A DIGEST OF FISH TAPEWORMS

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ABSTRACT. – Members of the following seven of a total of 19 cestode orders mature in ray-finned fishes (Actinopterygii): Amphilinidea (mainly in acipenseriforms and osteoglossiforms; 8 species in 6 genera), Bothriocephalidea (in several freshwater and marine fish groups; 129/47), Caryophyllidea (mainly in cyprinids and suckers, also in some catfishes; 117/42), Haplobothriidea (exclusively in bowfin; 2/1), Nippotaeniidea (in osmeriforms and perciforms; 6/1), freshwater Onchoproteocephalidea (mainly in catfishes 194/55), and Spathebothriidea (in several freshwater and marine fish groups; 6/5). Updated information on species diversity, host associations, interrelations and geographical distribution is provided for every group. The existing phylogenetic hypotheses suggest that tapeworms colonized ray-finned fishes several times and form several independent lineages. From a total of 461 fish tapeworms only 92 species are exclusively marine. So, freshwater species dominate the assemblage. No general patterns in host use can be observed at the level of fish definitive hosts because cestodes of fishes occur in not closely related host groups. Nevertheless, only three fish orders host almost three fourth of all tapeworms of fishes, namely Siluriformes (36 % of all cestode species), Cypriniformes (22 %) and Perciformes (16 %). Nearly two thirds (61 %) of fish tapeworms have a strict (oioxenous) specificity and one third (33 %) is stenoxenous. The highest proportion (8 %) of euryxenous species is among the bothriocephalideans, including one of the most opportunistic fish helminth, the invasive Asian fish tapeworm (*Schyzocotyle acheilognathi*), which has been reported from more than 200 fish species and axolotl, snakes and birds. Tapeworms of fishes are more diverse in the temperate zones of the northern hemisphere (Nearctic and Palearctic regions with 26 % and 23 % of all species) than in the tropics, with the exception of onchoproteocephalideans in South America (together with a very few other tapeworms represent 29 % of all species). However, this may reflect a lower sampling effort in tropical regions and the southern hemisphere. Caryophyllideans dominate in the Australasian (58 % of all species, but only 12 species found) and Nearctic (56 % of all species) regions, and together with oncoproteocephalideans in the Ethiopian (both 41 %; n = 39), Palearctic (both 37 %; n = 90) realms, and with bothriocephalideans in the Oriental realm (34 %; n = 36). The Neotropical region is dominated by onchoproteocephalideans (in fact almost exclusively members of the family Proteocephalidae; n = 112), which represent as many as 95 % of all species reported. The major part of the undescribed diversity of fish tapeworms regarding the total number of species can be expected in the latter region, but this concerns only a single cestode family, Proteocephalidae (order Onchoproteocephalidea).

INTRODUCTION

Tapeworms or cestodes (Platyhelminthes: Cestoda) are obligatory parasites that mature and sexually reproduce almost exclusively in the intestinal tract of all major groups of vertebrates (Khalil et al. 1994). With relatively few exceptions, a typical cestode is elongate, white or whitish, polyzoic, *i.e.* composed of a series of body parts called ‘proglottids’ that consecutively contain progressively maturing reproductive organs. This part of the body is called ‘strobila’ and more posterior proglottids are more mature, with egg-bearing proglottids called gravid always being more posterior than mature or hermaphroditic ones. The anterior end, which is attached to the host intestinal mucosa, is called the ‘scolex’; it is usually followed by the neck region or proliferative zone (Caira et al. 2012).

Recent collaborative efforts focused on mapping the global cestode diversity, and funded by the National Science Foundation-Planetary Biodiversity Inventory project “Tapeworms from vertebrate bowels of the earth”, resulted in the accumulation of previously unattainable amounts of new morphological and molecular data, covering a large part of taxonomic diversity of these parasitic flatworms (Caira & Jensen 2017). In the present account, major cestode groups, *i.e.* orders (see Khalil et al. 1994), that include species maturing in ray-finned fishes (Actinopterygii; furthermore called ‘fishes’) are reviewed with focus on their diversity and host associations. The present survey is inspired by an account by Caira & Jensen (2014) on cestodes of elasmobranchs (sharks and rays) and follows the same structure and focus, with only minor modifications that reflect differences between elasmobranch and fish tapeworms. Unlike Caira & Jensen (2014), the new order Onchoproteocephalidea Caira, Jensen, Wae-schenbach, Olson & Littlewood, 2014 is not considered in its whole extent for practical reasons, just the part cor-

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responding to the former order Proteocephalidea Mola, 1928, *i.e.* the family Proteocephalidae La Rue, 1911, which does not include taxa parasitizing elasmobranchs as adults.

**TAPEWORMS OF RAY-FINNED FISHES**

The first adult tapeworms from fishes were described as early as 1776 for marine taxa (*Taenia scorpii* Müller, 1776, now *Bothriocephalus scorpii*) and just 3 years later for freshwater taxa (*Taenia crassa* Bloch, 1779, now *Eubothrium crassum*). In total, 14 species were described during the 18th century, but most species of fish tapeworms were described during the 20th century (Fig. 1). Since 2000, the number of new species has been relatively low, not considering invalid taxa that were inadequately described mainly from the Indian subcontinent (see Kuchta & Scholz 2007, Ash et al. 2011 a,b, 2012; Kuchta et al. 2008 for extensive list of synonyms). Compared to almost 1,000 tapeworm species from elasmobranchs (see Caira & Jensen 2014), the proportion of recently described species is considerably lower, partly due to a lower research effort (fewer researchers working on fish tapeworms).

We now recognise 461 species belonging to 157 genera of fish tapeworms that are accommodated in seven of the 19 currently recognized cestode orders: Amphilinidea, Bothriocephalidea, Caryophyllidea, haplobothriidea, Nippotaeniidea, Onchoproteocephalidea and Spathebothriidea (Table I). These orders do not form a monophyletic group, but most of them (except Onchoproteocephalidea and Nippotaeniidea) belong to earlier evolved cestode lineages (Caira et al. 2014). Information on individual species and genera can be found in the Global Cestode Database (Caira et al. 2012), which also contains an extensive bibliography of taxonomic accounts on tapeworms. More detailed information is presented in a monograph edited by Caira & Jensen (2017), which summarizes main achievements of an NSF-PBI funded project.

Out of the seven orders listed above, four are species-poor, none of them exceeding 10 species (Table I). Since very few species of these minor orders have been described over the past several decades, discovery of many additional taxa seems unlikely. In contrast, the number of recently described species in species-rich orders, *i.e.* Caryophyllidea, Bothriocephalidea and Onchoproteocephalidea, is higher and it is probable that species diversity in these groups is considerably underestimated. This is valid mainly for fish cestodes in the Neotropical region (Proteocephalidae) and the Nearctic region (all three orders – see below).

