park 13°1'44''N, 12°59'23''W. Nile River basin – Ethiopia: Beshelo River near Old Bridge, 11°28'27.78''N, 39°13'47.84''E, Lake Awasa 7°4'3.05''N, 38°26'30.86''E, Lake Chamo 5°51'10.03''N, 37°34'3.97''E, Lake Langano 7°35'26.47''N, 38°45'12.26''E, Lake Tana 12°2'29.64''N, 37°19'6.25''E, Lake Ziway 7°59'44.72''N, 38°49'42.51''E. The Sudan: Kostí, White Nile 13°10'20''N, 32°40'20''E, Sennar Dam, Blue Nile 13°32'37''N, 33°38'12''E, Khartoum 15°35'03''N, 32°32'13''E, Al Kawah 13°44'48.66''N, 32°29'49.56''E, Er Roseires Dam 11°47'5.83''N, 34°23'45.03''E, Lake Nubia (Asuan Dam) 21°46'41.65''N, 31°18'36.24''E. Turkana basin – Kenya: Lake Turkana, Todonyang, Omo River delta 4°27'10''N, 35°56'30''E. Zambezi basin – Malawi: southeast arm of Lake Malawi 14°9'41.00''S, 35°0'48.00''E.

The worms for morphological studies, including scanning electron microscopical (SEM) observations and histology, were fixed with hot 4% formaldehyde solution (see Oros *et al*. 2010), whereas some tapeworms or their pieces were preserved in 96% molecular grade ethanol for DNA sequencing (see below). Whole mounts were stained with Mayer's hydrochloric carmine and mounted in Canada balsam. Cross sections of the strobila (thickness 15 μm) were stained with hematoxylin-eosin, using standard histological methodology (Scholz & Hanzelová 1998). Several scoleces and segments were prepared for SEM following the procedure outlined by Kuchta & Caira (2010). Terminology of microtriches follows Chervy (2009); names of fish follow those of Froese & Pauly (2011). Illustrations were made using a drawing attachment on an Olympus BX51 microscope with differential interference contrast optics. Measurements are given in the text as ranges followed in parentheses by the mean, standard deviation, and number of measurements made. Measurements in descriptions are given in micrometers unless otherwise stated.

Additional material of bothriocephalidean cestodes, which is listed in redescriptions of individual species, was provided by M. Barson (specimens from South Africa), R. A. Bray (Malawi), B. Koubková (Senegal) and E. N. Protasova (Ethiopia). In addition, type and voucher specimens were borrowed from several museum collections: The Natural History Museum, London, UK (acronym BMNH); Göteborgs Naturhistoriska Museum, Göteborg, Sweden (GNM); Institute of Parasitology, České Budějovice, Czech Republic (IPCAS); Muséum d'Histoire Naturelle, Geneva, Switzerland (MHNG); Muséum National d'Histoire Naturelle, Paris, France (MNHNP); Meguro Parasitological Museum, Tokyo, Japan (MPM); Naturhistorisches Museum, Vienna, Austria (NMW); Musée Royal de l'Afrique Centrale, Tervuren, Belgium (RMCA); The Royal Veterinary College, London, UK (RVC); United States National Parasite Collection, Beltsville, Maryland, USA (USNPC); Naturhistorisches Museum, Berlin, Germany (ZMB).

To assess phylogenetic relationships of African bothriocephalideans, a comparative analysis of partial sequences of the large subunit rDNA (lsrDNA) gene was performed. Seven samples were analysed: *B. acheilognathi* ex *Labeobarbus nedgia* Rüppell from Ethiopia (MHNG 55310; GenBank Accession No. JQ811839), *B. acheilognathi* ex *Poecilia reticulata* Peters from Czech Republic (IPCAS C-15; JQ811834), *I. ichthybori* ex *Ichthyborus besse* (Joannis) from the Sudan (IPCAS C-455; JQ811837), *K. gordoni* ex *Heterobranchus bidorsalis* Geoffroy Saint-Hilaire from Ethiopia (IPCAS C-609; JQ811838), *P. polypteri* ex *Polypterus senegalus* Cuvier from the Sudan (IPCAS C-464; JQ811836), *T. ciliotheca* ex *Clarias gariepinus* (Burchell) from Ethiopia (IPCAS C-466; JQ811835) and *Senga* sp. ex *Channa micropeltes* (Cuvier) from Cambodia (IPCAS C-495; JQ811840). Genomic DNA was extracted using a standard phenol-chloroform extraction (Sambrook & Russell 2001) from 96% ethanol preserved samples. The D1–D3 region of lsrDNA was amplified by PCR using the primers and conditions described previously in Brabec *et al*. (2012). All products were verified on a 1% agarose gel and purified with the QIAquick PCR Purification Kit (Qiagen). BigDye® Terminator v3.1 cycle sequencing reagents and a PRISM 3130xl automatic sequencer (Applied Biosystems) were used for bidirectional sequencing of the PCR products using the set of PCR and internal sequencing primers described previously (e.g. Brabec *et al*. 2012). Sequences were assembled and inspected for errors using Geneious Pro 5.1.6 (Drummond *et al*. 2010) and aligned using the E-INS-i algorithm in the program MAFFT (Katoh *et al*. 2005). The resulting alignments were checked in MacClade 4.08 (Maddison & Maddison 2000) and ambiguously aligned positions were manually excluded prior to phylogenetic analyses.

The phylogenetic relationships were evaluated by maximum likelihood (ML) and Bayesian inference (BI) methods. ML analyses were conducted using the program RAxML ver. 7.2.8-ALPHA (Stamatakis 2006; Stamatakis *et al*. 2008), employing the GTR+Γ substitution model. All model parameters and bootstrap nodal support values (1000 repetitions) were estimated using RAxML. BI trees were constructed using MrBayes ver. 3.1.2 (Ronquist & Huelsenbeck 2003), running 4 independent MCMCMC runs of 4 chains for 5 million generations and sampling tree topologies every 1000th generation. As in ML analyses, the GTR+Γ model was employed. Burn-in period was set to 2.5 million generations according to the standard deviation of split frequencies values (<0.01) and by checking for MCMC convergence using AWTY (Nylander *et al*. 2008).

Results

The present study, based on the evaluation of all type material available, voucher specimens and extensive quantity of newly collected tapeworms, has shown that only seven species of bothriocephalidean cestodes, all of the family Bothriocephalidae, occur in freshwater fish in Africa. Adult bothriocephalideans were found in 6 families of fish, namely Alestidae, Clariidae, Claroteidae, Cyprinidae, Distichodontidae and Polypteridae (Appendix 1). A comprehensive survey of cestodes considered to be valid is provided below, including redescriptions of all but one (*Bothriocephalus acheilognathi*) species and data on their synonyms, definitive hosts and geographical distribution. A new genus is proposed to accommodate *Polyonchobothrium gordoni* Woodland, 1937, and a new tapeworm species is described from *Bagrus meridionalis* from Malawi. The species are listed in alphabetical order.

Bothriocephalus acheilognathi Yamaguti, 1934

(Figs. 1, 2, 4, 12)

Syns. (only taxa reported from Africa; for other synonyms – see Pool & Chubb 1985; Pool 1987; Kuchta & Scholz 2007): *Bothriocephalus* (*Clestobothrium*) *kivuensis* Baer & Fain, 1958; *Bothriocephalus aegyptiacus* Ryšavý & Moravec, 1975; *Bothriocephalus barbus* Fahmy, Mandour & El-Naffar, 1978; *Bothriocephalus* sp. of Yimer (2000), Al-Bassel (2003), and Zekarias & Yimer (2007).

Type host: *Acheilognathus rhombeus* (Temminck & Schlegel) (Cypriniformes: Cyprinidae).

Other definitive hosts in Africa (for extensive list of hosts from other continents, see Dove & Fletcher 2000): *Barbus altianalis* Boulenger, *Barbus argenteus* Günther, *Barbus brevipinnis* Jubb, *Barbus bynni* (Forsskål), *Barbus mattozi* Guimarães, *Barbus paludinosus* Peters, *Barbus trimaculatus* Peters, *Cyprinus carpio* Linnaeus, *Labeobarbus aeneus* (Burchell), *Labeobarbus kimberleyensis* (Gilchrist & Thompson), *Labeobarbus marequensis* (Smith), *Labeobarbus nedgia* Rüppell (Cypriniformes: Cyprinidae).

Type locality: Lake Ogura, Kyoto Prefecture, Honshu, Japan (35°2'N, 135°53'E).

Distribution in Africa: Congo basin – Democratic Republic of the Congo; Incomati basin – South Africa; Limpopo basin – South Africa; Maputo basin – South Africa; Nile basin – Egypt, Ethiopia; Orange basin – South Africa.

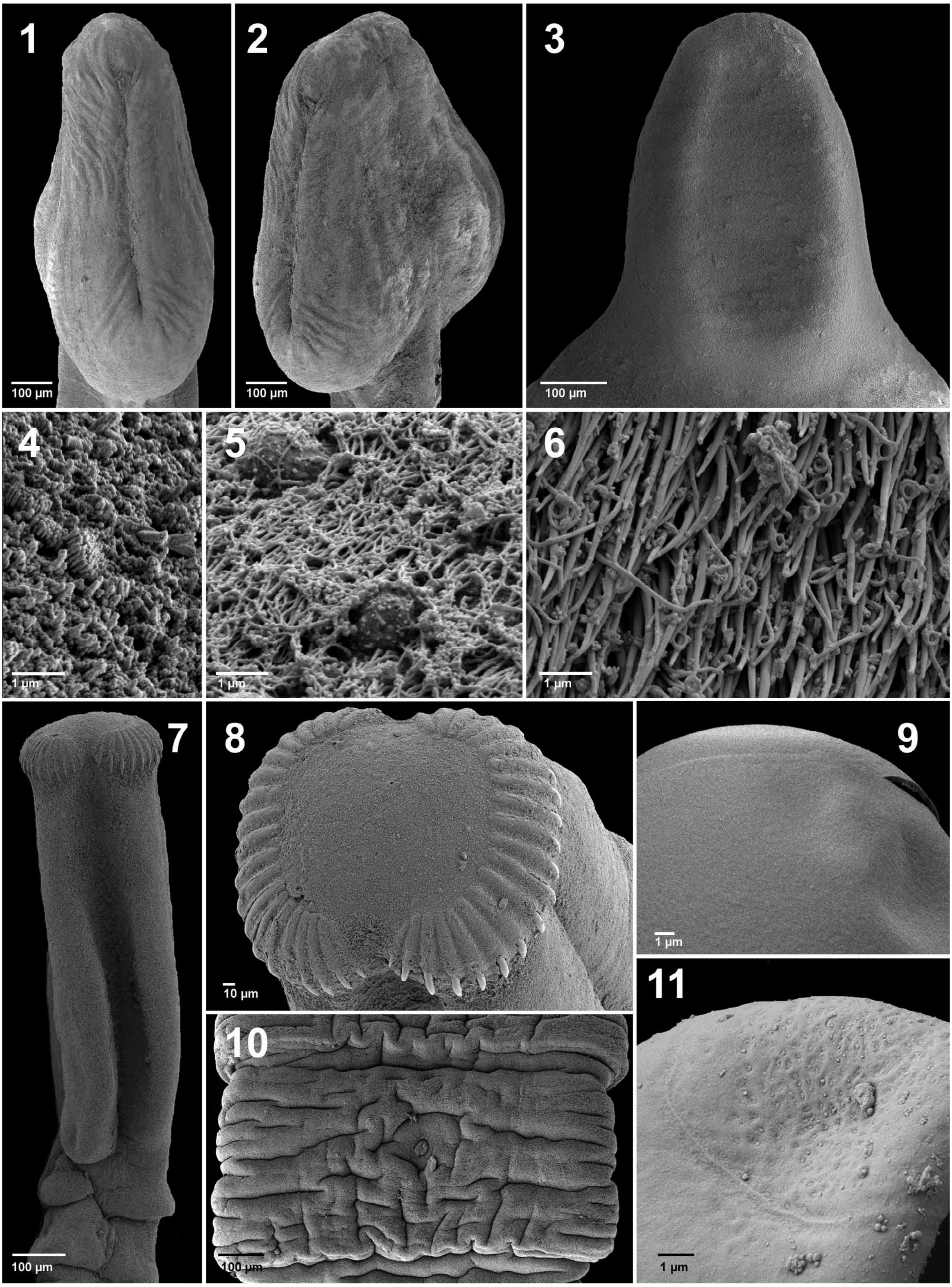
Prevalence and intensity of infection: Precise data are not available, but this cestode seems to be rather infrequent. Despite extensive sampling, the present authors found only a single barbel infected with *B. acheilognathi* in Ethiopia (out of 56 barbels examined; see Appendix 1). However, Bertasso & Avenant-Oldewage (2005) found prevalence up to 90% in *L. kimberleyensis* from South Africa.

Type material: MPM 23780 (holotype).

Material studied: Type material: holotype (one slide of whole mount and one slide of histological sections) of *B. acheilognathi*; holotype (one worm on 20 slides) of *B. aegyptiacus* ex *B. bynni* from Cairo, Egypt (IPCAS C–14); three syntypes (3 mounted scoleces and histological sections) of *B. kivuensis* ex *B. altianalis* from Lake Kivu, Democratic Republic of the Congo (MHNG 40332) (Fig. 12); vouchers: one specimen ex *L. kimberleyensis* from Vall Dam, South Africa, collected by M. Barson (MHNG 36429); one specimen of *Bothriocephalus* sp. ex *Hydrocynus* sp. (Craciformes: Alestidae) from Bagata, Kwilu, Democratic Republic of the Congo (MHNG 55308); new material: three specimens ex *L. nedgia* from Beshelo River, near Old Bridge, Ethiopia, collected by Moges Beletew (MHNG 55310) (Figs. 1, 2, 4).

Published records from Africa: Baer & Fain (1958, 1960); Ryšavý & Moravec (1975); Amin (1978); Fahmy *et al*. (1978); Boomker *et al*. (1980); Brandt *et al*. (1981); van As *et al*. (1981); El-Naffar *et al*. (1984); Basson & van As (1993); Paperna (1996); Schulz & Schoonbee (1999); Al-Bassel (2003); Bertasso & Avenant-Oldewage (2005); Retief *et al*. (2006, 2007, 2009); Zekarias & Yimer (2007); Degger & Avenant-Oldewage (2009); Degger *et al*. (2009); Stadtlander *et al.* (2011).

Remarks: Up to date, six species of *Bothriocephalus* Rudolphi, 1808 have been reported to occur in freshwater fish in Africa, especially in barbels (Cyprinidae: Barbinae) (Baer & Fain 1958; Tadros 1967; Ryšavý & Moravec 1975; Fahmy *et al*. 1978; Bertasso & Avenant-Oldewage 2005; Stadtlander *et al*. 2011). However, the present study has shown that apart from marginal occurrence of *B. claviceps* (see below), only one species, the Asian fish tapeworm, *Bothriocephalus acheilognathi*, actually parasitizes African fish. *Bothriocephalus prudhoei* Tadros, 1967 is invalidated (synonym of *Kirstenella gordoni* – see below) and three remaining species of *Bothriocephalus*, namely *B.* (*Clestobothrium*) *kivuensis* Baer & Fain, 1958; *B. aegyptiacus* Ryšavý & Moravec, 1975; and *B. barbus* Fahmy, Manour & El-Naffar, 1978, are synonyms of *B. acheilognathi* (see Pool 1987; Kuchta & Scholz 2007).



FIGURES 1–11. Scanning electron micrographs of the scoleces and the body surface. **1**, **2**, **4**, *Bothriocephalus acheilognathi* Yamaguti, 1934 ex *Labeobarbus nedgia* from Ethiopia (MHNG 55310). **1**, **2**, Scolex, dorsoventral and sublateral views. **4**, Surface of apical region of scolex. **3**, **6**, **9**, *Ichthybothrium ichthybori* Khalil, 1971 ex *Ichthyborus besse* from Sudan (IPCAS C-455). **3**, Scolex, dorsoventral view. **6**, Surface of apical region of scolex. **9**, Detail of operculum of egg. **5**, **7**, **8**, **10**, **11**, *Kirstenella gordoni* (Woodland, 1937) ex *Heterobranchus bidorsalis* from Kenya (IPCAS C-609). **5**, Surface of apical region of scolex. **7**, Scolex, dorsoventral view. **8**, Scolex, apical view. **10**, Mature segment, ventral view. **11**, Detail of operculum of egg.

Bothriocephalus acheilognathi has been introduced from its original distribution area in East Asia throughout the world (Scholz *et al*. 2011b). It is a pathogen of fry of cultured fish, especially carp and other cyprinids, and has been reported to cause mortalities (Williams & Jones 1994). Numerous bothriocephalidean tapeworms have been synonymized with *B. acheilognathi*, including African taxa (see Kuchta & Scholz 2007 for list of synonyms). Pool (1987) synonymized *B. aegyptiacus* and *B. kivuensis* with *B. acheilognathi*, whereas *B. barbus* was considered to be a synonym of *B. acheilognathi* by Kuchta & Scholz (2007). Molecular data confirm these synonymies (Fig. 62).

