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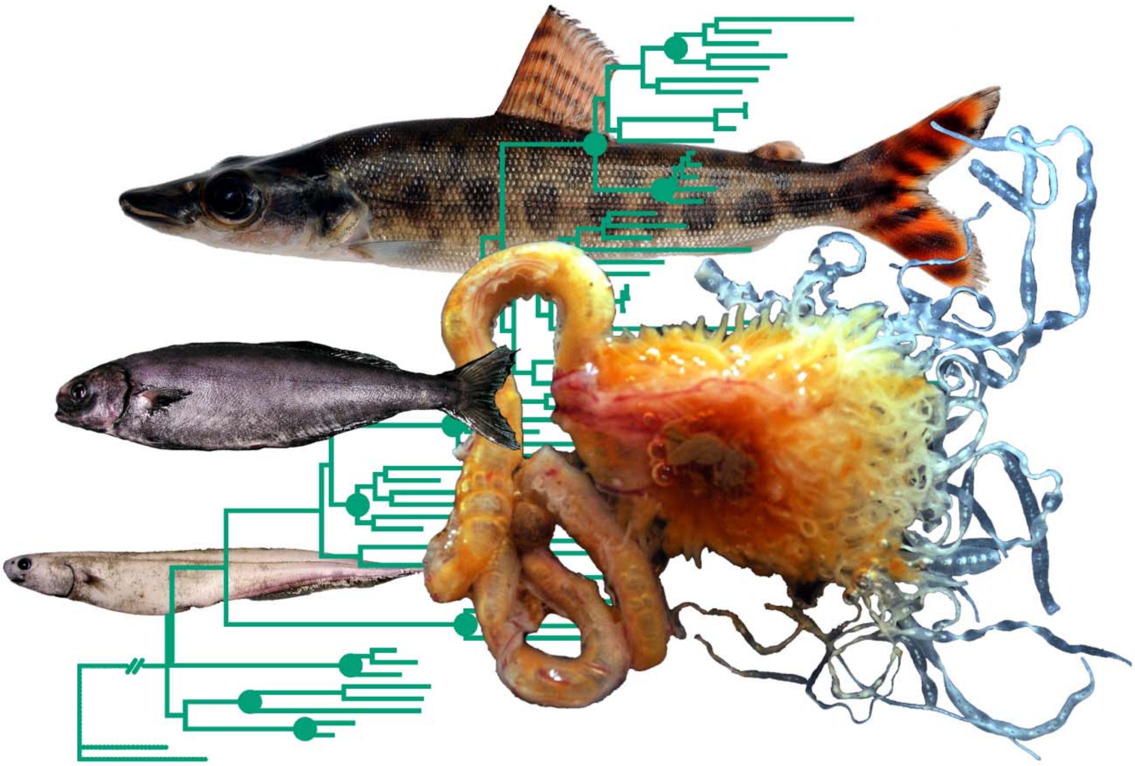
PŘÍRODOVĚDECKÁ FAKULTA

Evolution, biology and systematics of the Bothriocephalidea (Cestoda)



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Habilitační práce

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Habilitation thesis:

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Introduction

1. **Kuchta R.**, Scholz T. **2017**. Bothriocephalidea. In: J.N. Caira and K. Jensen (Eds.). *Tapeworms from vertebrate bowels of the earth 2008–2016*. Special publication No. 25. Natural History Museum, The University of Kansas, Allen Press, Inc., Lawrence, Kansas

Selected papers

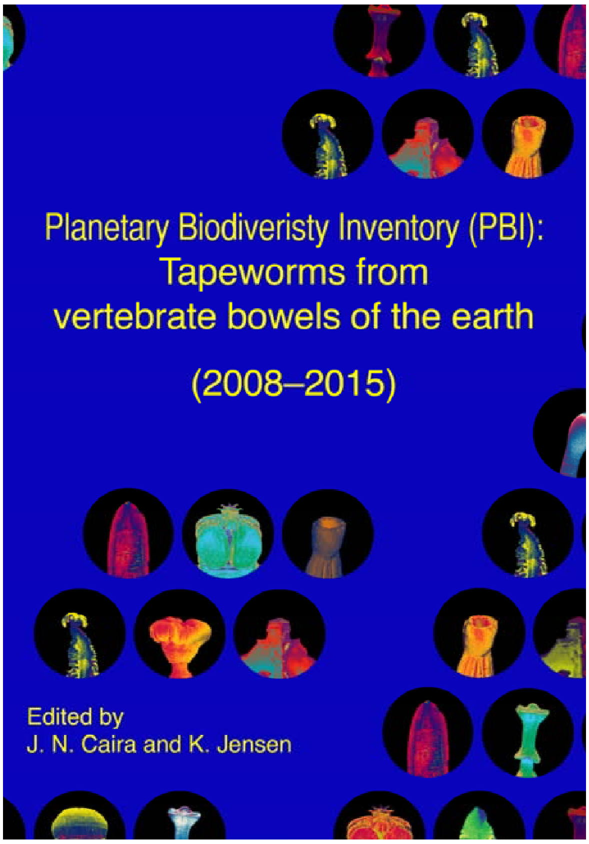
2. **Kuchta R.**, Scholz T., Brabec J., Bray R.A. **2008**. Suppression of the tapeworm order Pseudophyllidea (Platyhelminthes: Eucestoda) and the proposal of two new orders, Bothriocephalidea and Diphyllobothriidea. *International Journal for Parasitology* 38: 49–55. [IF=3.752]
3. **Kuchta R.**, Scholz T., Bray R.A. **2008**. Revision of the order Bothriocephalidea Kuchta, Scholz, Brabec & Bray, 2008 (Eucestoda) with amended generic diagnoses and keys to families and genera. *Systematic Parasitology* 71: 81–136. [IF=0.927]
4. **Kuchta R.**, Scholz T., Justine J.-L. **2009**. Two new species of *Bothriocephalus* Rudolphi, 180*8* (Cestoda: Bothriocephalidea) from marine fish off Australia and New Caledonia. *Systematic Parasitology* 73: 229–238. [IF=0.911]
5. **Kuchta R.**, Scholz T., Vlčková R., Říha M., Walter T., Yuniar A.T., Palm H. W. **2009**. Revision of tapeworms (Cestoda: Bothriocephalidea) from lizardfish (*Saurida:* Synodontidae) from the Indo-Pacific region. *Zootaxa* 1977: 55–67. [IF=0.891]
6. **Kuchta R.**, Burianová A., Jirků M., de Chambrier A., Oros M., Brabec J., Scholz T. **2012**. Bothriocephalidean tapeworms (Cestoda) of freshwater fish in Africa, including erection of *Kirstenella* n. gen. and description of *Tetracampos martinae* n. sp. *Zootaxa* 3309: 1–35. [IF=0.974]
7. Brabec J., Waeschenbach A.,Scholz T., Littlewood D.T.J., **Kuchta R. 2015**. Molecular phylogeny of the Bothriocephalidea (Cestoda): molecular data challenge morphology-based classification. *International Journal for Parasitology* 45: 761–771.

Introduction

Tapeworms (Platyhelminthes: Cestoda) are common intestinal parasites with complex life-cycles that infect all groups of vertebrates including man. They are currently divided into 19 orders and members of one of them, the Bothriocephalidea Kuchta, Scholz, Brabec et Bray, 2008, parasitise marine and freshwater bony fishes. The present habilitation thesis is based on candidate's long-term research on bothriocephalidean cestodes, which formed principal subject of his undergraduate (BC thesis on A comparative study of two sympatric species of the genus *Eubothrium* defended in 2000) and graduate studies (MSc thesis on the genus *Eubothrium* Nybelin, 1922 defended in 2002 and PhD thesis on taxonomic revision of "pseudophyllidean" cestodes including the newly erected order Bothriocephalidea and Diphyllobothriidea defended in 2007).

Since 2008, he actively participated at an international project funded by the National Science foundation (Planetary Biodiversity Inventory program) to map the cestode diversity globally. As leading expert in this and other cestode groups occurring in bony fishes, the candidate participated in preparation of 9 of 21 chapters in the monograph on cestodes generated as the principal outcome of this big international collaborative project (2008 – 2016). The chapter that summarises previous and current knowledge of the taxonomy, biology, host associations, geographic distribution and phylogenetic relationships of bothriocephalidean cestodes (Kuchta and Scholz, 2017) has been selected as an introduction chapter to this habilitation thesis.

Kuchta R., Scholz T. **2017**. Bothriocephalidea. In: J.N. Caira and K. Jensen (Eds.). *Tapeworms from vertebrate bowels of the earth 2008–2016*. Special publication No. 25. Natural History Museum, The University of Kansas, Allen Press, Inc., Lawrence, Kansas



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Bothriocephalidea Kuchta, Scholz, Brabec & Bray, 2008

By
Roman Kuchta[1] and Tomáš Scholz

BOTHRIOCEPHALIDEA AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. The Bothriocephalidea was erected as an independent order by Kuchta et al. (2008a) just before the inception of the PBI project. Prior to that, its taxa and those assigned to the second new order established by Kuchta et al. (2008a), the Diphyllobothriidea (see Chapter 8 this volume), had collectively been considered to compose the single order Pseudophyllidea Carus, 1863. The taxa assigned to the Bothriocephlidea had traditionally been divided into four families: Bothriocephalidae Blanchard, 1849, Echinophallidae Schumacher, 1914, Philobythiidae Campbell, 1977, and Triaenophoridae Lönnberg, 1889 (see Bray et al., 1994; Kuchta et al., 2008a). Taxa considered to validly belong to these families varied greatly among authors: Wardle and McLeod (1952) recognized a total of 22 genera with 44 valid species, Yamaguti (1959) 28 genera with 132 valid species, Protasova (1977) 32 genera with 96 valid species (and another 31 species designated as *species inquirendae*), and Schmidt (1986) listed 41 genera with 170 valid species. Following extensive review of specimens and the literature, Kuchta and Scholz (2007) critically re-evaluated bothriocephalidean membership. In that work they recognized 31 genera and only 125 valid species out of total of 305 nominal taxa (135 synonymized and 45 *species inquirendae* or of unclear status—dominant among these were the numerous insufficiently described species of *Senga* Dollfus, 1934 from snakeheads [*Channa* spp.] and the zig-zag eel, *Mastacembelus armatus* [Lacepède] in India and its neighboring countries).

Morphology. The last detailed taxonomic revision of the order (as the suborder Bothriocephalata), examining morphology at the species level, was that of Protasova (1977); however, as this monograph was published in Russian, its results were not widely accessible. Bray et al. (1994) presented a critical account of the order Pseudophyllidea, which included keys and very brief updated diagnoses of both bothriocephalidean and diphyllobothriidean genera.

When, informed by the earlier molecular work of Mariaux (1998), Kodedová et al. (2000), and Brabec et al. (2006), Kuchta et al. (2008a) formally dismantled the order Pseudophyllidea, they differentiated the Bothriocephalidea and Diphyllobothriidea from one another on the basis of the following characteristics: (i) the position of the genital pore, which is on the dorsal, dorsolateral, or lateral side of the proglottid, posterior to the ventral uterine pore in the Bothriocephalidea, but is located on the ventral surface anterior to the uterine pore in the Diphyllobothriidea; (ii) external seminal vesicle, which is lacking in the Bothriocephalidea, but present as a well-developed, muscular structure in the Diphyllobothriidea; (iii) enlarged distal part of the uterus in gravid proglottids,

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Kuchta, R. and T. Scholz. 2017. Bothriocephalidea Kuchta, Scholz, Brabec & Bray, 2008. *In* Planetary Biodiversity Inventory (2008–2016): Tapeworms from vertebrate bowels of the earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. XX–XX.

which is present in the Bothriocephalidea, but absent in the Diphyllobothriidea; and (iv) range of definitive hosts, which are mainly teleosts and never homeotherm vertebrates in the Bothriocephalidea, but are tetrapods and most frequently mammals in the Diphyllobothriidea.

The four families recognized prior to the PBI project are generally distinguished from one another (see Bray et al., 1994; Kuchta et al., 2008b) by genital pore position (median, sublateral, or lateral). The two families with a lateral gonopore (i.e., Philobythiidae and Triaenophoridae) differ in vitellarium shape (i.e., compact in the former and follicular in the latter) (see Bray et al., 1994). Because of uniformity in strobilar morphology, scolex morphology is one of the key diagnostic features for distinguishing among genera and their species. Developmental features, such as whether eggs embryonate while in utero (or not) and presence (or absence) of an egg operculum, are also informative (see Bray et al., 1994; Kuchta et al., 2008b).

HOST ASSOCIATIONS. Kuchta and Scholz (2007) nicely summarized the specturm of definitive hosts used by bothriocephalideans as follows. In total, 96% of the 125 valid species recognized by Kuchta and Scholz (2007) use Actinopterygii (ray-finned fishes) as definitive hosts, although three species of *Bothriocephalus* Rudolphi, 1808 parasitize North American lungless salamanders (Caudata: Plethodontidae Gray). Among Actinopterygii, teleosts serve as definitive hosts for the majority of bothriocephalideans. There are, however, five species that are interesting exceptions in that they parasitize more archaic actinopterygian groups. Specifically *Marsipometra hastata* (Linton, 1897) Cooper, 1917 and *M. parva* Simer, 1930 infect paddlefish, and *Eubothrium acipenserium* (Cholodkovsky, 1918) Dogiel & Bychowsky, 1939 infects sturgeons, both in the order Acipenseriformes, *Polyonchobothrium polypteri* (Leydig, 1853) Lühe, 1900 which is found in Polypteriformes (bichirs), and *Senga scleropagis* (Blair, 1978) Kuchta & Scholz, 2007 which has been reported from Osteoglossiformes (bony tongues).

Approximately 65% of all species in the order parasitize marine fishes, while only 32% are found in freshwater fishes. Three species (i.e., *Eubothrium acipenserium*, *E. crassum* [Bloch, 1779] Nybelin, 1922, and *E. salvelini* [Schrank, 1790] Nybelin, 1922) infect migratory fishes (i.e., sturgeons and salmonids) and thus may live in both types of environments. Among teleosts, the group that most commonly serves as definitive host for bothriocephalideans are the Perciformes, with 45 species parasitizing fishes of this order—15 of these cestodes specifically parasitize centrolophids. In some cases (e.g., the Japanese butterfish, *Psenopsis anomala* [Temminck & Schlegel] or the rudderfish, *Centrolophus niger* [Gmelin]), up to four species may co-occur in the same host species.

The prevalence of bothriocephalideans in their definitive hosts is usually low—rarely exceeding 10%. However, instances of prevalences reaching 100% with infection intensities of up to 1,000 individuals per host have been reported in the triaenophorid *Eubothrium crassum* in brown trout, *Salmo trutta* L. (see Kennedy, 1996) and in the echinophallid *Neobothriocephalus aspinosus* Mateo & Bullock, 1930 in the palm ruff, *Serioella violacea* Guichenot (see Mateo and Bullock, 1966). In fact, the most prevalent bothriocephalideans are generally echinophallids of the genera *Bothriocotyle* Ariola, 1900, *Echinophallus* Schumacher, 1914, *Neobothriocephalus* Mateo & Bullock, 1966, *Parabothriocephaloides* Yamaguti, 1934, *Parabothriocephalus* Yamaguti, 1934, and *Paraechinophallus* Protasova, 1975. There may also be marked differences in infection parameters within adjacent marine ecosystems . For example, the coastal waters off the mainland of Scotland seem to be poor for bothriocephalidean cestodes. Kuchta and Scholz (2007) reported finding only four cestode individuals in two fish species infected with either *Abothrium gadi* van Beneden, 1871 or *Bothriocephalus scorpii* (Müller, 1776) Cooper, 1917 out of the approximately 500 individuals of 37 fish species from 11 localities throughout coastal Scotland surveyed in the autumn of 2004. In contrast, during an investigation of the helminth fauna of deep-sea fishes off the Outer Hebrides, Scotland, carried out in the fall of 2005, Kuchta and Scholz (2007) found 20 of the 286 fish individuals representing a total of 42 fish species infected with five species of bothriocephalideans. Host specificity of bothriocephalideans is usually strict, with about 95% of species being at least stenoxenous (sensu Caira et al., 2003; i.e., restricted to a single host genus), and approximately 70% of species being oioxenous (sensu Euzet and Combs, 1980; i.e., known from 1 host species only). As few as seven species of bothriocephalideans are euryxenous (sensu Caira et al., 2003; i.e., occur in hosts of different families). For example, *Clestobothrium crassiceps* (Rudolphi, 1819) Lühe, 1899 and *B. scorpii* have been reported from as many as 30 species belonging to six families of marine fish each, although the latter taxon probably represents a species complex (Cooper, 1918; Protasova, 1977; Škeříková et al., 2004). However, the species of the *B. scorpii* complex, namely *B. barbatus* Renaud, Gabrion & Pasteur, 1983, *B. gregarius* Renaud, Gabrion & Pasteur, 1983, and *B. funiculus* Renaud & Garbion, 1984, represent *nomina nuda* because their original description did not comply with requirements of the International Code of Zoological Nomenclature (1999; Article 13) (see Renaud et al., 1983; Renaud and Gabrion, 1984; Kuchta and Scholz, 2007). Moreover, phylogenetic analyses revealed a close relationship among these species and *B. andresi* Porta, 1911 and *B. clavibothrium* Ariola, 1899; their status as valid species thus requires verification (see Škeříková et al., 2004). By far the most extreme example of euryxeny is *Bothriocephalus acheilognathi* Yamaguti, 1934 (now *Schyzocotyle acheilognathi* [Yamaguti, 1934] Brabec, Waeschenbach, Scholz, Littlewood, & Kuchta, 2015), which has been reported from approximately 200 species of freshwater fishes, representing 10 orders, and 19 families (Scholz et al., 2011). It should, however, be noted that the range of definitive hosts of many bothriocephalidean species and thus, their actual degree of host specificity, is not clearly understood because of the insufficiently resolved taxonomy not only of many of the bothriocephalidean genera, but also of their hosts.

GEOGRAPHIC DISTRIBUTION. The majority of bothriocephalidean species have been reported from the Atlantic (45 species) and Pacific (31 species) Oceans, with only 18 species known from the Indian Ocean (Kuchta and Scholz, 2007). The number of freshwater bothriocephalidean species occurring in Eurasia (27 species) is higher than that reported from North America (18 species). In contrast, the species richness of freshwater bothriocephalideans on other continents is very low; they are particularly rare in the freshwaters of South America, including the Amazon River basin. *Galaxitaenia toloi* Gil de Pertierra & Semenas, 2005 and *Ailinella mirabilis* Gil de Pertierra, 2006 were described from Argentinian Patagonia (Kuchta and Scholz, 2007). There are only four records, probably all of conspecific *Senga*-like bothriocephalideans, from unrelated freshwater teleosts representing four orders (Characiformes, Cyprinidontiformes, Perciformes, and Pleuronectiformes) in Brazil (Woodland, 1935; Rego, 1997; Kuchta and Scholz, 2007).

The occurence of marine bothriocephalideans varies also in ocean ecosystems. The shelf and epipelagic ocean faunas (down to a depth of 200 m) are relatively depauperate, represented solely by species of *Bothriocephalus*, *Clestobothrium* Lühe, 1899, and *Abothrium* van Beneden, 1871. The mesopelagic fauna (200 to 1,000 m) is also very species poor, typically consisting of *Bothriocephalus manubriformis* (Linton, 1889) Ariola, 1900 and *Fistulicola plicatus* (Rudolphi, 1819) Lühe, 1899 in xiphiid fishes (swordfish), and *Anchistrocephalus microcephalus* (Rudolphi, 1819) Monticelli, 1890 in sunfish (Molidae Bonaparte). In contrast, bathypelagic (1,000 to 4,000 m) fishes harbor a relatively rich fauna of bothriocephalidean cestodes. Species of nine genera, namely *Andycestus* Kuchta, Scholz & Bray, 2008; *Australicola* Kuchta & Scholz, 2006; *Bathycestus* Kuchta & Scholz, 2004; *Kimocestus* Kuchta, Scholz & Bray, 2008; *Milanella* Kuchta & Scholz, 2008; *Philobythoides* Campbell, 1977; *Philobythos* Campbell, 1979; *Pistana* Campbell & Gartner, 1982; and *Probothriocephalus* Campbell, 1979 are known only from deep-sea fishes (Kuchta et al., 2008b). The deepest record of a bothriocephalidean cestode is that of *Pistana eurypharyngis* Campbell & Gartner, 1982 from the pelican eel, *Eurypharynx pelecanoides* Vaillant, collected from 3,083 m (Campbell and Gartner, 1982). In general, the bothriocephalids are more common in benthic than in pelagic fishes.

PHYLOGENETIC RELATIONSHIPS. Dubinina (1980) and Yurakhno (1992) discussed possible relationships of pseudophyllidean cestodes, but the first cladistic assessment of the phylogenetic relationships of bothriocephalidean families was that of Bray et al. (1999) as part of a larger analysis of the, at that time, Pseudophyllidea overall. That study was based on morphological characters of the type genera of each of the 14 families recognized by Yurakhno (1992). Brabec et al. (2006) presented the first molecular phylogenetic analysis of pseudophyllidean cestodes, based on 18S and 28S rDNA sequence data for 17 bothriocephalidean species, including five species for which data were obtained from GenBank, and 12 species for which new data were generated. Their analyses confirmed the paraphyly of the order "Pseudophyllidea," which they found to consist of two unrelated clades, then informally designated as the "Bothriocephalidea" and "Diphyllobothriidea." Although Brabec et al. (2006) found the "Bothriocephalidea" to be monophyletic, two of its families (i.e., the Echinophallidae and the Triaenophoridae) were not. As noted above, the orders Bothriocephalidea and Diphyllobothriidea were formally proposed two years later once sufficient morphological and ecological (host range) evidence had been accumulated to support these molecular results (Kuchta et al., 2008a). In their analysis of the group in the context of cestodes overall, Waeschenbach et al. (2007) found their bothriocephalidean exemplar to group as the sister to the clade of all acetabulate orders (incl. *Litobothrium* Dailey, 1969), well away from the diphyllobothriidean exemplar included in their analyses.

CURRENT STATUS OF THE BOTHRIOCEPHALIDEA

DIVERSITY AND CLASSIFICATION. Over the course of the PBI project, three new species were described (Kuchta et al., 2009a, 2012; Gil de Pertierra et al., 2015) and five new genera were erected, while another three genera were resurrected (Kuchta et al., 2008b, 2012; Brabec et al., 2015). In total, the order now houses 132 species in 48 genera (Table 1). It is of note that only 38% of the 350 nominal species are valid. In addition, our work revealed at least ten undescribed species, the novelty of which is supported by both morphological and molecular data (Brabec et al., 2015).

Since 2008, more than 40 allegedly new species have been described by authors outside of the PBI project. However, with the exception of two species of *Clestobothrium* described by Gil de Pertierra et al. (2011), species were described in the "catch-all" genus *Senga* or in the invalid genus *Circumoncobothrium* Shinde, 1968, all from India and its neighboring countries. No less than 26 species were described from *Mastacembelus armatus*, despite the fact that this notoriously repeatedly examined teleost has already been reported to host as many as 60 of the 100 nominal species of *Senga* described. The remainder of the allegedly new species were described from the snakehead *Channa striata* (Bloch), which is another teleost that has been reported to host dozens of invalid, insufficiently described species of tapeworms (see Kuchta and Scholz [2007], Kuchta et al. [2008b], and Ash et al. [2011, 2015] for detailed treatments of the problems associated with the taxonomy of fish cestodes from India and its neighboring countries). Provisionally, 14 species of *Senga*, based on their type host, have been retained as valid (Table 1). Of particular note are the two new species of *Circumoncobothrium* (*C. clariasi* Kadam & Dhole, 2011 and *C. jadhavi* Shinde, 2013) described from the walking catfish *Clarias batrachus* (Linnaeus), which is not known to host bothriocephalideans, but harbors a number of caryophyllidean cestodes (see Ash et al., 2011). We believe these records are in error because on several collecting trips to India and Bangladesh over the course of the PBI project, more than 100 specimens of this fish were dissected and no bothriocephalidean tapeworms were found (Ash et al., 2011). The recently described species *Parabothriocephaloides magnus* Sedova & Gulyaev, 2012 is synonymized herein with the type species of the genus, *P. segmentatus* Yamaguti, 1934, because, beyond a slight difference in testis number, these species in fact do not differ morphologically from one another.

The validity of both genera erected by non-PBI personnel is highly suspect. In fact, *Aitodiscus* Srivastav & Narayan, 2012 is a synonym of *Senga*. It was proposed to accommodate *A. jalaunensis* Srivastav & Narayan, 2012 from *Channa punctata* (Bloch) in India, which is here identified as a junior synonym of *Senga visakhapatnamensis* Devi & Rao, 1973, described from the same fish host. *Indobothrium* Sedova & Gulyaev, 2009 was proposed to accommodate two species originally assigned to *Bothriocephalus* (i.e., *I. bengalensis* [Devil, 1975] Sedova & Gulyaev, 2009 and *I. branchiostegus* [Yamaguti, 1952] Sedova & Gulyaev, 2009). The new genus was characterized mainly by the markedly craspedote nature of the proglottids, but this character is present in several other species of *Bothriocephalus*, including *B. carangis* Yamaguti, 1968, *B. gadellus* Blend & Dronen, 2003, and *B. timii* Gil de Pertierra, Arredondo, Kuchta & Incorvaia, 2015. As a result, *Indobothrium* was synonymized with *Bothriocephalus* by Gil de Pertierra et al. (2015).

Regarding the overall species richness of bothriocephalideans (i.e., both described and undescribed), it is impossible to provide a reliable estimate because so many host groups, especially from marine environments, have not yet been examined. In freshwater, our molecular work suggests that a number of undescribed species of *Bothriocephalus* and *Ichthybothrium* Khalil, 1971 certainly exist in North America and Africa, respectively, and detailed study of bothriocephalideans in the Indomalayan biogeographic realm are also likely to reveal additional, undescribed species (see Brabec et al., 2015). However, most urgent is a revision of the infamous genus *Senga* with its more than 100 nominal species. Preliminary molecular data generated from well-fixed specimens from Cambodia, India, and Vietnam, collected over the course of the PBI project, lead us to believe that the actual number of species of *Senga* may be as low as five to ten.

MORPHOLOGY. In addition to revising the order, Kuchta et al. (2008b) and Brabec et al. (2015) provided emended generic diagnoses of all 48 genera based on a critical examination of a comprehensive selection of museum and newly collected material. They also presented the first scanning electron micrographs (SEM) of the scoleces of numerous taxa, which exhibited microtriches and tumuli-like globular surface structures, and they studied the surface ultrastructure of the eggs of several taxa for the first time. Beyond confirming that SEM micrographs of the scolex of specimens fixed with a standardized protocol (i.e., hot formalin fixation) are key for future comparative studies and species descriptions, as suggested by Kuchta and Scholz (2007) and Kuchta et al. (2008b), no new morphological characters were observed during the PBI project.

Although superficially the scoleces of different bothriocephalidean cestodes may look quite uniform because most taxa possess only two simple elongated bothria (e.g., Fig. 1M), in fact, the morphology of the scolex plays a crucial role mainly in generic identification. Across taxa, there is a high amount of variation in the shape of the scolex (e.g., Fig. 1); it may or may not bear an apical disc (but its presence may be influenced by fixation method) or hooks; the musculature of the bothria may be weakly developed, strong, or hypertrophied. When hooks are present, they can vary in size, shape, and number, and are not necessarily found in related taxa (e.g., Figs. 1B, F, O, and Q). In a few bothriocephalideans, the whole scolex or at least the bothria have been reduced (e.g., Fig. 1K), or the scolex including bothria has been strongly modified as in *Onchodiscus sauridae* Yamaguti, 1934 and *Ptychobothrium belones* (Dujardin, 1845) Lönnberg, 1889 (see Kuchta et al., 2008b, 2009b).

In contrast, the morphology of the strobila is rather uniform across bothriocephalideans, although some unique characters are present in species of the Echinophallidae. For example, the strobila can be folded along the longitudinal axis (convex dorsally and concave ventrally) as in *Bothriocotyle solinosomum* Ariola, 1900 (see Kuchta et al., 2008c). The cirrus of many echinophallids (e.g., *Paraechinophallus japonicus* [Yamaguti, 1934] Protasova, 1975; see Levron et al., 2008) is usually large and armed with massive spinitriches. All echinophallids, including *Echinophallus wageneri* (Monticelli, 1890) Schumacher, 1914 and *P. japonicus*, possess large, gladiate spinitriches on the posterior margins of their proglottids (Fig. 1R, S; see also Poddubnaya et al., 2007; Kuchta et al., 2008c; Levron et al., 2008).

HOST ASSOCIATIONS. Over the course of the PBI project, more than 8,000 host specimens of a total of over 500 species, the great majority from freshwater, were examined but only ten host species were found to be new hosts for bothriocephalideans (see Table 2). The Lepisosteiformes (gars), represented by *Lepisosteus oculatus* Winchell, from the USA, is a new host order; new host families are the Achiridae Rafinesque (American soles), represented by *Trinectes maculatus* (Bloch & Schneider) from the USA, the Bovichtidae Gill (thornfishes), represented by *Cottoperca gobio* (Günther) from Argentina (Brabec et al., 2015; Gil de Pertierra et al., 2015), the Platycephalidae Gill (flatheads), represented by *Platycephalus bassensis* Cuvier and *P. aurimaculatus* Knapp from Australia, and the Serranidae Innamura & Yabe (sea basses and groupers), represented by *Cephalopholis aurantia* × *spiloparaea* (Valenciennes) from New Caledonia (Brabec et al., 2015). The serranids represent the first records of reef fish hosting adult bothriocephalideans (Kuchta et al., 2009a). New host species records are *Bagrus meridionalis* Günther (Bagridae) from Lake Malawi in Africa (Kuchta et al., 2012), *Mastacembelus favus* Hora (Mastacembelidae Bleeker) from Vietnam and *Mesoborus crocodilus* Pellegrin (Distichodontidae Günther) from the Central African Republic (Brabec et al., 2015). Except for *T. maculatus* and *L. oculatus*, which represent new host records for the known cestodes, *Bothriocephalus claviceps* (Goeze, 1782) Rudolphi, 1810 and *B. cuspidatus* Cooper, 1917, respectively, the fish hosts listed above all harbor new species of bothriocephalideans.

Bothriocephalideans are most commonly found in fish of the families Centrolophidae Bonaparte and Synodontidae Gill. However, only nine out of 31 species of centrolophids and 20 of 73 species of synodontids have been studied for parasites and thus new sampling of other members of these families may reveal additional new bothriocephalidean species.

Bothriocephalideans are conspicuously absent from siluriforms in South America and Eurasia (around 150 species examined), but were relatively diverse in families of this order in the Ethiopian (in Clariidae Bonaparte) and Australia (Ariidae Berg); our preliminary

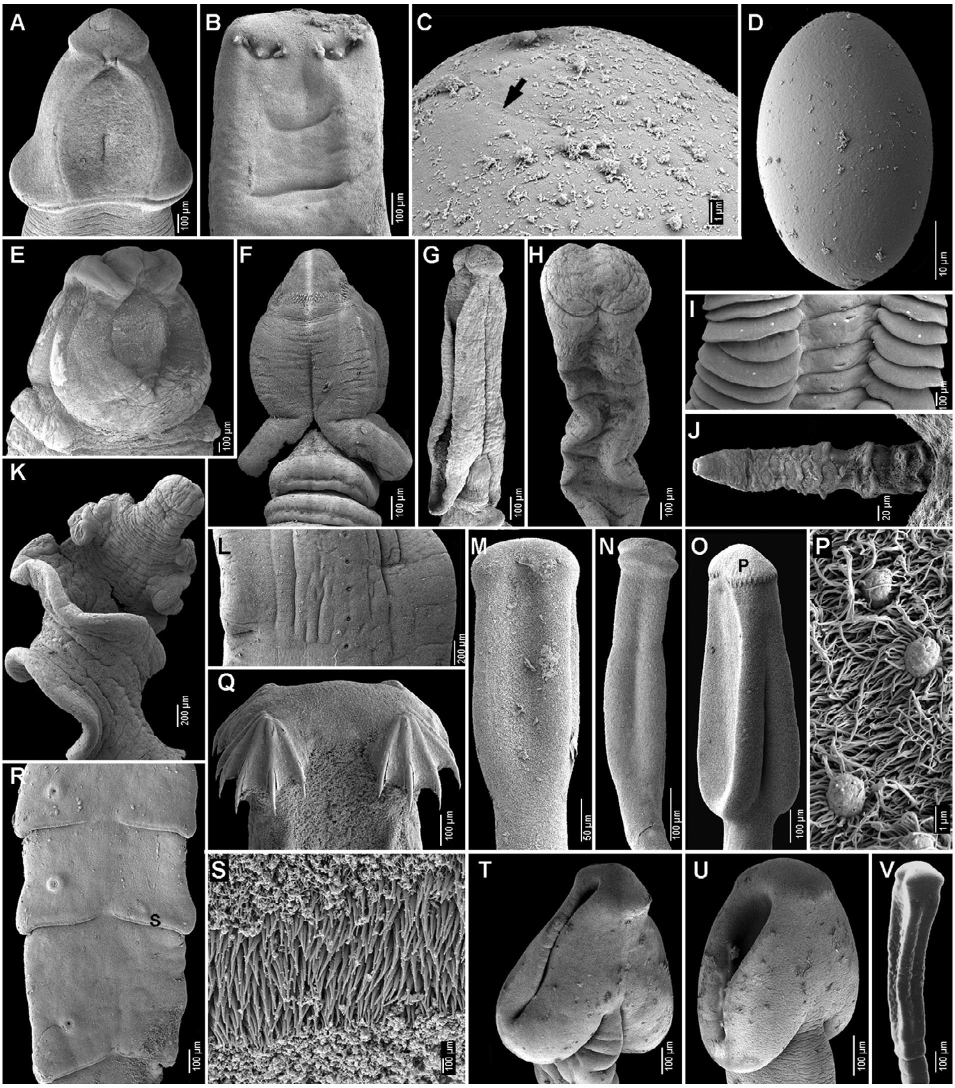

Figure 1. Scanning electron micrographs of selected bothriocephalideans. **(A)** Scolex of *Marsipometra hastata* ex *Polyodon spathula*, USA. **(B, C)** Scolex (B) and egg (C) with operculum (arrow) of *Triaenophorus nodulosus* ex *Esox lucius*, UK **(D)** Unoperculate egg of *Eubothrium salvelini* ex *Salvelinus alpinus*, UK. **(E)** Scolex of *Anchistrocephalus* n. sp. ex *Masturus lanceolatus*, Portugal. **(F)** Scolex of *A. microcephalus* ex *Mola mola*, USA. **(G, J)** Scolex (G) and cirrus with tegumental bumps (J) of Triaenophoridae n. gen. n. sp. ex *Hyperoglyphe antarctica*, Australia. **(H)** Scolex of Bothriocephalidae n. gen. n. sp. ex *Epinephelus coioides*, Indonesia. **(I)** Strobila of *Penetrocephalus ganapattii* ex *Saurida tumbil*, Indonesia. **(K, L)** Anterior region of body (K) and detail of strobila (L) of *Anantrum tortum* ex *Synodus foetens*, USA. **(M)** Scolex of *Bothriocephalus celinae* ex *Cephalopholis aurantia* × *spiloparaea*, New Caledonia. **(N)** Scolex of *Bothriocephalus scorpii* ex *Myoxocephalus scorpius*, UK. **(O, P)** Scolex (O) and tumuliform globular structures on scolex (P) of *Senga visakhapatnamensis* ex *Channa punctata*, India. **(Q)** Apical region of scolex of *Polyonchobothrium polypteri* ex *Polypterus senegalus*, Sudan. **(R, S)** Strobila with submedian genital pores (R) and posterior margin of proglottid armed with large gladiate spinitriches (S) of *Neobothriocephalus aspinosus* ex *Seriolella violacea*, Peru. **(T, U)** Scolex of *Schyzocotyle nayarensis* ex *Raiamas bola*, India. **(V)** Scolex of *Bothriocephalus claviceps* ex *Anguilla anguilla*, Czech Republic. Note: Small letters in (O) and (R) correspond to figure letters showing higher magnification images of these surfaces. Modified from Brabec et al. (2015).

molecular work suggests that members of the latter family host what is likely to be a new genus.

GEOGRAPHIC DISTRIBUTION. PBI project bothriocephalidean collecting efforts were focused mainly on insufficiently known freshwater fishes from the following four poorly sampled regions: sub-Saharan Africa (i.e., the Central African Republic, the Democratic Republic of the Congo, Gabon, Kenya) and the Sudan, Southeast Asia (i.e., Bangladesh, Cambodia, India, and Vietnam), South America (i.e., Brazil and Peru), Canada (i.e., Manitoba), and the USA (i.e., Alaska, Connecticut, Mississippi, Nebraska, South Carolina, Texas, and Wisconsin) (Table 2). Also examined were marine fishes from South America (i.e., Argentina and Peru), Southeast Asia (i.e., Vietnam), Europe (i.e, Norway, incl. Svalbard), and Oceania (i.e., Australia and New Caledonia).

In combination with pre-PBI project data, the following summary of the geographic distribution of bothriocephalideans is provided, with a focus on freshwater taxa, which represent about one third of all valid species as they were more intensively studied over the course of the PBI project.

Almost 3,400 freshwater teleosts of approx. 80 species were examined in the Palaearctic realm, with most of the specimens from Europe, followed by China and the Far East of Russia (Primorsky region). However, only six already known species (out of 12 known) of five genera were found. In the Nearctic realm, we found nine species in four genera including three putatively new species of *Bothriocephalus*.

In the Afrotropic realm, only eight species of five genera (1 new species and 1 new genus erected by the present authors—see Kuchta et al., 2012) are currently known. This total number of bothriocephalideans is rather low and most of these species are widely distributed throughout sub-Saharan Africa (Kuchta et al., 2012).

The cestode fauna of the Indomalayan realm is least known and may be relatively species-poor, even though the literature is littered with dozens of "species" of *Senga* and *Senga*-like genera described inadequately. Based on a critical review of the literature (see also Kuchta and Scholz [2007] and Kuchta et al. [2008b]) and examination of almost 1,600 freshwater teleosts of approx. 50 species from Bangladesh, Cambodia, India, Indonesia, and Vietnam, only 14 species of bothriocephalideans are tentatively recognized, including presumably five distinct species of *Senga* (the number indicated by the number of different fish hosts and genetic differences revealed by preliminary molecular data).

The most depauparate fauna of bothriocephalidean cestodes is that of the Australasian and Neotropical realms, with only two and four species reported, respectively. In addition, the prevalence of infection of freshwater teleosts with these species seems to be quite low, especially in South America, which corresponds to the fact that only one bothriocephalidean, which represents a new species of a new genus (Scholz and Kuchta, unpubl. data) was found in only one of more than 1,100 fishes of approx. 150 species examined from Amazonia (Table 2; de Chambrier et al., 2015).

In the case of marine bothriocephalidean species, data on their geographic distribution largely depend on sampling effort and may not fully correspond with the actual distribution of individual species, which are probably much larger than currently recognized. Some of the widely distributed species such *Anchistrocephalus microcephalus*, *Bothriocephalus manubriformis*, *Fistulicola plicatus*, *Plicatobothrium cypseluri* (Rao, 1959) Khalil, 1971, *Plicocestus janickii* (Markowski, 1971) Kuchta, Scholz & Bray, 2008, and *Ptychobothrium belones* occur, at a minimum, in two Oceans (i.e., the Atlantic and Pacific Oceans). *Abothrium gadi*, *Australicola platycephalus* (Monticelli, 1889) Kuchta & Scholz, 2007, and *Kimocestus ceratias* (Tkachev,

1979) Kuchta, Scholz & Bray, 2008 have been reported from almost all regions in Arctic and temperate regions, whereas *Bothriocephalus carangis* is known to occur in most tropical regions (Kuchta et al., 2008b; unpubl. data).

Overall, no conspicuous changes in distributional patterns compared to those outlined by Kuchta and Scholz (2007) have been detected over the course of the PBI project. The Atlantic Ocean hosts the most diverse fauna, with as many as 51 species reported (i.e., about 38% of all bothriocephalidean known diversity), whereas 39 species (29%) are known from the Pacific Ocean, largely as a result of pioneer studies of Satyu Yamaguti in Japan and Hawaii; only 23 species (17%) have been reported from the Indian Ocean.

As mentioned above, the parasite fauna of deep-sea fishes is characterized by the presence of bothriocephalidean cestodes, with 14 species in nine genera known only from teleosts living at depths greater than 1,000 m in the Atlantic, Indian and Pacific Oceans (see above and Kuchta et al., 2008b). In addition, one new taxon, possibly a new species of a new genus, was found in the roundnose grenadier, *Coryphaenoides rupestris* Gunnerus, off the coast of Norway and Scotland, but only immature specimens are available.

PHYLOGENETIC RELATIONSHIPS. Collecting trips conducted over the course of the PBI project (Table 2) considerably expanded the original dataset of Brabec et al. (2006) to include an additional 41 species in 18 genera for molecular phylogenetic analysis. The project's resulting multi-gene-based phylogenetic inferences (Fig. 2; Brabec et al., 2015) included sequence data for 59 species of 31 genera of bothriocephalideans (i.e., approx. 45% of valid species and approx. 72% genera in the order). This comprehensive dataset allowed for a relatively robust assessment of the phylogenetic relationships among the bothriocephalideans and the monophyly of individual families and genera. Some of Brabec et al.'s (2015) key conclusions are briefly summarized as follows:

(1) The earliest diverging lineages of the order represent species of the paraphyletic Triaenophoridae. It remains to be determined whether bothriocephalideans parasitizing freshwater (i.e., species of *Marsipometra* or *Bathybothrium*) or marine (i.e., species of *Abothrium* or *Parabothrium*) teleosts represent the earliest diverging lineages (Fig. 2). *Philobythoides* sp., the only representative of this family of parasites of bathypelagic fishes, which had previously been assigned to the Philobythiidae, was deeply nested among the paraphyletic triaenophorids as the sister lineage to a clade consisting of species of *Eubothrium*. The family Philobythiidae was thus suppressed.

(2) The Echinophallidae, essentially all of which exclusively parasitize pelagic fishes, are also paraphyletic.

(3) The Bothriocephalidae are monophyletic and consist of a single freshwater and several marine clades, which collectively represent the most derived clade in the order. Biogeographic patterns within the freshwater clade are indicative of rapid radiations having occurred in Africa and North America.

(4) The genus *Bothriocephalus*, as traditionally recognized, contains by far the greatest number of nominal species in the order. However, it represents an artificial assemblage of at least one marine and three unrelated freshwater clades/lineages. Thus, the genus *Bothriocephalus sensu stricto* will be limited to only marine species comprising a clade that includes the type species, *B. scorpii*. For the remaining species, new genera will have to be proposed, but they are provisionally kept in *Bothriocephalus* until these genera are sufficiently circumscribed.

(5) Two species previously assigned to *Bothriocephalus*, namely the Asian fish tapeworm *B. acheilognathi*, which is a widely distributed invasive parasite of numerous teleosts

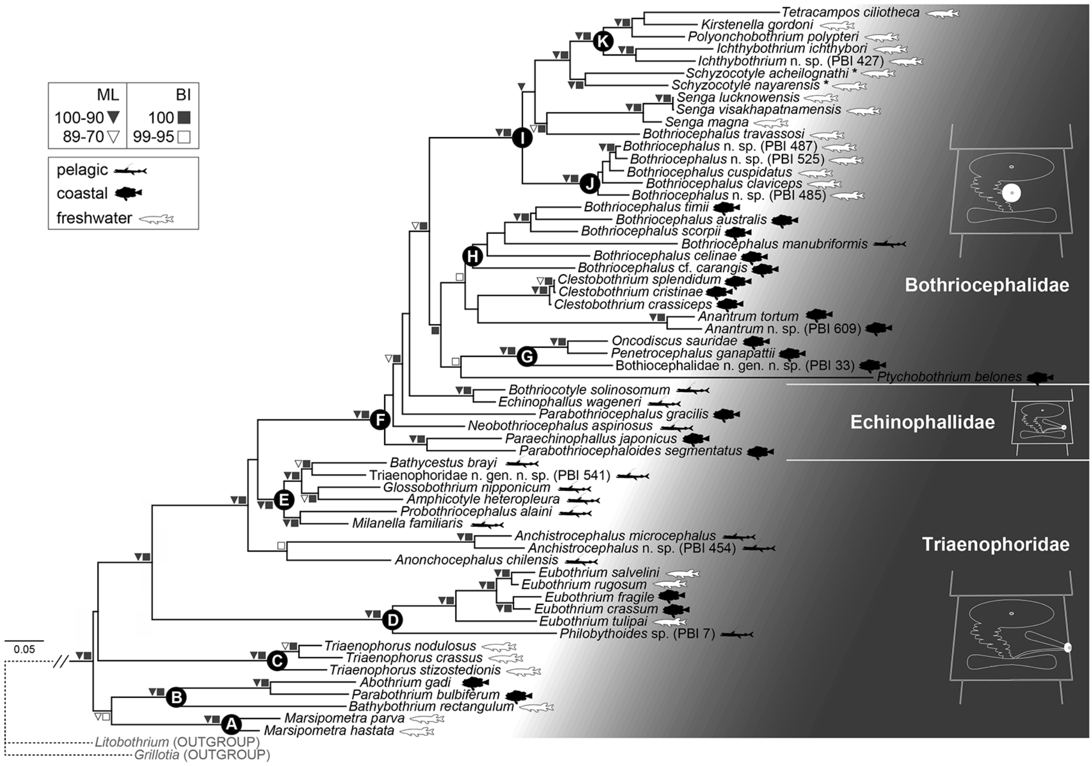

FIGURE 2. Phylogenetic tree of bothriocephalidean interrelationships resulting from maximum likelihood (ML) analysis of the concatenated, four-gene dataset with model parameters estimated separately for each partition. Partitions and models of nucleotide evolution implemented in the ML analysis were as follows: SSU rDNA (GTR+I+Γ), LSU rDNA (GTR+I+Γ), COI codon position 1 (TrN+I+Γ), COI codon position 2 (TVM+I+Γ), COI codon position 3 (TIM+I+Γ), 16S rRNA (GTR+I+Γ). Branch length scale bar indicates number of substitutions per site. Silhouettes indicate definitive host habitat. Current familial placements and corresponding genital pore positions (indicated by sold white circles) are presented to the right of the tree. Modified from Brabec et al. (2015).

(Scholz et al., 2011) and *Ptychobothrium nayarensis* Malhotra, 1983 from India, were transferred to the resurrected genus *Schyzocotyle* Akhmerov, 1960. Both taxa differ from species of *Bothriocephalus* in their possession of a heart-shaped scolex with narrow, deep bothria.

CONCLUSIONS

The period just prior to the PBI was a very active period in the taxonomic history of this group. The order Bothriocephalidea was erected by Kuchta et al. (2008a) and was revised based on morphological characters that same year (Kuchta et al., 2008b). Over the course of the PBI project, relatively few major taxonomic changes have been made, and the amount of new morphological, host association, and distribution data for the order was relatively limited, especially considering the extraordinarily high number of potential hosts examined over that period. In contrast, considerable progress has been made during the PBI project on assessment of the phylogenetic interrelationships of bothriocephalidean cestodes. This came largely from the phylogenetic analyses of data generated for multiple genes for an unprecedented number of bothrocephalidean taxa, which provided a robust phylogenetic framework of the evolutionary history of this relatively small, but ecologically quite heterogeneous group of bothriate cestodes. Considering the obstacles associated with collecting from poorly known marine fishes, especially those living in deep seas that typically exhibit low prevalences of infection, it is difficult to predict reliably how many bothriocephalidean species remain to be discovered and formally described.

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Table 1. List of valid and *incertae sedis* bothriocephalidean taxa with their type hosts. New taxa and taxonomic actions resulting from PBI activities indicated in bold.

VALID TAXA

Family Bothriocephalidae Blanchard, 1849
- *Anantrum* Overstreet, 1968
  - *Anantrum tortum* (Linton, 1904) Overstreet, 1968 (type) ex *Synodus foetens*
  - *Anantrum histocephalum* Jensen & Heckmann, 1977 ex *Synodus lucioceps*
- ***Andycestus* Kuchta, Scholz & Bray, 2008**
  - *Andycestus abyssmus* (Thomas, 1953) **Kuchta, Scholz & Bray, 2008** (type) ex *Eulophias tanneri*
- *Bothriocephalus* Rudolphi, 1808 (syn. *Indobothrium* Sedova & Gulyaev, 2009)
  - *Bothriocephalus scorpii* (Müller, 1776) Cooper, 1917 (type) ex *Myoxocephalus scorpius*
  - *Bothriocephalus andresi* Porta, 1911 ex *Citharus linguatula*
  - *Bothriocephalus antarcticus* Wojciechowska, Pisano & Zdzitowiecki, 1995 ex *Champsocephalus gunnari*
  - *Bothriocephalus apogonis* Yamaguti, 1952 ex *Apogon lineatus*
  - *Bothriocephalus atherinae* Chernyshenko, 1949 ex *Atherina boyeri*
  - ***Bothriocephalus australis* Kuchta, Scholz & Justine, 2009** ex *Platycephalus bassensis*
  - *Bothriocephalus bengalensis* Devi, 1975 ex *Carangoides plagiotaenia*
  - *Bothriocephalus branchiostegi* Yamaguti, 1952 ex *Branchiostegus japonicus*
  - *Bothriocephalus brotulae* Yamaguti, 1952 ex *Brotula multibarbata*
  - *Bothriocephalus carangis* Yamaguti, 1968 ex *Uraspis helfla*
  - ***Bothriocephalus celinae* Kuchta, Scholz & Justine, 2009** ex *Cephalopholis aurantia* x *spiloparaea*
  - *Bothriocephalus cepolae* Rudolphi, 1819 ex *Cepola macrophthalma*
  - *Bothriocephalus clavibothrium* Ariola, 1899 ex *Arnoglossus laterna*
  - *Bothriocephalus claviceps* (Goeze, 1782) Rudolphi, 1810 ex *Anguilla anguilla*
  - *Bothriocephalus cuspidatus* Cooper, 1917 ex *Sander vitreus*
  - *Bothriocephalus euryciensis* Schaeffer & Self, 1978 ex *Eurycea longicauda*
  - *Bothriocephalus fluviatilis* Yamaguti, 1952 ex *Leptobotia curta*
  - *Bothriocephalus formosus* Mueller & Van Cleave, 1932 ex *Percopsis omiscomaycus*
  - *Bothriocephalus gadellus* Blend & Dronen, 2003 ex *Gadella imberbis*
  - *Bothriocephalus japonicus* Yamaguti, 1934 ex *Anguilla japonica*
  - *Bothriocephalus kerguelensis* Prudhoe, 1969 ex *Notothenia cyanobrancha*
  - *Bothriocephalus lateolabracis* Yamaguti, 1952 ex *Lateolabrax japonicus*
  - *Bothriocephalus manubriformis* (Linton, 1889) Ariola, 1900 ex *Kajikia albida*
  - *Bothriocephalus monticelli* Ariola, 1899 ex *Trachypterus iris*
  - *Bothriocephalus nigropunctatus* von Linstow, 1901 ex *Sebastes norvegicus*
  - *Bothriocephalus occidentalis* (Linton, 1897) Lühe, 1899 ex *Sebastes* sp.
  - *Bothriocephalus pearsei* Scholz, Vargas-Vázquez & Moravec, 1996 ex *Cichlasoma urophthalmus*
  - *Bothriocephalus rarus* Thomas, 1937 ex *Triturus viridiscens*
  - *Bothriocephalus sciaenae* Yamaguti, 1934 ex *Pennahia argentata*
  - *Bothriocephalus tetragonus* Ariola, 1899 ex *Anarhichas minor*
  - *Bothriocephalus timii* Gil de Pertierra, Arredondo, Kuchta & Incorvaia, 2015 ex *Cottoperca gobio*
  - *Bothriocephalus travassosi* Tubangui, 1938 ex *Anguilla marmorata*
  - *Bothriocephalus typhlotritonis* Reeves, 1949 ex *Typhlotriton spelaeus*
- *Clestobothrium* Lühe, 1899
  - *Clestobothrium crassiceps* (Rudolphi, 1819) Lühe, 1899 (type) ex *Merluccius merluccius*
  - *Clestobothrium cristinae* Gil de Pertierra, Incorvaia & Arredondo, 2011 ex *Merluccius hubbsi*
  - *Clestobothrium gibsoni* Dronen & Blend, 2005 ex *Bathygadus macrops*
  - *Clestobothrium neglectum* (Lönnberg, 1893) Dronen & Blend, 2003 ex *Raniceps raninus*
  - *Clestobothrium splendidum* Gil de Pertierra, Incorvaia & Arredondo, 2011 ex *Merluccius australis*
- *Ichthybothrium* Khalil, 1971
  - *Ichthybothrium ichthybori* Khalil, 1971 (type) ex *Ichthyborus besse*
- ***Kirstenella* Kuchta, 2012 (in Kuchta et al., 2012)**
  - *Kirstenella gordoni* (Woodland, 1937) **Kuchta, 2012 (in Kuchta et al., 2012)** (type) ex *Heterobranchus bidorsalis*
- *Oncodiscus* Yamaguti, 1934 (syn. *Tetrapapillocephalus* Protasova & Mordvinova, 1986 **[new synonymy: Kuchta et al. (2009)]**)
  - *Oncodiscus sauridae* Yamaguti, 1934 (type) ex *Saurida tumbil*

- *Penetrocephalus* Rao, 1960 **(resurrected: Kuchta et al. [2009])**
  - *Penetrocephalus ganapattii* (Rao, 1954) Rao, 1960 (type) ex *Saurida tumbil*
- *Plicatobothrium* Cable & Michaelis, 1967 (syn. *Alloptychobothrium* Yamaguti, 1968 **(new synonymy: Kuchta et al. [2008b]**)
  - *Plicatobothrium cypseluri* (Rao, 1959) Khalil, 1971 (type) ex *Cypselurus poecilopterus*
- ***Plicocestus* Kuchta, Scholz & Bray, 2008**
  - *Plicocestus janickii* (Markowski, 1971) **Kuchta, Scholz & Bray, 2008** (type) ex *Coryphaena* sp.
- *Polyonchobothrium* Diesing, 1854
  - *Polyonchobothrium polypteri* (Leydig, 1853) Lühe, 1900 (type) ex *Polypterus bichir*
- *Ptychobothrium* Lönnberg, 1889
  - *Ptychobothrium belones* (Dujardin, 1845) Lönnberg, 1889 (type) ex *Belone belone*
  - *Ptychobothrium ratnagiriensis* Deshmukh & Shinde, 1975 ex *Chelipogon cyanopterus*
- *Schyzocotyle* Akhmerov, 1960 (syns. *Capooria* Malhotra, 1985, *Coelobothrium* Dollfus, 1970) **(new synonymy: Brabec et al. [2015])**
  - *Schyzocotyle acheilognathi* (Yamaguti, 1934) **Brabec, Waeschenbach, Scholz, Littlewood, & Kuchta, 2015** (type) ex *Acheilognathus rhombea*
  - *Schyzocotyle nayarensis* (Malhotra, 1983) **Brabec, Waeschenbach, Scholz, Littlewood, & Kuchta, 2015** ex *Raiamas bola*
- *Senga* Dollfus, 1934 (syn. *Aitodiscus* Srivastav & Narayan, 2012 **[new synonymy: present study]**)
  - *Senga besnardi* Dollfus, 1934 (type) ex *Betta splendens*
  - *Senga bagariusi* (Chincholikar & Shinde, 1977) Kuchta & Scholz, 2007 ex *Bagarius* sp.
  - *Senga filiformis* Fernando & Furtado, 1963 ex *Channa micropeltes*
  - *Senga gangesii* Gairola & Malhotra, 1986 ex *Mystus vittatus*
  - *Senga lucknowensis* Johri, 1956 ex *Mastacembelus armatus*
  - *Senga magna* (Zmeev, 1936) Protasova, 1977 ex *Siniperca chuatsi*
  - *Senga malayana* Fernando & Furtado, 1963 ex *Channa striata*
  - *Senga ophiocephalina* (Tseng, 1933) Kuchta & Scholz, 2007 ex *Channa argus*
  - *Senga pahangensis* Furtado & Chau-lan, 1971 ex *Channa micropeltes*
  - *Senga pathankotensis* Duggal & Bedi, 1989 ex *Labeo rohita*
  - *Senga pycnomera* (Woodland, 1924) Dollfus, 1934 ex *Channa marulius*
  - *Senga scleropagis* (Blair, 1978) Kuchta & Scholz, 2007 ex *Scleropages leichardti*
  - *Senga taunsaensis* Zaidi & Khan, 1976 ex *Channa gachua*
  - *Senga visakhapatnamensis* Devi & Rao, 1973 ex *Channa punctata*
- *Taphrobothrium* Lühe, 1899
  - *Taphrobothrium japonense* Lühe, 1899 (type) ex *Muraenesox cinereus*
- *Tetracampos* Wedl, 1861 **(resurrected: Kuchta et al. [2008b])**
  - *Tetracampos ciliotheca* Wedl, 1861 (type) ex *Clarias anguillaris*
  - ***Tetracampos martinae* Kuchta, 2012 (in Kuchta et al., 2012)** ex *Bagrus meridionalis*

FAMILY ECHINOPHALLIDAE SCHUMACHER, 1914

- *Bothriocotyle* Ariola, 1900
  - *Bothriocotyle solinosomum* Ariola, 1900 (type) ex *Centrolophus niger*
- *Echinophallus* Schumacher, 1914
  - *Echinophallus wageneri* (Monticelli, 1890) Schumacher, 1914 (type) ex *Centrolophus niger*
  - *Echinophallus lonchinobothrium* (Monticelli, 1890) Kuchta & Scholz, 2007 ex *Coryphaena hippurus*
  - *Echinophallus peltocephalus* (Monticelli, 1893) Kuchta & Scholz, 2007 ex *Schedophilus ovalis*
  - *Echinophallus seriolellae* Korotaeva, 1975 ex *Seriolella brama*
  - *Echinophallus stossichi* (Ariola, 1896) Kuchta & Scholz, 2007 ex *Trachypterus trachypterus*
- ***Mesoechinophallus* Kuchta, Scholz & Bray, 2008**
  - *Mesoechinophallus hyperogliphe* (Tkachev, 1979) **Kuchta, Scholz & Bray, 2008** (type) ex *Hyperoglyphe japonica*
  - *Mesoechinophallus major* (Takao, 1986) **Kuchta, Scholz & Bray, 2008** ex *Pagrus major*
- *Neobothriocephalus* Mateo & Bullock, 1966
  - *Neobothriocephalus aspinosus* Mateo & Bullock, 1966 (type) ex *Seriolella violacea*
  - *Neobothriocephalus mamaevi* (Tkachev, 1978) Kuchta & Scholz, 2007 ex *Seriolella tinro*
- *Parabothriocephaloides* Yamaguti, 1934 (syn. *Paratelemerus* Gulyaev, Korotaeva & Kurochkin, 1989 **(resurrected: Kuchta et al. [2008b]**))
  - *Parabothriocephaloides segmentatus* Yamaguti, 1934 (type) ex *Psenopsis anomala*
  - *Parabothriocephaloides psenopsis* (Gulyeav, Korotaeva & Kurochkin, 1989) Kuchta & Scholz, 2007 ex *Psenopsis humerosa*
  - *Parabothriocephaloides seriolella* (Gulyeav, Korotaeva & Kurochkin, 1989) Kuchta & Scholz, 2007 ex *Seriolella brama*
  - *Parabothriocephaloides wangi* Kuchta, Scholz & Bray, 2008 ex *Psenopsis anomala* **(nomen novum: Kuchta et al.**

[2008b])

- *Parabothriocephalus* Yamaguti, 1934
  - *Parabothriocephalus gracilis* Yamaguti, 1934 (type) ex *Psenopsis anomala*
  - *Parabothriocephalus johnstoni* Prudhoe, 1969 ex *Macrourus whitsoni*
  - *Parabothriocephalus macruri* Campbell, Correia & Haedrich, 1982 ex *Macrourus berglax*
  - *Parabothriocephalus sagitticeps* (Sleggs, 1927) Jensen, 1976 ex *Sebastes paucispinis*
- *Paraechinophallus* Protasova, 1975
  - *Paraechinophallus japonicus* (Yamaguti, 1934) Protasova, 1975 (type) ex *Psenopsis anomala*
- *Pseudamphicotyla* Yamaguti, 1959 **(transferred from Triaenophoridae: Kuchta et al. [2008b])**
  - *Pseudamphicotyla quinquarii* (Yamaguti, 1952) Yamaguti, 1959 ex *Pentaceros japonicus*

FAMILY TRIAENOPHORIDAE LÖNNBERG, 1889 (SYN. PHILOBYTHIIDAE CAMPBELL, 1977) **(NEW SYNONYMY: BRABEC ET AL. [2015])**

- *Abothrium* van Beneden, 1871
  - *Abothrium gadi* van Beneden, 1871 (type) ex *Gadus morhua*
- *Ailinella* Gil de Pertierra & Semenas, 2006
  - *Ailinella mirabilis* Gil de Pertierra & Semenas, 2006 (type) ex *Galaxias maculatus*
- *Amphicotyle* Diesing, 1863
  - *Amphicotyle heteropleura* (Diesing, 1850) Lühe, 1902 (type) ex *Centrolophus niger*
- *Anchistrocephalus* Monticelli, 1890
  - *Anchistrocephalus microcephalus* (Rudolphi, 1819) Monticelli, 1890 (type) ex *Mola mola*
  - *Anchistrocephalus aluterae* (Linton, 1889) Linton, 1941 ex *Aluterus schoepfii*
- *Anonchocephalus* Lühe, 1902
  - *Anonchocephalus chilensis* (Riggenbach, 1896) Lühe, 1902 (type) ex *Genypterus chilensis*
  - *Anonchocephalus argentinensis* Szidat, 1961 ex *Xystreurys rasile*
  - *Anonchocephalus patagonicus* Suriano et Labriola, 1998 ex *Paralichthys patagonicus*
- *Australicola* Kuchta & Scholz, 2006
  - *Australicola platycephalus* (Monticelli, 1889) (type) Kuchta & Scholz, 2007 ex *Beryx decadactylus*
- *Bathybothrium* Lühe, 1902 (syn. *Fissurobothrium* Roitman, 1965) **(new synonymy: Kuchta et al. [2008b])**
  - *Bathybothrium rectangulum* (Bloch, 1782) Lühe, 1902 (type) ex *Barbus barbus*
  - *Bathybothrium unicum* (Roitman, 1965) Kuchta & Scholz, 2007 ex *Gobio cynocephalus*
- *Bathycestus* Kuchta & Scholz, 2004
  - *Bathycestus brayi* Kuchta & Scholz, 2004 (type) ex *Notacanthus bonaparte*
- *Eubothrioides* Yamaguti, 1952
  - *Eubothrioides lamellatus* Yamaguti, 1952 (type) ex *Zenopsis nebulosa*
- *Eubothrium* Nybelin, 1922
  - *Eubothrium rugosum* (Batsch, 1786) Nybelin, 1922 (type) ex *Lota lota*
  - *Eubothrium acipenserinum* (Cholodkovsky, 1918) Dogiel & Bychowsky, 1939 ex *Acipenser stellatus*
  - *Eubothrium arcticum* Nybelin, 1922 ex *Lycodes pallidus*
  - *Eubothrium crassum* (Bloch, 1779) Nybelin, 1922 ex *Salmo salar*
  - *Eubothrium fragile* (Rudolphi, 1802) Nybelin, 1922 ex *Alosa fallax*
  - *Eubothrium parvum* Nybelin, 1922 ex *Mallotus villosus*
  - *Eubothrium salvelini* (Schrank, 1790) Nybelin, 1922 ex *Salvelinus alpinus*
  - *Eubothrium tulipai* Ching & Andersen, 1983 ex *Ptychocheilus oregonensis*
  - *Eubothrium vittevitellatus* Mamaev, 1968 ex *Trichodon trichodon*
- *Fistulicola* Lühe, 1899
  - *Fistulicola plicatus* (Rudolphi, 1819) Lühe, 1899 (type) ex *Xiphias gladius*
- *Galaxitaenia* Gil de Pertierra & Semenas, 2005
  - *Galaxitaenia toloi* Gil de Pertierra & Semenas, 2005 (type) ex *Glaxias platei*
- *Glossobothrium* Yamaguti, 1952 **(transferred from Echinophallidae: Kuchta et al. [2008b])**
  - *Glossobothrium nipponicum* Yamaguti, 1952 (type) ex unknown marine fish related to *Psenopsis anomala*
- ***Kimocestus* Kuchta, Scholz & Bray, 2008**
  - *Kimocestus ceratias* (Tkachev, 1979) **Kuchta, Scholz & Bray, 2008** (type) ex *Ceratias holboelli*
- *Marsipometra* Cooper, 1917
  - *Marsipometra hastata* (Linton, 1897) Cooper, 1917 (type) ex *Polyodon spathula*
  - *Marsipometra parva* Simer, 1931 ex *Polyodon spathula*
- *Metabothriocephalus* Yamaguti, 1968
  - *Metabothriocephalus menpachi* Yamaguti, 1968 (type) ex *Myripristis amaena*
- *Milanella* Kuchta & Scholz, 2008
  - *Milanella familiaris* Kuchta & Scholz, 2008 (type) ex *Centrolophus niger*

Parabothrium Nybelin, 1922
  Parabothrium bulbiferum Nybelin, 1922 (type) ex *Pollachius pollachius*
Philobythoides Campbell, 1979
  Philobythoides stunkardi Campbell, 1979 (type) ex *Alepocephalus agassizii*
Philobythos Campbell, 1977
  Philobythos atlanticus Campbell, 1977 (type) ex *Acanthochaenus luetkenii*
Pistana Campbell & Gartner, 1982
  Pistana eurypharyngis Campbell & Gartner, 1982 (type) ex *Eurypharynx pelecanoides*
Probothriocephalus Campbell, 1979
  Probothriocephalus muelleri Campbell, 1979 (type) ex *Alepocephalus agassizii*
  Probothriocephalus alaini Scholz & Bray, 2001 ex *Xenodermichthys copei*
  Probothriocephalus atlanticus (Protasova & Parukhin, 1986) Bray, Jones, & Andersen, 1994 ex *Symbolophorus boops*
  Probothriocephalus berycis (Protasova & Parukhin, 1986) Bray, Jones, & Andersen, 1994 ex *Beryx splendens*
  Probothriocephalus electronus (Protasova & Parukhin, 1986) Bray, Jones, & Andersen, 1994 ex *Electrona paucirastra*
Pseudeubothrioides Yamaguti, 1968
  Pseudeubothrioides lepidocybii Yamaguti, 1968 (type) ex *Lepidocybium flavobrunneum*
Triaenophorus Rudolphi, 1793
  Triaenophorus nodulosus (Pallas, 1760) Rudolphi, 1793 (type) ex *Esox lucius*
  Triaenophorus crassus Forel, 1868 ex *Esox lucius*
  Triaenophorus stizostedionis Miller, 1945 ex *Sander vitreus*

TAXA *INCERTAE SEDIS*

Dactylobothrium choprai Srivastav, Khare & Jadhav, 2006 ex *Channa punctata*—*genus* and *species inquirenda*; *incertae sedis*

TABLE 2. Summary of fish (and elasmobranch) hosts examined for tapeworms (by country) over the course of the PBI project by the ~~present~~ authors and their colleagues.