Fishes also serve as intermediate or paratenic hosts of tapeworm larvae called, generally, metacestodes (see Chervy 2002). However, it is beyond the scope of this review to deal with cestode larvae from fishes, which belong to several cestode orders such as (listed alphabetically) Cyclophyllidea (family Gryporhynchidae), Diphyllobothriidea, Haplobothriidea, Lecanicephalidea, Onchoproteocephalidea, Phyllobothriidea, Rhinebothriidea, ‘Tetraphyllidea’ and Trypanorhyncha (Williams & Jones 1994, Scholz et al. 2004, Caira & Jensen 2017). Instead, a survey of cestode orders with adults in fishes is provided below with brief information on (i) a brief history of every cestode order and its classification, (ii) current understanding of species diversity, host associations, distribution and evolutionary relationships, and (iii)
gaps in our knowledge and challenges for future research (prospects).

There are approximately 32,500 species of fishes (Nelson 2006). Considering that freshwaters may constitute less than 0.3 % of available global water, it is remarkable that there are more than 15,000 freshwater fish species. Similarly, the number of tapeworms parasitizing freshwater fishes is considerably higher than that of marine cestode taxa, the latter represented by a few amphilinideans and spathebothriideans, and a handful of bothriocephalideans. In contrast, the orders Caryophyllidea, Haplobothriidea, Nippotaeniidea and large part of the Proteocephalidea of the order Onchoproteocephalidea from fishes are restricted to freshwaters (Fig. 2).

**Amphilinidea Poche, 1922**

With eight species in six genera (one of these species parasitizes freshwater turtles), the Amphilinidea is one of the least species-rich orders of fish tapeworms. Scholz & Kuchta (2017) overviewed this apparently early evolved group of cestodes (Caira et al. 2014). Species of this small order markedly differ in their body plan from ‘typical’ tapeworms in possessing a dorsoventrally flattened, monozoic, leaf-like body without proglottids or any distinct scolex, even though a small sucker-like organ may be present anteriorly (Dubinina 1982, Gibson 1994a). A cirrus-sac is absent and gonopores open at or near the posterior end of the body. Unusual among cestodes is also a long, N-shaped or looped tubular uterus, which opens at the anterior end of the body. The eggs do not have an operculum and contain a decacanth larva (lycophora) with ten embryonic hooks (Rohde 1994).

**Table I.** – Numbers of species and genera of cestode orders in ray-finned fishes.

<table>
<thead>
<tr>
<th>Order</th>
<th>Total No. of species</th>
<th>No. in fish</th>
<th>Freshwater</th>
<th>Marine</th>
<th>No. of genera</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amphilinidea</td>
<td>8</td>
<td>7 (88 %)</td>
<td>6</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>Bothriocephalidea</td>
<td>131</td>
<td>129 (98 %)</td>
<td>41</td>
<td>88</td>
<td>47</td>
</tr>
<tr>
<td>Caryophyllidea</td>
<td>117</td>
<td>117 (100 %)</td>
<td>117</td>
<td>–</td>
<td>42</td>
</tr>
<tr>
<td>Haplobothriidea</td>
<td>2</td>
<td>2 (100 %)</td>
<td>2</td>
<td>–</td>
<td>1</td>
</tr>
<tr>
<td>Nippotaeniidea</td>
<td>6</td>
<td>6 (100 %)</td>
<td>6</td>
<td>–</td>
<td>1</td>
</tr>
<tr>
<td>Onchoproteocephalidea*</td>
<td>318</td>
<td>194 (61 %)</td>
<td>194</td>
<td>–</td>
<td>55</td>
</tr>
<tr>
<td>Spathebothriidea</td>
<td>6</td>
<td>6 (100 %)</td>
<td>3</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>688</td>
<td>461 (67 %)</td>
<td>359</td>
<td>92</td>
<td>157</td>
</tr>
</tbody>
</table>

*only members of the family Proteocephalidae.

Fig. 2. – Zoogeography of seven orders of tapeworms parasitizing fishes as adults (some of the 359 species of freshwater fish tapeworms occur in more than one zoogeographical realm).
In contrast, relationships of the amphilinideans with the Gyrocotyliida and remaining tapeworms (Eucestoda), as well as their classification at a higher level (genera, subfamilies and families) have been debated for long time (Bandoni & Brooks 1987, Xylander 2001). Molecular phylogenetic studies on the amphilinideans are rather scarce and the genes of four species sequenced exhibit much higher levels of divergence compared to those of other tapeworms, which makes their alignment difficult (Olson et al. 2001, Waeschenbach et al. 2007). Nevertheless, a basal position of the amphilinideans among tapeworms as one of the two of their earliest diverging groups is not questioned (Scholz & Kuchta 2017).

Unlike other tapeworms, amphilinideans occur as adults exclusively in the body cavity of their hosts that are not closely related to each other: Australian freshwater turtles, earlier diverged fishes such as sturgeons and osteoglossiform fishes (e.g. Arapaima gigas) and more recently evolved perciform teleosts (Gibson 1994a). Host specificity is relatively strict, even though Gigantolina magna (Southwell, 1915) has been reported from three families of perciform fishes (Gibson et al. 2005). Life cycles have been partly or completely elucidated in four species of three genera including one species from freshwater turtle (Janicki 1928, Rašín 1931, Dubinina 1974, Rohde & Georgi 1983, Gibson et al. 1987, Rohde 1994). The geographic distribution of the amphilinideans does not follow any general pattern: whereas two species of Amphilina occur in northern temperate zones (Holartic region), the remaining taxa occur in the southern hemisphere and the tropics (Indian Ocean and freshwaters of Australia and South America).

Ecological data on amphilinideans are relatively scarce, with by far the most detailed information existing on Amphilina foliacea (Rudolphi, 1819), a parasite of sturgeons in the Palearctic region, especially on seasonal patterns in its occurrence and maturation (Chubb 1982). Veterinary importance of the amphilinideans is negligible, but they represent one of the key groups for our understanding of the evolutionary history of tapeworms.

**BOTHRIOCHEPHALIDAE** Kuchta, Scholz, Brabec & Bray, 2008

This is one of the species-richest orders of fish tapeworms, with only two species parasitizing news in North America (Kuchta & Scholz 2007, 2017a). The order was erected by Kuchta et al. (2008a) who split the previous order Pseudophyllidea into two orders, the Bothrioccephalidea and the Diphyllobothriidea. Most bothrioccephalideans have a rather thick, medium- to large-sized strobila of rather uniform morphology including extensive vitelline follicles filling most of the cortex. Scolex morphology is one of key diagnostic features (Protasova 1977, Bray et al. 1994, Kuchta et al. 2008b).

Recent taxonomic studies that included a critical review of all bothrioccephalidean genera (Kuchta et al. 2008b) have revealed that the order currently contains 131 species in 47 genera (Kuchta & Scholz 2007, 2017a). This number is much lower than that of nominal species that appeared in the literature (350 until 2007). A high number of species have been synonymized, especially insufficiently described taxa from snakeheads (Channa spp.) and zig-zag eel (Mastacembelus armatus) in the Indian subcontinent. The order is now divided into three families that are distinguished from each other by the position of the genital pore: median in the Bothrioccephalidae, sublateral in the Echinocephalidae and lateral in the Triaenophoridae (Bray et al. 1994, Kuchta et al. 2008b, Brabec et al. 2015).