The host spectrum of *B. acheilognathi* is extraordinarily wide and includes more than 200 species of unrelated fish (Scholz *et al*. 2011b), with cyprinids representing the most suitable definitive hosts. In Africa, it has been recorded in 12 cyprinid species of two native genera, *Barbus* (7 spp.) and *Labeobarbus* (4 spp.), as well as in introduced *Cyprinus caprio* (Stadtlander *et al.* 2011). Records from the Nile basin, South Africa, as well as the Congo basin suggest that *B. acheilognathi* is present throughout the continent wherever suitable cyprinid hosts are available. Surprisingly, there are no records from *Labeo* spp., suggesting that members of this speciose pan-African cyprinid genus constituting a significant component of ichthyofauna of many African basins are not suitable hosts. Such presumed unsuitability of *Labeo* spp. as hosts for *B. acheilognathi* might be the reason of its apparent absence in basins in which cyprinids are dominated by *Labeo* spp. This assumption is supported by the absence of *B. acheilognathi* in Lake Turkana (this study, Appendix 1), where none of the examined cyprinids, i.e. 42 *Labeo* spp. and 11 *Barbus bynni*, was infected (ratio of examined fish does not reflect real ratio in the lake in which two *Barbus* spp. in very low densities share the lake with huge populations of two *Labeo* spp.).

Findings of *B. acheilognathi* in clariid catfish in Ethiopia, Nigeria and Zimbabwe (Anosike *et al*. 1992; Yimer 2000; Moyo *et al*. 2009; Bichi & Yelwa 2010) may represent accidental findings due to predation, but extraordinarily high values of prevalence (up to 60%; Moyo *et al*. 2009) indicate that *Clarias* Scopoli catfish may harbour this parasite more frequently. Unfortunately, no voucher specimens of these remarkable, but suspicious findings have been preserved, which casts doubts upon correct identification of the worms found. It thus cannot be excluded that the authors misidentified *Tetracampos ciliotheca* Wedl, 1861, which is a very frequent and abundant intestinal parasite of *Clarias* catfish in Africa (see below) and the scolex of which somewhat resembles that of *B. acheilognathi*, especially when hooklets on the apical disc are detached after death of worms.

Tapeworms from *Tilapia* sp. (Characiformes: Cichlidae) and *Hydrocynus* sp. identified as *Bothriocephalus* sp. (Khalil & Thurston 1973; present study), may represent incidental infection of *B. acheilognathi*, but species identification could not be confirmed, because the specimen from *Tilapia* sp. is not available and the worm from *Hydrocynus* sp. is without scolex.

Bothriocephalus acheilognathi is distributed throughout Africa, but its abundance is considerably lower than in newly colonized regions, especially in Europe and North America (García-Prieto & Osorio-Sarabia 1991; Williams & Jones 1994; Salgado-Maldonado & Pineda-López 2003). The absence of records from West Africa is probably artificial, because great majority of parasitological studies on cyprinids in this region were obviously focused solely on ectoparasitic monogeneans (see Khalil & Polling 1997).

Ichthybothrium ichthybori Khalil, 1971

(Figs. 3, 6, 9, 13, 14)

Syns: "immature *Bothriocephalus*" of Woodland (1936); "unidentified ptychobothriid cestode" of Khalil (1969, 1971a).

Type host: *Ichthyborus besse* (Joannis) (Characiformes: Ichthyboridae).

Other definitive host: *Ichthyborus quadrilineatus* (Pellegrin) (new host).

Type locality: White Nile near Khartoum, the Sudan.

Distribution: Upper Guinea – Sierra Leone (Moa River in Mano or Pujehun) ; Nile basin – the Sudan (Khartoum and Kostí).

Prevalence and intensity of infection: Nile, Kostí, the Sudan; 67%, n = 6, intensity 15–35 (Khalil 1971b); 50%, n = 4, intensity 1–8 (present study).

Type material: Holotype – incomplete worm on 2 slides (USNPC 71666) and 2 paratypes – 3 worms on 3 slides (USNPC 71667).

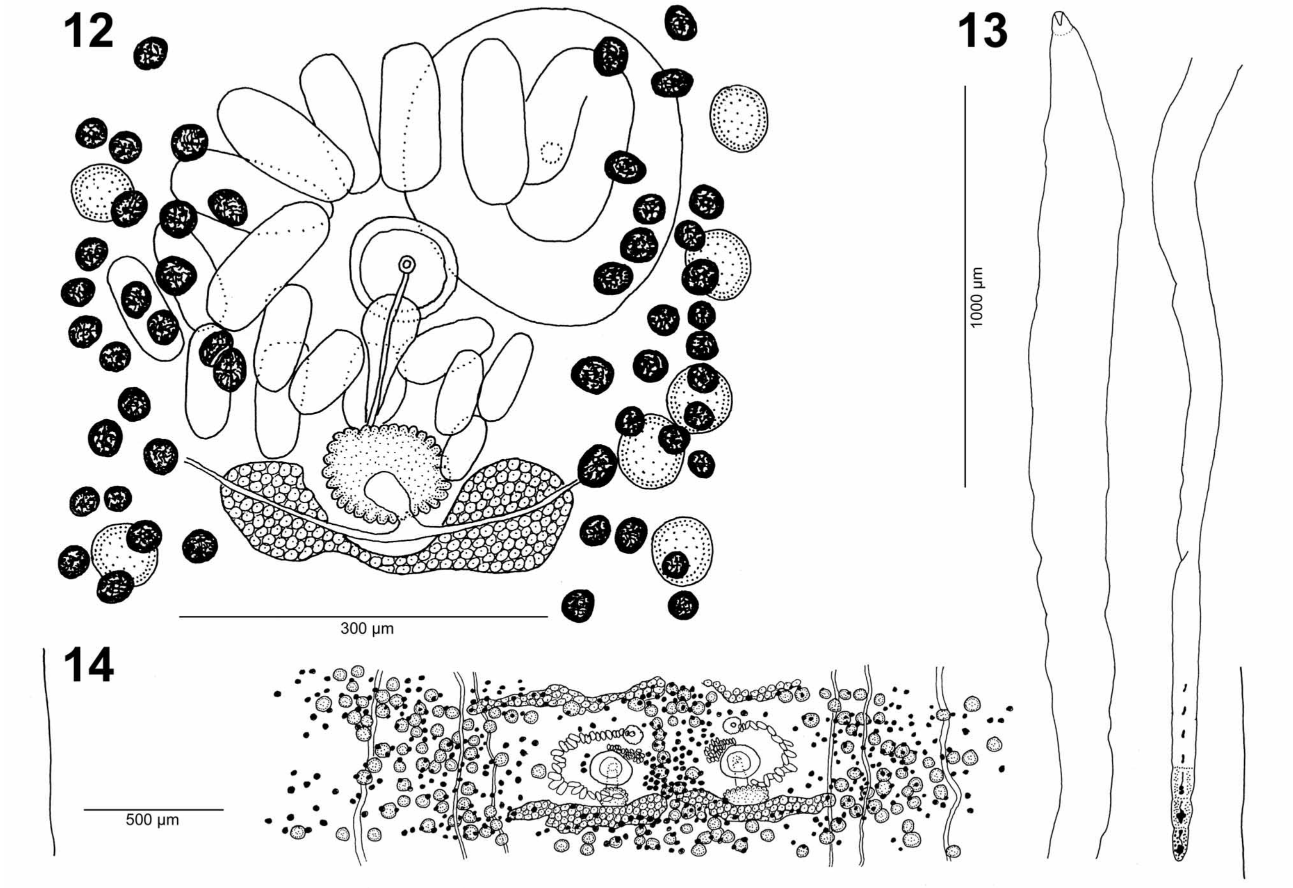
Material studied: Type material (USNPC 71666, 71667); vouchers: several slides collected by W.N.F. Woodland from *I. quadrilineatus* in Sierra Leone (BMNH 1977.3.28.147–179); new material: 9 specimens from Kostí, the Sudan (IPCAS C-455).

Published records: Woodland (1936); Khalil (1969, 1971a, b); Kuchta *et al*. (2008b).

Re-description (based on 3 mature and 6 immature worms from Kostí; measurements of holotype in brackets)**:** Bothriocephalidea, Bothriocephalidae. Strobila up to 10.0 [4.2] cm long; maximum width 3.7 [1.5] mm. External and internal segmentation weakly developed; segments variable in shape from wider than long to longer than wide, acraspedote (Fig. 13). Two pairs of longitudinal osmoregulatory canals; dorsal canals narrow (diameter up to 10); ventral canals wide (diameter up to 15), connected by transverse anastomoses. Inner longitudinal musculature weakly developed, formed by few muscle fibres. Surface of strobila uniformly covered with capilliform filitriches.

Scolex oval to lanceolate, much narrower than anterior part of strobila (Figs. 3, 13), 490–630 [495] long by 340–530 wide [413]. Apical disc absent. Bothria shallow, elongate, 240–360 [360] long by 140–200 [186] wide (Fig. 3). Surface of scolex covered with capilliform filitriches; tumuliform globular structures not observed (Fig. 6). Neck absent, first segments appear immediately posterior to scolex (Fig. 13).

Strobila with immature segments very long, representing up to 93% [58%] of total length. Mature segments, i.e. with spermatozoa in vas deferens, of two markedly different forms (morphotypes): longer than wide (486–614 by 374–529) [749–1,187 by 564–700] with one genital complex per segment or much wider than long (315–557 by 3,370–3,745) with two or three genital complexes per segment; segment length/width ratio 1.08–1.09 [1.19–1.78] or 0.08–0.16 (Figs. 13, 14). Gravid segments longer than wide (736–831 by 374–523) [1,080–1,280] or wider than long (425–621 by 2,550–3,360); segment length/width ratio 1.59–1.96 [1.50–1.74] or 0.13–0.24.



FIGURES 12–14. Line drawings. **12**, Detail of genital complex of gravid segment, dorsal view, eggs not illustrated, type specimen of *Bothriocephalus kivuensis* Baer & Fain, 1958 (= *B. acheilognathi* Yamaguti, 1934) ex *Barbus altianalis* from Democratic Republic of the Congo (MHNG 40332). **13**, **14**, *Ichthybothrium ichthybori* Khalil, 1971 ex *Ichthyborus besse* from the Sudan (IPCAS C-455). **13**, Complete worm with single genital complex per segment. **14**, Mature segment with double genital complexes.

Testes medullary, oval, 37–69 [48–57] in number per proglottid (110–120 testes in segments with duplicate or triplicate proglottides), 36–50 long by 22–43 wide [77–96 by 54–69], forming 2 narrow longitudinal bands (20–36 [22–29] testes per band), confluent between segments, absent medially and near lateral margins (Fig. 14). Cirrus-sac large, thin-walled (thickness of sac wall up to 32 [35]), spherical, 107–143 in diameter [106–135]; equatorial to pre-equatorial (at 42–50% [41–48%] of length of mature segment from anterior margin). Vas deferens forms numerous loops anterolateral to cirrus-sac, cirrus unarmed, opening into genital atrium (Fig. 14). Genital pore dorsal, sub-median, pre-equatorial (at 8–12% [4–10%] of length of mature segment from anterior margin), enlarging in gravid segments (Fig. 14).

Ovary asymmetrical, elongated or V-shaped, lobulate, 41–143 [131–213] long by 135–394 [186–251] wide (Fig. 14). Vagina a straight, thin-walled tube, with sac-like extension in proximal part, 64–83 [44–60] long by 23–52 [26–27] wide, opens posterior to cirrus-sac into genital atrium; vaginal sphincter absent (Fig. 14). Vitelline follicles numerous, small, spherical, 10–25 [30–45] long by 17–35 [25–30] wide, cortical, form 2 wide longitudinal bands confluent between segments, separated medially, rarely connected by several follicles in postovarian region (Fig. 14).

Uterine duct forms numerous tightly coiled loops, filled with eggs, enlarged in gravid segments. Uterine pore thick-walled, opens slightly posterior to midlength of uterus. Eggs oval, thin-walled, operculate, unembryonated, 38–46 [45–50] long by 27–30 [32–33] wide (Fig. 9).

Remarks: This tapeworm was described by Khalil (1971b) from the Sudan and placed in a newly proposed genus *Ichthybothrium* Khalil, 1971. It is characterized by a lanceolate scolex, which is narrower than the anterior end of the strobila (Figs. 3, 13) and possesses shallow bothria, but no apical disc. The strobila has weakly developed segmentation and its large proportion (more than 90% in some specimens) consists of immature proglottides without genital complexes (called “pregenital region” by Khalil 1971b).

Specimens recently collected near the type locality differ markedly from the type specimens in the shape of the segments and number of genital complexes per segment, with duplication or even triplication of genital complexes (proglottides) within mature and gravid segments (Kuchta *et al*. 2008b). Marked differences in the size of the worms may be influenced by crowding effect, because worms in more heavily infected hosts (intensity of infection 8–35 worms) are smaller (maximum length 6.2 cm) and consist of just a few mature and gravid segments, which are longer than wide (length/width ratio 1.08–1.96: 1) and usually contain only one genital complex (Khalil 1971b) (Fig. 13). In contrast, tapeworms from mono- or light infections are up to 10 cm long, their strobila is formed by numerous mature and gravid segments, which are much wider than long (length/width ratio 0.08–0.24: 1), and each of them contains two or even three genital complexes (Kuchta *et al*. 2008b; present study) (Fig. 14).

Khalil (1971b) correctly reported the cortical position of vitelline follicles in the diagnosis of *I. ichthybori*, but erroneously described vitelline follicles to be medullary in the diagnosis of the genus. The surface of the scolex and strobila was studied using SEM for the first time and a uniform pattern of capilliform filitriches was observed. Khalil (1971b) also reported the presence of “minute hair-like processes” on the scolex and “long hair-like processes” around the uterine pore, which may also represent capilliform filitriches (Fig. 6). However, tumuliform globular structures commonly observed in many bothriocephalideans (Kuchta *et al.* 2008b), including all other studied species, are missing in *I. ichthybori* (Fig. 6).

Ichthybothrium ichthybori is a rather frequent parasite of *Ichthyborus besse*, with high prevalence of infection (50–67%) and a relatively high intensity of infection. However, its fish host is rare and thus only a limited number of records of this tapeworm exist in the literature. Examination of several slides with immature cestodes designated as “immature *Bothriocephalus*” from *Neoborus quadrilineatus* (= *Ichthyborus quadrilineatus*) collected by W.N.F. Woodland in Sierra Leone (BMNH 1977.3.28.147–179) (Woodland 1936) has shown that they belong to *I. ichthybori*.

Kirstenella Kuchta n. gen.

Diagnosis: Bothriocephalidea, Bothriocephalidae. Medium-sized worms. Segmentation present. Segments trapeziform, craspedote. Scolex elongate. Bothria elongate, shallow. Apical disc present, as wide as, or slightly wider, than bothrial part of scolex, armed with large, simple hooks arranged in two lateral semicircles. Neck absent. Testes in two lateral fields, continuous between segments. Cirrus-sac thick-walled, spherical, large, representing as much as 1/6–2/5 of segment width; internal seminal vesicle present; cirrus unarmed. Genital pore dorsal, median. Ovary compact, bilobed, transversely elongate. Vagina posterior to cirrus-sac, enlarged distally. Vitelline follicles cortical, in two lateral fields continuous between segments. Uterine duct sinuous, S-shaped, enlarging in gravid segments. Uterus small, oval. Uterine pore median. Eggs operculate, unembryonated. In freshwater siluriforms. Africa.

Etymology: The new genus is named in honour of Kirsten Jensen, University of Kansas at Lawrence, USA, for her outstanding contribution to cestode systematics.

Type and only species: *Kirstenella gordoni* (Woodland, 1937) Kuchta, n. comb.

Remarks: The new genus is placed in Bothriocephalidae Lönnberg, 1889 because it possesses the median genital pore, follicular vitellaria, and a ventral uterine pore (Kuchta *et al*. 2008a, b). It is typified by combination of the following characteristics: (1) scolex is elongate with a small apical disc armed with two lateral semicircles of hooks; (2) cirrus-sac is large (its width represents as much as 1/6–2/5 of the width of segments) and it is situated perpendicularly; (3) a low number of testes (less than 75 per segment); (4) vagina is enlarged distally; (5) vitellaria are cortical.

Kirstenella differs from all but three bothriocephalid genera (*Polyonchobothrium* Diesing, 1854, *Senga* Dollfus, 1934 and *Tetracampos* Wedl, 1861) in the presence of an apical disc armed with two lateral semicircles of large hooks (Kuchta *et al*. 2008b). The new genus can be distinguished from *Tetracampos* by the presence of cortical (instead of medullary) vitelline follicles and presence of operculate, thin-walled (vs. unoperculated, with hyaline membrane) eggs. The new genus can be distinguished from *Polyonchobothrium* and *Senga* mainly by the relative size of the cirrus-sac, which is markedly larger (ratio of its width to the width of segments 16–39%) than that of species of *Senga* (ratio 4–10%) and *Polyonchobothrium* (ratio 5–10%), and is situated more perpendicularly in *Kirstenella*, whereas longitudinally or obliquely in the two remaining genera (Figs. 19, 22, 38, 39). Moreover, *Polyonchobothrium* has a markedly wider apical disc (350–510 µm) and much larger hooks (up to 190 µm) mostly distributed in 4 quadrants, whereas *Kirstenella* has a slender apical disc (230–300 µm) with smaller apical hooks (shorter than 90 µm) distributed in 2 semicircles. Hooks of *Senga* have an indistinct blade and handle (data not shown), whereas those of *Kirstenella* have the blade well differentiated from the handle (Figs. 16, 18).