Biogeographic realm Country	No. fish spcms. examined	No. fish species	No. of fish spcms. infected	No. fish species infected	No. of species of Bothriocephalidea	No. of species of Caryophyllidea	No. of species of Onchoproteocephalidea	No. of speices of larval Cyclophyllidea (Gryporhynchidae)	No. of speices of larval Diphyllobothriidea	Members of other cestode orders*	Collector(s)†	Collection date(s)
AFROTROPIC												
Central African Rep.	103	42	3	3	1	2	1	0	0		MJ	IX. 2012
Dem. Rep. Congo	38	16	15	3	1	2	2	0	0		MJ	VII. 2008
Gabon	59	21	0	0	0	0	0	0	0		AC	XI. 2010
Kenya	906	38	142	9	3	4	8	3	0		MJ, MO	2006–2010
Sudan	629	56	177	23	3	7	12	7	0		AC, MJ< TS	XI. 2008, III. 2009
TOTAL (AFROTROPIC)	*1735*		*173*	*PREVALENCE: 19%*								
NEARCTIC												
Canada	77	15	32	12	1	4	2	0	0		MO	VII. 2013
USA (AK)	97	9	23	7	1	0	0	0	5	2 Phyll.	MO, RK	VII. 2013;
USA (MS, SC, TX)	196	30	77	20	4	21	7	0	0		MO, RK	III. 2012
TOTAL (NEARCTIC)	*370*		*132*	*PREVALENCE: 36%*								
NEOTROPIC												
Brazil	242	57	44	17	0	0	30	0	0		AC, TS	IV–VI. 2013
Peru	897	130	210	31	0	0	63	1	0	1 Rhine.	AC, RK, TS	2005–2011
TOTAL (NEOTROPIC)	*1139*		*187*	*PREVALENCE: 22%*								
INDOMALAYA												
Bangladesh	242	35	25	8	1	7	2	0	1		AC, MO, TS	III. 2011
Cambodia	156	22	19	5	1	1	2	0	0		AC, RK, TS	X. 2010
India	915	38	115	21	3	11	5	0	0		AC, MO, TS	II. 2009, III. 2011
Vietnam	273	29	11	4	2	1	0	0	0		AC, RK, TS	X. 2010
TOTAL (INDOMALAYA)	*1586*		*170*	*PREVALENCE: 11%*								
PALEARCTIC												
Bulgaria	450	31	35	10	1	3	2	0	1		VH	VI. 2009, 2010, 2012
China	1707	32	147	9	1	5	2	0	0		MO	III. 2009, III. 2010, IX. 2013
Italy	195	15	25	3	0	0	1	0	1		MO, RK	VIII. 2011; II. 2013
Norway	48	3	3	3	1	0	0	0	0	1 Gyro., 1 Tryp.	MO, RK, TS	V. 2010
Portugal	85	7	5	1	0	1	0	0	0		TS	IX. 2009
Russia (Far East)	302	22	73	13	3	4	7	0	0	1 Nippo.	AC, TS	VI. 2011
Russia (Volga)	256	12	69	7	0	3	2	0	1		VH	VII. 2009
Slovakia	305	32	34	11	2	6	1	1	1	1 Amphi., 1 Nippo.	MO, RK	2010–2013
Svalbard	48	7	5	2	0	0	0	0	1	2 Spathe.	RK	VII. 2008
TOTAL (PALEARCTIC)	*3396*		*396*	*PREVALENCE: 12%*								
TOTAL	**8226**		**1289**	**PREVALENCE: 16%**								

* *Abbreviations:* Amphi., Amphilinidea; Gyro., Gyrocotylidea; Nippo., Nippotaeniidea; Phyllo., Phyllobothriidea (larva); Rhine., Rhinebothriidea; Spathe., Spathebothriidea; Tryp., Trypanorhyncha.

† *Abbreviations:* AC, Alain de Chambrier (Switzerland); MJ, Miloslav Jirků (Czech Republic [CR]); MO, Mikuláš Oros (Slovakia); RK, Roman Kuchta (CR); TS, Tomáš Scholz (CR); VH, Vladimíra Hanzelová (Slovakia)

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Rapid Communication

Suppression of the tapeworm order Pseudophyllidea (Platyhelminthes: Eucestoda) and the proposal of two new orders, Bothriocephalidea and Diphyllobothriidea

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Abstract

Pseudophyllidea van Beneden in Carus, 1863, a well recognised order of tapeworms (Platyhelminthes: Eucestoda), is suppressed because it is composed of two phylogenetically unrelated groups, for which the new names Bothriocephalidea and Diphyllobothriidea are proposed. The new orders differ from each other in the following characters: (i) position of the genital pore: on the dorsal, dorsolateral or lateral aspects and posterior to the ventral uterine pore in the Bothriocephalidea versus on the ventral aspect of segments and anterior to the uterine pore in the Diphyllobothriidea; (ii) the presence of a muscular external seminal vesicle in the Diphyllobothriidea, which is absent in the Bothriocephalidea; (iii) the presence of a uterine sac in the Bothriocephalidea, which is absent in the Diphyllobothriidea; and (iv) the spectrum of definitive hosts: mainly teleost fishes, never homoiothermic vertebrates in the Bothriocephalidea, versus tetrapods, most frequently mammals, in the Diphyllobothriidea, with species of *Diphyllobothrium*, *Spirometra* and *Diplogonoporus* parasitic in humans. The Diphyllobothriidea, which includes 17 genera in four families (*Digramma* is synonymised with *Ligula*), is associated with cestode groups that have a range of plesiomorphic characters (Haplobothriidea and Caryophyllidea), whereas the Bothriocephalidea, consisting of 41 genera grouped in four families, is the sister-group to the 'acetabulate' or 'tetrafossate' cestodes, which are generally regarded as having derived characters.

Keywords: Systematics; New classification; Bothriocephalidea new order; Diphyllobothriidea new order; Differential diagnosis; Cestoda

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1. Introduction

The order Pseudophyllidea van Beneden in Carus, 1863 (Platyhelminthes: Cestoda) is one of the major groups of tapeworms and consists mostly of parasites of marine and freshwater fish, although some genera are specific to mammals or, more rarely, to birds, reptiles and amphibians (Schmidt, 1986; Bray et al., 1994). The order also includes several important parasites of humans, such as species of *Diphyllobothrium*, *Spirometra* and *Diplogonoporus*, as well as pathogens of fish both in aquaculture and free-living, such as species of *Bothriocephalus*, *Eubothrium*, *Ligula*, *Schistocephalus* and *Triaenophorus* (Williams and Jones, 1994; Kassai, 1999; Muller, 2002; Chai et al., 2005).

The first tapeworm placed in the Pseudophyllidea was the "broad fish tapeworm", *Diphyllobothrium latum*, a large parasite of humans, which was briefly described by Linnaeus (1758) under the name *Taenia lata*. One century later, van Beneden in Carus (1863) proposed the name Pseudophyllidea for one of the five groups, among which he accommodated all previously described genera of tapeworms (Cestoda). The taxon Pseudophyllidea was erected by van Beneden, not by Carus as claimed in the literature (Wardle and McLeod, 1952; Yamaguti, 1959; Schmidt, 1986; Bray

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et al., 1994). Van Beneden should therefore be considered the author of the taxon because it was cited with his name when first proposed (Carus, 1863, p. 482) ("Fam. Pseudophyllidea van Ben.") as a family. Major contributions to the systematics of the group were made by Lühe (1902), Wardle and McLeod (1952), Yamaguti (1959), Protasova (1977), Delyamure et al. (1985), Yurakhno (1992), and more recently by Bray et al. (1994, 1999).

The precise position of the Pseudophyllidea within the 'true' tapeworms (Eucestoda) has changed frequently, but pseudophyllideans have usually been placed close to the most basal orders, such as the Caryophyllidea and Spathebothriidea (see Hoberg et al., 1997, 2001 and references therein). Pseudophyllideans have been treated as a monophyletic group in most classifications and have been typified mainly by the possession of two bothria on the scolex (Schmidt, 1986; Jones et al., 1994).

Hoberg et al. (1997) examined the phylogeny of the Eucestoda based on a suite of 49 characters derived from comparative morphological and ontogenetic studies. In the Pseudophyllidea, these authors found as many as 10 characters of the 49 analysed to be multistate and claimed that the Pseudophyllidea may prove to be paraphyletic or polyphyletic. Indeed, the molecular data of Mariaux (1998), based on partial sequences of the 18S rRNA gene, those of Kodedová et al. (2000), who analysed complete sequences of this gene from cestodes of 'lower' vertebrates, and Olson et al. (2001), who compared sequences of the 18S and 28S rRNA genes of members of all recognised orders, indicated paraphyly or polyphyly of the pseudophyllideans.

Brabec et al. (2006) provided evidence that the Pseudophyllidea actually consisted of two unrelated clades, differing markedly from each other in their phylogenetic position within the Eucestoda. An analysis of sequences of the 18S and 28S rRNA genes of 25 representatives of all of the pseudophyllidean families recognised by Bray et al. (1994) has shown that one group, provisionally named 'Diphyllobothriidea' therein, formed a sister group to the Haplobothriidea, a very small group composed of two species in one genus (Brabec et al., 2006). In turn, these taxa were closely related to monozoic caryophyllideans and the putatively most basal spathebothriideans (Brabec et al., 2006). The second clade, 'Bothriocephalidea', is apparently derived, because it appeared as a sister group to the 'higher' ('acetabulate' or 'tetrafossate') tapeworms (Brabec et al., 2006; Waeschenbach et al., 2007) (Fig. 1).

Therefore, the order Pseudophyllidea is formally suppressed in this paper and new orders are proposed to accommodate two unrelated clades possessing dorsal and ventral longitudinal grooves on the scolex called bothria (Bray et al., 1994). In addition, both new orders are characterised and their differential diagnoses, based on morphological and life-cycle characteristics found during a systematic revision of the order (Kuchta, 2007; Kuchta and Scholz, 2007), are provided to reflect the results of recent phylogenetic studies.

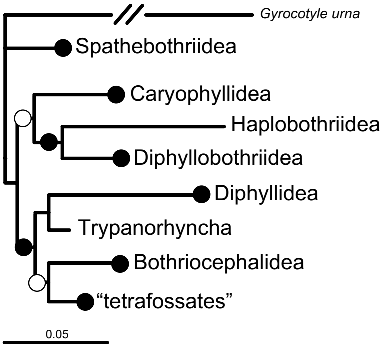

Fig. 1. Phylogenetic tree of basal tapeworms (Eucestoda) inferred from SSU + LSU data (sequences of the small and large subunits of the rRNA gene; modified from Brabec et al., 2006). Bayesian majority rule consensus tree with nodal support based on Bayesian posterior probabilities. Nodal support of 1.00 and >0.90 indicated by filled and open circles, respectively.

2. Results

2.1. Proposal of new orders

2.1.1. ***BOTHRIOCEPHALIDEA* new order** *Figs. 1 and 2a, c–f*

2.1.1.1. Synonyms: Pseudophyllidea van Beneden in Carus (1863) *in part*; Pseudophyllidea van Beneden in Carus (1863) *sensu* Wardle et al. (1974); Bothriocephalata Freze (1974); Bothriocephalinea Euzet (1982).

2.1.1.2. Diagnosis. Cestoda: Eucestoda. Small to large tapeworms. Strobila usually segmented. Segmentation complete, incomplete, or rarely absent. Segments usually craspedote, wider than long, anapolytic. Two pairs of main osmoregulatory canals; ventral canals usually wider, thin-walled; dorsal canals narrow, thick-walled. Scolex variable in shape, unarmed, or rarely with hooks, may be replaced by pseudoscolex or *scolex deformatus*. Scolex with dorsal and ventral longitudinal grooves, termed bothria. Apical disc present or absent. Neck present or absent. Reproductive organs single in segment, rarely two symmetrical sets of proglottids present in segment. Testes numerous, medullary, usually in two lateral fields. Sperm ducts convoluted; external seminal vesicle absent. Cirrus-sac with or without internal seminal vesicle; cirrus unarmed or armed with spines or tegumental bulbs. Genital pores on dorsal surface (median or submedian) or lateral, irregularly alternating. Ovary medullary, usually bilobed, compact, folliculate or dendritic, posterior. Vitellarium follicular, extensive, exceptionally single, cortical, less often medullary or paramuscular (between bundles of inner longitudinal muscles). Uterus variable in shape, divided into tubular, convoluted uterine duct that may enlarge and compact or diverticulate (branched) uterine sac; ventral uterine pore present or absent. Eggs with or without operculum, egg may be embryonated in uterus; free ciliated coracidium may be present, usually when eggs are not embryonated in uterus. One or two intermediate hosts: procercoids develop in copepods (Crustacea), plerocercoids, if present, in fish.

Adults in intestine of fish, exceptionally in amphibians (newts).

2.1.2. **DIPHYLLOBOTHRIIDEA new order** Figs. 1 and 2b, g

2.1.2.1. Synonyms: Pseudophyllidea van Beneden in Carus (1863) *in part*; Diphyllidea Wardle et al. (1974) (*nec* van Beneden in Carus, 1863); Diphyllobothriata Freze (1974); Diphyllobothriinea Euzet (1982); Polygonoporiata Yurakhno (1992).

2.1.2.2. Diagnosis. Cestoda: Eucestoda. Medium-sized to large tapeworms. Strobila usually segmented. Segmentation complete or incomplete; rarely absent. Segments craspedote or acraspedote, usually wider than long, anapolytic. Two pairs of main osmoregulatory canals; ventral canals usually wider, thin-walled; dorsal canal narrow, thick-walled. Scolex variable in shape, always unarmed, with dorsal and ventral longitudinal grooves, termed bothria. Apical disc absent, or rarely present. Neck present or absent. Reproductive organs single in segment, rarely double or multiple proglottids in segment. Testes numerous, medullary, usually in single field. Sperm ducts convoluted, with thick-walled, muscularised external seminal vesicle attached to proximal part of cirrus-sac. Cirrus-sac usually thick-walled; cirrus unarmed. Internal seminal vesicle occasionally present. Genital pore ventral (median or submedian). Ovary medullary, usually bilobed, posterior. Vitelline follicles numerous, cortical, rarely paramuscular (between bundles of inner longitudinal muscles), circum-medullary. Uterus tubular, variable in shape, opening to exterior through uterine pore situated posterior to genital pore; uterine sac absent. Eggs usually operculate, unembryonated; free, ciliated coracidium present. Usually two intermediate hosts: procercoids develop in copepods (Crustacea), plerocercoids in vertebrates. Adults in intestine of tetrapods, most frequently in mammals.

2.2. *Differential diagnosis*

The new orders, previously included within the Pseudophyllidea, were differentiated from other cestode orders currently recognised as valid (Khalil et al., 1994; Olson et al., 2001; Caira et al., 2005) by the morphology of the scolex which possesses dorsal and ventral longitudinal grooves (i.e. bothria) serving as attachment organs, external segmentation, proglottization and a follicular vitellarium (Jones et al., 1994).

The Bothriocephalidea differs from the Diphyllobothriidea in the following characteristics:

(i) The genital pores (openings of the cirrus-sac and vagina) are median, submedian or sublateral on the dorsal surface or are lateral, whereas they are on the ventral surface in the Diphyllobothriidea;
(ii) The uterine pore is anterior to the genital pore, whereas it is posterior in the Diphyllobothriidea;
(iii) An external seminal vesicle is absent, but is present in the Diphyllobothriidea;
(iv) A uterine sac is present, but is lacking in the Diphyllobothriidea;
(v) The spectrum of definitive hosts includes fish, with a few taxa found in newts, which contrasts with that of the Diphyllobothriidea which are found only in tetrapods, never in fish.

Both new orders belong among the 'bothriate' groups (previously also named less appropriately 'difossate' – see Olson et al., 2001), the attachment organs of which are not separated from the surrounding tissue by a well demarcated plasma membrane (*lamina basalis*) (Caira et al., 1999, 2001; Jones et al., 2004). However, the position of the Bothriocephalidea and Diphyllobothriidea among other major groups of the 'bothriate' tapeworms remains unclear, as do the relationships among basal tapeworms (Olson and Caira, 1999; Kodedová et al., 2000; Olson et al., 2001; Olson and Tkach, 2005; Waeschenbach et al., 2007). Therefore, putative sister groups of the Bothriocephalidea and Diphyllobothriidea are not unequivocally identifiable.

Nevertheless, recent molecular data indicate that the Diphyllobothriidea are associated with the taxa that have a range of plesiomorphic characters, namely the Haplobothriidea and Caryophyllidea (Fig. 1) (Waeschenbach et al., 2007). All three groups share the following characters, some of them, however, being present also in other 'bothriate' groups (for more data see Khalil et al., 1994; Hoberg et al., 1997, 2001; Olson et al., 2001): (i) the genital pores and uterus open on the ventral side of the segment; (ii) the vitellarium consists of numerous follicles usually distributed throughout the segment; (iii) the operculate, unembryonated eggs; (iv) the male genital pore is anterior to the uterine pore. The last character, present also in the Spathebothriidea and Gyrocotylidea, might represent a symplesiomorphy retained by the basal tapeworms (Cestoda).

Besides possessing a strobila with well-developed external segmentation, the polyzoic Diphyllobothriidea can also be distinguished from the monozoic (non-segmented) Caryophyllidea by scolex morphology (see Mackiewicz, 1994, 2003), the anterior or equatorial position of the uterus (confined to the posterior part of the body in the Caryophyllidea), parasitism in tetrapods, never in fish (versus teleost fish as the only definitive hosts in the latter group), a two-host life cycle involving copepods (versus tubificid oligochaetes in the Caryophyllidea), and other morphological, ultrastructural, spermiological and biological characters reviewed by Mackiewicz (1972, 1994, 2003) and Hoberg et al. (1997, 2001).

The order Haplobothriidea contains only two species in one genus, *Haplobothrium*, parasitic in a relict fish species, the bowfin (*Amia calva*), and its affinities and systematic position have been controversial (Jones, 1994). As an independent family, the Haplobothriidae Cooper, 1917, was placed within the Pseudophyllidea by Wardle and McLeod (1952), Yamaguti (1959) and Schmidt (1986), whereas

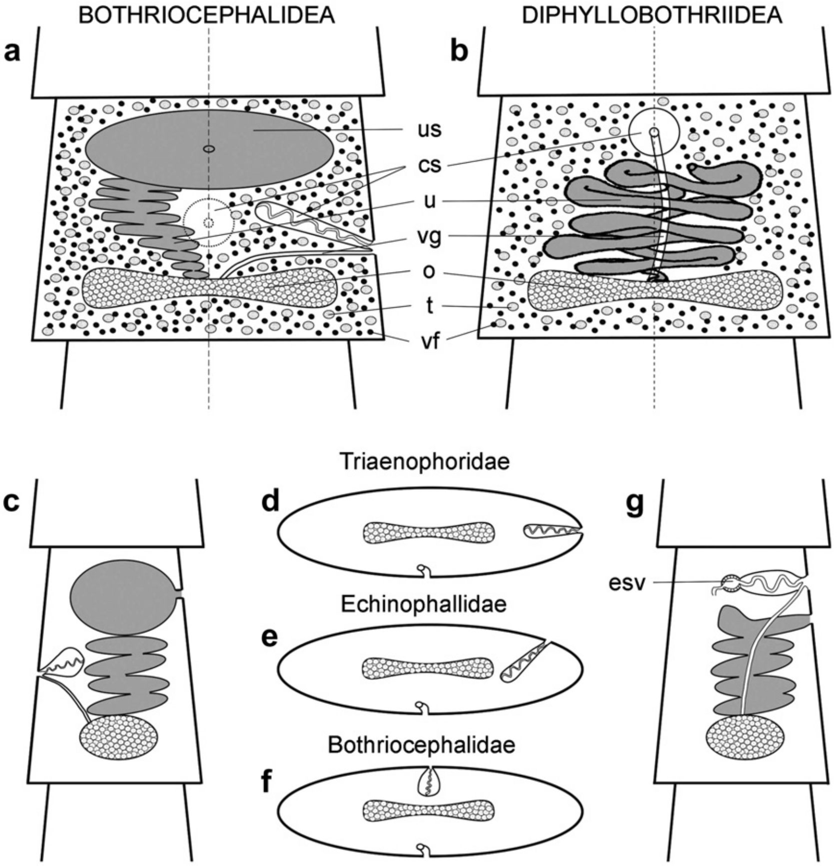

Fig. 2. Schematic drawings of differential morphological characteristics of the new orders Bothriocephalidea (a, c–f) and Diphyllobothriidea (b and g). (a) and (b), ventral view; (c) and (g), lateral view; (d–f), cross-section. *Abbreviations:* cs, cirrus-sac; esv, external seminal vesicle; o, ovary; t, testes; u, uterus; us, uterine sac; vf, vitelline follicles; vg, vagina.

Euzet (1959, 1974) and Dubinina (1980) considered haplobothriideans to be a sister group of the Pseudophyllidea. The anatomy of the segments and the life-cycle patterns are characteristic of the Diphyllobothriidea (Jones, 1994), but haplobothriids differ markedly in possessing a tentacle-bearing primary scolex (absent in the Diphyllobothriidea), an undivided secondary scolex depressed on four sides and a dilated uterine sac (a uterine sac is absent in diphyllobothriideans) (Bray et al., 1994; Jones, 1994).

The phylogenetic position of the Bothriocephalidea is also not resolved satisfactorily (Waeschenbach et al., 2007), but molecular data indicate that it may be a sister-group to the ‘acetabulate’ (‘tetrafossate’) tapeworms, which are generally regarded as having derived characters (Hoberg et al., 1997, 2001; Olson et al., 2001; Brabec et al., 2006; Waeschenbach et al., 2007). ‘Acetabulate’ cestodes differ from bothriocephalideans in possessing acetabulate attachment organs, i.e. bothridia, suckers or both (Caira et al., 1999, 2001).

Molecular analyses have also indicated possible relationships between bothriocephalideans, diphyllideans and trypanorhynchs, the latter being parasites of elasmobranchs (Brabec et al., 2006; Waeschenbach et al., 2007). Although members of the latter two orders also possess bothria or bothria-like attachment organs (Olson et al., 2001; Jones et al., 2004), they are markedly different in their scolex morphology. The scolex of diphyllideans consists of a ‘head’ and a cephalic peduncle (Khalil, 1994), whereas that of the Trypanorhyncha possesses a unique rhyncheal apparatus with four armed, retractable tentacles (Campbell and Beveridge, 1994).

2.3. List of families and genera recognised in the new orders

2.3.1. *Order* ***BOTHRIOCEPHALIDEA new order***

2.3.1.1. *Bothriocephalidae Blanchard, 1849.*

Synonyms: Ptychobothriidae Lühe, 1902; Acompsocephalidae Rees, 1969.

Type-genus: Bothriocephalus Rudolphi, 1808.

Other valid genera: Anantrum Overstreet, 1968; *Clestobothrium* Lühe, 1899; *Ichthybothrium* Khalil, 1971; *Oncodiscus* Yamaguti, 1934; *Penetrocephalus* Rao, 1960; *Plicatobothrium* Cable & Michaelis, 1967; *Polyonchobothrium* Diesing, 1854; *Ptychobothrium* Lönnberg, 1889; *Senga* Dollfus, 1934; *Taphrobothrium* Lühe, 1899; *Tetracampos* Wedl, 1861.

2.3.1.2. *Echinophallidae Schumacher, 1914.*

Synonym: Parabothriocephalidae Yamaguti, 1934.

Type-genus: Echinophallus Schumacher, 1914.

Other valid genera: Bothriocotyle Ariola, 1900; *Neobothriocephalus* Mateo & Bullock, 1966; *Parabothriocephaloides* Yamaguti, 1934; *Parabothriocephalus* Yamaguti, 1934; *Paraechinophallus* Protasova, 1975; *Pseudamphicotyla* Yamaguti, 1959.

2.3.1.3. Philobythiidae Campbell, 1977.

Type-genus: Philobythos Campbell, 1977.

Other valid genus: Philobythoides Campbell, 1979.

2.3.1.4. Triaenophoridae Lönnberg, 1889.

Synonyms: Amphicotylidae Lühe, 1889; Ancistrocephalidae Protasova, 1974.

Type-genus: Triaenophorus Rudolphi, 1793.

Other valid genera: Abothrium van Beneden, 1871; *Ailinella* Gil de Pertierra & Semenas, 2006; *Amphicotyle* Diesing, 1863; *Anchistrocephalus* Monticelli, 1890; *Anonchocephalus* Lühe, 1902; *Australicola* Kuchta & Scholz, 2006; *Bathybothrium* Lühe, 1902; *Bathycestus* Kuchta & Scholz, 2004; *Eubothrioides* Yamaguti, 1952; *Eubothrium* Nybelin, 1922; *Fistulicola* Lühe, 1899; *Galaxitaenia* Gil de Pertierra & Semenas, 2005; *Glossobothrium* Yamaguti, 1952; *Marsipometra* Cooper, 1917; *Metabothriocephalus* Yamaguti, 1968; *Parabothrium* Nybelin, 1922; *Pistana* Campbell & Gartner, 1982; *Pseudeubothrioides* Yamaguti, 1968; *Probothriocephalus* Campbell, 1979.

Remarks. A detailed revision of the order with amended generic diagnoses and keys to identification is in preparation (Kuchta et al., in preparation).

2.3.2. Order ***DIPHYLLOBOTHRIIDEA*** **new order**

2.3.2.1. Diphyllobothriidae Lühe, 1910.

Synonyms: Baylisiidae Yurakhno, 1992; Baylisiellidae Yurakhno, 1992; Ligulidae Claus, 1868; Glandicephalidae Yurakhno & Maslev, 1995; Schistocephalidae Yurakhno, 1992.

Type-genus: Diphyllobothrium Cobbold, 1858.

Other valid genera: Baylisia Markowski, 1952; *Baylisiella* Markowski, 1952; *Diplogonoporus* Lönnberg, 1892; *Flexobothrium* Yurakhno, 1979; *Glandicephalus* Fuhrmann, 1921; *Ligula* Bloch, 1782; *Plicobothrium* Rausch & Margolis, 1969; *Pyramicocephalus* Monticelli, 1890; *Schistocephalus* Creplin, 1829; *Spirometra* Faust, Campbell & Kellogg, 1929; *Tetragonoporus* Skriabin, 1961.

Remarks. Based on molecular data (Luo et al., 2003; Logan et al., 2004), *Digramma* Cholodkovsky, 1914 is synonymised with *Ligula*, in agreement with Wardle and McLeod (1952), who considered *Digramma* to be merely a rare diplogonadic type of *Ligula*. *Multiductus* Clarke, 1962 was synonymised with *Tetragonoporus* Skriabin, 1961 by Delyamure and Skriabin (1968). Bray et al. (1994) considered *Polygonoporus* Skriabin, 1967 to be a synonym of *Hexagonoporus* Gubanov in Delyamure, 1955, which, however, is considered herein to be a *genus inquirendum* because the original description is incomplete (no data on the scolex, etc.).

2.3.2.2. Cephalochlamydidae Yamaguti, 1959.

Type-genus: Cephalochlamys Blanchard, 1908.

Other valid genus: Paracephalochlamys Jackson & Tinsley, 2001.

2.3.2.3. Scyphocephalidae Freze, 1974.

Type-genus: Scyphocephalus Riggenbach, 1898.

Other valid genera: Bothridium Blainville, 1824; *Duthiersia* Perrier, 1873.

3. Discussion

Molecular data (Brabec et al., 2006; Waeschenbach et al., 2007) provided evidence that both new orders, previously placed in the Pseudophyllidea, are phylogenetically distinct. The present study includes the results of molecular analyses and a subsequent morphology-based evaluation of most ‘pseudophyllidean’ genera in proposing a new ordinal classification. Several morphological characters typical of each of these groups were found, which enabled us to distinguish them from one another. They were also distinguishable based on their host groups. In contrast, the presence of paired, dorsal and ventral grooves, termed bothria, on the scolex may represent a homoplastic character, because it appears in phylogenetically distinct cestode groups. However, the possible homologies of bothria and bothrium-like attachment organs present in the so-called ‘bothriate’ eucestodes, including diphyllideans and trypanorhynchs, are yet to be identified (Caira et al., 1999, 2001; Olson et al., 2001; Jones et al., 2004).

The Pseudophyllidea has previously been split into two or three groups by some authors (Freze, 1974; Euzet, 1982; Yurakhno, 1992; Bray et al., 1999; Hoberg et al., 2001), but none of them suppressed the order as such and both of the taxa here raised to ordinal level have almost always been considered to be members of the monophyletic order Pseudophyllidea (Hoberg et al., 1997, 2001). Wardle et al. (1974) were the first to separate genera of the current diphyllobothriideans (referred to as ‘Diphyllidea’) from bothriocephalideans, for which the original name of the order (‘Pseudophyllidea’) was used. However, these authors provided neither justification for the separation of the groups, nor a differential diagnosis. In addition, the nomenclature they proposed was confusing, especially in the case of the former group, because the name Diphyllidea, considered by Wardle et al. (1994) to be a *nomen oblitum*, has been widely used for cestodes parasitic in elasmobranchs (Khalil et al., 1994; Tyler, 2006).

The term ‘Pseudophyllidea’ has been used for a long time for those segmented tapeworms that possessed paired attachment organs formed by dorsal and ventral longitudinal grooves or tubes in the case of the genus *Bothridium*. However, the composition of the order has changed considerably, as has its delimitation from other cestode orders. Several cestode groups now recognised as independent ordinal taxa (Khalil et al., 1994), such as the monozoic caryophyllideans, the non-segmented spathebothriideans and the haplobothriideans, have previously been placed in the Pseudophyllidea (Lühe, 1899, 1902; Nybelin, 1922; Fuhrmann, 1931; Wardle and McLeod, 1952; Brooks et al., 1991). Mola (1921, 1928) even included lecanicephalideans from elasmobranchs in the order. Since retaining the name 'Pseudophyllidea' for only one of the groups previously considered to constitute the pseudophyllidean tapeworms could potentially cause great confusion, this name is suppressed and two new names are proposed to accommodate the newly erected orders.

Similarly, two suborders erected by Freze (1974), Diphyllobothriata and Bothriocephalata, are not elevated to ordinal status in order to prevent possible confusion, based on the following reasons: (i) Freze (1974) did not provide any justification for his new classification nor did he present differential diagnoses of component taxa (suborders, superfamilies, families and subfamilies), some of which were proposed as new taxa; (ii) the revised classification of the Pseudophyllidea appeared only as abstract from an international congress; the text contains only one introductory sentence and then a list of the higher taxa included; (iii) the names of the suborders erected by Freze (1974) did not follow widely accepted rules and did not end with "-idea"; thus, Freze's (1974) names would cause confusion; (iv) the International Code of Zoological Nomenclature does not apply for taxon names above the family level.

The Bothriocephalidea was considered to be composed of four families by Bray et al. (1994), but molecular data indicate that some families may be paraphyletic or polyphyletic (Brabec et al., 2006). Similarly, several genera, including the largest genus *Bothriocephalus*, may include unrelated species groups (Škeříková et al., 2004; Kuchta, 2007).

Regarding the patterns of host associations, a putatively more basal position of the Diphyllobothriidea compared with that of the Bothriocephalidea, most members of which are parasites of teleost fish, indicates that diphyllobothriideans may represent an example of early colonization of tetrapods (Hoberg et al., 1999).

Bray et al. (1999) suggested that egg morphology and development, as described by Freeman (1973), could be integrated into phylogenetic appraisals of 'pseudophyllidean' cestodes. However, it should be emphasized that the data on egg morphology and development, although potentially very promising (see Beveridge, 2001), are difficult to use in the systematics of the 'Pseudophyllidea', as argued by Bray et al. (1994), because reliable information is absent on the most significant characters previously used to delimit genera and families, such as the presence or absence of an operculum and embryonation of eggs (Freze, 1974; Protasova, 1977; Schmidt, 1986). In addition, almost no data are available on the life-cycles and postembryonic development of marine species that form a major part of the Bothriocephalidea (see Kuchta and Scholz, 2007).

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Revision of the order Bothriocephalidea Kuchta, Scholz, Brabec & Bray, 2008 (Eucestoda) with amended generic diagnoses and keys to families and genera

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Abstract The tapeworm order Bothriocephalidea Kuchta, Scholz, Brabec & Bray, 2008 (Platyhelminthes: Eucestoda), which has until recently formed part of the suppressed order Pseudophyllidea, is revised. Four new genera, namely *Andycestus* n. g. [type- and only species *A. abyssmus* (Thomas, 1953) n. comb.], *Plicocestus* n. g. [type- and only species *P. janickii* (Markowski, 1971) n. comb.] (both Bothriocephalidae), *Mesoechinophallus* n. g. [type-species *M. hyperogliphe* (Tkachev, 1979) n. comb.; other species *M. major* (Takao, 1986) n. comb. (Echinophallidae)] and *Kimocestus* n. g. [type- and only species *K. ceratias* (Tkachev, 1979) n. comb.] (Triaenophoridae) are proposed. *Parabothriocephaloides* Yamaguti, 1934, *Penetrocephalus* Rao, 1960 and *Tetracampos* Wedl, 1861 are resurrected as valid genera, whereas *Alloptychobothrium* Yamaguti, 1968 (newly synonymised with *Plicatobothrium* Cable & Michaelis, 1967), *Capooria* Malhotra, 1985 and *Coelobothrium* Dollfus, 1970 (syns of *Bothriocephalus* Rudolphi 1808), *Fissurobothrium* Roitman, 1965 (syn. of *Bathybothrium* Lühe, 1902), *Paratelemerus* Gulyaev, Korotaeva & Kurochkin, 1989 (syn. of *Parabothriocephaloides* Yamaguti, 1934) and *Tetrapapillocephalus* Protasova & Mordvinova, 1986 (syn. of *Oncodiscus* Yamaguti, 1934) are considered to be invalid. A recently erected genus, *Dactylobothrium* Srivastav, Khare & Jadhav, 2006, and its type- and only species, *D. choprai* Srivastav, Khare & Jadhav, 2006, are considered to be unrecognisable, because their descriptions contain a number of obvious errors and also indicate that a mixture of several taxa, probably of at least two cestode orders, were studied. *Parabothriocephaloides wangi* nom. nov. is proposed for *Parabothriocephalus psenopsis* Wang, Liu & Yang, 2004 from *Psenopsis anomala* in China in order to avoid a secondary homonymy. All 46 genera considered to be valid are revised, with their generic diagnoses amended on the basis of a critical examination of extensive museum and newly collected specimens. Despite apparent paraphyly or polyphyly of some bothriocephalidean families, especially the Triaenophoridae, the current classification restricted to four families, proposed by Bray et al. (1994), namely the Bothriocephalidae, Echinophallidae, Philobythiidae and Triaenophoridae, is provisionally retained with slight modifications until more molecular data on most genera are available. Keys to families and genera are provided.

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Introduction

Systematics of the Bothriocephalidea – historical overview

The order Bothriocephalidea Kuchta, Scholz, Brabec & Bray, 2008 has been proposed recently (Kuchta et al., 2008a) to accommodate those tapeworms of the previously recognised order Pseudophyllidea Beneden in Carus, 1863 which are characterised by: (i) the genital pore on the dorsal, dorsolateral or lateral aspects of the segment and posterior to the ventral uterine pore; (ii) the absence of a muscular external seminal vesicle; (iii) the presence of a sacciform uterus (forming a sac and, therefore, sometimes known as a uterine sac); and (iv) the spectrum of definitive hosts: mainly teleost fishes, never homoiothermic vertebrates (Kuchta et al., 2008a). The order Pseudophyllidea was one of the major cestode groups and consisted mostly of parasites of marine and freshwater teleost fish, but some genera were specific to mammals and, less frequently, to birds, reptiles and amphibians (Schmidt, 1986; Bray et al., 1994).

Pseudophyllideans were typified mainly by the possession of two bothria on the scolex (Yamaguti, 1959; Schmidt, 1986; Bray et al., 1994). The bothrium is an attachment organ formed by a longitudinal groove or depression of different shape and depth on the ventral and dorsal surfaces of the scolex (Wardle & McLeod, 1952). The margins of the bothria are delimited by a feebly developed musculature, formed by diffuse muscle fibres, which are not separated from the surrounding tissue by a well demarcated plasma membrane (*lamina basalis*) (Fuhrmann, 1931; Caira et al., 1999).

The most notable contributions to the systematics of the Pseudophyllidea around the turn of the 19th and 20th Centuries were those of Lühe (1899, 1902). Another important contribution was made by Nybelin (1922), who revised the cestodes of fish now placed in the Caryophyllidea, Spathebothriidea, Pseudophyllidea and Proteocephalidea, and established several new species and genera, such as *Eubothrium* Nybelin, 1922 and *Parabothrium* Nybelin, 1922.

A very important contribution to the systematics of cestodes, including pseudophyllideans, was that presented by Wardle & McLeod (1952). These authors recognised 40 genera (23 bothriocephalidean and 17 diphyllobothriidean) within seven families. The Caryophyllidea and Spathebothriidea, treated as pseudophyllideans by some previous researchers, such as Nybelin (1922) and Fuhrmann (1931), were removed from the Pseudophyllidea as independent orders and this status has been widely accepted (Wardle & McLeod, 1952; Schmidt, 1986; Khalil et al., 1994; Hoberg et al., 1997, 2001; Mariaux, 1998; Olson et al., 2001).

Thirty years later, the same authors (Wardle et al., 1974) published an updated version of their monograph and presented a different view on tapeworm systematics. They split pseudophyllidean tapeworms into two independent orders, the Pseudophyllidea Beneden in Carus, 1863 *sensu stricto* with 24 genera, corresponding more or less to the present Bothriocephalidea (see Kuchta et al., 2008a), but also including the Haplobothriidea Joyeux & Baer, 1961, currently recognised as a separate order (Khalil et al., 1994), and Diphyllidea Wardle, McLeod & Radinovsky, 1974 (*nec* Diphyllidea Beneden in Carus, 1863, considered by these authors to be a *nomen oblitum* – see p. 64, and comprising exclusively parasites of elasmobranchs) with 16 genera. The latter order corresponds in its composition, i.e. inclusion of the Diphyllobothriidae Lühe, 1910 and Cephalochlamydidae Yamaguti, 1959, to the present Diphyllobothriidea (see Kuchta et al., 2008a).

Another revision of the cestodes, including pseudophyllideans, was made by Yamaguti (1959), as a part of his extensive series of monographs on all groups of helminths. This author recognised nine pseudophyllidean families with a total of 44 genera (28 bothriocephalidean and 16 diphyllobothriidean). In the proceedings of a conference, Euzet (1982) divided the Pseudophyllidea into two suborders based on the position of the genital pore, i.e. the Bothriocephalinea and Diphyllobothriinea, but did not propose them formally as new taxa. Schmidt (1986) listed 10 families, including the Haplobothriidae Meggitt, 1924 (now considered as a separate order – see Khalil et al., 1994), with as many as 58 valid genera (*Haplobothrium* Cooper, 1914, 40 bothriocephalidean and 17 diphyllobothriidean).

The systematics of the Pseudophyllidea was also treated in detail by Russian authors in two volumes of a series "*Fundamentals of Cestodology*", which were based on the system proposed by Freze (1974). He recognised two new suborders, the Bothriocephalata Freze, 1974 (with the superfamilies Bothriocephaloidea Blanchard, 1849 and Amphicotyloidea Lühe, 1902) and the Diphyllobothriata Freze, 1974 (with the superfamilies Diphyllobothrioidea Lühe, 1910 and Scyphocephaloidea Freze, 1974). This system was followed by Dubinina (1987) in the keys to the parasites of freshwater fish of the USSR.

Protasova (1974, 1977) reviewed the suborder Bothriocephalata, which she divided into seven families in two superfamilies. She recognised 96 valid species in 32 genera, not considering another 31 taxa treated as *species inquirendae*. Although Protasova (1977) redescribed some taxa on the basis of her own observations, keys were provided only to families, subfamilies and some genera. The author discussed the possible evolution of individual groups of the Bothriocephalata on the basis of the development of the uterus, but her conclusions have not been supported by molecular data (Brabec et al., 2006).

The most recent and widely recognised taxonomic monograph of cestodes, with generic diagnoses and keys to all genera was edited by Khalil et al. (1994). The Pseudophyllidea was treated by Bray, Jones & Andersen (1994) and the number of families was reduced to six (Bothriocephalidae, Cephalochlamydidae, Diphyllobothriidae, Echinophallidae, Philobythiidae and Triaenophoridae), with a total of 56 valid genera (40 bothriocephalidean and 16 diphyllobothriidean).

Molecular taxonomy

The Pseudophyllidea was previously considered to be a relatively basal, monophyletic group of “difossate” cestodes (Hoberg et al., 1997, 2001). However, the results of Mariaux (1998), based on partial sequences of the 18S rRNA gene, as well as those of Kodedová et al. (2000), who analysed complete sequences of this gene of cestodes from the “lower” vertebrates, indicated the presence of two unrelated clades and, thus, paraphyly or polyphyly of the pseudophyllideans.

The most comprehensive molecular study by Brabec et al. (2006), based on sequences of the 18S and 28S rRNA genes of 25 representatives of all pseudophyllidean families recognised by Bray et al. (1994), provided unequivocal evidence that the Pseudophyllidea actually consists of two unrelated clades, markedly differing in their phylogenetic position within major groups of the Eucestoda (Brabec et al., 2006). The subsequent study of Waeschenbach et al. (2007) confirmed these data.

Recently, two new orders, the Bothriocephalidea and Diphyllobothriidea, have been proposed to accommodate these unrelated assemblages of taxa circumscribed by molecular data and previously forming the Pseudophyllidea (Kuchta et al., 2008a). The Bothriocephalidea has been revised on the basis of a critical examination of literature and the morphological and molecular study of museum and newly collected specimens of most genera. In the present paper, the updated diagnoses of all families and genera of the Bothriocephalidea, and keys to their identification are provided, including the proposal of four new genera.

Materials and methods

Material studied

The data used for the revision were obtained from three main sources:

(i) a critical examination of the extensive literature, with a focus on the original descriptions of the type-species of each genus; the data on bothriocephalideans used for constructing the Global Cestode Database (see Caira et al., 2006; www.tapeworms.org) were also considered;

(ii) study of type- and voucher specimens of bothriocephalideans available in the following helminthological collections: Natural History Museum, London, UK (BMNH); Parasitological Institute, Russian Academy of Sciences, Moscow, Russia (GELAN); 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, Berlin, Germany (NMB); Naturhistorisches Museum, Vienna, Austria (NMW); United States National Parasite Collection, Beltsville, Maryland, USA (USNPC); Zoological Institute, Russian Academy of Sciences (ZIRAS); and Zoological Museum, University of Oslo, Norway (ZMUO);

(iii) morphological, ultrastructural (scanning electron microscopy – SEM) and molecular evaluation of freshly collected material. A major part of this material was collected during field expeditions of the two first authors and their collaborators in Europe (Czech Republic, Finland, Italy, Norway, Russia, Scotland, Slovakia), North Atlantic off the Outer Hebrides, North Sea, Mediterranean Sea, Africa (Ethiopia, Sudan), Asia (Indonesia, Japan, Thailand) and Latin America (Mexico, Peru). Extensive material of other taxa was also kindly provided by a number of foreign collaborators, whose names are listed in the Acknowledgements. In total, representatives of 43 of the 46 valid genera of the Bothriocephalidea were studied.

Processing and evaluation of newly collected cestodes

New material of bothriocephalidean cestodes was obtained from freshly killed hosts obtained from local fisherman or caught using trawl nets. Tapeworms taken alive from the intestine were rinsed in saline and immediately fixed with hot (almost boiling) 4% formaldehyde solution, then transferred to 70% ethanol for storage, stained with Mayer's carmine, dehydrated through a graded ethanol series, cleared in clove oil (eugenol) and mounted in Canada balsam as permanent preparations. Cross and longitudinal 12 μm thick sections were prepared using a standard histological procedure, stained with haematoxylin-eosin and then mounted in Canada balsam (Scholz & Hanzelová, 1998). Several scoleces and segments were prepared for scanning electron microscopy (SEM) using the methodology outlined by Scholz et al. (1998). The specimens were mounted on stubs, sputter-coated with gold-palladium and examined using a JEOL 7401F scanning electron microscope. Line drawings were made with a drawing tube of an Olympus microscope BX-51 with Nomarski interference contrast. Measurements were made using a computer program QuickPHOTO MICRO 2.1. Inc.

The names of fish hosts were corrected, where necessary, according to the FishBase database (Froese & Pauly, 2008).

Order Bothriocephalidea Kuchta, Scholz, Brabec & Bray, 2008

Syns Pseudophyllidea Beneden in Carus, 1863 in part; Pseudophyllidea Carus, 1863 *sensu* Wardle, McLeod & Radinovsky (1974) in part; Bothriocephalata Freze, 1974 in part; Bothriocephalinea Euzet, 1982 in part

Diagnosis: Eucestoda. Small to large tapeworms. Strobila proglottised. Segmentation complete or incomplete, rarely absent. Segments usually craspedote, wider than long, anapolytic. Scolex variable in shape, usually unarmed, rarely with hooks, may be replaced by pseudoscolex or *scolex deformatus*. Scolex usually with one dorsal and one ventral bothria of different shape and depth in individual taxa. Apical disc present or absent. Neck present or absent. Reproductive organs single, rarely paired in segment (genitalia duplicated). Testes numerous, medullary, usually in two lateral fields, interrupted or confluent medially and continuous between segments. Vas deferens sinuous; external seminal vesicle absent. Cirrus-sac with or without internal seminal vesicle; cirrus unarmed or armed with spines or tegumental protuberances. Genital pore on dorsal surface, median, sublateral or lateral, irregularly alternating. Ovary medullary, usually bilobed, compact, follicular or dendritic, posterior. Vitellarium formed by numerous follicles, exceptionally compact, cortical, medullary or both. Uterine duct sinuous, may enlarge in gravid segments. Uterus forming sac variable in shape, compact or diverticulate (branched). Ventral uterine pore present or absent, anterior to genital pore. Eggs operculate or without operculum, embryonated in uterus or not; ciliated coracidium may develop within egg capsule in water. One or rarely two intermediate hosts (procercoids in copepods, plerocercoids in fish). Adults in intestine of fish, exceptionally in amphibians (salamanders).

Families: Bothriocephalidae Blanchard, 1849; Echinophallidae Schumacher, 1914; Philobythiidae Campbell, 1977; Triaenophoridae Lönnberg, 1889.

Remarks: The order is typified, as is the Diphyllobothriidea, by having paired attachment organs called bothria, but differs from the latter in the characters listed above (see also Kuchta et al., 2008a). Despite the fact that bothriocephalideans mature in fish, especially teleosts, all available data suggest that they are more highly derived than diphyllobothriideans. Results of recent molecular studies on basal cestodes (Brabec et al., 2006; Waeschenbach et al., 2007) indicate that the Bothriocephalidea is the sister taxon to the 'tetrafossate' (acetabulate) cestodes.

Key to the families of the Bothriocephalidea

The key corresponds to that provided by Bray et al. (1994) with slight modifications. As discussed below, it is apparent that bothriocephalidean families are not natural groupings of phylogenetically related taxa, especially members of the largest and most diverse family Triaenophoridae (see Brabec et al., 2006). Nevertheless, a new classification of families is not proposed here because of lack of molecular and other data on numerous groups which could not be placed in newly proposed families. Therefore, the present classification should be considered as tentative until sufficient information on phylogenetic relationships of bothriocephalidean genera is available.

1a. Genital pore median … Bothriocephalidae (p. 85)
1b. Genital pore lateral or sublateral 2
2a. Genital pore sublateral … Echinophallidae (p. 86)
2b. Genital pore lateral 3
3a. Vitellarium compact ..... Philobythiidae (p. 86)
3b. Vitellarium follicular … Triaenophoridae (p. 87)

Diagnoses of the families of the Bothriocephalidea

Bothriocephalidae Blanchard, 1849

Syns Ptychobothriidae Lühe, 1902; Acompsocephalidae Rees, 1969

Diagnosis: Small to medium-sized tapeworms. Strobila flattened or rarely spirally twisted. Segmentation present or absent. Segments craspedote or not, usually wider than long. Scolex variable in shape, usually with two bothria, exceptionally absent. Apical disc present or absent, rarely armed with hooklets. Segments with one set of genitalia, rarely duplicated. Testes medullary, mostly in two lateral bands, confluent or separated medially. Cirrus-sac small, thin-walled; cirrus unarmed. Genital pore median or slightly submedian. Ovary posterior, usually transversely elongate. Vagina posterior to cirrus-sac. Vitelline follicles usually cortical, may be intermingled with longitudinal muscle fibres or rarely medullary. Uterine duct sinuous, passing around cirrus-sac. Uterus spherical to oval, rarely lobulate. Uterine pore median or submedian. Eggs operculate or not, embryonated or not. Usually one intermediate host (Crustacea: Copepoda). Adults in intestine of marine and freshwater fish, exceptionally in amphibians (salamanders).

Type-genus: *Bothriocephalus* Rudolphi, 1808.

Other genera: *Anantrum* Overstreet, 1968; ***Andycestus* n. g.**; *Clestobothrium* Lühe, 1899; *Ichthybothrium* Khalil, 1971; *Oncodiscus* Yamaguti, 1934; *Penetrocephalus* Rao, 1960; *Plicatobothrium* Cable & Michaelis, 1967; ***Plicocestus* n. g.**; *Polyonchobothrium* Diesing, 1854; *Ptychobothrium* Lönnberg, 1889; *Senga* Dollfus, 1934; *Taphrobothrium* Lühe, 1899; *Tetracampos* Wedl, 1861.

Key to the genera of the Bothriocephalidae

1a. Segmentation absent or incomplete 2
1b. Segmentation present 5
2a. Scolex with developed bothria 3
2b. Scolex elongate or clavate, without bothria .... *Anantrum* (p. 92)
3a. Scolex elongate, much longer than wide 4
3b. Scolex oval .... *Ichthybothrium* (p. 107)
4a. Scolex tear-shaped, without apical disc; uterus lobulate .... *Andycestus* n. g. (p. 93)
4b. Scolex very large, elongate, bothrial margins crenulated, apical disc present; uterus oval .... *Plicocestus* n. g. (p. 121)
5a. Scolex oval, elongate to sagittate 6
5b. Scolex with crenulate margins of bothria or replaced by *scolex deformatus* 11
6a. Scolex unarmed 7
6b. Scolex armed 9
7a. Vitelline follicles medullary, intermingled with testes; eggs embryonated … ..... *Taphrobothrium* (p. 125)
7b. Vitelline follicles cortical; eggs unembryonated 8
8a. Scolex without sphincter surrounding anterior aperture of bothria .... *Bothriocephalus* (p. 97)
8b. Scolex with sphincter surrounding anterior aperture of bothria .... *Clestobothrium* (p. 99)
9a. Eggs unembryonated, without external hyaline membrane 10
9b. Eggs embryonated, with external hyaline membrane .... *Tetracampos* (p. 126)
10a. Apical disc of scolex prominent, quadrilobed, wider than scolex proper … *Polyonchobothrium* (p. 122)
10b. Apical disc of scolex not prominent, narrower than scolex proper .... *Senga* (p. 125)

11a. Segments with prominent posterolateral wing-like projections 12
11b. Segments without posterolateral wing-like projections 13
12a. Scolex replaced by *scolex deformatus*, encapsulated in pseudocyst .... *Penetrocephalus* (p. 118)
12b. Scolex compressed laterally, bothrial margins crenulated .... *Oncodiscus* (p. 113)
13a. Posterior margins of scolex not projecting posteriorly over anterior part of strobila, bothrial margins crenulated internally .... *Ptychobothrium* (p. 124)
13b. Posterior margins of scolex projecting over anterior part of strobila, bothrial margins crenulated externally .... *Plicatobothrium* (p. 120)

Echinophallidae Schumacher, 1914

Syns Acanthophallidae Cholodkovsky, 1914 (pre-occ.); Amphitretidae Cholodkovsky, 1914 (pre-occ.); Parabothriocephalidae Yamaguti, 1934

Diagnosis: Small to large tapeworms. Strobila flattened, rarely spiral and concave ventrally. Segmentation present or incomplete. Genitalia single or paired (duplicated in segment). Segments craspedote, wider than long. Posterolateral margins of segments or pseudosegments usually armed with band of giant spiniform microtriches. Scolex present or replaced by pseudoscolex. Apical disc present or absent. Bothria weakly developed, may possess sucker-like structure on elongate posterior end. Testes medullary. Cirrus-sac large, usually thick-walled. Cirrus usually armed with spines. Genital pore sublateral. Ovary posterior, lobulated to dendritic. Vagina posterior to cirrus-sac. Vitelline follicles cortical, rarely paramuscular or medullary. Uterine duct sinuous. Uterus oval. Uterine pore ventral, median or submedian. Eggs operculate or not, unembryonated. In intestine of marine, often centrolophid teleosts (Perciformes).
Type-genus: *Echinophallus* Schumacher, 1914.
Other genera: *Bothriocotyle* Ariola, 1900; ***Mesoechinophallus* n. g.**; *Neobothriocephalus* Mateo & Bullock, 1966; *Parabothriocephaloides* Yamaguti, 1934; *Parabothriocephalus* Yamaguti, 1934; *Paraechinophallus* Protasova, 1975; *Pseudamphicotyla* Yamaguti, 1959.

Remarks: *Pseudamphicotyla* was placed by Bray et al. (1994) in the Triaenophoridae, but it is here considered to be a member of the Echinophallidae because of the presence of a sublateral genital pore and a cirrus armed with spines. On the other hand, *Glossobothrium* and *Metabothriocephalus*, which both possess a lateral genital pore, an unarmed cirrus and lack large spiniform microtriches on the posterolateral margin of segments, which is a characteristic typical of most echinophallids, are now transferred to the Triaenophoridae.

Key to the genera of the Echinophallidae

1a. Genitalia single in segment 2
1b. Genitalia paired in segment 6
2a. Scolex present 3
2b. Scolex replaced by pseudoscolex .... *Parabothriocephaloides* (p. 115)
3a. Bothria without posterior slit-like depression 4
3b. Bothria with posterior slit-like depression .... *Bothriocotyle* (p. 98)
4a. Bothria not divided into several loculi 5
4b. Bothria divided into several loculi .... *Pseudamphicotyla* (p. 123)
5a. Cirrus-sac without conspicuous swelling in proximal part .... *Parabothriocephalus* (p. 116)
5b. Cirrus-sac with conspicuous spherical swelling in proximal part .... *Neobothriocephalus* (p. 112)
6a. Genital pore markedly sublateral; cirrus smaller 7
6b. Genital pore close to lateral margins; cirrus large, with large spines .. *Paraechinophallus* (p. 117)
7a. Scolex present; vitelline follicles only ventrally; cirrus armed .... *Echinophallus* (p. 100)
7b. Scolex replaced by *scolex deformatus*; vitelline follicles circumsegmental; cirrus unarmed .... *Mesoechinophallus* n. g. (p. 109)

Philobythiidae Campbell, 1977

Diagnosis: Small tapeworms. Strobila flattened. Segmentation present. Segments craspedote, trapeziform. Scolex oval, unarmed; bothria oval to elongate; apical disc weakly developed or absent. One set of genitalia per segment. Testes medullary, in one or two fields

confluent anteriorly. Cirrus-sac small; cirrus unarmed. Genital pore lateral. Vagina anterior to cirrus-sac. Ovary posterior, compact. Vitellarium compact, medullary, dendritic to lobed, forming transverse band posterior to ovary. Uterine duct straight, short. Uterus inverted V-shaped in mature segments, enlarging in gravid segments, slightly lobed or branched. Uterine pore median. Eggs embryonated, covered with membraneous capsule. In intestine of deep-sea teleosts.
Type-genus: *Philobythos* Campbell, 1977.
Other genus: *Philobythoides* Campbell, 1979.

Key to the genera of the Philobythiidae

1a. Scolex with apical disc; uteus trilobulate; 3–5 oncospheres within membraneous capsule……. ……………………… *Philobythos* (p. 119)
1b. Scolex without apical disc; uterus transverse elongate; single oncospheres within membraneous capsule ……… *Philobythoides* (p. 119)

Triaenophoridae Lönnberg, 1889

Syns Amphicotylidae Lühe, 1889; Ancistrocephalidae Protasova, 1974

Diagnosis: Medium-sized to large tapeworms. Segmentation usually present. Single set of genitalia in segment, rarely paired (duplicated). Segments mostly wider than long, craspedote. Scolex of variable shape, rarely replaced by *scolex deformatus*. Apical disc present or not, unarmed, exceptionally armed with hooks. Bothria present, exceptionally absent, shallow to well-developed, occasionally with projecting posterior margins. Testes medullary. Cirrus-sac small to large; cirrus unarmed or rarely covered with small protuberances. Genital pore lateral. Ovary posterior. Vagina posterior or anterior to cirrus-sac. Vitelline follicles cortical or medullary, may intrude between inner longitudinal musculature. Uterine duct sinuous. Uterus compact or lobulate. Uterine pore present or not, ventral, median or submedian. Eggs operculate or not, embryonated or not. Ciliated coracidium present or not. In intestine of freshwater and marine teleosts.
Type-genus: *Triaenophorus* Rudolphi, 1793.
Other genera: *Abothrium* Beneden, 1871; *Ailinella* Gil de Pertierra & Semenas, 2006; *Amphicotyle* Diesing, 1863; *Anchistrocephalus* Monticelli, 1890; *Anonchocephalus* Lühe, 1902; *Australicola* Kuchta & Scholz, 2006; *Bathybothrium* Lühe, 1902; *Bathycestus* Kuchta & Scholz, 2004; *Eubothrioides* Yamaguti, 1952; *Eubothrium* Nybelin, 1922; *Fistulicola* Lühe, 1899; *Galaxitaenia* Gil de Pertierra & Semenas, 2005; *Glossobothrium* Yamaguti, 1952; ***Kimocestus* n. g.**; *Marsipometra* Cooper, 1917; *Metabothriocephalus* Yamaguti, 1968; *Milanella* Kuchta & Scholz, 2008; *Parabothrium* Nybelin, 1922; *Pistana* Campbell & Gartner, 1982; *Pseudeubothrioides* Yamaguti, 1968; *Probothriocephalus* Campbell, 1979.
Genus dubium and *incertae sedis*: *Dactylobothrium* Srivastav, Khare & Jadhav, 2006.