Two thirds (67 %) of the species are known from marine and one third (33 %) from freshwater fishes. As many as 51 species of bothrioccephalideans occur in the Perciformes, especially centrolophids (16 species), and in snakeheads and cyprinids (7 and 6 species, respectively) (Kuchta & Scholz 2017a; present study). Approximately one third of the species diversity is known from 14 fish families and the remaining species have been reported from additional 103 fish families with only one or two bothrioccephalidean species reported in each. Interestingly, bothrioccephalideans are almost absent in catfishes (Siluriformes; 5 species only), which are common hosts of proteocephalid cestodes (see below). Host specificity of most bothrioccephalideans is strict, with two thirds (67 %) of the species being oioxenous, i.e. known only from one fish host. Just seven species are euryxenous, occurring in fishes of different families (Fig. 3), with the widest spectrum of definitive hosts (~ 30 species of marine teleosts) in Clesitobothrium crassiceps (Rudolphi, 1819) and the invasive Asian fish tapeworm, Schyzocotyle acheilognathi (Yamaguti, 1934) (syn. Bothrioccephalus acheilognathi), which has been reported from more than 200 species of freshwater fishes (Scholz et al. 2011a, Kuchta & Scholz 2017a).

The prevalence and intensity of infection with bothrioccephalideans vary considerably, but are generally low (prevalence usually below 10 %), with some notable exceptions, with prevalence up to 100 % and intensity of infection up to 1,000 individuals per host (Kuchta & Scholz 2017a). Life cycles have been at least partly elucidated in 11 species of the genera Bathybothrium Lühe, 1902 (1 species), Bothrioccephalus Rudolphi, 1802 (3 spp.), Eubothrium Nybelin, 1922 (3), Schyzocotyle Akhermov, 1960 (1) and Triaenophorus Rudolphi, 1793 (3 spp.) (Protasova 1977). In all cases, cestodes serve as first and usually only intermediate host. Second or paratenic hosts may be also involved, but three-host life cycle has been experimentally confirmed only in species of Triaenophorus (see Kuperman 1973).

Marine bothrioccephalideans have been found in the Atlantic (45 species), Pacific (41) and Indian (21) Oceans,
but it is probable that a lower number of species reported from other oceans reflects a lower sampling effort rather than the actual paucity of these cestodes. In freshwaters, 18 species are known from the Palearctic, 12 from Oriental, 11 from Nearctic and six from Ethiopian regions. Surprisingly, very few bothriocephalideans are known from the Neotropical region (4 species; almost exclusively out of the most diverse tropical Amazon and Paraná River basins), whereas the occurrence of only two species of bothriocephalideans in the Australian realm apparently corresponds to the depauperate fauna of freshwater fishes in this region. The cestode fauna of the Oriental (Indomalayan) region is less known and probably not extraordinarily species-rich, even though the literature is

Fig. 3. – Host specificity and host spectrum of fish tapeworms with more detailed data on the three largest orders (Bothriocephalidea, Caryophyllidea and Onchoproteocephalidea – family Poteocephalidae).

Graphs below:

Host spectrum of all fish tapeworms by frequencies of 36 fish orders. Fish icons showing the most common fish orders. Clockwise from the right (blue): Siluriformes (white icon), Cypriniformes (white icon), Perciformes (white icon), Osmeriformes (white icon), Gadiformes, Gadidae, Boletidae, Bovichtidae, Cepolidae, Citharidae, Clupeidae, Distichodontidae, Eurypharyngidae, Gymnotidae, Holocentridae, Channichthyidae, Istiophoridae, Lateolabracidae, Lotidae, Malacanthidae, Mastacembelidae, Monacanthidae, Moridae, Muraenesocidae, Notacanthidae, Nototheniidae, Osmeridae, Osphronemidae, Osteoglossidae, Perciformes, Percopsidae, Scombridae, Serranidae, Sisoridae, Stomatomidae, Terapontidae.

Host spectrum of the bothriocephalideans by frequencies of 97 reported fish families. Fish icons show the most common fish orders. Clockwise from the right (blue): Centriscidae, Channidae, Cyprinidae, Synodontidae, Merluccidae, Percidae, Bovichtidae, Anguillidae, Siluridae, Ictaluridae, Auchenipteridae, Clariidae, Lepisosteidae, Centrarchidae, Cichlidae, Nemacheilidae, Percidae, Bagridae, Cyprinidae, Doradidae, Erythrinidae, Gasterosteidae, Gymnotidae, Hepatapteridae, Salmonidae, Amblyopsidae, Cetopsidae, Claroteidae, Cobitidae, Malapteruridae, Mochokidae, Osmeridae, Serrasalmidae, Schilbeidae, Atherinopsidae, Catostomidae, Centrarchidae, Cyprinodontidae, Elopidae, Fundulidae, Gobiidae, Goodeidae, Characidae, Nemacheilidae, Poeciliidae, Siluridae, Terapontidae.

Host spectrum of the caryophyllideans by frequencies of 12 reported fish families. Fish icons show the most common fish orders. Clockwise from the right (blue): Catostomidae, Cyprinidae, Claridae, Plotosidae, Cobitidae, Mochokidae, Heteropneustidae, Characidae, Mormyridae, Alestidae, Bagridae, Cichlidae.

Host spectrum of onchoproteocephalideans (proteocephalids) by frequencies of 47 reported fish families. Fish icons show the most common fish orders. Clockwise from the right (blue): Pimelodidae, Siluridae, Ictaluridae, Auchenipteridae, Claridae, Lepisosteidae, Centrarchidae, Cichlidae, Nemacheilidae, Percidae, Bagridae, Cyprinidae, Doradidae, Erythrinidae, Gasterosteidae, Gymnotidae, Hepatapteridae, Salmonidae, Amblyopsidae, Cetopsidae, Claroteidae, Cobitidae, Malapteruridae, Mochokidae, Osmeridae, Serrasalmidae, Schilbeidae, Aesthrotrygonidae, Ariidae, Anguillidae, Aphanidae, Atherinidae, Bryconidae, Clarichthyidae, Diplomyidae, Eleotridae, Esocidae, Gobiidae, Channidae, Loricariidae, Pangasiidae, Plecobdosidae, Polypteridae, Sisoridae, Synbranchidae, Trionychidae, Moronidae.

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littered by dozens of inadequate descriptions of more than 100 'species' of Senga Dollfus, 1934 (and related genera Circumoncobothrium Shinde, 1968 and Polyonchobothrium Diesing, 1854) from snakeheads (Channa spp.) and the zig-zag eel (Mastacembelus armatus) in the Indian subcontinent (see Kuchta & Scholz, 2007, Kuchta et al. 2008b). The shelf, epipelagic and mesopelagic fauna of marine fishes is poor, whereas bathypelagic fishes host a rather rich and morphologically peculiar fauna of bothrioccephalids, especially members of the Echinophilidae, with a number of monotypic genera (Kuchta et al. 2008b, Klimpel et al. 2009).

The recently published phylogenetic analyses of data of 59 species of 31 bothrioccephalidean genera generated for four genes revealed that species of the paraphyletic Triaenophoridae represent the earliest diverging lineages of the order, but freshwater or marine origin of bothrioccephalids remains unclear. The Echinophilidae is also paraplectic, whereas the Bothrioccephalidae is monophyletic and was revealed as the most derived clade (Brabec et al. 2015).