Kirstenella gordoni (Woodland, 1937) Kuchta, n. comb.

(Figs. 7, 8, 10, 11, 15–22)

Syns: *Polyonchobothrium gordoni* Woodland, 1937; *Polyoncobothrium gordoni* (Woodland, 1937) Yamaguti, 1959; *Bothriocephalus prudhoei* Tadros, 1967; *Polyonchobothrium* sp. of Fagbenro *et al.* (1993); *Senga gordoni* (Woodland, 1937) Kuchta & Scholz, 2007.

Type host: *Heterobranchus bidorsalis* Geoffroy Saint-Hilaire (Siluriformes: Clariidae).

Other definitive hosts: *Clarias anguillaris* (Linnaeus) (Siluriformes: Clariidae), *Schilbe mystus* (Linnaeus) (Siluriformes: Schilbeidae). Both species are considered accidental/atypical hosts – see the Remarks section.

Type locality: Waanje River near Pujehun, Sierra Leone.

Distribution: Gambia basin – Senegal (Lampsar River, Taoué River, Gambia River); Turkana basin – Ethiopia (lower Omo River) and Kenya (Lake Turkana – restricted to the northernmost freshwater region part of the lake; see Remarks); Upper Guinea – Sierra Leone (Moa River); Niger basin – Mali (Lake Debo), Nigeria (River Ogbase); Nile basin – the Sudan (White Nile, Kostí) and Uganda (Lake Victoria).

Prevalence and intensity of infection: Lake Turkana – Omo River delta, Todonyang, Kenya, 60%, n = 10; intensity 1–6 (present study); Ethiopia – Omo River, Omorate, 50%, n = 2, intensity 1 (present study); Nile basin – the Sudan, 20%, n = 5, intensity 1 (present study); Niger basin – Nigeria, 22%, n = 185 (Fagbenro *et al.* 1993).

Type material: Syntypes (several slides with fragments of worms and their histological sections) (BMNH 1965.2.24.36–45).

Material studied: Type material: several syntypes; holotype and paratypes of *Polyonchobothrium gordoni* from Waanje River, Sierra Leone (BMNH 1965.2.24.36–45); *Bothriocephalus prudhoei* ex *Clarias anguillaris*, Malakal, the Sudan (BMNH 1998.10.15.6.7; RVC C. 1262); vouchers: Ptychobothriidae gen. sp. ex *H. bidorsalis*, Mali, Lake Dabo (MNHNP bd10); *P. clarias* ex *H. bidorsalis*, Taoué River, Senegal (RMCA 34695; D.T.F. Puylaert; 15.iii.1966); *Polyonchobothrium* sp. ex *H. bidorsalis*, Waanje River, Sierra Leone (BMNH 1965.2.24.62–65; collected by W.N.F. Woodland); *Polyonchobothrium* sp. ex *Schilbe mystus*, Lake Victoria, Uganda (BMNH

1957.12.30.34–38); new material: 1 specimen ex *H. bidorsalis*, White Nile in Kostí, the Sudan (MHNG 49379; 26.iii.2006); 1 specimen from Omo River, Omorate, Ethiopia (MHNG 63067; 15.iv.2006); 15 specimens from Omo River delta, Todonyang, Lake Turkana, Kenya (MHNG 69955); 3 specimens from Niokolo-Koba National Park, River Gambia, Senegal collected by B. Koubková (2006; Sen 272-1). The new material is deposited in BMNH (Nos. 2012.3.20.26–28), IPCAS (No. C-609), MHNG (Nos. 55339, 63254, 82036, 82038) USNPC (No. 105390) and ZMB (No. 7524).

Published records: Woodland (1937); Tadros (1968); Khalil (1973); Fagbenro *et al.* (1993).

Re-description (based on 10 whole mounts and 1 scolex observed by SEM; measurements from Woodland, 1937 in brackets): Bothriocephalidea, Bothriocephalidae. Strobila up to 10 [1.0–1.5] cm long; maximum width 875 [1,350]. External and internal segmentation present; segments wider than long, markedly craspedote, several ridges on surface of segments (Figs. 10, 15).

Two pairs of longitudinal osmoregulatory canals; dorsal canals narrow (diameter up to 7); ventral canals wide (diameter up to 14), connected by transverse anastomoses. Inner longitudinal musculature well developed, muscle fibres diffused (Fig. 21). Surface of strobila covered with capilliform filitriches.

Scolex oval, narrow (Figs. 7, 15, 17), 926–1,480 (1,160 ± 168) [280–380] long by 224–419 (317 ± 65) [310–516] wide (n = 15). Apical disc weakly developed, 230–300 (265 ± 18) wide by 74–102 (87 ± 10) long, armed with 40–42 (41 ± 1) [36–42] small hooks 16–88 (67 ± 19; n = 103) long. Hooks variable in size, arranged in two semicircles, smallest on periphery above each bothrium and increasing into middle of semicircle with largest hook 83–88 (86 ± 3; 3) [64] long (Figs. 8, 16, 18). Bothria elongate, shallow, 757–1,355 (1,025 ± 230) long by 73–98 (84 ± 11) wide (n = 7) (Figs. 7, 17). Surface of scolex covered with capilliform filitriches and tumuliform globular structures (diameter around 1) (Fig. 5). Neck absent, first segments appearing immediately posterior to scolex (Figs. 7, 15, 17).

Immature segments 112–257 (191 ± 43) long by 217–531 (340 ± 101) wide; segment length/width ratio 0.27–0.94: 1 (n = 15) (Fig. 15). Mature segments wider than long, 134–371 (242 ± 74) long by 283–998 (667 ± 201) wide; segment length/width ratio 0.23–0.66: 1 (n = 24) (Fig. 22). Gravid segments wider than long, 188–573 (326 ± 97) long by 704–1,104 (869 ± 114) wide; segment length/width ratio 0.24–0.79: 1 (n = 20) (Fig. 15).

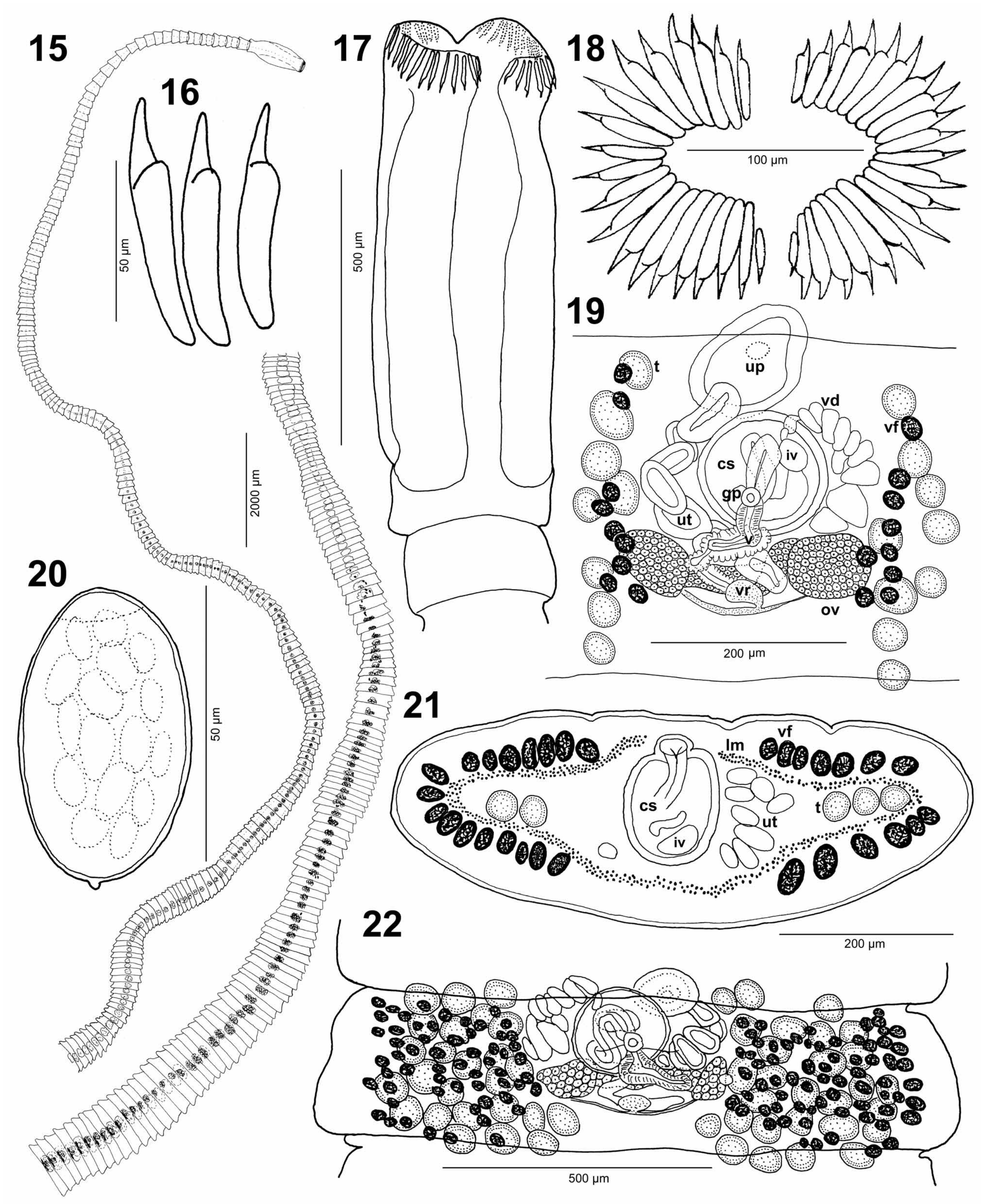
Testes medullary, oval, 70–133 (86 ± 20; 10) [under 30] in number per segment, 23–51 (35 ± 9) long by 26–45 (36 ± 6) wide [69 × 44 in sections] (n = 10) in diameter, forming 2 narrow longitudinal bands, 34–72 (47 ± 11) testes per band, confluent between segments, absent medially and near lateral margins (Fig. 22). Cirrus-sac large, thick-walled (thickness of sac wall 7–14), spherical, 92–161 (121 ± 21) long by 91–171 (132 ± 20) wide, length/width ratio 0.66–1.15: 1 (n = 24), pre-equatorial to postequatorial (at 30–69% of length of mature segment from anterior margin; n = 10). Internal seminal vesicle present, Vas deferens forms numerous loops posterolateral to cirrus-sac; internal sperm ducts strongly coiled, cirrus unarmed, opening into genital atrium (Figs. 19, 21, 22). Genital pore dorsal, median, pre-equatorial (Fig. 22).

Ovary asymmetrical, compact, bilobed, 44–95 (70 ± 16) long by 224–455 (332 ± 7) wide (n = 16) (Figs. 19, 22). Vagina a straight, thin-walled tube, 22–52 in diameter, opens posterior to cirrus-sac into genital atrium; vaginal sphincter absent (Fig. 19). Vitelline follicles numerous, small, spherical, 11–17 (14 ± 2; 8) [51 × 22] in diameter, cortical, form 2 wide longitudinal bands confluent between segments, separated medially, rarely connected by several follicles in postovarian region (Fig. 22).

Uterine duct forms numerous tightly coiled loops, filled with eggs, enlarged in gravid segments (Fig. 15). Uterus thick-walled, median, spherical, enlarged in gravid segments, occupies 4–30% of segment surface (Fig. 15). Uterine pore thick-walled, opens slightly posterior to midlength of uterus (Figs. 19, 22). Eggs oval, thin-walled, operculate, unembryonated, with abopercular knob, 30–43 (38 ± 4) lo ng by 21–33 (28 ± 4) wide [47 × 31] (n = 11) (Figs. 11, 20).

Remarks: *Polyonchobothrium gordoni* Woodland, 1937 was described from *Heterobranchus bidorsalis* from Sierra Leone. Woodland (1937) mentioned similarity of his new species with *Tetracampos ciliotheca* Wedl, 1861 in the shape of the body ("great part of strobila tightly coiled") and differentiated both taxa by the number and size of apical hooks.

Tadros (1967) described a new species *Bothriocephalus prudhoei* Tadros, 1967 based on material collected by K.N. Soliman from *Clarias anguillaris* in the Sudan in 1958. Only one complete specimen with several pieces of strobila was available, but the apical part of its scolex is missing. Kuchta and Scholz (2007) considered *B. prudhoei* to be a junior synonym of *T. ciliotheca*, but re-examination of the type material did not support this synonymy. In fact, strobilar morphology, including the presence of a large cirrus-sac, is identical to that of *K. gordoni*.



FIGURES 15–22. Line drawings of *Kirstenella gordoni* (Woodland, 1937) ex *Heterobranchus bidorsalis* from Kenya (IPCAS C-609). **15**, Complete worm. **16**, Detail of hooks. **17**, Scolex, dorsoventral view. **18**, Complete circle of hooks. **19**, Detail of genital complex of mature segment, dorsal view. **20**, Egg. **21**, Cross-section of gravid segment at level of cirrus-sac. **22**, Mature segment, dorsal view.

Abbreviations: cs, cirrus-sac; gp, genital pore; iv, internal seminal vesicle; lm, inner longitudinal muscles; ov, ovary; t, testes; up, uterine pore; ut, uterus; v, vagina; vd, vas deferens; vf, vitelline follicles; vr, viteline reservoir.

Therefore, *B. prudhoei* is synonymized with this species, even though *B. prudhoei* was not found in its type host *H. bidorsalis*, but in *Clarias*, which is considered herein to be an accidental host.

Tadros (1968) compared *Polyonchobothrium gordoni* with *P. cylindraceum* forma *major* Janicki, 1926 and concluded that these species were closely related and could be separated from each other by the number and size of the hooks. Kuchta & Scholz (2007) transferred *P. gordoni* to *Senga* because they considered *Polyonchobothrium* Diesing, 1854 to be monotypic (see Kuchta *et al.* 2008b). However, the present study has shown that *P. gordoni* differs from all species of *Senga*, which occur exclusively in the Indomalayan Region, in several morphological characteristics considered to be of generic importance. Therefore, the new genus, *Kirstenella*, is proposed to accommodate *P. gordoni* (see above).

No reliable record of *Kirstenella gordoni* has been published since the original description of the species, but new material of this tapeworm was collected by the present authors and their collaborators in Ethiopia, Kenya, Senegal and the Sudan (Fig. 61). Tapeworms from *H. bidorsalis* from Lake Debo, Nigeria, identified as Ptychobothriidae gen. sp. (MNHNP bd10), and those from the same host from the rivers Lampsar and Taoué in Senegal (RMCA 34695), identified by Khalil (1973) as *Polyonchobothrium clarias*, are conspecific with *K. gordoni*.

Heterobranchus currently comprises 4 species and represents a sister clade to African species of the genera *Clarias* and *Bathyclarias* Jackson (Pouyaud *et al.* 2009), but only *H. bidorsalis* is known as the definitive host of *K. gordoni*. In Turkana basin, the occurrence of *K. gordoni* most probably reflects distribution of its host, *H. bidorsalis*, which is restricted to the Omo River and freshwater part of the Turkana Lake, i.e. Omo River delta and adjacent northernmost part of the lake. Interestingly, *K. gordoni* has not been found in any of 547 members of the genus *Clarias* (abundant and sympatric with *H. bidorsalis*) examined in this study (Appendix 1), further supporting the presumed narrow host specificity. Mature tapeworms morphologically indistinguishable from *K. gordoni* were found in the the catfish *Schilbe mystus* (BMNH 1957.12.30.34–38), which might represent atypical host that became infected via predation.

Polyonchobothrium polypteri (Leydig, 1853) Lühe, 1900

(Figs. 23–27, 33–40)

Syns: *Tetrabothrium polypteri* Leyding, 1853; *Onchobothrium* (*Polyonchobothrium*) *septicolle* Diesing, 1854; *Anchistrocephalus polypteri* (Leyding, 1853) Monticelli, 1890; *Ptychobothrium armatum* Fuhrmann, 1902; *Ancistrocephalus polypteri* (Leyding, 1853) Hesse, 1922; *Polyonchobothrium pseudopolypteri* Meggitt, 1930; *Oncobothriocephalus armatum* (Fuhrmann, 1902) Yamaguti, 1959; *Polyoncobothrium polypteri* (Leyding, 1853) Yamaguti, 1959.

Type host: *Polypterus bichir* Lacépède (Polypteriformes: Polypteridae).

Other definitive hosts: *Polypterus endlicheri* Heckel; *Polypterus senegalus* Cuvier.