Key to the genera of the Triaenophoridae

1a. Scolex armed …………………………… 2
1b. Scolex unarmed ………………………… 3
2a. Scolex armed with several alternating rows of small hooks around apical disc ……………… …………………………*Anchistrocephalus* (p. 92)
2b. Scolex armed with four trident-shaped hooks .. …………………… *Triaenophorus* (p. 127)
3a. Scolex replaced by *scolex deformatus* ……. 4
3b. Scolex usually present …………………… 5
4a. Vitelline follicles intermingled with testes, circumsegmental, continuous between segments .. …………………………*Abothrium* (p. 88)
4b. Vitelline follicles only ventral, not intermingled with testes, in two fields in posterior part of segment …………… *Parabothrium* (p. 117)
5a. Vagina opening anterior to or at same level as cirrus-sac ……………………………… 6
5b. Vagina opening posterior cirrus-sac ……… 11
6a. Vagina opening anterior to cirrus-sac …….. 7
6b. Vagina opening at same level as cirrus-sac … ……………………………*Bathybothrium* (p. 95)
7a. Scolex clearly demarcated from neck (or anterior part of strobila) ………………………… 8
7b. Scolex not clearly demarcated from neck ……. ………………… *Metabothriocephalus* (p. 111)
8a. Segments numerous, wider than long or quadrate, craspedote ……………………………… 9
8b. Segments few in number, longer than wide, acraspedote ………………*Ailinella* (p. 89)
9a. Seminal receptacle absent; uterus without diverticula ………………………………… 10
9b. Seminal receptacle large; uterus branched, with numerous lateral diverticula …………………… ………………………….. *Marsipometra* (p. 108)

10a. Genital atrium deep; uterus transverse oval ... . *Australicola* (p. 95)
10b. Genital atrium shallow; uterus transverse elongate .... *Eubothrium* (p. 101)
11a. Ovary compact to lobed 12
11b. Ovary dendritic .... *Pistana* (p. 120)
12a. Cirrus-sac with markedly thickened distal wall 13
12b. Cirrus-sac without thickened distal wall ... 15
13a. Cirrus with small protuberances; bothria without sucker-like structure posteriorly 14
13b. Cirrus smooth; bothria with sucker-like structure posteriorly ..... *Glossobothrium* (p. 105)
14a. Scolex sagittate, with very long free posterior margins; vitelline follicles cortical .... *Kimocestus* n. g. (p. 107)
14b. Scolex sagittate; vitelline follicles medullary, limited to ventral surface .... *Anonchocephalus* (p. 94)
15a. Bothria without posterior sucker-like depression 16
15b. Bothria with posterior sucker-like depression .... *Amphicotyle* (p. 89)
16a. Vitelline follicles circumsegmental 17
16b. Vitelline follicles only in posterior part of segment; bothrial margins crenulate .... *Eubothrioides* (p. 101)
17a. Cirrus-sac postequatorial to equatorial; osmoregulatory canals narrow 18
17b. Cirrus-sac markedly pre-equatorial; osmoregulatory canals wide .... *Pseudeubothrioides* (p. 123)
18a. Segments trapeziform or slightly longer than wide 19
18b. Segments much wider than long, with extended posterolateral margins .... *Fistulicola* (p. 103)
19a. Uterus oval to elongate 20
19b. Uterus pyriform in first gravid segments .... *Milanella* (p. 111)
20a. Vitelline follicles continuous between segments 21
20b. Vitelline follicles in two ventrolateral fields, separated between segments .... *Galaxitaenia* (p. 105)
21a. Scolex linguiform to elongate; bothria without posterior margins ... *Probothriocephalus* (p. 122)
21b. Scolex sagittate; bothria with well-developed posterior margins .... *Bathycestus* (p. 96)

Diagnoses of the genera of the Bothriocephalidea

Based on the evaluation of numerous type- and voucher specimens and the examination of extensive new material of taxa of most (91%) of the bothriocephalidean genera, supplemented by a critical review of the literature, all genera of the Bothriocephalidea considered to be valid are characterised in the present study in order to update the information presented in the most comprehensive taxonomic treatment of the group (Bray et al., 1994). The authors have not been able to examine specimens of four genera (*Dactylobothrium*, *Eubothrioides*, *Galaxitaenia* and *Pseudamphicotyla*) so their diagnoses are based on the literature, which is often incomplete or even erroneous. This implies that future studies based on appropriately fixed material and sequences of suitable genes might show some differences in diagnoses of individual genera. In addition, some genera, in particular *Bothriocephalus*, are probably paraphyletic or polyphyletic and may also contain a number of invalid taxa. A critical revision of the species composition of individual genera was not amongst the aims of this study, but a preliminary list of species tentatively considered to be valid, with their synonyms, type-hosts and distribution has been published by Kuchta & Scholz (2007).

The genera are listed alphabetically irrespective of the family to which they belong (see lists of genera of individual families above). This arrangement also seems to us to be more appropriate because it is probable that the current familial classification, including placement of genera in individual bothriocephalidean families, will change when more molecular data are available. In addition, we felt this arrangement would assist the reader to recover information easily.

Abothrium Beneden, 1871 (Figs. 4A, 5A)

Diagnosis: Bothriocephalidea, Triaenophoridae. Large worms. Strobila robust with well developed inner longitudinal musculature formed by several layers of massive bundles of muscular fibres. Segmentation present. Segments much wider than long, slightly craspedote. Scolex modified to *scolex deformatus*, unarmed. Apical disc and bothria absent. Neck not distinguishable. Testes in two lateral fields, separated between segments. Cirrus-sac small, with internal seminal vesicle; cirrus unarmed. Genital pore marginal. Ovary compact, median. Vagina posterior to cirrus-sac. Vitelline follicles medullary, in two lateral fields, separated between segments. Uterine duct sinuous, short. Uterus thin-walled, transverse elongate, occupying most of segment volume in terminal gravid segments. Uterus opening by rupture of segment wall. Eggs unoperculate, embryonated. In marine teleosts (Gadiformes). North Atlantic and Pacific Oceans.

Type- and only species: *A. gadi* Beneden, 1871 ex gadiform fish (*Gadus*, *Melanogrammus* and *Merluccius*).

Material studied: *A. gadi* ex *Melanogrammus aeglefinus* (L.) from the North Atlantic Ocean (IPCAS C-439).

Remarks: *Abothrium* originally included several species parasitic in marine and freshwater fish, but Nybelin (1922) proposed two new genera, *Eubothrium* and *Parabothrium*, to accommodate all but one species previously placed in *Abothrium*. Therefore, *Abothrium* is now monotypic and can be differentiated from other triaenophorids by the possession of a modified scolex (*scolex deformatus*), which is deeply embedded in the intestinal mucosal layer, and medullary vitelline follicles.

According to Williams (1960), who provided a very detailed morphological description of *A. gadi*, and Bray et al. (1994), *Abothrium* possesses a uterine pore ("uterine pore median"), but the pore was not observed in the specimens studied. This corresponds to the observations of Protasova (1977), who noted that no real uterine pore is present and eggs are released by rupture of the wall of segments.

Ailinella **Gil de Pertierra & Semenas, 2006 (Figs. 1A, 5E)**

Diagnosis: Bothriocephalidea, Triaenophoridae. Small worms. Strobila weakly muscular, without discernible inner longitudinal musculature, consisting of a small number of elongate segments, easy to detach. Segmentation present. Scolex elongate, with truncate anterior end. Bothria shallow, transversely oval, with prominent posterior margins. Apical disc present. Neck present. Testes in one central field, separated between segments, surrounding ovary laterally and posteriorly. Cirrus-sac small, oval; internal seminal vesicle present; cirrus unarmed. Genital pore marginal. Ovary compact, asymmetrical. Vagina anterior to cirrus-sac. Vitelline follicles surrounding internal genital organs. Uterine duct enlarged in gravid segments. Uterus elongate. Uterine pore midventral. Eggs operculate, unembryonated. In freshwater teleosts (*Galaxias*). Patagonia, Argentina.

Type- and only species: *A. mirabilis* Gil de Pertierra & Semenas, 2006 ex *Galaxias maculatus* (Jenyns) (Osmeriformes: Galaxiidae), Patagonia.

Material studied: *A. mirabilis* ex *Galaxias maculatus* (IPCAS C-438 – paratype).

Remarks: This monotypic genus was erected recently to accommodate a new species of bothriocephalidean cestodes found in a galaxiid fish from southern Argentina (Patagonia). It differs markedly from other triaenophorid genera in possessing a tiny strobila composed of a low number of elongate segments, the absence of an inner longitudinal musculature, the distribution of testes which surround the ovary posteriorly, and the shape of the scolex and bothria.

In the morphology of the strobila, which is composed of a few easily detached segments, *A. mirabilis* superficially resembles the nippotaeniid *Nippotaenia contorta* Hine, 1977 reported from *Galaxias maculatus* in New Zealand, which apparently led to the misidentification of *Ailinella* material from this host in Argentina as *Nippotaenia* sp. (see references in Gil de Pertierra & Semenas, 2006). Another triaenophorid cestode, *Galaxitaenia toloi* Gil de Pertierra & Semenas, 2005, has recently been described from a congeneric fish host, *Galaxias platei* Steindachner. It can easily be distinguished from *A. mirabilis* by a number of morphological characteristics (see Figs. 2A, 6J, and Gil de Pertierra & Semenas, 2005, 2006).

Amphicotyle **Diesing, 1863 (Figs. 1B, 5B)**

Diagnosis: Bothriocephalidea, Triaenophoridae. Medium-sized worms. Segmentation present. Strobila robust, composed of markedly craspedote (velum-like or pectinate), very short and wide segments; each segment consisting of two pseudosegments, posterior one being slightly larger. Longitudinal musculature well developed. In stained preparation, numerous intensely stained corpuscles present throughout strobila, reaching scolex. Scolex trapeziform with freely projecting posterior margins in lateral view. Bothria elongate, shallow, with spherical, sucker-like depression near posterior margin. Apical disc present. Neck absent. Testes

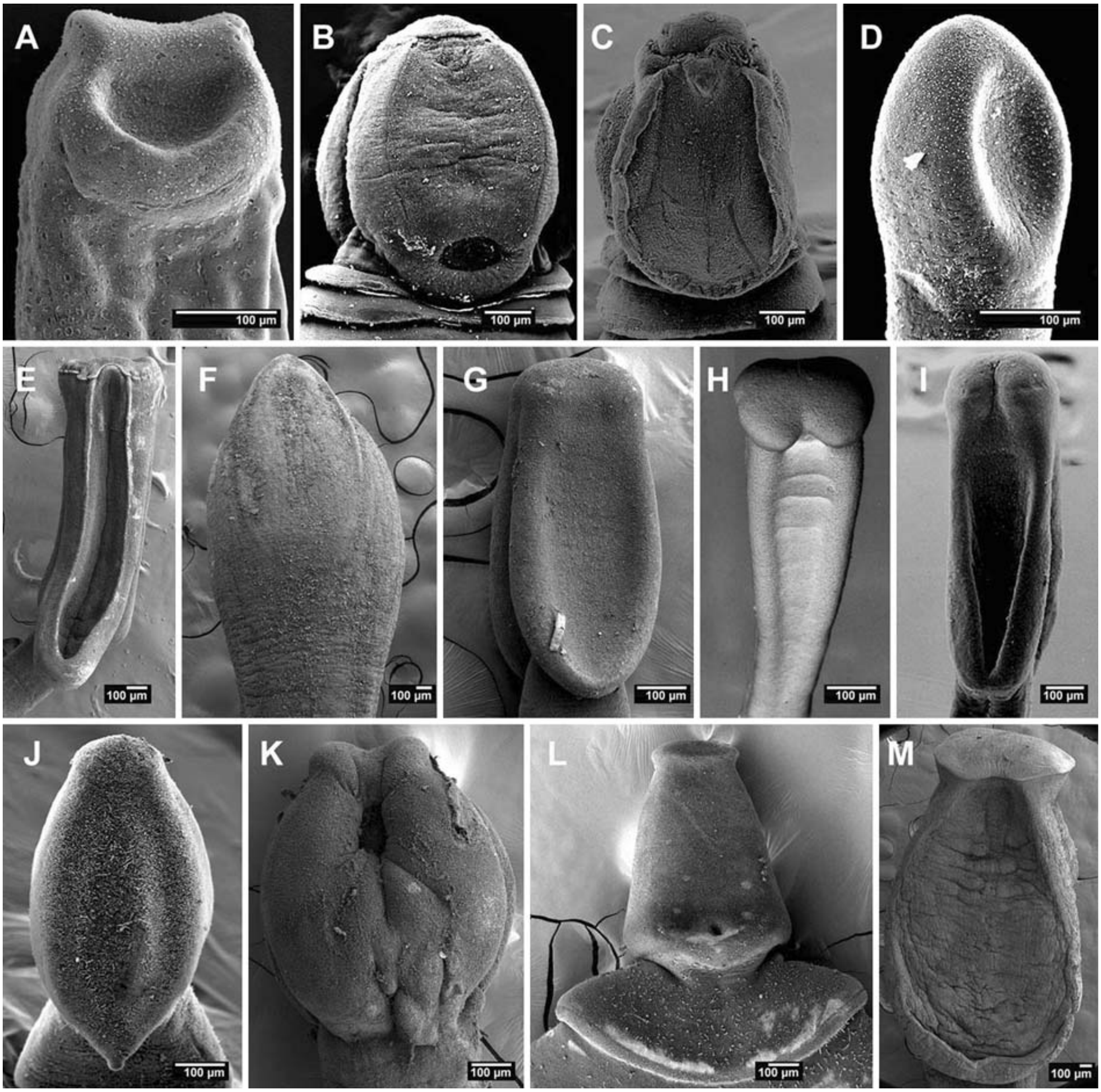


Fig. 1 Scanning electron micrographs of scoleces of bothriocephalidean cestodes. (**A**) *Ailinella mirabilis* ex *Galaxias maculatus*, adapted from Gil de Pertierra & Semenas (2006); (**B**) *Amphicotyle heteropleura* ex *Centrolophus niger*, adapted from Kuchta et al. (2008b); (**C**) *Anchistrocephalus microcephalus* ex *Mola mola*, original; (**D**) *Bathybothrium rectangulum* ex *Barbus barbus*, original; (**E**) *Anonchocephalus chilensis* ex *Genypterus maculatus*, original; (**F**) *Australicola platycephalus* ex *Beryx decadactylus*, original; (**G**) *Bathycestus brayi* ex *Notacanthus bonaparte*, original; (**H**) *Bothriocephalus claviceps* ex *Anguilla anguilla*, original; (**I**) *Eubothrium rugosum* ex *Lota lota*, adapted from Kuchta et al. (2005); (**J**) *Bothriocotyle solinosomum* ex *C. niger*, adapted from Kuchta et al. (2008b); (**K**) *Clestobothrium crassiceps* ex *Merluccius merluccius*, original; (**L**) *Echinophallus wageneri* ex *Centrolophus niger*, adapted from Kuchta et al. (2008b); (**M**) *Fistulicola plicatus* ex *Xiphias gladius*, original

forming large field continuous between segments. Cirrus-sac large, pyriform, thick-walled; cirrus unarmed, with tegumental invaginations (folds) in its lumen. Genital pore lateral. Ovary irregularly shaped, lobulate, in dorsal medulla, with lobes intruding among muscle bundles of inner longitudinal musculature. Vagina posterior to cirrus-sac. Vitelline follicles circumcortical, including posterior velum-like processes

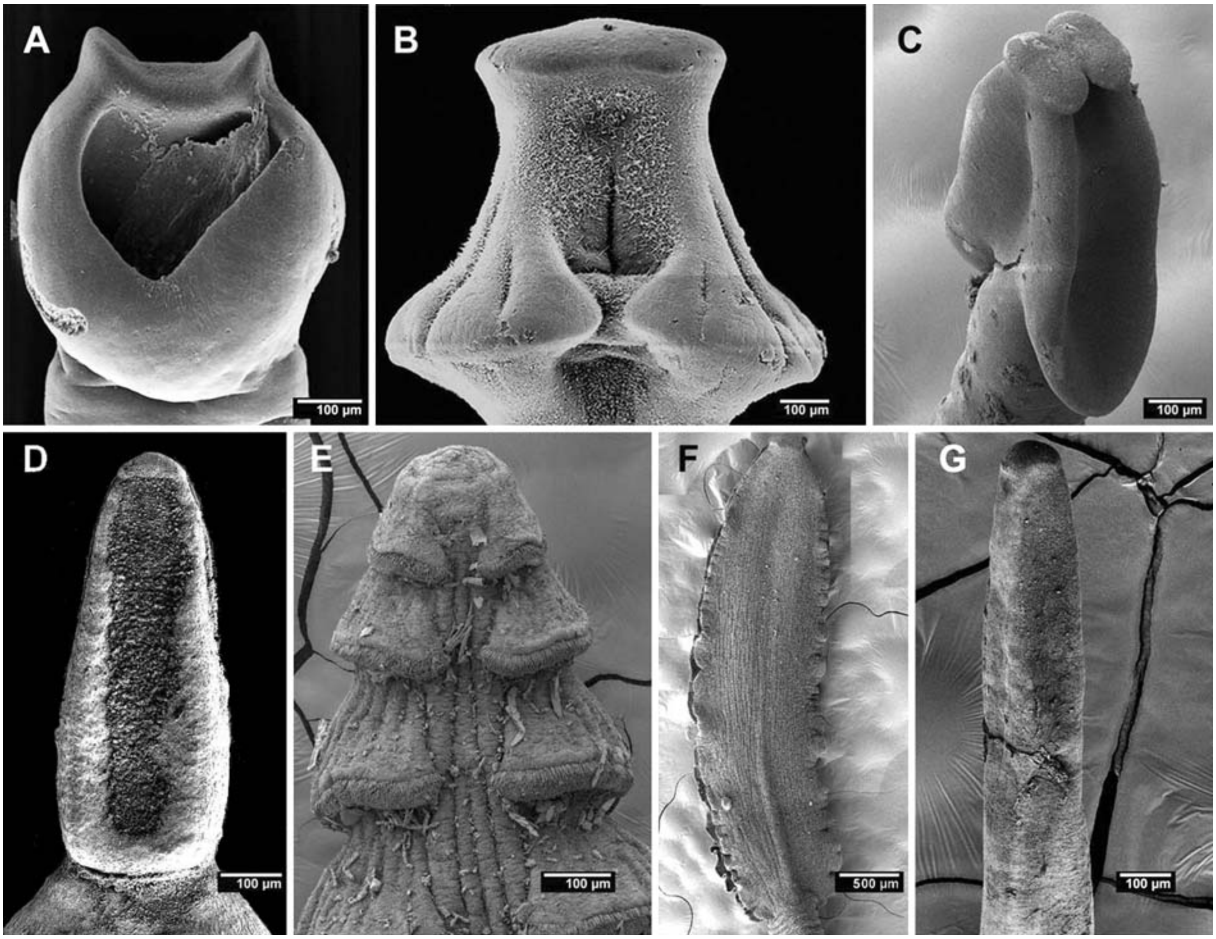


Fig. 2 Scanning electron micrographs of scoleces of bothriocephalidean cestodes. (**A**) *Galaxitaenia toloi* ex *Galaxias platei*, adapted from Gil de Pertierra & Semenas (2005); (**B**) *Marsipometra hastata* ex *Polyodon spathula*, original; (**C**) *Milanella familiaris* ex *Centrolophus niger*, adapted from Kuchta & Scholz (2008); (**D**) *Neobothriocephalus aspinosus* ex *Seriolella violacea*, original; (**E**) *Parabothriocephaloides seriolella* ex *Seriolella brama*, original; (**F**) *Plicocestus janickii* ex *Coryphaena* sp., original; (**G**) *Probothriocephalus alaini* ex *Xenodermichthys copei*, original

of segments. Uterus median, thin-walled, transversely oval, occupying large part of gravid segments. Uterine pore not observed. Eggs operculate, unembryonated. In marine fish (*Centrolophus*). Mediterranean Sea, Atlantic and Pacific Oceans.

Type- and only species: *A. heteropleura* (Diesing, 1850) ex *Centrolophus pompilius* (L.) [now *C. niger* (Gmelin)] (Perciformes: Centrolophidae).

Material studied: *A. heteropleura* ex *C. niger* from Trieste, Adriatic Sea (NMW 2600 – holotype); *A. heteropleura* ex *C. niger* from the Outer Hebrides, North Atlantic Ocean (not "*A. heteropleura*" from the same host, sequenced by Brabec et al., 2006) (IPCAS C-453); *Amphicotyle* sp. ex *C. niger* from the Outer Hebrides, North Atlantic Ocean (IPCAS C-454).

Remarks: Kuchta et al. (2008b) have recently redescribed *A. heteropleura* on the basis of freshly collected material. Tkachev (1979a,b) described *A. ceratias* Tkachev, 1979 from *Ceratias holboelli* Krøyer and *A. kurochkini* Tkachev, 1979 from *Seriolella* sp., but the former taxon is here accommodated in *Kimocestus* n. g. (see p. 107) as a new combination, *K. ceratias*, whereas *A. kurochkini* was synonymised with *Glossobothrium nipponicum* Yamaguti, 1952 by Kuchta & Scholz (2007) (see p. 107).

Amphicotyle sp. found in *Schedophilus medusophagus* (Cocco) by Gaevskaya & Kovaleva (1991) (see

p. 107 – *Kimocestus*) and in *Myctophum spinosum* (Steindachner) by Noble & Collard (1970) may belong to *Amphicotyle*, but no morphological descriptions of either taxon were provided to confirm their generic allocation.

The internal morphology of *A. heteropleura* can be observed only in histological sections, including one of the most characteristic features of the genus, the dorsal position of the ovary in the medulla with intrusion of some ovarian lobes between the wide and narrow bundles of the inner longitudinal musculature (see fig. 13 in Schumacher, 1914; Kuchta et al., 2008b).

Anantrum Overstreet, 1968 (Figs. 4B, 5F)

Syn. *Acompsocephalum* Rees, 1969

Diagnosis: Bothriocephalidea, Bothriocephalidae. Medium-sized worms. Strobila may be spirally twisted and with rippled margins. Segmentation absent. Scolex unarmed, elongate or clavate, without bothria and apical disc. Neck absent or present. Testes in two lateral fields. Cirrus-sac small, thick-walled; internal seminal vesicle present; cirrus unarmed. Genital pore median. Ovary bilobed, with slightly lobulate lateral wings. Vagina posterior to cirrus-sac. Seminal receptacle present. Vitelline follicles cortical, in two wide lateral bands. Uterine duct sinuous, enlarging in gravid proglottides. Uterus elongate. Uterine pore submedian. Eggs operculate, unembryonated. In marine teleosts (*Synodus*). Atlantic and Pacific Oceans.

Type-species: *A. tortum* (Linton, 1905) ex *Synodus foetens* (L.) (type-host) and *S. intermedius* (Spix & Agassiz) (Aulopiformes: Synodontidae), Beaufort, North Carolina (type locality), and Bermuda, Atlantic Ocean.

Other species: *A. histocephalum* Jensen & Heckmann, 1977 ex *Synodus lucioceps* (Ayres), Los Angeles, California, USA, Pacific Ocean.

Material studied: *A. tortum* ex *Synodus intermedius* from Bermuda (BMNH 1976.4.12.132-144 – see Rees, 1969); *A. histocephalum* ex *S. lucioceps* (USNPC 74110 – holotype, 74111 – paratype, 74825 – voucher).

Remarks: Linton (1905) described *Dibothrium tortum* from *Synodus foetens* from Bermuda. Overstreet (1968), who found conspecific cestodes, proposed *Anantrum* to accommodate *D. tortum*. One year later, Rees (1969), apparently unaware of Overstreet's paper, erected the new genus *Acompsocephalum* to accommodate the same species.

In 1977, another species of *Anantrum* was described (Jensen & Heckmann, 1977). It differs markedly from the type-species in some morphological characteristics, such as the presence of the *scolex deformatus* and neck (absent in *A. tortum*), and a well-developed inner longitudinal musculature formed by massive bundles of muscle fibres (versus very feeble in *A. tortum*) (Overstreet, 1968; Rees, 1969; Jensen & Heckmann, 1977). However, these species are retained in the same genus because they lack external segmentation, their strobila has the same shape and they occur in the same group of fish hosts.

Anchistrocephalus Monticelli, 1890 (Figs. 1C, 5C)

Syns *Ancistrocephalus* Lühe, 1899; *Amphigonoporus* Mendes, 1944; *Pachybothrium* Pozdniakov, 1983

Diagnosis: Bothriocephalidea, Triaenophoridae. Large worms. Segmentation present. Strobila robust; segments craspedote, wider than long. Single genitalia per segment, rarely genitalia duplicated in some segments. Scolex sagittate. Bothria elongate, with well-developed lateral and posterior margins. Apical disc armed with small hooks with wide base, arranged in one to several rows. Neck absent. Testes in two lateral continuous fields, confluent near posterior margin of segment. Cirrus-sac elongate; cirrus with small protuberances. Genital pore lateral. Ovary lobulate, slightly submedian (poral). Vagina posterior to cirrus-sac. Vitelline follicles limited to dorsal layer of segments, largely medullary, penetrating to cortex dorsolaterally, forming two wide fields confluent posteriorly. Uterine duct strongly sinuous. Uterus oval, aporal, opening by rupture of segment wall. Eggs operculate, unembryonated. In marine teleosts (Tetraodontiformes). Mediterranean Sea, Atlantic, Pacific and Indian Oceans.

Type-species: *A. microcephalus* (Rudolphi, 1819) ex *Orthragoriscos molas* (L.) [now *Mola mola* (L.)] (type-host) and *Mola ramsayi* (Giglioli) (Tetraodontiformes: Molidae).

Other species: *A. aluterae* (Linton, 1889) Linton, 1941 ex *Aluterus schoepfii* (type-host), Woods Hole, USA, and *A. monoceros* (L.) (new host) from Java, Indonesia.

Material studied: *Anchistrocephalus microcephalus* ex *M. mola* from Mediterranean Sea and Pacific Ocean (IPCAS C-195); *A. aluterae* ex *Aluterus schoepfii* (Walbaum), Woods Hole, USA (USNPC 8904 – see Linton, 1941); *A. aluterae* ex *Aluterus monoceros*, Pelabuhan Ratu, Java, Indonesia (IPCAS C-500).

Remarks: The genus was established by Monticelli (1890) to accommodate *Bothriocephalus microcephalus* Rudolphi, 1819. Lühe (1899) changed the name to *Ancistrocephalus*, but this emendation is invalid according to the ICZN and *Ancistrocephalus* becomes a synonym of *Anchistrocephalus*.

Amphigonoporus Mendes, 1944 was differentiated from *Anchistrocephalus* only by the absence of hooks around the base of the apical disc and the doubling of the genitalia. However, Kennedy & Andersen (1982) provided evidence that the scolex hooks may easily disappear, most probably as a consequence of fixation, and that some segments of *Anchistrocephalus microcephalus* contain doubled genitalia. The absence of scolex hooks and the presence of paired genitalia in some segments of *A. microcephalus* were also observed in the specimens studied by the present authors. Therefore, the invalidity of *Amphigonoporus*, first proposed by Kennedy & Andersen (1982), is accepted herein, although Bray et al. (1994) resurrected the genus based on the presence of duplicated genitalia.

Bray et al. (1994) considered *Pachybothrium* Pozdniakov, 1983 a synonym of *Amphigonoporus* and, therefore, *Pachybothrium* now falls into synonymy with *Anchistrocephalus*.

Dibothrium imbricatum Diesing, 1850, described from a marine turtle, was placed in *Anchistrocephalus* by Lühe (1900), but was considered a *species dubia* by the same author (Lühe, 1902). Another species of *Anchistrocephalus*, *A. aluterae* (Linton, 1889) Linton, 1941 from *Aluterus schoepfii*, was considered to be a *species inquirendum* by Protasova (1977). On the basis of a study of new material from a new host (*Aluterus monoceros*), collected by T. Walter in the Indian Ocean, *Anchistrocephalus aluterae* is considered to be a valid species.

Andycestus n. g. (Figs. 4C, 5D)

Diagnosis: Bothriocephalidea, Bothriocephalidae. Small worms. Segmentation absent. Scolex obclavate, sharply pointed, markedly narrower than strobila. Bothria elongate, with indistinct margin in anterior part of scolex. Apical disc absent. Neck absent. Testes in two lateral fields, continuous longitudinally. Cirrus-sac oval to spherical; cirrus unarmed. Genital pore median. Ovary bilobed, dumbbell-shaped. Vagina posterior to cirrus-sac. Vitelline follicles cortical, in two lateral fields. Uterine duct sinuous. Uterus stellate (rosette-like). Uterine pore median. Eggs pyriform, with operculum on wider pole, unembryonated. In deep-sea teleosts (*Eulophias*). North Atlantic Ocean.

Type- and only species: *A. abyssmus* (Thomas, 1953) n. comb., ex *Echiostoma tanneri* (Gill) (now *E. barbatum* Lowe) (Perciformes: Stomiidae), Bermuda, Atlantic Ocean.

Material studied: *A. abyssmus* ex *E. barbatum* (USNPC 48746 – holotype).

Etymology: The genus is named for Andrew (= Andy) P. Shinn from the Institute of Aquaculture, University of Stirling, UK, for his valuable contribution to fish parasitology and generous help with obtaining material of fish cestodes in Scotland and the North Atlantic Ocean.

Differential diagnosis: This tapeworm was originally described as *Bothriocephalus abyssmus* Thomas, 1953. It has been found only once, but differs in several features from all other taxa currently placed in *Bothriocephalus* and thus warrants erection of the new genus *Andycestus* to accommodate it. It is characterised by: (i) pyriform eggs (only *Eubothrioides* has been reported to possess pyriform eggs but it is a member of the Triaenophoridae, i.e. it has a lateral genital pore); (ii) the shape of the scolex, which is obclavate and markedly narrower than the adjacent anterior part of the strobila; (iii) the stellate uterus with 4–8 diverticula; (iv) the absence of external segmentation (only *Anantrum*, *Plicocestus* and *Probothriocephalus* have a completely or partly unsegmented strobila but they differ in scolex and strobilar morphology).

Remarks: Examination of the holotype of *A. abyssmus* showed some discrepancies from the original description: (1) the spines on the cirrus reported by Thomas (1953) and illustrated in his figure 9 were not found; (2) the shape of the bothria was incorrectly described and illustrated in the original description (figs. 1–3 in Thomas, 1953), because they are not in fact slit-like, but relatively shallow and wide, with lateral margins disappearing towards the anterior end of the scolex (Fig. 4C); and (3) the vaginal sphincter was not observed, although Thomas (1953 – p. 270) stated "Vagina,…, with sphincter muscles,…"; in fact, the wall of the proximal part of the vaginal canal is thickened, but no sphincter could be found.

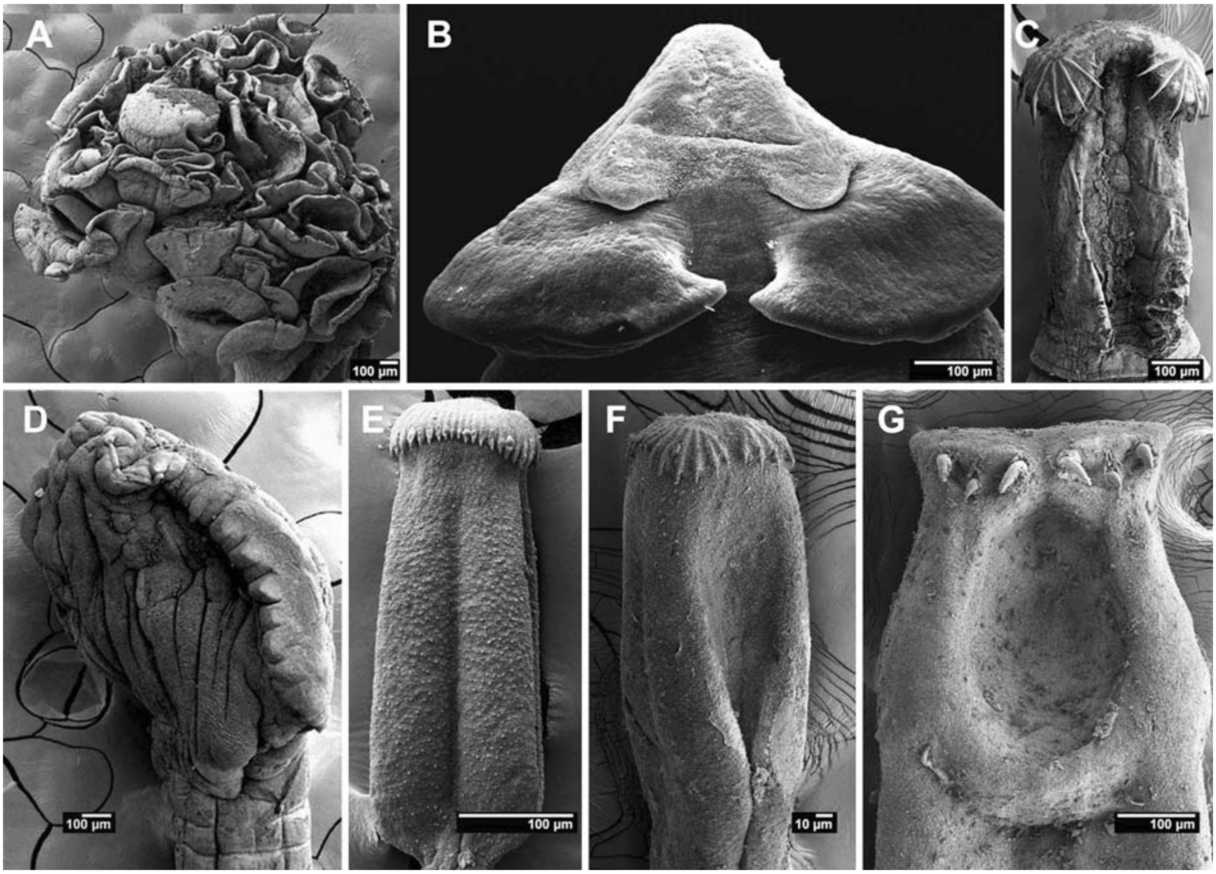


Fig. 3 Scanning electron micrographs of scoleces of bothriocephalidean cestodes. (**A**) *Oncodiscus sauridae* ex *Saurida tumbil*, original; (**B**) *Paraechinophallus japonicus* ex *Psenopsis anomala*, adapted from Levron et al. (2008b); (**C**) *Polyonchobothrium polypteri* ex *Polypterus bichir*, original; (**D**) *Ptychobothrium belones* ex *Strongylura leiura*, original; (**E**) *Senga filiformis* ex *Channa micropeltes*, original; (**F**) *Tetracampos ciliotheca* ex *Clarias anguillaris*, original; (**G**) *Triaenophorus nodulosus* ex *Esox lucius*, adapted from Kuchta et al. (2007)

Anonchocephalus Lühe, 1902 (Figs. 1E, 5G)

Syn. *Anoncocephalus* Yamaguti, 1959

Diagnosis: Bothriocephalidea, Triaenophoridae. Medium-sized worms. Segmentation present. Strobila with segments wider than long or quadrate, slightly craspedote. Scolex sagittate, unarmed. Bothria with free posterior margins. Apical disc present. Neck absent. Testes in two lateral fields, confluent posteriorly. Cirrus-sac large, pyriform, with markedly thickened distal part; cirrus armed with small protuberances. Genital pore marginal. Ovary compact, irregularly-shaped, slightly poral. Vagina posterior to cirrus-sac, with thick-walled distal part. Vitelline follicles medullary, ventral to testes. Uterine duct strongly sinuous, enlarged in gravid segments, containing chambers separated by septa. Uterus muscular, spherical to lobulate, not growing in gravid segments, with numerous chambers. Uterine pore ventral, median to submedian. Eggs operculate, unembryonated, with knob. In marine teleosts (Ophidiidae, Paralichthyidae). Pacific Ocean.

Type-species: *A. chilensis* (Riggenbach, 1896) ex *Genypterus chilensis* (Guichenot) (type-host), *G. blacodes* (Forster), *G. brasiliensis* Regan and *G. maculatus* (Tschudi) (Ophidiiformes: Ophidiidae), coast of Chile (type-locality), Pacific Ocean.

Other species: *A. argentinensis* Szidat, 1961 ex *Xystreurys rasile* (Jordan); *A. patagonicus* Suriano & Labriola, 1998 ex *Paralichthys patagonicus* Jordan (both hosts Pleuronectiformes: Paralichthyidae).

Material studied: *A. chilensis* ex *Genypterus maculatus*, Rise Survey, New Zealand (IPCAS C-440).

Remarks: Riggenbach (1896) described *Bothriotaenia chilensis* from *Genypterus chilensis* from Chile, and Lühe (1902) proposed *Anonchocephalus* to accommodate it. Gulyaev & Tkachev (1988) redescribed the species based on material from *G. blacodes* from the western Pacific. Bray et al. (1994) reported incorrectly the absence of an apical disc, but it is actually present (see fig. 1 in Gulyaev & Tkachev, 1988, and fig. 10.83 in Bray et al., 1994) and, as did Suriano & Labriola (1998) and Pereira (2000), described the cirrus to be armed with spines (in fact, the cirrus is covered with small protuberances) and eggs as embryonated (actually, the eggs are unembryonated, without a formed oncosphere with oncospheral hooks).

The three species of *Anonchocephalus* are morphologically very similar and their validity needs confirmation. However, it is worth mentioning that the two taxa of doubtful validity were described from fish of a different order (Pleuronectiformes) than the type-species (Ophidiiformes).

The genus is characterised by having vitelline follicles ventral to the testes, which form two wide lateral fields connected postovarially, the cirrus covered with tegumental protuberances (as in *Kimocestus* n. g.) and the presence of numerous chambers within the uterus.

Australicola **Kuchta & Scholz, 2006 (Figs. 1F, 5L)**

Diagnosis: Bothriocephalidea, Triaenophoridae. Large worms. Segmentation present. Strobila massive, with very short and wide, strongly craspedote segments. Scolex unarmed, massive, tapering anteriorly. Bothria oval, shallow. Apical disc small, quadrate in apical view. Neck present, long. Testes in two wide longitudinal fields, confluent anteriorly. Cirrus-sac small, elongate; internal seminal vesicle present; cirrus unarmed. Genital pore marginal; genital atrium narrow and deep. Ovary dendritic, on poral side. Vaginal canal strongly convoluted, anterior to cirrus-sac. Seminal receptacle present. Vitelline follicles cortical, with some follicles penetrating between muscle fibres of inner longitudinal musculature; follicles forming transverse equatorial field, separated between segments. Uterine duct sinuous. Uterus transverse oval. Uterine pore oval, thick-walled. Eggs operculate, unembryonated. Parasites of deep-sea teleosts (*Beryx*). Atlantic, Indian and Pacific Oceans.

Type- and only species: *A. platycephalus* (Monticelli, 1889) Kuchta & Scholz, 2007 (syn. *A. pectinatus* Kuchta & Scholz, 2006) ex *Beryx decadactylus* Cuvier (type-host) and *B. splendens* Lowe (Beryciformes: Berycidae).

Material studied: *A. pectinatus* ex *B. splendens* (holotype and paratypes – see Kuchta & Scholz, 2006); *A. platycephalus* ex *B. decadactylus* (BMNH 2007.3.29.1); *A. platycephalus* ex *B. decadactylus* from Mozambique (IPCAS C-441) and *B. splendens* from Agadir, 27.2.1953 (MNHNP C 91); *A. platycephalus* ex *Beryx decadactylus* and *B. splendens* from unknown locality, most probably from the Atlantic Ocean (MNHNP C 85).

Remarks: *Australicola* was proposed to accommodate the new species *Australicola pectinatus* Kuchta & Scholz, 2006 from *B. splendens* from Tasmania. After description of this taxon (Kuchta & Scholz, 2006), material of *Bothriocephalus platycephalus* Monticelli, 1889 from *Beryx decadactylus* (BMNH 2007.3.29.1) was studied and its conspecificity with *A. pectinatus* was established. On the basis of priority, Kuchta & Scholz (2007) synonymised *A. pectinatus* with *A. platycephalus* (Monticelli, 1889) n. comb, and the latter taxon became the type-species of the monotypic genus *Australicola*.

Australicola is characterised mainly by its large strobila composed of a large number of markedly craspedote segments with convex posterior margins, a dendritic ovary, a very deep and narrow genital atrium, circumcortical vitelline follicles forming wide transverse fields separated between segments and the scolex being quadrate in apical view.

Kuchta & Scholz (2006) reported the eggs to be unoperculate, but present SEM observations have revealed the presence of an operculum.

Bathybothrium **Lühe, 1902 (Figs. 1D, 5I)**

Syn. *Fissurobothrium* Roitman, 1965

Diagnosis: Bothriocephalidea, Triaenophoridae. Small worms. Segmentation present. Strobila with acraspedote segments wider than long, becoming quadrate in last mature and gravid segments. Scolex oval to heart-shaped. Bothria oval. Apical disc absent. Testes in two wide lateral bands, confluent anteriorly. Cirrus-sac elongate to pyriform; internal seminal vesicle present; cirrus unarmed. Genital pore lateral. Ovary irregular in shape, median. Vagina opening ventral to cirrus-sac. Vitelline follicles medullary, forming two lateral fields separated medially. Uterine duct sinuous. Uterus oval in first gravid segments, enlarging to form lateral diverticula with secondary branches in terminal segments. Uterine pore rudimentary, median. Eggs unoperculate, embryonated or not. In freshwater teleosts (Cyprinidae). Eurasia.

Type-species: *B. rectangulum* (Bloch, 1782) ex *Cyprinus barbus* L. (now *Barbus barbus*) (type-host), *Barbus* spp., *Gymnodiptychus dybowskii* (Kessler) and *Schizothorax intermedius* McClelland (Cypriniformes: Cyprinidae), Europe and Asia.

Other species: *B. unicum* (Roitman, 1965) ex *Gobio cynocephalus* Dybowski (Cypriniformes: Cyprinidae), Far East (Russia, Mongolia).

Material studied: *B. rectangulum* ex *Barbus barbus*, Jihlava River, Czech Republic (IPCAS C-17); *Fissurobothrium unicum* ex *Gobio cynocephalus*, Mongolia (ZIRAS 59 – see Scholz & Ergens, 1990).

Remarks: *Bathybothrium* has been monotypic, containing only its type-species specific to barbels (*Barbus* spp.) (Schmidt, 1986; Bray et al., 1994). However, *Fissurobothrium*, a genus proposed by Roitman (1965) to accommodate *F. unicum* Roitman, 1965, was invalidated by Kuchta & Scholz (2007), when they transferred its type- and only species, *F. unicum*, to *Bathybothrium*. This taxonomic action implicated invalidation of *Fissurobothrium*, although its synonymy with *Bathybothrium* was not mentioned explicitly by Kuchta & Scholz (2007).

Fissurobothrium is identical in all but one morphological character with *Bathybothrium* (two other differences are not considered to be reliable, namely the dorsal position of the uterine pore reported for *F. unicum*, which is apparently erroneous because all bothriocephalideans have the ventral uterine pore; and the alleged presence of unembryonated eggs, because the taxonomic importance of embryonation of eggs in bothriocephalidean cestodes is questionable – see Bray et al., 1994). The only actual difference between the two genera is in the distribution of the vitelline follicles, those of *Bathybothrium* being limited to two lateral bands in the medulla, whereas the follicles of *Fissurobothrium* were reported to be cortical (Roitman, 1965; Bray et al., 1994). However, the reliability of this characteristic of *Fissurobothrium* is questionable for the following reasons: (i) no cross sections of mature segments of *F. unicum* were provided in the original description; (ii) distribution of vitelline follicles as illustrated in his fig. 2a by Roitman (1965) (limited to the most lateral part of the segments external to the osmoregulatory canals) is doubtful because vitelline follicles are never limited to a very narrow lateral margin of the strobila external to the osmoregulatory canals in any bothriocephalidean cestode; and (iii) Roitman (1965, p. 129) mentioned that some follicles may also be present in the medulla (but this contradicts the distribution of follicles illustrated very schematically in his fig. 2).

F. unicum was described on the basis of a single specimen found in one of 141 gudgeons (*Gobio cynocephalus* Dybowski) examined, i.e. with a prevalence of 0.75% (Roitman, 1965). Scholz & Ergens (1990) reported the finding of an immature cestode resembling *F. unicum* in its scolex morphology from gudgeon in Mongolia; the worm had been previously identified as *F. unicum* by M.N. Dubinina and is deposited in St Petersburg (ZIRAS 59).

On the basis of the dubious nature of the characteristics used by Bray et al. (1994) to differentiate the genera (Roitman, 1965 distinguished his new genus only from *Marsipometra*, ignoring apparent morphological similarities with *Bathybothrium*, also parasitic in cyprinid fish), *Fissurobothrium* is considered here to be invalid. Its type- and only species, *F. unicum*, is provisionally retained as *B. unicum* (Roitman, 1965) – see Kuchta & Scholz (2007), but its validity is doubtful and it may well be conspecific with *B. rectangulum*, with which it shares many taxonomically important characteristics, including the shape of the scolex and bothria and the shape of the uterus in gravid segments.

Bathycestus Kuchta & Scholz, 2004 (Figs. 1G, 5J)

Diagnosis: Bothriocephalidea, Triaenophoridae. Medium-sized worms. Segmentation present. Strobila with trapeziform, craspedote segments, wider than long in anterior part of strobila, but acraspedote, quadrate to elongate in posterior part. Scolex unarmed, sagittate. Bothria elongate, shallow, with free posterior margins. Apical disc weakly developed, unarmed. Neck present. Testes forming two lateral fields, continuous between segments, confluent in postovarian space. Cirrus-sac large, elongate, with proximal part angled anteromedially; cirrus unarmed. Genital pore lateral. Ovary compact, slightly asymmetrical. Vagina posterior to cirrus-sac, with thickened distal part. Vitelline follicles circumcortical. Uterine duct sinuous. Uterus elongate, thick-walled, median. Uterine pore medioventral. Eggs unoperculate, unembryonated. Parasites of deep-sea teleosts (*Notacanthus*). North Atlantic Ocean.

Type- and only species: *B. brayi* Kuchta & Scholz, 2004 ex *Notacanthus bonaparte* Risso and *N. chemnitzii* Bloch (new host record) (Notacanthiformes: Notacanthidae), Goban Spur (type-locality), North-east Atlantic.

Material studied: *B. brayi* ex *N. bonaparte* (holotype and paratypes – see Kuchta & Scholz, 2004) and new material from *N. bonaparte* and *N. chemnitzii*, Outer Hebrides, North Atlantic Ocean, autumn 2005 (IPCAS C-303).

Remarks: The genus was erected on the basis of specimens found in *N. bonaparte*, but apparently conspecific cestodes were then collected from *N. chemnitzii* by one of us (R.K.) during the autumn of 2005. In the original description, the neck was reported to be absent because the first segments start immediately after the scolex (figs. 2 and 3 in Kuchta & Scholz, 2004). However, newly collected tapeworms possess a neck, because the first segments start at a distance after the scolex (Fig. 1G). The absence of the neck in the type-specimens seems to be caused by contraction.

***Bothriocephalus* Rudolphi, 1808 (Figs. 1H, 5H)**

Syns *Dibothrium* Diesing, 1850; *Schyzocotyle* Akhmerov, 1960; *Coelobothrium* Dollfus, 1970; *Capooria* Malhotra, 1985

Diagnosis: Bothriocephalidea, Bothriocephalidae. Small, medium-sized to large worms. Segmentation present. Strobila usually with craspedote segments wider than long. Scolex of variable shape, elongate, occasionally oval or heart-shaped; apical disc usually present, unarmed; bothria shallow and elongate, rarely deep, with simple (non-crenulate) margins. Neck absent. Testes in two lateral fields, continuous between segments. Cirrus-sac oval to spherical, elongate to pyriform in cross-section; cirrus unarmed. Genital pore median. Ovary median, transversely elongate or bilobed, compact. Vagina posterior to cirrus-sac. Vitelline follicles numerous, cortical, circumsegmental. Uterine duct sinuous, usually enlarging in gravid segments. Uterus spherical to transversely oval, occupying most median space in terminal segments. Uterine pore median or slightly submedian. Eggs operculate, unembryonated. In marine and freshwater teleosts. Cosmopolitan.

Type-species: *B. scorpii* (Müller, 1776) ex *Cottus scorpius* L. (now *Myoxocephalus scorpius*) (Scorpaeniformes: Cottidae).

Other species: About 30–35 (see Kuchta & Scholz, 2007). *Capooria barilii* Malhotra, 1985, *Coelobothrium monodi* Dollfus, 1970, *C. oitense* Kugi & Matsuo, 1990 and *C. gambusiense* Yang, Wang, Peng, Zhou & Liu, 2005 were synonymized with *B. acheilognathi* Yamaguti, 1934 by Kuchta & Scholz (2007) (see 'Remarks').

Material studied: *B. acheilognathi* Yamaguti, 1934 ex *Cyprinus carpio* L., Czech Republic (IPCAS C-15); *B. apogonis* Yamaguti, 1952 ex *Apogon lineatus* Temminck & Schlegel, Japan (MPM SY0385-89 – holotype); *B. brotulae* Yamaguti, 1952 ex *Brotula multibarbata* Temminck & Schlegel, Japan (MPM SY6803-4 – holotype); *B. carangis* Yamaguti, 1968 ex *Carangoides ferdau* (Forsskål), Hawaii (MPM 15377-9 – holotype); *B. claviceps* (Goeze, 1782) ex *Anguilla anguilla* (L.), Czech Republic (IPCAS C-16); *B. japonicus* Yamaguti, 1934 ex *A. japonica* Temminck & Schlegel, Japan (MPM 22905 – holotype); *B.* "*gregarius*" Renaud et al., 1983 ex *Psetta maxima* (L.), North Sea; *B. lateolabracis* Yamaguti, 1952 ex *Lateolabrax japonicus* (Cuvier), Japan (MPM SY0384 – holotype); *B. manubriformis* (Linton, 1889) ex *Istiophorus platypterus* (Shaw), Maldives (IPCAS C-496); *B. rarus* Thomas, 1934 ex *Notophthalmus viridescens* (Rafinesque), USA (IPCAS C-502); *B. sciaenae* Yamaguti, 1934 ex *Pennahia argentata* (Houttuyn), Japan (MPM SY3034-5 – holotype); *B.* "*scorpii*" (Müller, 1776) ex *Hemitripterus americanus* (Gmelin), Canada (IPCAS C-233); *Coelobothrium monodi* Dollfus, 1970 ex *Varicorhinus damascinus umbla* (Valenciennes) [now *Capoeta damascina* (Valenciennes)], Nasratabad, Iran (MNHNP bD 52/73-75 – holotype).

Remarks: This is by far the largest genus of the Bothriocephalidea, containing almost 100 nominal species, many of them, however, probably being invalid or *species inquirendae* (Protasova, 1977 listed as many as 28 taxa as *species inquirendae*; Kuchta & Scholz, 2007 listed 33 valid species). In addition, it seems that the genus is a composite taxon formed by unrelated species and should be split into several natural groupings (see Škeříková et al., 2004).

Molecular data indicate that marine and freshwater taxa form two unrelated assemblages (J. Brabec, pers. comm).

The type-species, *B. scorpii*, has been reported from almost 50 genera of marine fish of unrelated families and orders (Protasova, 1977). It is obvious that many, if not most, records are erroneous, as confirmed by the descriptions of several sibling species of the *B. scorpii* species complex (Renaud et al., 1984; Robert & Gabrion, 1991).

In the present revision, two taxa, *B. abyssmus* Thomas, 1953 and *B. janickii* Markowski, 1971, are transferred to newly proposed genera, *Andycestus* (see p. 93) and *Plicocestus* (see p. 121), respectively, because they possess several morphological characteristics which warrant their separate generic status. In addition, *Penetrocephalus* is resurrected as a valid genus, contradicting the conclusions of Protasova (1977) and Bray et al. (1994), because it differs markedly from species of *Bothriocephalus* (see *Penetrocephalus* p. 118).

Coelobothrium Dollfus, 1970 was proposed to accommodate a new species, *C. monodi*, described from the barbel *Capoeta damascina* (Cyprinidae: Barbinae) from Iran (Dollfus, 1970). The species is identical in all but one morphological characteristic with *B. acheilognathi*, sharing the shape of the scolex, which lacks an apical disc, the very deep bothria and the utilisation of a barbel as a host. *B. acheilognathi* has been found in numerous species of barbels (Barbinae) in Africa, Europe and Asia (Pool, 1987). The only difference is the alleged absence of an operculum in the eggs of *C. monodi*, but this character has been questioned by Tadros (1966) and Bray et al. (1994). The species is here considered, as first proposed by Kuchta and Scholz (2007), a synonym of *B. acheilognathi*, as are *Coelobothrium oitense* Kugi & Matsuo, 1990 from *Tribolodon hakonensis* (Günther) (Cyprinidae) in Japan and *C. gambusiense* Yang, Wang, Peng, Zhou & Liu, 2005 from *Gambusia affinis* (Baird & Girard) (Poeciliidae) in China. These species are morphologically identical and thus conspecific with *B. acheilognathi* Yamaguti, 1934, a widely distributed parasite of cyprinid, poeciliid and many other freshwater fish (Pool & Chubb, 1985; Pool, 1987; Scholz, 1997; Salgado-Maldonado & Pineda-López, 2003). *B. acheilognathi* is typified by a spherical to heart-shaped scolex with deep bothria identical to that in the above-listed Japanese and Chinese taxa as well as the type-species of *Coelobothrium*, *C. monodi*. In *C. gambusiense*, the eggs are reported to be operculate. Because of the synonymy of all species of *Coelobothrium* with *B. acheilognathi*, first proposed by Kuchta & Scholz (2007), *Coelobothrium* automatically became a junior synonym of *Bothriocephalus*, even though Kuchta & Scholz (2007) did not formally invalidate the former genus.

Capooria barilii Malhotra, 1985 was described from the cyprinid fish *Barilius bola* (Hamilton) (now *Raiamas bola*) in India as a new species of a new genus of the family Diphyllobothriidae [sic!]. Bray et al. (1994) considered it a *genus inquirendum* superficially resembling members of the family Bothriocephalidae. The morphology of *C. barilii* in fact entirely corresponds to that of *B. acheilognathi*. Since both taxa occur in the same fish host and are morphologically indistinguishable, *C. barilii* was synonymised with *B. acheilognathi* by Kuchta & Scholz (2007) and thus *Capooria* became a junior synonym of *Bothriocephalus*.

Bothriocephalus needs revision and several new genera will probably be recognised, as also indicated by molecular data (Škeříková et al., 2004). For example, *B. macrobothrium* Monticelli, 1889 from *Trachipterus* sp., was reported to have a lateral genital pore, which should place it among triaenophorids rather than the bothriocephalids. Some of the more recently described species of *Bothriocephalus*, such as *B. branchiostegi* Yamaguti, 1952 and *B. atherinae* Chernyshenko, 1949 are also of uncertain generic status.

Bothriocotyle Ariola, 1900 (Figs. 1J, 5K)

Diagnosis: Bothriocephalidea, Echinophallidae. Large worms. Segmentation present. Strobila folded along longitudinal axis (convex dorsally and concave ventrally) in spiral; segments craspedote, much wider than long. Strobila with numerous intensely stained corpuscles. Posterolateral margins of dorsal surface of segments covered with narrow band of large spiniform microtriches. Scolex unarmed, ovoid. Bothria shallow, pointed posteriorly, with narrow slit-like depression at its posterior extremity. Apical disc weakly developed. Neck absent. Testes in two lateral fields, confluent medially near posterior margin, continuous between segments. Cirrus-sac large, with very thick wall, with proximal part surrounded by gland-cells; cirrus armed with large spines. Genital pore sublateral. Ovary bilobed, poral, posteromedian to cirrus-sac, follicular. Vaginal canal sinuous, posterior to cirrus-sac, with terminal part markedly distended, thick-walled, armed with microtriches in proximal part of distended terminal portion. Vitelline follicles medullary, circumsegmental. Uterine duct sinuous, poral. Uterus median, oval. Uterine pore median. Eggs operculate, unembryonated. In marine teleosts (*Centrolophus*). Mediterranean Sea, Atlantic and Pacific Oceans.

Type- and only species: *B. solinosomum* Ariola, 1900 ex *Centrolophus pompilius* (L.) (now *C. niger* (Gmelin)) (Perciformes: Centrolophidae).

Material studied: *B. solinosomum* ex *C. niger*, off Outer Hebrides, Atlantic Ocean and New Zealand, Pacific Ocean (IPCAS C-442) (see Kuchta et al., 2008b); *Bothriocotyle* sp. ex *Seriolella punctata* (Forster), Stanley Area, Tasmania (IPCAS C-501).

Remarks: Yamaguti (1959) transferred the genus to the family Amphicotylidae (now considered to be a synonym of the Triaenophoridae – see Bray et al., 1994; Kuchta et al., 2008a) and proposed a new subfamily, the Bothriocotylinae, but subsequent authors have placed the genus back into the Echinophallidae (see Protasova, 1977; Schmidt, 1986; Bray et al., 1994; Kuchta et al., 2008a).

The genus is well defined by the shape of the strobila, which is folded along its longitudinal axis and forms a spiral, and the shape of the scolex, the bothria of which possess a small, narrow slit-like depression at their posterior extremity. The species has been recently redescribed by Kuchta et al. (2008b).

Tapeworms found in *Seriolella punctata* from Tasmania, collected by T. H. Cribb, probably belong to a new, undescribed species.

Clestobothrium **Lühe, 1899 (Figs. 1K, 6A)**

Diagnosis: Bothriocephalidea, Bothriocephalidae. Medium-sized worms. Segmentation present. Strobila with markedly craspedote segments wider than long. Scolex widely oval to spherical, robust. Bothria deep, may be connected by apical groove, surrounded by large sphincter. Apical disc absent. Testes in two lateral fields, usually separated medially, continuous between segments. Cirrus-sac small, oval, with internal seminal vesicle; cirrus unarmed. Genital pore median. Ovary transversely elongate or bilobed. Vagina posterior to cirrus-sac. Vitelline follicles cortical, circumsegmental. Uterine duct sinuous, enlarging in gravid segments. Uterus oval. Uterine pore slightly submedian. Eggs operculate, unembryonated. In marine teleosts (Gadiformes). Atlantic and Pacific Oceans.

Type-species: *C. crassiceps* (Rudolphi, 1819) ex *Merluccius* spp. (type-host *Gadus merluccius* L., now *Merluccius merluccius*) (Gadiformes: Merlucciidae), *Zeus faber* L. (Zeidae: Zeiformes) and *Scorpaena* sp. (new host records) (Scorpaeniformes: Scorpaenidae).

Other species: *C. gibsoni* Dronen & Blend, 2005 ex *Bathygadus macrops* Goode & Bean (Macrouridae), Gulf of Mexico; *C. neglectum* (Lönnberg, 1893) ex *Raniceps raninus* (L.) (Gadidae), Baltic Sea off Sweden.

Material studied: *C. crassiceps* ex *Merluccius australis* (Hutton), Chile, Pacific Ocean (BMNH 1994.6.7.36) and ex *Scorpaena* sp., Atlantic coast of France (MHNG 42008); *C. neglectum* ex *Raniceps raninus*, North Sea (BMNH 1984.10.1.1-3); *Clestobothrium* sp. ex *Zeus faber*, Plymouth, UK, originally identified as *Fistulicola dalmatina* (Stossich, 1897) (BMNH 1966.2.24.23).

Remarks: The type-species, *C. crassiceps*, has been reported from fish of several genera, but these records need to be confirmed. The genus was differentiated from *Bothriocephalus* by the possession of a sphincter on the bothria (Rees, 1958) and by the lack of an operculum on the eggs. The presence of an operculum has, however, recently been confirmed in its type-species, *C. crassiceps*, as well as one of two other congeneric taxa, *C. gibsoni* – see Draoui & Maamouri (1997) and Dronen & Blend (2005). In fact, *Clestobothrium* differs from other bothriocephalid genera only in the possession of a sphincter surrounding the anterior aperture of the bothria (Rees, 1958; Bray et al., 1994).

Tadros (1967) and Kornyushin & Kulakovskaya (1984) placed *Bothriocephalus acheilognathi* Yamaguti, 1934 in *Clestobothrium*, because it also possesses a spherical or heart-shaped scolex with deep bothria. However, the former species lacks a circular sphincter around the bothrial aperture found in species of *Clestobothrium* and its segments are only slightly craspedote or acraspedote (versus markedly craspedote in *Clestobothrium*). In addition, molecular data inferred from sequences of three genes provide evidence that *B. acheilognathi* and *C. crassiceps* are unrelated and their morphological similarity is a consequence of the convergent evolution of their scolex (Škeříková et al., 2004).

***Echinophallus* Schumacher, 1914 (Figs. 1L, 6C)**

Syns *Amphitretus* Blanchard, 1894 (pre-occ.); *Acanthocephallus* Lühe, 1910 (pre-occ.); *Atelemerus* Guiart, 1935

Diagnosis: Bothriocephalidea, Echinophallidae. Large, very wide worms. Segmentation present; each segment formed by two pseudosegments, each containing paired proglottides, i.e. two parallel sets of genitalia. Strobila flat, convex dorsally and concave ventrally along longitudinal axis. Segments markedly craspedote, much wider than long, with frilled (velum-like) posterior margins on ventral surface. Numerous intensely stained corpuscles present throughout strobila. Posterodorsal margins of dorsal surface of pseudosegments covered with narrow band of large spiniform microtriches. Scolex unarmed, pyramidal to trapeziform, narrower than first segments. Bothria very shallow, with slit-like incision in posterior extremity. Apical disc slightly developed. Neck absent. Testes exclusively on ventral side of medulla, forming narrow, transverse bands along anterior and posterior margins of segments between genital pores. Cirrus-sac large, elongate, thick-walled, with proximal part surrounded by gland-cells; cirrus armed with large spines. Genital pore sublateral. Ovary bilobed, follicular, posteromedian to cirrus-sac. Vagina posterior to cirrus-sac, thick-walled, with markedly distended distal part surrounded by large ring-like sphincter. Vitelline follicles cortical and medullary, along ventral layer of inner longitudinal musculature. Uterine duct sinuous, enlarging in gravid segments. Uterus oval, submedian. Uterine pore submedian, near anterior margin of segments. Eggs oval, operculate, unembryonated. In marine teleosts (Centrolophidae). Mediterranean Sea, Atlantic and Pacific Oceans.

Type-species: *E. wageneri* (Monticelli, 1890) (syns *Atelemerus acanthoides* Guiard, 1935; *Diplogonoporus settii* Ariola, 1895) ex *Centrolophus pompilius* (L.) [now *C. niger* (Gmelin)] (Perciformes: Centrolophidae).

Other species: *E. seriolellae* Korotaeva, 1975 ex *Seriolella brama* (Günther); *E. peltocephalus* (Monticelli, 1893) (syn. *Bothriocephalus loennbergii* Ariola, 1895) ex *Schedophilus ovalis* (Cuvier), off Italy, Mediterranean Sea; *E. lonchinobothrium* (Monticelli, 1890) ex *Coryphaena hippurus* L., Mediterranean Sea; *E. stossichi* (Ariola, 1896) ex *Trachipterus trachypterus* (Gmelin), Mediterranean Sea.

Material studied: *E. wageneri* – vouchers ex *Centrolophus niger*, North Atlantic Ocean (IPCAS C-443); *Echinophallus* sp. ex *Pseudocaranx dentex* (Bloch & Schneider), New Zealand (BMNH 1975.4.26.39-45).

Remarks: This genus was proposed by Schumacher (1914) to accommodate *Bothriocephalus wageneri* Monticelli, 1890. Kuchta et al. (2008b), who redescribed the species on the basis of newly collected material, synonymised *Atelemerus acanthoides* Guiart, 1935 and *Diplogonoporus settii* Ariola, 1895 with *E. wageneri*.

Kuchta & Scholz (2007) listed eight nominal taxa of *Echinophallus* with five valid species. *Bothriocephalus lonchinobothrium* Monticelli, 1890 and *B. peltocephalus* Monticelli, 1893 were transferred to *Echinophallus* (see Kuchta & Scholz, 2007). Ariola (1895) described *B. loennbergi* Ariola, 1895, which was later considered to be a junior synonym of *E. peltocephalus* (Monticelli, 1893) by the same author (Ariola, 1900). Ariola (1896) described two cestodes with double genital complexes from fish of the genus *Trachipterus*. *B. trachypteri* Ariola, 1896 from *T. liopterus* Valenciennes (now *T. trachypterus*) was considered to be a junior synonym of *B. stossichi* Ariola, 1896 by Ariola (1900), because they parasitise conspecific hosts. Protasova (1977) listed "*Bothriocephalus trachypteri-iris* Ariola, 1896", but in fact this species was not named as such in the original paper of Ariola (1896). He just mentioned a tapeworm from this fish host. Therefore, *Bothriocephalus trachypteri-iris* Ariola, 1896 represents a *nomen nudum*.

All the taxa described superficially and inadequately by Monticelli and Ariola from off Italy are tentatively placed in *Echinophallus* on the basis of their redescriptions made by Ariola (1900). The type-material of these species was allegedly deposited in the helminthological collection of the University of Naples, Italy, but was not available to the present authors despite several requests.

E. seriolellae was reported by Ichihara (1974b) as *Echinophallus* sp. from *Seriolella brama* off Japan. *Atelemerus major* Takao, 1986, described from *Pagrus major* (Temminck & Schlegel) off China, is placed in *Mesoechinophallus* (see below).