The species-richest genus Bothriocphalus, which includes 33 valid species according to Kuchta & Scholz (2017a), is polyphyletic, being composed from at least three not closely related freshwater and one marine lineages, the latter including the type species B. scorpii. Schyzocotyle acheilognathi, which may be pathogenic for heavily infected small fish (Scholz et al. 2011a), and only few other bothrioccephalids are of veterinary importance, such as plerocercoids (metacestodes) of species of Triaenophorus Rudolphi, 1793 and adults of the species of Eubothrium Nybelin, 1922 (see Williams & Jones 1994, Schaeble et al. 2014).

**CARYOPHYLLIDEA van Beneden in Carus, 1863**

Caryophyllidea was treated by many authors as belonging to the Pseudophyllidea (e.g. Nybelin 1922, Fuhrmann 1931). The order consists of four families, namely the Balanotaeniidae, Capingentidae, Caryophyllaeidae and Lycocotylidae (see Mackiewicz 1994). Classification at the family level is based on the position of the inner longitudinal muscle in relation to the testes and vitelline follicles (Mackiewicz 1972, 1994). Even though a high number (dozens) of inadequately described from clariid and heteropneustid catfishes in India and neighboring countries have been invalidated by Ash et al. (2011a, b), the total number of species recognized as valid (117 species in 42 genera – Scholz & Oros 2017) still makes this order the third species-richest among fish tapeworms.

Caryophyllideans are unique among the ‘true’ tapeworms (Eucestoda) in the possession of a monozoic body, *i.e.* they lack any internal and external proglottisation, with a single set of genital organs, thus resembling two ‘cestodarian’ orders, the Gyrocotyliidea and the Amphilinidea (see above). Unlike species of these two early diverged orders, caryophyllideans possess a scolex, albeit rather simple. The scolex of caryophyllideans bears shallow grooves, loculi or frills (Mackiewicz 1994, Scholz & Oros, 2017). The ovary is usually H-shaped, in the posterior part of the body. The genital pores are ventral, anterior to the ovary. Eggs are operculate and do not contain a formed embryo (oncosphere) in the uterus in all but one genus (Wenyonia Woodland, 1923).

The caryophyllideans are exclusively intestinal parasites of freshwater teleosts with 85 species reported from cypriniform and 29 from siluriform fishes. Only few species of the Lytocestus with 2 species and monotypic Lytocestoides are known from mormyrids (Osteoglossiformes), characiform and cichlid (Periformes) fishes, respectively. Within families, 40 % of caryophyllideans parasitize North American suckers (Catostomidae), 26 % cyprinids, 10 % clariid catfishes and just a few caryophyllideans have been reported from 12 additional fish families. The degree of host specificity of caryophyllideans for their fish hosts is rather variable, even within individual genera, *e.g.* in Khawia Hsü, 1935 and Caryophyllaeus Gmelin, 1790 (see Scholz et al. 2011b, unpubl. data). In addition, there is a number of doubtful host records that cannot be verified due to the absence of voucher specimens for scrutiny. This is mainly a problem in the Indomalayan Region (Ash et al. 2011a, b, 2012), but also into some extent in North America (see Hoffman 1999).

Nevertheless, the caryophyllideans seem to be rather host specific with more than a half of caryophyllideans being oioxenous and almost another half stenoxenous, with only 4 species reported from different host families, *i.e.* euryxenous.

Freshwater annelids of the family Naididae, especially species previously placed in the Tubificidae (Tubifex tubifex, Limnodrilus spp.), serve as only intermediate hosts (Mackiewicz 1972, Demshin 1975). Larvae (plerocercoids) of some species, *e.g.* Archigetes sieboldi Leuckart, 1878, may be progenetic, *i.e.* precociously produce eggs in intermediate host. As evidenced by Olson et al. (2008), this progenetic development represents a secondary reduction of the life cycle, not plesiomorphic condition of procestodes. Rate of infection with caryophyllideans varies among species and fluctuates considerably during year, especially in temperate zones with conspicuous seasonality in the occurrence and maturation (Chubb 1982).

Caryophyllideans are common parasites of freshwater teleosts in the Nearctic (57 species), Palearctic (33), Ethiopian (16) and Indomalayan (12) zoogeographical regions; 7 species have been reported from the Australasian realm (Mackiewicz 1972, Scholz & Oros 2017, present study). Interestingly, caryophyllideans do not occur in the Neotropical region (a very few published records are unreliable and cannot be verified as no vouchers are preserved – Rego et al. 1999; records from the introduced carp in cultures are not considered). The absence of caryophyllideans in the Neotropics is most probably related to the
lack of suitable fish definitive hosts (potential intermediate hosts, i.e. naïdids, occur in South America – Harman et al. 1988). Even though the fish fauna of South America is rich in catfishes (Froese & Pauly 2017), no groups of siluriforms related to those that harbour caryophyllideans in the Afrotropical, Australian and Oriental regions (e.g. Bagridae, Claridae, Heteropneustidae, Mochokidae, Tandainidae, etc.) are present there.

Molecular phylogenetic studies confirm monophyly of caryophyllideans, but also reveal the non-monophyly of three of the four families (the family Balanotaeniidae is mono-generic) (Olson et al. 2008, Brabec et al. 2012, Scholz & Oros 2017). In contrast, most genera seem to be mono-generic) (Olson 2017). All nippotaeniideans occur in freshwater fishes of the families Eleotridae, Gobiidae, Odontobutidae (all Perciformes), Galaxiidae and Retropinnidae (Osmeriformes). The life cycle includes only one intermediate host, planktonic copepods (Yamaguti 1951, Demshin 1985, Shimazu 1997); metacestodes in copepods called plerocercoids already possess the scolex with an apical sucker.

The distribution of nippotaeniideans is considerably disjunct, with three species occurring in eastern Asia (China, Japan, eastern Russia) and three endemic to New Zealand (Hine 1977, Bray 1994, Scholz et al. 2017). Nippotaenia perccotti (Akhermov, 1941) from the Chinese sleeper, Percottus gleni, erroneously identified as Nippotaenia sogmarda Yamaguti & Miyata, 1940 in the literature, is an invasive species that has expanded its range from its original distribution area in eastern Asia to eastern and central Europe (Koštufová et al. 2008, Scholz et al. 2017).

The position of the Nippotaeniidea among cestodes has been a matter of discussion, but molecular data provide a strong evidence of a close relation of this order to the so-called ‘higher tetrafossates’ of Olson & Tkach (2005), i.e. the Tetrabothriidea, Mesocestoididae and Cyclophyllidea (see Waeschenbach et al. 2012, Cairà et al. 2014). At present, sequence data are available for four of the six known species of the order (Scholz et al. 2017).