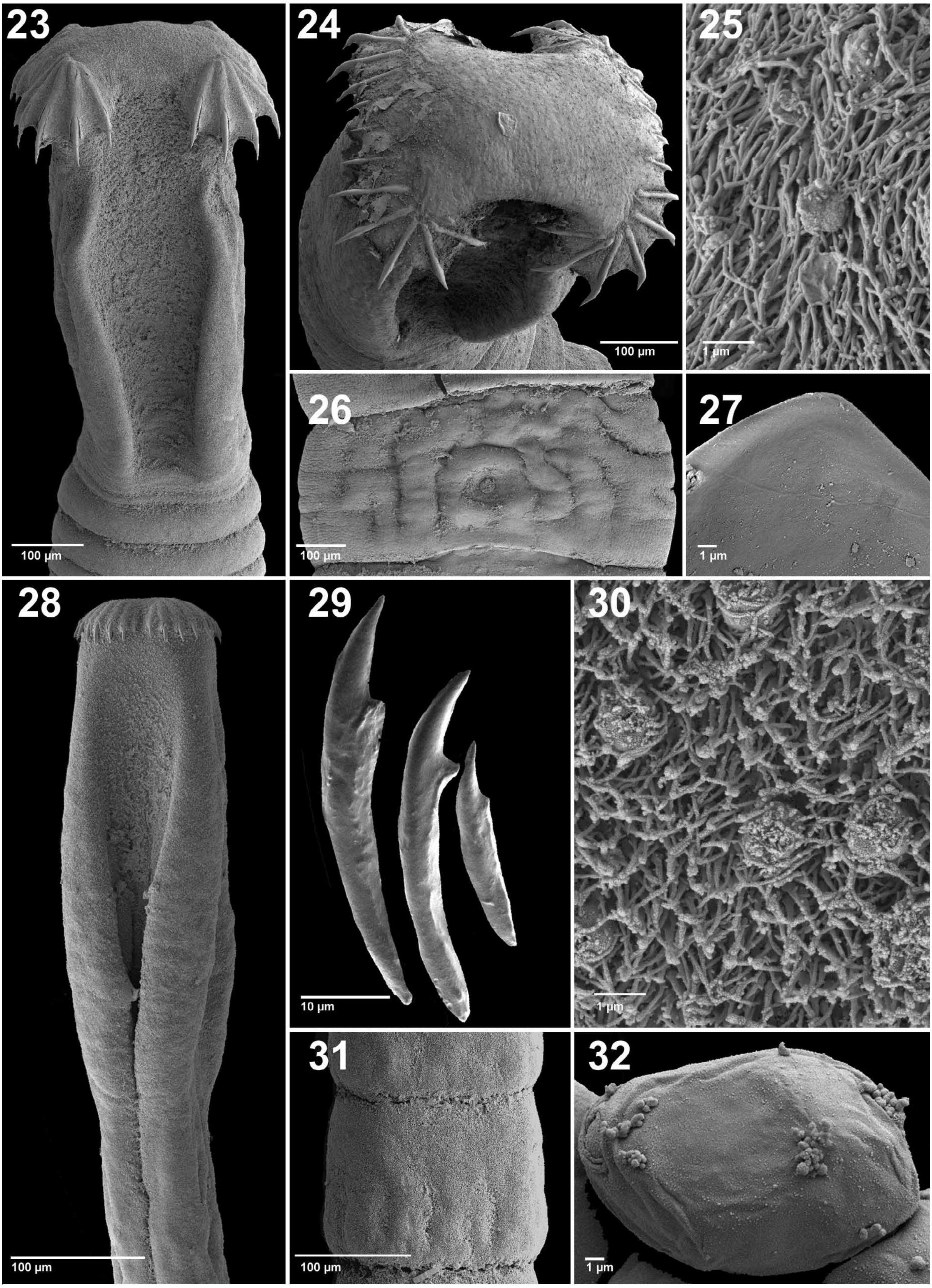
Type locality: Nile River in Egypt.

Distribution: Congo basin – Democratic Republic of the Congo (Brazzaville); Gambia basin – Senegal; Lake Chad – Chad; Turkana basin – Kenya, Lake Turkana (*Polypterus* spp. occur only sporadically in saline part of the lake and *P. polypteri* is therefore probably restricted to the freshwater part of the Turkana Lake, i.e. Omo River delta and upstream and adjacent northernmost part of the lake); Niger basin – Nigeria, Ivory Coast, Mali; Nile basin – Egypt, Ethiopia, the Sudan; Ogoué basin – Gabon; Zambezi basin – Malawi.

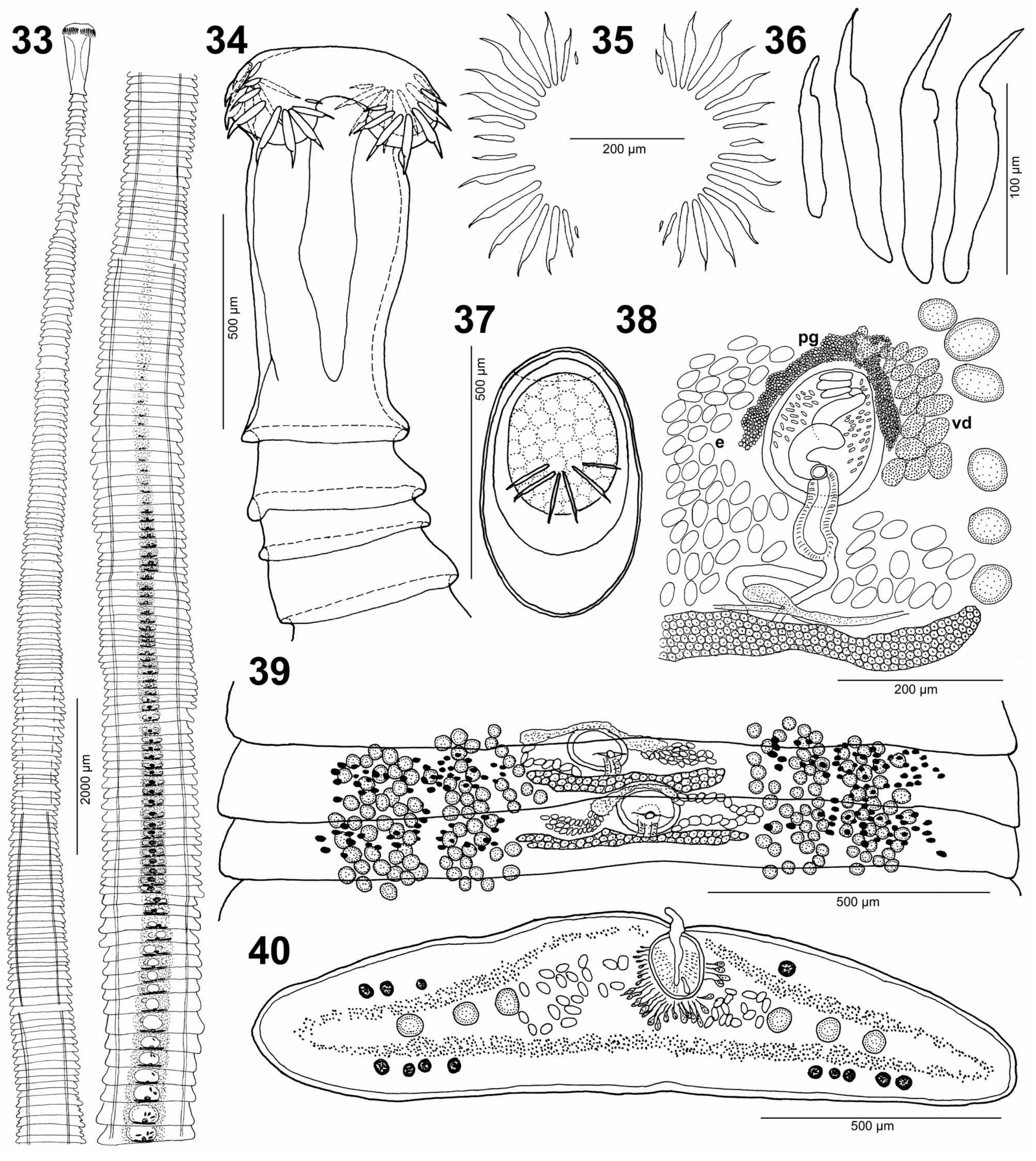
Prevalence: Nile basin – the Sudan, 8–25%, n = 21, intensity 15–50 (present study), 43%, n = 312, 10–70 (Khalil 1969); Turkana Lake – Kenya, 75%, 8, intensity up to 50 (present study); Niger basin – Nigeria, 94%, n = 84, intensity 1–226 (mostly juveniles) (Shotter & Medaiyedu 1978).

Life cycle: Not known, but plerocercoids of *P. polypteri* have been found in the following fish of different families, which may serve as second intermediate or paratenic hosts: *Auchenoglanis occidentalis* (Valenciennes) (Siluriformes: Claroteidae); *Barbus bynni* (Cypriniformes: Cyprinidae); *Lates niloticus* (Linnaeus) (Perciformes: Latidae); *Mormyrops anguilloides* (Linnaeus) (Mormyriformes: Mormyridae); *Schilbe uranoscopus* Rüppell (Siluriformes: Schilbeidae); *Sarotherodon galilaeus* (Linnaeus); *Stigmatochromis woodi* (Regan); and *Oreochromis niloticus* (Linnaeus) (Perciformes: Cichlidae) (see below).

Type material: Not known to exist. To enable future comparison of the species with other taxa, the specimen found in *P. bichir* (field No. T 169/08) from Lake Turkana – Omo River delta, Todonyang, Kenya is designated as neotype and it is deposited in IPCAS (No. C-464).



FIGURES 23–32. Scanning electron micrographs of the scoleces and the body surface. **23–27**, *Polyonchobothrium polypteri* (Leydig, 1853) ex *Polypterus bichir* from Kenya (IPCAS C-464). **23**, Scolex, dorsoventral view. **24**, Apical disc. **25**, Surface of apical region of scolex. **26**, Gravid proglottid, dorsal view. **27**, Detail of operculum of egg. **28–32**, *Tetracampos ciliotheca* Wedl, 1861 ex *Clarias anguillaris* from the Sudan (IPCAS C-466). **28**, Scolex, dorsoventral view. **29**, Detail of hooks. **30**, Surface of apical region of scolex. **31**, Gravid proglottid, dorsoventral view. **32**, Egg.



FIGURES 33–40. Line drawings of *Polyonchobothrium polypteri* (Leydig, 1853) ex *Polypterus* spp. from Kenya and the Sudan (IPCAS C-464). **33**, Complete worm. **34**, Scolex, dorsoventral view. **35**, Complete circle of hooks. **36**, Detail of hooks. **37**, Egg. **38**, Detail of genital complex of mature segment, dorsal view. **39**, Mature segment, dorsal view, neotype. **40**, Cross-section of the gravid segment at the level of cirrus-sac.
Abbreviations: e, eggs; pg, prostatic glands; vd, vas deferens.

Material studied: Type material: syntype of *Ptychobothrium armatum* Fuhrmann, 1902 (one slide and vial with 9 scolexes and several pieces of strobila) ex *Turdus parochus* from Egypt (ZBM E.2361); probably syntype of *Onchobothrium septicolle* Diesing, 1854 ex *P. bichir* from Egypt collected by Kollar in 1847 or 1852 (NMW 2612–3); vouchers: ex *P. endlicheri* from Brazzaville, Republic of the Congo (MHNG 41938–9; RMCA 30156); ex *P. endlicheri* from Mali (MNHNP C75); ex *P. senegalus* from Sierra Leone (BMNH 1965.2.24.46–53, 1977.6.28.3–4); ex *P. bichir* from Kainji Dam, Nigeria (BMNH 1970.8.24.38); ex "*Silurus* sp." from Bamba, Mali

(MHNG 45401); *Polyonchobothrium clarias* ex *Chrysichthys thonneri* Steindachner from Gabon (RMCA 33752); plerocercoids: *Polyonchobothrium* sp. ex *Auchenoglanis occidentalis* (Valenciennes) from unknown locality collected by McClelland (RVC C1106–7); ex *Barbus bynni* from unknown locality collected by McClelland (RVC C1105); ex *Mormyrops anguilloides* (Linnaeus) from unknown locality collected by McClelland (RVC C1103); ex *Schilbe uranoscopus* from unknown locality collected by McClelland (RVC C1109); new material (see Appendix 1 for details): around 100 worms collected from 7/8 (7 of 8 examined) *Polypterus bichir* from Kenya, Lake Turkana and the Sudan, Sennar Dam; 1/3 *P. endlicheri* from the Sudan, White Nile, Kostí; 1/13 *P. senegalus* from the Sudan. The new material is deposited in BMNH (Nos. 2012.3.120.1–13), IPCAS (No. C-464), MHNG (Nos. 62880, 82040–82047), USNPC (Nos. 105392–105394, 105401–105403) and ZMB (Nos. 7515–7516).

Published records: Leydig (1853); Klaptocz (1906); Hesse (1922); Janicki (1926); Joyeux & Baer (1928); Meggitt (1930); Ukoli (1965); Khalil (1969, 1973); Shotter & Medaiyedu (1978); Troncy (1978); Jones (1980).

Re-description (based on 20 complete worms from Ethiopia, Kenya and the Sudan): Bothriocephalidea, Bothriocephalidae. Strobila up to 10 cm long (up to 20 cm according to Khalil, 1969); maximum width 2.3 mm. External and internal segmentation present; segments wider than long, markedly craspedote (Fig. 33).

Two pairs of longitudinal osmoregulatory canals; dorsal canals narrow (diameter up to 16); ventral canals wide (diameter up to 20), connected by transverse anastomoses. Longitudinal musculature well developed, muscle fibres diffused (Fig. 40). Surface of strobila covered with capilliform filitriches.

Scolex elongate (Figs. 23, 34), 700–1,490 (1,065 ± 198) long by 260–430 (350 ± 44) wide (n = 19). Apical disc prominent, wider than scolex proper, usually four-lobed in apical view, 350–510 (410 ± 45) wide by 145–255 (200 ± 33) long (n = 17), armed with 27–35 (32 ± 2; n = 12) large hooks, 14–165 (106 ± 37; n = 314) long (Jones 1980 reported hooks up to 190 µm long), arranged usually in four quadrants (6–9 hooks in each quadrant). Hooks variable in size in each quadrant, smallest being on periphery and increasing to middle of quadrant, with largest hook 120–165 (152 ± 13; n = 10) in centre (Figs. 24, 35, 36). Bothria elongate, shallow, 580–1,020 (790 ± 37) long by 100–235 (163 ± 40) wide (n = 13) (Figs. 23, 34). Surface of scolex covered with capilliform filitriches and tumuliform globular structures (diameter around 1) (Fig. 25). Neck absent, first segments appear immediately posterior to scolex (Figs. 23, 33, 34).

Immature segments 80–247 long by 270–2130 wide; length/width ratio 0.06–1.04: 1 (n = 45) (Fig. 33). Mature segments wider than long, 125–300 (178 ± 56) long by 1,400–2,300 (1,830 ± 386) wide; length/width ratio 0.06–0.60: 1 (n = 12) (Fig. 39). Gravid segments wider than long, 170–810 (415 ± 240) long by 775–1,680 (1,155 ± 254) wide; length/width ratio 0.12–0.76: 1 (n = 13) (Fig. 33).

Testes medullary, oval, 30–65 (48 ± 9; n = 18) in number per segment (up to 72 according to Jones 1980), 37–81 (57 ± 14) long by 22–41 (34 ± 7) wide (n = 14), forming 2 narrow longitudinal bands (17–38 testes per band), confluent between segments, absent medially and near lateral margins (Fig. 39). Cirrus-sac large, thick-walled (thickness of sac wall 3–8), pyriform, oblique, with proximal part curved anterolaterally, 46–182 (111 ± 34) long by 51–179 (130 ± 30) wide (length/width ratio 0.70–1.06: 1) (n = 20), pre-equatorial to equatorial (at 30–51% of length of mature segment from its anterior margin; n = 10) (Figs. 38–40). Internal seminal vesicle absent. Vas deferens forms numerous loops lateral to cirrus-sac; internal sperm duct strongly coiled; cirrus unarmed, opening into genital atrium (Figs. 26, 38–40). Numerous prostatic glands around anterior part of cirrus-sac (Figs. 38–40). Genital pore dorsal, median, near anterior margin of segment, transversely elongate (Fig. 39).

Ovary slightly asymmetrical, compact, transversely elongate, 20–50 (40 ± 10) long by 100–550 (410 ± 150) wide (n = 10) (Fig. 39). Vagina a straight, thick-walled wide tube, 22–37 (28 ± 4; n = 15) in diameter, opens posterior to cirrus-sac into genital atrium; vaginal sphincter absent (Fig. 38). Vitelline follicles cortical, numerous, small, spherical, 19–41 (28 ± 5; n= 15) in diameter, form 2 wide longitudinal bands confluent between segments, separated medially to form ventral and dorsal bands (Fig. 39), rarely connected by several follicles in postovarian region.