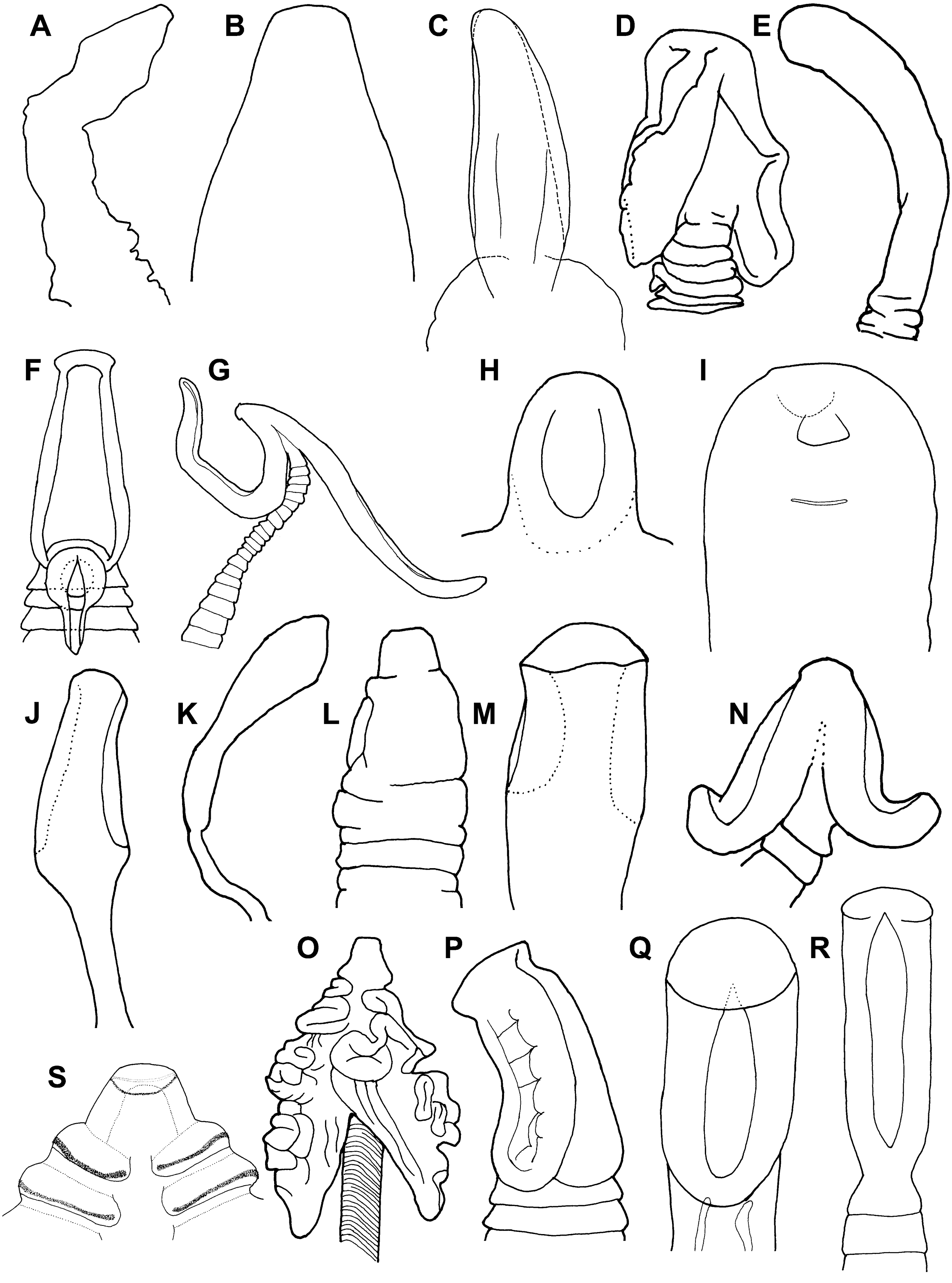
Tapeworms found in *Pseudocaranx dentex* from off New Zealand (BMNH 1975.4.28.39-45) belong to *Echinophallus* and may represent a new species. However, its description is not possible because of poor quality of the available material (Kuchta, 2007).

***Eubothrioides* Yamaguti, 1952 (Figs. 4D, 6B)**

Diagnosis: Bothriocephalidea, Triaenophoridae. Medium-sized worms. Segmentation present. Segments markedly trapeziform, craspedote. Scolex sagittate, unarmed. Bothria elongate, narrow, with slightly crenulate margins. Apical disc absent. Neck absent. Testes in two lateral fields, separated between segments. Cirrus-sac small; cirrus unarmed. Genital pore lateral. Ovary compact, slightly poral. Vagina posterior or dorsal to cirrus-sac. Vitelline follicles circumcortical, forming one transverse field in posterior half of segment. Uterine duct sinuous. Uterus small. Uterine pore median, near anterior margin of segment. Eggs pyriform, operculate, unembryonated. In marine teleosts (*Zenopsis*). Pacific Ocean (Japan).
Type- and only species: *E. lamellatus* Yamaguti, 1952 ex *Zenopsis nebulosa* (Temminck & Schlegel) (Zeiformes: Zeidae).
Material studied: None (the type- and only material was lost – J. Araki, Meguro Parasitological Museum, pers. comm.).
Remarks: This genus was erected to accommodate a new species, *E. lamellatus*, which has not been found since its description. It is easily distinguished from all triaenophorids in possessing markedly trapeziform segments with circumcortical vitelline follicles limited to the posterior half of the segments and a sagittate scolex with long bothria possessing crenulated lateral margins.

***Eubothrium* Nybelin, 1922 (Figs. 1I, 6D)**

Syn. *Leuckartia* Moniez, 1879 pre-occ.
Diagnosis: Bothriocephalidea, Triaenophoridae. Medium-sized to large worms. Segmentation present. Strobila with markedly craspedote, trapeziform segments, much wider than long. Scolex oval to elongate, may be deformed (*E. rugosum*). Bothria elongate. Apical disc present, with margin entire or with two to several incisions in margin. Testes in two lateral fields, confluent posteriorly, continuous between segments. Cirrus-sac small, elongate; cirrus unarmed. Genital pore marginal. Ovary irregular, compact or slightly lobulated, median or slightly poral. Vagina anterior to cirrus-sac. Vitelline follicles cortical, paramuscular or medullary, circumsegmental, forming two transverse lateral fields, separated or confluent medially, usually separated between segments. Uterine duct short. Uterus transversely elongate, near anterior margin of segment, enlarging to fill most space in terminal segments. Eggs released after rupture of segment wall. Eggs unoperculate, embryonated. In marine and freshwater teleosts. Eurasia, North America, Atlantic and Pacific Oceans.
Type-species: *E. rugosum* (Batsch, 1786) ex *Gadus lota* L. (now *Lota lota*) (Gadiformes: Lotidae), Eurasia and North America.
Other species: *E. acipenserinum* Cholodkovsky, 1918 ex sturgeons (*Acipenser*, *Huso*), Black and Caspian Seas; *E. arcticum* Nybelin, 1922 ex *Lycodes pallidus* Collett (Perciformes: Zoarcidae), Greenland, Atlantic Ocean; *E. crassum* (Bloch, 1779) ex salmoniform fish, mainly *Salmo* spp., Eurasia and North America; *E. fragile* (Rudolphi, 1802) ex *Alosa fallax* (Lacépède), Baltic and Celtic Seas; *E. parvum* Nybelin, 1922 ex *Mallotus villosus* (Müller) (both Clupeiformes: Clupeidae), North Atlantic Ocean; *E. salvelini* (Schrank, 1790) ex *Salvelinus* spp. and *Oncorhynchus* spp., Eurasia and North America; *E. tulipai* Ching & Andersen, 1983 ex *Ptychocheilus oregonensis* (Richardson) (Cypriniformes: Cyprinidae), North America; *E. vittevitellatus* Mamaev, 1968 ex *Trichodon trichodon* (Tilesius) (Perciformes: Trichodonidae), North Pacific Ocean.
Material studied: *E. acipenserinum* ex *Acipenser stellatus* Pallas, Caspian Sea (IPCAS C-423), *E. crassum*, *E. fragile*, *E. parvum*, *E. salvelini* (see Scholz et al., 2003 and Kuchta et al., 2005 for data on hosts and localities), *E. tulipai* ex *Ptychocheilus oregonensis* (see Ching & Andersen, 1983), *E. vittevitellatus* ex *Trichodon trichodon* (see Kennedy & Andersen, 1988).
Remarks: Based on the position of the vitelline follicles, species of *Eubothrium* can be divided into three groups. Marine species (*E. crassum*, *E. fragile*, *E. parvum*, *E. vittevitellatus*) have most of the vitelline follicles cortical, whereas taxa living primarily in freshwater hosts (*E. salvelini*, *E. rugosum*, *E. tulipai*) have follicles in the medulla (Kuchta et al., 2005; present study). *E. acipenserinum* represents an intermediate form with paramuscular vitellaria, i.e. vitelline follicles between bundles of inner longitudinal musculature. Bray et al. (1994) reported a uterine pore in *Eubothrium*, but in fact the eggs leave the uterus by rupture of the body wall (Protasova, 1977).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◀**Fig. 4** Drawings of scoleces of bothriocephalidean cestodes. (**A**) *Abothrium gadi* ex *Melanogrammus aeglefinus*, adapted from Williams (1960); (**B**) *Anantrum tortum* ex *Synodus intermedius*, adapted from Rees (1969); (**C**) *Andycestus abyssmus* ex *Echiostoma barbatum*, original; (**D**) *Eubothrioides lamellatus* ex *Zenopsis nebulosa*, adapted from Yamaguti (1952); (**E**) *Parabothrium bulbiferum* ex *Pollachius pollachius*, adapted from Bray et al. (1994); (**F**) *Glossobothrium nipponicum* ex *Seriolella brama*, adapted from Gulyaev & Korotaeva (1980); (**G**) *Kimocestus ceratias* ex *Ceratias holboelli*, original; (**H**) *Ichthybothrium ichthybori* ex *Ichthyborus besse*, adapted from Khalil (1971); (**I**) *Metabothriocephalus menpachi* ex *Myripristis bernardi*, paratype (MPM 15386), original; (**J**) *Parabothriocephalus gracilis* ex *Psenopsis anomala*, original; (**K**) *Penetrocephalus penetratus* ex *Saurida tumbil*, adapted from Rao (1960); (**L**) *Philobythoides stunkardi* ex *Alepocephalus agassizii*, adapted from Campbell (1979); (**M**) *Philobythos atlanticus* ex *Acanthochaenus luetkenii*, adapted from Bray et al. (1994); (**N**) *Pistana eurypharyngis* ex *Eurypharynx pelecanoides*, adapted from Campbell & Partner (1982); (**O**) *Plicatobothrium cypseluri* ex *Cheilopogon spinolotopterus*, adapted from Yamaguti (1968); (**P**) *Pseudamphicotyla quinquarii* ex *Pentaceros japonicus*, adapted from Yamaguti (1952); (**Q**) *Pseudeubothrioides lepidocybii* ex *Lepidocybium flavobrunneum*, adapted from Yamaguti (1968); (**R**) *Taphrobothrium japonense* ex *Muraenesox cinereus*, adapted from Yamaguti (1934); (**S**) *Mesoechinophallus hyperogliphe* ex *Hyperoglyphe japonica*, original

E. tulipai differs in its morphology from other congeners and it may well belong to another genus. However, the existing material, which was not well fixed, does not permit us to propose a new genus for this taxon.

Fistulicola Lühe, 1899 (Figs. 1M, 6K)

Syn. *Pseudeubothrium* Yamaguti, 1968

Diagnosis: Bothriocephalidea, Triaenophoridae. Large worms. Segmentation present. Strobila with well developed inner musculature formed by several rows of muscle bundles separated by fine transverse and dorsoventral muscle fibres. Segments wider than long, strongly craspedote with extended posterolateral margins (projections). Scolex unarmed, sagittate; pseudoscolex may be present. Bothria elongate, with prominent posterior margins. Apical disc present. Neck absent. Testes in single field, continuous between segments. Cirrus-sac small, with strongly thickened middle and distal portion; cirrus unarmed, smooth. Genital pore lateral. Ovary transversely elongate, with lobulated lateral wings. Vagina posterior to cirrus-sac, with spherical sphincter. Vitelline follicles circumcortical, extending into lateral projections of segment. Uterine duct strongly sinuous, muscular distally. Uterus transverse oval. Uterine pore submedian. Eggs operculate, unembryonated. In marine teleost (*Xiphias*, *Zeus*). Mediterranean Sea, Atlantic and Pacific Oceans.

Type- and only species: *F. plicatus* (Rudolphi, 1819) [syns *F. dalmatinus* (Stossich, 1897); *Pseudeubothrium xiphiados* Yamaguti, 1968] ex *Xiphias gladius* L. (Perciformes: Xiphiidae), Atlantic and Pacific Oceans.

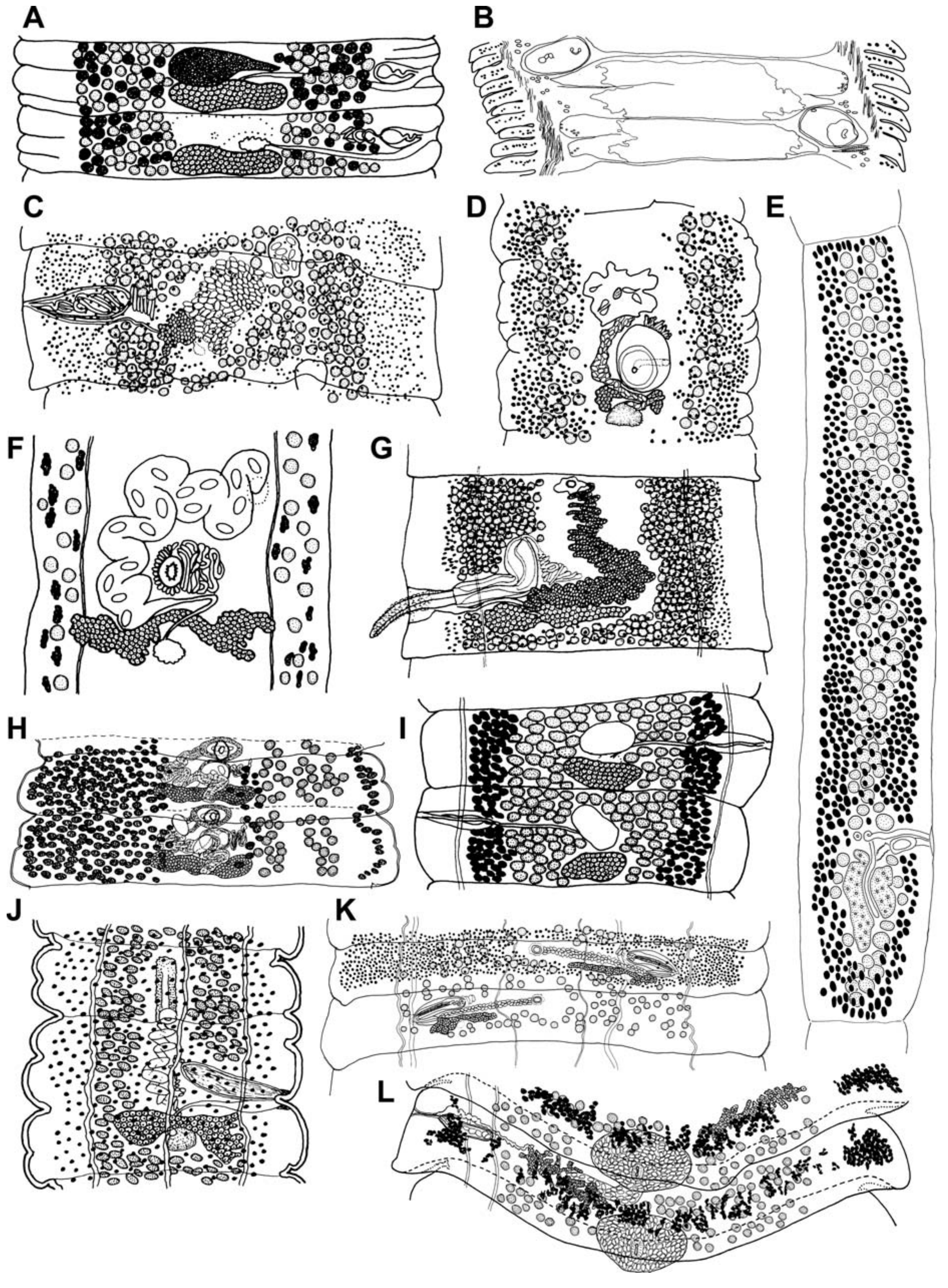
Material studied: *F. plicatus* ex *X. gladius*, Mediterranean Sea (NMB 1778/81 – holotype) and Atlantic Ocean (IPCAS C-444); *P. xiphiados* Yamaguti, 1968 ex *X. gladius*, Pacific Ocean (USNPC 63871 – holotype; MPM15376 YB 3101-33 – paratypes).

Remarks: *F. plicatus* is a large tapeworm with a massive strobila, which makes the internal organs difficult to observe. It was studied by Linton (1890) and Lühe (1899, 1900), but neither of these authors provided sufficient details of the internal morphology. New material from the Mediterranean Sea (Italy), kindly provided to the present authors by S. Mattiucci, P. Merella and G. Garippa, was taken from frozen hosts and is thus of very poor quality and unsuitable for a detailed morphological study.

Stossich (1897) described *Bothriocephalus dalmatinus* from *Zeus faber* L. from the Mediterranean Sea. This species is morphologically identical with *F. plicatus*, with which it was synonymised (Kuchta & Scholz, 2007), although the latter taxon was reported from a phylogenetically unrelated fish host (Zeiformes: Zeidae).

Pseudeubothrium, described by Yamaguti (1968) to accommodate *P. xiphados* Yamaguti, 1968, from the swordfish (*Xiphias gladius*), was synonymised with *Fistulicola* by Bray et al. (1994, p. 224) because the characteristics used to differentiate this taxon were doubtful or unsuitable for separating the genera. This synonymy is accepted in the present paper.

Bray et al. (1994) also reported the eggs of *Fistulicola* to be embryonated in the uterus. However, eggs of *F. plicatus* are laid unembryonated and coracidia containing oncospheres (hexacanths) are formed after 6-8 days in water, as described by Euzet (1962), who also successfully infected marine copepods [*Acartia discaudata* (Giesbrecht) and *A. latisetosa* (Kricagin)] with oncospheres of *F. plicatus*. Experimental infection of mullets [*Liza aurata* (Risso)] with copepods harbouring procercoids was unsuccessful (Euzet, 1962).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◀**Fig. 5** Drawings of segments of bothriocephalidean cestodes. (**A**) *Abothrium gadi* ex *Gadus morhua*, adapted from Williams (1960); (**B**) *Amphicotyle heteropleura* ex *Centrolophus niger*, longitudinal section of gravid segment, adapted from Kuchta et al. (2008b); (**C**) *Anchistrocephalus microcephalus* ex *Mola mola*, original; (**D**) *Andycestus abyssmus* ex *Echiostoma barbatum*, original; (**E**) *Ailinella mirabilis* ex *Galaxias maculatus*, adapted from Gil de Pertierra & Semenas (2006); (**F**) *Anantrum tortum* ex *Synodus intermedius*, adapted from Rees (1969); (**G**) *Anonchocephalus chilensis* ex *Genypterus blacodes*, adapted from Gulyaev & Tkachev (1988); (**H**) *Bothriocephalus claviceps* ex *Anguilla anguilla*, vitelline follicles illustrated mostly in left side of segment and testes only in right side, adapted from Scholz (1997); (**I**) *Bathybothrium rectangulum* ex *Barbus barbus*, adapted from Scholz (1989); (**J**) *Bathycestus brayi* ex *Notacanthus bonaparte*, adapted from Kuchta & Scholz (2004); (**K**) *Bothriocotyle solinosomum* ex *Centrolophus niger*, vitelline follicles not illustrated in posterior segment, adapted from Kuchta et al. (2008b); (**L**) *Australicola platycephalus* ex *Beryx splendens*, adapted from Kuchta & Scholz (2006)

Galaxitaenia Gil de Pertierra & Semenas, 2005 (Figs. 2A, 6J)

Diagnosis: Bothriocephalidea, Triaenophoridae. Small to medium-sized worms. Segmentation present. Strobila with slightly craspedote segments wider than long to square in terminal segments. Scolex unarmed, globular. Bothria deep, cup-shaped. Apical disc present, may possess anteriorly directed, rounded corner-like projections. Neck present. Testes in two fields, confluent anteriorly. Cirrus-sac large, pyriform; cirrus unarmed. Genital pore marginal. Ovary bilobed, with lobulate lateral wings. Vagina posterior, rarely ventral to cirrus-sac. Vitelline follicles medullary, in two ventrolateral fields, separated medially and between segments. Uterine duct short. Uterus oval, becoming branched in terminal gravid segments. Uterine pore present. Eggs unoperculate, embryonated. Parasites of freshwater teleosts (*Galaxias*). Patagonia, Argentina.

Type- and only species: *G. toloi* Gil de Pertierra & Semenas, 2005 ex *Galaxias platei* Steindachner (Osmeriformes: Galaxiidae), Patagonia.

Material studied: None.

Remarks: This genus has recently been described from a galaxiid fish from Patagonia and can be differentiated from other genera by combinations of several characteristics listed by Gil de Pertierra & Semenas (2005), especially by the typical shape of the scolex and the distribution of vitelline follicles, which are limited to the ventral layer of the medulla and form two longitudinal fields separated medially and between segments.

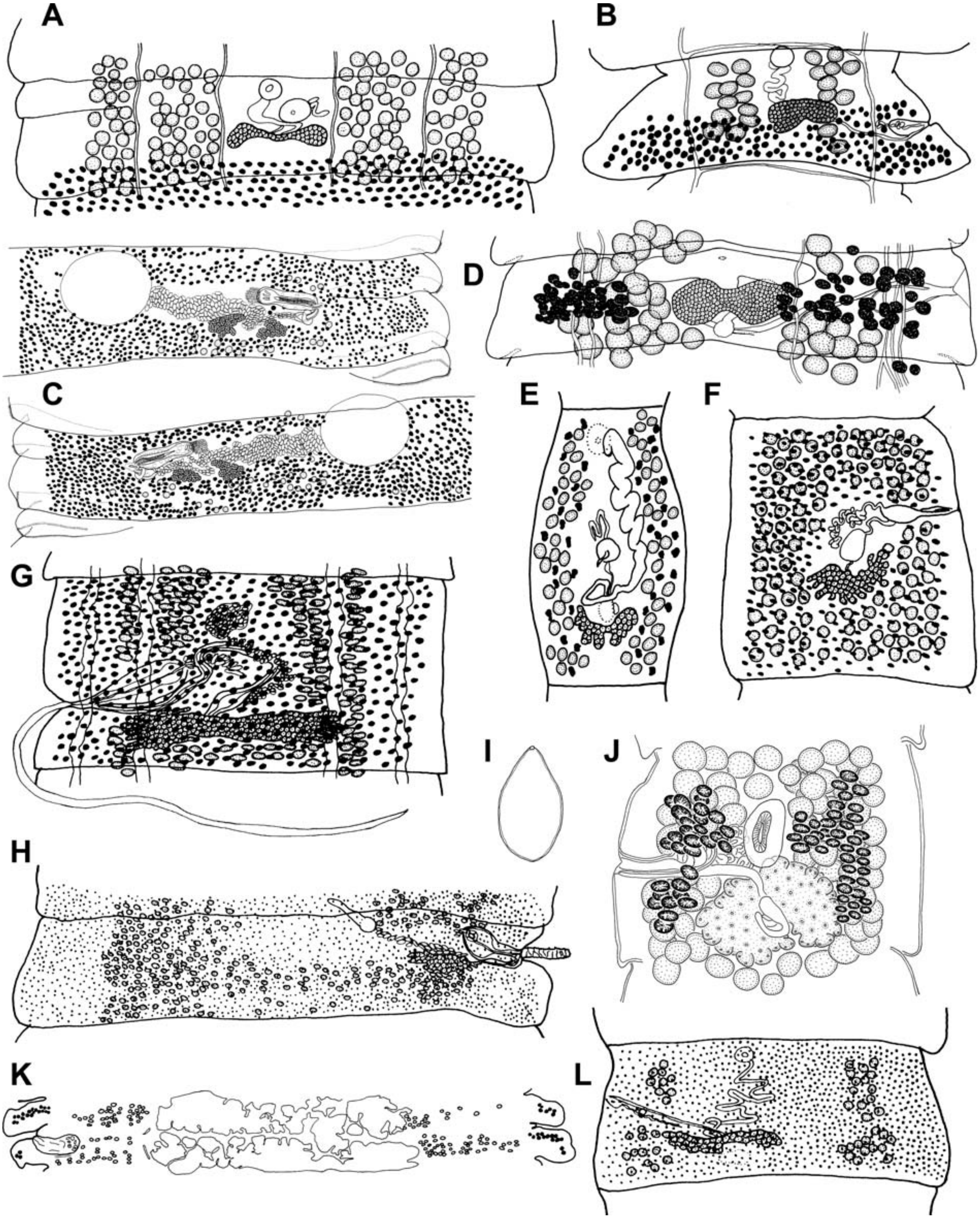
Glossobothrium Yamaguti, 1952 (Figs. 4F, 6G)

Diagnosis: Bothriocephalidea, Triaenophoridae. Small worms. Segmentation present. Strobila with craspedote segments wider than long. Ventral osmoregulatory canals wide. Scolex elongate, unarmed. Bothria with sucker-like structure at posterior margin, with small linguiform appendage projecting posteriorly. Apical disc well developed. Neck absent. Testes in two lateral fields, confluent posteriorly. Cirrus-sac large, pyriform, slightly angled anteriorly, with markedly thickened wall in middle part; cirrus extremely long, armed with small microtriches. Genital pore marginal. Ovary bilobed, reticulate. Vagina with proximal muscular dilatation, forms large sigmoid loop in median field, opening posterior to cirrus-sac. Vitelline follicles extensive, cortical, form compact circumsegmental field. Uterine duct sinuous, following course of proximal part of vaginal canal. Uterus oval to transverse elongate, near anterior margin of segment. Uterine pore median, near posterior margin of uterus. Eggs operculate, unembryonated. In marine teleost (Centrolophidae). Pacific and Indian Oceans.

Type- and only species: *G. nipponicum* Yamaguti, 1952 ex "marine fish", related to *Psenopsis anomala* (Temminck & Schlegel) (Perciformes: Centrolophidae), Japan.

Material studied: *G. nipponicum* ex *Seriolella brama* (Günther) (Centrolophidae), off Hawaii (see Gulyaev & Korotaeva, 1980) (IPCAS C-445/1), ex *Hyperoglyphe japonica* (Döderlein), off Japan (see Ichihara, 1974a) (MPM 14610-11) and ex *Xenolepidichthys dalgleishi* Gilchrist (Zeiformes: Grammicolepididae), Mozambique, Indian Ocean (IPCAS C-445/2).

Remarks: *Glossobothrium* is unique among bothriocephalideans in possessing a sucker-like structure bearing a linguiform appendage at the posterior margin of each bothrium and an extremely long cirrus, which is armed with numerous tiny microtriches. Yamaguti (1952) described the species from an unknown fish supposedly related to *Psenopsis anomala*, but the type-material has been lost from Yamaguti's collections deposited in the Meguro Parasitological Museum in Tokyo. Ichihara (1974a) reported the finding of *G. nipponicum* in *Hyperoglyphe japonica* (Centrolophidae) from Japan. The species was then redescribed by Gulyaev & Korotaeva (1980) on the basis of specimens found in *Seriolella brama* from off Hawaii. The specimens collected by L.W. Reimer from *Xenolepidichthys*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◀**Fig. 6** Drawings of segments of bothriocephalidean cestodes. (**A**) *Clestobothrium crassiceps* ex *Merluccius merluccius*, vitelline follicles illustrated only posteriorly, adapted from Protasova (1977); (**B**) *Eubothrioides lamellatus* ex *Zenopsis nebulosa*, adapted from Yamaguti (1952); (**C**) *Echinophallus wageneri* ex *Centrolophus niger*, adapted from Kuchta et al. (2008b); (**D**) *Eubothrium rugosum* ex *Lota lota*, adapted from Kuchta et al. (2005); (**E**) *Ichthybothrium ichthybori* ex *Ichthyborus besse*, adapted from Khalil (1971); (**F**) *Marsipometra hastata* ex *Polyodon spathula*, adapted from Beaver & Simer (1940); (**G**) *Glossobothrium nipponicum* ex *Seriolella brama*, adapted from Gulyaev & Korotaeva (1980); (**H, I**) *Kimocestus ceratias* ex *Ceratias holboelli*, original, I. egg; (**J**) *Galaxitaenia toloi* ex *Galaxias platei*, adapted from Gil de Pertierra & Semenas (2005); (**K**) *Fistulicola plicatus* ex *Xiphias gladius*, longitudinal section of gravid segment, original; (**L**) *Metabothriocephalus menpachi* ex *Myripristis argyromus*, adapted from Yamaguti (1968)

dalgleishi from off Mozambique fully correspond in their morphology to *G. nipponicum* and are also considered to be conspecific. Tantalean et al. (1982) found cestodes tentatively placed in *Glossobothrium* in *Hemilutjanus macrophthalmos* (Tschudi) (Perciformes: Serranidae) from Peruvian waters, but their description is incomplete and only the scolex was illustrated; voucher specimens were lost (M. Tantalean – pers. comm.).

Tkachev (1979a) described *Amphicotyle kurochkini* from *Seriolella* sp., but this species has been considered a junior synonym of *G. nipponicum* (V. Gulyaev, pers. comm; Kuchta & Scholz, 2007).

Bray et al. (1994) placed *Glossobothrium* in the Echinophallidae because they synonymised the Parabothriocephalidae with the Echinophallidae, the genus having been placed in the Parabothriocephalidae by Yamaguti (1959). However, *Glossobothrium* is considered here to belong to the Triaenophoridae because it possesses a lateral genital pore, the cirrus is armed with small microtriches rather than with large spines (see Levron et al., 2008a), and the posterior margin of segments is not covered with the blade-like spiniform microtriches present in most echinophallids (Poddubnaya et al., 2007; Levron et al., 2008b).

Ichthybothrium Khalil, 1971 (Figs. 4H, 6E)

Diagnosis: Bothriocephalidea, Bothriocephalidae. Small worms. Segmentation incomplete. Strobila weakly muscular; segments acraspedote. Usually one set of reproductive organs per segment, rarely genitalia duplicated or even triplicated. Scolex oval, much narrower than beginning of strobila, unarmed. Bothria elongate, shallow. Apical disc absent. Neck absent. Cirrus-sac thick-walled; cirrus unarmed. Testes in two lateral fields. Genital pore median. Ovary bilobed, median. Vagina posterior to cirrus-sac. Vitelline follicles cortical, in two fields confluent medially, circumsegmental. Uterine duct sinuous, enlarging in gravid segments. Uterus oval, thin-walled. Uterine pore median, near anterior margin of segment. Eggs unoperculate, embryonated. In freshwater teleosts (*Ichthyborus*). Africa (Sudan).

Type- and only species: *I. ichthybori* Khalil, 1971 ex *Ichthyborus besse* (Joannis) (Characiformes: Ichthyboridae), Sudan, Africa.

Material studied: *I. ichthybori* ex *Ichthyborus besse*, Sudan (USNPC 71666, 71667 – holotype and paratype; IPCAS C-455 – new material).

Remarks: The genus is monotypic and differs from other bothriocephalids in the shape of the scolex, which is markedly narrower than the anterior end of the strobila, and the presence of a long anterior part of the strobila without genital complexes or their primordia. Khalil (1971) correctly reported the cortical position of vitelline follicles in the species diagnosis, but erroneously stated “Vitelline follicles lateral in medullary parenchyma” in the generic diagnosis of *Ichthybothrium* (Khalil, 1971, p. 378).

The new material recently collected from the type-host near the type-locality (White Nile at Kostí) differs markedly from the type-specimens in the shape of the segments, which are in fact markedly wider than long. Khalil’s specimens are unnaturally elongate, most probably due to fixation of too relaxed or dead worms. In addition, genitalia were duplicated or even triplicated in some segments of the new material.

Kimocestus n. g. (Figs. 4G, 6H, I)

Diagnosis: Bothriocephalidea, Triaenophoridae. Large worms. Segmentation present. Strobila with wide segments, much wider than long, markedly craspedote. Scolex unarmed, sagittate, with very long free posterior margins. Bothria very long, narrow. Apical disc present. Neck absent. Testes in two lateral fields, confluent posteriorly. Cirrus-sac pyriform, with markedly thickened distal part; internal seminal vesicle present; cirrus armed with small protuberances. Genital pore lateral. Ovary follicular, submedian. Vagina posterior to cirrus-sac, with thickened terminal distal part. Vitelline follicles cortical, circumsegmental.

Uterine duct strongly sinuous, narrow. Uterus pyriform to spindle-shaped in last mature and first gravid segments, enlarging in gravid segments to form thick-walled spherical to broadly oval, unlobed sac. Uterine pore medioventral. Eggs pyriform, unoperculate, unembryonated. In deep-sea teleosts (*Ceratias*). Indian and Atlantic Oceans.

Type- and only species: *K. ceratias* (Tkachev, 1979) n. comb. (syn. *Amphicotyle ceratias* Tkachev, 1979) ex *Ceratias holboelli* Krøyer (Lophiiformes: Ceratiidae), off South Australia, Indian Ocean.

Material studied: *K. ceratias* ex *C. holboelli*, North Atlantic Ocean (48°40′N; 45°36′W, at depth 1,128–1,224 m), 12.vii. 1996 (BMNH 2007.3.29.2; IPCAS C-446).

Etymology: This genus is named for Dr Kim S. Last, who collected the new material, which made it possible to redescribe the species (the type-specimens of *Amphicotyle ceratias*, allegedly deposited in the Laboratory of Parasitology of Marine Animals, TINRO, Vladivostok – Nos. GC 79001 & 79002, were not available to the present authors and most probably do not exist).

Differential diagnosis: The new genus is most similar to *Anonchocephalus*, with which it shares several characteristics unique or rare among triaenophorids, such as markedly craspedote segments, the shape of the cirrus-sac, the distal part of which has a markedly thickened wall, the cirrus covered with small protuberances, a thick-walled distal part of the vaginal canal, and the relative position of the terminal genitalia and the uterine duct.

Kimocestus, however, differs from *Anonchocephalus* (and other triaenophorid genera as well) in the following characters: (i) the scolex has extremely long posterior projections on the bothria (versus sagittate, without long posterior projections in *Anonchocephalus*); (ii) the vitelline follicles are completely cortical and circumsegmental (versus exclusively medullary and limited to the ventral layer of the medulla in *Anonchocephalus*); (iii) the ovary is follicular (versus compact or slightly lobate in *Anonchocephalus*); (iv) the cirrus-sac contains an internal seminal vesicle, which is missing in *Anonchocephalus*; and (v) the uterus is spindle-shaped in the last mature and first gravid segments and enlarges markedly to become transversely oval to spherical in more developed gravid segments in *Kimocestus*, whereas in *Anonchocephalus* the uterus does not enlarge much and remains relative small, becoming broadly oval in the terminal gravid segments, and most eggs are maintained within numerous chambers (septate compartments) of a strongly enlarged uterine duct.

Remarks: The new genus is proposed on the basis of the new material which is apparently conspecific with *Amphicotyle ceratias* described by Tkachev (1979b). This species, originally described only superficially from specimens in a poor state (see the very schematic illustrations in Tkachev, 1979b), cannot be placed in *Amphicotyle*, because it has a markedly different scolex (Fig. 1B), which lacks posterior sucker-like depression, a weakly developed inner musculature, a different distribution of vitelline follicles, and other morphological characteristics (see diagnosis of *Amphicotyle* – p. 89).

Gaevskaya & Kovaleva (1991) reported *Amphycotyle* sp. [sic!] from *Schedophilus medusophagus* (Cocco) in the Atlantic Ocean, but the authors provided only an illustration of the scolex with the first segments (see fig. 16 of Gaevskaya & Kovaleva, 1991). The morphology of the scolex is similar to that of *K. ceratias* illustrated by Tkachev (1979b, fig. a) and the tapeworm may well be conspecific.

Marsipometra Cooper, 1917 (Figs. 2B, 6F)

Diagnosis: Bothriocephalidea, Triaenophoridae. Medium-sized worms. Segmentation present. Strobila with mature and gravid segments square to longer than wide, slightly craspedote. Scolex pyramidal or sagittate, with well-developed posterior margins. Bothria oval to elongate. Apical disc present, dome-shaped. Neck present. Testes in two lateral fields, confluent anteriorly and posteriorly. External sperm duct (vas deferens) lined in terminal part with numerous prostatic glands. Cirrus-sac large, may be curved anteriorly; internal seminal vesicle present; cirrus unarmed. Genital pore lateral. Ovary median, compact, with slightly lobulate lateral wings. Vaginal canal crossing cirrus-sac, opening anterior or ventral to cirrus-sac. Seminal receptacle present. Vitelline follicles medullary, usually forming two ventrolateral fields, confluent posteriorly and continuous between segments. Uterine duct sinuous. Uterus lobulate or with long lateral diverticula in gravid segments. Uterine pore median. Eggs unoperculate, embryonated. In freshwater sturgeons (paddle-fish). North America.

Type-species: *M. hastata* (Linton, 1897) ex *Polyodon spathula* (Walbaum) (Acipenseriformes: Polyodontidae), North America (Mississippi).

Other species: *M. confusa* Simer, 1930 and *M. parva* Simer, 1930, both ex *P. spathula*, Mississippi, North America.

Material studied: *M. hastata* (IPCAS C-447); *M. confusa* (USNPC 9276 – paratype); *M. parva* (USNPC 9275 – paratype), Mississippi, USA.

Remarks: The genus was proposed to receive *Dibothrium hastatum* described from the paddle-fish *Polyodon spathula* by Linton (1897). Cooper (1917) placed the genus in the new subfamily Marsipometrinae, but Nybelin (1922) transferred it to the Amphicotylidae, which is now considered to be a synonym of the Triaenophoridae.

The genus is well characterised by the shape of the scolex, the branched uterus with numerous lateral diverticula, numerous prostatic glands along the terminal part of the external sperm duct, the presence of a seminal receptacle and medullary vitelline follicles forming two ventrolateral fields.

Records of *Marsipometra* from *Mastacembelus armatus* (Lacépède) and *Wallago attu* (Bloch & Schneider) in Bangladesh and *Cyprinus carpio* L. in Indonesia (Arthur, 1992; Khanum & Farhana, 2000; Arthur & Ahmed, 2002) are undoubtedly erroneous, because the genus is specific to paddle-fish and its distribution is limited to the southeastern part of USA.

Mesoechinophallus n. g. (Figs. 4S, 7M)

Diagnosis: Bothriocephalidea, Echinophallidae. Large, very wide worms. Segmentation incomplete, missing along mid-line of strobila. Segments markedly craspedote, much wider than long. Posterolateral margins of segments covered with narrow band of large spiniform microtriches. Scolex replaced by trapeziform pseudoscolex with two shallow, bothrium-like depressions; apical part of pseudoscolex lined with ring of large spiniform microtriches. Neck absent. Testes in one field, continuous between segments. Cirrus-sac large, elongate, thick-walled, with proximal part surrounded by gland-cells; cirrus unarmed. Genital pore sublateral. Ovary bilobed, follicular, posteromedian to cirrus-sac. Vagina posterior to cirrus-sac, thin-walled; distal part surrounded by small ring-like sphincter. Vitelline follicles cortical. Uterine duct sinuous, enlarging in gravid segments. Uterus oval, submedian. Uterine pore submedian, near anterior margin of segments. Eggs oval, operculate, unembryonated. In marine teleosts (Centrolophidae, Sparidae). Pacific Ocean.

Type-species: *M. hyperogliphe* (Tkachev, 1979) n. comb. (syn. *Paraechinophallus hyperogliphe* Tkachev, 1979) ex *Hyperoglyphe japonica* (L.) (Perciformes: Centrolophidae) (mispelled as *Hyperogliphe japonica*), off Hawaii, Pacific Ocean.

Other species: *Mesoechinophallus major* (Takao, 1986) n. comb. (syn. *Atelemerus major* Takao, 1986) ex *Pagrus major* (Temminck & Schlegel) (Perciformes: Sparidae), off Kyushu, Japan.

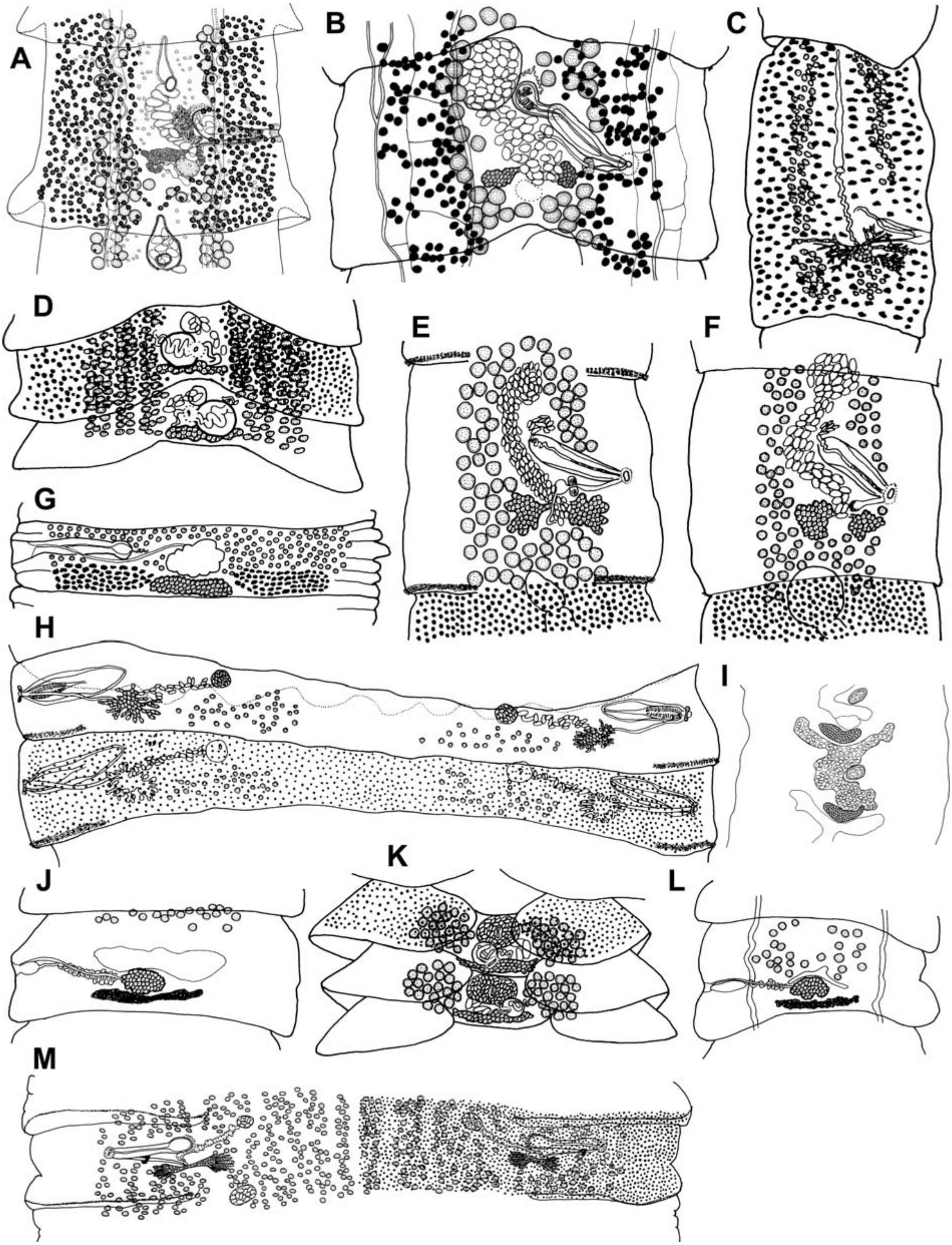
Material studied: *M. hyperogliphe* (designated as *Echinophallus* sp.) ex *H. hyperoglyphe* from Japan (MPM 14609, 14752) collected by Ichihara. The type-specimens of *Paraechinophallus hyperogliphe*, which should have been deposited in the Laboratory of Parasitology of Marine Animals, TINRO, Vladivostok, were not available to the present authors and most probably do not exist.

Etymology: The generic name reflects the fact that *Mesoechinophallus* possesses some morphological characteristic intermediate between *Echinophallus* and *Paraechinophallus*.

Differential diagnosis: The new genus is closely related to *Echinophallus* and *Paraechinophallus*, with which it shares the possession of double sets of proglottids per segment. It differs from these genera in the absence of large spines on the cirrus.

Remarks: The new genus is proposed on the study of new material that is apparently conspecific with *Paraechinophallus hyperogliphe* described by Tkachev (1979c), the type-material of which has not been available and probably does not exist. This species, originally described only superficially with illustrations not providing sufficient information about its morphology (Tkachev, 1979c), cannot be placed in *Paraechinophallus*, because it has incomplete segmentation along the mid-line of the strobila, a markedly sublateral position of the genital pore, the vaginal sphincter is lacking and the cirrus is unarmed.

Takao (1986) described *Atelemerus major* from sea bream *Pagrus major* off China, but *Atelemerus* Takao, 1986 is invalid (see Bray et al., 1994; Kuchta et al., 2008b; present study) and the species was preliminary placed in *Paraechinophallus* by Kuchta & Scholz (2007). Although the validity of *P. major* is questionable (the type- and only specimens, probably deposited in the Department of Parasitology, Kurume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◀ **Fig. 7** Drawings of segments of bothriocephalidean cestodes. (**A**) *Milanella familiaris* ex *Centrolophus niger*, adapted from Kuchta & Scholz (2008); (**B**) *Neobothriocephalus aspinosus* ex *Seriolella violacea*, original; (**C**) *Pistana eurypharyngis* ex *Eurypharynx pelecanoides*, adapted from Campbell & Partner (1982); (**D**) *Oncodiscus sauridae* ex *Saurida tumbil*, vitelline follicles illustrated only in first segment, adapted from Yamaguti (1934); (**E**) *Parabothriocephaloides segmentatus* ex *Psenopsis anomala*, vitelline follicles illustrated only posteriorly, adapted from Yamaguti (1934); (**F**) *Parabothriocephalus gracilis* ex *Psenopsis anomala*, vitelline follicles illustrated only posteriorly, adapted from Yamaguti (1934); (**G**) *Parabothrium bulbiferum* ex *Pollachius pollachius*, adapted from Williams (1960); (**H**) *Paraechinophallus japonicus* ex *Psenopsis anomala*, vitelline follicles illustrated only in posterior segment, original; (**I**) *Plicatobothrium cypseluri* ex *Cheilopogon spilonopterus*, vitelline follicles and testes not illustrated, paratype MPM 15388 (YB 3485), original; (**J**) *Philobythoides stunkardi* ex *Alepocephalus agassizii*, adapted from Campbell (1979); (**K**) *Penetrocephalus penetratus* ex *Saurida tumbil*, vitelline follicles illustrated only in first segment, original; (**L**) *Philobythos atlanticus* ex *Acanthochaenus luetkenii*, adapted from Bray et al. (1994); (**M**) *Mesoechinophallus hyperogliphe* ex *Hyperoglyphe japonica*, vitelline follicles illustrated only in right side of segment, original

University School of Medicine, Japan, Col.. No. 79-01-05, were not available to the present authors to obtain more data on its morphology), the species is provisionally placed in *Mesoechinophallus* as a new combination.

***Metabothriocephalus* Yamaguti, 1968 (Figs. 4I, 6L)**

Diagnosis: Bothriocephalidea, Triaenophoridae. Small worms. Segmentation present. Strobila with slightly craspedote segments wider than long. Scolex spherical, unarmed. Bothria very small, shallow, subapical; transversely oval, slit-like depression posterior to bothria. Apical disc small, weakly developed. Neck present. Testes few in number, in two lateral fields median to main osmoregulatory canals. Cirrus-sac small; internal seminal vesicle present; cirrus unarmed. Genital pore lateral. Ovary bilobed, transversely elongate, poral. Vagina anterior to cirrus-sac. Vitelline follicles cortical, circumsegmental. Uterine duct forming numerous transverse loops in gravid segments, filled with formed eggs. Uterus oval, thick-walled, not enlarging in gravid segments. Uterine pore median, near anterior margin of segments. Eggs allegedly operculate, unembryonated. In marine teleosts (*Myripristis*, *Chlorophthalmus*). Indian and Pacific Oceans.

Type- and only species: *Metabothriocephalus menpachi* Yamaguti, 1968 ex *Myripristis argyromus* Jordan & Evermann [now *M. amaena* (Castelnau)] (type-host), *M. berndti* Jordan & Evermann and *M. chryseres* Jordan & Evermann (Beryciformes: Holocentridae), off Hawaii (type-locality) and Tahiti, Pacific Ocean.

Material studied: *M. menpachi* (USNPC 63874 – holotype, MPM 15386 – paratypes, MPM 15385, 15387 – vouchers); *Metabothriocephalus* sp. (see 'Remarks') ex *Chlorophthalmus agassizi* Bonaparte (Aulopiformes: Chlorophthalmidae), off Mozambique (IPCAS C-448).

Remarks: The genus was described by Yamaguti (1968), who placed it in the Parabothriocephalidae, which was then synonymised with the Echinophallidae by Bray et al. (1994). However, the genus actually belongs to the Triaenophoridae because it possesses lateral genital pores; in addition, it lacks the characteristics typical of echinophallids, such as the cirrus armed with spines and a band of large, spiniform microtriches at the posterior margin of segments (Poddubnaya et al., 2007; Levron et al., 2008a,b).

Specimens from *C. agassizi* from Mozambique collected by L.W. Reimer are considered to be congeneric because they are identical in most morphological characteristics, such as the presence of a slit-like depression posterior to the bothria, a long neck and very small cirrus-sac, the shape and poral position of the ovary, a low number of testes and numerous vitelline follicles filling most of the cortex of the whole segments. They probably represent a new species because they possess a slightly different scolex, an elongate rather than a spherical uterine pore, more testes forming wider lateral fields, a genital pore opening in a deep transverse incision on the lateral margin of the segment, and a different fish host (Aulopiformes).

***Milanella* Kuchta & Scholz, 2008 (Figs. 2C, 7A)**

Diagnosis: Bothriocephalidea, Triaenophoridae. Medium-sized worms. Segmentation present. Segments trapeziform, markedly craspedote, with velum-like posterior margin and horn-like posterolateral projections. Strobila with intensely stained corpuscles, most numerous in anterior part of strobila. Scolex sagittate, projecting posteriorly over first segment. Apical disc well developed. Bothria elongate. Neck absent. Testes in two narrow lateral bands, separated medially, continuous between segments. Cirrus-sac large, pyriform, thin-walled, with proximal part bent anteriorly; cirrus unarmed. Genital pore lateral, postequatorial, irregularly alternating. Genital atrium deep. Ovary asymmetrical, slightly poral, deeply lobed. Vagina thick-walled, posterior to cirrus-sac, without sphincter. Vitelline follicles numerous, cortical, circumsegmental. Uterine duct sinuous, enlarging in gravid segments. Uterus near anterior margin of segments, pyriform in first gravid segments, then becoming widely oval to elongate. Uterine pore near posterior end of uterus. Eggs operculate, unembryonated.

Type- and only species: *M. familiaris* Kuchta & Scholz, 2008 ex *Centrolophus niger* (Gmelin) (Perciformes: Centrolophidae), off Outer Hebrides, North Atlantic Ocean.

Material studied: See Kuchta & Scholz (2008).

Remarks: This genus was erected by Kuchta & Scholz (2008), who provided a detailed differential diagnosis. *Milanella* is typified by combination of the following characteristics: (1) trapeziform, markedly craspedote segments with velum-like posterior margins and horn-like posterolateral projections; (2) the uterus is pyriform in the first gravid segments, becoming widely oval to elongate in the posterior part of the strobila; (3) an arrow-shaped scolex with prominent posterior margins, a well-developed apical disc and elongate, simple bothria; (4) intensively stained corpuscles which are most numerous in the anterior part of the strobila; (5) a large pyriform, thin-walled cirrus-sac with the proximal part curved anteromedially; (6) a deeply lobate ovary; and (7) the absence of a neck (Kuchta & Scholz, 2008).

Bray et al. (1994) provided an illustration (fig. 10.66) of a mature segment of the tapeworm designated as *Amphicotyle heteropleura*, but it actually belongs to *Milanella familiaris* (see Kuchta & Scholz, 2008). Similarly, Brabec et al. (2006) misidentified the latter cestode as *A. heteropleura*.

***Neobothriocephalus* Mateo & Bullock, 1966 (Figs. 2D, 7B)**

Diagnosis: Bothriocephalidea, Echinophallidae. Medium-sized tapeworms. Segmentation may be incomplete (missing along mid-line of strobila). Strobila with craspedote segments with enlarged posterolateral margin. Scolex lanceolate, unarmed. Bothria shallow. Apical disc present. Neck absent. Testes in two lateral fields, confluent posteriorly. Cirrus-sac large, thick-walled, oriented obliquely, with conspicuous spherical swelling (basal bulb) in proximal part near anterior margin of segment, surrounded by gland-cells; cirrus unarmed. Genital pore sublateral. Ovary reniform, lobulated. Vagina posterior to cirrus-sac, with ring-like sphincter. Receptaculum seminis present. Vitelline follicles largely cortical, with some follicles entering medulla, forming two lateral fields separated medially, not reaching lateral margins of segments. Uterine duct sinuous, enlarging in gravid segments. Uterus oval to spherical. Uterine pore submedian. Eggs operculate, unembryonated. In marine teleosts (*Seriolella*). Pacific Ocean.

Type-species: *N. aspinosus* Mateo & Bullock, 1966 ex *Neptomenus crassus* Starks (now *Seriolella violacea* Guichenot) (Perciformes: Centrolophidae), off Lima, Peru (type-locality) and Chile.

Other species: *N. mamaevi* (Tkachev, 1978) ex *Seriolella tinro* Gavrilov, New Zealand.

Material studied: *N. aspinosus* from *S. violacea*, off Lima, Peru (USNPC 61639-40 – holotype and paratype, 97383 – vouchers; IPCAS C-449).

Remarks: Mateo & Bullock (1966) reported an asymmetrical shape of the eggs due to a lateral swelling. Although a large number of live specimens were observed by the present authors and their eggs were studied *in vivo* and using SEM, such a lateral swelling was never found. The type-host was designated as *Neptomenus crassus* (this name is not listed in FishBase – Froese & Pauly, 2008, but is listed as a synonym of *Seriolella violacea* in other databases), in which the cestode occurs with very high prevalences (almost 100% – see Iannacone, 2003) and intensity of infection (4,800 tapeworms in 19 infected fish according to Mateo & Bullock, 1966).

Riffo (1991), Oliva et al. (2004) and González et al. (2008) found tapeworms identified as *Neobothriocephalus aspinosus* in *Hippoglossina macrops* Steindachner (Pleuronectiformes: Paralichthyidae), but with a very low prevalence (6%). This record in a different fish host should be confirmed, but the voucher material does not exist.

Pseudamphicotyla mamaevi Tkachev, 1978 described from *Seriolella tinro* from off New Zealand belongs to *Neobothriocephalus* (V. Gulyaev, pers.

comm.; Kuchta & Scholz, 2007) and may be conspecific with *N. aspinosus*, but no material is available.

Oncodiscus **Yamaguti, 1934 (Figs. 3A, 7D)**

Syn. *Tetrapapillocephalus* Protasova & Mordvinova, 1986

Diagnosis: Bothriocephalidea, Bothriocephalidae. Medium-sized worms. Segmentation present, may be incomplete (missing along mid-line of strobila). Strobila craspedote, segments with prominent posterolateral wing-like projections. Scolex oval or irregularly-shaped, usually compressed laterally. Bothria narrow, elongate, with strongly folded margins. Apical disc flattened, armed with numerous tiny hooklets which detach readily. Neck absent. Testes in two lateral fields. Cirrus-sac large, thick-walled; cirrus unarmed. Genital pore median. Ovary transversely elongate, lobulate. Vagina opening lateral or anterolateral to cirrus-sac, thick-walled distally. Vitelline follicles cortical, in two lateral fields, reaching posterolateral projections of segment. Uterine duct sinuous, enlarging in gravid segments. Uterus thick-walled. Uterine pore median, at some distance from anterior margin of segment or almost equatorial. Eggs operculate, unembryonated. In marine teleosts (*Saurida*). Pacific and Indian Oceans.

Type- and only species: *O. sauridae* Yamaguti, 1934 (syns *O. fimbriatus* Subhapradha, 1955; *O. waltairensis* Shinde, 1975; *O. maharashtrae* Jadhav & Shinde, 1981; *Bothriocephalus indicus* Ganapati & Rao, 1955; *Tetrapapillocephalus magnus* Protasova & Mordvina, 1986) ex *Saurida argyrophanes* (Richardson) [now *S. tumbil* (Bloch, 1795)] (type-host), *S. longimanus* Norman (new host), *S. micropectoralis* Shindo & Yamada and *S. undosquamis* (Richardson) (Aulopiformes: Synodontidae), Pacific and Indian Oceans.

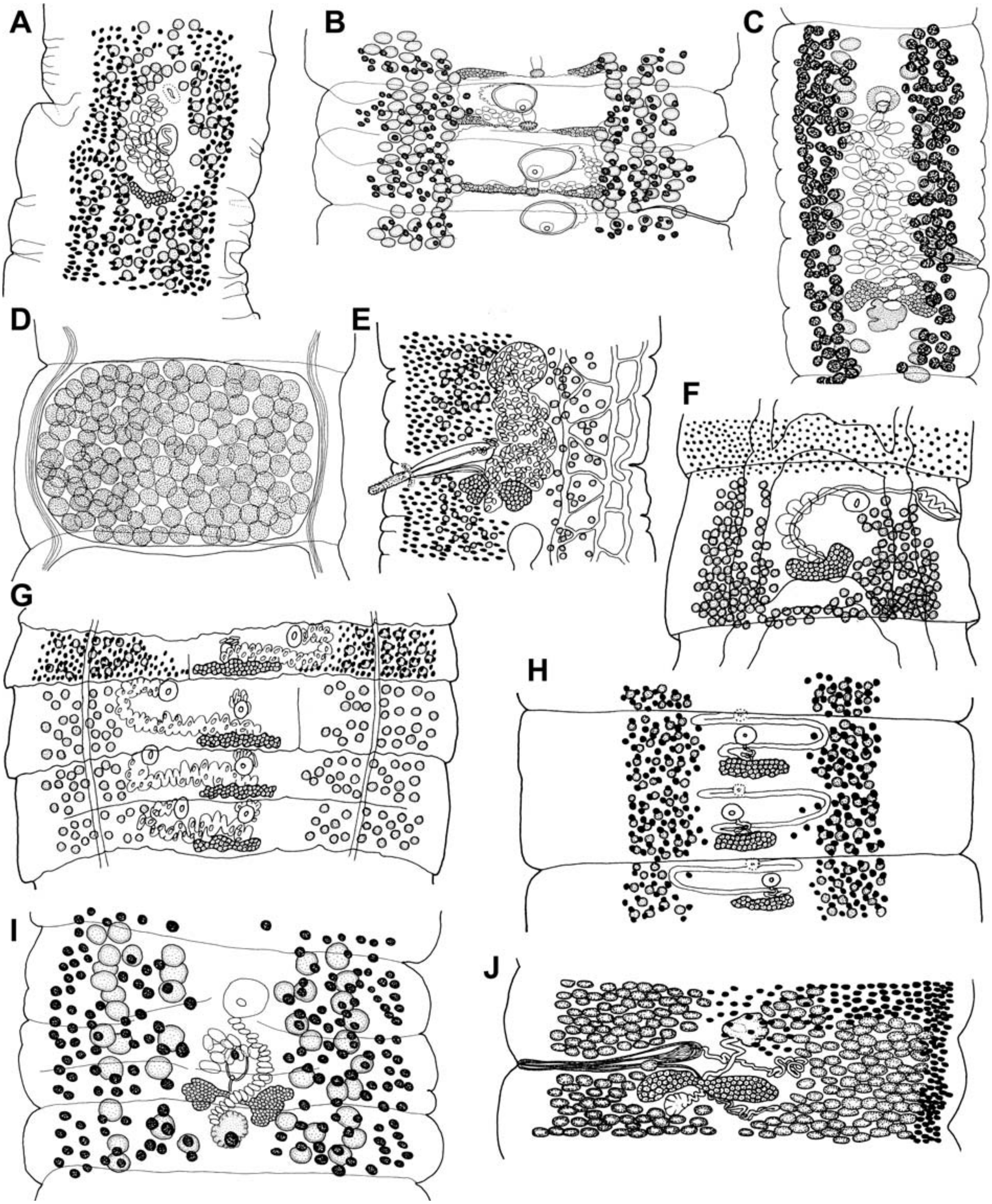
Material studied: *O. sauridae* ex *Saurida tumbil* (MPM SY 3042 – holotype, SY 3043 and SY 3165-67 – paratypes, SY 5613-18 – vouchers), Inland Sea, Japan, vouchers ex *Saurida tumbil*, *S. longimanus* and *S. micropectoralis*, Pelabuhan Ratu, Java, Indonesia (IPCAS C-456); *T. magnus* ex *S. undosquamis* from the Indian Ocean (GELAN 696 – holotype).

Remarks: This genus was erected by Yamaguti (1934) to accommodate *O. sauridae* from *Saurida argyrophanes* (now *S. tumbil*) and was revised by Khalil & Abu-Hakima (1985), who studied specimens from *S. tumbil* and *S. undosquamis*. These authors synonymised two species, *O. fimbriatus* Subhapradha, 1955 and *O. waltairensis* Shinde, 1975, which had been described from *S. tumbil* from India (off the Madras coast and the Bay of Bengal). This synonymy is accepted herein.

Khalil & Abu-Hakima (1985) also discussed the taxonomic status of another species, *O. maharashtrae*, described by Jadhav & Shinde (1981) as a member of the Tetraphyllidae [sic!] from the spiral valve of the stingray *Trygon sephen* (Forsskål) (now *Pastinachus sephen*) (Dasyatidae) off Bombay on the west coast of India. It is actually a bothriocephalid cestode, not a tetraphyllidean, because it has a medial genital pore and extensive vitelline follicles (apparently misinterpreted as testes by the authors – see their schematic figs. 2 and 3 and allegedly high number of testes – Jadhav & Shinde, 1981), and operculate eggs.

Unlike Khalil & Abu-Hakima (1985), who considered *O. maharashtrae* to be a *species inquirenda*, Kuchta & Scholz (2007) considered it a synonym of *O. sauridae* because it corresponds in its morphology, including the presence of minute hooks on an apical disc, a wide scolex with folded margins and the presence of posterolateral wing-like projections on segments. It is obvious that the finding of this bothriocephalid tapeworm in a stingray was accidental due to consumption of a true fish host (*Saurida*). *Bothriocephalus indicus* Ganapati & Rao, 1955, also described from *S. tumbil* off the eastern coast of India (Andhrapradesh), was considered a further junior synonym of *O. sauridae* by Kuchta & Scholz (2007), because its morphology conforms perfectly to that of *O. sauridae*.

Protasova & Mordvinova (1986) proposed *Tetrapapillocephalus* to accommodate their new species *T. magnus* described from *S. undosquamis*, which also hosts *O. sauridae* (see above), in the Indian Ocean, and erected a new subfamily, the Tetrapapillocephalinae Protasova & Mordvinova, 1986. The genera differ, allegedly, only in the absence of tiny hooklets on the apical disc in *Tetrapapillocephalus*. However, the hooklets can be easily lost during handling or when dead tapeworms are found (Khalil & Abu-Hakima, 1985). Indeed, examination of the type-material of *T. magnus* has shown that they are in a poor state, apparently due to *post mortem* autolysis. In addition, the Russian authors did not compare their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◀**Fig. 8** Drawings of scoleces of bothriocephalidean cestodes. (**A**) *Plicocestus janickii* ex *Coryphaena* sp., original; (**B**) *Polyonchobothrium polypteri* ex *Polypterus bichir*, original; (**C**) *Probothriocephalus alaini* ex *Xenodermichthys copei*, adapted from Scholz & Bray (2001); (**D**) *Tetracampos ciliotheca* ex *Clarias anguillaris*, original; (**E**) *Pseudamphicotyla quinquarii* ex *Pentaceros japonicus*, vitelline follicles illustrated only in left side of segment, adapted from Yamaguti (1952); (**F**) *Pseudeubothrioides lepidocybii* ex *Lepidocybium flavobrunneum*, vitelline follicles illustrated only anteriorly, adapted from Yamaguti (1968); (**G**) *Taphrobothrium japonense* ex *Muraenesox cinereus*, vitelline follicles illustrated only in first segment, adapted from Yamaguti (1934); (**H**) *Ptychobothrium belones* ex *Belone belone*, adapted from Yamaguti (1934); (**I**) *Senga filiformis* ex *Channa micropeltes*, original; (**J**) *Triaenophorus nodulosus* ex *Esox lucius*, adapted from Scholz (1989)

new genus with *Oncodiscus*, although its type- and only species parasitises the same fish host. Therefore, *T. magnus* was synonymised with *O. sauridae* by Kuchta & Scholz (2007).