**NIPPOTAENIIDEA Yamaguti, 1939**

This is another species-poor order of exclusively freshwater fish tapeworms, with only six recognized species that are currently placed in a single genus, *Nippotaenia* Yamaguti, 1939 (the genus *Amurotaenia* Akhermov, 1941 was not recognized as valid by Scholz et al. 2017). Because of a unique morphology of the scolex of *N. chaenogobii*, which possesses a single apical sucker, the order has been generally accepted (Khalil et al. 1994). Nippotaeniideans are small- to medium-sized tapeworms with a cylindrical body; some species are hyperapolytic. The genital pore is sublateral, pre-equatorial. The vitellarium is compact, composed of two lobes. The uterus forms transverse loops in the medulla. The eggs are spherical, three-layered, with fully formed hexacanth when released in water (Shimazu 1997).

**HAPLOBOTHRIIDEA Joyeux & Baer, 1961**

This is by far the smallest cestode order because it contains only two species in one genus; in addition, validity of *Haplobothrium bistrobilae* Premvati, 1969 is questionable (Kuchta & Scholz 2017b). The order is closely related to the Diphyllobothriidea by morphological (Jones 1994), ultrastructural (MacKinnon & Burt 1985) and molecular (Waeschenbach et al. 2007) data. Haplobothriideans possess several unique traits, such as a primary and secondary strobila as a result of peculiar asexual reproduction, a primary scolex with evertible tentacles (not homologous with those of the Trypanorhyncha), a secondary scolex with bothrium-like attachment grooves, and an armed cirrus (Kuchta & Scholz 2017b). The eggs of *Haplobothrium* spp. are operculate and embryonated in the uterus.

Both species of the order are specific to a freshwater relict fish host, bowfin, *Amia calva*, the only extant member of the order Amiiformes (Holostei), which occurs only in USA and a small portion of Canada. The life cycle of the type species, *H. globuliforme* Cooper, 1914, includes three hosts: a copepod that eats a freely swimming, ciliated larva called ceracidium (similar to that of some bothrioccephalideans and diphyllobothriideans), a freshwater teleost that hosts plerocercoids in its liver, and bowfin that becomes infected after predation on infected second (fish) intermediate host (Essex 1929, Thomas 1930, Meinloth 1947).

**ONCHOPROTEOCEPHALIDEA Cairà, Jensen, Waeschenbach, Olson & Littlewood, 2014**

(Previously Proteocephalidea Mola, 1928 – in part)

Molecular phylogenetic analyses demonstrated close relationships of cestodes of the order Proteocephalidea, which contains largely tapeworms parasitising freshwater teleosts with some members of the ‘tetrathyridian’ family Onchobothriidae. Therefore, Cairà et al. (2014)
proposed a new order Onchoproteocephalidea to include the former order Proteocephalidea and genetically related, but morphologically distinct onchobothrid genera. In the present account, focus will be given just on those taxa of the Onchoproteocephalidea that parasitize fishes, i.e. great proportion of members of the previous order Proteocephalidea, which includes just a single family, Proteocephalidae. Therefore, we will refer to proteocephalids (instead of onchoproteocephalideans) in the following text. Proteocephalids are also parasites of reptiles and amphibians, and one species was described from marsupials (de Chambrier et al. 2017).

A recent overview of this group by de Chambrier et al. (2017) reports 318 species in 67 genera of proteocephalids, which makes the Onchoproteocephalidea the species-richest order among cestodes as to the number of species parasitizing fishes. Despite great progress achieved over the last decade (de Chambrier et al. 2017), the current knowledge of proteocephalid diversity remains insufficient. The number of still undescribed species is likely high, in particular in the Neotropical Region (de Chambrier et al. 2015a, 2017); also North American proteocephalids are in serious need of revision (Scholz & Choudhury 2014).

The Proteocephalidae is composed of a number (usually 13) of subfamilies (see de Chambrier et al. 2017), which are differentiated from each other mainly by the position of genital organs (testes, ovary, vitellarium and uterus) in relation to the inner longitudinal musculature (Rego 1994, 1995). Proteocephalids are typified by possessing a scolex bearing four spherical to elongate, usually uniloculate (rarely bi- or triloculate) suckers. The scolex possesses an apical concentration of gland cells, a functional or vestigial apical sucker or a rostellum-like muscular organ with hooks that is arguably homologous with the rostellum of cyclophyllideans (Scholz et al. 1998, Caira & Jensen 2014, Ash et al. 2015, de Chambrier et al. 2017). Genital pores open into a genital atrium on the lateral margin of proglottids. The vitellarium forms two bands of follicles lateral to the testes. The uterus forms lateral diverticula and contains usually spherical eggs with a hyaline membrane that swells in the water to enable the eggs to float (Freze 1965, Scholz 1999).

Catfishes (Siluriformes) are the principal definitive hosts (69%; i.e. 133 species from fishes), followed by percoform (with 16 spp.), cypriniform and characiform fishes (5 spp. in each). Fishes of few other fish orders are involved (Fig. 3). In the case of fish families, the most dominant are pimelodid catfishes distributed in the Neotropics with 69 species, which represents 34% of species diversity, followed by silurid, ictalurid, auchenipterid and clarid catfishes (each 5%) (Fig. 3).

Hosts of almost all proteocephalids are freshwater, with just a very few species that have entered brackish waters, e.g. Proteocephalus gobiorum Dogiel & Bychowsky, 1939 in gobiids (Gobiidae) from the Black Sea and Proteocephalus chamelensis Pérez-Ponce de León, Brooks & Berman, 1995 from the Pacific sleeper Gobiomorus maculatus (Eleotridae) in Mexico, but no proteocephalids are known from marine hosts. Proteocephalids occur globally, but there are remarkable differences between individual zoogeographical realms. The highest number of species occurs in the Neotropical region with 106 spp. (e.g. catfishes of the families Pimelodidae and some other Siluriformes, Characiformes, Perciformes, Gymnotiformes, etc.; de Chambrier & Vaucher 1999). The proteocephalid fauna of the Palearctic (33 spp.) and Nearctic (29 spp.) regions is also rather rich, outnumbering considerably that of the Ethiopian region (16 spp.) (Fig. 2). The highest number of nominal ‘species’ of proteocephalids was in fact described from the Oriental region, especially from the Indian subcontinent (species of the genera Gangesia Woodland, 1924, Silurotaenia Nybelin, 1942 and related ‘genera’ from catfishes such as Wallago attu and Sperata senghala), but the great majority of these inadequately described taxa are synonyms of 11 valid species (Ash et al. 2012, 2015). Interestingly, the proteocephalid fauna in a large part of tropical Asia (Thailand, past Indochina, Indonesia, etc.) is very poor and no proteocephalids are known from freshwater fishes of the Australian region (de Chambrier et al. 2017).