Uterine duct winding, forms numerous tightly coiled loops, filled with eggs, enlarged in gravid segments (Fig. 33). Uterus thin-walled, median, spherical, enlarged in gravid segments, occupying 23–36% of segment surface (Fig. 33). Uterine pore thick-walled, opens anterior to midlength of uterus. Eggs oval, thin-walled, operculate, may be embryonated, 30–50 (40 ± 7) long by 20–45 (30 ± 6) wide (n = 20), fully formed oncosphere 22–37 (28 ± 4) long by 18–30 (23 ± 4) wide (n = 15) (Figs. 27, 37).

Remarks: *Polyonchobothrium polypteri* was described as *Tetrabothrium polypteri* based on worms found in *Polypterus bichir* from the Nile River in Egypt by Leydig (1853), who described only scolex morphology. Taxonomic history of the species, which was transferred to several genera, was reviewed by Jones (1980), who redescribed the taxon on the basis of tapeworms collected by L. F. Khalil in three species of bichirs (*P. bichir*, *P.*

endlicheri and *P. senegalus*) from the White Nile at Jebel-Awlia (south of Khartoum, the Sudan). This redescription was detailed, but it seems that tapeworms studied by Jones (1980) may have been relaxed too long in the water, because their segments were unnaturally long in relation to their width (see figs. 14 and 15 in Jones 1980). In our new material from *Polypterus* spp. from Kenya and the Sudan, which was observed alive, segments were invariably much wider than long and markedly craspedote.

Jones (1980) provided erroneous measurements of the eggs (396–444 µm by 264–288 µm), which was apparently caused by an incorrect position of the decimal point, and reported the eggs to be unoperculate when laid. However, we observed operculate eggs in the new material from the Sudan (Figs. 27, 37).

Kuchta *et al*. (2008a, b) considered *Polyonchobothrium* to be monotypic, with *P. polypteri* representing its type and only species, because species previously placed in *Polyonchobothrium* (see Kuchta & Scholz 2007 for list of synonyms) actually belong to other genera (*Kirstenella*, *Senga* and *Tetracampos*). *Polyonchobothrium* differs from other bothriocephalidean genera in scolex morphology, especially in the possession of a prominent apical disc, usually divided into four separate lobes, each of them armed with 6–9 massive hooks up to 190 µm long.

Polyonchobothrium polypteri is considered here to be a specific parasite of bichirs (Polypteridae), which represent an ancient lineage of ray-finned fish (Actinopterygii) endemic to Africa. Polypterids are phylogenetically distant from teleosts and other freshwater fish, such as paddlefish, sturgeons, gars and bowfins (Suzuki *et al*. 2010). Adult worms were found in other hosts, such as *Chrysichthys thanneri* (present study; RMCA 33752) or "*Silurus* sp." (present study, Joyeux & Baer 1928; MHNG 45401), but they may represent just atypical hosts.

Fuhrmann (1902) described *Ptychobothrium armatum* from a trush reported under the name *Turdus parochus* from Egypt. However, trush of this name has never been described, which casts doubts upon the actual host of these specimens. Examination of the type material (ZBM E.2361) has shown that *Polyonchobothrium polypteri* was misidentified. The most probable explanation of this unusual finding of a specific parasite of bichir in a passeriform bird is mislabelling of samples. Bichi & Yelwa (2010) reported *P. polypteri* in clariid catfish (*Clarias gariepinus*) in Nigeria. This finding may represent misidentification of *Tetracampos ciliotheca*, which is a typical parasite frequently infecting that host (see below).

Larvae (plerocercoids), juvenile or immature specimens of *P. polypteri* have been found by the present authors in the intestine of several unrelated fish, such as claroteid catfish, mormyrids, barbels, Nile perch and tilapias, which may serve as paratenic or postcyclic hosts (Appendix 1).

Seasonality in the occurrence and maturation of *P. polypteri* has been indicated by previous authors, because immature specimens were found in spring (March and April by Jones, 1980) in the Sudan and from July to September in Nigeria (Ukoli 1965), whereas fully mature specimens were present only in autumn (October) in the Sudan (Jones 1980). Even though immature worms dominated in all newly collected samples, material from Kenya and the Sudan was represented by mixture of immature, mature and gravid worms in March 2006 (the Sudan), September 2008 and 2009 (Kenya). In November 2008 (the Sudan) only immature worms were found.

Shotter & Medaiyedu (1977) reported the highest prevalence and intensity of infection *P. polypteri* in bichirs from Nigeria in fish of the total length of 300–350 mm. Based on a high proportion of immature worms to mature ones (3,879 versus 866 specimens, i.e. ratio 4.5: 1), these authors supposed that many juvenile worms did not reach maturity, possibly due to effective immune reaction of fish hosts.

***Tetracampos ciliotheca* Wedl, 1861**

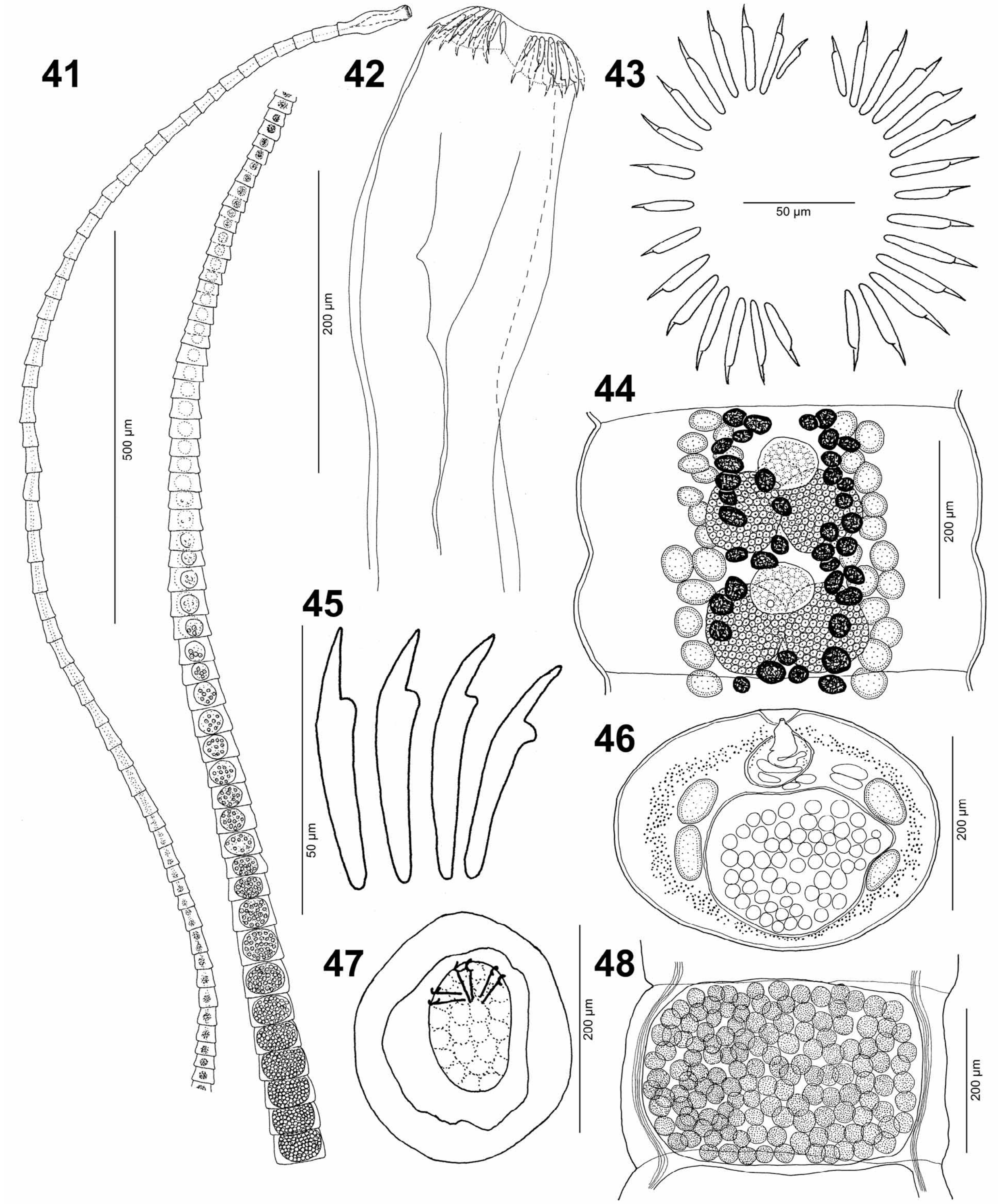
(Figs. 28–32, 41–52)

Syns: *Clestobothrium clarias* Woodland, 1925; *Polyonchobothrium cylindraceum* forma *major* Janicki, 1926; *P. cylindraceum* forma *minor* Janicki, 1926; *Polyonchobothrium fulgidum* Meggitt, 1930; *Polyonchobothrium clarias* (Woodland, 1925) Meggitt, 1930; *Polyonchobothrium ciliotheca* (Wedl, 1861) Dollfus, 1934; *Polyoncobothrium ciliotheca* (Wedl, 1861) Yamaguti, 1959; *Polyoncobothrium clarias* (Woodland, 1925) Yamaguti, 1959.

Type host: *Clarias anguillaris* (Linnaeus) (Siluriformes: Clariidae).

Other definitive hosts: *Clarias gariepinus* (Burchell), *Clarias liocephalus* Boulenger, *Clarias werneri* Boulenger.

Life cycle: Khalil & Thurston (1973) observed hatching of eggs in 10 minutes after their transfer to tap water. Liberated coracidia had embryophore 36–42 µm long by 30–35 µm wide, cilia 18 µm long and embryonic hooks 1 µm in length (Diab 2007). Freshwater copepods serve as the first intermediate hosts, in which procercoids developed within 20–26 days. Developed procercoids (252–610 µm long) were infective for small fish, such as tilapias (*Oreochromis niloticus*). Experimentally infected tilapias were exposed to *C. gariepinus*, in which adult worms were found (Diab 2007; Ramadan 2007). Small fish that harbour immature cestodes in natural conditions, such as schilbeid and mochokid catfish (*Schilbe uranoscopus*, *Synodontis membranacea* and *S. zambezensis*) and tilapias (*Oreochromis niloticus*, *Sarotherodon galilaeus*) (Douellou 1992; Owolabi 2008; Eissa *et al.* 2011a, b), may play a role of paratenic hosts.



FIGURES 41–48. Line drawings of *Tetracampos ciliotheca* Wedl, 1861 ex *Clarias anguillaris* from the Sudan (IPCAS C-466). **41**, Complete worm. **42**, Scolex, dorsoventral view. **43**, Complete circle of hooks. **44**, Gravid segment, ventral view. **45**, Detail of hooks. **46**, Cross-section of gravid segment at level of cirrus-sac. **47**, Egg. **48**, Gravid segment entirely filled with eggs.

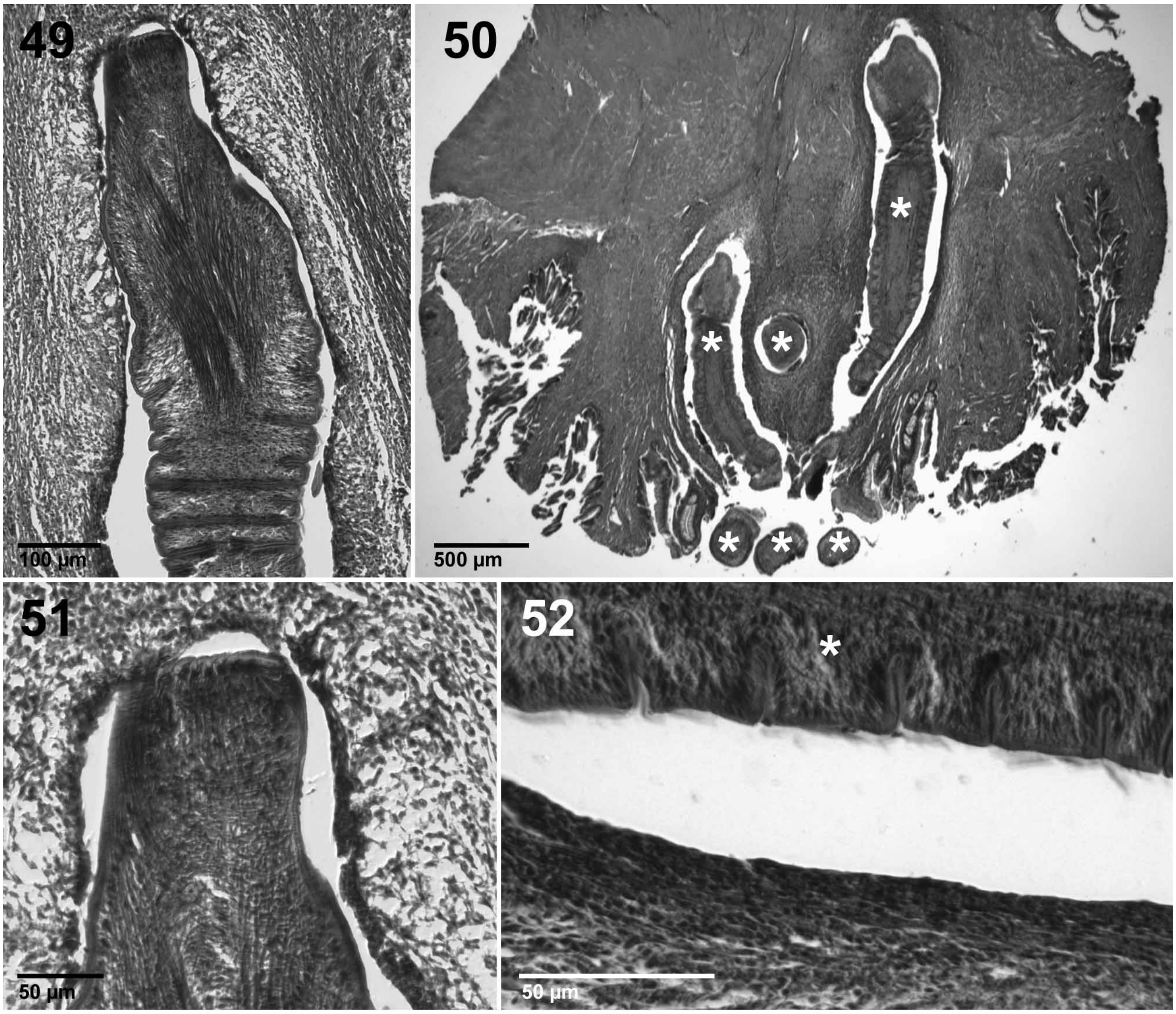
Type locality: Egypt, Nile River.

Distribution: Lower Guinea – Gabon; Gambia basin – Senegal; Turkana basin – Kenya (all parts of the Lake Turkana); Limpopo basin – South Africa; Upper Guinea – Sierra Leone (Moa River); Niger basin – Mali, Nigeria; Nile basin – Egypt, Ethiopia, the Sudan, Tanzania, Uganda; Volta basin – Ghana; Zambezi basin – Zimbabwe, Malawi. Besides Africa, *T. ciliotheca* has been reported also from Asia – Israel and Turkey, probably as a consequence of introduction with host – see Remarks (Paperna 1964; Soylu & Emre 2005; present study).

Prevalence and intensity of infection: Usually high, with values between 52% and 100% in most studies from Egypt, Nigeria and South Africa (Aderounmu & Adeniyi 1972; Shotter 1980; Faisal *et al*. 1989; Anosike *et al*. 1992; Barson & Avenant-Oldewage 2006). In the present study the overall prevalence was 5–17% in the Sudan, 26% in Ethiopia and 33% in Kenya (Appendix 1).

Type material: Not known to exist. To enable taxonomic comparative studies in the future, the specimen from *Clarias* sp. from Blue Nile, Sennar Dam, the Sudan (field No. Sud 438) is designated as neotype and is deposited in IPCAS (No. C-466).