Protasova & Mordvinova (1986) illustrated one scolex of the same species, allegedly, found in *Beryx splendens* Lowe (Beryciformes: Berycidae), but this fish probably represents only a paratenic or accidental host, because only immature specimens were found (Protasova, pers. comm.).

Parabothriocephaloides **Yamaguti, 1934 (Figs. 2E, 7E)**

Syn. *Paratelemerus* Gulyaev, Korotaeva & Kurochkin, 1989

Diagnosis: Bothriocephalidea, Echinophallidae. Small worms. Segmentation incomplete (lacking along mid-line of strobila). Strobila pectinate; craspedote segments possess paired posterolateral expansions on dorsal and ventral surface, covered with band of large spiniform microtriches. Scolex replaced by cone-shaped or trapeziform pseudoscolex. Neck absent. Testes in two lateral fields, confluent posteriorly, continuous between segments. Cirrus-sac medium-sized to very large, thick-walled, oriented anteromedially; cirrus armed with spines. Genital pore sublateral. Ovary bilobed, with lobulate to dendritic lateral wings, submedian (poral). Vagina posterior to cirrus-sac, with distended terminal part; large, ring-like vaginal sphincter usually present, but may be absent in some segments of same worm. Vitelline follicles cortical, circumsegmental. Uterine duct sinuous, enlarging in gravid segments. Uterus oval, not expanding in gravid segments. Uterine pore median, near anterior margin of segments. Eggs operculate, unembryonated. In centrolophid fish (*Psenopsis*, *Seriolella*). Pacific and Indian Oceans.

Type-species: *P. segmentatus* Yamaguti, 1934 ex *Psenopsis anomala* (Temminck & Schlegel) (Perciformes: Centrolophidae), Inland Sea, Japan (type-locality) and China.

Other species: *P. psenopsis* (Gulyaev, Korotaeva & Kurochkin, 1989) Kuchta & Scholz, 2007 ex *Psenopsis humerosa* Munro; *P. seriolella* (Gulyaev, Korotaeva & Kurochkin, 1989) Kuchta & Scholz, 2007 ex *Seriolella brama* (Günther), off north-western Australia; *P. wangi* nom. nov. for *Parabothriocephalus psenopsis* Wang, Liu & Yang, 2004 ex *Psenopsis anomala*, off Xiamen, South China Sea, China (see Remarks).

Material studied: *P. segmentatus* ex *Psenopsis anomala* (MPM 22332 SY 3051 – holotype, SY 3052 – paratype, SY 5603-12 – vouchers), Inland Sea, Japan; *P. wangi* ex *Psenopsis anomala*, South China Sea, China (IPCAS C-457; C-458); *P. psenopsis* ex *Psenopsis humerosa* (IPCAS C-451 – holotype & paratypes); *P. seriolella* ex *S. brama* (IPCAS C-450 – holotype & paratypes), off north-western Australia; specimens of the two last species were kindly provided by V. Gulyaev and are now deposited in the IPCAS.

Remarks: The genus was described by Yamaguti (1934), but Bray et al. (1994) synonymised it with *Parabothriocephalus*, because they did not consider the presence or absence of a pseudoscolex, the presence of posterolateral expansions on the segments and a vaginal sphincter and the distribution of the vitellarium to represent valid generic characters.

Based on a study of a high number of echinophallid taxa, it is concluded herein that the two last characters are actually not suitable for differentiation of individual genera. However, the presence or absence of a pseudoscolex and the presence of paired posterolateral expansions are considered to be generic characteristics. In addition, *Parabothriocephaloides* and *Parabothriocephalus* differ markedly in the shape of the strobila (pectinate in the former genus), the degree of external segmentation (incomplete in all segments of *Parabothriocephaloides*) and the presence of a wide band of giant spiniform microtriches on posterolateral expansions of segments in the former genus (versus much smaller microtriches in

Parabothriocephalus). On the basis of the above-listed differences, *Parabothriocephaloides* is resurrected. This taxonomic action is also supported by molecular data because *Parabothriocephaloides* and *Parabothriocephalus* appear in unrelated clades of the echinophallid cestodes (Kuchta, 2007, fig. 10).

Gulyaev et al. (1989) erected a new genus, *Paratelemerus*, to accommodate two new species, *Paratelemerus psenopsis* from *Psenopsis anomala* and *Paratelemerus seriolella* from *Seriolella brama*, both taxa found off Australian waters. Bray et al. (1994) retained this genus as valid, differentiating it from other echinophallids in possessing a very large cirrus-sac, reaching the aporal part and to the anterior edge of segments. Indeed, both taxa of Gulyaev et al. (1989) have extremely large cirrus-sacs, but the size of the sac is not considered here to be a valid generic character, because there is a wide range of intrageneric variation in the relative and absolute size of the cirrus-sac in members of the Echinophallidae, including members of *Parabothriocephaloides* and *Parabothriocephalus*. This makes it impossible to clearly demarcate the "very large" and "large" cirrus-sacs present in some morphologically similar taxa. Therefore, both species of *Paratelemerus* were transferred to *Parabothriocephaloides* as new combinations by Kuchta & Scholz (2007), which also implies that these authors invalidated the former genus as a junior synonym of *Parabothriocephaloides*, although they did not explicitly mention this synonymy.

Parabothriocephalus psenopsis Wang, Liu & Yang, 2004, described from *Psenopsis anomala*, apparently belongs to *Parabothriocephaloides* because of the possession of all morphological characteristics typical of this genus now resurrected from previous synonymy with *Parabothriocephalus*. Because of homonymy with *Parabothriocephaloides psenopsis* (Gulyaev, Korotaeva & Kurochkin, 1989), a new name, *Parabothriocephaloides wangi* nom. nov., is proposed to accommodate the taxon described by Wang et al. (2004).

***Parabothriocephalus* Yamaguti, 1934 (Figs. 4J, 7F)**

Diagnosis: Bothriocephalidea, Echinophallidae. Small to medium-sized worms. Segmentation present, may be incomplete (along mid-line of strobila) in last mature and gravid segments. Strobila with craspedote segments. Posterolateral margins of segments covered with large microtriches. Scolex elongate, unarmed. Bothria elongate, shallow. Apical disc absent. Neck absent. Testes in two lateral fields, confluent posteriorly, continuous between segments. Cirrus-sac medium-sized to large, thick-walled, mainly in distal part, oriented slightly anteromedially; cirrus armed with spines. Genital pore sublateral. Ovary with two asymmetrical, strongly lobulate wings. Vagina posterior to cirrus-sac, distended in terminal part, sometimes (*P. gracilis*) armed with small spines in proximal end of distended region; vaginal sphincter present or absent, even in different segments of same worm. Vitelline follicles cortical, with some follicles entering medulla, or medullary, in one almost complete circumsegmental field. Uterine duct sinuous, sigmoid, enlarging in gravid segments. Uterus oval, not enlarging in gravid segments. Uterine pore median, near anterior margin of segments. Eggs operculate, unembryonated. In marine fish (Centrolophidae, Macrouridae, Sebastidae). Atlantic and Pacific Oceans.

Type-species: *P. gracilis* Yamaguti, 1934 ex *Psenopsis anomala* (Temminck & Schlegel) (Perciformes: Centrolophidae), Inland Sea, Japan (type-locality) and China.

Other species: *P. johnstoni* Prudhoe, 1969 ex *Macrourus whitsoni* (Regan) and *M. holotrachys* Günther (new host), Weddell Sea, Antarctic; *P. macrouri* Campbell, Correia & Haedrich, 1982 ex *M. berglax* Lacépède and *M. carinatus* (Günther) (all Gadiformes: Macrouridae), off Newfoundland and the Falkland Islands, Atlantic Ocean; *P. sagitticeps* (Sleggs, 1927) ex *Sebastes paucispinus* Ayres (Scorpaeniformes: Sebastidae), off California, Pacific Ocean.

Material studied: *P. gracilis* ex *Psenopsis anomala* (MPM 22330 – holotype, 22331 – paratype, SY 5607-12 – vouchers), Inland Sea, Japan and vouchers, Sea of Japan, China (IPCAS C-459); *P. johnstoni* ex *Macrourus whitsoni*, Weddell Sea (IPCAS C-460); *P. macrouri* ex *M. berglax* from off Newfoundland (USNPC 77098, 77099 – holotype and paratype); *P. sagitticeps* ex *Sebastes paucispinis*, Californian coastal waters (USNPC 73463-73467); *Parabothriocephalus johnstoni* (designated as the syntype of "*Priapacanthus macrouri*" by R. Dollfus, but never published and thus is a *nomen nudum*) ex *Macrourus holotrachys*, off Heard and Kerguelen Islands (MNHNP dB 52/1-11).

Remarks: Unlike *Parabothriocephaloides*, which was synonymised with the present genus by Bray et al. (1994), but is resurrected here (see above), the scolex is present in species of *Parabothriocephalus*, although it may be detached. Segments are usually distinctly delineated, but segmentation may be incomplete along the midline of mature and gravid segments. As already observed in the type-species (Yamaguti, 1934) and confirmed in the present study, the vaginal sphincter may be present in some segments, whereas it is absent in others in the same worm, which renders this character taxonomically useless. The genus includes species parasitic in phylogenetically distant fish groups, but the morphology of these species justifies their placement in the same genus. Wang et al. (2004) described *Parabothriocephalus psenopsis*, which has been transferred to *Parabothriocephaloides* and a new name, *Parabothriocephaloides wangi*, is proposed to avoid the homonymy with *Parabothriocephaloides psenopsis* (Gulyaev, Korotaeva & Kurochkin, 1989) Kuchta & Scholz, 2007 (see above).

Specimens from the collection of R. Dollfus ("*Priapacanthus macrouri*") deposited in MNHNP belong to *Parabothriocephalus johnstoni* and, therefore, *M. holotrachys* is a new host for this species.

Parabothrium **Nybelin, 1922 (Figs. 4E, 7G)**

Diagnosis: Bothriocephalidea, Triaenophoridae. Large worms. Segmentation present. Strobila robust; segments with prominent longitudinal grooves. *Scolex deformatus* present, unarmed. Bothria absent. Apical disc absent. Neck undistinguishable. Testes in two dorsolateral fields, separated between segments, confluent in anterior part of segment. Cirrus-sac large, elongate; internal seminal vesicle present; cirrus unarmed. Genital pore lateral. Ovary compact. Vagina anterior to cirrus-sac, with sphincter in terminal part. Vitelline follicles medullary, on ventral layer of medulla only, forming two lateral fields in posterior part of segments. Uterine duct short, sinuous. Uterus large, oval, lobulate. Uterine pore rudimentary; eggs released by rupture of segment wall. Eggs unoperculate, embryonated. In marine teleosts (Gadidae). Atlantic Ocean.

Type- and only species: *P. bulbiferum* Nybelin, 1922 [syn. (?) *Taenia gadipollachii* Rudolphi, 1810 in part] ex *Gadus pollachius* L. (now *Pollachius pollachius*) (type-host), *P. virens* (L.) and *G. morhua* L. (Gadiformes: Gadidae).

Material studied: *P. bulbiferum* ex *Pollachius pollachius*, coll. O. Nybelin, 5.iv.1905 (MNHNP C 96 – syntype), and vouchers, North Atlantic Ocean (BMNH 1982.4.26.257-259).

Remarks: This genus resembles *Abothrium* in several morphological features, such as the presence of the *scolex deformatus*, a robust strobila with well-developed inner longitudinal musculature and a thick-walled cirrus-sac with an internal seminal vesicle. It can be easily distinguished from *Abothrium* by the distribution of vitelline follicles and testes (limited to the dorsal medulla), the size of the cirrus-sac and the position of the vagina, which possesses a large sphincter in *Parabothrium*. A detailed description of *P. bulbiferum* (reported as *Parabothrium gadipollachii*) was provided by Williams (1960). The present study confirmed almost all characteristics reported by Williams (1960); slight differences were found only in the distribution of the longitudinal musculature.

There have been controversies over the designation of the type-species of the genus. Some authors (Williams, 1960; Bray et al., 1994) considered Rudolphi's *Taenia gadipollachii* to be the type-species. However, it is not evident from the original description of *T. gadipollachii* whether Rudolphi (1810) actually studied *Parabothrium*, *Abothrium gadi* or a mixture of tapeworms of both taxa. These tapeworms occur frequently in gadid fish and are almost indistinguishable from each other on the basis of gross morphology. They had been confused until Nybelin (1922) redescribed both taxa on the basis of a thorough evaluation of freshly collected material, including cross-sections. In order to avoid the confusion caused by a very simple and inadequate original description of *Taenia gadipollachii*, Nybelin (1922) proposed *Parabothrium bulbiferum* as a new name for tapeworms found in gadids that do not belong to *Abothrium gadi*. *P. bulbiferum* is considered here, in accordance with Nybelin (1922), Schmidt (1986) and other authors, to be the type-species of *Parabothrium* and *Taenia gadipollachii* is placed among the tentative synonyms of this taxon.

Paraechinophallus **Protasova, 1975 (Figs. 3B, 7H)**

Diagnosis: Bothriocephalidea, Echinophallidae. Small worms. Segmentation present, may be incomplete along mid-line of anterior segments. Each segment

formed by two pseudosegments which contain paired (parallel) genitalia. Strobila craspedote; anterior segments with paired posterolateral wing-like appendages on dorsal and ventral surface of body; more posterior segments with posterior margins possessing numerous tongue-shaped lappets, wider and shorter on ventral surface; margins of segments covered with large spiniform microtriches. Scolex replaced by trapeziform pseudoscolex with two shallow, bothrium-like depression. Neck absent. Testes in two transverse lateral fields, separated medially, absent along anterior margin of segments. Cirrus-sac large, massive, muscular; cirrus large, armed with very large spines, often evaginated. Genital pore close to lateral margin of segments. Ovary bilobed, lobulate to dendritic, near lateral margin. Vagina posterior or posteroventral to cirrus-sac; vaginal sphincter absent. Vitelline follicles cortical, circumsegmental. Uterine duct winding. Uterus oval, submedian. Uterine pore submedian. In marine teleosts (Centrolophidae, Nomeidae). Pacific Ocean.
Type- and only species: *P. japonicus* (Yamaguti, 1934) (syn. *Echinophallus japonicus* Yamaguti, 1934) ex *Psenopsis anomala* (Temminck & Schlegel) (Perciformes: Centrolophidae), Inland Sea, Japan (type-locality) and off China.
Material studied: *P. japonicus* ex *Psenopsis anomala* (MPM 22333 SY 3061 – holotype, SY 3060, 3062-65 – paratypes, SY 7150-56 – vouchers), Inland Sea, Japan; vouchers, Japan and China (IPCAS C-461); *Paraechinophallus* sp. ex *Psenes* cf. *cyanophrys* Valenciennes (Perciformes: Nomeidae) (IPCAS C–494), Pelabuhan Ratu, Java, Indonesia.
Remarks: *Paraechinophallus* is very similar to *Echinophallus*, but differs in the more lateral position of the genital pores, the presence of a pseudoscolex (a true, primary scolex is present in *Echinophallus*) and incomplete segmentation in the anterior segments, which possess paired posterolateral wing-like appendages on the ventral and dorsal surface of the strobila. The cirrus of species of *Paraechinophallus* is often evaginated and covered with large spines. In the possession of an armed cirrus, *Paraechinophallus* differs markedly from *Mesoechinophallus*, the cirrus of which is smooth (see p. 109).

Paraechinophallus sp. found in *Psenes* cf. *cyanophrys* from off Java by T. Walter may represent a new species, but the material is of too poor a quality for the description of a new species.

Penetrocephalus Rao, 1960 (Figs. 4K, 7K)
Diagnosis: Bothriocephalidea, Bothriocephalidae. Medium-sized worms. Segmentation present, may be incomplete (missing along mid-line of strobila). Strobila craspedote; segments with prominent posterolateral wing-like projections. Scolex unarmed, replaced by long, claviform *scolex deformatus* with terminally tapered anterior end. Neck long, slender, penetrating intestinal wall, encapsulated on mesentery or in liver, coiled in cyst and often degenerating to become filamentous. Testes in two lateral fields, continuous between segments. Cirrus-sac oval; cirrus armed with fine spines. Genital pore slightly submedian. Ovary transversely elongate, bilobed. Vagina lateral or anterolateral to cirrus-sac. Vitelline follicles numerous, cortical, forming two lateral fields reaching posterolateral projections, absent along mid-line of body. Uterine duct sinuous, enlarging in gravid segments. Uterus thick-walled. Uterine pore median. Eggs operculate, unembryonated. In marine teleosts (*Saurida*). Indian Ocean.
Type- and only species: *P. ganapattii* (Rao, 1954) Rao, 1960 (syn. *Bothriocephalus penetratus* Subhapradha, 1955) ex *Saurida tumbil* (Bloch) (type-host), *S. micropectoralis* Shindo & Yamada and *S. undosqamis* (Richardson) (Aulopiformes: Synodontidae), off Waltair, India, Indian Ocean.
Material studied: *P. ganapattii* – vouchers ex *S. micropectoralis*, *S. tumbil* and *S. undosqamis*, off Pelabuhan Ratu, Java, Indonesia (IPCAS C-462).
Remarks: *Penetrocephalus* was erected by Rao (1960) for *Bothriocephalus ganapattii* Rao, 1954, but misspelled as '*Penetrocephalus ganapatii*'. Subhapradha (1955) described apparently conspecific cestodes as *B. penetratus*. Protasova (1977) and Bray et al. (1994) considered *B. ganapatii* as a *nomen nudum* and retained this taxon in *Bothriocephalus* considering *Penetrocephalus* to be its synonym.

However, the original description of *B. ganapatii*, although incomplete and with only two photomicrographs of the *scolex deformatus*, enables differentiation of the new genus from *Bothriocephalus* (see Rao, 1954). Therefore, *B. ganapattii* is considered to be valid and thus becomes the type-species of *Penetrocephalus*, in accordance with Rao (1960).

Based on morphological descriptions by Rao (1954, 1960) and Subhapradha (1955) as well as examination of new material from Indonesia, *Penetrocephalus* Rao, 1960 is resurrected, because it differs from *Bothriocephalus* in several characteristics: (i) the unique scolex morphology (*scolex deformatus*) and its penetration through the intestinal wall; (ii) the presence of a slender, filamentous neck coiled in the cyst with the scolex outside the intestinal wall; (iii) the presence of prominent posterolateral wing-like projections on the segments, similar to those of *Oncodiscus*. The validity of *Penetrocephalus* is also supported by molecular data (Kuchta, 2007, fig. 10).

Philobythoides **Campbell, 1979 (Figs. 4L, 7J)**

Diagnosis: Bothriocephalidea, Philobythiidae. Small tapeworms. Segmentation present. Strobila craspedote, with trapeziform segments wider than long. Scolex oval, unarmed. Bothria elongate to oval. Apical disc absent. Neck absent. Testes forming transverse band near anterior margin of segment or in two lateral fields. Cirrus-sac small; cirrus unarmed. Genital pore marginal. Ovary oval, slightly poral. Vagina anterior to cirrus-sac. Vitellarium medullary, lobed, forming single transverse band posterior to ovary. Uterine duct straight, short. Uterus inverted V-shaped in mature segments, enlarging to become transversely elongate, slightly lobed in gravid segments. Uterine pore median. Single oncosphere covered with membraneous capsule. In deep-sea teleosts (*Alepocephalus*). North Atlantic Ocean.

Type- and only species: *P. stunkardi* Campbell, 1979 ex *Alepocephalus agassizii* Goode & Bean (Osmeriformes: Alepocephalidae), North Atlantic.

Material studied: *P. stunkardi* (USNPC 74873, 74874 – holotype and paratype); *Philobythoides* sp. ex *Alepocephalus rostratus* Risso, North Atlantic Ocean (BMNH 1999.9.27.7-8).

Remarks: *Philobythoides* and *Philobythos* are unique among bothriocephalidean cestodes in having a compact vitellarium posterior to the ovary. The genera can be distinguished from each other by the shape of the scolex, the absence of an apical disc and neck in the former genus, the shape of the uterus in gravid segments (transversely elongate in the former genus versus three-lobed in *Philobythos*), and a single oncosphere within each membraneous capsule in *Philobythoides* versus three to five oncospheres grouped together in *Philobythos*. There are also slight differences in the relative position of the uterus, genital pore and ovary.

The specimens collected by R.A. Bray from *A. rostratus* are almost identical in their morphology with *P. stunkardi*, the only difference being in the distribution of testes, which form two lateral bands continuous between segments in the new material, whereas they are limited to the anteriormost region of the segments in *P. stunkardi*. Based on this difference, it is probable that the tapeworms from *A. rostratus* represent a new species of *Philobythoides*, but the internal morphology of both of the specimens available was difficult to observe, which makes it inadvisable to propose them as a new species.

Philobythos **Campbell, 1977 (Figs. 4M, 7L)**

Diagnosis: Bothriocephalidea, Philobythiidae. Small tapeworms. Segmentation present. Strobila craspedote, with trapeziform segments, wider than long, with rounded posterolateral projections. Scolex oval, unarmed. Bothria elongate. Apical disc present. Neck present. Testes few in number, forming two irregular fields, confluent posteriorly. Cirrus-sac small, oval; cirrus unarmed. Genital pore marginal. Ovary compact, oval. Vagina anterior to cirrus-sac. Seminal receptacle present. Vitellarium medullary, dendritic to lobed, forming single transverse band posterior to ovary. Uterine duct straight, short. Uterus wide, inverted V-shaped, with oval anteromedian part and straight, elongate lateral wings, enlarging in gravid segments to form three large sac-like compartments. Uterine pore median. Oncospheres grouped together in clusters of three to five, covered with membranous capsule. In deep-sea teleosts. North Atlantic Ocean.

Type- and only species: *P. atlanticus* Campbell, 1977 ex *Acanthochaenus luetkenii* Gill (Stephanoberyciformes: Stephanoberycidae), North Atlantic Ocean.

Material studied: *P. atlanticus* (BMNH 1991.7.2.34-36, USNPC 74324, 74325, 74326 – holotype and paratypes); *Philobythos* sp. ex *Spectrunculus grandis* (Günther) (Ophidiiformes: Ophidiidae), North Atlantic Ocean (BMNH 1997.10.20.1-2); "*Philobythos*" sp. ex *Coryphaenoides rupestris* Gunnerus (Gadiformes: Macrouridae), North Atlantic Ocean (IPCAS C-463).

Remarks: This genus can be easily distinguished from all but one bothriocephalidean genera (*Philobythoides*) by the possession of a compact, postovarian vitellarium. *Philobythoides* differs in the characters listed above. Tapeworms found by R.A. Bray in *Spectrunculus grandis* undoubtedly belong to *Philobythos*, but their conspecificity with *P. atlanticus* is doubtful because of several morphological differences; they may well represent a new species.

P. atlanticus was also reported from *Coryphaenoides rupestris* by Zubchenko (1985). Immature cestodes collected from the same host from the North Atlantic Ocean, studied by the present authors, have a scolex different from that of *P. atlanticus*. They almost certainly belong to another, probably new, genus of the Echinophallidae or Triaenophoridae (see Kuchta, 2007).

Pistana Campbell & Gartner, 1982 (Figs. 4N, 7C)

Diagnosis: Bothriocephalidea, Triaenophoridae. Medium-sized worms. Segmentation present. Strobila with slightly craspedote segments, longer than wide. Scolex sagittate, unarmed. Bothria elongate, with freely projecting posterior margins. Apical disc absent. Cirrus-sac large, elongate, bent anteriorly; cirrus unarmed. Testes in two narrow lateral fields, continuous between segments. Genital pore lateral. Ovary dendritic, slightly poral. Vagina posterior to cirrus-sac. Vitelline follicles cortical, circumsegmental. Uterine duct sinuous. Uterus elongate, narrowing anteriorly, reaching anterior margin of segments. Uterine pore median, near posterior base of uterus. Eggs operculate, unembryonated. In deep-sea teleosts (*Eurypharynx* and *Saccopharynx*). North Atlantic Ocean.

Type- and only species: *P. eurypharyngis* Campbell & Gartner, 1982 ex *Eurypharynx pelecanoides* Vaillant and *Saccopharynx ampullaceus* (Harwood) (new host) (Saccopharyngiformes: Saccopharyngidae), North Atlantic Ocean.

Material studied: *P. eurypharyngis* ex *E. pelecanoides* (USNPC 76928, 76929 – holotype and paratype) and *S. ampullaceus*, North Atlantic Ocean (BMNH 1997.10.20.4).

Remarks: This genus is unique in several characters, such as a dendritic ovary, elongate segments, hastate scolex and an elongate uterus narrowing anteriorly. Specimens from *S. ampullaceus*, which represents a new host, are identical with the type-material, except for a slightly different shape of the bothria, which have shorter posterior projections than those of the type-material (compare figs. 1 and 2 in Campbell & Gartner, 1982 with fig. 10.69 in Bray et al., 1994). However, they are considered to be conspecific.

Although Campbell & Gartner (1982) reported the eggs of *Pistana* to be embryonated, they in fact do not contain formed six-hooked oncospheres, as is obvious from fig. 3 in the original description, and thus are considered to be unembryonated.

***Plicatobothrium* Cable & Michaelis, 1967 (Figs. 4O, 7I)**

Syn. *Alloptychobothrium* Yamaguti, 1968

Diagnosis: Bothriocephalidea, Bothriocephalidae. Small worms. Segmentation complete or not. Strobila acraspedote; segments wider than long. Inner longitudinal musculature formed by double concentric layers of muscle fibres. Scolex sagittiform, projecting posteriorly over anterior part of strobila, laterally compressed, unarmed. Bothria deep, with strongly crenulate margins. Apical disc present. Neck absent. Cirrus-sac small, oval, slightly directed anterolaterally; cirrus unarmed. Testes in two lateral fields, separated medially and between segments. Genital pore median. Ovary triangular to V-shaped. Vagina posterior to cirrus-sac. Vitelline follicles between fibres of external and internal circles of inner longitudinal muscles, circumsegmental. Uterine duct sinuous. Uterus oval to Y-shaped, with wide stem oblique to perpendicular anterolateral branches. Uterine pore inconspicuous. Eggs unoperculate, embryonated. In marine teleosts (flying fish – *Cypselurus* and *Cheilopogon*). Cosmopolitan.

Type- and only species: *P. cypseluri* (Rao, 1959) Khalil, 1971 (syns *Ptychobothrium cypseluri* Rao, 1959; *Alloptychobothrium spinolotopteri* Yamaguti, 1968; *Plicatobothrium raoi* Khalil, 1971; *P. cypseluri* Cable & Michaelis, 1967) ex *Cypselurus poecilopterus* (Valenciennes) (type-host), *C. oligolepis* (Bleeker), *Cheilopogon cyanopterus* (Valenciennes) and *C. spilonotopterus* (Bleeker) (Beloniformes: Exocoetidae), Atlantic, Indian and Pacific Oceans, Red Sea.

Material studied: *P. cypseluri* Cable & Michaelis, 1967 ex *Cheilopogon cyanopterus* from Jamaica (USNPC 61346 – holotype); *Alloptychobothrium spinolotopteri* ex *C. spilonotopterus*, Hawaii (USNPC 63875 – holotype; MPM 15388 YB 3481-100 – paratypes); *Alloptychobothrium* sp. ex *Cypselurus oligolepis*, Red Sea (BMNH 1991.7.17-70); *Ptychobothrium cypseluri* ex *Cypselurus* sp. (BMNH 1969.12.3.8).

Remarks: *Plicatobothrium* was erected by Cable & Michaelis (1967) for their new species *Plicatobothrium cypseluri* from the Caribbean flying fish *Cypselurus bahiensis* (now *Cheilopogon cyanopterus*). However, the authors were not aware of *Ptychobothrium cypseluri* Rao, 1959 (now transferred to *Plicatobothrium* as its type-species) described from another flying fish in India, *Cypselurus poecilopterus*, by Rao (1959). The taxa are apparently conspecific, because they are identical in their morphology, including the presence of vitelline follicles between two concentric layers of muscle bundles of the inner longitudinal musculature. They also parasitise congeneric fish hosts. Therefore, the former taxon proposed by Cable & Michaelis (1967) becomes a synonym and homonym of *Plicatobothrium cypseluri* (Rao, 1959).

Khalil (1971) also supposed conspecificity of these taxa, but he did not formally synonymise them because of the unavailability of the types of the Indian species. In order to avoid homonymy, he proposed, in our opinion incorrectly, to rename Rao's species, which has priority, to *Plicatobothrium raoi* nom. nov. Protasova (1977) also considered these species synonymous, but, following Khalil's (1971) proposal, ignored the priority of Rao's specific name "*cypseluri*".

Yamaguti (1968) erected *Alloptychobothrium* to accommodate his new species *A. spilonotopteri* from another flying fish, *Cypselurus spinolotopterus* (now *Cheilopogon spinolotopterus*), from Hawaii. He admitted that his new species closely resembled *Plicatobothrium cypseluri* of Cable & Michaelis (1967) and that both taxa might belong to the same genus. Nevertheless, he regarded them as distinct species in separate genera on the basis of the alleged difference in the shape of the ovary (V-shaped in *Plicatobothrium*) and the uterus (conspicuously Y-shaped in this genus).

However, Yamaguti (1968) was incorrect in describing the shape of the ovary, which does not have its lateral wings "directed posterial", as claimed (Yamaguti, 1968, p. 32). Observation of Yamaguti's material, carried out by the two senior authors (R.K. & T.S.), has shown that Yamaguti's illustration of a mature segment (fig. 6B) is in fact inverted, as indicated by the position of the vagina and uterine duct. Thus, the ovary is in fact V-shaped, as in *Plicatobothrium cypseluri*, the cirrus-sac is directed posteromedially and the uterus has a central stem with two lateral wings, thus being Y-shaped. The slight difference in the position of the lateral wings reflects the fact that specimens described by Rao (1959) and Cable & Michaelis (1967) were more elongate than those studied by Yamaguti (1968).

On the basis of the above-mentioned morphological features, the three taxa, found in congeneric fish, are considered conspecific. Therefore, *Alloptychobothrium* is synonymised with *Plicatobothrium* and *A. spilonotopteri* becomes a junior synonym of *P. cypseluri* (Rao, 1959). Kuchta & Scholz (2007) correctly listed *A. spinolopteri* as a synonym of *P. cypseluri* but they erroneously mentioned Khalil (1971) as the first author who proposed this synonymy.

Plicocestus n. g. (Figs. 2F, 8A)

Diagnosis: Bothriocephalidea, Bothriocephalidae. Small, slender worms. Segmentation absent. Strobila with plicate lateral margins. Inner musculature composed of two layers around vitelline follicles. Scolex markedly elongate, very long in comparison with strobila, unarmed. Bothria very long, groove-like, with plicate lateral margins. Apical disc weakly developed. Neck absent. Testes forming single wide longitudinal field along median line. Cirrus-sac oval, median; cirrus unarmed. Genital pore median. Ovary transversely elongate, lobulate. Vagina posterior to cirrus-sac. Vitelline follicles paramuscular, limited to ventral layer of proglottids, between external and internal concentric layers of inner longitudinal musculature. Uterine duct sinuous, enlarged in gravid proglottids. Uterus and uterine pore median. Eggs unoperculate, unembryonated. In marine fish (*Coryphaena*). Indian and Atlantic Oceans.

Type- and only species: *P. janickii* (Markowski, 1971) n. comb., ex *Coryphaena* sp. (type-host) and *Coryphaena hippurus* L. (Perciformes: Coryphaenidae), Atlantic and Indian Oceans.

Material studied: *P. janickii* ex *Coryphaena* sp. (BMNH 1970.7.30.51-55 – holotype).

Etymology: The name of the new genus is derived from the most characteristic feature, i.e. the presence of plicate lateral margins of the bothria and strobila.

Differential diagnosis: Markowski (1971) described *Bothriocephalus janickii* from *Coryphaena* sp. in the Indian Ocean. The same species was subsequently found in *C. hippurus* from the Bay of Bengal (Devil, 1975) and off Puerto Rico (Dyer et al., 1997). On the basis of a study of the holotype of this species, a new genus is proposed to accommodate *B. janickii*. The new genus differs from all bothriocephalid genera, including *Anantrum* and *Andycestus*, the only two genera that lack segmentation, in the shape and size of the scolex [very long (5 mm) in comparison with the length of the slender strobila, about 1 mm wide], the plicate lateral margins of the bothria and the presence of two concentric layers of inner longitudinal musculature which surround paramuscular vitelline follicles present only in the ventral region of the strobila.

Polyonchobothrium Diesing, 1854 (Figs. 3C, 8B)

Syn. *Oncobothriocephalus* Yamaguti, 1959

Diagnosis: Bothriocephalidea, Bothriocephalidae. Medium-sized worms. Segmentation present. Strobila with markedly craspedote, trapeziform segments. Scolex elongate, narrowing posteriorly. Bothria elongate, shallow. Apical disc prominent, wider than scolex proper, four-lobed in apical view, armed with large hooks arranged in four quadrants (6–9 hooks in each quadrant). Neck absent. Testes in two lateral fields, continuous between segments. Cirrus-sac pyriform, thick-walled; internal seminal vesicle present; cirrus unarmed. Genital pore median. Ovary compact, transversely elongate. Vagina posterior to cirrus-sac. 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 unoperculate, unembryonated. In freshwater polypterids. Africa.

Type- and only species: *P. polypteri* (Leydig, 1853) ex *Polypterus bichir* Lacépède (type-host), *P. endlicheri* Heckel and *P. senegalus* Cuvier (Polypteriformes: Polypteridae), Egypt (type-locality), River Nile, Africa.

Material studied: *Polyonchobothrium polypteri* ex *Polypterus senegalus*, Sudan (IPCAS C-464).

Remarks: The taxonomic history of the genus was reviewed by Protasova (1977) and Jones (1980). The type-species was first described briefly by Leydig (1853) as *Tetrabothrium polypteri*. Jones (1980) provided a detailed account of the morphology of *Polyonchobothrium polypteri* based on specimens from three species of bichir (*Polypterus bichir*, *P. endlicheri* and *P. senegalus*) from the Sudan. Specimens newly collected from *P. senegalus* in the Sudan are identical with those redescribed by Jones (1980).

In the present study, the validity of the monotypic genus *Polyonchobothrium* is confirmed, following Bray et al. (1994). The genus is well differentiated from the two other bothriocephalid genera from freshwater fish with an apical disc armed with small hooks in the following characteristics (the marine *Oncodiscus* with a markedly different scolex and strobilar morphology is not considered): (i) the scolex is elongate, narrowing posteriorly, with a prominent apical disc, wider than the scolex proper, with elongate, narrow bothria; (ii) the hooks on the apical disc are large, reaching up to 190 µm in length (Jones, 1980) (versus < 100 µm, usually *c.*50 µm in *Senga* and *Tetracampos*); and (iii) the strobila is massive and composed of markedly craspedote, trapeziform segments.

Oncobothriocephalus Yamaguti, 1959, the genus erected to accommodate *Ptychobothrium armatum* Fuhrmann, 1902 from *Turdus parochus* in Egypt, has been invalidated by Tadros (1968), Protasova (1977), Schmidt (1986) and Bray et al. (1994); this synonymy is also accepted herein.

Probothriocephalus Campbell, 1979 (Figs. 2G, 8C)

Syns *Flexiphallus* Protasova & Parukhin, 1986; *Heterovitellus* Protasova & Parukhin, 1986; (?) *Partitiotestis* Protasova & Parukhin, 1986

Diagnosis: Bothriocephalidea, Triaenophoridae. Small to medium-sized worms. Segmentation absent, incomplete or present. Scolex elongate. Bothria shallow. Apical disc absent. Neck present. Testes in two lateral fields, confluent medially at postovarian level. Cirrus-sac oval to elongate; cirrus unarmed. Genital pore lateral, postequatorial. Ovary bilobed, slightly poral. Vagina posterior to cirrus-sac. Vitelline follicles cortical, circumsegmental, continuous between segments. Uterine duct strongly sinuous, enlarged in gravid segments. Uterus oval to spherical. Uterine pore median. Eggs operculate or allegedly not, unembryonated. In deep-sea teleosts. Atlantic and Indian Oceans.

Type-species: *P. muelleri* Campbell, 1979 ex *Alepocephalus agassizi* Goode & Bean (Osmeriformes: Alepocephalidae), north-western Atlantic Ocean.

Other species: *P. alaini* Scholz & Bray, 2001 ex *Xenodermichthys copei* (Gill) (Alepocephalidae), North Atlantic Ocean; *P. atlanticus* (Protasova & Parukhin, 1986) (syn. *Heterovitellus atlanticus* Protasova & Parukhin, 1986) ex *Symbolophorus boops* (Richardson) (Myctophiformes: Myctophidae), South Atlantic Ocean; (?) *P. berycis* (Protasova & Parukhin, 1986) (syn. *Partitiotestis berycis* Protasova & Parukhin, 1986) ex *Beryx splendens* Lowe (Bericiformes:

Bericidae), Indian Ocean; and *P. electronus* (Protasova & Parukhin, 1986) (syn. *Flexiphallus electrona* Protasova & Parukhin, 1986) ex *Electrona paucirastra* Bolin (Myctophidae), Indian Ocean.

Material studied: *P. muelleri* (USNPC 74875, 74876 – holotype and paratype); *P. alaini* (BMNH 1998.3.31.25; IPCAS C-452 – holotype and vouchers); *P. atlanticus* (GELAN K-88 – holotype); *P. berycis* (GELAN 669 – holotype); *P. electronus* (GELAN 670 – holotype).

Remarks: Protasova & Parukhin (1986) described three new species from deep-sea fish from the Atlantic and Pacific Oceans and proposed three new genera to accommodate them. Bray et al. (1994) synonymised all three genera with *Probothriocephalus*, a genus that was not considered by Protasova & Parukhin (1986) when they erected their new genera.

Examination of the holotypes (and only existing specimens) of all three taxa described by Protasova & Parukhin (1986) showed that the tapeworms were in poor condition and thus unsuitable for morphological study, including the erection of new taxa. The worms are contracted and deformed, probably due to fixation under pressure; it is also probable that the tapeworms were already dead when fixed. Despite these obstacles, it was possible to confirm the synonymy of *Flexiphallus* and *Heterovitellus* with *Probothriocephalus* as proposed by Bray et al. (1994), because there are no characteristics to justify the generic status of the two former genera.

On the other hand, *Partitiotestis* seems to be different from *Probothriocephalus* (including *Flexiphallus* and *Heterovitellus* as its synonyms), because it possesses trapeziform, craspedote segments, the vagina is anterior to the cirrus-sac and the scolex is elongate, widening towards its anterior end. However, the very poor quality of the only existing specimen does not allow retention of the genus. Therefore, *Partitiotestis* is tentatively retained as a possible synonym of *Probothriocephalus* until new material becomes available.

Pseudamphicotyla Yamaguti, 1959 (Figs. 4P, 8E)

Diagnosis: Bothriocephalidea, Echinophallidae. Large worms. Segmentation present. Strobila with craspedote segments wider than long. Osmoregulatory system reticulate, with several longitudinal canals. Scolex elongate. Bothria divided into several loculi by transverse septal grooves, with posterior margin projecting over first segments. Apical disc conspicuous. Testes in two lateral fields, continuous between segments. Cirrus-sac large, thick-walled, oriented anteromedially; cirrus armed with spines. Genital pore sublateral, markedly postequatorial. Ovary bilobed, submedian (poral). Vagina posterior to cirrus-sac. Vitelline follicles cortical, occasionally intruding into medulla, circumsegmental. Uterine duct sinuous, enlarging in gravid segments. Uterus globular to oval. Uterine pore median. Eggs reported to be unoperculate, probably unembryonated. In marine teleosts (*Pentaceros*). Pacific Ocean.

Type- and only species: *P. quinquarii* (Yamaguti, 1952) Yamaguti 1959 ex *Quinquarius japonicus* (now *Pentaceros japonicus* Steindachner) (Perciformes: Pentacerotidae), off Japan, Pacific Ocean.

Material studied: None (the type- and only material was lost – J. Araki, Meguro Parasitological Museum, pers. comm.).

Remarks: Yamaguti (1952) described the species as a member of *Amphicotyle*, but later (Yamaguti, 1959) proposed a new genus, *Pseudamphicotyla*, to accommodate this taxon because of the unique morphology of its bothria. The species has never been found since the original description. Protasova (1977) placed the genus in the family Echinophallidae, but Bray et al. (1994) considered that *Pseudamphicotyla* belonged within the Triaenophoridae. The genus is herein considered to be a member of the Echinophallidae because of the sublateral genital pore and spined cirrus.

Another species, *Pseudamphicotyla mamaevi* Tkachev, 1978 was transferred to *Neobothriocephalus* by Kuchta & Scholz (2007) (see *Neobothriocephalus* – p. 112).

Pseudeubothrioides Yamaguti, 1968 (Figs. 4Q, 8F)

Diagnosis: Bothriocephalidea, Triaenophoridae. Small worms. Segmentation present. Strobila with slightly craspedote segments wider than long to square in terminal gravid segments. Ventral osmoregulatory canals very wide, connected with transverse anastomoses in each segment. Scolex unarmed, elongate. Bothria narrowing anteriorly. Apical disc wide, dome-shaped. Neck present. Testes in two lateral fields, confluent at postovarian level. Cirrus-sac small, with proximal part inclined anteromedially; cirrus unarmed. Genital pore lateral, pre-equatorial. Ovary bilobed, median. Vagina posterior to cirrus-sac. Vitelline follicles cortical, circumsegmental, forming single compact field, continuous between segments. Uterine duct strongly sinuous, taking arcuate course similar to vagina and vas deferens, enlarging in gravid segments. Uterus thick-walled, oval, not enlarging in gravid segments. Uterine pore slightly submedian (poral), at same level as genital pore. Eggs unembryonated. In marine teleosts (*Lepidocybium*). Pacific Ocean (off Hawaii).

Type- and only species: *P. lepidocybii* Yamaguti, 1968 ex *Lepidocybium flavobrunneum* (Smith) (Perciformes: Gempylidae), off Hawaii.

Material studied: *P. lepidocybii* (USNPC 63872 – holotype, MPM 15377 YB 3434-35 – paratypes).

Remarks: This genus was established by Yamaguti (1968), who provided a fairly detailed morphological description. However, he did not mention whether the eggs were operculate and did not present any cross-sections. Yamaguti's (1968) illustration of the scolex (his fig. 2A) is somewhat misleading because the apical disc is in fact not divided by the anterior margins of the bothria. Observation of the holotype has shown that the dome-shaped apical disc is muscular, compact and slightly overlaps the anteriormost extremity of the bothrium on each surface (Fig. 4Q).

The genus is characterised by the possession of very wide ventral osmoregulatory canals with transverse anastomoses in the postovarian region of each segment, the arcuate course of the strongly sinuous uterine duct beside the vas deferens, a dome-shaped apical disc, the inclined (oblique) position of the cirrus-sac and a markedly anterior (pre-equatorial) position of the genital pore.

Ptychobothrium Lönnberg, 1889 (Figs. 3D, 8H)

Diagnosis: Bothriocephalidea, Bothriocephalidae. Medium-sized worms. Segmentation present, may be incomplete. Strobila with acraspedote segments wider than long. Scolex sagittiform to fan-shaped, laterally compressed, unarmed; apical disc present; bothria deep, with smooth or slightly crenulate internal margins. Neck absent. Testes closely packed, in two relatively narrow lateral fields, separated medially. Cirrus-sac small, oval; cirrus unarmed. Genital pore median, pre-equatorial. Vaginal pore posterior to cirrus-sac. Ovary transversely elongate, compact. Vitelline follicles medullary, with some follicles penetrating between muscle fibres of inner longitudinal musculature (paramuscular), forming two large lateral fields separated medially, continuous between segments. Uterine duct strongly sinuous, S-shaped in first gravid segments, enlarging to fill most of space of terminal segments. Uterus widely oval, thick-walled. Uterine pore slightly submedian. Eggs unoperculate, embryonated. In marine teleosts (Belonidae). Atlantic, Indian and Pacific Oceans, Red Sea.

Type-species: *P. belones* (Dujardin, 1845) (syn. *Dibothrium restiforme* Linton, 1891) ex *Esox belone* L. (now *Belone belone*) (type-host), *Strongylura* spp. and *Tylosurus* spp. (Beloniformes: Belonidae).

Other species: *P. ratnagirensis* Deshmukh & Shinde, 1975 ex *Exocoetus bahiensis* (Valenciennes) (Beloniformes: Belonidae), Indian Ocean.

Material studied: *P. belones* ex *Strongylura leiura* (Bleeker), off Maldives, Indian Ocean (IPCAS C-465).

Remarks: This genus was erected by Lönnberg (1889) for *Bothriocephalus belones* Dujardin, 1845 and its validity has been widely accepted (Protasova, 1977; Bray et al., 1994; present study). Janicki (1926) provided a morphological description of *P. belones* based on specimens from *Belone choram* Rüppell (now *Tylosurus choram*) in the Red Sea, but he misinterpreted the orientation of the mature segments and reported the ovary to be situated near the anterior margins of the segments (see fig. 4 in Janicki, 1926, which is inverted, with the posterior margin at the top).

In strobilar morphology, *Ptychobothrium* closely resembles *Plicatobothrium* (see above); species of both genera also possess a fairly similar, sagittiform scolex (although that of *Ptychobothrium* may be fan-shaped), the only minor difference between the genera being in the extent of plication of the lateral margins of the bothria (only internal, not external margins are plicated in *Ptychobothrium*). The spectrum of fish hosts is also similar (beloniform fish), but *Ptychobothrium* taxa have been reported from belonids, whereas *Plicatobothrium cypseluri* is specific to flying fish (*Cypselurus* and *Cheilopogon*). Further studies, including molecular data, may demonstrate the relationship of these genera.

Several bothriocephalid species described from freshwater fish from India and Thailand have been placed in *Ptychobothrium* on the basis of the superficial resemblance of their scoleces to those of species of *Ptychobothrium*. However, *Ptychobothrium* is an exclusively marine genus and all freshwater taxa are considered to be conspecific with *Bothriocephalus acheilognathi* Yamaguti, 1934 (see Kuchta & Scholz, 2007).

Senga **Dollfus, 1934 (Figs. 3E, 8I)**

Syn. *Circumoncobothrium* Shinde, 1968.

Diagnosis: Bothriocephalidea, Bothriocephalidae. Small to medium-sized worms. Segmentation present. Strobila with acraspedote or slightly craspedote segments usually wider than long. Scolex oval to sagittate, with maximum width near posterior margin. Bothria oval to elongate. Apical disc present, but weakly developed, armed with small hooks, usually arranged in two semicircles. Neck absent. Testes in two lateral fields, continuous between segments. Cirrus-sac oval, medium-sized. Genital pore median. Ovary bilobed, lobulate. Vagina posterior to cirrus-sac. Vitelline follicles cortical, circumsegmental or in two longitudinal, medially separated fields, continuous between segments. Uterine duct sinuous. Uterus oval, enlarging in gravid segments. Uterine pore slightly submedian. Eggs unoperculate, unembryonated. In freshwater teleosts. Asia, Africa and Australia.

Type-species: *S. besnardi* Dollfus, 1934 ex *Betta splendens* Regan (Perciformes: Osphronemidae), aquarium in Paris.

Other species: The number of species considered to be valid was reduced to 15 by Kuchta & Scholz (2007), but it is almost certain that their actual number is much lower.

Material studied: *S. besnardi* ex *Betta splendens* (MNHNP bD 10/20-23 – syntypes); *S. filiformis* Fernando & Furtado, 1963 ex *Channa micropeltes* (Cuvier), Thailand, Asia (IPCAS C-495); *S. gordoni* (Woodland, 1937) ex *Heterobranchus bidorsalis* Geoffroy Saint-Hilaire, Sierra Leone, Africa (BMNH 1965.2.24.36-45 – cotype); *S. pycnomera* (Woodland, 1924) ex *Channa marulius* (Hamilton) (Perciformes: Channidae), India, Asia (BMNH 1965.2.24.54-58 – cotype); *S. pahangensis* Furtado & Chau-Lan, 1971 ex *Channa micropeltes* (Cuvier), Malaysia, Asia (BNMH 1970.7.30.51-55 – holotype).

Remarks: *Senga* was established by Dollfus (1934) for the new species, *S. besnardii*, which was found in *Betta splendens*, a fish occuring in South-East Asia, from an aquarium near Paris. The taxonomic history of the genus is rather complicated and was reviewed by Tadros (1966) and Protasova (1977). Most authors, including Protasova (1977) and Bray et al. (1994), considered *Senga* to be a valid genus distinct from *Polyonchobothrium*. In this paper, both genera are also retained as valid taxa, but tapeworms from catfishes of the genus *Clarias*, previously placed either in *Polyonchobothrium* or *Senga*, are transferred to *Tetracampos*, which is resurrected (see p. 126).

This implies that *Senga* now contains mainly species from freshwater fish (snakeheads, mastacembelids, etc.) in the Indomalayan Region, with one taxon, *Senga scleropagis* (Blair, 1978) (synonym *Polyonchobothrium scleropagis* Blair, 1978), described from the osteoglossiform fish *Scleropages leichardti* Günther in Australia. *Senga gordoni* (Woodland, 1937) described from *Heterobranchus* catfish in Africa was tentatively transferred to *Tetracampos* by Kuchta & Scholz (2007). However, recent examination of the type-material of *S. gordoni* has shown that the taxon should be retained in *Senga* until its generic position is resolved, because it differs from *T. ciliotheca* in the number of characteristics, including the shape of the strobila and gravid segments (unpubl. data).

Bray et al. (1994) synonymised *Circumoncobothrium* Shinde, 1968 with *Senga*. The genus had been differentiated from *Senga* only by an uninterrupted circle of hooks on the apical disc. This synonymy is accepted herein. *Senga* requires revision because many species, often found in the same fish host, have been inadequately described. Besides the poor-quality of the descriptions of almost all of the Indian taxa, their type-specimens either do not exist or they are unavailable and never sent for study on request. It is very probable that only one valid species parasitises each fish host species and that all other taxa are invalid (Kuchta & Scholz, 2007). New, well-fixed, fresh material from the type-hosts and type-localities of all taxa is necessary to rectify the systematics of *Senga*.

Rego (1997) reported a species of *Senga* from a freshwater fish in Brazil, but the worms were not mature and could not be identified to the species level; in addition, as vouchers do not exist, confirmation of the generic position is not possible.

Taphrobothrium **Lühe, 1899 (Figs. 4R, 8G)**

Diagnosis: Bothriocephalidea, Bothriocephalidae. Large worms. Segmentation present, may be incomplete.

Strobila with craspedote segments, wider than long, with notched posterior borders. Scolex elongate. Bothria elongate, shallow. Apical disc prominent, unarmed. Neck absent. Testes in two lateral fields, continuous between segments. Cirrus-sac oval, small; cirrus unarmed. Genital pore median. Vagina posterior to cirrus-sac. Ovary transversely elongate, compact. Vitelline follicles medullary, intermingled with testes, forming two lateral fields, separated medially, continuous between segments. Uterine duct strongly sinuous, enlarging in gravid segments. Uterus thin-walled, oval, submedian. Uterine pore submedian (lateral to ovarian wings). Eggs operculate, embryonated. In marine teleosts (*Muraenesox*). Pacific Ocean (off Japan).

Type- and only species: *T. japonense* Lühe, 1899 ex *Muraenesox cinereus* (Forsskål) (Anguilliformes: Muraenesocidae), Inland Sea, Japan.

Material studied: *T. japonense* ex *M. cinereus*, Inland Sea, Japan (MPM 22328 SY 3036-37 – vouchers).

Remarks: This genus was established and briefly described by Lühe (1899) and later redescribed in detail by Yamaguti (1934) based on specimens from off Japan. Cestodes identified as *Taphrobothrium* were also reported from the snakehead *Channa marulius* (Hamilton) in Bangladesh by Arthur & Ahmed (2002), but this finding is apparently erroneous. The genus is typified mainly by the medullary position of the vitelline follicles, the markedly submedian uterine pore and the presence of uterine operculate eggs containing a six-hooked oncosphere (Yamaguti, 1934).

***Tetracampos* Wedl, 1861 (Figs. 3F, 8D)**

Diagnosis: Bothriocephalidea, Bothriocephalidae. Small worms. Segmentation present. Strobila tiny, oval or spherical in cross-section, with acraspedote segments. Inner longitudinal musculature formed by wide band of individual 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. Neck absent. Testes not numerous, large, in two lateral fields, continuous between segments. Cirrus-sac spherical; cirrus unarmed. Genital pore median. Ovary bilobed. 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, absent in immature and most gravid segments. Uterine duct short. Uterus thick-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 catfish (*Clarias*). Africa, Asia.

Type- and only species: *T. ciliotheca* Wedl, 1861 (for synonyms see Kuchta & Scholz, 2007) ex *Heterobranchus anguillaris* (L.) (now *Clarias anguillaris*) (type-host) and *C. gariepinus* (Burchell) (Siluriformes: Clariidae), Egypt (type-locality), Nile River Basin, Africa, Asia.

Material studied: *T. ciliotheca* ex *C. anguillaris*, Sudan and *C. gariepinus* from Ethiopia (IPCAS C-466); *Polyonchobothrium clarias* (Woodland, 1925) ex *C. anguillaris* (BMNH 1965.2.24.29-35 – holotype); *P. fulgidum* Meggitt, 1930 ex *C. anguillaris* (BMNH 1932.5.31.801-806 – 'cotype').

Remarks: Wedl (1861) erected *Tetracampos* to accommodate *T. ciliotheca* found in *Heterobranchus anguillaris* (now *Clarias anguillaris*) in Egypt. Since the original description was incomplete, most subsequent authors considered *T. ciliotheca* a *nomen nudum* or placed it in the Proteocephalidea or Tetraphyllidea (Southwell, 1925; Janicki, 1926).

In the present paper, the genus is resurrected on the basis of an examination of the new material from the type-host in the Sudan, its comparison with type specimens of the taxa described from African catfish and a critical study of the literature, including the original description of *T. ciliotheca* by Wedl (1861). The taxon can be easily differentiated from other bothriocephalids because of the oval to cylindrical shape of the tiny strobila in cross-section, the unique morphology of its eggs (see fig. 30 a,b in Wedl, 1861) and the appearance of the gravid segments, most of which is occupied by the uterus replete with eggs (Fig. 8D). Wedl (1861) described a ciliated layer on the eggs of *T. ciliotheca*, but we did not observe this layer. The scolex described and illustrated by Wedl (1861, fig. 29) corresponds with that of the tapeworms recently found in African catfish as well as those previously placed in the genera *Polyonchobothrium* and *Senga* (see Protasova, 1977 for review).

The present study has also revealed the medullary position of vitelline follicles of *Tetracampos*, a feature found in only two other bothriocephalidean cestodes (*Ptychobothrium* and *Taphrobothrium*). Janicki (1926) provided a very detailed description of *Polyonchobothrium cylindraceum* [synonymised with *P. clarias* (Woodland, 1925) by Tadros, 1968] from *Clarias anguillaris*, and first reported the cylindrical shape of the strobila and the medullary position of the vitelline follicles (in his *forma major*) and a typical shape and morphology of the eggs (in the *forma minor*).

Meggitt (1930) described *P. fulgidum* from the same host. It is apparent, that *P. clarias*, *P. cylindraceum* and *P. fulgidum* are conspecific with *T. ciliotheca* and are considered to be its junior synonyms (see Kuchta & Scholz, 2007).

Tadros (1968) synonymised all bothriocephalid genera possessing an apical disc armed with hooks, namely *Polyonchobothrium*, *Tetracampos*, *Senga* and *Oncobothriocephalus*. However, his synonymy has not been widely accepted, although Dubinina (1987) considered *Polyonchobothrium* and *Senga* to be synonymous.

***Triaenophorus* Rudolphi, 1793 (Figs. 3G, 8J)**

Diagnosis: Bothriocephalidea, Triaenophoridae. Medium-sized worms. Segmentation absent. Scolex trapeziform to rectangular. Bothria shallow, oval. Apical disc armed with four trident-shaped hooks. Neck present. Testes numerous, forming continuous field throughout strobila. Cirrus-sac pyriform, large, thick-walled; internal seminal vesicle present; cirrus unarmed. Genital pore lateral. Ovary irregularly-shaped, slightly poral. Vagina dorsal to cirrus-sac. Seminal receptacle present. Vitelline follicles cortical, circumsegmental. Uterine duct slightly sinuous. Uterus oval. Uterine pore slit-like, slightly submedian. Eggs operculate, unembryonated. In carnivorous freshwater teleosts (*Esox*, *Sander*). Circumboreal.
Type-species: *T. nodulosus* (Pallas, 1781) ex *Esox lucius* L., *E. masquinongy* Mitchill and *E. reicherti* Dybowski (Esociformes: Esocidae), circumboreal.
Other species: *T. crassus* Forel, 1868 ex *Esox lucius*, *E. masquinongy* and *E. reicherti*, Eurasia and North America; *T. stizostedionis* Miller, 1945 ex *Sander vitreus* (Mitchill) (Perciformes: Percidae), North America.
Material studied: See Kuchta et al. (2007).
Remarks: This genus was revised by Kuperman (1973). It is well characterised by the presence of four large, trident-shaped hooks on the apical disc, an unsegmented strobila and a large, thick-walled cirrus-sac. The life-cycle includes copepods as first and freshwater fish as second intermediate hosts; plerocercoids are located in the liver or in the musculature (Kuperman, 1973). Eggs laid into water are usually unembryonated but their precocious development within the uterus of live worms was reported as a consequence of elevated water temperature (Kuperman, 1973).

Four species, *T. amurensis* Kuperman, 1968, *T. meridionalis* Kuperman, 1968, *T. orientalis* Kuperman, 1968 and *T. procerus* Özcelik, 1979, were invalidated by Dubinina (1987) and Kuchta et al. (2007).

Addendum

***Dactylobothrium* Srivastav, Khare & Jadhav, 2006 gen. inq.**

Diagnosis: Bothriocephalidea, Triaenophoridae. Medium-sized worms. External segmentation present. Scolex oval to sagittate, with two elongate bothria. Apical disc, called rostellum [sic!], present, armed with four rows of hooklets, with hooks in fourth row markedly larger. Neck absent. Testes in two lateral fields. Cirrus-sac small, oval; cirrus unarmed. Genital pore marginal. Ovary bilobed, median, postequatorial. Vagina anterior to cirrus-sac. Seminal receptacle present, near anterior margin of segments [sic!], allegedly connected with neighbouring segments by medially situated duct (?). Vitelline follicles cortical, forming two lateral fields, allegedly limited to lateralmost part of segments, external to osmoregulatory canals (?). Uterine duct sinuous. Uterus forming lateral diverticula from central, medially situated uterine stem. Uterine pore pre-equatorial. Eggs operculate, with laterally (?) situated operculum. In freshwater teleosts (Channidae). India.
Type- and only species: *D. choprai* Srivastav, Khare & Jadhav, 2006 ex *Channa punctatus* (Bloch) (correct name *C. punctata*) (Perciformes: Channidae), India.
Material studied: None.
Remarks: This genus was erected recently to accommodate a new species, *D. choprai*. It was placed in

the family Parabothriocephalidae, which is a synonym of the Echinophallidae. However, this cestode possesses a lateral genital pore and thus should be placed in the Triaenophoridae.

The description of *D. choprai* contains several morphological characteristics that make its description doubtful: (i) the scolex is reported to possess "rostellar hooks" [sic!], but a rostellum is not present in any bothriate cestode (Khalil et al., 1994); (ii) the scolex resembles that of species of *Senga*, including the shape and size of the hooks in the fourth row; however, no known bothriocephalidean cestode possesses two types of hooks, as reported for *D. choprai*; (iii) the position of the vitelline follicles (limited to a very narrow band along the lateral margin of segments, just external to the osmoregulatory canals) is different from that found in all other bothriocephalidean cestodes; in fact, the distribution of vitelline follicles in *D. choprai* correspond to that of proteocephalidean tapeworms (Rego, 1994); (iv) the presence of a medially situated longitudinal duct connecting the seminal receptacles in all segments has not been reported in any bothriocephalidean cestode (such a structure is present in some amabiliid cestodes of birds – Jones, 1994) and would represent, if it actually exists, a unique characteristic of *D. choprai*; however, the position of the seminal receptacle near the anterior margin of the segment is questionable because it has never been observed in this position in any bothriocephalidean tapeworm; (v) the shape of the uterus in gravid segments differs markedly from that of all bothriocephalideans and resembles the uterus typical of proteocephalidean cestodes (Rego, 1994); and (vi) the eggs of *D. choprai* are reported to be operculate but the operculum is illustrated as lateral [sic!] (fig. 6 in Srivastav et al., 2006).

All the above-listed questionable characteristics demonstrate that the description of *Dactylobothrium* and its type-species, *D. choprai*, is dubious and inadequate. It is probable that the authors in fact studied a mixture of several taxa, at least one of them having been a proteocephalidean tapeworm (possibly *Gangesia* – see the illustrations of mature and gravid segments in figs. 4 & 5 of Srivastav et al., 2006). Since the type-material does not exist (A.K. Srivastav, pers. comm.), although the holotype was mentioned to have been deposited in the Parasitological Laboratory of the Bipin Bihari College, the genus and species are unrecognisable. *Dactylobothrium* is here considered to be a *genus inquirendum* and *incertae sedis*.

Discussion

Systematics of the Bothriocephalidea: problems and obstacles

The systematics of the Bothriocephalidea (previously forming a part of the recently suppressed order Pseudophyllidea – Kuchta et al., 2008a) has been controversial for a long time, resulting from a number of obstacles and difficulties, some of which are:

(i) Many species occur in marine teleosts, including deep-sea fish, which make them difficult to obtain; in addition, prevalences are often low in some host groups and thus their parasites are found only exceptionally;

(ii) The morphology of most species is fairly uniform and thus the number of morphological characteristics available for differentiation is small, even in well-fixed material;

(iii) Many of them have a large, thick strobila, which complicates observations of their internal morphology; longitudinal or sagittal sections may help considerably but some characteristics of the strobilar morphology still remain difficult to assess;

(iv) The quality of many whole-mounts (permanent preparations) deposited in museum collections is poor; usually details of fixation are not available but it is possible that some specimens may have been retrieved after the death of the host; they may have also been deformed due to their strong flattening or contracted when cold fixative was used;

(v) The type-material of many taxa described in the 19th Century is not available and type-specimens of virtually all taxa described more recently from some regions, such as India, are also unavailable, if they exist at all;

(vi) Some morphological characters may depend to a great extent on fixation and/or methods of observation (e.g. the operculum of the eggs is often observable only using scanning electron microscopy or when fresh eggs are studied – see Kuchta et al., 2008b);

(vii) A number of taxa have been described superficially and much information necessary for their differentiation is missing;

(viii) A relatively low number of taxa are available for DNA analyses, which makes it impossible to assess the phylogenetic relationships of individual taxa; molecular markers may serve as a powerful tool, especially when morphological differences between taxa are negligible, which is the case of many bothriocephalidean cestodes.