No general pattern in the degree of host specificity can be observed in proteocephalids from fishes. Most Neotropical species exhibit oioxenous (65%) or stenoxenous (31%) host specificity (Fig. 3), whereas several taxa in the Palearctic, Nearctic and Ethiopian regions are stenoxenous or even euryxenous (Freze 1965, Schmidt 1986, Scholz & Hanzelová 1998, de Chambrier et al. 2017). Most strange is the host specificity of Testudotaenia testudo (Magath, 1924), which was confirmed to occur in softshell turtle Apalone spinifera and the bowfin Amia calva (see de Chambrier et al. 2009). Prevalence of infection with proteocephalids may be high, even 100% in some cases, but fluctuates usually between 10-25% (de Chambrier & Vaucher 1999, de Chambrier et al. 2006, 2015a). In contrast, intensity of infection is generally low, with just a few specimens in a single host. A notable exception is the record of more than 12,000 tapeworms of seven species from the pimelodid catfish Phractocephalus hemioliopterus in Brazil; the dominant species, which is 2.0-8.5 mm long, was represented by 10,641 individuals (Ruedi & de Chambrier 2012). Veterinary importance of proteocephalids is low, with only a few species reported as potential pathogens of cultured fish, such as Proteocephalus longicollis (Zeder, 1800) (syns. P. exiguus La Rue, 1911 and P. neglectus La Rue, 1911) in cultures of rainbow trout (Oncorhynchus mykiss) in Europe (Williams & Jones 1994).

Collaborative efforts over the past several decades made it possible to update generic diagnoses of as many as 54 of the currently recognized 67 genera, including some taxa specific to reptilian hosts (de Chambrier & Chambrier, 2017, 67 (2)
The current classification of subfamilies is artificial because most subfamilies are not monophyletic neither are most species-rich genera, and a better circumscription is pending. This task is complicated by the lack of morphological and other autapomorphies of individual lineages due to a high degree of homoplasy of characters previously used in the taxonomy of proteocephalids, especially position of reproductive organs in the cortex and medulla and scolex morphology (Scholz et al. 2013, de Chambrier et al. 2015b, 2017). It seems that the Acanthotaeniinae (parasites of reptiles throughout the world) or Gangesiinae (specific to catfishes in Asia) are the earliest lineages, but neither of them is monophyletic. Whereas the fauna of proteocephalids in the Palearctic seems to include closely related taxa, Nearctic proteocephalids belong to several lineages not closely related to one another, including those belonging to the most recently evolved superclade comprising largely Neotropical taxa from catfishes (de Chambrier et al. 2015b). African taxa are monophyletic (except for Sandonella sandoni [Lyndale, 1960] of the monotypic Sandonellinae), even though they were classified in four genera of three different subfamilies (de Chambrier et al. 2015b). Neotropical proteocephalids are non-monophyletic and their interrelations remain unresolved (de Chambrier et al. 2015b, 2017).

**SPATHEBOTHRIIDEA Wardle & McLeod, 1952**

This small order, which includes only six species in five genera from marine and freshwater fishes, has been recently reviewed by Kuchta et al. (2014) and Kuchta & Scholz (2017c). The authors concluded that it may be a relictual group that was once diverse and widespread. Its members are in four monotypic genera and share peculiar morphological traits, but their hosts and geographical distribution do not show much commonality (Kuchta et al. 2014).

Morphologically, spathebothriideans differ from almost all tapeworms in the possession of an internally proglottised body with multiple genital complexes, but the lack of external proglottisation (Gibson 1994b, Kuchta & Scholz 2017c). Male and female genital pores are median and may alternate, being situated on the ventral or on the dorsal side of the same strobila (Protasova & Roitman 1995). Scolex morphology differs considerably across genera, with no differentiated scolex in *Spathebothrium* and a funnel-like scolex in species of the remaining genera (Kuchta et al. 2014). The eggs are operculated and those of marine species possess polar filaments (Kuchta & Scholz 2017c). Marine and freshwater amphipods (Gammaridae, rarely Mysidae) serve as intermediate hosts (Protasova & Roitman 1995). Plerocercoids in amphipods may reach sexual maturity and produce eggs, thus being progenetic (Protasova & Roitman 1995, Kuchta et al. 2014).

Spathebothriideans occur in a number of distantly related groups of fishes, such as the early evolved sturgeons (Acipenseriformes) and much more recently derived fish orders, e.g. Pleuronectiformes, Salmoniformes and Scorpaeniformes (see Protasova & Roitman 1995, Kuchta et al. 2014). Species of three genera occur in fishes of a single family each, namely Bothrimonus in sturgeons, Didymobothrium in the Soleidae, and Spathebothrium in the Liparidae. In contrast, species of Cyathocephalus and Diplocotyle occur in a wide spectrum of freshwater and anadromous fishes, and in several marine groups of fishes, respectively. Species of three genera have an Arctic and subarctic distribution, whereas Bothrimonus occurs in the Caspian Sea and Didymobothrium in the Mediterranean Sea (Protasova & Roitman 1995, Marques et al. 2007, Kuchta & Scholz 2017c). Prevalence of infection generally fluctuates around 20 %, but may reach in exceptional cases up to 100 % (Kuchta et al. 2014).

It seems that the spathebothriideans evolved more recently than the monozoic caryophyllideans (Olson et al. 2001, Waeschenbach et al. 2007, Caira & Jensen 2017). Molecular data also indicate that the spathebothriideans originated in marine hosts whereas the taxa occurring in freshwaters are more derived. The marine *Spathebothrium simplex* Linton, 1922, which bears undifferentiated scolex, appears to be the earliest diverging extant taxon of the order (Kuchta et al. 2014). The veterinary importance of spathebothriideans is negligible, except for *Cyathocephalus truncatus* (Pallas, 1781), which has been reported to cause mortality of heavily infected salmonids (Protasova & Roitman 1995).

**PHYLOGENETIC RELATIONSHIPS**

Tapeworms that mature in fishes do not form a monophyletic group. Instead, they belong to several more distantly related lineages that are scattered throughout the phylogenetic tree of cestodes without any obvious pattern (Caira et al. 2014). This indicates that fishes have been colonized by cestodes independently several times. Molecular phylogenetic analyses revealed all but one of the orders of fish tapeworms as monophyletic, but their position among the Cestoda and interrelations with other cestode groups remain uncertain due to a generally low support for basal nodes of the cestode tree (Waeschenbach et al. 2007, 2012). Nevertheless, the Bothriocephalidea seem to be the most evolved groups of bothriate cestodes, whereas proteocephalids belong, together with elasmobranch tapeworm genera with which they form the new order Onchoprotocephalidea, among large and insufficiently resolved lineages of ‘Tetraphyllidea-like’ tapeworms (Caira et al. 2014). In contrast, the position of the Nippotaeniidea, which is unique among tapeworms in possessing a scolex with a large apical sucker as the principal organ of attachment, seems to be well resolved.

Most recent molecular data (Waeschenbach et al. 2012, Caira et al. 2014) have confirmed the general scenario of cestode evolution outlined by Olson et al. (2001), i.e. basal position of two small orders that possess a larva called lycocephora, which contains a decacanth, i.e. embryo with 10 embryonic hooks. In most analyses, the Gyrocotylidea, which includes 10 species in one genus that parasitize holocephalans (chimaeras or rat fishes — Gibson 1994c, Kuchta et al. 2017), was revealed as the earliest evolved group followed by the amphilinideans, with which they were placed in the Cestodaria based on the possession of a decacanth larva. However, monophyly of this subclass has not been supported. In addition, the position of the amphilinideans among cestodes remains uncertain, especially because of extraordinary divergence of their nuclear ribosomal genes (Waeschenbach et al. 2007).