Material studied: Type material: *Clestobothrium clarias* Woodland, 1925 ex *C. anguillaris* (BMNH 1965.2.24.29–35); *Polyonchobothrium fulgidum* Meggitt, 1930 ex *C. anguillaris* (BMNH 1932.5.31.801–806); *Polyonchobothrium interruptus – nomen nudum* (USNPC 74291–2); vouchers: *P. cylindraceum* ex *C. anguillaris*



FIGURES 49–52. Photomicrographs of histological sections of *Tetracampos ciliotheca* Wedl, 1861 in the intestinal wall of *Clarias gariepinus* from Ethiopia (IPCAS C-466). **49**, Cross-section of the intestinal wall at the level of the scolex. **50**, Cross-section of the intestinal wall with several parts of the worm. **51**, Detail of apical part of the scolex in the intestinal wall. **52**, Detail of the parasite and host surface. * indicates the body of the parasite.

from Mali, Diafarabe (MNHNP C79); *P. clarias* ex *C. anguillaris* from Senegal, Guerina (RMCA 34773) and Ghana (BMNH 1976.4.12.155–161); ex *C. gariepinus* from Nigeria, Lekki Lagoon and Kainji Dam (BMNH 2004.2.18.38, 1970.8.24.37); from Tanzania, Lake Victoria, Mwanza Gulf (MHNG 33983), Zimbabwe, Save-Runde River Floodplain (BMNH 2006.9.1.6) and Sierra Leone (BMNH 1965.2.24.59–6); ex *Heterobranchus bidorsalis* from Senegal, Guerina (RMCA 34723); ex *Schilbe uranoscopus* from unknown locality, collected by McClelland (RVC C1108); *T. ciliotheca* ex *Clarias* sp. from Egypt, Luxor, collected by A. de Chambrier (MHNG 31547; 17.iv.2001); ex *C. gariepinus* from South Africa, Rietvlei Dam, collected by M. Barson and from Turkey, Antalya (IPCAS C–466); new material: tens of *T. ciliotheca* ex 2/18 *C. anguillaris* from the Sudan, Kostí and Sennar Dam; 12 worms ex 3/23 *C. anguillaris* from Senegal, Niokolo-Koba National Park, Gambia River collected by B. Koubková (2004; Sen 52, 53, 121); 84/322 *C. gariepinus* from Ethiopia, Lake Tana and Great Rift Lakes (Awasa, Langano and Ziway), 14/43 *C. gariepinus* from Kenya, Lake Turkana and 5/30 *C. gariepinus* from the Sudan, Al Kawa, Khartoum, Er Roseires Dam, Sennar Dam; 4/88 *Clarias* sp. from the Sudan, Khartoum, Lake Nubia (Asuan Dam), Sennar Dam; one *C. gariepinus* from Lake Malawi, collected by S. Hendrix (SSH96-09-M-1). The new material is deposited in BMNH (Nos. 2012.3.20.16–25), IPCAS (No. C-466), MHNG (Nos. 55309, 55337, 55338, 62879, 62904, 63006–63328), USNPC (Nos. 105395–105400, 105404–105408) and ZMB (Nos. 7517–7523).

Published records: Wedl (1861); Woodland (1925); Janicki (1926); Meggitt (1930); Tadros (1968); Khalil (1969, 1973); Aderounmu & Adeniyi (1972); Khalil & Thurston (1973); Amin (1978); Tadros *et al*. (1979); Shotter (1980); Wabuke-Bunoti (1980); Onwuliri & Mgbemena (1987); Faisal *et al*. (1989); Mashego & Saayman (1989); Imam & El-Askalany (1990); Imam *et al*. (1991a, b); Anosike *et al*. (1992); Douellou (1992); Al-Bassel (2003); El-Garhy (2003); Rizkalla *et al*. (2003); Hamanda & Abdrabouh (2004); Oniye *et al*. (2004); Akinsanya & Otubanjo (2006); Barson & Avenant-Oldewage (2006); Olofintoye (2006); Diab (2007); Ayanda (2008, 2009a, b); Barson *et al*. (2008); Mwita & Nkwengulila (2008); Moyo *et al*. (2009); Bichi & Yelwa (2010); Madanire-Moyo & Barson (2010); Madanire-Moyo *et al*. (2010); Eissa *et al*. (2011a, b).

Re-description (based on 25 complete worms from Ethiopia, Kenya and the Sudan): Bothriocephalidea, Bothriocephalidae. Strobila small, oval or almost spherical in cross section, up to 30 mm long; maximum width 475. External and internal segmentation present; segments wider than long, acraspedote (Figs. 31, 41, 44).

Two pairs of osmoregulatory canals; dorsal canals narrow; ventral canals wide, connected by transverse anastomoses. Inner longitudinal musculature well developed, muscle fibres diffused (Fig. 46). Surface of strobila covered with capilliform filitriches.

Scolex elongate to ovoid, 285–510 (396 ± 62) long by 115–245 (165 ± 42) wide (n = 20) (Figs. 28, 42). Apical disc weakly developed, 104–290 (156 ± 63) wide and 35–120 (97 ± 24) high (n = 20), armed with 25–35 (29 ± 2; n = 18) small hooks (Amin 1978 reported as many as 41 hooks) 12–51 (37 ± 7; n = 537) long, arranged in two lateral semicircles separated from each other on dorsal and ventral side. Hooks variable in size in each semicircle, with largest hook 40–51 (46 ± 3; n = 20) in each corner of apical dic (Figs. 29, 43, 45). Bothria elongate, shallow, 200–410 (308 ± 56) long by 57–120 (79 ± 22) wide (n = 20) (Figs. 28, 42). Surface of scolex covered with capilliform filitriches and numerous tumuliform globular structures (diameter around 1) (Fig. 30). Neck absent, first segments appearing immediately posterior to scolex (Fig. 41).

Immature segments 80–235 (144 ± 39) long by 84–261 (167 ± 57) wide; length/width ratio 0.41–2.58: 1 (n = 38) (Fig. 41). Mature segments wider than long by, 90–400 (182 ± 68) long by 135–480 (255 ± 96) wide; length/width ratio 0.3–1.0: 1 (n = 41) (Fig. 41). Gravid segments wider than long, 178–488 (198 ± 69) long by 180–455 (316 ± 71) wide; length/width ratio 0.5–1.2: 1 (n = 35) (Figs. 31, 41, 44, 48).

Testes medullary, spherical, 5–15 (10 ± 3; n = 21) in number per segment, 21–48 (33 ± 7; n = 60) in diameter, forming 2 narrow longitudinal bands (4–9 testes per band), confluent between segments, absent medially and near lateral margins (Fig. 44). Cirrus-sac large, thin-walled (thickness of sac wall up to 4), oval, 32–66 (48 ± 9) long by 28–68 (45 ± 10) wide (length/width ratio 0.77–1.73: 1) (n = 15), equatorial (39–59% of length of mature segment; n = 10) (Fig. 46). Internal seminal vesicle absent; cirrus unarmed, opening into genital atrium. Vas deferens forms numerous loops lateral to cirrus-sac; internal sperm ducts strongly coiled. Genital pore dorsal, median, pre-equatorial.

Ovary symmetrical, forming two spherical lobes, 31–91 (59 ± 18) long by 76–183 (113 ± 29) wide (n = 14) (Fig. 44). Vagina a straight, thin-walled tube, 6–16 (11 ± 4; n = 9) in diameter, opens posterior to cirrus-sac into genital atrium; vaginal sphincter absent. Vitelline follicles few, small, spherical, 12–40 (19 ± 8; n = 28) in diameter, medullary, distributed among testes, visible only in some mature and gravid proglottides (Fig. 44).

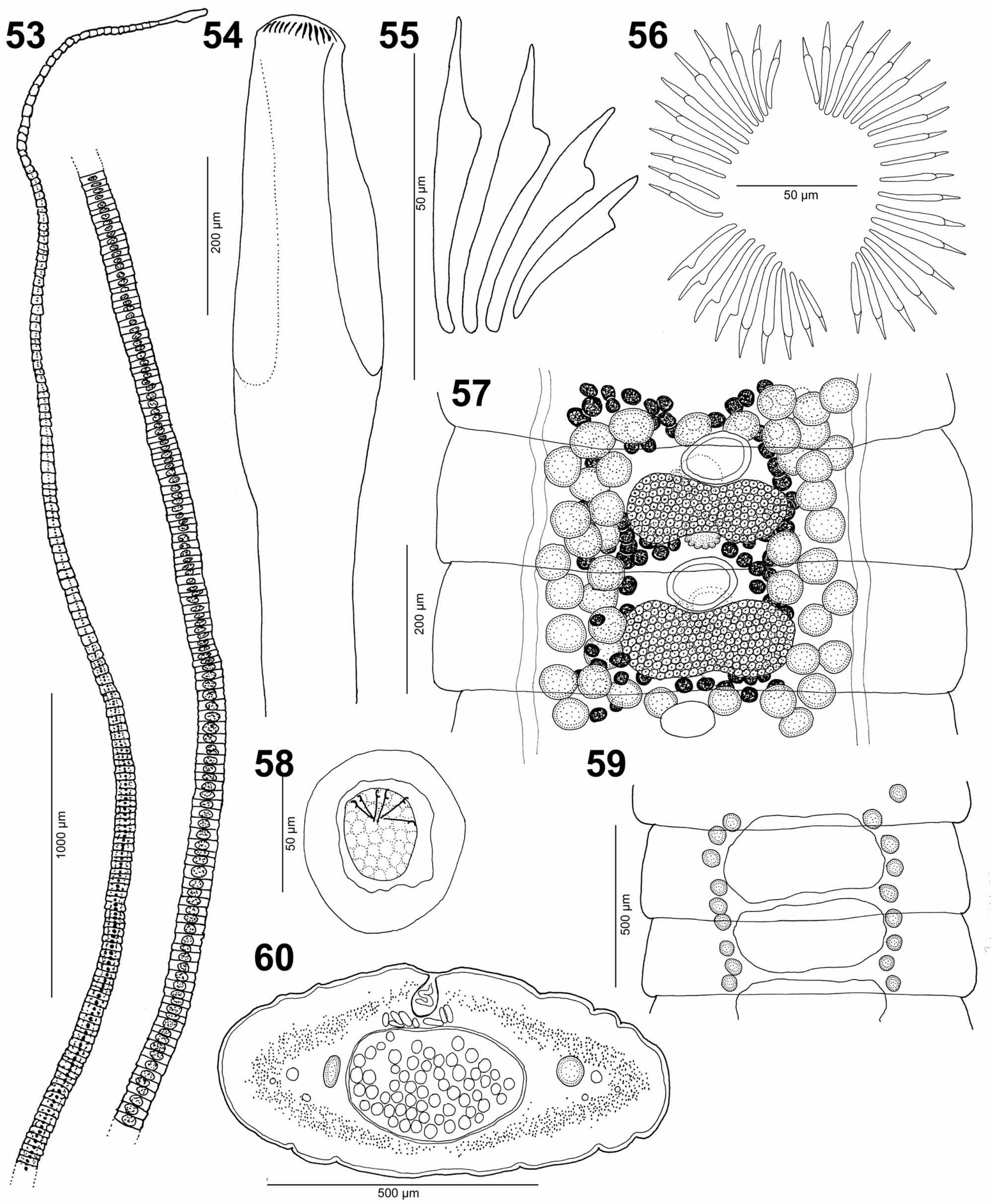
Uterine duct winding, short, filled with eggs (Fig. 41). Uterus thin-walled, median, spherical, enlarged in gravid segments, occupying 57–80% of segment surface (Figs. 41, 48). Uterine pore thick-walled, opens in centre of uterus. Eggs widely oval to spherical, 28–72 (46 ± 9) long by 27–51 (40 ± 6) wide (n = 46), with external hyaline membrane and internal granular layer surrounding fully formed oncospheres, 17–45 (27 ± 8) long by 17–31 (23 ± 4) wide (n = 41) in terminal segments; eggs enlarging during their development in uterus (Figs. 32, 47).

Remarks: Taxonomic history of bothriocephalideans parasitic in clariid catfish in Africa is complicated because apparently conspecific tapeworms were reported under different species names and were placed in several genera. Most commonly, they were identified as *Polyonchobothrium clarias* (Woodland, 1925), but this species is a junior synonym of *Tetracampos ciliotheca* (see Kuchta *et al*. 2008b). Wedl (1861) described *T. ciliotheca* from cestodes parasitic in *Heterobranchus anguillaris* (= *Clarias anguillaris*) from Egypt. Since the original description was incomplete, most subsequent authors considered *T. ciliotheca* as a *nomen nudum* or placed it in the order Proteocephalidea or even Tetraphyllidea, because its eggs possess a transparent, hyaline external envelope (Southwell 1925; Janicki 1926). Kuchta *et al*. (2008a, b) resurrected the genus with *T. ciliotheca* as its type and only species because it differs from other bothriocephalideans in egg morphology, the possession of an unflattened strobila, almost round in cross section, and medullary position of vitelline follicles. The latter characteristic is also present in two other bothriocephalidean cestodes, *Ptychobothrium* Lönnberg, 1889 and *Taphrobothrium* Lühe, 1899, but they parasitize marine teleosts and their morphology is otherwise markedly different (see Kuchta *et al*. 2008b).

Tetracampos ciliotheca is a common parasite of clariid catfish and it is widely distributed throughout Africa, with most published reports from Egypt, Nigeria, South Africa and the Sudan (see above). The cestode has also been reported from Israel (Paperna 1964 – as *P. clarias*) and Turkey [Soylu & Emre 2005 – as *Polyonchobothrium magnum* (Zmeev, 1936); present study], apparently as a consequence of import of African species of *Clarias* to these countries. Records of *T. ciliotheca* in other catfish, such as *Heterobranchus bidorsalis* from Senegal (present study; Khalil 1973; RMCA 34723), *Bagrus bayad* from Egypt (Imam *et al*. 1991a) and *Chrysichthys auratus* from the Sudan (present study), may represent incidental infections or these fish may serve as postcyclic or accidental hosts.

Omar M. Amin deposited tapeworms found in *C. anguillaris* from Egypt under the name *Polyonchobothrium interruptus* (USNPC 74291–2), but that species has never been formally described and thus represents *nomen nudum*. In 1978 Amin himself identified these tapeworms as *Polyonchobothrium clarias* (= *T. ciliotheca*).

Host-parasite relationships of *T. ciliotheca* and its fish host have been studied by several authors (most of them referred to this species as *Polyonchobothrium clarias* – see above). The tapeworms penetrates deeply into the mucosa of the intestinal wall and may cause mechanical injury by the attachment of the apical crown of hooks on the scolex (Tadros 1979; Akinsanya & Otubanjo 2006; present study Figs. 49–52). Adults of *T. ciliotheca* were also found in the gall bladder (Amin 1978; Shotter 1980; Faisal *et al*. 1989; Barson *et al*. 2008), where tapeworms may cause formation of nodular outgrowths in the mucosa (Wabuke-Bunoti 1980). Faisal *et al*. (1989) reported complete penetration of *T. ciliotheca* tapeworms through the intestinal wall, with their attachment in the liver, spleen and ovary. In fish with perforated intestine, the intestinal contents filled the peritoneal cavity (Wabuke-Bunoti 1980). Despite the high number of examined hosts and observed cestodes, we never found *T. ciliotheca* tapeworms in extraintestinal localization.



FIGURES 53–60. Line drawings of *Tetracampos martinae* Kuchta, n. sp. ex *Bagrus meridionalis* from Lake Malawi (IPCAS C-608). **53**, Total view of the worm with anterior and posterior part of the body. **54**, Scolex, lateral view. **55**, Detail of hooks. **56**, Complete circle of hooks. **57**, Gravid segment, ventral view, eggs not illustrated. **58**, Egg. **59**, Gravid segment, eggs not illustrated. **60**, Cross-section of the gravid segment in the level of cirrus-sac.

Tetracampos martinae Kuchta n. sp.

(Figs 53–60)

Type host: *Bagrus meridionalis* (Linnaeus) (Siluriformes: Bagridae).

Type locality: Deep waters of the southeast arm of Lake Malawi, Malawi (14°06′S, 35°03′E).

Distribution: Zambezi basin – Lake Malawi.

Type material: Holotype and paratype (IPCAS C-608) (field No. SSH96-09-K-1).

Material studied: Two type specimens (IPCAS C-608).

Etymology: The new species is named in honour of Martina Borovková, Institute of Parasitology, Academy of Sciences of the Czech Republic, for her extraordinary technical support.

Description (based on 2 specimens, 1 without scolex): Bothriocephalidea, Bothriocephalidae. Strobila up to 19 cm long, oval in cross section; maximum width 1 mm. External and internal segmentation present; segments wider than long, slightly craspedote (Fig. 53).

Two pairs of longitudinal osmoregulatory canals; dorsal canals narrow (diameter up to 10); ventral canals wide (diameter up to 25), connected by transverse anastomoses. Inner longitudinal musculature well developed, muscle fibres diffused (Fig. 60).

Scolex elongate, with maximum width near posterior margin of scolex (Fig. 54), 620 long by 160 wide. Apical disc weakly developed, 100 wide and 28 high, armed with 39 small hooks 44–100 (75 ± 5; n = 15) long, arranged in two lateral semicircles separated from each other on dorsal and ventral side (Fig 56). Hooks variable in size in each semicircle, with largest hook in each corner of apical disc (Figs 55, 56). Bothria elongate, shallow, 409 long by 80 wide. Neck present (Fig. 53).

Immature segments 78–135 long by 191–560 wide (n = 10) (Fig. 53). Mature segments wider than long, 103–211 long by 690–724 wide; segment length/width ratio 0.15–0.29: 1 (n = 10). Gravid segments wider than long, 220–380 long by 1015–1059 wide; segment length/width ratio 0.21–0.37: 1 (n = 10) (Figs 53, 57, 59).

Testes medullary, oval, 15–19 (n = 10) in number per segment, 36–72 (51 ± 10; 10) in diameter, forming 2 narrow longitudinal bands (7–10 testes per band), confluent between segments, absent medially and near lateral margins (Fig. 57). Cirrus-sac small, thin-walled (thickness of sac wall up to 6), pyriform, 46–59 long by 59–75 wide (length/width ratio 0.61–0.93: 1) (n = 10), pre-equatorial (at 13–44% of length of mature segment from anterior margin; n = 10) (Figs. 57, 60). Internal seminal vesicle absent; cirrus unarmed (Fig. 60). Vas deferens forms numerous loops posterolateral to cirrus-sac; internal sperm ducts strongly coiled. Genital pore dorsal, median, near anterior margin of segment, transversely elongate (Fig. 60).