In the present study, the above-listed obstacles also hindered the proposal of a new system for the order based solely on natural relationships reflecting the evolution of individual bothriocephalidean lineages. However, an extensive range of material, both from museum collections and new collections from all over the world, was examined, which enabled us to provide new data on numerous taxa. This material also made it possible to infer molecular phylogenetic trees of several genera of bothriocephalidean families (Brabec et al., 2006).

However, it was not feasible to carry out a large-scaled revision of all genera of both new orders because some of them, such as *Bothriocephalus*, are species rich and a critical evaluation of their species composition will require further studies based on additional material. Revisions of other genera, such as *Oncodiscus* and *Senga*, are in progress.

Classification

In the present study, a somewhat conservative approach had to be applied regarding the family level classification, and the generic composition of some families may well be paraphyletic. This is particularly the case with the Triaenophoridae, the most genus-rich family (22 genera), which includes several unrelated groups, as indicated by previous authors (Nybelin, 1922; Yamaguti, 1959; Protasova, 1977; Schmidt, 1986; Brabec et al., 2006). A more detailed study of some genera, such as *Bothriocephalus* or *Senga*, may also reveal that they represent artificial assemblages of phylogenetically distinct taxa.

In general, the system proposed by Bray et al. (1994) has been accepted in the present study, even though this classification is grossly simplified and apparently unrelated genera are grouped together (see Brabec et al., 2006; fig. 10 in Kuchta, 2007). However, the concept of Protasova (1974, 1977), based on splitting bothriocephalideans into many families, is not accepted here because it does not correspond to the natural groupings of bothriocephalidean genera, e.g. those of the Amphicotylidae and Ptychobothriidae, inferred from DNA sequences (Brabec et al., 2006; Waeschenbach et al., 2007).

Although several genera of bothriocephalidean tapeworms have recently been invalidated (Protasova, 1977; Bray et al., 1994; present study), a remarkable generic diversity of bothriocephalideans is obvious, with most genera being monotypic or containing only a few species (Kuchta & Scholz, 2007; present study). The present study has also demonstrated that five previously known species merit placement in four newly proposed genera (*Andycestus*, *Kimocestus*, *Mesoechinohallus* and *Plicocestus*); another three genera (*Parabothriocephaloides*, *Penetrocephalus* and *Tetracampos*) have been resurrected.

Evaluation of specimens of taxa (preferably type-species) of most genera of the Bothriocephalidea made it possible to construct a matrix of 80 morphological and biological characters for 45 bothriocephalidean genera (see www.paru.cas.cz/images/staff/104-3-DataMatrix.pdf). However, analysis of this morphology-based data matrix did not provide significant resolution because it resulted in almost complete polytomies (data not shown). Therefore, these data were not used to propose changes in generic or familial classifications but they may be useful for future systematic studies when natural assemblages of bothriocephalideans are identified. Insufficient resolution of phylogenetic trees inferred from this data matrix also indicates that many morphological characters are homoplastic and thus unsuitable for phylogenetic studies.

Evolution and phylogeny

Freze (1974) and Protasova (1974, 1977) proposed a new system of the suborder Bothriocephalata, dividing it into two superfamilies, the Amphicotyloidea, with the families Amphicotylidae, Echinophallidae and Ptychobothriidae, and the Bothriocephaloidea, containing the Bothriocephalidae, Ancistrocephalidae, Parabothriocephalidae and Triaenophoridae. The most important character for differentiation of individual families was the presence or absence of an operculum on the eggs and their embryonation in the uterus. However, the reliability of these characters was questioned by Bray et al. (1994), because they may be difficult to assess in permanent preparations. SEM should be used to study the surface morphology of the eggs or freshly laid eggs should be observed (Kuchta et al., 2008b). Since most previous authors did not use SEM or did not have the opportunity to study fresh eggs, controversy exists in reporting these characters in identical taxa by different authors (Bray et al., 1994; Kuchta et al., 2008b). Although embryonation *in utero*, i.e. development of the oncosphere within the egg, was reported to depend on the temperature in *Triaenophorus* (see Kuperman, 1973), such a variability in the presence of embryonated or unembryonated eggs within the uterus of the same species has not been observed in any other bothriocephalidean cestode.

The genera *Bothriocephalus* and *Clestobothrium* were separated mainly by the presence or absence of an operculum on the eggs and were even placed in different superfamilies (the Bothriocephaloidea and Ptychobothrioidea, respectively) on the basis of this character (Protasova, 1977). However, the type-species of *Clestobothrium*, *C. crassiceps*, actually has operculate eggs, as observed in fresh material by Draoui & Maamouri (1997). The degree of embryonation in the uterus is easy to assess in some cases, but not in others, because it may depend on the temperature, as observed in species of *Triaenophorus* by Kuperman (1973).

Unreliability of the characters related to egg morphology and the degree of their development in the uterus led Bray et al. (1994) to reduce the number of valid families of bothriocephalidean cestodes to four. Indeed, molecular data do not support the validity of the Amphicotylidae, Parabothriocephalidae and Ptychobothriidae, as defined by Freze (1974) and Protasova (1977), but they indicate paraphyly of some families, in particular the Triaenophoridae (Brabec et al., 2006; Kuchta, 2007).

The Bothriocephalidae is polyphyletic forming at least two separated groups: a “freshwater” clade (*Bothriocephalus acheilognathi*, *B. claviceps*, *Ichthybothrium*, *Polyonchobothrium* and *Tetracampos*) and a “marine” clade (with *Anantrum*, *Clestobothrium*, *Bothriocephalus manubriformis* and *B. scorpii*) (Kuchta, 2007; J. Brabec, pers. comm.). The positions of *Penetrocephalus* and *Ptychobothrium* remain unclear and the monophyly of Echinophallidae is also not supported (Brabec et al., 2006; Kuchta, 2007).

Triaenophorids are undoubtedly paraphyletic, with some taxa representing the most basal bothriocephalideans, whereas others are highly derived. The family appears to include at least four unrelated clades, the most basal being that which contains three freshwater genera, *Triaenophorus*, *Marsipometra* and *Bathybothrium*, and the marine genus *Abothrium*. The only member of the Philobythiidae sequenced is a sister taxon to *Eubothrium*, both taxa being also basal to the remaining bothriocephalideans (Brabec et al., 2006).

Lönnberg (1897) considered *Triaenophorus* to be one of the most basal taxa within the “Pseudophyllidea” (but spathebothriideans were also included). Nybelin (1922) suggested that the original type of “pseudophyllidean” holdfast is represented by that found in the extant genera *Triaenophorus* and *Eubothrium*. Freeman (1973) also considered the genera *Marsipometra* and *Eubothrium*, together with *Cephalochlamys* (Diphyllobothriidea), to be the most primitive “pseudophyllideans”. Similarly, Gulyaev (2002) proposed that the Triaenophoridae represent the most basal group of the “Pseudophyllidea”. On the other hand, Protasova (1977) considered *Bothriocephalus* and *Ptychobothrium* to be the most basal and *Eubothrium* and *Triaenophorus* as the most highly derived, but this hypothesis can be rejected based on the available data (Brabec et al., 2006; Kuchta, 2007).

Regarding the possible coevolution of bothriocephalidean cestodes with their hosts, the presence of some basal taxa in evolutionarily ancient host groups, such as *Marsipometra* in paddle-fish (Polyodontidae) and *Eubothrium acipenserinum* in sturgeons (Acipenseridae), indicates a long co-evolutionary history, whereas parasitism of bichirs (Polypteriformes) by members of an apparently derived genus *Polyonchobothrium* (Bothriocephalidae) contradicts this scenario. Infection of salamanders with species of *Bothriocephalus* is undoubtedly a result of secondary host-switching. However, much more data are needed before the evolutionary history of host-parasite relationships of bothriocephalideans can be assessed.

The crucial parts of the present revision are the amended diagnoses of all genera of the new order Bothriocephalidea (see Kuchta et al., 2008a) based on the examination of all available material. They should serve as a solid basis for further systematic and phylogenetic studies of these highly diverse and widely distributed cestodes.

Diversity and biogeography

The order Bothriocephalidea includes bothriate tapeworms from marine and freshwater fish, with a few species found in salamanders (Amphibia) (Protasova, 1977; Schmidt, 1986; Bray et al., 1994; Kuchta et al., 2008a). They are grouped provisionally in the four families recognised by Bray et al. (1994), i.e. Bothriocephalidae (with 14 genera), Echinophallidae (8), Philobythiidae (2) and Triaenophoridae (22).

Bothriocephalideans have a worldwide distribution, including the Arctic and Antarctic regions. A majority of taxa have been found in the Atlantic Ocean (about 36% of described species) and Pacific Oceans (25%); 22% of bothriocephalidean species have been described from Eurasia and 14% from North America (Kuchta & Scholz, 2007).

A preliminary list of valid species of the Bothriocephalidea with tentative synonyms was published by Kuchta & Scholz (2007). These authors also provided more detailed data on the diversity and zoogeographical distribution of this group.

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Two new species of *Bothriocephalus* Rudolphi, 1808 (Cestoda: Bothriocephalidea) from marine fish off Australia and New Caledonia

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Abstract Two new species of bothriocephalidean tapeworms, *Bothriocephalus australis* n. sp. from the flatheads *Platycephalus bassensis* Cuvier (type host) and *P. aurimaculatus* Knapp off southern Australia and *B. celineae* n. sp. from a hybrid serranid *Cephalopholis aurantia* (Val.) × *C. spiloparaea* (Val.) from off New Caledonia, are described. *B. australis* is unique in the possession of the combination of the three characters: an elongate, obliquely situated cirrus-sac; a wide genital atrium surrounded by chromophilic cells; and a well-developed apical disc. *B. celineae* is typified by the presence of a low number of testes per segment (14–26), forming one or two incomplete longitudinal bands on each side of segment, and the small size of the strobila (total length 24 mm) which consists of less than 100 segments.

Résumé Deux nouvelles espèces de cestodes Bothriocephalidea, *Bothriocephalus australis* n. sp. de poissons-crocodiles *Platycephalus bassensis* Cuvier (hôte-type) et *P. aurimaculatus* Knapp du Sud de l'Australie et *B. celineae* n. sp. d'un Serranidae hybride *Cephalopholis aurantia* (Val.) × *C. spiloparaea* (Val.) de Nouvelle-Calédonie, sont décrites. *B. australis* est défini par la combinaison unique de trois caractères: un sac du cirre allongé et situé obliquement, un atrium génital large entouré par des cellules chromophiles et un disque apical bien développé. *B. celineae* est caractérisé par la présence d'un petit nombre de testicules par segment (14–26) formant une ou deux bandes longitudinales incomplètes de chaque côté du segment, et la petite taille du strobile (longueur totale 24 mm) qui consiste en moins de 100 segments.

Introduction

Bothriocephalidean tapeworms are parasites of poikilotherm vertebrates, especially teleost fish (Kuchta & Scholz, 2007; Kuchta et al., 2008a). *Bothriocephalus* Rudolphi, 1808 is by far the largest genus of the order, containing more than 100 nominal species. Many of these, however, are probably invalid or *species inquirendae* (Yamaguti, 1959; Protasova, 1977). Based on a critical review of the literature and a comprehensive evaluation of extensive material (Kuchta et al., 2008b), Kuchta & Scholz (2007) listed only 33 valid species, as many species have been found only once and their validity needs to be

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confirmed. Nevertheless, there may be a number of cryptic species, such as those of the *B. scorpii* (Müller, 1776) complex (Renaud et al., 1984; Robert & Gabrion, 1991). In addition, molecular data indicate that the genus is an assemblage of unrelated taxa and should be split into several natural groups (Škeříková et al., 2004; Kuchta, 2007).

Taxonomic evaluation of bothriocephalidean cestodes from marine fish off Australia and New Caledonia has shown that they belong to two new species of *Bothriocephalus*. Their descriptions are provided below.

Materials and methods

Numerous specimens of *Bothriocephalus* were found in three freshly killed flathead *Platycephalus bassensis* Cuvier caught off the northern coast of Tasmania (collected by Dr I. Dyková in November, 2003), in several specimens of *P. aurimaculatus* Knapp caught off the Bass Strait coast of Cape Otway, Victoria (collected by Dr I. Beveridge on 31.xii.2007) and in one specimen of *P. aurimaculatus* caught off the Port Macdonnell, South Australia (collected by Dr K. Hutson on 8.v.2007).

Another species of the same genus was found in a hybrid of the serranids *Cephalopholis aurantia* (Valenciennes) and *C. spiloparaea* (Valenciennes) caught off the reef slope, New Caledonia; collected by one of us (J.-L.J.) on 22.viii.2006 (Randall & Justine, 2008).

The tapeworms were fixed with hot (almost boiling) 4% formaldehyde solution for morphological studies, including scanning electron microscopy and histology. Part of the strobila of some of the tapeworms was fixed in 96% alcohol for molecular study (Brabec et al., 2006). The specimens for morphological study were stained with Schuberg hydrochloric carmine solution and mounted as permanent slides in Canada balsam. Parts of the strobila were also cross-sectioned using a standard histological procedure (Scholz & Hanzelová, 1998). Several scoleces and segments were prepared for SEM observations using the methodology outlined by Scholz et al. (1998). Illustrations were made using a drawing attachment on an Olympus BX51 microscope with differential interference contrast optics. Measurements in descriptions are given in micrometres unless otherwise stated; measurements of the holotype are given in brackets.

***Bothriocephalus australis* n. sp.**

Type-host: Sand flathead *Platycephalus bassensis* Cuvier (Scorpaeniformes: Platycephalidae).
Other host: Toothy flathead *P. aurimaculatus* Knapp.
Site: Intestine.
Type-locality: Off northern coast of Tasmania (November, 2003).
Other localities: Off Cape Otway, Victoria; off Port Macdonnell, South Australia (31.xii.2007).
Type-material: Australian Helminthological Collection, South Australian Museum, Adelaide, Australia (holotype SAMA AHC 29631 and 11 vouchers SAMA AHC 29633-43); Institute of Parasitology, BC AS CR, České Budějovice, Czech Republic (4 paratypes and 11 vouchers IPCAS C-510); Natural History Museum, London, UK (3 paratypes BMNH 2009.3.12.1-3 and 10 vouchers BMNH 2009.3.12.4-13).
Etymology: The specific name *australis* refers to the southern hemisphere where these tapeworms were found.

Description (Figs. 1–2)

[Based on holotype, 5 paratypes and 11 vouchers.] Strobila up to 22 [8] cm long; maximum width 3 mm. External and internal segmentation present, incomplete anteriorly; secondary segmentation present; segments wider than long, markedly craspedote (Fig. 1A,E).

Two pairs of longitudinal osmoregulatory canals; dorsal canals narrow (diameter 7–11); ventral canals wide (diameter 11–14), connected by transverse anastomoses. Longitudinal musculature well developed, formed by large bundles of muscle fibres (Fig. 1G,H).

Surface of strobila covered with capilliform filitriches; posterior margins of segments covered with narrow band of coniform spinitriches (Fig. 2C,D).

Scolex arrow-shaped in lateral view, oval in dorsoventral view (Figs. 1B,C, 2A,B), 874–1357 [1357] long, 491–619 [573] wide (n = 10). Apical disc well developed, 390–504 [454] wide dorsoventrally, 128–189 [155] high, with deep incisions on dorsal and ventral sides (Fig. 2E). Bothria elongate, shallow, 694–1319 [1063] long, 397–414 [409] wide (n = 10) (Fig. 2A,B). Surface of scolex covered with capilliform filitriches and tumuliform globular structures *c.*2 wide (Fig. 2B,D,E). Neck absent, first segments appearing immediately posterior to scolex (Fig. 1A–C).

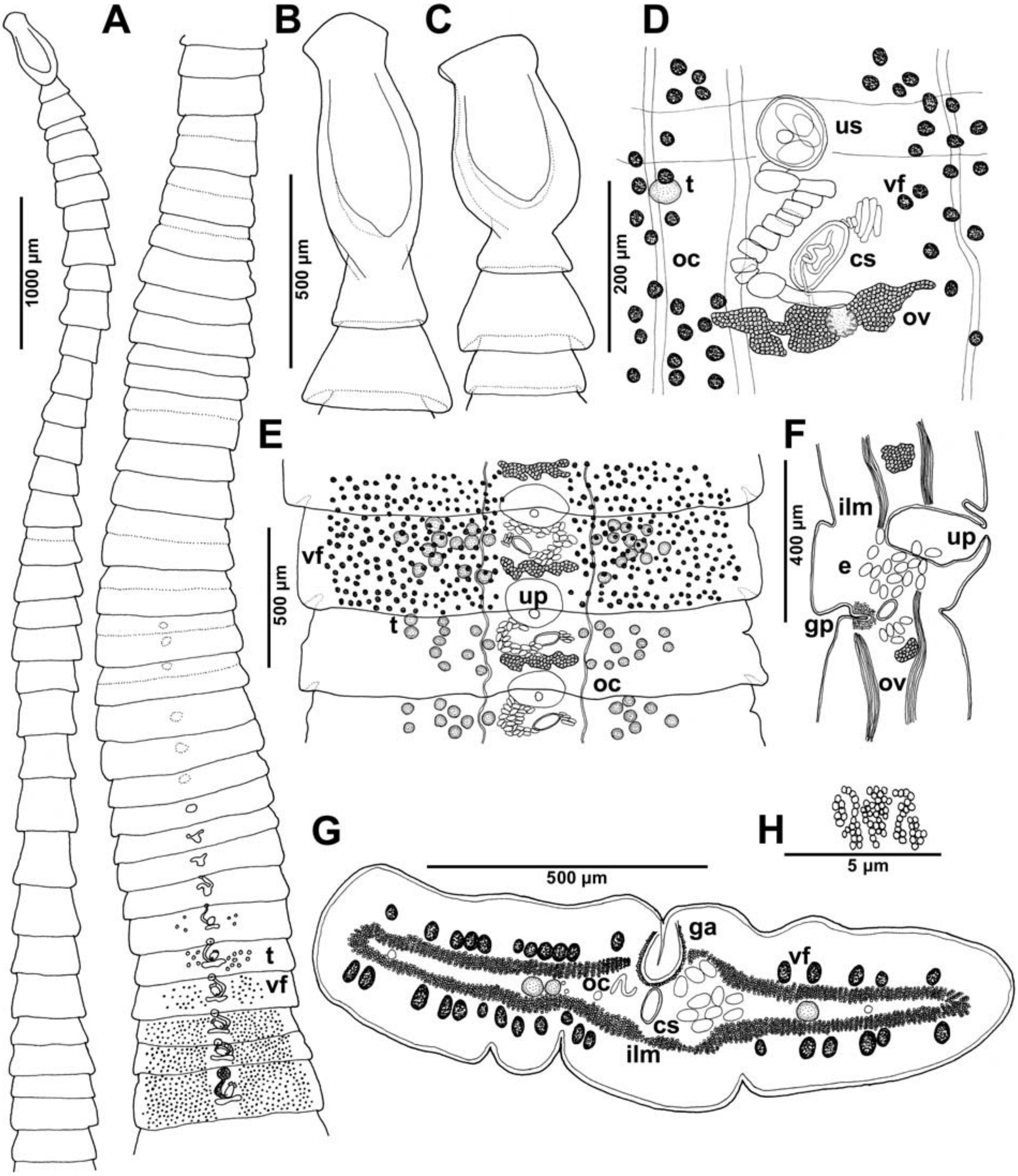


Fig. 1 *Bothriocephalus australis* n. sp. A, B, D, E, holotype (SAMA AHC 29631); C, F–H, paratype (IPCAS C-510). A, entire anterior part of the strobila; B,C, scolex, dorsoventral view; D, detail of mature segment, ventral view; E, diagrammatic drawing of gravid segments, with vitelline follicles illustrated only in the anterior segment, ventral view; F, sagittal section of gravid segments at the level of the cirrus-sac; G, cross-section at the level of the cirrus-sac; H, detail of a cross-section of longitudinal musculature. *Abbreviations*: cs, cirrus-sac; e, eggs; ga, genital atrium; gp, genital pore; ilm, inner longitudinal muscles; oc, osmoregulatory canals; ov, ovary; t, testes; up, uterine pore; us, uterus; vf, vitelline follicles

Immature segments 165–338 long, 368–1847 wide (n = 16) (Fig. 1A). Mature segments, i.e. with spermatozoa in vas deferens, wider than long, 215–434 long, 1,123–1,870 wide; segment length/width ratio 0.17–0.36:1 (n = 16). Gravid segments wider than long, 231–500 long, 1,447–1,949 wide; segment length/width ratio 0.16–0.33:1 (n = 16) (Fig. 1A,E).

Testes medullary, oval, 21–45 [21–24] (n = 16) in number per segment, 36–52 [36–52] (n = 16) in diameter, forming 2 narrow longitudinal bands (10–23 testes per band), non-confluent between segments, absent medially and near lateral margins (Fig. 1A,E). Cirrus-sac large, thin-walled (thickness of sac wall up to 10), elongate, oblique, with proximal part curved anterolaterally (Fig. 1D–F), 81–114 long, 37–50 wide (length/width ratio 1.9–2.3:1) (n = 16), pre-equatorial (32–52% of length of mature segment; n = 16). Vas deferens forms numerous loops posterolateral to cirrus-sac; internal sperm ducts strongly coiled; cirrus unarmed, opening into genital atrium (Figs. 1D,F, 2G). Genital pore median (Fig. 1A,E), near anterior margin of segment, transversely elongate. Genital atrium deep, wide, surrounded by chromophilic cells (Figs. 1F,G, 2G).

Ovary asymmetrical, lobulate, 153–239 [197–232] long, 42–97 [50–70] wide (n = 16) (Fig. 1D,E). Vagina a straight, thin-walled tube, 12–19 in diameter, opens posterior to cirrus-sac into genital atrium; vaginal sphincter absent (Fig. 1D). Vitelline follicles numerous, small, spherical, 28–42 [28–36] in diameter (n = 16), cortical, form 2 wide longitudinal bands confluent between segments, separated medially, rarely connected by several follicles in postovarian region (Fig. 1A,D,E,G).

Uterine duct winding, forms numerous tightly coiled loops, filled with eggs, enlarged in gravid segments (Fig. 1A,D,E). Uterus thin-walled, median, spherical, enlarged in gravid segments, up to 398 [312] long and 422 [358] wide (Fig. 1D–F). Uterine pore thick-walled, opens slightly posterior to mid-length of uterus (Figs. 1F, 2H). Eggs oval, thin-walled, operculate, unembryonated, 55–60 long, 33–39 wide (n = 20) (Fig. 2F,H).

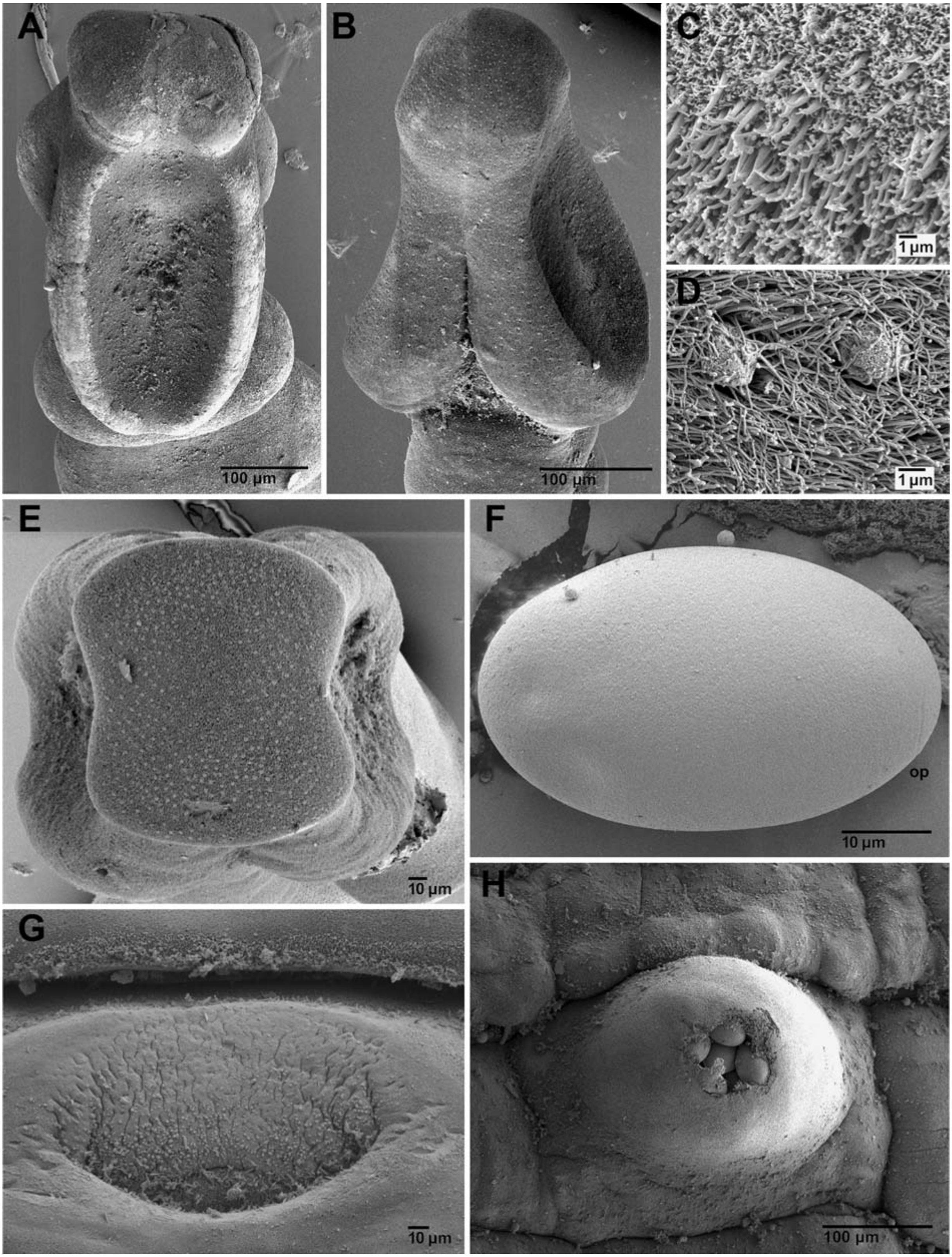
Remarks

The new tapeworm is placed in *Bothriocephalus* because of the presence of segmentation, an unarmed scolex without a sphincter surrounding the anterior aperture of the bothria, a median genital pore and cortical vitelline follicles (see Kuchta et al., 2008b for an amended diagnosis of the genus and keys to bothriocephalidean genera). *B. australis* n. sp. differs from most bothriocephalid species in the presence of a deep and wide genital atrium surrounded with chromophilic cells. However, this feature is not easy to see without the use of scanning electron microscopy (the shape of the atrium) and histology (presence of chromophilic cells). The new species can also be differentiated from all but two species of *Bothriocephalus* in the possession of an elongate cirrus-sac situated obliquely, with the proximal part curved anterolaterally. A similar cirrus-sac is present in *B. kerguelensis* Prudhoe, 1969 and *B. carangis* Yamaguti, 1968, but the former species differs mostly in the size of the cirrus-sac, which is larger (250 × 57 *vs* 81–114 × 37–50 µm in *B. australis*) and much longer than wide (4:1 *vs* 1.9–2.3:1 in *B. australis*), the size of the ovary, which is larger in *B. kerguelensis* (400 × 300 *vs* 153–239 µm in *B. australis*), the size of testes, which are larger (120 *vs* 21–45 µm in *B. australis*), the spectrum of definitive hosts (*Notothenia cyanobrancha* Richardson and *N. rossii* Richardson – Perciformes *vs* Scorpaeniformes in *B. australis*) and the geographical distribution (Antarctic waters *vs* off the south-eastern coast of Australia in *B. australis*). *B. carangis* differs mainly in the presence of a massive vaginal sphincter (lacking in *B. australis*), the incomplete segmentation (missing medially), a slightly greater number of testes (30–110 *vs* 21–45 in *B. australis*), a larger cirrus-sac (200–350 × 80–110 *vs* 81–114 × 37–50 µm in *B. australis*), larger eggs (60–68 × 32–40 *vs* 55–60 × 33–39 µm) and the spectrum of definitive hosts [*Carangoides ferdau* (Forsskål) and *Uraspis helvola* (Forster) – Perciformes *vs* Scorpaeniformes in *B. australis*].

Fig. 2 Scanning electron micrographs of *Bothriocephalus australis* n. sp. voucher. A, scolex, dorsoventral view; B, scolex, lateral view; C, detailed view of the posterior margin of a segment; D, detail of tumuliform globular structures on the apical disc; E, apical disc, apical view; F, freshly liberated egg; G, detail of the genital pore; H, detail of the uterine pore. *Abbreviation*: op, operculum ▶

Bothriocephalus celineae n. sp.

Type-host: A hybrid between the golden hind *Cephalopholis aurantia* (Val.) and the strawberry hind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G
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C. spiloparaea (Val.) (Perciformes: Serranidae). The fish specimen is deposited in the Muséum National d'Histoire Naturelle, Paris, France, as MNHN 2007-0256 (Randall & Justine, 2008).
Site: Intestine.
Type-locality: Outer slope of the barrier reef off Nouméa, New Caledonia, Pacific Ocean (22.viii.2006; 22°27′S, 166°21′E).
Type-material: Muséum National d'Histoire Naturelle, Paris, France (holotype MNHN JNC1926).
Etymology: The species is named for Céline Levron, Institute of Parasitology, BC, AS CR, for her valuable contribution to the ultrastructural studies of fish tapeworms and trematodes.

Description (Fig. 3)

[Based on holotype]. Strobila small, 2.4 cm long; maximum width 570. External and internal segmentation present. Number of segments 97; secondary segmentation present; segments wider than long, slightly craspedote (Fig. 3A).

Two pairs of longitudinal osmoregulatory canals; dorsal canals narrow (diameter 4–5); ventral canals wide (diameter 6–7), connected by transverse anastomoses. Longitudinal musculature well developed, formed by bundles of muscle fibres (Fig. 3E).

Scolex elongate, 347 long, 93 wide in lateral view (Fig. 3B). Apical disc weakly developed, 101 wide in lateral view, 34 high (Fig. 3B). Bothria elongate, 281–294 long (Fig. 3B). Neck present, 85 long (Fig. 3B).

Immature segments 80–487 long, 143–367 wide (n = 10) (Fig. 3A). Mature segments, wider than long, 491–524 long, 255–414 wide; segment length/width ratio 0.5–0.8:1 (n = 3). Gravid segments wider than long, 516–567 long, 347–498 wide; segment length/width ratio 0.6–0.9:1 (n = 10) (Fig. 3A,C).

Testes medullary, oval, 14–26 in number per segment (n = 16), 36–54 in diameter (n = 30), forming single longitudinal band of testes (6–14 per band) on each side, rarely with some testes in second row, non-confluent between segments, absent medially and near lateral margins (Fig. 3A,C). Cirrus-sac small, thin-walled, oval (Fig. 3C–E), 46–57 long, 32–49 wide (length/width ratio 1.1–1.5:1) (n = 12). Vas deferens forms numerous loops anterolateral to cirrus-sac; internal sperm ducts and cirrus not observed; genital atrium deep (Fig. 3D,E). Genital pore median (Fig. 3C), slightly pre-equatorial (at 35–60% of length of segment; n = 12).

Ovary asymmetrical, compact, bilobed, 111–188 long, 46–98 wide (n = 12) (Fig. 3C,D). Vagina thin-walled, 16–20 in diameter, straight, opens posterior to cirrus-sac into genital atrium; vaginal sphincter absent (Fig. 3C,D). Vitelline follicles numerous, small, spherical, 12–25 in diameter (n = 30), cortical, form 2 wide longitudinal bands separated between segments, separated medially, rarely connected by several follicles in postovarian region (Figs. 3A,C).

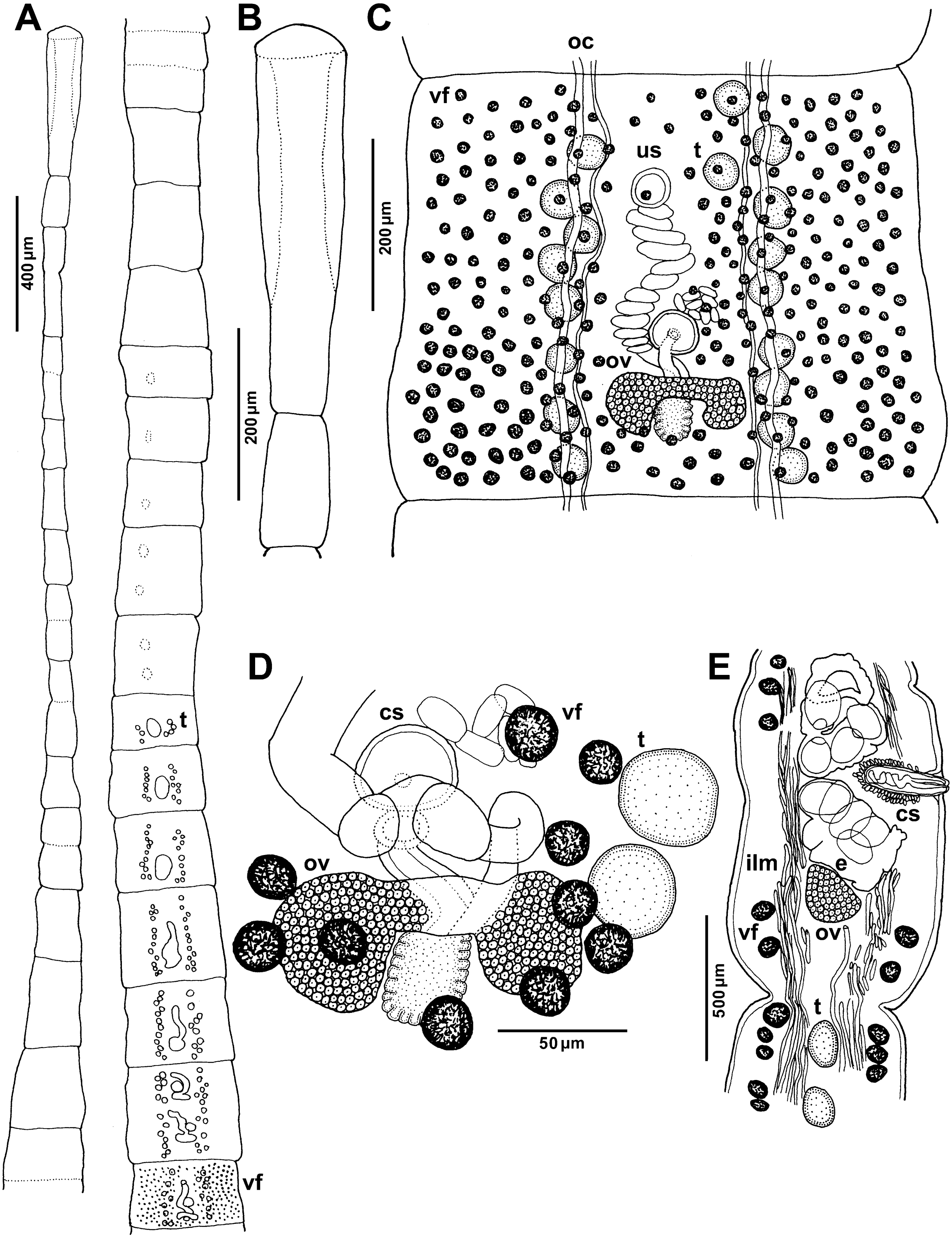
Uterine duct winding, forms numerous, tightly coiled loops, filled with eggs and enlarged in gravid segments (Fig. 3C). Uterus thin-walled, median, spherical, enlarged in gravid segments, up to 88 long and 79 wide (Fig. 3C,E). Uterine pore thick-walled, markedly pre-equatorial (at 16–27% of segment length; n = 12) (Fig. 3C,E). Eggs oval, thin-walled, operculate, unembryonated, 41–50 long, 29–35 wide (n = 10).

Fig. 3 *Bothriocephalus celineae* n. sp. holotype (MNHN JNC1926). A, entire anterior part of the strobila; B, scolex, lateral view; C, diagrammatic drawing of a mature segment; D, detail of a mature segment; E, sagittal section of gravid segments at the level of the cirrus-sac. *Abbreviations*: cs, cirrus-sac; e, eggs; ilm, inner longitudinal muscles; oc, osmoregulatory canals; ov, ovary; t, testes; us, uterus; vf, vitelline follicles

▶

Remarks

Although only one tapeworm specimen was found, it is so markedly different from its congeners that it is proposed as a new taxon. The new species is placed in *Bothriocephalus* because of the presence of a median genital pore, segmentation, an unarmed scolex without sphincter surrounding the anterior aperture of the bothria and cortical vitelline follicles (Kuchta et al., 2008b). *B. celineae* n. sp. differs from all congeneric species mainly in the small number of testes per segment (14–26, each band of testes is usually being formed by a single row) and the small strobila (maximum length 24 mm), consisting of less than 100 segments. Most bothriocephalids are longer than 10 cm (Protasova, 1977; Kuchta, 2007). The number of testes is less than 40 in just four species, namely *B. apogonis* Yamaguti, 1952 ex *Apogon lineatus*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Temminck & Schlegel off Japan (*c*.30 testes), *B. branchiostegi* Yamaguti, 1952 ex *Branchiostegus japonicus* (Houttuyn) off Japan (*c*.20 testes), *B. gadellus* Blend & Dronen, 2003 ex *Gadella imberbis* (Vaillant) from the Gulf of Mexico (up to 33 testes) and *B. kerguelensis* Prudhoe, 1969 ex *Notothenia cyanobrancha* Richardson in Antarctic waters (up to 30 testes). However, most of these species differ in the greater size of the strobila (more than 10 cm) and number of segments, the oval shape of the scolex with a well-developed apical disc (*vs* an elongate scolex with a weakly developed apical disc in *B. celineae*), the absence of a neck and the host spectrum (see below).

Discussion

Bothriocephalidean tapeworms are one of the most common parasites of marine teleosts (Kuchta & Scholz, 2007; Kuchta et al., 2008a). *Bothriocephalus* is the most speciose and taxonomically complicated genus of the order (Kuchta & Scholz, 2007; Kuchta et al., 2008b); this is mainly caused by a very uniform strobilar morphology of most taxa and poor descriptions of many of them (Protasova, 1977; Kuchta & Scholz, 2007; Kuchta et al., 2008b).

Both of the new taxa are described from the Australian region. As many as 12 valid marine species of *Bothriocephalus* have been described from the Indo-Pacific, namely *B. antarcticus* Wojciechowska, Pisano & Zdzitowiecki, 1995, *B. apogonis*, *B. bengalensis* Devi, 1975, *B. branchiostegi*, *B. brotulae* Yamaguti, 1952, *B. carangis*, *B. kerguelensis*, *B. lateolabracis* Yamaguti, 1952, *B. manubriformis* (Linton, 1889), *B. sciaenae* Yamaguti, 1934, *B. scorpii* and *B. travassosi* Tubangui, 1938 (see Kuchta & Scholz, 2007). From the Australian region, two species of *Bothriocephalus* are known, the freshwater *B. acheilognathi* Yamaguti, 1934 and the marine *B. scorpii*. The latter species was reported from off New Zealand ex *Pseudophycis bachus* (Forster) (Robinson, 1959). McKinnon & Featherston (1982) described the scolex of *B. scorpii* as penetrating the intestine wall of *P. bachus*, a typical character of the triaenophorid genera *Abothrium* van Beneden, 1871 and *Parabothrium* Nybelin, 1920, which are also known from gadiform fishes. The identification of tapeworms from *P. bachus* as *B. scorpii* is thus questionable and needs to be confirmed.

Adult cestodes have never been reported from flathead (Schmidt, 1986) and only larval trypanorhynchs and phyllobothriids have been found (Hooper, 1983; Palm, 2004). Platycephalids inhabit temperate and tropical coastal waters of the Indo-West Pacific (Jordan & Richardson, 1908). There are 16 valid species of *Platycephalus*, 14 of which are known from Australian waters (Froese & Pauly, 2009). Flathead are highly carnivorous, feeding on small fishes and crustaceans. They can be found in a wide range of depths (10–350 m) and are commercially fished (Froese & Pauly, 2009). Some species are cultivated in experimental aquaculture programmes in Japan. Conspecific cestodes have also been found in dusky flathead *P. fuscus* Cuvier, 1829 (I. Beveridge, pers. comm.), but were not been available to the present authors. No data on the pathogenic influence of these cestodes on their hosts are available and no macroscopical changes in the host intestine were observed, even in heavy infections of *B. australis* (unpublished data).

The Epinephelinae, or groupers, comprise 15 genera (Heemstra & Randall, 1993). *Cephalopholis* Bloch & Schneider is the second most speciose genus after *Epinephelus* Bloch and contains 23 species, according to Froese & Pauly (2009). Adult bothriocephalidean cestodes have not yet been described from groupers, discounting the unpublished finding of Yuniar (2005), who reported tapeworms tentatively identified as *Bothriocephalus* sp. from *Epinephelus coioides* (Hamilton) off Indonesia. Only larval trypanorhynchs (Palm, 2004; Beveridge et al., 2007; Abdou & Palm, 2008; Justine, 2008) are known from groupers.

The finding of *B. celineae* in the hybrid *C. aurantia* × *C. spiloparaea* is exceptional for several reasons: (a) it was the only adult bothriocephalidean cestode found in hundreds of examined groupers (epinepheline serranids); (b) it was found in an hybrid specimen, rarely found in the wild (Randall & Justine, 2008); and (c) the fish specimen was caught at some depth off the outer slope of the reef. Species of *Cephalopholis* off New Caledonia negative for adult bothriocephalidean cestodes included *C. argus*, *C. boenak*, *C. miniata*, *C. sonnerati* and *C. urodeta*, plus two specimens of one of the parent species of the hybrid, *C. spiloparaea*. More than 20 species of groupers, including members of *Epinephelus*, *Plectropomus* and *Variola*, were also uninfected (Justine, 2007, 2008).

No species of *Platycephalus* has been recorded off New Caledonia, but four specimens of *Cymbacephalus beauforti* (Platycephalidae) were examined and they had no bothriocephalid tapeworms. The prevalence of adult bothriocephalid cestodes in most coral reef fish is probably extremely low. At New Caledonia, although more than 300 species of fish have been examined, other than in the present work, adult bothriocephalids have been recorded only in two species of *Saurida* (Synodontidae) (Kuchta et al., 2009).

A comparative analysis of a partial sequence of the large submit of the rRNA gene (LSU; length 1,438 bp) with sequences of available species of *Bothriocephalus* has shown that the most closely related species is *B. scorpii*, which differed in 2.4% of the nucleotides from *B. australis* n. sp. and 3.6% from *B. celineae* n. sp.. Both new species differed from each other in 4.4% of the nucleotides (J. Brabec, unpublished data).

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Article

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Revision of tapeworms (Cestoda: Bothriocephalidea) from lizardfish (*Saurida*: Synodontidae) from the Indo-Pacific region

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Abstract

Bothriocephalidean cestodes reported from lizardfish (*Saurida* Valenciennes in Cuvier & Valenciennes) were revised on the basis of newly collected material from type-hosts and available type- and voucher specimens. Instead of nine taxa of four genera listed in the literature, only *Oncodiscus sauridae* Yamaguti, 1934 and *Penetrocephalus ganapattii* (Rao, 1954) are considered valid and thus both genera become monotypic. Both taxa are redescribed, including the first scanning electron micrographs and data on intraspecific variability. Both species are unique among bothriocephalid cestodes in the lateral position of the vagina in relation to the cirrus-sac. *Oncodiscus sauridae* found in *Saurida longimanus* Norman, *S. nebulosa* Valenciennes (new host record), *S. tumbil* (Bloch) and *S. undosquamis* (Richardson) differs from *P. ganapattii* found in *S. micropectoralis* Shindo & Yamanda and *S. tumbil* in the following characters: (i) scolex shape (fan-shaped, with crenulated bothrial margins in *O. sauridae*, replaced by a *scolex deformatus* in *P. ganapattii*); (ii) site of scolex attachment (in the intestinal lumen in the former taxon versus penetrating through the intestinal wall, and encysted on pyloric caeca in *P. ganapattii*); (iii) shape of segments (usually only slightly wider than long in *O. sauridae* versus very short, much wider than long in *P. ganapattii*); and (iv) number of testes (50–100 per segment in *O. sauridae* whereas fewer than 60 in *P. ganapattii*). *Bothriocephalus sauridae* Ariola, 1900 is considered a *species inquirendum*, although conspecificity with *O. sauridae* is very probable. The present study demonstrates the necessity of using standard procedures, especially adequate fixation methods of freshly collected cestode material (hot 4% formaldehyde solution is strongly recommended for morphological studies), because most previous descriptions were based on poor-quality material, including partly macerated worms missing hooklets on the apical disc of the scolex in *O. sauridae*.

Key words: Bothriocephalidae, Eucestoda, Indo-Pacific, Pseudophyllidea, lizardfish, *Oncodiscus sauridae*, *Penetrocephalus ganapattii*, *Saurida*, Synodontidae, tapeworm

Introduction

Fish parasitological studies in the Indo-Pacific region have indicated that several species have a wide range of distribution throughout the region, causing taxonomic confusion due to duplicate species descriptions (e.g. Palm & Overstreet 2000). Palm (2000, 2004) summarized the trypanorhynch cestode fauna from the southern Indonesian coast, demonstrating significant overlap of species composition in Indian and southern Indonesian waters. Lönnberg (1893) described the first tetraphyllidean cestode from Java, and Yamaguti (1954) studied

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tetraphyllidean and trypanorhynchan cestodes from the southern Sulawesi coast. However, other information on cestodes parasitic in fish especially from the Indonesian archipelago, a centre of marine biodiversity, is scarce.

Lizardfish of the genus *Saurida* Valenciennes in Cuvier & Valenciennes (Aulopiformes: Synodontidae) are common on the Indo-West Pacific continental shelf, with 21 species recognised as valid (Froese & Pauly 2008). As many as nine nominal cestode species of four genera have been described from four species of lizardfish (Kuchta and Scholz 2007; Kuchta *et al.* 2008b), namely *Bothriocephalus sauridae* Ariola, 1900; *B. ganapattii* Rao, 1954 [= *Penetrocephalus ganapatii* (Rao, 1954) Rao, 1960]; *Bothriocephalus indicus* Ganapati & Rao, 1955; *Bothriocephalus penetratus* Subhapradha, 1955; *Oncodiscus sauridae* Yamaguti, 1934; *O. fimbriatus* Subhapradha, 1955; *O. waltairensis* Shinde, 1975; *O. maharashtrae* Jadhav & Shinde, 1981; and *Tetrapapillocephalus magnus* Protasova & Mordvinova, 1986.

The genus *Oncodiscus* Yamaguti, 1934 was revised by Khalil & Abu-Hakima (1985) on the basis of material collected from *Saurida undosquamis* (Richardson) from Kuwait Bay and Australian waters. The authors synonymised two species, *O. fimbriatus* Subhapradha, 1955 and *O. waltairensis*, both found in *Saurida tumbil* (Bloch) from the Bay of Bengal off India, with *O. sauridae* described from *Saurida argyrophanes* (Richardson) (syn. of *S. tumbil*). These synonymies were accepted by Kuchta & Scholz (2007) and Kuchta *et al.* (2008b), who presented a preliminary list of valid taxa of bothriocephalideans, including new synonymies of species parasitic in lizardfish. However, they did not provide detailed data on their morphology and morphometry.

The purpose of the present study is a revision of bothriocephalidean tapeworms from lizardfish based on newly obtained material from Indonesia and New Caledonia. The morphology and morphometry of the valid species are described, comparing the new material with type and voucher specimens from different museum collections. The re-descriptions of *Oncodiscus sauridae* and *Penetrocephalus ganapattii* including details of the surface ultrastructure are presented in this paper.

Material and methods

The present study was based on morphological and biometrical evaluation of freshly collected specimens as well as on tapeworms deposited in museum collections. New material was isolated from 153 freshly killed lizardfish of 4 species [*S. longimanus* Norman – 52, *S. micropectoralis* Shindo & Yamada – 11, *S. tumbil* – 46, *S. undosquamis* – 44] obtained from local fisherman in Pelabuhan Ratu, Java, Indonesia and examined by the present authors (R.K., A.T.Y., T.W. and H.W.P.) from 2001 to 2008. Other cestodes were collected from 24 lizardfish of 3 species [*Saurida gracilis* (Quoy & Gaimard) – 1, *S. nebulosa* Valenciennes – 1, *S. undosquamis* – 22] in New Caledonia by J.-L. Justine from 2003 to 2006.

Tapeworms collected by the present authors were obtained from freshly killed lizardfish. They were washed in saline and specimens for morphological studies, including scanning electron microscopy (SEM) observations and histology, were fixed with hot 4% formaldehyde solution. Remaining tapeworms or their pieces were fixed with 96% ethanol for molecular study (see Brabec *et al.* 2006). Whole mounts were stained with Schuberg'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 Scholz *et al.* (1998).

The following material was studied:

Oncodiscus sauridae

(i) type material (9 specimens) ex *Saurida argyrophanes* (now *S. tumbil*) from the Inland Sea and East China Sea, Japan (Meguro Parasitological Museum, Tokyo, Japan – acronym MPM): holotype [MPM 23176 (SY 3042)], paratypes [MPM 23176 (SY 3043), MPM 23177 (SY 3165-67)];

(ii) three specimens ex *Chirocentrus dorab* (Forsskål) from Toyama Bay, Toyama Prefecture, Honshū, Japan, Japan Sea (collected by S. Yamaguti) [MPM 23178 (SY5616-18)];

(iii) six specimens ex *S. tumbil* from Pelabuhan Ratu, Java, Indonesia (helminthological collection of the Institute of Parasitology, BC AS CR, České Budějovice – IPCAS C-456/1; Natural History Museum, London, UK – BMNH 2008.9.5.3; Invertebrate Collection, Muséum d'Histoire Naturelle, Genève, Switzerland – MHNG INVE 62588);

(iii) six specimens ex *S. longimanus* from Pelabuhan Ratu, Java, Indonesia (IPCAS C-456/2; BMNH 2008.9.5.6 and 2008.11.7.1; Zoologisches Museum Berlin – ZMB 7447 and 7448);

(iv) one specimen ex *S. undosquamis* from Pelabuhan Ratu, Java, Indonesia and two specimens from off Nouméa, New Caledonia (IPCAS C-456/3; Muséum National d'Histoire Naturelle, Paris, France – MNHN JNC502, 2588);

(v) one specimens from *S. nebulosa* from off Nouméa, New Caledonia (MNHN JNC2474).

Tetrapapillocephalus magnus

(i) The holotype ex *S. undosquamis* from the Indian Ocean (Parasitological Institute, Russian Academy of Sciences, Moscow, Russia – GELAN): holotype (GELAN 696);

(ii) plerocercoid on the slide with the holotype of *Partitiotestis berycis* Protasova & Parukhin, 1986 (GELAN 986).

Penetrocephalus ganapattii

(i) two specimens ex *S. tumbil* from Pelabuhan Ratu, Java, Indonesia (IPCAS C-462/1; MHNG INVE 62589; ZMB 7449).

(ii) three specimens ex *S. micropectoralis* from Pelabuhan Ratu, Java, Indonesia (IPCAS C-462/2; BMNH 2008.9.5.7–8; MHNG INVE 62590; ZMB 7450).

Illustrations were made using a drawing attachment on the Olympus BX51 microscope with Nomarski interference contrast. Types or vouchers of the taxa described by Indian authors were not available and they most probably do not exist or have never been deposited (B. Jadhav – personal comm.).

Results

Based of the evaluation of types, vouchers and newly collected specimens, two taxa belonging to two monotypic genera, *Oncodiscus sauridae* and *Penetrocephalus ganapattii*, are considered valid. They represent nine nominal species of four bothriocephalidean genera that were formerly described from lizardfish. Both species are redescribed herein, with all measurements are given in micrometers (µm); those of the type material are in parentheses.

Oncodiscus sauridae Yamaguti, 1934

Figs. 1–8, 14–18, 21, 24

Syns. *O. fimbriatus* Subhapradha, 1955; *O. waltairensis* Shinde, 1975; *O. maharashtrae* Jadhav & Shinde, 1981; *Bothriocephalus indicus* Ganapati & Rao, 1955; *Tetrapapillocephalus magnus* Protasova & Mordvinova, 1986

Type host: *Saurida argyrophanes* (now *S. tumbil*).

Other hosts: *S. longimanus*, *S. nebulosa* (new host), *S. undosquamis*.

Site of infection: Scolex in the pyloric caeca or embedded in the intestinal wall, strobila in the intestinal lumen.

Type locality: Inland Sea, Tarumi-ku, Kobe, Hyōgo Prefecture, Kyūshū, Japan, Pacific Ocean.

Distribution: Indian Ocean (India, Indonesia, Kuwait, Mozambique); Pacific Ocean (Australia, Japan, New Caledonia).

Prevalence: In Indonesia, *S. longimanus* – 12%; *S. tumbil* – 9%; *S. undosquamis* – 5%. In New Caledonia, 9% of *S. undosquamis* were infected (J.-L. Justine – unpublished data).

References: Subhapradha (1955); Devi (1975); Khalil & Abu-Hakima (1985); Protasova & Mordvinova (1986).

Re-description: Bothriocephalidea, Bothriocephalidae. Medium-sized worms, up to 130 (90) mm long. Strobila with craspedote segments with prominent posterolateral wing-like projections, overlapping following segment (Figs. 5, 16, 17). External segmentation present, but may be incomplete (missing medially). Two pairs of longitudinal osmoregulatory canals present. Longitudinal musculature well developed, formed by numerous bundles of muscle fibres (Fig. 7). Surface covered with small filiform microtriches similar in shape and size.

Scolex oval, irregularly-shaped or fan-shaped (Figs. 1, 2, 4, 14, 15), usually compressed laterally, 1,120–3,140 (1,710–4,000) long by 860–2,380 (1,360–2,190) wide. Bothria well developed, with conspicuously crenulated margins turned laterally (Figs. 1, 2, 4, 14, 15). Apical disc well developed, 310–890 (780–1,250) wide, 140–400 (160–370) high, consisting of two lateral lobes, armed with up to four irregular rows of tiny hooklets (Figs. 2, 3, 15, 18, 24); hooklets easy to detach, especially in dead specimens (Figs. 1, 4), 21–26 (12–24) long, with largest hooklets in second and third rows, and diminishing in size from top of lateral lobes to junction of lobes, where rows may be interrupted. Neck absent, first segments starting immediately posterior to scolex (Figs. 1, 15).

Immature segments much wider than long, 25–110 (45–165) long by 400–1,510 (230–850) wide. Mature segments wider than long, 50–810 (80–380) long by 310–1,715 (755–1,070) wide (Fig. 5). Gravid segments wider than long to rectangular or, exceptionally, slightly longer than wide, 190–2000 (180–700) long by 615–1865 (985–1520) wide (Figs. 16, 17).

Testes medullary, oval, 50–100 (60–100) in number per segment, 22–66 (30–61) long by 11–38 (25–50) wide, in two lateral fields, usually separated medially, continuous between segments (Fig. 5). Cirrus-sac submedian, irregularly alternating, thick-walled, round or slightly oval, 70–215 (85–135) in diameter, just anterodorsal to ovary (Figs. 5, 6, 8). Cirrus armed with filiform microtriches. Cirrus opening to small genital atrium lateral to median line of segment (Fig. 7). Genital pore dorsal, median, slightly postequatorial (Fig. 5).

Ovary transverse elongate, bilobed, lobulate, median, near posterior margin of segment, 200–630 (225–460) wide (Figs. 5, 6). Vagina tubular, dorsal to ovarian bridge, arched lateral or anterolateral to cirrus-sac (Figs. 5, 6). Vitelline follicles numerous, cortical, circumsegmental (Fig. 7), oval, 13–40 (7–28) in diameter, in two lateral fields, often separated medially, reaching to posterolateral projections (Figs. 5, 7). Uterine duct well developed, sinuous, ending in muscular, thick-walled uterine sac situated medially (Figs. 5, 6); sac markedly enlarged in last gravid segments. Uterine pore medioventral, at distance from anterior margin of segment or almost equatorial. In some segments, pore extremely large due to collapse of wall of uterus (Fig.

16). Eggs oval, operculate, unembryonated, 55–64 (60–63) long by 32–45 (39–42) wide, with operculum 11–20 in diameter (Fig. 21).

Remarks: *Oncodiscus sauridae* was described by Yamaguti (1934) from *Saurida argyrophanes* (now *S. tumbil*) and redescribed by Khalil & Abu-Hakima (1985), who collected new material and added morphological data to the original description. The total length of 9 mm was given by Yamaguti (1934) for the holotype, but this specimen measures in fact 90 mm (present study).

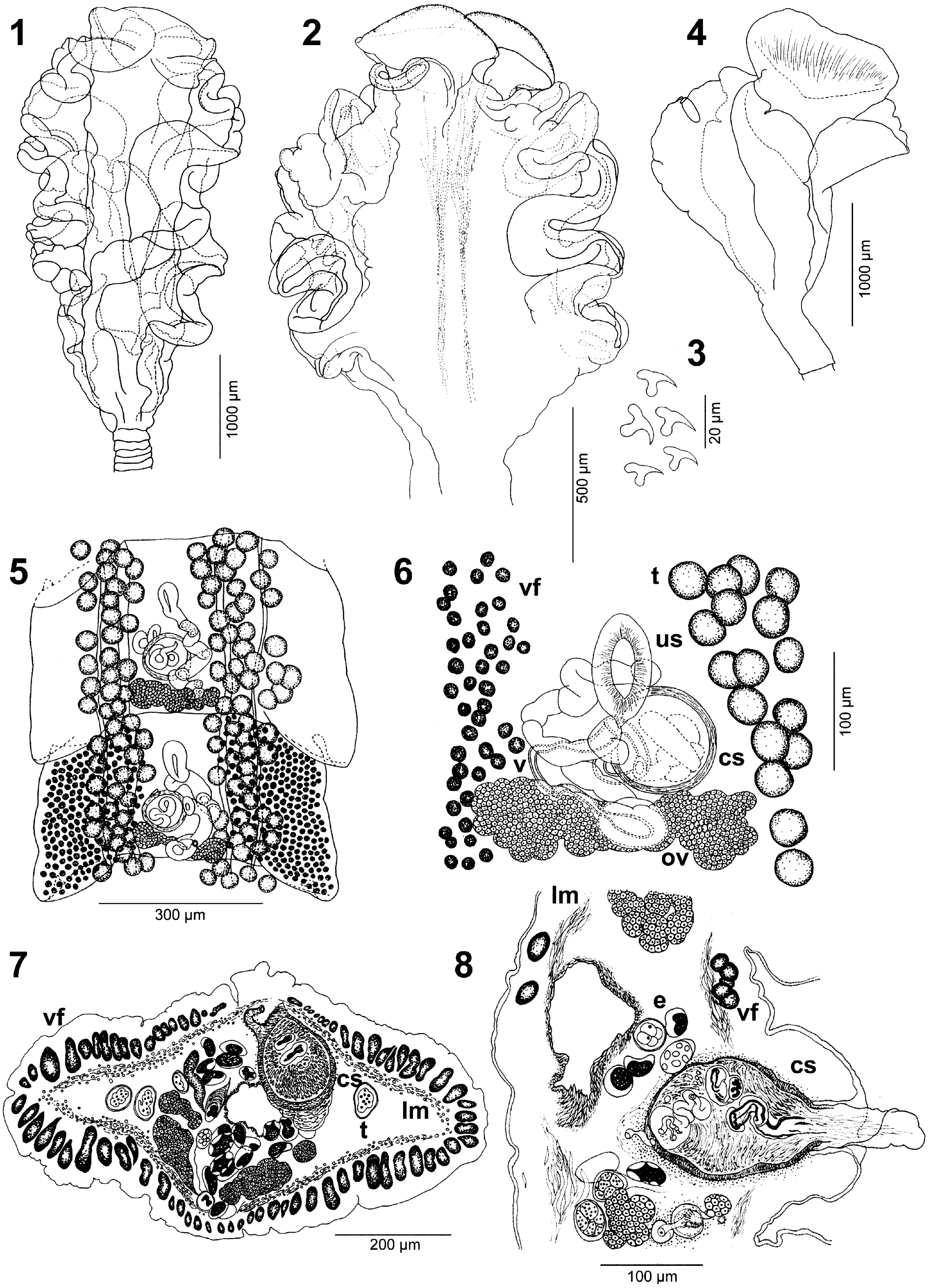
Besides *O. sauridae*, another three species of *Oncodiscus*, namely *O. fimbriatus*, *O. waltairensis*, and *O. maharashtrae*, were erected. They were differentiated mainly by the shape of the scolex, the presence or absence of a median longitudinal furrow, the presence or absence hooklets on the apical disc, the number of testes and the presence or absence of an operculum in the eggs (Subhapradha 1955; Shinde 1975; Jadhav & Shinde 1981). However, these characters are unsuitable for species differentiation in this group of cestodes. The shape of the scolex and the presence of furrows and hooklets on the apical disc are not stable characters because they depend into a great extent on the state in which worms were fixed and on fixation procedure (Kuchta & Scholz 2007). In dead tapeworms or in worms that have been relaxed for too long in water, the hooklets detach (one of Yamaguti's paratypes of *O. sauridae* lacks hooklets on the apical disc due to tissue destruction – Fig. 1), the scolex shape changes and tegumental furrows may appear as a consequence of deformation of the scolex, especially when fixation by pressure between two glass slides is used (Khalil & Abu-Hakima 1985; present study).

The number of testes is variable in *O. sauridae* and may considerably differ even between segments of the same specimen. The maximum number of testes in *O. sauridae* was found to reach up to 100, which corresponds to the data from the original description (Yamaguti 1934). Jadhav & Shinde (1981) reported as many as 350 testes in one segment of *O. maharashtrae*, but it is apparent that the authors confused vitelline follicles with testes. Vitelline follicles enlarge in the posterior part of the strobila and may reach a similar size compared to that of the testes in gravid segments.

Another feature which was used for species differentiation, i.e. the presence or absence of an operculum in the eggs, can easily be overlooked unless scanning electron microscopy is used (Bray *et al.* 1994; Kuchta *et al.* 2008a; present study). Yamaguti (1934) described a median longitudinal furrow on the scolex of *O. sauridae*. On the basis of the absence of that structure, Subhapradha (1955) proposed *O. fimbriatus*. However, this structure does not represent a species-distinguishing character. Such a furrow is missing in one of the paratypes of *O. sauridae* and it is much less developed in other specimens of the type series. This indicates that its presence depends on the level of worm contraction or fixation procedure (S. Yamaguti strongly flattened the worms, which may have caused unnatural deformations of the scolex and strobila).

Khalil & Abu-Hakima (1985) synonymized *O. fimbriatus* and *O. waltairensis* with *O. sauridae*, but they considered *O. maharashtrae* to be a *species inquirendum*. This species was described from *Pastinachus (Trygon) sephen* (Forsskål) (Dasyatidae) from off Bombay, India. Unlike Khalil & Abu-Hakima (1985), the present authors (Kuchta & Scholz 2007; Kuchta *et al.* 2008b; this study) consider *O. maharasthrae* to be a synonym of *O. sauridae* which occurred in an unusual (postcyclic or accidental) host.

All three species from India were described on the basis of only a few, apparently macerated and deformed specimens. In addition, the descriptions of the taxa from the Indian Ocean were superficial and no histological sections were made (Ariola 1900; Subhapradha 1955; Shinde 1975; Jadhav & Shinde 1981; Protasova & Mordvinova 1984). *Bothriocephalus indicus* was described from *Saurida tumbil*. It is obvious from its morphology that the authors erroneously placed these specimens in the genus *Bothriocephalus* Rudolphi, 1808, because species of this genus are devoid of a fan-shaped scolex with crenulated bothrial margins (Ganapati & Rao 1955). In fact, *B. indicus* is identical in its morphology with *O. sauridae* (the absence of hooklets on an apical disc is apparently due to poor state of specimens studied), parasitizes the same species of fish hosts and occurs in the same region. Therefore, the synonymy of *B. indicus* with *O. sauridae*, first proposed by Kuchta & Scholz (2007), is confirmed in the present study.