Members of the smallest cestode order, Haplobothriidea, invariably form a sister group to the Diphyllobothriidea (Brabec et al. 2006, Waeschenbach et al. 2007, 2012). However, the haplobothriideans are kept as a separate order because of their peculiar morphology, life cycle and evolutionary ancient definitive hosts (Kuchta et al. 2008a, Kuchta & Scholz 2017b).

Whereas the caryophyllideans, spathebothriideans, and to some extent also haplobothriideans, appear to be closely related, the remaining groups parasitizing fishes are apparently not closely related to each other. The evolutionary history of cestodes was reflected in the development of attachment organs on the anterior end called the scolex (Caira & Jensen 2014). The anterior end of members of the earliest evolved groups such as the gyrocotylideans, amphilinideans, some spathebothriideans (Spathebothrium) and caryophyllideans is devoid of sophisticated attachment structures. Species of more recently evolved groups including the bothrioccephalideans and haplobothriideans called bothriates possess paired attachment grooves, bothria, whereas the most recently derived cestode orders including the proteocephalids and nippo- taeniideans have acatabulate attachment structures, i.e. bothridia or suckers (Olson et al. 2001, Caira & Jensen, 2014).

KEY MORPHOLOGICAL FEATURES

There are no specific morphological features shared by all members of the seven orders that include parasites of fishes. The principal groups of fish tapeworms even differ from each other in key characteristics such as mono- zoic (2 orders) and polyzoic body plan (5 orders), external proglottization (absent in 3 orders), scolex type (no true scolex in 2 orders, simple scolex in 1 order, bothriote structures in 2 orders and acatabulate structures in 2 orders), form of the uterus (tubular in basal groups versus usually sacciform in more evolved orders), and egg morphology (tanned eggs in most orders, hyaline external membrane in 2 more recently derived orders). Most fish tapeworms possess a vitellarium in form of separate, usually numerous follicles, but the arrangement of vitelline follicles markedly differs between individual orders. The same is valid for the ovary and male genital organs (testes, vas deferens and cirrus-sac).

A key morphological feature in several orders of fish cestodes is the position of genital organs (testes, ovary, vitellarium and uterus) in relation to the inner longitudinal musculature. This feature was even used for circumscription of families and subfamilies in the Caryophyllidea (see Mackiewicz 1994) and Proteocephalidae (see Rego 1994). However, there is increasing evidence that this character is homoplastic, not reflecting the evolutionary history of these cestode groups (Olson et al. 2008, Brabec et al. 2015, de Chambrier et al. 2015b).

Scolex morphology is another key morphological feature that has been widely used in differentiating species and genera of fish cestodes (Schmidt 1986, Khalil et al. 1994). Even though morphology of the scolex is undoubtedly of taxonomic importance in many cestode groups, there is some recent information based on molecular data that shape of the scolex may be homoplastic, thus not reflecting actual interrelations of morphologically similar taxa (see, e.g. Scholz et al. 2013, Brabec et al. 2015, Scholz et al. 2011b for the onchoprotocehalideans, bothriocephalideans and caryophyllideans, respectively).

GENERAL HOST ASSOCIATIONS

Fish tapeworms are not restricted to a single or a few host groups as obvious from a survey of individual cestode orders hosted by fishes provided above. No general patterns in host use can be observed at the level of fish definitive hosts because cestodes of fishes occur in distantly related host groups. Nevertheless, only three fish orders host almost three fourth of all tapeworms of fishes, namely Siluriformes (35 % of all cestode species), Cypriniformes (22 %) and Perciformes (15 %) (Fig. 3).

Host associations of individual tapeworms differ even within individual genera, from strictly oioxenous to stenoxenous or even euryxenous. Nevertheless, it can be summarised that host specificity of fish tapeworms is usually strict, i.e. stenoxenous (61 % of all species) or oioxenous (33 % of species), whereas the number of euryxenous taxa is much lower (6 %). The highest proportion (8 %) of euryxenous species is among the bothriocephalideans, including one of the most opportunistic fish helminth, is the invasive Asian fish tapeworm (Schyzocotyle achenognathi), which has been reported from more than 200 fish species and even other vertebrates. In other cestode
orders, most specific seem to be onchoproteocephalideans with 65% of species oioxenous and only 4% euryxenous (Fig. 3). Even though a more reliable assessment of host associations of fish tapeworms is complicated by a high number of questionable or unreliable host records, especially of caryophyllideans in North America (Hoffman 1999), it seems that, overall, fish tapeworms exhibit somewhat less strict host specificity compared to that of elasmobranch tapeworms (Caira & Jensen 2014, 2017).

ASSOCIATIONS WITH RAY-FINNED FISHES

Adult tapeworms have been reported from fishes of 36 orders, with the highest numbers of species occurring in the Siluriformes (35% of all cestode species), Cypriniformes (22%) and Perciformes (15%) (Fig. 3). Fishes have been colonized by tapeworms independently several times because their tapeworms do not form a monophyletic assemblage. Instead they belong to several distantly related lineages of cestodes. Some host groups such as perciform fishes and catfishes (Siluriformes) are parasitized by early evolved cestodes (amphilinideans and caryophyllideans), but also more recently derived tapeworms (bothriocephalideans, proteocephalids and nippotaeniideans). It is also worth noting that even more recently derived groups such as bothriocephalideans and proteocephalids parasitize both evolutionary ancient fishes such as bichirs, sturgeons, bowfin and gars as well as members of much more recently evolved fishes, e.g. perciforms.

The widest host spectrum is in bothriocephalideans which have been reported from as many as 97 fish families. However, with the exception of Centrolophidae (10% of cestode species), Channidae (4%) and Cyprinidae (4%), all other host families are reported to harbour less than four bothriocephalidean species each (in total, more than 4/5 of bothriocephalidean taxa – Fig. 3). In contrast, caryophyllideans occur in only 12 fish families, with a dominant role played by species of the Catostomidae, Cyprinidae and Clariidae as definitive hosts (more than 3/4 of all caryophyllidean species – Fig. 3). Host spectrum may encompass a wide spectrum of not closely related lineages of fishes even within a single genus, e.g. in Bothriocephalus and Proteocephalus Weinland, 1858. However, these species-rich genera are non-monophyletic assemblages, except for the Proteocephalus-aggregate (de Chambrier et al. 2004, 2015b, Brabec et al. 2015).

This incongruence between parasite and host evolutionary histories has been detected in two of the three largest groups of fish tapeworms, i.e. the Bothrioccephalidea (see Brabec et al. 2015) and the Proteocephalidea (see de Chambrier et al. 2015b). Caryophyllideans occur only in fishes of two orders, namely Cypriniformes and Siluriformes (three species from osteglossiform and perciform fishes are not considered) and molecular data indicate that group of definitive hosts and geographical distribution may have played a key role in the evolution of these fish cestodes (Olson et al. 2008, Brabec et al. 2012, A. Waeschenbach – unpubl. data), but possible co-evolution of individual caryophyllidean lineages with their cypriniform and siluriform hosts has not been tested.