Ovary symmetrical, circular biscuit-shaped, lobulate, 84–107 long by 199–242 wide (n = 10) (Fig. 57). Vagina a straight, thin-walled tube, 5–11 in diameter, opens posterior to cirrus-sac into genital atrium; vaginal sphincter absent. Vitelline follicles numerous, small, spherical, 24–40 in diameter (n = 25), medullary, form 2 wide longitudinal bands confluent between segments, separated medially, rarely connected by several follicles in postovarian region (Fig. 57).

Uterine duct winding, short, filled with eggs. Uterus thin-walled, median, spherical, enlarged in gravid segments, up to 277 long and 450 wide (Fig. 59). Uterine pore thick-walled, opens in centre of uterus. Eggs oval to spherical, 40–64 long by 41–53 wide (n = 10), with external hyaline membrane and internal granular layer surrounding fully formed oncospheres 28–45 long by 30–36 wide (n = 10) in terminal segments; eggs enlarging during their development in uterus (Figs 53, 58).

Remarks: Tapeworms from *Bagrus meridionalis* from Lake Malawi are placed in *Tetracampos* based on the medullary position of vitelline follicles and morphology of eggs, which are unique characters of the genus, missing in all other bothriocephalideans possessing the scolex armed with hooks on the apical disc, i.e. species of *Kirstenella*, *Oncodiscus* Yamaguti, 1934, *Polyonchobothrium* and *Senga* (see Kuchta *et al*. 2008b). The new species differs from congeneric *T. ciliotheca* in the following characteristics: (i) much longer and dorsoventrally flattened strobila (19 cm vs. oval, much smaller strobila less than 3 cm); (ii) larger hooks (up to 100 µm long vs. shorter than 52 µm); and (iii) mature and gravid segments much wider than long vs. almost quadrate in *T. ciliotheca*. The definitive host of *T. martinae* is *Bagrus meridionalis*, which is endemic to Lake Malawi, whereas *T. ciliotheca* is specific to *Clarias* spp. *Tetracampos martinae* is the second species of *Tetracampos*, the diagnosis of which is emended below to reflect morphological differences between both species of the genus.

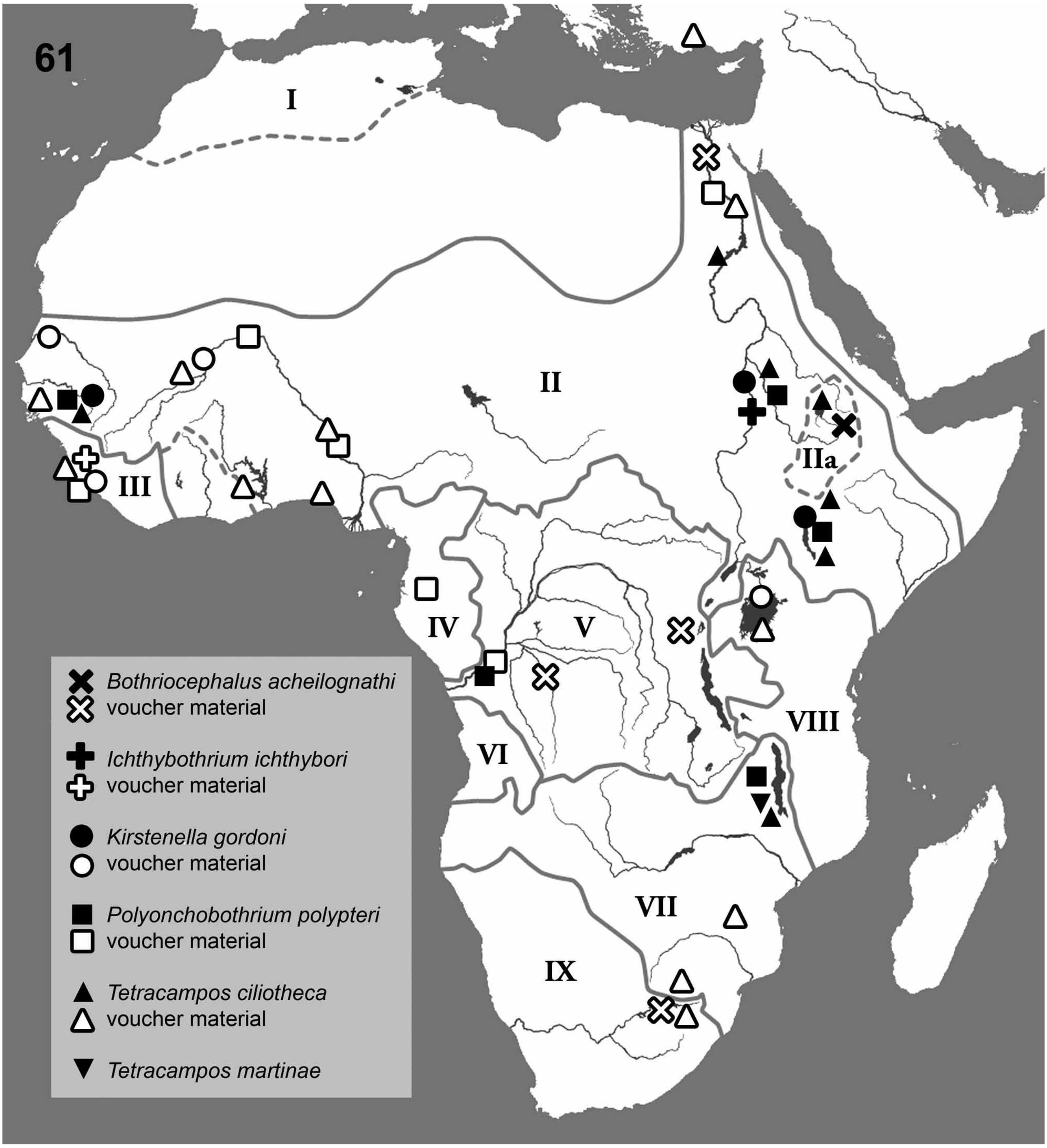


FIGURE 61. Distribution map of African bothriocephalideans according to existing voucher material (unconfirmed literature records not included). Ichthyological provinces are marked as follows: I. Maghreb, II. Nilo Sudan, IIa. Abyssinian subprovince, III. Upper Guinea, IV. Lower Guinea, V. Congo, VI. Quanza, VII. Zambezi, VIII. East Coast, IX. Southern province (map orig. M. Jirků; delimitation of ichthyological provinces modified from Lévêque *et al*. 2008).

Tetracampos Wedl, 1861

Amended diagnosis: Bothriocephalidea, Bothriocephalidae. Small worms. Segmentation present. Strobila with acraspedote or slightly craspedote segments. Inner longitudinal musculature formed by numerous diffused muscle fibres. Scolex elongate to ovoid, with maximum width near middle part or slightly posteriorly. Bothria shallow, elongate. Apical disc weakly developed, armed with small hooks. Testes not numerous, large, in two lateral fields, continuous between segments. Cirrus-sac spherical; cirrus unarmed. Genital pore dorsal, median. Ovary bilobed, circular biscuit-shaped, with very wide lateral lobes. Vagina posterior to cirrus-sac. Vitelline follicles not numerous, difficult to observe, medullary, externally protruding among innermost fibres of internal longitudinal musculature, in two lateral fields on dorsal and ventral side, may absent in immature and most gravid segments. Uterine duct short. Uterus thin-walled, compact, markedly enlarging in gravid segments to occupy almost all space of terminal segments. Uterine pore slightly submedian. Eggs oval to spherical, with external hyaline membrane and internal granular layer surrounding fully formed oncospheres in terminal segments; eggs enlarging during their development in uterus, with fully formed oncosphere armed with three pairs of embryonic hooks. In freshwater catfishes (*Clarias*, *Bagrus*). Endemic to Africa, introduced to Asia.

Type species: *T. ciliotheca* Wedl, 1861.

Additional species: *T. martinae* Kuchta, n. sp.

Additional species

Bothriocephalus claviceps (Goeze, 1782) Rudolphi, 1810

Type locality: Unknown (? Germany).

Distribution in Africa: Nile basin – Egypt.

Type material: Not known to exist.

Material studied: *Bothriocephalus claviceps* ex *Anguilla* sp. from Egypt (BMNH 1932.5.31.780–780).

References: Meggitt (1930); Tadros (1967).

Remarks: Meggitt (1930) identified immature fragments of tapeworms from unidentified eels [most probably *Anguilla anguilla* (Linnaeus), the only eel occurring in the region], allegedly found by A. Looss in Egypt, as *B. claviceps*. Examination of the vouchers confirmed this identification. *Bothriocephalus claviceps* is a specific parasite of eels in the Holarctic Region (Scholz *et al.* 2004) and its occurrence in Africa represents the southernmost range of its distribution area, apparently related to occasional migration of eels to the rivers in North Africa including the lower Nile. Based on the distribution of *A. anguilla*, it is possible that future studies will reveal the presence of *B. claviceps* also in Maghreb ichthyofaunistic province, which has Palaearctic affinities and includes Morocco, northern Algeria and Tunisia[1]. Since the distribution of this Holarctic tapeworm in Africa is restricted to lower Nile and possibly Maghreb province, it is not included into the key below.

Phylogenetic relationships

Phylogenetic analysis of five African species encompassing all five genera of bothriocephalidean cestodes reported from freshwater fish in Africa provided strong support of their monophyly (Fig. 62). A sister group of the African clade forms *Senga* sp. from Cambodia, Asia, whereas *Bothriocephalus claviceps,* which has Holarctic distribution and has been reported from Egypt (see above), is a sister taxon to this clade (*Senga* and African taxa).

This analysis, inferred from partial sequences of the lsrDNA (region D1–D3) has also shown close relationships of species devoid of hooks on the apical disc (*Bothriocephalus acheilognathi* and *Ichthybothrium ichthybori*), even though their definitive hosts are phylogenetically distant. Similarly, species of three genera possessing hooks on the apical disc, i.e. *Kirstenella*, *Polyonchobothrium* and *Tetracampos*, which parasitize unrelated fish hosts, form a well supported clade, with *T. ciliotheca* representing a sister taxon to the remaining two species.

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[1] One specimen of *Bothriocephalus claviceps* has been recently (24 April 2012) found in eel (*Anguilla anguilla*) from northwestern Algeria (Orna 35°41'49"N, 0°37'59"W) by one of the authors (T. S.).

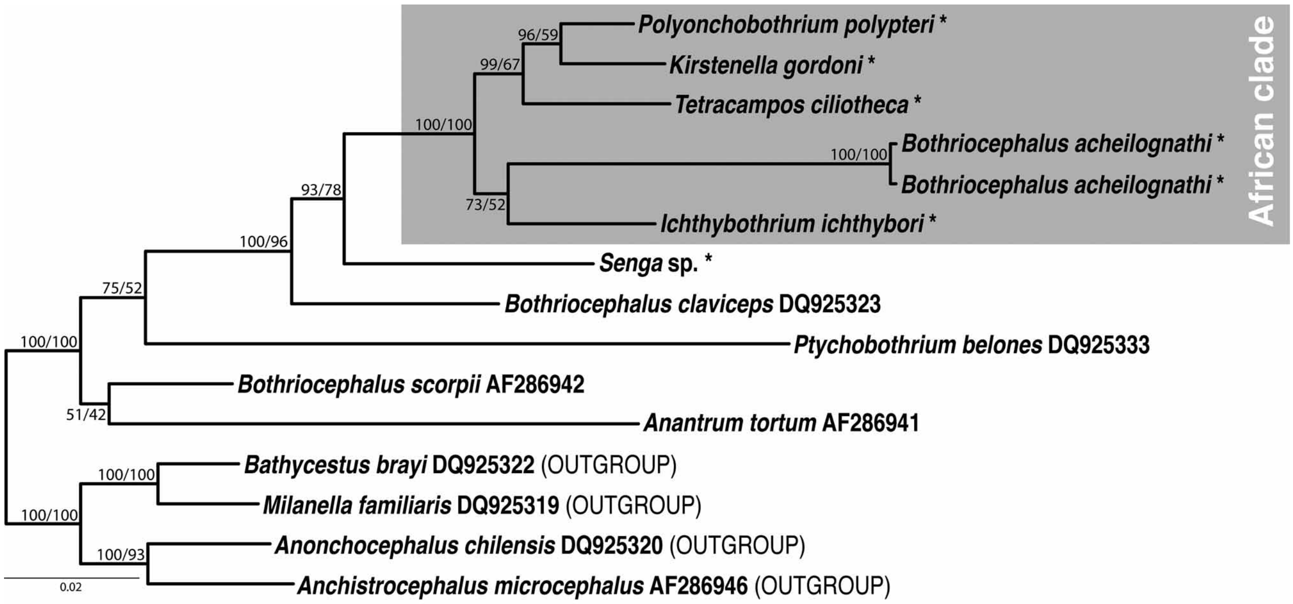

FIGURE 62. Interrelationships of 6 African bothriocephalideans and their relatives based on Bayesian inferrence analysis of partial sequences of the large subunit rDNA (lsrDNA). Rooted phylogram with node labels showing Bayesian posterior probabilities/bootstrap support values. Newly characterized sequences are marked with an asterisk.

Remarkably, the representative of *Senga*, another genus possessing an apical disc armed with spines similar in their number, size and shape to those in *Kirstenella* and *Tetracampos*, and with a very similar strobilar morphology to that of species of the three African genera listed above, is not closely related. This indicates that hooks on the apical disc of species of *Senga* and three African genera may not be homologous.

Key to the freshwater bothriocephalideans from Africa

In order to facilitate identification of bothriocephalidean cestodes found in the freshwater fish in Africa, a simple key based on gross morphology is provided.

1 Apical part of scolex unarmed (without hooks) 2
\- Apical part of scolex armed (with hooks) 3
2 Scolex heart-shaped, with deep, narrow bothria; external segmentation present . . . . *Bothriocephalus acheilognathi*
\- Scolex elongate to lanceolate, with shallow and wide bothria; external segmentation absent . . . . *Ichthybothrium ichthybori*
3 Scolex large (> 700 μm); vitelline follicles cortical, numerous; testes numerous (> 30, usually more than 100); eggs with hard shell (capsule) 4
\- Scolex small (< 650 μm); vitelline follicles medullary; testes few (5–20); eggs with transparent, hyaline outer envelope 5
4 Apical disc prominent, wider than scolex, armed with < 36 large, massive hooks, up to 190 μm long; cirrus-sac small (ratio of cirrus-sac width to width of segment 5–10%). . . . . *Polyonchobothrium polypteri*
\- Apical disc weakly developed, as wide as scolex or narrower, armed with > 40 hooks shorter than 90 μm; cirrus-sac large (ratio of cirrus-sac width to width of segment 16–39%) . . . . *Kirstenella gordoni*
5 Small worms (< 30 mm in total length), with almost cylindrical strobila (widely oval to spherical in cross section); < than 35 small hooks (< 51 μm) on apical disc . . . . *Tetracampos ciliotheca*
\- Large worms (total length up to 190 mm), with dorsoventrally flattened strobila; > than 36 hooks on apical disc, hooks large, up to 100 μm long . . . . *Tetracampos martinae*

Discussion

Tapeworms of the order Bothriocephalidea are common parasites of freshwater fish with cosmopolitan distribution (Kuchta *et al*. 2008b). Only species of the family Bothriocephalidae Blanchard, 1849 parasitize African freshwater fish. In Africa, adults of bothriocephalidean cestodes have been reported from 30 fish species representing 10 families of 4 orders (Characiformes, Cypriniformes, Polypteriformes and Siluriformes) (Appendix 1 and the Results section). Total number of bothriocephalidean species, i.e. 7 species in 5 genera, is low, especially when compared with the Holarctic Region, i.e. 21 species in 6 genera (Protasova 1977; Hoffman 1999; Kuchta & Scholz 2007). Six species in four genera are endemic to Africa, with three genera being monotypic (only the genus *Tetracampos* includes two species). The number of fish genera, the species of which serve as definitive hosts of bothriocephalideans in Africa, is also low, but each species seems to be restricted to a particular (definitive) host genus as follows: *Anguilla* (definitive host of *Bothriocephalus claviceps*), *Bagrus* (*Tetracampos martinae*), *Barbus*, *Cyprinus* and *Labeobarbus* (*Bothriocephalus acheilognathi*), *Clarias* (*Tetracampos ciliotheca*), *Heterobranchus* (*Kirstenella gordoni*), *Ichthyborus* (*Ichthybothrium ichthybori*), and *Polypterus* (*Polyonchobothrium polypteri*). Fish of the genera *Chrysichthys*, *Hydrocynus*, *Schilbe*, *Synodontis*, and *Tilapia* seem to represent postcyclic, paratenic or accidental hosts of bothriocephalidean cestodes (see the Results section). Immature tapeworms or their larvae (plerocercoids) have been found in fish of 7 families (Claroteidae, Cichlidae, Cyprinidae, Latidae, Mochokidae, Mormyridae and Schilbeidae) (Appendix 1 and the Results section). It remains unclear whether these fish serve as second intermediate or paratenic hosts of bothriocephalidean tapeworms.