FIGURES 1–8. *Oncodiscus sauridae* Yamaguti, 1934. **1**, Scolex of paratype (MPM SY 3043); lateral view. **2**, **3**, Voucher (MPM SY 5616) ex *Chirocentrus dorab*; **2**, scolex; **3**, detail of hooklets. **4**, Scolex of the holotype of *Tetrapapillocephalus magnus* (GELAN 696). **5**, Schematic drawing of mature segments ex *Saurida longimanus* (IPCAS C-456/2); vitelline follicles illustrated only in the posterior segment; ventral view. **6**, Detail of mature segment ex *S. tumbil* (IPCAS C-456/1); vitelline follicles illustrated only on the left side and testes only on right side, ventral view. **7**, **8**, Histological sections of gravid segments ex *S. tumbil* (IPCAS C-456/1) at level of cirrus-sac; **7**, cross-section; **8**, sagittal section. Abbreviations: cs – cirrus-sac; e – eggs; lm – inner longitudinal muscles; ov – ovary; t – testes; us – uterine sac; v – vagina; vf – vitelline follicles.

Bothriocephalus sauridae was very briefly described on basis of specimens without a scolex that were collected from *Saurida nebulosa* off the eastern coast of Africa (Zanzibar) (Ariola 1900). The species was considered to be a *species inquirendum* (Protasova 1977; Kuchta & Scholz 2007; present paper), but its conspecificity with *O. sauridae* is very probable. In the same region, *O. sauridae* (reported to as *Tetrapapillocephalus magnus*) was found in *S. undosquamis* by Protasova & Mordvinova (1986).

Morphological and morphometrical examination of the specimens of *Tetrapapillocephalus magnus* (holotype and voucher), which are both in poor condition, shows a high similarity with *O. sauridae*. The taxa differ only in the absence of tiny hooklets on the apical disc in the former. However, hooklets can be easily lost during handling or when dead tapeworms are collected (Khalil & Abu-Hakima 1985; present study).

The scolex of *Tetrapapillocephalus magnus* (= *O. sauridae*) illustrated in the original description (Protasova & Mordvinova 1986) belongs to another specimen, not representing the holotype as indicated (Fig. 4). This immature specimen was found in *Beryx splendens* Lowe; it is mounted onto the same slide with the holotype of *Partitiotestis berycis* Protasova & Parukhin, 1986 (GELAN 986). Numerous immature tapeworms conspecific with *T. magnus* were found in this host, but only one specimen was mounted (Protasova – pers. com.). Besides this report, no further data exist on the occurrence of *O. sauridae* in berycid fish (Kuchta & Scholz 2007; Kuchta *et al.* 2008b) and it is possible that *B. splendens* represents an accidental or paratenic host only.

It is interesting to note that we examined some unusual material from clupeid fish (*Chirocentrus dorab*) from the Japan Sea, in the collection of Yamaguti (MPM), collected 19.vi. 1928. These specimens are conspecific with *O. sauridae* (also identified as *Oncodiscus* by Yamaguti), but this finding was never published. In addition, no other occurrence of any bothriocephalid tapeworm has been reported from this host. This finding may represent misidentification of the host, or an accidental or paratenic host.

***Penetrocephalus ganapattii* (Rao, 1954) Rao, 1960**

Figs. 9–13, 19, 20, 22, 23

Syns. *Bothriocephalus ganapattii* Rao, 1954; *Bothriocephalus penetratus* Subhapradha, 1955.

Type host: *Saurida tumbil*.

Other hosts: *S. micropectoralis*, *S. undosquamis*.

Site of infection: The scolex and neck (*scolex deformatus*) is coiled within a cyst on the wall of pyloric caeca, whereas the strobila lies freely in the intestinal lumen.

Type locality: Coast of Waltair, Bay of Bengal, Andhra Pradesh, India, Indian Ocean.

Distribution: Indian Ocean (India, Indonesia).

Prevalence: In Indonesia, *S. micropectoralis* – 27%; *S. tumbil* – 5%.

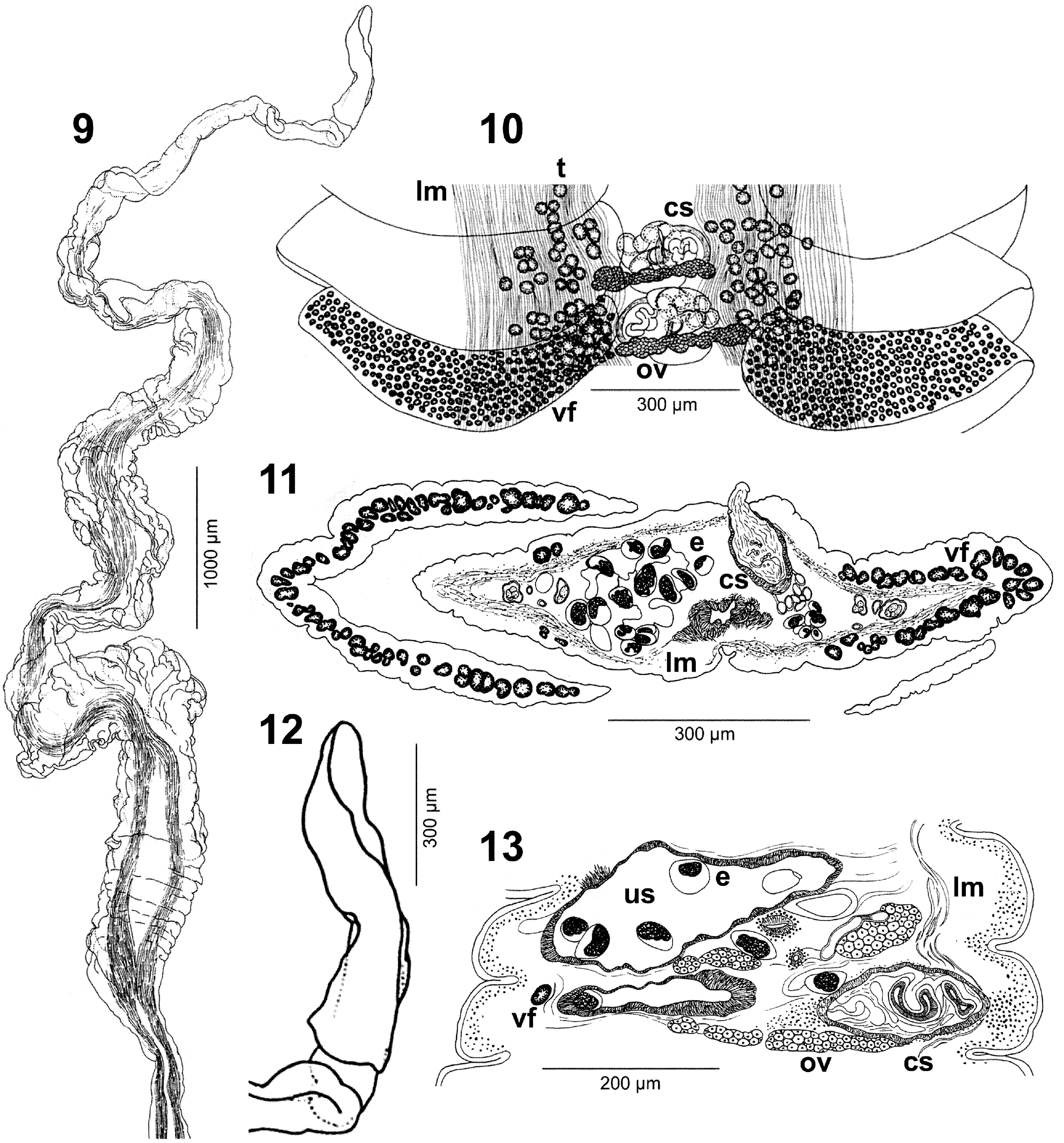
References: Subhapradha (1955); Rao (1960); Devi (1975); Radhakrishnan *et al.* (1983).

Re-description: Bothriocephalidea, Bothriocephalidae. Large worms, up to 125 mm long. Strobila with markedly craspedote segments with prominent lateral wing-like projections (Figs. 10, 19, 23). External segmentation present, may be incomplete (missing medially). Two pairs of longitudinal osmoregulatory canals present. Longitudinal musculature well developed, forming numerous bundles of muscle fibres (Figs. 10, 11). Surface covered with small filiform microtriches similar in shape and size.

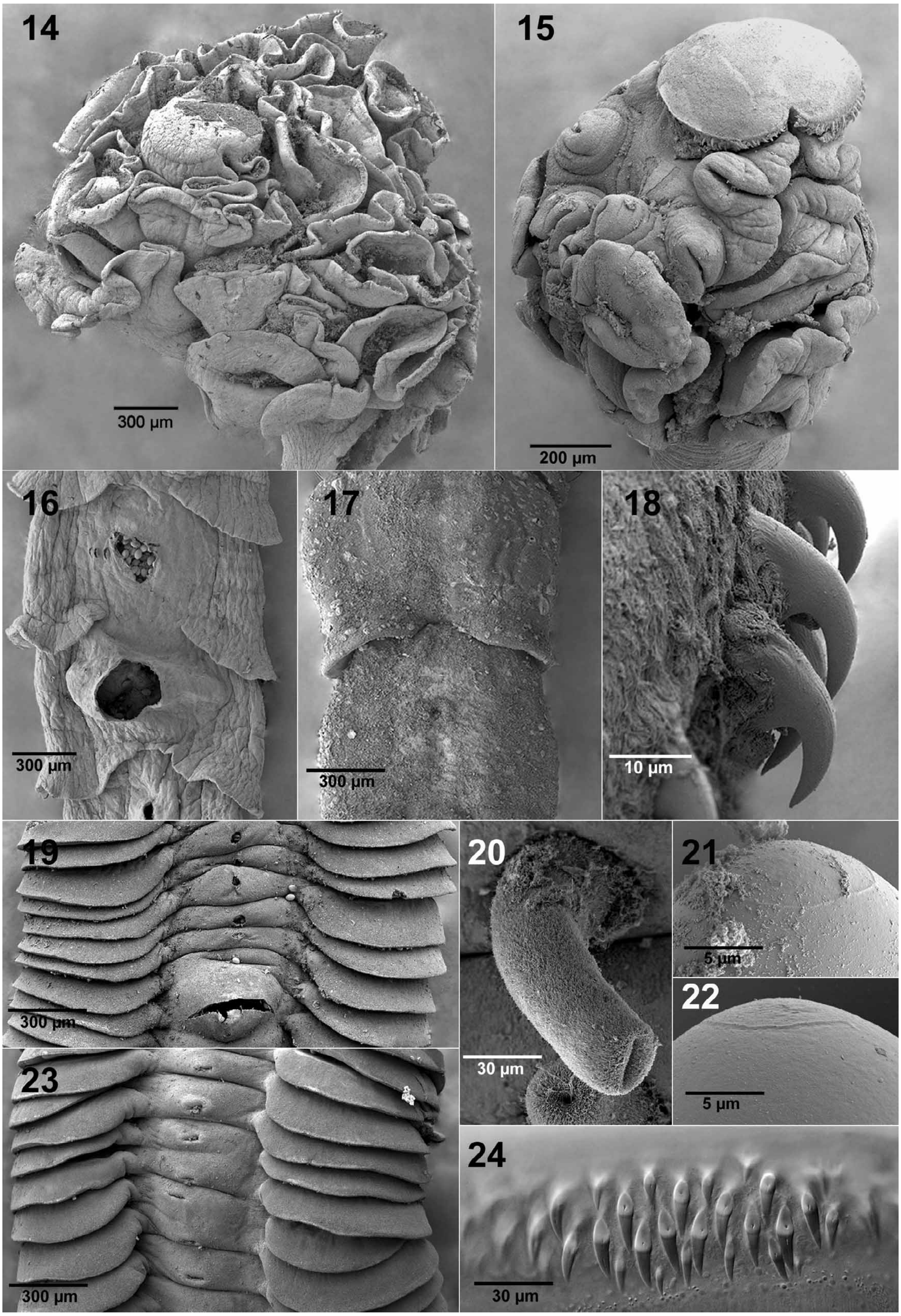
Scolex unarmed, 700–750 long by 150–200 wide, changed to *scolex deformatus* (Fig. 9, 12). Apical disc absent. Anterior part of body including neck often degenerated, becoming filiform (Fig. 9), up to 60 mm long, penetrating through intestinal wall, and encysted on pyloric caeca.

Segments short, much wider than long (up to 14 times in mature segments). Immature segments 50–620 long by 100–2,540 wide. Mature segments 40–220 long by 1,080–2,900 wide (Fig. 10). Gravid segments 70–620 long by 890–3,140 wide (Figs. 19, 23).

Testes medullary, oval, 40–60 in number per segment, 10–60 long by 10–40 wide, in two lateral fields separated medially, continuous between segments (Fig. 10). Cirrus-sac submedian (Fig. 11), irregularly alternating, round or slightly oval, 65–195 in diameter, just anterior to ovary (Fig. 10, 13). Cirrus unarmed, covered with long filiform microtriches (Fig. 20), opening to small genital atrium. Genital pore dorsal, slightly submedian (Figs. 11, 23).



FIGURES 9–13. *Penetrocephalus ganapattii* (Rao, 1954) ex *Saurida micropectoralis* (IPCAS C-462/2). **9**, **12**, Schematic drawing of *scolex deformatus*. **10**, Schematic drawing of mature segment; vitelline follicles illustrated only in the posterior segment; ventral view. **11**, **13**, Histological sections of gravid segments at the level of cirrus-sac; **11**, cross-section; **13**, sagittal section. Abbreviations: cs – cirrus-sac; e – eggs; lm – inner longitudinal muscles; ov – ovary; t – testes; us – uterine sac; vf – vitelline follicles.



FIGURES 14–23. Photomicrographs. **14–18**, **21**, **24**, *Oncodiscus sauridae* Yamaguti, 1934. **14**, Scolex; ex *Saurida longimanus*. **15**, Scolex; ex *S. tumbil*. **16**, **17**, Gravid strobila; **16**, Ventral view; **17**, Dorsal view. **18**, **24**, Detail of hooklets; **18**, SEM photomicrograph; **24**, Photomicrograph. **21**, Operculum of the egg. **19**, **20**, **22**, **23**, *Penetrocephalus ganapattii* (Rao, 1954). **19**, **23,** Gravid strobila; **19**, Ventral view; **23**, Dorsal view. **20**, Detailed view of the envaginated cirrus. **22**, Operculum of the egg.

Ovary transverse elongate, lobulate, median, 240–720 wide (Fig. 10). Vagina tubular, lateral or anterolateral to cirrus-sac. Vitelline follicles cortical, oval, 10–40 in diameter, numerous, in two lateral fields separated medially, reaching to posterolateral projections (Fig. 10, 11). Uterine duct sinuous, leading to thick-walled, median uterus (Figs. 10, 13), dilated ventrally in gravid segments. Uterine pore ventral, median, at distance from anterior margin of segment (Fig. 19). Eggs oval, operculate, unembryonated, 50–74 long by 33–42 wide; operculum 9–18 in diameter (Fig. 22).

Remarks: The original description of *Bothriocephalus ganapattii* was very brief (Rao, 1954), which led Protasova (1977) and Bray *et al.* (1994) to consider *B. ganapattii* a *nomen nudum*. However, the species is clearly recognizable on the basis of its original description because it possesses a *scolex deformatus* that penetrates the intestine and forms a cyst in the mesentery or in the liver (Rao 1954). Subhapradha (1955), probably not aware of Rao's (1954) publication, described an apparently conspecific cestode, *Bothriocephalus penetratus*. Both taxa parasitize the same fish host in the same region and are morphologically indistinguishable. Therefore, they are considered synonymous (Rao 1960; Kuchta & Scholz 2007; Kuchta *et al.* 2008b).

Rao (1960) proposed a new genus, *Penetrocephalus*, to accommodate *B. ganapattii* (the type- and only species was misspelled as *P. ganapatii*). The genus was invalidated by Protasova (1977) and Bray *et al.* (1994), but resurrected by Kuchta *et al.* (2008b); the validity of the genus is also supported by molecular data (Kuchta 2007, fig. 10).

Discussion

The present study contributes to our knowledge of the fish parasite biodiversity from Indonesian coastal waters, a centre of marine biodiversity within the Indo-Pacific region. It confirms the previous conclusions of Khalil & Abu-Hakima (1985) and Kuchta & Scholz (2007) regarding synonymy of bothriocephalid cestodes described from lizardfish. Based on the present data, only two out of nine nominal species are considered valid (*Bothriocephalus sauridae* is kept as a *species inquirendum*). The invalidity of the monotypic genus *Tetrapapillocephalus*, as first proposed by Kuchta & Scholz (2007), is confirmed.

Evaluation of freshly collected specimens from Indonesia and New Caledonia has shown high intraspecific and even individual variability in many characters, some of them having been used by previous authors for erection of new taxa (shape of the scolex and apical disc, presence/absence of hooklets on the apical disc and longitudinal furrows on the scolex, measurements of segments, etc.). The present study also demonstrated that poor-quality material, especially macerated cestodes or worms fixed under pressure, should not be used for taxonomic studies in bothriocephalidean cestodes (Kuchta & Scholz 2007).

Oncodiscus sauridae and *Penetrocephalus ganapattii* differ from other bothriocephalid cestodes in the position of the vaginal pore, which is anterolateral to the male pore (opening of the cirrus-sac), whereas in other species of the family Bothriocephalidae it is posterior to the male pore (Kuchta *et al.* 2008b). *O. sauridae* and *P. ganapattii* are also characterized by the shape of segments which possess posterolateral projections, markedly developed mainly in the latter taxon. Similar structures are known only in some echinophallids (Kuchta *et al.* 2008a, b) and several species provisionally placed in *Bothriocephalus*, namely *B. antarcticus* Wojciechowska, Pisano & Zdzitowiecki, 1995; *B. bengalensis* Devil, 1975; *B. branchiostegi* Yamaguti, 1952; and *B. gadellus* Blend & Dronen, 2003 (Protasova 1977; unpublished data).

The species from lizardfish share some morphological characters, especially of the strobila, but they can easily be distinguished from one another. The most important characters are: (i) the scolex shape (fan-shaped, with crenulated bothrial margins (Ganapati & Rao 1955). in *O. sauridae*, whereas replaced by a *scolex deformatus* in *P. ganapattii*); (ii) site of scolex attachment (in the intestinal lumen in the former versus penetrating through the intestinal wall and encysted on pyloric caeca in *P. ganapattii*); (iii) shape of segments (only slightly wider than long in *O. sauridae* versus very short, much wider than long in *P. ganapattii*); and (iv) the number of testes (50–100 per segment in *O. sauridae* whereas fewer than 60 in *P. ganapattii*). A comparative analysis of LSU sequences of both taxa from Indonesia has also shown differences, because a partial sequence of the large submit of the rRNA gene (LSU; length 1438 bp) differed in 0.974% (sequence similarity 0.990) (J. Brabec – unpublished data).

The taxa redescribed above may occur sympatrically and may infect even the same host specimen of *Saurida tumbil* and *S. undosquamis*. On the other hand, *S. longimanus* and probably *S. nebulosa* harbour only *O. sauridae*, whereas *S. micropectoralis* is infected with *P. ganapattii* only (Rao 1954, 1960; Subhapradha 1955; Devi 1975; Shinde 1975; Jadhav & Shinde 1981; Khalil & Abu-Hakima 1985; Kuchta *et al.* 2008b; present study). Kuchta *et al*. (2008b) put wrongly *S. micropectoralis* as a host of *O. sauridae*. Neither *O. sauridae* nor *P. ganapattii* were found in *Saurida gracilis* (Quoy & Gaimard) from New Caledonia. *O. sauridae* is more widely distributed in the Indopacific and occurs from the Persian Gulf and coast of Mozambique throughout India and Indonesia up to the Pacific coast of Australia, New Caledonia and Japan. On the other hand, *P. ganapattii* was found only in the coastal waters of India and Indonesia, but never in the Pacific Ocean (Subhapradha 1955; Devi 1975; Radhakrishnan *et al.* 1983; present study).

Radhakrishnan *et al.* (1983) observed seasonal variation in the prevalence of infection of *S. tumbil* off India, with the highest prevalence (up to 100% for *P. ganapattii* and up to 20% for *O. sauridae*) from October to November and the lowest from January to February (35%). The present values from *S. tumbil* are much lower (9% in *O. sauridae* and 4% in *P. ganapattii*), but most hosts from Indonesia were dissected in the rainy season (from January to March) when the prevalence is probably at its minimum (Radhakrishnan *et al.* 1983).

Several authors described the cysts with the scolex of *P. ganapattii* occurring in the fish liver (Rao 1954; Subhapradha 1955; Radhakrishnan *et al.* 1983), but this site of infection was not confirmed in the newly collected material. In fact, the tapeworm forms cysts in the wall of the pyloric caeca, immediately next to the liver, which may have given the impression of its location in this organ. Penetration through the intestinal wall and the presence of a s*colex deformatus* is known also in another bothriocephalid cestode, *Anantrum histocephalum* Jensen & Heckmann, 1977, and two species of triaenophorids, namely *Abothrium gadi* Beneden, 1871 and *Parabothrium bulbiferum* Nybelin, 1922, but none of these species form extraintestinal cysts (Kuchta *et al.* 2008b).

Palm (2000, 2004) reported 54 different trypanorhynch cestodes species from the southern Java coast, Indonesia. Lönnberg (1893) and Yamaguti (1954) listed 5 elasmobranch cestodes from Java and Sulawesi, and recent studies describe further tetraphyllidean cestodes from Borneo (Caira *et al.* 2007; Twohig *et al.* 2008). On the contrary, only four bothriocephalideans have been reported so far from Indonesia, namely *Anchistrocephalus aluterae* (Linton, 1889), *Oncodiscus sauridae*, *Paraechinophallus* sp., and *Penetrocephalus ganapattii* (Kuchta *et al.* 2008b), making this region of major scientific interest for future fish parasitological research.

Finding *O. sauridae* in New Caledonia represents the first bothriocephalid tapeworm reported from these waters (Justine 2007).

Acknowledgments

The authors are grateful to Dr. Jean-Lou Justine for providing unpublished data and *O. sauridae* specimens from New Caledonia and to Jan ("Honza") Brabec for data on DNA sequences of studied taxa. The identification of most hosts from New Caledonia was kindly confirmed (from photographs) by Ronald Fricke (Staatliches Museum für Naturkunde, Stuttgart, Germany) and by John E. Randall (Bishop Museum, Hawaii, USA). The present study was partially supported by the Grant Agency of the Czech Republic (projects Nos. 524/04/0342 and 524/08/0885), Institute of Parasitology, Biology Centre AS CR (projects Z60220518 and LC522), and Faculty of Science, University of South Bohemia (MSM 6007665801). Collections in Indonesia were supported by the German Academic Exchange Service (DAAD) (T.W, A.T.Y.), the German Research Council (DFG PA 664/4-1) (H.W.P.), and the German Federal Ministry for Education and Science [BMBF Grant Nos. 03F0391(471)A] within the framework of the joint Indonesian-German research programme SPICE (Science for the Protection of Indonesian Coastal Marine Ecosystems).

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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.

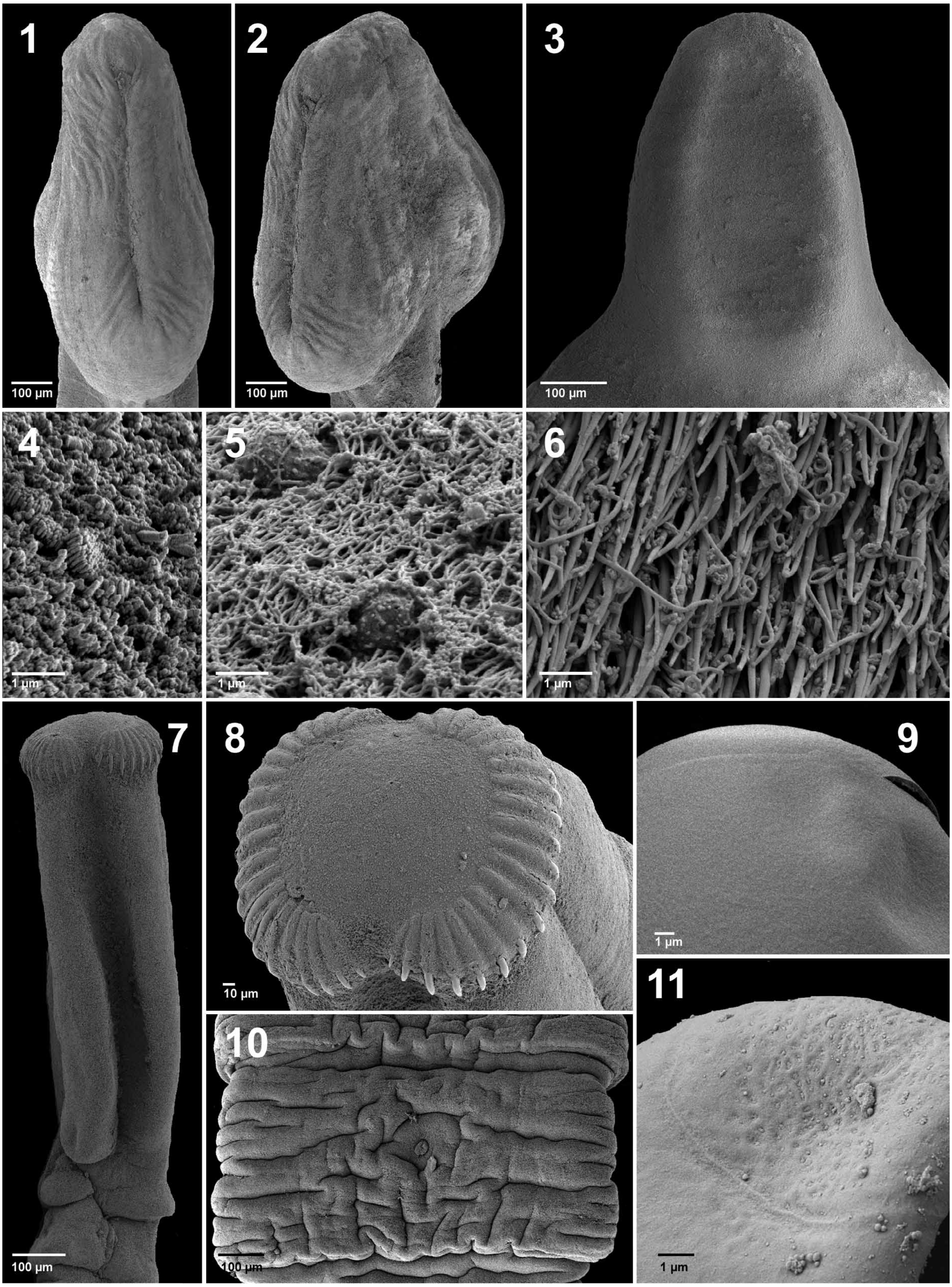
Prevalence and intensity of infection: Precise data are not available, but this cestode seems to be rather infrequent. Despite extensive sampling, the present authors found only a single barbel infected with *B. acheilognathi* in Ethiopia (out of 56 barbels examined; see Appendix 1). However, Bertasso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

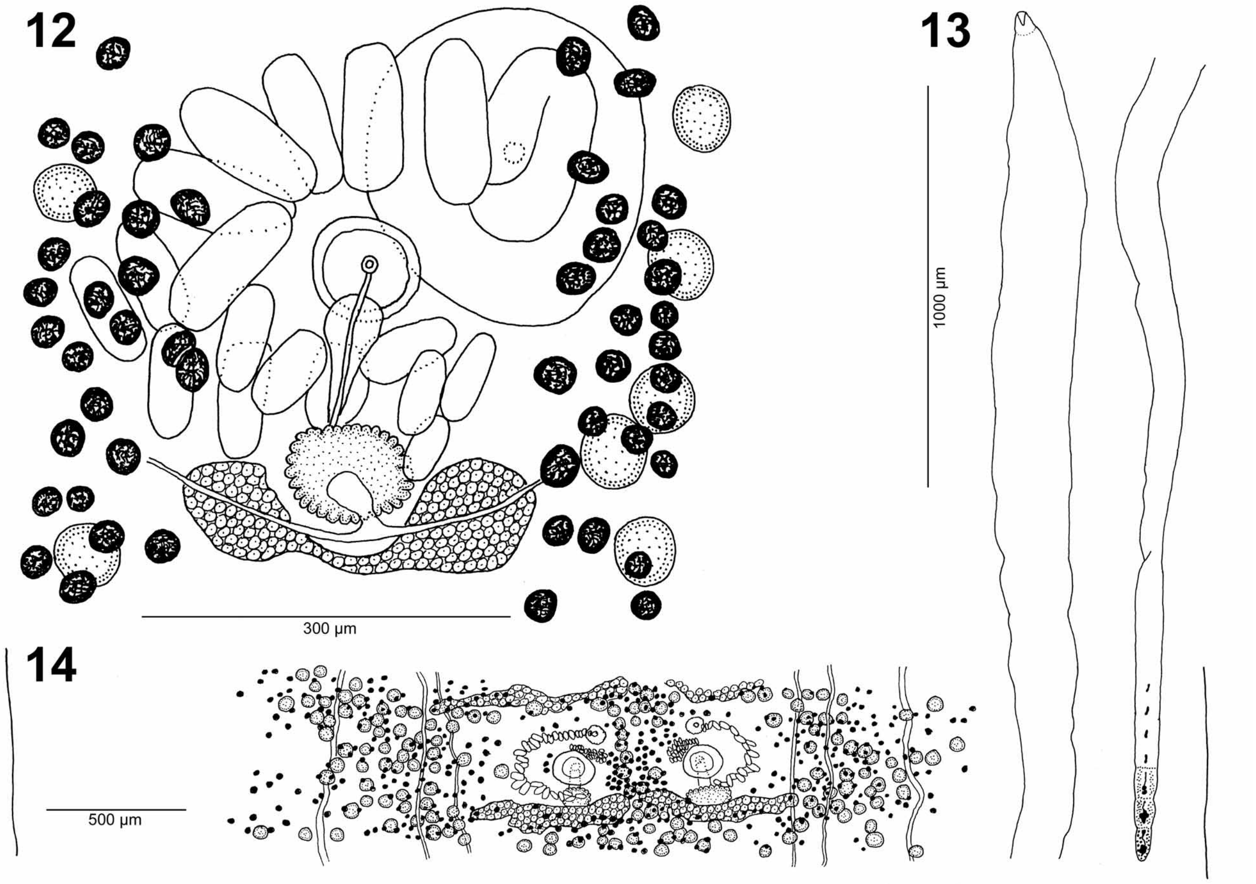
Material studied: Type material (USNPC 71666, 71667); vouchers: several slides collected by W.N.F. Woodland from *I. quadrilineatus* in Sierra Leone (BMNH 1977.3.28.147–179); new material: 9 specimens from Kostí, the Sudan (IPCAS C-455).

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).

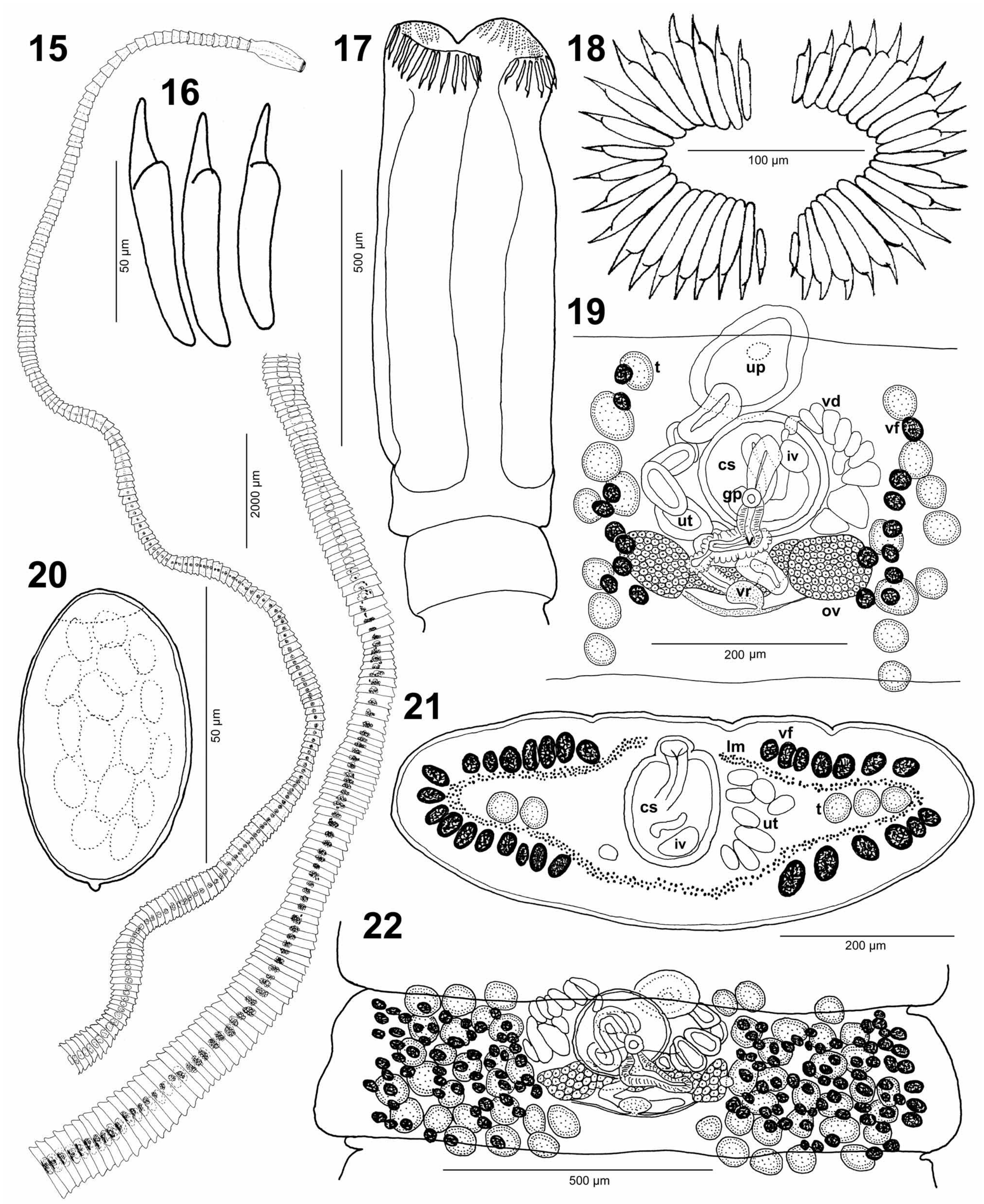
Testes medullary, oval, 70–133 (86 ± 20; 10) [under 30] in number per segment, 23–51 (35 ± 9) long by 26–45 (36 ± 6) wide [69 × 44 in sections] (n = 10) in diameter, forming 2 narrow longitudinal bands, 34–72 (47 ± 11) testes per band, confluent between segments, absent medially and near lateral margins (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.

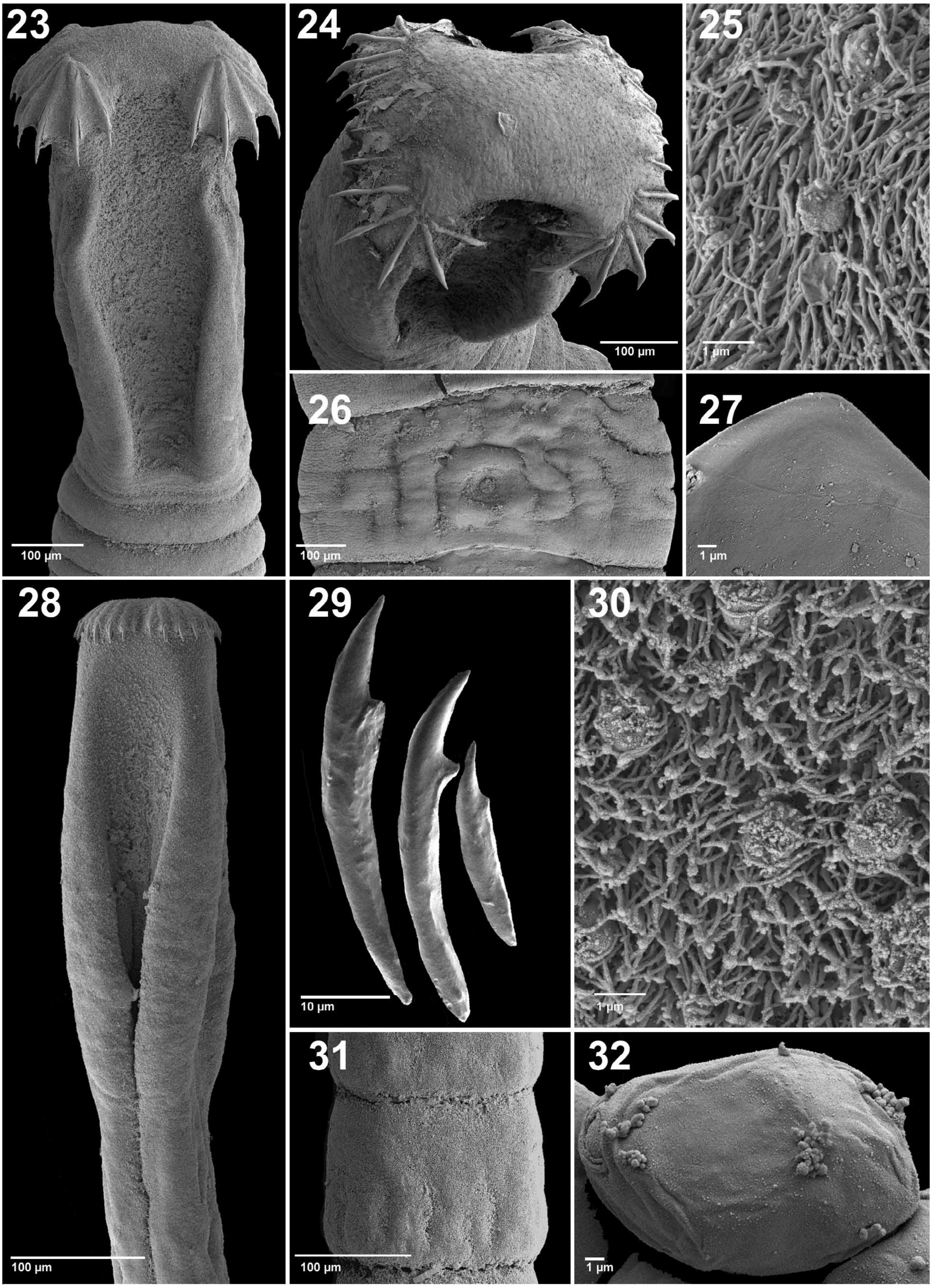
Type locality: Nile River in Egypt.

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.

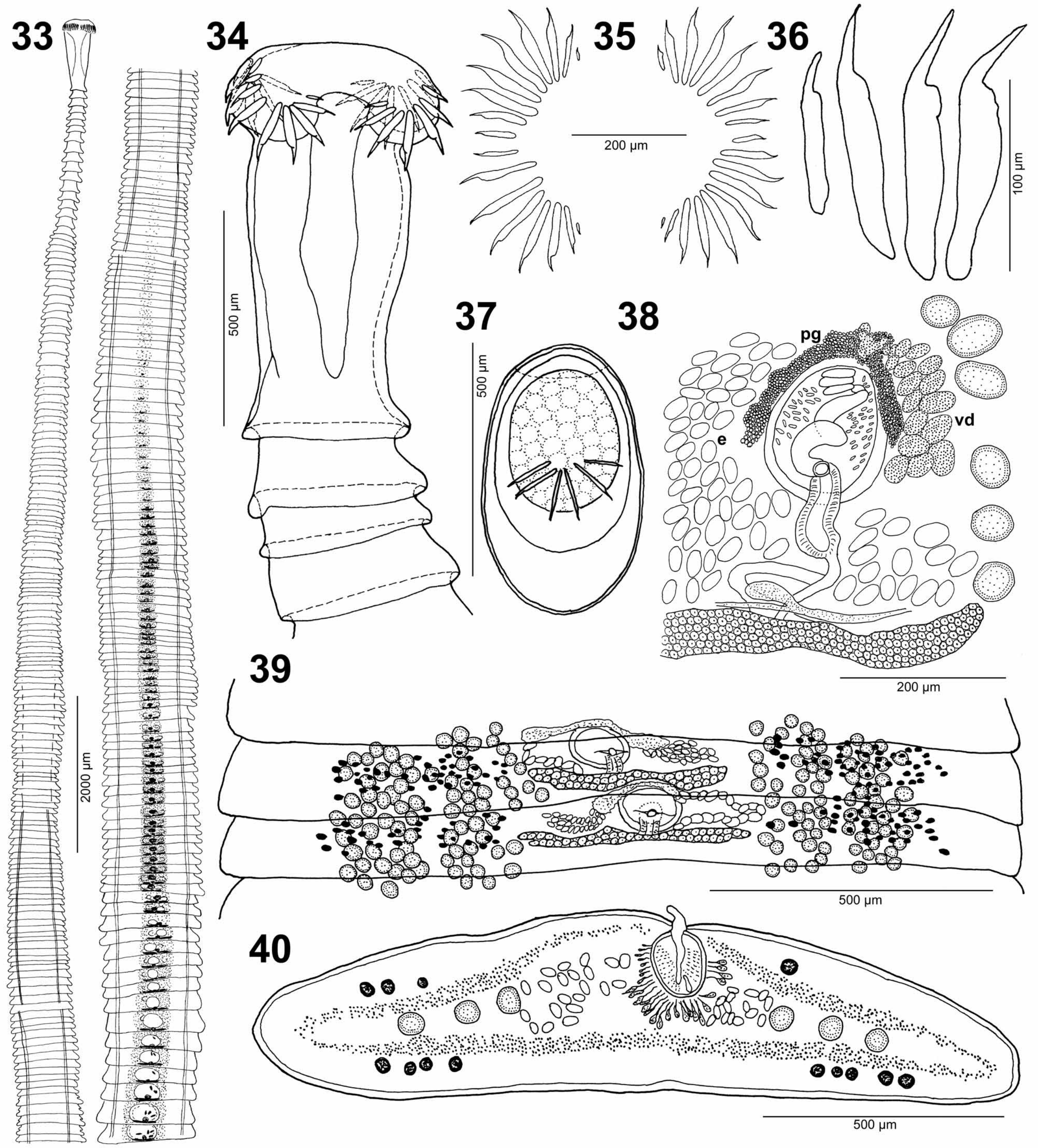
Prevalence: Nile basin – the Sudan, 8–25%, n = 21, intensity 15–50 (present study), 43%, n = 312, 10–70 (Khalil 1969); Turkana Lake – Kenya, 75%, 8, intensity up to 50 (present study); Niger basin – Nigeria, 94%, n = 84, intensity 1–226 (mostly juveniles) (Shotter & Medaiyedu 1978).

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**

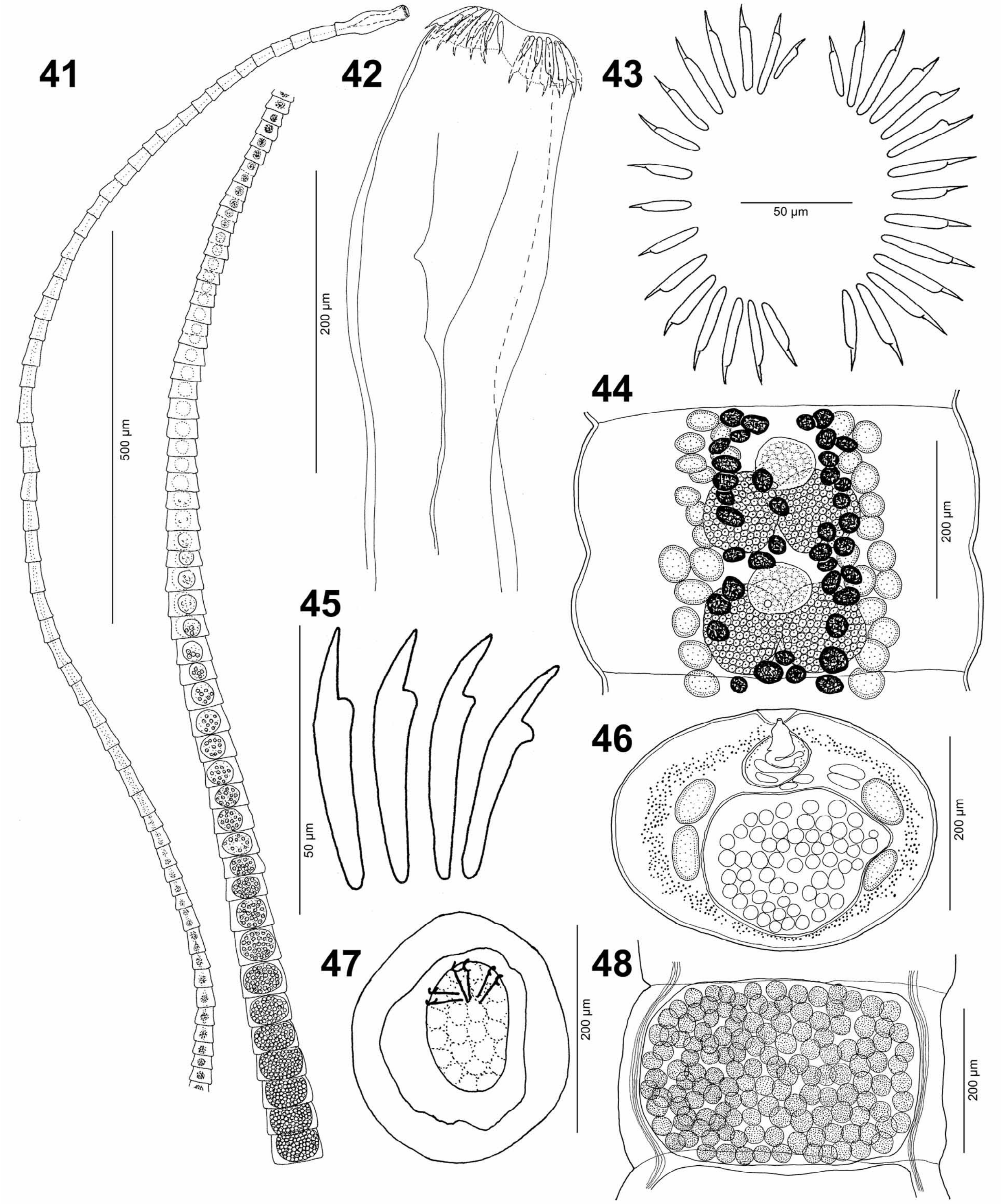
(Figs. 28–32, 41–52)

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.

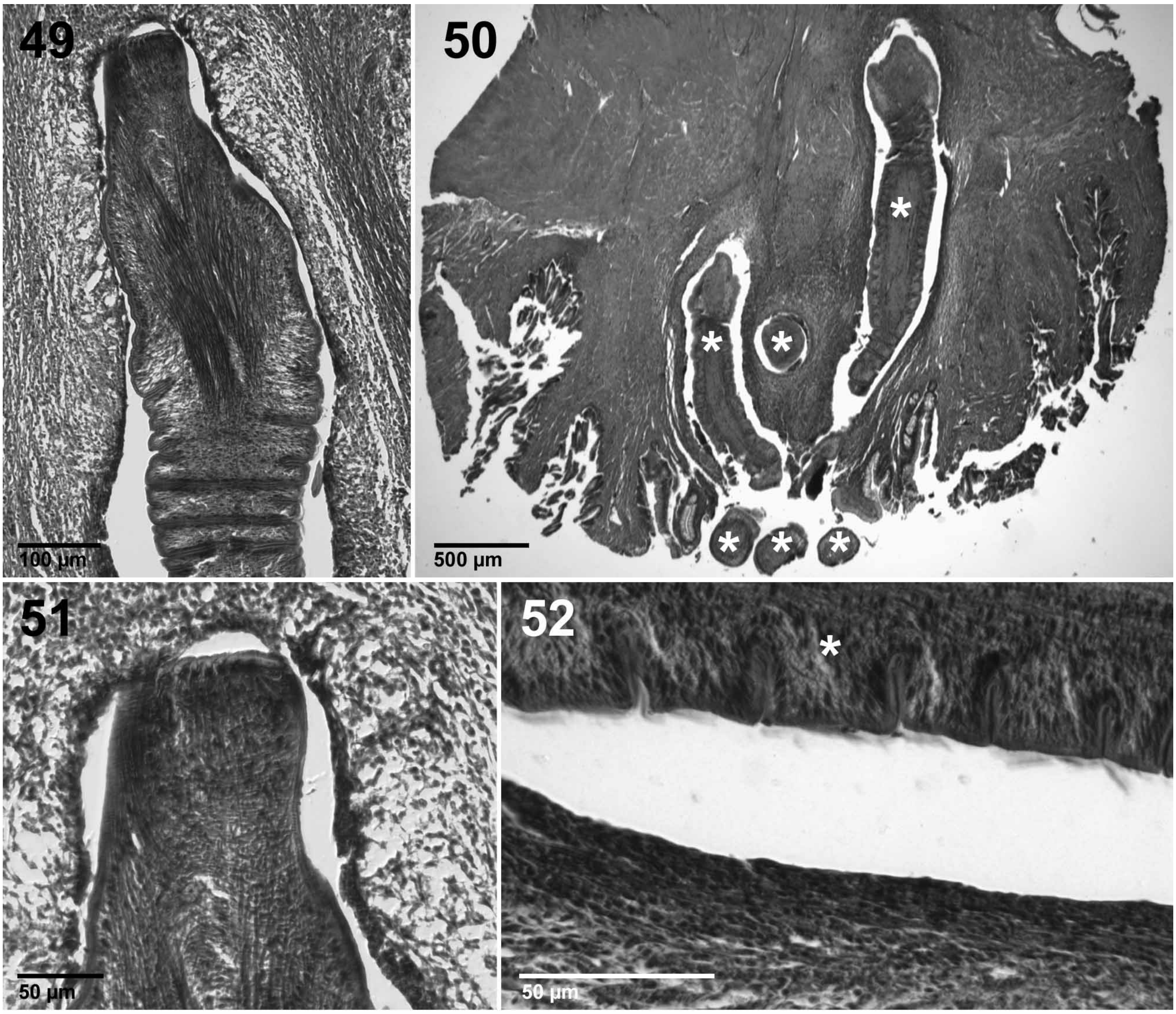
Type locality: Egypt, Nile River.

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).

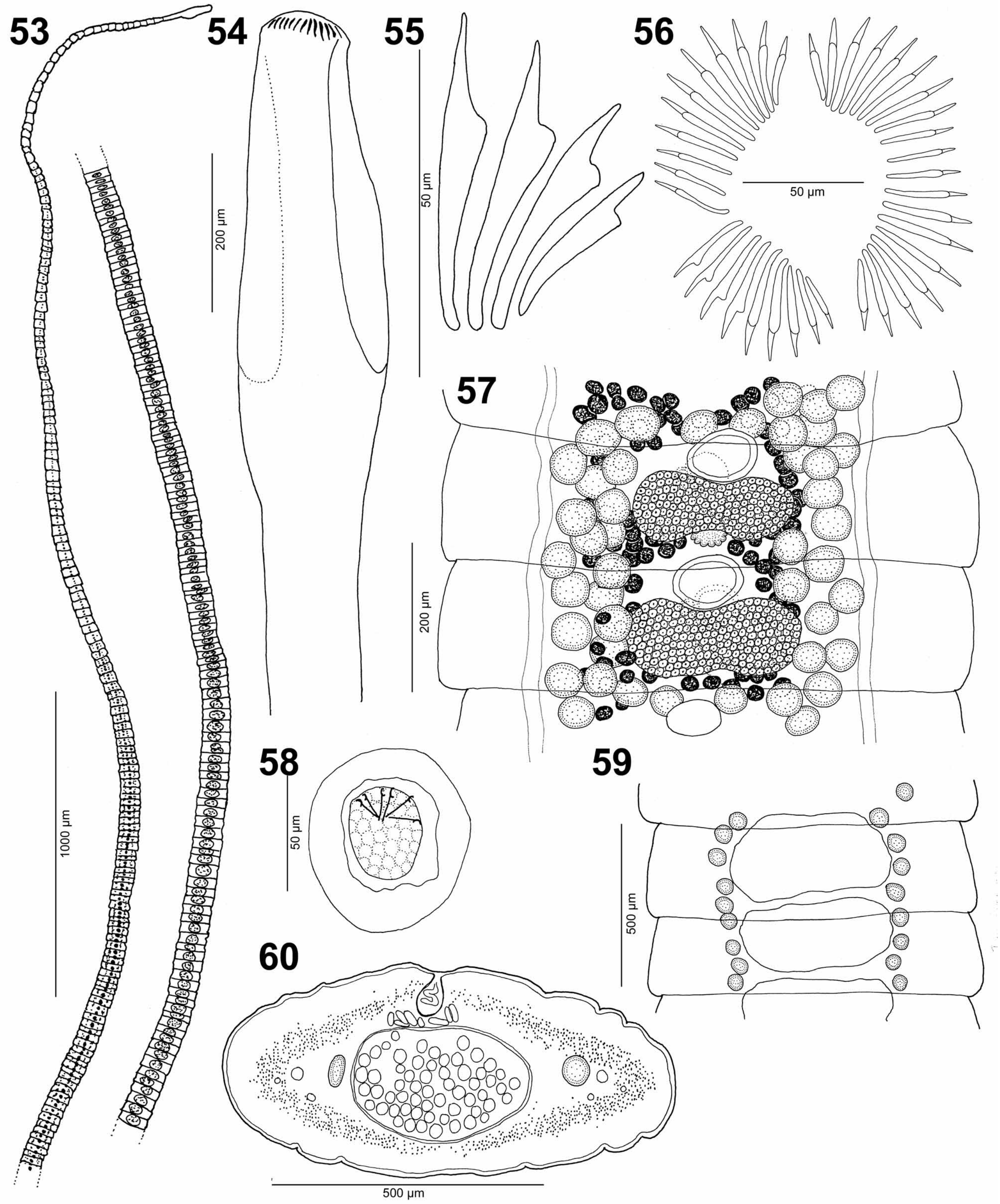
Uterine duct winding, short, filled with eggs (Fig. 41). Uterus thin-walled, median, spherical, enlarged in gravid segments, occupying 57–80% of segment surface (Figs. 41, 48). Uterine pore thick-walled, opens in centre of uterus. Eggs widely oval to spherical, 28–72 (46 ± 9) long by 27–51 (40 ± 6) wide (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.

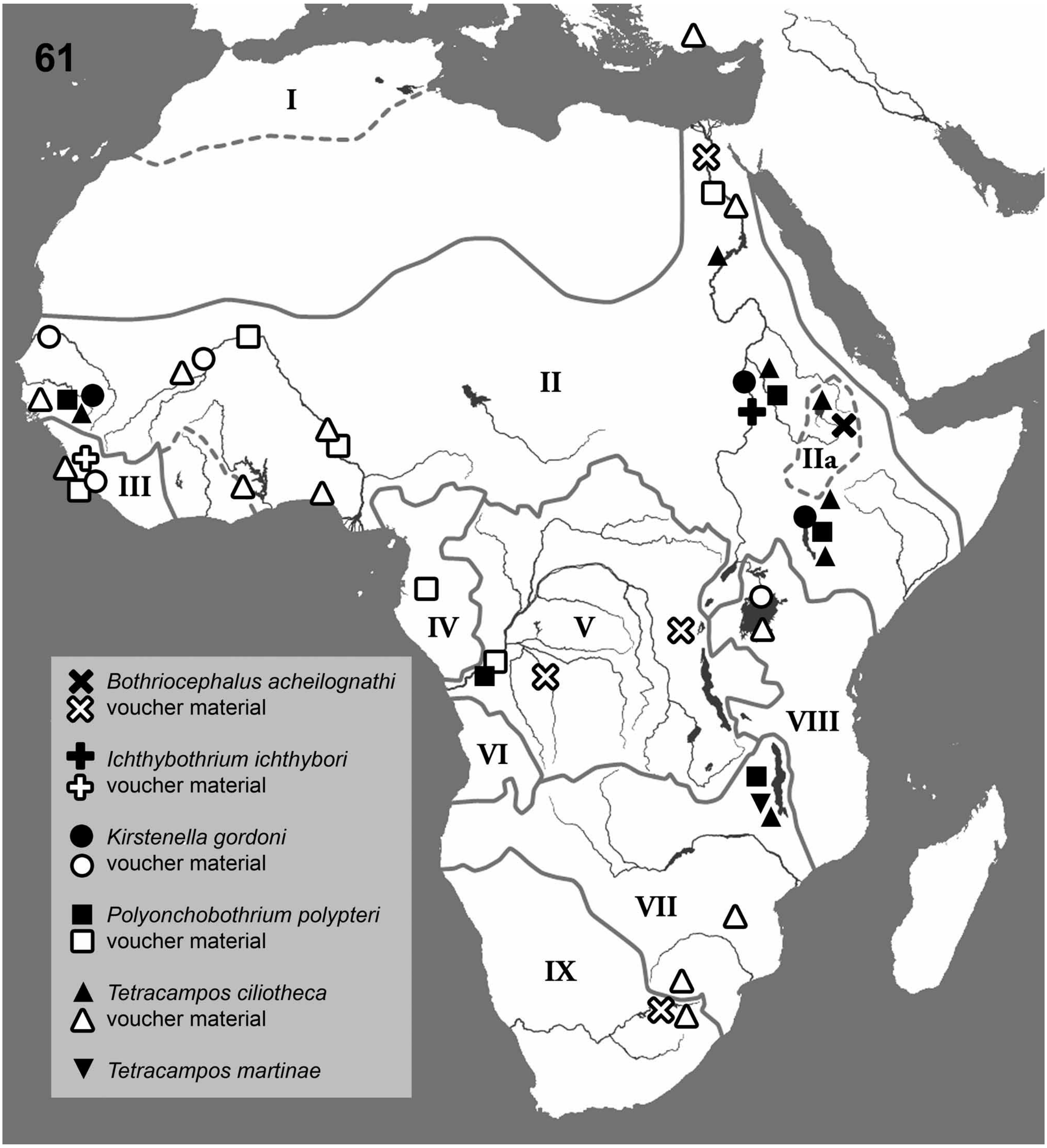


FIGURE 61. Distribution map of African bothriocephalideans according to existing voucher material (unconfirmed literature records not included). Ichthyological provinces are marked as follows: I. Maghreb, II. Nilo Sudan, IIa. Abyssinian subprovince, III. Upper Guinea, IV. Lower Guinea, V. Congo, VI. 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.).

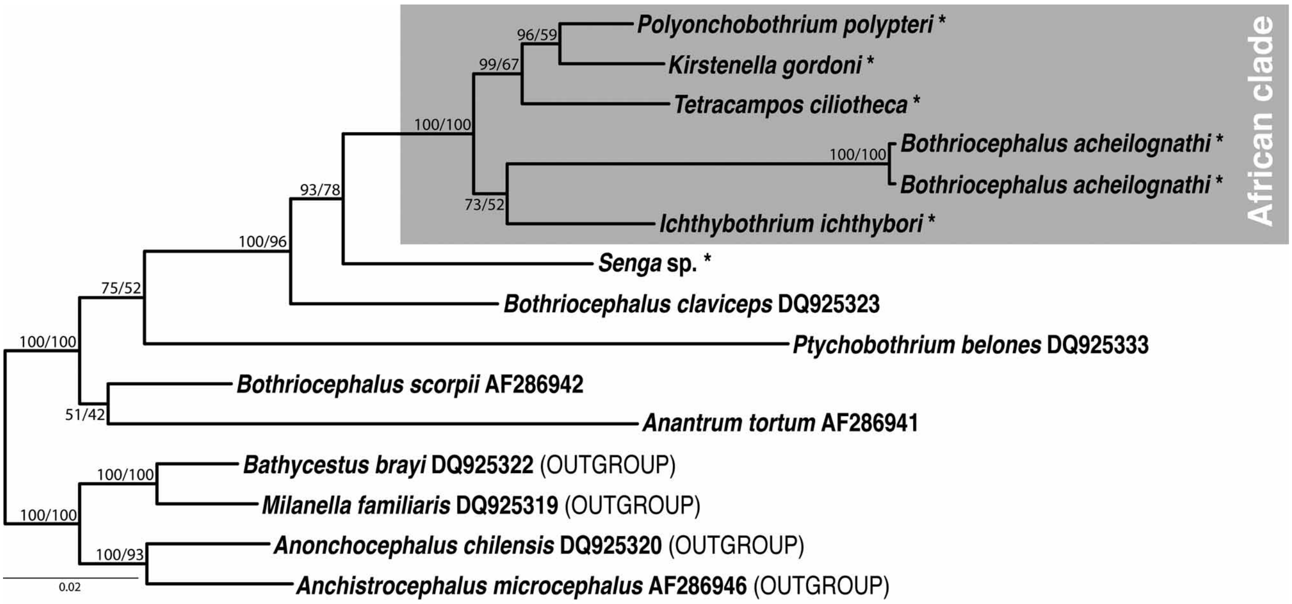

FIGURE 62. Interrelationships of 6 African bothriocephalideans and their relatives based on Bayesian inferrence analysis of partial sequences of the large subunit rDNA (lsrDNA). Rooted phylogram with node labels showing Bayesian posterior probabilities/bootstrap support values. Newly characterized sequences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

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Molecular phylogeny of the Bothriocephalidea (Cestoda): molecular data challenge morphological classification

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ABSTRACT

In this study, the relationships of the cestode order Bothriocephalidea, parasites of marine and freshwater bony fish, were assessed using multi-gene molecular phylogenetic analyses. The dataset included 59 species, covering approximately 70% of currently recognised genera, a sample of bothriocephalidean biodiversity gathered through an intense 15 year effort. The order as currently circumscribed, while monophyletic, includes three non-monophyletic and one monophyletic families. Bothriocephalidae is monophyletic and forms the most derived lineage of the order, comprised of a single freshwater and several marine clades. Biogeographic patterns within the freshwater clade are indicative of past radiations having occurred in Africa and North America. The earliest diverging lineages of the order comprise a paraphyletic Triaenophoridae. The Echinophallidae, consisting nearly exclusively of parasites of pelagic fish, was also resolved as paraphyletic with respect to the Bothriocephalidae. *Philobythoides* sp., the only representative included from the Philobythiidae, a unique family of parasites of bathypelagic fish, was sister to the genus *Eubothrium*, the latter constituting one of the lineages of the paraphyletic Triaenophoridae. Due to the weak statistical support for most of the basal nodes of the Triaenophoridae and Echinophallidae, as well as the lack of obvious morphological synapomorphies shared by taxa belonging to the statistically well-supported lineages, the current family-level classification, although mostly non-monophyletic, is provisionally retained, with the exception of the family Philobythiidae, which is recognised as a synonym of the Triaenophoridae. In addition, *Schyzocotyle* is resurrected to accommodate the invasive Asian fish tapeworm, *Schyzocotyle acheilognathi* (Yamaguti, 1934) n. comb. (syn. *Bothriocephalus acheilognathi* Yamaguti, 1934), which is of veterinary importance, and *Schyzocotyle nayarensis* (Malhotra, 1983) n. comb. (syn. *Ptychobothrium nayarensis* Malhotra, 1983). The genus is morphologically characterised by a wide, heart-shaped scolex with narrow, deep bothria.

1. Introduction

Over the past decade, a global collaborative effort has been undertaken to relate cestode classifications to their phylogeny on the basis of available molecular sequence data (Caira, 2011). Among the 19 currently recognised cestode orders (Caira et al., 2014), a few of the early diverging 'true' tapeworm (Eucestoda) groups differ from the others by possessing one or two pairs of bothria on the scolex ('bothriate', or formerly 'bifossate', cestodes), which act as sucking grooves and facilitate attachment to the host's gastrointestinal tract. Bothriate cestodes include the order Bothriocephalidea Kuchta, Scholz, Brabec & Bray, 2008, a globally distributed group of teleost fish parasites. Molecular phylogenetic studies (Brabec et al., 2006; Waeschenbach et al., 2007, 2012) consider the Bothriocephalidea as the most derived of all bothriate taxa, forming the sister clade to the group consisting of the Litobothriidea Dailey, 1969, which lack paired attachment organs, and the acetabulate taxa, which bear (mostly) four muscular, sucker-like attachment organs, each separated from the surrounding tissue by a basal membrane.

The order Bothriocephalidea was established by Kuchta et al. (2008a) as a result of splitting the paraphyletic Pseudophyllidea van Beneden in Carus, 1863 into two monophyletic clades—Diphyllobothriidea Kuchta, Scholz, Brabec & Bray, 2008 and Bothriocephalidea—on the basis of a number of unique morphological, biological (notably life cycle features and spectrum of host use) and molecular characteristics (Brabec et al., 2006; Kuchta et al., 2008a). Current bothriocephalidean taxonomy recognises 134 species and 48 genera (unpublished data; see Caira et al.,

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2012; www.tapeworms.uconn.edu accessed Feb 2015) and includes some of the first historically described cestode taxa (i.e. *Triaenophorus* Rudolphi, 1793 and *Bothriocephalus* Rudolphi, 1808).

As adults, bothriocephalidean cestodes parasitise teleost fish (Teleostei) almost exclusively, with both species of *Marsipometra* Cooper, 1917, *Polyonchobothrium polypteri* (Leydig, 1853), and *Eubothrium acipenserinum* (Cholodkovsky, 1918), parasitising archaic fish groups, namely paddlefish (Acipenseriformes), bichirs (Polypteriformes), and sturgeons (Acipenseriformes), respectively. Exceptions include three species of *Bothriocephalus* that have been described from salamanders (Plethodontidae) (Kuchta and Scholz, 2007). Two thirds of the known taxa are found in marine and one third in freshwater environments. Among marine bothriocephalideans, species diversity increases with ocean depth, where the richest fauna (nine genera) has been reported from bathypelagic and benthopelagic fish living deeper than 1000 m (Kuchta et al., 2008b; Klimpel et al., 2009). Freshwater bothriocephalideans are distributed mainly in Eurasia (27 species) and North America (18 species; some species are Holarctic in distribution). The species richness of the other continents is conspicuously depauperate (Kuchta and Scholz, 2007).

Early systematic treatments of the group were contributed by Lönnberg (1897), Lühe (1899, 1902), Nybelin (1922) and Fuhrmann (1931). Protasova (1974, 1977) reviewed the group (as suborder Bothriocephalata Freze, 1974), recognising 32 genera and 96 valid species, introducing a taxonomic categorisation largely based on egg morphology (presence or absence of an operculum) and uterine development, dividing bothriocephalideans into two superfamilies—Amphicotyloidea Lühe, 1889 and Bothriocephaloidea Blanchard, 1849. Two decades later, Bray et al. (1994) contributed keys to the pseudophyllidean genera and classified members of the currently recognised order into four families on the basis of the genital pore position: Bothriocephalidae Blanchard, 1849 (median), Echinophallidae Schumacher, 1914 (submarginal), Philobythiidae Campbell, 1977 and Triaenophoridae Lönnberg, 1889 (marginal), the latter two being further distinguished by vitellarium and egg characteristics (see Bray et al., 1994; Kuchta et al., 2008b). Bray et al. (1999) were the first to evaluate the phylogenetic relationships of the Bothriocephalidea using a matrix consisting of 36 morphological characters developed from a set of 14 nominotypical genera representing families sensu Yurakhno (1992), complemented by the Philobythiidae.

The first and most recent molecular phylogenetic analysis, focused on the interrelationships of the Bothriocephalidea, was performed by Brabec et al. (2006) using sequences of the nuclear rRNA genes (rDNA) of 17 bothriocephalidean species. Their study supported the monophyletic status of the order and suggested paraphyly of the families Triaenophoridae and Echinophallidae. However, due to the limited taxon sampling, they were unable to test the validity of several other families, e.g. Amphicotylidae Lühe, 1889, Parabothriocephalidae Yamaguti, 1934 and Ptychobothriidae Lühe, 1902 of Protasova (1977). Since then, phylogenetic interrelationships of the group have not been further evaluated, mainly due to the difficulties with collecting bothriocephalidean specimens preserved for molecular work as a result of their low prevalence and occurrence in rarely collected definitive hosts, e.g. deep-sea fish. Kuchta and Scholz (2007) provided an updated list of valid species and Kuchta et al. (2008b) carried out a taxonomic revision of the order, following the family classification proposed by Bray et al. (1994).

The present study was carried out with the following three aims. First, to undertake a comprehensive molecular phylogenetic evaluation of the Bothriocephalidea using a four gene dataset [small subunit (18S) nuclear rDNA (ssrDNA); partial large subunit (28S) nuclear rDNA (lsrDNA – domains D1–D3); partial cytochrome *c* oxidase subunit I (*cox*1); partial large subunit (16S) mitochondrial rDNA (*rrn*L)] based on a comprehensive sampling of taxa. Second, to examine congruence of the traditional classification based largely on morphological characters with the newly generated molecular data. Finally, to test monophyly of particularly problematic genera, with a particular focus on the genus *Bothriocephalus*.

2. Materials and methods

2.1. Sampling

Specimens sequenced *de novo* were obtained from freshly killed fish collected and processed following the procedure described by Kuchta et al. (2012). Most specimens were fixed in 96–99% molecular-grade ethanol and their morphological vouchers, i.e. hologenophores (the specimen from which the molecular sample was taken) and paragenophores (a putatively conspecific specimen voucher collected together with the molecular specimen; see Pleijel et al., 2008 for details), were fixed in hot 4% formalin for morphological study. Several scoleces and proglottids were prepared for scanning electron microscopy (SEM) following the procedure outlined by Kuchta et al. (2012).

In total, 59 species of bothriocephalideans were analysed in this study (see Table 1). In addition to existing described taxa, eight species and two genera new to science were included to maximise the diversity of morphological forms and definitive host spectrum. Scanning electron micrographs of key morphological characters including some of these undescribed taxa are presented in Fig. 1.

2.2. Molecular and phylogenetic analyses

Total genomic DNA (gDNA) was extracted using the DNeasy Blood and Tissue kit or the BioSprint 96 robotic workstation in combination with the BioSprint 96 DNA Blood kit (QIAGEN, Netherlands) following the manufacturer's instructions. PCR protocols, primer use and PCR purification followed the methodology described in Scholz et al. (2013). Sequencing of both strands of PCR products was carried out on an Applied Biosystems 3730 DNA Analyser, using Big Dye version 1.1. Contiguous sequences of complete ssrDNA (1859–2138 bp), partial lsrDNA (domains D1–D3; 1242–2111 bp), partial *cox*1 (493–612 bp) and partial *rrn*L (365–885 bp) were assembled using Sequencher 4.8 (GeneCodes Corporation, Ann Arbor, USA) and sequence identity was checked with the Basic Local Alignment Search Tool (BLAST) (www.ncbi.nih.gov/BLAST/).

Sequences were aligned using either the E-INS-i (lsrDNA, ssrDNA, *rrn*L) or the G-INS-i translation code aware (*cox*1) algorithm of the program MAFFT (Katoh and Standley, 2013) implemented in Geneious ver. 7 (Kearse et al., 2012) and ambiguously aligned positions were manually excluded from subsequent analyses (full data sets available at http://dx.doi.org/10.5519/0071217). Phylogenetic relationships were estimated from individual genes as well as from the concatenated dataset using maximum likelihood (ML) and Bayesian inference (BI) methods. Best ML estimates were obtained from 100 search replicates using the program GARLI ver. 2.0 (Zwickl, D.J., 2006. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Ph.D. dissertation, The University of Texas at Austin, USA). BI was carried out using MrBayes ver. 3.2 (Ronquist et al., 2012), running four independent Metropolis coupled Markov chain Monte Carlo (MC^3) runs of four chains, each, for 10 million generations, sampling tree topologies every 1000th generation. The burn-in period was determined as the point when standard deviation of split frequencies values were

Table 1
List of taxa included in the analyses with details on host, locality and museum collection vouchers. GenBank numbers in bold indicate data generated in this study.

Cestode species	Host species	Env[a]	Country[b] and locality	PBI[c] and Coll.[d] Nos.; voucher type[e]	GenBank Accession numbers[i]			
					ssrDNA	lsrDNA	*rrn*L	*cox*1
Abothrium gadi	*Gadus morhua*	P/B	GB, Fair Isle, North Sea	PBI-6; C-439; P	AJ228773	AF286945	**KR780834**	**KR780779**
Amphicotyle heteropleura	*Centrolophus niger*	P/W	NZ, Chatham Rise	PBI-542; C-453; H	**KR780965**	**KR780918**	–	**KR780826**
Anantrum tortum	*Synodus foetens*	C/B	US, SC, Charleston	PBI-14; C-669; H	**KR780927**	**KR780883**	**KR780837**	–
Anantrum sp.	*Synodus myops*	C/B	US, MS, Ocean Springs	PBI-609; C-684; H	**KR780966**	**KR780919**	–	**KR780831**
Anchistrocephalus microcephalus	*Mola mola*	P/W	Unknown locality	PBI-9; N/A; -	AJ287473	AF286946	JQ268539	JQ268539
Anonchocephalus chilensis	*Genypterus blacodes*	P/B	AR, Patagonian Shelf	PBI-10; C-440; H	DQ925304	DQ925320	–	**KR780782**
Bathybothrium rectangulum	*Barbus barbus*	F	CZ, River Rokytná	PBI-5; C-17/4; P	DQ925305	DQ925321	**KR780833**	**KR780778**
Bathycestus brayi	*Notacanthus bonaparte*	P/B	GB, Outer Hebrides	PBI-13; B-2003.9.3.01; P	**KR780926**	**KR780882**	–	**KR780785**
Bothriocephalidae gen. sp.	*Epinephelus coioides*	C/B	ID, Java, Segara Anakan	PBI-33; C-686; H	**KR780941**	**KR780894**	**KR780853**	**KR780801**
Bothriocephalus australis	*Platycephalus aurimaculatus*	C/B	AU, Cape Otway	PBI-18; C-510/1; P	**KR780930**	**KR780886**	**KR780841**	**KR780789**
Bothriocephalus cf. *carangis*	*Uraspis uraspis*	C/W	ID, Pelabuhan Ratu	PBI-20; C-687/1; P	**KR780931**	**KR780888**	**KR780842**	**KR780790**
Bothriocephalus celinae	*Cephalopholis aurantia* × *spiloparaea*	C/B	NC, Barrier Reef	PBI-962; M-1926; H	**KR780968**	**KR780921**	–	**KR780828**
Bothriocephalus claviceps	*Trinectes maculatus*	F	US, MS, Benndale	PBI-526; C-16; H	**KR780957**	**KR780910**	**KR780871**	**KR780818**
Bothriocephalus cuspidatus	*Sander vitreus*	F	US, WI, Turtle-Flambeau	PBI-489; C-269; H	**KR780955**	**KR780908**	**KR780869**	**KR780816**
Bothriocephalus manubriformis	*Istiophorus platypterus*	P/W	MV, Indian Ocean	PBI-19; C-496/1; P	–	**KR780887**	–	–
Bothriocephalus scorpii	*Myoxocephalus scorpius*	C/B	GB, North Sea	PBI-17; C-233; H	AJ228776	AF286942	**KR780840**	**KR780788**
Bothriocephalus timii	*Cottoperca gobio*	C/B	AR, Patagonian Shelf	PBI-16; C-646; P	**KR780929**	**KR780885**	**KR780839**	**KR780787**
Bothriocephalus travassosi	*Anguilla marmorata*	F/C	CN, South China	PBI-535; C-688; P	**KR780959**	**KR780912**	**KR780872**	**KR780820**
Bothriocephalus sp.	*Lepisosteus oculatus*	F	US, MS, Benndale	PBI-525; C-689; H	**KR780954**	**KR780907**	**KR780868**	**KR780815**
Bothriocephalus sp.	*Lepomis gibbosus*	F	US, MN, Lake Peter	PBI-487; [g]; H	**KR780953**	**KR780906**	**KR780867**	**KR780814**
Bothriocephalus sp.	*Micropterus dolomieu*	F	US, WI, Lake Little Trout	PBI-485; [g]; H	**KR780952**	**KR780905**	**KR780866**	**KR780813**
Bothriocotyle solinosomum	*Centrolophus niger*	P/W	NZ, Chatham Rise	PBI-35; C-442/1; P	**KR780943**	**KR780896**	**KR780855**	**KR780803**
Clestobothrium crassiceps	*Merluccius merluccius*	C/B	GB, North Sea	PBI-15; C-498; P	**KR780928**	**KR780884**	**KR780838**	**KR780786**
Clestobothrium cristinae	*Merluccius hubbsi*	C/B	AR, Patagonia	PBI-402; A-511; P	**KR780948**	**KR780901**	**KR780862**	**KR780830**
Clestobothrium splendidum	*Merluccius australis*	C/B	AR, Patagonia	PBI-401; A-512; P	**KR780967**	**KR780920**	**KR780877**	**KR780827**
Echinophallus wageneri	*Centrolophus niger*	C/W	NZ, Chatham Rise	PBI-34; C-443; P	**KR780942**	**KR780895**	**KR780854**	**KR780802**
Eubothrium crassum	*Salmo salar*	FC/W	GB, River Tay	PBI-8; C-271; P	**KR780924**	**KR780880**	**KR780836**	**KR780781**
Eubothrium fragile	*Alosa fallax*	C/W	GB, River Severn	PBI-40; C-398; P	**KR780946**	**KR780899**	**KR780860**	**KR780808**
Eubothrium rugosum	*Lota lota*	F	RU, Rybinsk Reservoir	PBI-538; C-327; P	**KR780961**	**KR780914**	**KR780874**	**KR780822**
Eubothrium salvelini	*Salvelinus alpinus*	F	GB, Scotland, Loch Doyn	PBI-540; C-126; P	**KR780963**	**KR780916**	**KR780876**	**KR780824**
Eubothrium tulipai	*Ptychocheilus oregonensis*	F	US, OR, River Willamette	PBI-484; [h]; H	**KR780951**	**KR780904**	**KR780865**	**KR780812**
Glossobothrium nipponicum	*Schedophilus velani*	P/W	SN, Atlantic	PBI-533; C-445; H	**KR780958**	**KR780911**	–	**KR780819**
Ichthybothrium ichthybori	*Ichthyborus besse*	F	SD, Kosti	PBI-24; C-455; H	**KR780933**	JQ811837	**KR780845**	**KR780793**
Ichthybothrium sp.	*Mesoborus crocodilus*	F	CF, Mongambe	PBI-427; C-690; H	**KR780949**	**KR780902**	**KR780863**	**KR780810**
Kirstenella gordoni	*Heterobranchus bidorsalis*	F	ET, River Omo	PBI-27; C-609; H	**KR780936**	JQ811838	**KR780848**	**KR780796**
Marsipometra hastata	*Polyodon spathula*	F	US, MS	PBI-4; C-447; P	DQ925313	AY584867	–	**KR780777**
Marsipometra parva	*Polyodon spathula*	F	US, MS, Chotard Lake	PBI-524; C-691; H	**KR780956**	**KR780909**	**KR780870**	**KR780817**
Milanella familiaris	*Centrolophus niger*	P/W	GB, Outer Hebrides	PBI-11; C-454; H	DQ925303	DQ925319	–	**KR780783**
Neobothriocephalus aspinosus	*Seriolella violacea*	P/W	PE, Lima, Pacific	PBI-37; C-449; P	**KR780944**	**KR780897**	**KR780857**	**KR780805**
Oncodiscus sauridae	*Saurida tumbil*	C/B	ID, Java, Pelabuhan Ratu	PBI-32; C-456; H	**KR780940**	**KR780893**	**KR780852**	**KR780800**
Parabothriocephaloides segmentatus	*Psenopsis anomala*	C/W	CN, coast of Xiamen	PBI-39; C-457; P	DQ925314	DQ925330	**KR780859**	**KR780807**
Parabothriocephalus gracilis	*Psenopsis anomala*	C/W	CN, coast of Xiamen	PBI-38; C-459; P	**KR780945**	**KR780898**	**KR780858**	**KR780806**
Parabothrium bulbiferum	*Pollachius pollachius*	C/B	NO, Trondheimsleia	PBI-539; C-620; H	**KR780962**	**KR780915**	**KR780875**	**KR780823**
Paraechinophallus japonicus	*Psenopsis anomala*	C/W	CN, coast of Xiamen	PBI-36; C-461; P	DQ925315	DQ925331	**KR780856**	**KR780804**

(*continued on next page*)

Table 1 (*continued*)

Cestode species	Host species	Env[a]	Country[b] and locality	PBI[c] and Coll.[d] Nos.; voucher type[e]	GenBank Accession numbers[i]			
					ssrDNA	lsrDNA	*rrn*L	*cox*1
Penetrocephalus ganapattii	*Saurida tumbil*	C/B	ID, Java, Pelabuhan Ratu	PBI-31; C-462; H	**KR780939**	**KR780892**	**KR780851**	**KR780799**
Philobythoides sp.	*Alepocephalus rostratus*	P/B	GB, North Atlantic	PBI-7; B-1999.9.27.7-8; H	DQ925316	DQ925332	**KR780835**	**KR780780**
Polyonchobothrium polypteri	*Polypterus senegalus*	F	SD, Khartoum	PBI-25; C-464; P	**KR780934**	JQ811836	**KR780846**	**KR780794**
Probothriocephalus alaini	*Xenodermichthys copei*	P/W	GB, North Atlantic	PBI-12; C-452; P	**KR780925**	**KR780881**	–	**KR780784**
Ptychobothrium belones	*Strongylura leiura*	P/W	MV, Indian Ocean	PBI-21; C-465; H	DQ925317	DQ925333	**KR780843**	**KR780791**
Senga lucknowensis	*Mastacembelus armatus*	F	VN, Lake Ba-Be	PBI-29; [h]; H	**KR780938**	**KR780891**	**KR780850**	**KR780798**
Senga magna	*Siniperca chuatsi*	F	RU, River Ilistaya	PBI-537; C-694; H	**KR780960**	**KR780913**	**KR780873**	**KR780821**
Senga visakhapatnamensis	*Channa punctata*	F	IN, Kaliachak	PBI-28; [h]; H	**KR780937**	**KR780890**	**KR780849**	**KR780797**
Schyzocotyle acheilognathi n. comb.	*Cyprinus carpio*	F	CZ, Terezínský pond	PBI-23; C-15; H	**KR780932**	**KR780889**	**KR780844**	**KR780792**
Schyzocotyle nayarensis n. comb.	*Barilius* sp.	F	IN, West Bengal	PBI-963; C-695; H	**KR780969**	**KR780922**	**KR780878**	**KR780829**
Tetracampos ciliotheca	*Clarias gariepinus*	F	ET, Lake Zeway	PBI-26; C-466; P	**KR780935**	JQ811835	**KR780847**	**KR780795**
Triaenophoridae gen. sp.	*Hyperoglyphe antarctica*	P/B	AU, Port Macdonnell	PBI-541; C-692; H	**KR780964**	**KR780917**	–	**KR780825**
Triaenophorus crassus	*Coregonus lavaretus*	F	DE, Lake Titisee	PBI-42; C-350; H	DQ925318	DQ925334	–	–
Triaenophorus nodulosus	*Esox lucius*	F	GB, Loch Lomond	PBI-3; C-28; P	**KR780923**	**KR780879**	**KR780832**	**KR780776**
Triaenophorus stizostedionis	*Sander vitreus*	F	US, WI, Winnebago Lake	PBI-41; C-657; P	**KR780947**	**KR780900**	**KR780861**	**KR780809**
Grillotia erinaceus TRY[f]	*Raja radiata*		GB; OUTGROUP		AJ228781	AF286967		
Grillotia pristiophori TRY[f]	*Pristiophorus nudipinnis*		AU; OUTGROUP				EF103924	EF103924
Litobothrium janovyi LIT[f]	*Alopias superciliosus*		MX; OUTGROUP		AF124468	AF286930		
Litobothrium nickoli LIT[f]	*Alopias pelagicus*		MX; OUTGROUP				JQ268549	JQ268549

[a] Env, Environment: C, coastal; F, freshwater; P, pelagic; B, benthic; W, water column.

[b] Country codes: AR, Argentina; AU, Australia; CF, Central African Republic; CN, China; CZ, Czech Republic; DE, Germany; ET, Ethiopia; GB, Great Britain; ID, Indonesia; IN, India; MV, Maldives; MX, Mexico; NC, New Caledonia; NO; Norway; NZ, New Zealand; PE, Peru; PT, Portugal; RU, Russia; SD, Sudan; SN, Senegal; US, United States of America (state codes: MN, Minnesota; MS, Mississippi; OR, Oregon; SC, South Carolina; WI, Wisconsin); VN, Vietnam.

[c] PBI-No: unique specimen ID related to a National Science Foundation (Planetary Biodiversity Inventory) project; see http://www.tapewormdb.uconn.edu/index.php/parasites/molecular_search/.

[d] Coll, collection: A, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; B, Natural History Museum, London, Great Britain (BMNH); C, Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic; M, Museum National d'Histoire Naturelle, Paris, France.

[e] Molecular vouchers (see Pleijel et al., 2008 for terminology): H, hologenophore; P, paragenophore.

[f] LIT, Litobothriidea; TRY, Trypanorhyncha.

[g] Deposited in personal collection of A. Choudhury, St. Norbet's College, DePere, WI, USA.

[h] Deposited in personal collection of R. Kuchta, Institute of Parasitology, CAS, Czech Republic.

[i] ssrDNA, small subunit (18S) nuclear rDNA; lsrDNA, partial large subunit (28S) nuclear rDNA; *rrn*L, partial large subunit (16S) mitochondrial rDNA; *cox*1, partial cytochrome c oxidase subunit I.

<0.01, and by checking for Markov chain Monte Carlo (MCMC) convergence using 'are we there yet?' (AWTY; Nylander et al., 2008).

The partitioning scheme for the concatenated dataset and models of nucleotide evolution for each gene were selected according to the Bayesian information criterion (BIC) in PartitionFinder 1.1.0 (Lanfear et al., 2012), limiting the model choice to those available for a given phylogenetic program; see Fig. 2 and Supplementary Figs. S1–S4 legends for the best fitting models and partitioning scenarios. In the concatenated analysis, model parameters were estimated separately for each partition. ML bootstrap support was estimated using GARLI, running three independent search replicates for each of the 1,000 bootstrap resamples. Bootstrap results were summarised in PAUP* ver. 4.0a136.

2.3. Morphological character mapping

A consensus topology based on the ML estimate of the concatenated dataset was generated by collapsing statistically poorly supported [either <70 ML bootstraps or <95 BI posterior probabilities (PP)] internal nodes and nodes not consistently found across single-gene ML analyses, using the program MacClade ver. 4.06 (Maddison and Maddison, 2005). A character matrix composed of 22 morphological and one ecological (aquatic realm, i.e. freshwater versus marine) characters scored for each of the 59 ingroup taxa present in the molecular phylogenies was constructed (Figs. 1 and 3, Supplementary Table S1). Characters were selected based on their importance for historical bothriocephalidean classification, or based on their putative systematic utility (as inferred by the combined expertise of the authors). Mapping of these characters on the consensus topology was carried out using MacClade assuming accelerated transformation (Supplementary Fig. S5).

2.4. Data accessibility

Most molecular vouchers, i.e. hologenophores and paragenophores (see Table 1 for accession numbers) were deposited in the Helminthological collection of the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice (see http://www.paru.cas.cz/en/collections/). A few specimens were also deposited in the Natural History Museum (NHM), London, UK (B); Museum National d'Histoire Naturelle, Paris, France (M); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (A).

Planetary Biodiversity Inventory (PBI) numbers refer to the samples used for a large-scale molecular phylogenetic study of tapeworms as part of a National Science Foundation, USA, (NSF)-PBI project (see Acknowledgments); data on individual samples sequenced can be found under a given PBI number at http://tapewormdb.uconn.edu/index.php/parasites/molecular_search/.

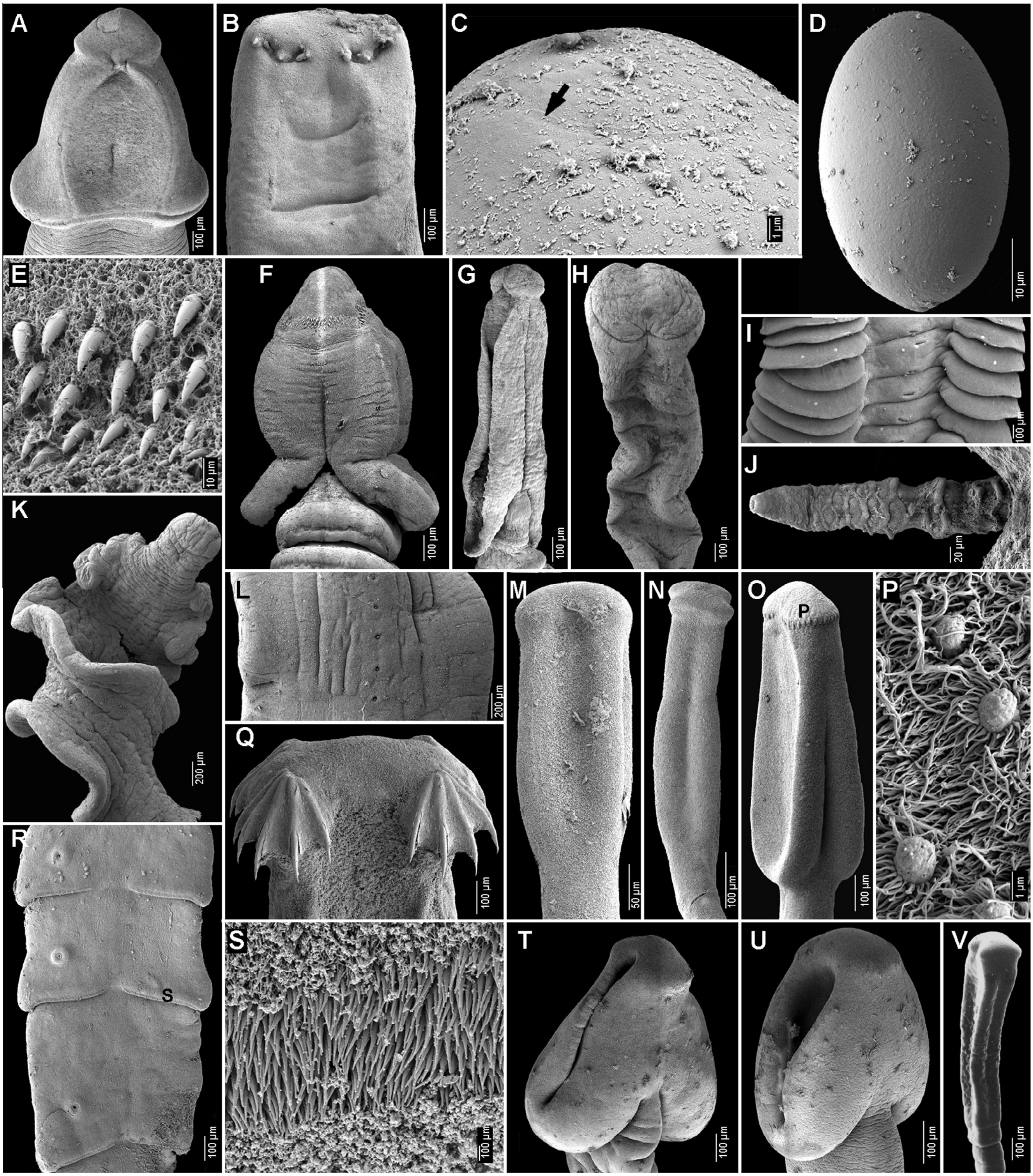

Fig. 1. Scanning electron micrographs of selected bothriocephalideans. (A) Scolex of *Marsipometra hastata* ex *Polyodon spathula*, USA. (B, C) Scolex and egg with operculum (arrow) of *Triaenophorus nodulosus* ex *Esox lucius*, Great Britain (GB). (D) Unoperculate egg of *Eubothrium salvelini* ex *Salvelinus alpinus*, GB. (E, F) Scolex of *Anchistrocephalus microcephalus* ex *Mola mola*, USA. (E) Detail of apical disc with hooks. (G, J) Scolex and everted cirrus with tegumental bumps of Triaenophoridae gen. sp. (PBI-541) ex *Hyperoglyphe antarctica*, Australia. (H) Scolex of Bothriocephalidae gen. sp. (PBI-33) ex *Epinephelus coioides*, Indonesia. (I) Portion of strobila of *Penetrocephalus ganapattii* ex *Saurida tumbil*, Indonesia. (K, L) Anterior part of the body and detail of strobila of *Anantrum tortum* ex *Synodus foetens*, USA. (M) Scolex of *Bothriocephalus celinae* ex *Cephalopholis aurantia* × *spiloparaea*, New Caledonia. (N) Scolex of *Bothriocephalus scorpii* ex *Myoxocephalus scorpius*, GB. (O, P) Scolex and tumuliform globular structures of *Senga visakhapatnamensis* ex *Channa punctata*, India. (Q) Apical part of the scolex of *Polyonchobothrium polypteri* ex *Polypterus senegalus*, Sudan. (R, S) Portion of strobila with submedian genital pores and posterior margin of proglottids armed with large spinitriches of *Neobothriocephalus aspinosus* ex *Seriolella violacea*, Peru. (T, U) Scolex of *Schyzocotyle nayarensis* ex *Barilius* sp., India; note variation in appearance of bothrial opening. (V) Scolex of *Bothriocephalus claviceps* ex *Anguilla anguilla*, Czech Republic. Note: small letters correspond to panels showing higher magnification images at locations indicated.

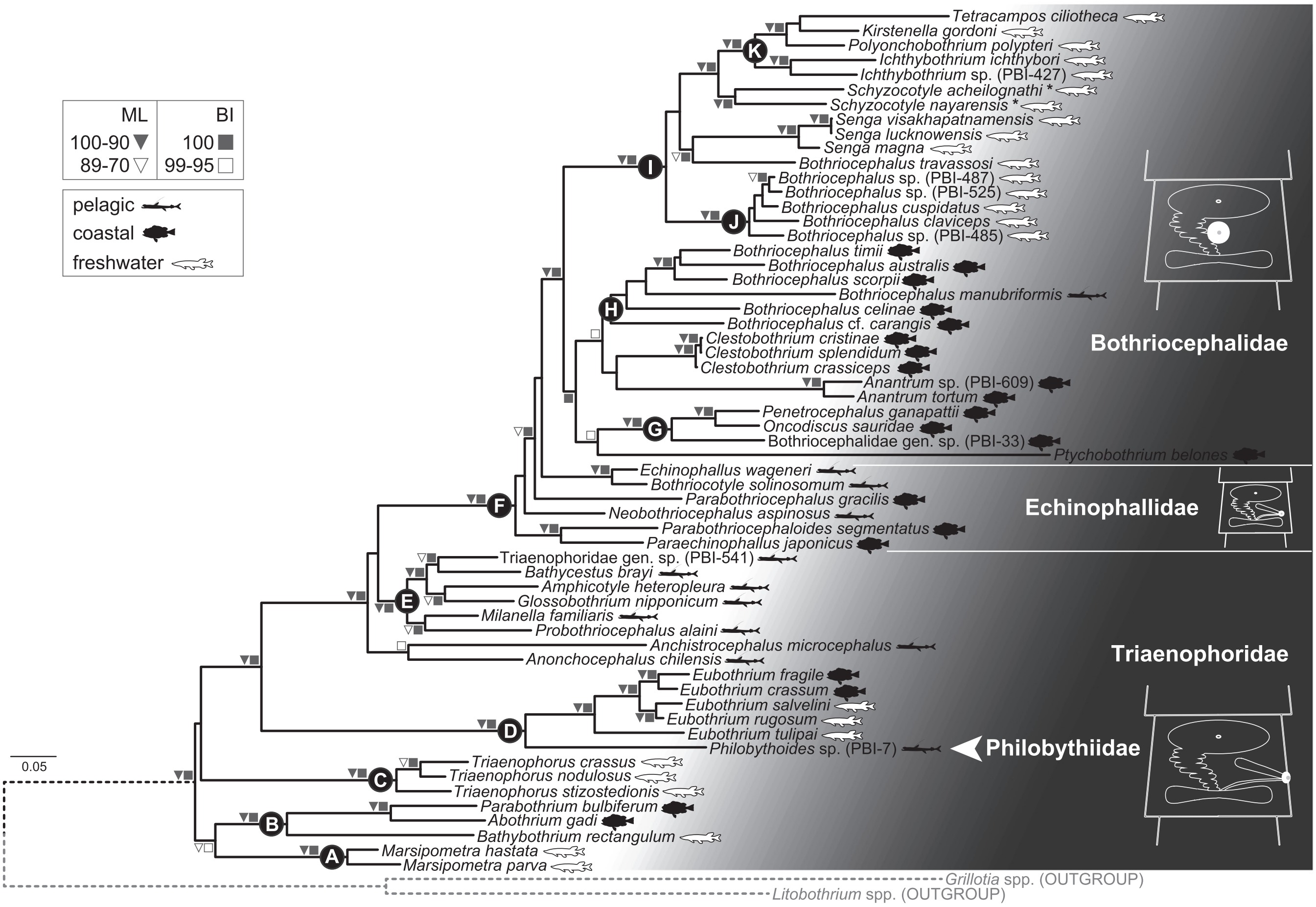

Fig. 2. Maximum likelihood (ML) phylogram of the Bothriocephalidea resulting from the analysis of the concatenated four-gene dataset, where model parameters were estimated separately for each partition. Partitions and models of nucleotide evolution were as follows: ssrDNA (GTR+I+Γ), lsrDNA (GTR+I+Γ), *cox*1 codon position 1 (TrN+I+Γ), *cox*1 codon position 2 (TVM+I+Γ), *cox*1 codon position 3 (TIM+I+Γ), *rrn*L (GTR+I+Γ). Branch length scale bar indicates number of substitutions per site. Silhouettes mark definitive host habitat. Current families and corresponding genital pore position are depicted at right. See Section 3 for comments on the designated Clades A–K. * indicates species of the resurrected genus *Schyzocotyle*, i.e. *Schyzocotyle acheilognathi* (Yamaguti, 1934) n. comb. (syn. *Bothriocephalus acheilognathi* Yamaguti, 1934) and *Schyzocotyle nayarensis* (Malhotra, 1983) n. comb. (syn. *Ptychobothrium nayarensis* Malhotra, 1983). BI, Bayesian inference.

Individual alignments are available from a data portal of the NHM, London at http://dx.doi.org/10.5519/0071217.

3. Results

The topology recovered from analyses of the concatenated four-gene dataset is presented in Fig. 2. Individual gene trees are given in Supplementary Figs. S1–S4. The overall topology and nodal stability of single-gene phylogenetic estimates based on ssr- and lsrDNA data partitions (Supplementary Figs. S1, S2) did not differ substantially from that resulting from the concatenated analysis. Nodal support in the *cox*1 and *rrn*L analyses (Supplementary Figs. S3, S4) was overall poor, with *cox*1 tree terminal nodes being placed on notably longer branches (Supplementary Fig. S3). However, strongly supported clades in single-gene phylogenies were present in trees resulting from analysis of the concatenated dataset. Important topological features of the phylogenetic trees resulting from individual gene analyses (see Supplementary Figs. S1–S4) are summarised and compared with the concatenated dataset in Table 2.

Exclusion of long-branching taxa from the concatenated dataset, one at a time (namely species of *Anantrum* Overstreet, 1968, *Anchistrocephalus microcephalus* (Rudolphi, 1819), *Bothriocephalus manubriformis* (Linton, 1889), species of *Eubothrium* Nybelin, 1920 + *Philobythoides* Campbell, 1979, *Ptychobothrium belones* (Dujardin, 1845), and outgroup taxa) had no effect on the resulting topology, i.e. an identical tree (apart from the excluded taxon) to that tree presented in Fig. 2 was always recovered (results not shown). In summary, the ML estimate resulting from the concatenated dataset represents well the consensus phylogenetic signal detected in all of the ML estimates constructed within the scope of this study, and demonstrates both the contribution and limitations of the currently available molecular data in furthering our understanding of the systematics of this order. In comparison to the single-gene and taxon-restricted phylogenies, the concatenated dataset resulted in a phylogenetic estimate that received the highest nodal support overall, with all of the highly supported bothriocephalidean lineages present. To facilitate discussion, clades that were well supported, shared biogeographic distributions or are taxonomically well founded are referred to with letters A through K (Fig. 2). Poorly supported lineages are not explicitly labeled.

3.1. Family composition of the Bothriocephalidea and circumscription of main lineages

Species of the family Triaenophoridae comprised a series of the earliest diverging lineages and thus the family is not monophyletic (Fig. 2). These lineages are supported Clades A–E; we note that in

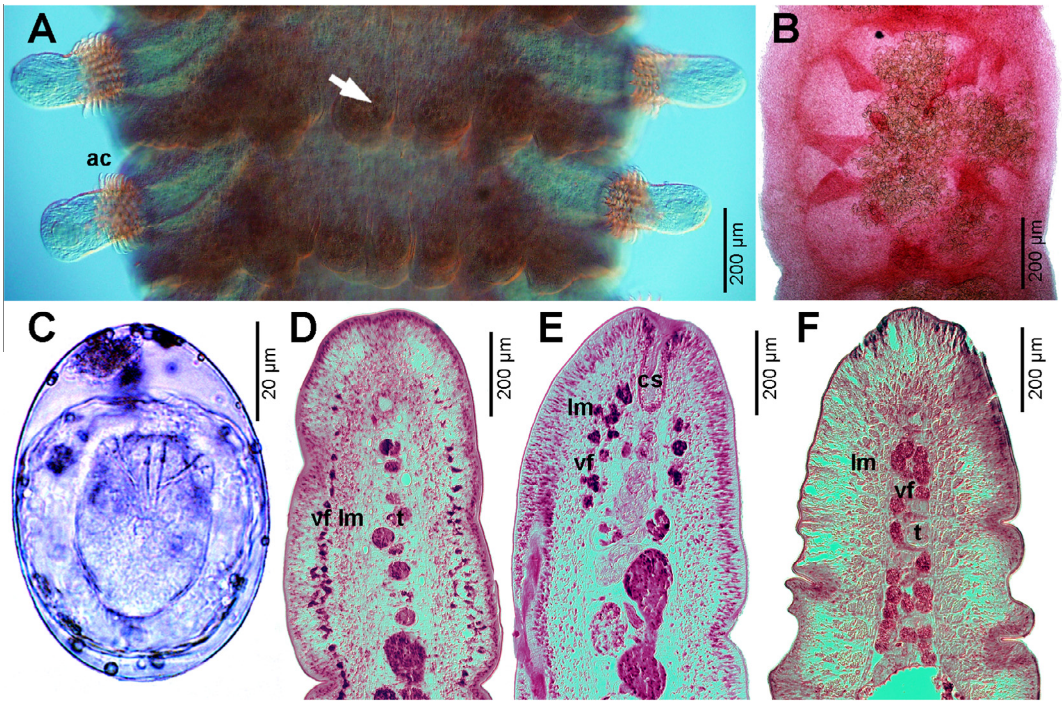

Fig. 3. Photomicrographs of selected morphological characters treated in Supplementary Fig. S5. (A) Proglottids of *Paraechinophallus japonicus* ex *Psenopsis anomala* showing presence of two genital complexes per proglottid; arrow indicates notched posterior margins (Character 3) of the proglottid and armed cirrus (ac). (B) Gravid proglottid of *Bathybothrium rectangulum* ex *Barbus barbus* showing lobulated terminal part of the uterus (Character 20). (C) Embryonated egg of *Eubothrium crassum* ex *Salmo salar* showing non-ciliated embryophore (Character 22) and unoperculate egg (Character 21). (D–F) Cross-sections of the mature proglottids showing status of vitelline follicle position (Character 15). (D) Cortical in *Eubothrium fragile* ex *Alosa fallax*. (E) In medulla with some follicles entering between inner muscle bundles in *Eubothrium rugosum* ex *Lota lota*. (F) Medullary in *Abothrium gadi* ex *Gadus morhua*. cs, cirrus sac; lm, longitudinal muscles; t, testes; vf, vitelline follicles.

Table 2
Nodal bootstrap support for monophyly of Clades A–K estimated from analyses of concatenated and single-gene data partitions.

Clade	Nodal bootstrap support for individual data partitions				
	Concatenated	ssrDNA	lsrDNA	*rrn*L	*cox*1
A, *Marsipometra*	100	96	99	na[a]	100
B, Abothriinae	100	100	53	44	88
C, *Triaenophorus*	100	100	100	100[a]	100[a]
D, *Eubothrium* and *Philobythoides*	100	100	100	100	2
E, Bathypelagic triaenophorids	63	1	98	na	7
F, Bothriocephalidae and Echinophallidae	72	99	98	64	21
G, Coastal fish (Indian Ocean)	100	100	100	83	17
H, Marine *Bothriocephalus* sensu stricto	32	34	12	18[a]	0
I, Freshwater bothriocephalids	100	100	97	58	63
J, Nearctic species of *Bothriocephalus*	100	100	100	89	99
K, African bothriocephalids	100	90	61	80	3

ssrDNA, small subunit (18S) nuclear rDNA; lsrDNA, partial large subunit (28S) nuclear rDNA; *rrn*L, partial large subunit (16S) mitochondrial rDNA; *cox*1, partial cytochrome c oxidase subunit I; na, not available.

[a] Based on limited taxon samples.

Clade D the single representative of the Philobythiidae (*Philobythoides* sp.) was sister to the triaenophorid genus *Eubothrium*. Beyond Clades A–E, the Triaenophoridae assemblage includes a weakly supported clade composed of the triaenophorid genera *Anchistrocephalus* and *Anonchocephalus*. The family Echinophallidae was also paraphyletic. Thus, among four historically recognised families of the order Bothriocephalidea, only the Bothriocephalidae was resolved as monophyletic relative to the other families (Fig. 2). This family represents the most derived clade in the order and is comprised of well-supported Clades G, I, J, K, as well as the relatively unstable Clade H (Fig. 2). Furthermore, it includes monophyletic lineages of uncertain position within the Bothriocephalidae, consisting of species of *Anantrum* Overstreet, 1968 and *Clestobothrium* Lühe, 1899 and the single-species *Ptychobothrium belones*.

Owing to the limited statistical support for several clades and a lack of morphological support for most of the well-supported clades (marked Clades A–K, see Sub-Sections 3.1.1.–3.1.5 and Fig. 2), we have refrained from proposing a new family-level classification for the Bothriocephalidea. However, we briefly circumscribe these clades on the basis of available molecular, morphological and biological data to facilitate the aggregation of additional data in the future and the ultimate proposition of a new family-level classification.

3.1.1. Early diverging triaenophorid lineages – basal Triaenophoridae

While it is impossible to unequivocally identify the earliest branching clade of the Bothriocephalidea, 'triaenophorid' Clades A, B and C represent the most basal lineages. Clade A consists of the 'Marsipometrinae' (*Marsipometra*), parasites of freshwater paddlefish, and formed the sister group to Clade B, which consists of 'Abothriinae', an assemblage of parasites of marine gadiforms (*Abothrium* van Beneden, 1871, *Parabothrium* Nybelin, 1920) and freshwater barbels (*Bathybothrium* Lühe, 1902). The precise position of Clade C, which encompasses the 'Triaenophori inae' (*Triaenophorus*), parasites of freshwater pikes, remains unresolved.

Each of these three triaenophorid lineages is characterised by a mutually not corresponding set of morphological and biological features (for details, see Supplementary Fig. S5). Of note, members of Clade B seem to lack a ciliated embryophore stage and egg operculum (see Fig. 1C), the presence of which is common to many other bothriocephalideans (see Section 3.1.2). In contrast, restriction to the freshwater environment unites all of the early diverging triaenophorids except *Parabothrium* and *Abothrium*.

3.1.2. Derived triaenophorid lineages – derived Triaenophoridae

There are at least three other clades that include members of the traditional family Triaenophoridae that form a well-supported clade group with all of the remaining Bothriocephalidea to the exclusion of the Clades A–C. These triaenophorids are also paraphyletic and cannot be readily characterised by shared morphological or biological features.

Clade D consists of the clade we call 'Eubothriinae' (*Eubothrium* and *Philobythoides*; the latter genus traditionally classified in its own family, the Philobythiidae). Species of the genus *Eubothrium* occur in a wide range of marine and freshwater fish throughout the northern hemisphere, whereas *Philobythoides* is found in bathypelagic fish only. Characters that unite members of Clade D are the absence of a ciliated embryophore and also of an egg operculum, as also is the case for Clade B (see Section 3.1.1) (Figs. 1C; 3C).

The second clade is composed of *Anchistrocephalus* Monticelli, 1890 and *Anonchocephalus* Lühe, 1902 (strongly supported only by Bayesian PP). These tapeworms parasitise pelagic, globally distributed sunfish and bathydemersal cusk-eels of the southeastern Pacific Ocean, respectively, and represent the sister to the larger group containing Clade E and the remaining Bothriocephalidea (Figs. 1 and 2).

Clade E, called herein the 'Amphicotylinae' (Amphicotylinae Lühe, 1889 contained *Amphicotyle* Diesing, 1863 and *Eubothrium*; the remaining genera listed below were accommodated in other subfamilies or have been erected recently; see Protasova, 1977), consists of six monotypic genera (*Amphicotyle*, *Bathycestus* Kuchta & Scholz, 2004, *Glossobothrium* Yamaguti, 1952, *Probothriocephalus* Campbell, 1979, *Milanella* Kuchta & Scholz, 2008 and Triaenophoridae gen. sp.) (Fig. 1G, J). While forming a well-supported monophyletic group, members of Clade E parasitise unrelated groups of bathypelagic and bathydemersal teleosts and display distinct morphological characteristics such as a large cirrus and the proximal part of the cirrus-sac angled anteriomedially (see Kuchta et al., 2008b; Supplementary Fig. S5).

3.1.3. Echinophallidae

The family Echinophallidae was recovered as an early diverging paraphyletic assemblage in Clade F. As currently configured, the Echinophallidae includes as many as four lineages with *Bothriocotyle* Ariola, 1900 + *Echinophallus* Schumacher, 1914 and *Parabothriocephaloides* Yamaguti, 1934 + *Paraechinophallus* Protasova, 1975 always forming well-supported pairs, respectively. Members of the Echinophallidae parasitise marine centrolophid fish with a high prevalence and share several unique morphological characteristics, including submarginal genital pores and posterior margins of the proglottids armed with large spinitriches (see Figs. 1R, S; 3A; Supplementary Fig. S5).

3.1.4. Marine Bothriocephalidae – early diverging Bothriocephalidae

Two clades of the Bothriocephalidae are recovered. One constituted of the marine taxa (albeit only with support from Bayesian PP), almost all of which exclusively parasitise coastal demersal marine teleosts (with the exception of *B. manubriformis*), and the other of freshwater taxa (Clade I, see Section 3.1.5). Well-supported groups within the marine clade include Clade G, in which Bothriocephalidae gen. sp. (PBI-33) was sister to *Penetrocephalus ganapattii* (Rao, 1954) + *Oncodiscus sauridae* Yamaguti, 1934, and several monogeneric lineages including *Anantrum* spp., *Clestobothrium* spp. and part of *Bothriocephalus* sensu stricto.

All members of Clade G, which is represented here by all recognised species, infect marine coastal fish in the western Indo-Pacific region and are characterised by markedly craspedote proglottids with prominent posterior margins (Fig. 1I). All members of the *Clestobothrium* clade occur in pelagic gadiforms, whereas those of *Anantrum*, including *Anantrum* sp., parasitise reef lizard fish (Synodontidae). *Anantrum* spp. are unique among bothriocephalideans in that they possess a spirally twisted strobila with rippled margins (Fig. 1K). They also lack separation between proglottids (Fig. 1L), but this character appears also in other mutually not closely related bothriocephalideans (*Ichthybothrium* Khalil, 1971, *Probothriocephalus*, *Triaenophorus*) (Supplementary Fig. S5).

3.1.5. Freshwater Bothriocephalidae

Clade I consists of four well-supported subclades of freshwater bothriocephalids: (i) Clade J is comprised of Nearctic species of *Bothriocephalus* sensu lato (three of which are new species) and *B. claviceps* (Goeze, 1782) with Holarctic distribution, (ii) species of *Senga* Dollfus, 1934 + *Bothriocephalus travassosi* Tubangui, 1938, predominantly from the Indomalayan region [exceptions include *S. magna* (Zmejev, 1936) from the Russian Far East and China, i.e. the Palaearctic region], (iii) *Schyzocotyle acheilognathi* (syn. *Bothriocephalus acheilognathi*; see Section 3.3) + *S. nayarensis* (syn. *Ptychobothrium nayarensis*; see Section 3.3) from Asia, and (iv) Clade K comprised of five morphologically distinct bothriocephalids from the Ethiopian biogeographic region (see Kuchta et al., 2012). Most species of *Senga* parasitise snakeheads (Channidae) and spiny eels (Mastacembelidae), however, *S. magna* parasitises Mandarin fish (*Siniperca chuatsi*) and *B. travassosi* parasitises eels.

3.2. Monophyly of bothriocephalidean genera and non-monophyly of *Bothriocephalus*

Our phylogenetic analyses, which covered 59 bothriocephalidean species, supported the monophyly of *Clestobothrium* (all three valid species), *Eubothrium* (five of nine valid species), *Ichthybothrium* (one valid species + one new), *Marsipometra* (both valid species), *Senga* (three species—the number of valid species is questionable; see Kuchta and Scholz, 2007; Kuchta et al., 2008b) and *Triaenophorus* (all three valid species) (Fig. 2).

In contrast, our analyses revealed paraphyly of *Bothriocephalus*, the bothriocephalidean genus with the highest number of nominal species and also the best represented genus in this study (14 of 38 species including three new to science; Table 1). In fact, our results suggest that currently valid species of *Bothriocephalus* might represent at least four unrelated genera: (i) six species in Clade H (including the type species *B. scorpii* Müller, 1776 and thus *Bothriocephalus* sensu stricto), (ii) five species in Clade J, and two lineages in Clade I: (iii) two species reassigned to *Schyzocotyle* below, and (iv) *Bothriocephalus travassosi*. Due to incomplete taxon sampling of the genus (11 named species out of 35 after Kuchta and Scholz, 2007; Gil de Pertierra et al., 2015), only one taxonomic action is proposed here—the resurrection of *Schyzocotyle* Akhmerov, 1960 to accommodate *B. acheilognathi* and *P. nayarensis*.

3.3. Resurrection of Schyzocotyle Akhmerov, 1960

Based on our results, *Schyzocotyle*, as established by Akhmerov (1960) to accommodate *Schyzocotyle fluviatilis* Akhmerov, 1960 (synonymised with *B. acheilognathi* by Dubinina, 1982), is resurrected as the oldest available name to accommodate *S. acheilognathi* (Yamaguti, 1934) n. comb. and *Schyzocotyle nayarensis* (Malhotra, 1983) n. comb., both of which are characterised by possession of a heart-shaped scolex (Fig. 1T,U); amended diagnosis of the genus is provided below.

Schyzocotyle Akhmerov, 1960 (Fig. 1T,U).

Synonyms: *Bothriocephalus* Rudolphi, 1808 *in part*; *Ptychobothrium* Lönnberg, 1889 *in part*; *Coelobothrium* Dollfus, 1970; *Capooria* Malhotra, 1985.

Diagnosis: Bothriocephalidea, Bothriocephalidae. Medium-sized worms. Strobila usually with acraspedote proglottids wider than long. Proglottids separated from each other. Scolex heart-shaped; apical disc weakly developed, unarmed; bothria narrow, deep, with simple (non-crenulate) margins. Neck absent. Testes in two lateral fields, continuous between proglottids. Cirrus-sac spherical; cirrus unarmed. Genital pore median. Ovary median, transversely bilobed, compact. Vagina posterior to cirrus-sac. Vitelline follicles numerous, circumcortical. Uterine duct sinuous, usually enlarged in gravid proglottids. Uterus spherical to transversely oval, occupying most median space in terminal proglottids. Uterine pore median. Eggs operculate, unembryonated, coracidium present. In freshwater teleosts. Cosmopolitan (due to human introductions; most likely native to South and East Asia or Africa).

Type-species: *Schyzocotyle fluviatilis* Akhmerov, 1960 [syn. of *Schyzocotyle acheilognathi* (Yamaguti, 1934) n. comb.]; for synonyms of *S. acheilognathi* – see Kuchta and Scholz, 2007).

Other species: *Schyzocotyle nayarensis* (Malhotra, 1983) new combination (syn. *P. nayarensis* Malhotra, 1983).

Remarks: Akhmerov (1960) described *Schyzocotyle fluviatilis* n. gen. n. sp. from specimens found in the redfin, *Pseudaspius leptocephalus* (Pallas, 1776) (Cyprinidae), from Petropavlovsk Lake in the Far East of Russia, but erroneously placed the genus in the family Cyathocephalidae of the order Spathebothriidea, because Akhmerov (1960) misinterpreted the scolex morphology of the species (he reported the bothria to open on the apex of the scolex; see Fig. 3.1 in his paper). Dubinina (1982) synonymised the species with *B. acheilognathi*, thus invalidating *Schyzocotyle*. However, she did not consider the conspicuous difference in scolex morphology between *B. acheilognathi* and other species of *Bothriocephalus*, which possess an elongate scolex with shallow, long bothria (Kuchta et al., 2008b).

In addition to its phylogenetic position within the Bothriocephalidae as a lineage distantly related to any other group including other species of *Bothriocephalus*, the genus *Schyzocotyle* is newly characterised morphologically by the possession of a heart-shaped scolex with a weakly developed apical disc and narrow, deep bothria. Cyprinid fishes are the most appropriate hosts for its species but *S. acheilognathi* has colonised hosts of a wide range of fish orders and families throughout the world (Scholz et al., 2012).

3.4. Analysis of morphological and biological characters

From 22 morphological characters that we scored and mapped onto the consensus topology [see Fig. 1 and 3, Supplementary Fig. S5; a consensus topology based on the ML estimate of the concatenated dataset was generated by collapsing statistically poorly supported (either <70 ML bootstraps or <95 BI PP) internal nodes and nodes not consistently found across single-gene ML analyses], only Character 6 (describing the longitudinal position of the genital pore) proved to be of phylogenetic utility. While all members of the family Bothriocephalidae exhibit genital pores that are median, the earliest diverging clades (i.e. paraphyletic Triaenophoridae and Philobythidae), exhibit marginal genital pores and the paraphyletic Echinophallidae exhibit submarginal genital pores (Figs. 1I, L, R, 2). Embryonated and unoperculate (or membranous) eggs (Characters 19 and 21, respectively) are present in species of some of the early diverging triaenophorid lineages (Clades A, B and D, and Clades A and D, respectively; Fig. 1), but they are also present in the relatively derived bothriocephalid taxa, i.e. *Ptychobothrium*, *Tetracampos* Wedl, 1861 (both characters) and *Polyonchobothrium* Diesing, 1854 (Character 19). Furthermore, early diverging Clades B and D are unique in lacking a ciliated embryophore, i.e. coracidium (Character 22, Supplementary Fig. S5). However, the state of this ontogenetic character remains unknown for a significant number of bothriocephalideans. Clades A–C are further characterised by having an internal seminal vesicle (Character 14, Supplementary Fig. S5), but this character is again not exclusive to these clades and is also found elsewhere within the Echinophallidae (*Parabothriocephalus gracilis* Yamaguti, 1934) and Bothriocephalidae (*Anantrum* spp., *Bothriocephalus manubriformis* and *Kirstenella gordoni* Kuchta in Kuchta et al., 2012).

In terms of aquatic habitat use, taxa in Clades A, C and I are exclusively restricted to hosts that occur in freshwater habitats (Character 23), the remaining bothriocephalideans [with the exception of *Bathybothrium rectangulum* (Bloch, 1782), *Eubothrium rugosum* (Batsch, 1786), *Eubothrium salvelini* (Schrank, 1790), *E. tulipai* Ching & Andersen, 1983] are marine or migrate between sea and freshwaters with their hosts [*B. claviceps*, *B. travassosi*, *E. crassum* (Bloch, 1779), *E. fragile* (Rudolphi, 1802)]. Most of the marine triaenophorids and echinophallids specialised to pelagic, mainly bathypelagic fish (Clade E, *Anchistrocephalus*, *Anonchocephalus, Philobythoides* sp.), whereas all the marine bothriocephalids utilise coastal or reef demersal fish, with the exception of *B. manubriformis* from pelagic fish.

4. Discussion

The results of our analyses challenge the current family-level classification of Bothriocephalidea while confirming the importance of genital pore position as a morphological trait that may have reflected the evolutionary history of the order at the level of families. Among bothriocephalideans, genital pore position occurs in three discrete states (Fig. 2). It is plausible to assume that early diverging groups possessed a marginally (laterally) placed genital pore that, after the cladogenesis of all triaenophorid bothriocephalideans, probably shifted to a submarginal (sublateral) position in echinophallids. Later on, the genital pore shifted to a median position, forming an autapomorphy of the most derived bothriocephalidean family (Fig. 2; Character 6 in Supplementary Fig. S5).

Gulyaev (2002) argued that genital pore position represents one of the key characters, if not the key character, for reconstructing the evolutionary history of cestodes. However, the shift in genital pore position is a relatively unique event among cestodes and, with only a few exceptions, genital pore position does not vary among taxa within orders. Most early diverging cestode orders (Caryophyllidea, Diphyllidea, Diphyllobothriidea, Spathebothriidea) have median genital pores, whereas marginal, occasionally submarginal, genital pores are typical of the acetabulate orders. Exceptions include the Mesocestoididae which have median genital pores and the bothriate orders Trypanorhyncha and Litobothriidea, which have marginal genital pores except for the trypanorhynchan family Tentaculariidae, which has submarginal pores (Caira et al., 2014).

Most bothriocephalideans are relatively uniform in strobilar morphology and, thus, even slight differences in the scolex morphology have been employed to distinguish genera (see Kuchta et al., 2008b; Fig. 1). However, it now seems clear that similarities in scolex morphology among some taxa (see, e.g., Fig. 1M–O, V) may have arisen through convergent evolution. Similar situations have been described in several other cestode groups such as the Caryophyllidea (e.g., Barčák et al., 2014; Hanzelová et al., 2015), Proteocephalidea (e.g., Scholz et al., 2013; de Chambrier et al., 2015) and some lineages of the paraphyletic 'Tetraphyllidea' (e.g., Caira et al., 2014).

The basal position of Clades A–C seems to be firmly established. This, again, corresponds to the opinions of Gulyaev (2002), who considered the Triaenophoridae to represent the most basal family of the 'Pseudophyllidea'. Contrary to that, Protasova (1977) considered *Triaenophorus* and *Eubothrium* as the most derived lineages. In the analyses of ssrDNA (Supplementary Fig. S1), freshwater species of *Triaenophorus* (Clade C) appeared as the earliest divergent lineage. This genus was already considered the most basal taxon by Lönnberg (1897) and Nybelin (1922), while Freeman (1973) reserved the most basal position for *Marsipometra* (Clade A in the present study), together with *Eubothrium* and the diphyllobothriidean *Cephalochlamys* from clawed frogs. Clade B in our analyses corresponds to the subfamily Abothriinae proposed by Nybelin (1922) to accommodate 'pseudophyllidean' taxa with unoperculate and embryonated eggs from marine gadiform fish (species of *Abothrium* and *Parabothrium*) and freshwater cyprinids (*Bathybothrium*) in the northern hemisphere.

Mapping morphological characters that are typically employed in the systematic studies of the Bothriocephalidea (Kuchta, R., 2007. Revision of the paraphyletic "Pseudophyllidea" (Eucestoda) with description of two new orders Bothriocephalidea and Diphyllobothriidea. Ph.D. Thesis. Faculty of Biological Sciences, University of South Bohemia, České Budějovice, Czech Republic; Kuchta et al., 2008b) onto the bothriocephalidean phylogeny failed to reveal characters that might represent synapomorphies of clades at the family level. This is also valid for egg morphology and uterine shape (both considered as key characters in previous studies, e.g., Protasova, 1974, 1977; Bray et al., 1994; Kuchta et al., 2008b). However, traits such as egg morphology and the presence of a ciliated embryophore during ontogeny (Characters 19, 21 and 22 – see Supplementary Fig. S5) characterise some of the clades/subclades. Although these characters remain to be evaluated in a significant proportion of bothriocephalidean species, both the absence of a ciliated embryophore (Character 22) and the egg operculum (Character 21) are typical of a large number of members of the earliest diverging clades and may represent plesiomorphic states (Figs. 1–3).

Although the degree of congruence between host and parasite phylogenies has not been explicitly tested, our results suggest that host-parasite co-phylogeny has not played a major role in the evolutionary history of these cestodes. For example, ancient hosts, such as bichirs and arowanas (Osteoglossidae), serve as definitive hosts for some of the most derived bothriocephalidean taxa (*Polyonchobothrium*, *Senga*). In contrast, morphologically divergent groups that inhabit the same aquatic realm (freshwater versus marine) and zoogeographical regions, in the case of freshwater taxa (Ethiopian and Nearctic regions), host phylogenetically closely related cestodes.

It is also important to note that 16 of the 48 valid bothriocephalidean genera are missing from the current dataset. Most of these are monotypic and because they parasitise rarely sampled hosts, their tissues are difficult to obtain (see Kuchta et al., 2008b). Only two of the missing genera, both of which are monotypic and belong to the family Triaenophoridae, occur in freshwater, namely *Ailinella* Gil de Pertierra & Semenas, 2006 and *Galaxitaenia* Gil de Pertierra & Semenas, 2005, both from Patagonian galaxiids. Since these genera are the only Neotropical representatives of the Bothriocephalidea, knowledge of their interrelationships with other bothriocephalideans might provide important information concerning the geographic distribution and radiation of the order.

Species of the other 14 genera missing in the analyses differ mainly in their scolex morphology (see Kuchta et al., 2008b). Additional sampling is thus important to uncover whether convergent evolution of unique morphological characters, especially those related to the scolex, has occurred within the cestodes. Further missing genera include the following marine forms: triaenophorids from bathypelagic and bathydemersal fish (species of *Australicola* Kuchta & Scholz, 2006, *Eubothrioides* Yamaguti, 1952, *Kimocestus* Kuchta, Scholz & Bray, 2008, *Philobythos* Campbell, 1977, *Pistana* Campbell & Gartner, 1982, *Pseudeubothrioides* Yamaguti, 1968), pelagic swordfish (*Fistulicola* Lühe, 1899) and coastal reef fish (*Metabothriocephalus* Yamaguti, 1968), echinophallids from coastal and pelagic fish (*Mesoechinophallus* Kuchta, Scholz & Bray, 2008, *Pseudamphicotyla* Yamaguti, 1959), and bothriocephalids from coastal or pelagic fish (*Andycestus* Kuchta, Scholz & Bray, 2008, *Plicatobothrium* Cable & Michaelis, 1967, *Plicocestus* Kuchta, Scholz & Bray, 2008, *Taphrobothrium* Lühe, 1899).

Despite the limitations identified above, it seems apparent that the Bothriocephalidea is composed of a larger number of molecularly well-defined clades than traditional views would suggest. Most lack morphological synapomorphies and instead can be defined unequivocally only by a combination of non-unique biological and ecological characteristics. In some cases, these clades include taxa from unrelated hosts and different aquatic environments. As a consequence, future efforts must be focused on finding novel morphological, biological and ecological traits, in addition to resampling representatives of genera not yet molecularly characterised. Meanwhile, the search for molecular markers capable of adding resolution and stability to the internal nodes continues. Available evidence suggests that many of the major cladogenetic events within the Bothriocephalidea have failed to leave their mark on the morphology, biology, host associations or distribution of these parasites.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ijpara.2015.05.006.

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