The geographical distribution of African bothriocephalideans (Fig. 61) exhibits an interesting pattern because most species are widely distributed across much of Sub-Saharan Africa, which corresponds with wide distributional areas of their specific definitive hosts, i.e. bichirs and clariid catfish in particular. In North Africa, one bothriocephalidean species common in Europe, i.e. *B. claviceps*, has been found, but it seems to be a rare parasite limited in its distribution to Egypt. According to distribution of its definitive host *A. anguilla*, it is possible that future studies will reveal its presence also in northwestern Africa, i.e. Maghreb ichthyological province, which includes Morocco, northern Algeria and Tunisia (Maghreb province is not considered in following discussion due to its Palaearctic affinities (s ee Footnote on page 24).

In general, the distribution ranges of African bothriocephalideans overlap with those of the host taxa. Therefore, absence of widely distributed species from some areas is most probably a result of inadequate sampling, rather than their real absence. For example, the absence of the most widely distributed species, *T. ciliotheca*, in the Congo basin harboring several *Clarias* spp. is unlikely, since it is known to be common (locally with prevalence up to 100%) in four *Clarias* spp. from West, East and South Africa. This assumption is, though indirectly, further supported by the isolated record of *P. polypteri* from the Congo basin (Brazzaville) and Lower Guinea (Gabon), which are located over 1,300 km from the nearest known localities in East and West Africa (Fig. 61).

Somewhat restricted ranges, but also correlating with those of hosts, are apparent in *I. ichthyobori* and *K. gordoni* known only from the Nilo-Sudan and Upper Guinea ichthyological provinces. In addition, *T. martinae* is described herein from *Bagrus meridionalis*, a catfish endemic to Lake Malawi. Further investigations are needed to assess whether this tapeworm is endemic to the lake/host or whether it occurs elsewhere downstream in the Congo basin (which would imply a wider host spectrum).

The most widely distributed species is *T. ciliotheca*, which has been found in East Coast, Nilo-Sudan, Southern, Upper Guinea and Zambezi ichthyological provinces (Fig. 61). It is also the most common bothriocephalidean parasite in Africa, with prevalence reaching up to 100% and intensity of infection up to several tens of specimens. However, its distribution has been expanded to western Asia as a result of exports of *Clarias* catfish, especially *C. gariepinus*, as indicated by records from Israel and Turkey (Paperna 1964; Soylu & Emre 2005; present study). *Polyonchobothrium polypteri*, a specific parasite of bichirs, has been reported from all but two ichthyological provinces. Its absence in South Africa probably corresponds with the absence of bichirs in that region (Froese & Pauly 2011). On the other hand, its absence in the East Coast province is rather a result of undersampling. *Kirstenella gordoni* (confirmed in 3 ichthyological provinces), and *Ichthybothrium ichthybori* (2 ichthyological provinces) possibly also occurs further southwards as implied by the distribution of their respective host genera. *Bothriocephalus acheilognathi*, which has been originally described from East Asia (Yamaguti 1934), was reported from 3 provinces covering huge area from the very North (Egypt) down to Southern Africa (doubtful records from *Clarias* spp. from the Niger and Zambezi river basins are not considered). In conclusion, sampling effort in individual parts of Africa has not been comparable and future systematic studies will certainly reveal the occurrence of some species in other river basins.

According to the current knowledge, the Nilo-Sudan ichthyological province might seem to be a continental hotspot of bothriocephalidean diversity since it harbors six of the seven species known from Africa. These figures, which are merely a result of a relatively high number of ichthyoparasitological studies carried out in this region, do not necessarily reflect biogeographical reality. The Nilo-Sudan province harbors a relatively rich fish fauna comprising 38 families, 119 genera with 361 species, of which much fewer than 100 are endemic (Chapman 2001; Lévêque *et al*. 2008). In terms of fish diversity, this province is surpassed by much smaller Congo ichthyological province covering 4 million square km. Knowledge of Congolean ichthyofauna is still incomplete, but available information clearly show that it harbors a very diverse fish assemblage characterized by exceptionally high degree of endemism. Excluding the biodiverse Lake Tanganyika, the Congo basin comprises 31 families, over 170 genera and almost 800 species, of which almost 600 (over 80%) are endemic (Lévêque *et al*. 1997; Chapman 2001). Importantly, some 20% of the Congolean ichthyofauna consists of siluriform catfish taxa, which are hosts of more than half of the African endemic bothriocephalideans. Given these figures and narrow host specificity, it seems probable that more bothriocephalideans remain undescribed not only in the Congo basin, but also in other undersampled ichthyofaunistic provinces harboring markedly diverse and highly endemic fish faunas. Description of a new species, *T. martinae* from Lake Malawi (Zambezi ichthyological province) provided herein, as well as record of *Polyonchobothrium* sp. from a cultured snakehead *Parachanna obscura* (Günther) (Perciformes: Channidae) in River State, Nigeria (Ogbulie *et al*. 2003) further support this assumption.

Although the fauna of fish parasites of the Nilo-Sudan and South African provinces is becoming relatively well known, large areas harboring majority of African fish diversity with the highest rates of endemism on the continent remain virtually unsampled. This applies especially to the Congo and Lower Guinea, and to a much lesser degree, to Quanza and East Coast ichthyological provinces, the parasite fauna of which remains poorly known. Future studies will almost certainly reveal existence of new taxa in these regions due to the narrow host specificity of bothriocephalideans shown in this study and concentration of endemic fish taxa, many of which are potential hosts for bothriocephalideans.

The present study has shown that many interesting findings of bothriocephalidean tapeworms could not be confirmed because no voucher specimens have been deposited. This applies mainly for more recent studies, especially those from Egypt, Nigeria and South Africa. In contrast, most cestodes found by researchers in the first half of the 20th century, such as W. N. F Woodland, F. J. Meggitt, L. F. Khalil, etc., were deposited in international collections, which enabled us to re-examine this valuable material, often from countries, in which a systematic parasitological research has long been impossible to perform. It is thus desirable that new material should be appropriately fixed using the hot formalin method, adequately described and voucher specimens deposited in internationally recognized collections (see Kuchta *et al*. 2008b; Oros *et al*. 2010; Ash *et al*. 2011 for methods). Preferentially, newly collected material should include samples for molecular analyses, which should be clearly assigned to particular tapeworm specimen from which it has been taken. Such material can be easily obtained by preservation of a few segments from the very end of strobila in absolute ethanol. Importantly, host should be properly determined and whenever possible, photographed and its tissue sample should be preserved in absolute ethanol and deposited together with the parasite to allow ex post confirmation of its identity.

Based on the present study, it is possible to conclude that the African fauna of bothriocephalidean cestodes is species poor (with only 7 instead of 19 species listed from this continent in the literature), but most taxa, which form a monophyletic clade, are widely distributed throughout this continent and exhibit a narrow host specificity to particular host genus. Low species richness, narrow host specificity and wide geographical distribution throughout Africa, which seem to be the principal characteristics of bothriocephalideans in the Ethiopian zoogeographical region, have also been observed in other cestodes parasitic in freshwater teleosts in this continent, i.e. caryophyllideans (Schaeffner *et al*. 2011a) and proteocephalideans (de Chambrier *et al*. 2007, 2008, 2009, 2011; Scholz *et al*. 2009, 2011a), and this general pattern thus may be typical for cestodes of African freshwater fish.

All cestode species prefer the anterior part of the intestine or spiral valve, but *T. ciliotheca* has been reported to occur in the gall bladder and other organs (see above), which has not been confirmed in this study. The scolex is attached by bothria and apical hooks may help to that attachment and may damage intestinal mucosa of the host (Tadros *et al*. 1979).

Preliminary data on phylogenetic relationships of African species, inferred from partial lsrDNA sequences of five species representing all five African genera, showed that they form a monophyletic group (Fig. 62), despite their different morphology and unrelated fish hosts. This indicates that evolution of bothriocephalideans in Africa has a long history from common ancestor resulting in high morphological divergence of individual taxa that adapted to unrelated host groups.

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APPENDIX 1. List of dissected fish from Democratic Republic of the Congo (2008; CON); Ethiopia (2006; ET); Gabon (2010; GAB); Kenya (2008 –2010; KET) and the Sudan (2006, 2008 & 2009; SUD). Abbreviation: *, larvae or plerocercoids in the intestine.

GENUS	SPECIES	SUD	ET	GAB	KET	CON	CESTODE SPECIES
ALESTIDAE							
Alestes	*baremoze*	6	–	–	19	–	
Alestes	*dentex*	3	–	–	8	–	
Brycinus	*kingsleyae*	–	–	1	–	–	
Brycinus	*opisthotaenia*	–	–	1	–	–	
Brycinus	*macrolepidotus*	–	–	4	–	–	
Brycinus	*nurse*	42	–	–	–	–	
Brycinus	*minutus*	–	–	–	4	–	
Brychonaethiops	*microstoma*	–	–	2	–	–	
Hydrocynus	*brevis*	1	–	–	–	–	
Hydrocynus	*forskahlii*	1	–	–	43	–	
Hydrocynus	*vittatus*	1	–	–	–	–	
ANADANTIDAE							
Ctenopoma	*petherici*	1	–	–	–	–	
Ctenopoma	*kingsleyae*	–	–	2	–	–	
BAGRIDAE							
Bagrus	*bajad*	9	–	–	36	–	
Bagrus	*docmak*	8	3	–	5	–	
Bagrus	***meridionalis***	–	–	–	–	–	*Tetracampos martinae*
Pseudobagrus	*albomarginatus*	–	–	1	–	–	
CLAROTIDAE							
Auchenoglanis	*biscutatus*	7	–	–	–	–	
Auchenoglanis	***occidentalis***	28	–	–	32	**1/7**	*Polyonchobothrium polypteri**
Auchenoglanis	sp.	10	–	–	–	–	
Clarotes	*laticeps*	29	–	–	–	–	
Chrysichthys	***auratus***	**1/43**	–	6	10	–	*Tetracampos ciliotheca*
Chrysichthys	*nigrodigitatus*	–	–	6	–	–	
Chrysichthys	*thysi*	–	–	2	–	–	
Chrysichthys	*thonneri*	–	–	–	–	–	
Parauchenoglanis	sp.	–	–	4	–	–	
LATIDAE							
Lates	***niloticus***	5	–	–	**5/34**	–	*Polyonchobothrium polypteri**
Lates	*longispinis*	–	–	–	1	–	
CICHLIDAE							
Haplochromis	*macconneli*	–	–	–	4	–	
Haplochromis	*rudolfianus*	–	–	–	9	–	
Hemichromis	*bimaculatus*	3	–	–	–	–	
Hemichromis	*elongatus*	–	–	–	–	1	
Hemichromis	*exsul*	–	–	–	3	–	
Hemichromis	*fasciatus*	5	–	2	–	–	
Oreochromis	*niloticus*	13	2	–	72	–	
Sarotherodon	*galilaeus*	5	–	–	38	–	
Tilapia	*tholloni*	–	–	–	–	2	
Tilapia	*zillii*	3	–	–	27	–	
CITHARINIDAE							
Citharinus	*citharus*	–	–	–	45	–	
CLARIDAE							
Clariallabes	sp.	–	–	–	–	1	
Clarias	***anguillaris***	**2/18**	–	–	–	–	*Tetracampos ciliotheca*
Clarias	*buthupogon*	–	–	2	–	1	
Clarias	***gariepinus***	**5/30**	**84/322**	–	**14/43**	1	*Tetracampos ciliotheca*
Clarias	*camerunensis*	–	–	2	–	–	
Clarias	*werneri*	5	–	–	–	–	
Clarias	sp.	**4/88**	–	4	–	3	*Tetracampos ciliotheca*
Heterobranchus	***bidorsalis***	**1/13**	**1/2**	–	**6/11**	–	*Kirstenella gordoni*
Platyallabes	*tihoni*	–	–	–	–	1	
CYPRINIDAE							
Barbus	*bynni*	2	–	–	11	–	
Barbus	*holotaenia*	–	–	2	–	–	
Barbus	*humilis*	–	19	–	–	–	
Barbus	*neglectus*	1	–	–	–	–	
Barbus	sp.	2	–	–	–	–	
Cyprinus	*caprio*	1	–	–	–	–	
Garra	*tana*	–	1	–	–	–	
Labeobarbus	*brevicephalus*	–	2	–	–	–	
Labeobarbus	*intermedius*	–	7	–	–	–	
Labeobarbus	*megastoma*	–	1	–	–	–	
Labeobarbus	***nedgia***	–	**1/3**	–	–	–	*Bothriocephalus acheilognathi*
Labeobarbus	*platydorsus*	–	1	–	–	–	

Labeobarbus	*tsanensis*	–	4	–	–	–	
Labeo	*horie*	5	–	–	38	–	
Labeo	*niloticus*	9	–	–	4	–	
Labeo	sp.	1	–	–	–	–	
Leptocypris	*niloticus*	–	–	–	5	–	
DISTICHODONTIDAE							
Distichodus	*rostratus*	2	–	–	–	–	
Distichodus	*nefasch*	1	–	–	30	–	
Distichodus	*notospilus*	–	–	1	–	–	
Ichthyborus	***besse***	**2/5**	–	–	–	–	*Ichtnybothrium ichthybori*
Xenocharax	*spilurus*	–	–	7	–	–	
GYMNARCHIDAE							
Gymnarchus	*niloticus*	1	–	–	2	–	
HEPSETIDAE							
Hepsetus	*odoe*	–	–	3	–	–	
HETEROTIDAE							
Heterotis	*niloticus*	19	–	–	12	–	
CHANNIDAE							
Parachanna	*obscura*	5	–	–	–	–	
Parachanna	sp.	–	–	–	–	2	
MALAPTERURIDAE							
Malapterurus	*electricus*	33	–	–	1	–	
Malapterurus	*gossei*	–	–	–	–	17	
MOCHOKIDAE							
Synodontis	*acanthomias*	–	–	–	–	4	
Synodontis	*batensoda*	5	–	–	–	–	
Synodontis	*caudovittata*	4	–	–	–	–	
Synodontis	*frontosa*	44	–	–	62	–	
Synodontis	*euptera*	4	–	–	–	–	
Synodontis	*filamentosa*	1	–	–	–	–	
Synodontis	*membranacea*	4	–	–	–	–	
Synodontis	*nigrita*	20	–	–	–	–	
Synodontis	*serrata*	23	–	–	–	–	
Synodontis	*schall*	91	1	–	104	–	
Synodontis	*sorex*	1	–	–	–	–	
Synodontis	sp.	32	–	–	–	–	
MORMYRIDAE							
Hyperopisus	*bebe*	4	–	–	1	–	
Hyperopisus	sp.	1	–	–	–	–	
Marcusenius	*cyprinoides*	9	–	–	–	–	
Marcusenius	*moorii*	–	–	1	–	–	
Mormyrops	*anguilloides*	4	–	–	–	1	
Mormyrus	*caschive*	15	–	–	–	–	
Mormyrus	*hasselquisti*	1	–	–	–	–	
Mormyrus	*kannume*	23	–	–	2	–	
Mormyrus	*niloticus*	4	–	–	–	–	
Mormyrus	sp.	16	–	–	–	–	
Pollimyrus	*isidori*	7	–	–	–	–	
NOTHOBRANCHIDAE							
Epiplatys	*bifasciatus*	2	–	–	–	–	
Epiplatys	*spilargyreius*	2	–	–	–	–	
POECILIIDAE							
Aplocheilichthys	*jeanneli*	–	–	–	4	–	
Aplocheilichthys	*rudolfianus*	–	–	–	2	–	
POLYPTERIDAE							
Polypterus	***bichir***	**1/1**	–	–	**6/8**	–	*Polyonchobothrium polypteri*
Polypterus	***endlicheri***	**1/3**	–	–	–	–	*Polyonchobothrium polypteri*
Polypterus	*ornatipinnis*	–	–	–	–	1	
Polypterus	***senegalus***	**1/13**	–	–	8	–	*Polyonchobothrium polypteri*
Polypterus	**sp.**	**1/4**	–	–	–	–	*Polyonchobothrium polypteri*
PROTOPTERIDAE							
Protopterus	*aethiopicus*	3	–	–	1	–	
Protopterus	*annectens*	4	–	–	–	–	
SCHILBEIDAE							
Schilbe	*grenfelli*	–	–	5	–	1	
Schilbe	*intermedius*	2	–	–	–	–	
Schilbe	*multitaeniatus*	–	–	1	–	–	
Schilbe	*mystus*	1	–	–	–	–	
Schilbe	*uranoscopus*	2	–	–	5	–	
Schilbe	sp.	2	–	–	–	–	
TETRAODONTIDAE							
Tetraodon	*lineatus*	5	–	–	13	–	
Tetraodon	*miurus*	–	–	–	–	1	
TOTAL COLLECTED	**120 spp.**	**821**	**368**	**59**	**757**	**44**	
TOTAL DISSECTED							**2049**