Most fish tapeworms occur in freshwater hosts (359 spp. of a total 461, i.e. 78%), whereas the number of species in marine hosts in considerably lower, with only a very few species among amphilinideans (1 of 8, i.e. 13%) and spathebothriideans (1 of 5, i.e. 20%; if anadromous hosts and sturgeons in the Caspian Sea are not considered), and none among caryophyllideans, haplobothriideans, proteocephalids and nippotaeniideans. The only order with dominant occurrence in marine fishes is the Bothriocephalidea, with 68% of valid species known from marine hosts.

Even though tapeworms of fishes were studied for a longer time than those in elasmobranchs, the number of elasmobranch tapeworms currently recognized as valid is more than double that reported in ray-finned fishes because Caira & Jensen (2017) report as many as 1033 species in 200 genera of 10 orders. It is partly due to the extraordinary progress in studies on elasmobranch tapeworms over the last two decades, when more than 250 species and 50 genera have been described (Caira & Jensen 2014, 2017). In contrast, the number of new taxa from fishes described since 2000 is much lower (Fig. 1; see also Scholz & Choudhury 2014 and corresponding chapters on fish tapeworms in Caira & Jensen 2017). However, it is obvious that elasmobranch tapeworms represent key elements of cestode evolution (Caira & Jensen 2014, 2017).

LIFE CYCLES

The life cycles of tapeworms of fishes are relatively well known, at least compared with those of elasmobranch tapeworms (Caira & Jensen 2014, Poulin et al. 2016). However, there are conspicuous differences in our knowledge of development and transmission between individual cestode orders. Whereas life cycles of a number of cestodes parasitizing fishes in freshwaters have been studied for a long time, those of marine species are insufficiently known (Poulin et al. 2016). Moreover, most of the existing knowledge is based on life cycle studies carried out in the middle of the 20th Century, with key contributions of North American, European and Soviet authors (Wardle & McLeod 1952, Freze 1965, Demshin 1975, Protasova 1977, Williams & Jones 1994, Scholz 1999, Chervy 2002).

In contrast, negligible attention has been paid to studies on the development and ontogeny of fish cestodes over the last decades (Scholz & Choudhury 2014). Even though recent application of molecular methods provides a powerful tool for elucidating life-cycles by matching larval stages with corresponding adults (see Jensen &
Bullard 2010 for an exemplary study), there are almost no recent studies focused on the development and transmission patterns of cestodes of fishes.

Different evolutionary origins of the various groups of fish tapeworms are also reflected in their different intermediate hosts. Crustaceans are dominant intermediate hosts for six of the seven groups of fish tapeworms, but species of both earliest evolved groups, i.e. the Amphilinidae and Spathebothriidae, use amphipods rather than planktonic copepods as do haplobothriideans, bothriocephalideans, proteocephalids and nippotaeniideans (Freze 1965, Protasova 1977, Dubinina 1982). Interestingly, presumably the most basal group of eucestodes, caryophyllideans, use oligochaetes as their intermediate hosts similarly as do some groups of the much more recently evolved cyclophyllideans (species of the families Dilepididae and Hymenoolepididae – Demshin 1975).

**GEOGRAPHICAL DISTRIBUTION**

Distribution of fish tapeworms markedly differs from each other, without exhibiting any obvious general pattern (Fig. 2). However, this may reflect a lower sampling effort in tropical regions and the southern hemisphere. The bothriocephalidean tapeworms of marine fishes may have global distribution if their hosts occur worldwide, but the existing data are fragmentary, partly due to uneven sampling effort throughout the globe. Little is known especially about geographical distribution of cestodes of 'deep-sea' fishes (Kuchta et al. 2008b, Klimpel et al. 2009). Species parasitizing widely distributed fish hosts, such as Anchistrocephalus microcephalus (Rudolphi, 1819) in sunfish Mola mola or Bothriocephalus manubriformis (Linton, 1889) in swordfish Xiphias gladius, may have cosmopolitan distribution, whereas others, e.g. Bothriocephalus australis Kuchta, Scholz & Justine, 2005 from flatheads (Platycephalidae) known only off South Australia, have a more restricted distribution related to the occurrence of their fish hosts. Unlike the Bothriocephalidea, the spathebothriideans parasitizing marine fish (the monotypic Didymobothrium and Spathebothrium) have more restricted distribution areas (Protasova & Roitman 1995, Gibson et al. 2005).

Tapeworms of freshwater fishes are more diverse in the temperate zones of the northern hemisphere (Nearctic and Palearctic regions with 26 % and 23 % of all species) than in the tropics, with the notable exception of the proteocephalids in South America. The caryophyllideans dominate in the Australian (58 % of all species, but only 7 species found) and Nearctic (56 %; n = 57) regions, and together with the proteocephalids in the Ethiopian (both 41 %; n = 16), Palearctic (both 37 %; n = 33) realms, and with the bothriocephalideans and caryophyllideans in the Oriental region (both 34 %; n = 13). The Neotropical region is remarkably dominated by the proteocephalids, which represent as many as 95 % of all species reported. The major part of the undescribed diversity of fish tapeworms regarding the total number of species can be expected in the latter region, but this concerns only a single cestode family, Proteocephalidae (order Onchoproteocephalidea).

Distribution areas of individual species of the tapeworms of freshwater fishes are usually restricted to only one zoogeographical region, except for invasive species that have been introduced to non-native regions with their fish hosts. However, species of several genera, usually species-rich ones, may occur in more than one zoogeographical realm. This is also the case of the amphilinid genus Nesolecithus Poche, 1922, with two species, N. africanus Donges & Harder, 1966 and N. janickii Poche, 1922, present in osteoglossomorph fishes in adjacent regions of West Africa and South America, thus indicating a Gondwanan origin (Gibson et al. 1987).

Invasive species are found among the caryophyllideans, bothriocephalideans and nippotaeniideans. In the former order, parasites of common and grass carp have been introduced since the 1960's from eastern Asia to Europe, with some imports to North America (Khawia iovensis Calentene & Ulmer, 1961, syn. of K. japonensis [Yamaguti, 1934]) and Africa (Atractolytocestus huroensis Anthony, 1965) (Oros et al. 2009, 2011, 2015, Scholz et al. 2011b, 2015). The most spectacular example of invasive species is the Asian fish cestode, Schyzocotyle acheilognathi (syn. Bothriocephalus acheilognathi), which has been introduced to all zoogeographical regions (Scholz et al. 2011a). Anthropogenic and natural expansions of the Amur sleeper, Percottus gleni, from eastern Asia to Europe has resulted in the introduction of Nippotaenia perccotti (see Scholz et al. 2017).

**PROSPECTS**

A collaborative effort supported mainly by an NSF-PBI funded project (2008-2016; see Caira & Jensen 2017) made possible to considerably advance our knowledge of the species diversity, interrelations, host associations and geographical distribution of tapeworms including those parasitizing fishes (see de Chambrier et al. 2017, Kuchta & Scholz 2017a, b, c, Scholz & Kuchta 2017, Scholz & Oros 2017). However, these studies have also detected serious gaps that still exist in our knowledge of cestode diversity, their phylogenetic relationships and evolutionary history. The focus of future research should be on unravelling the actual diversity of caryophyllidean and other cestodes of freshwater fishes in the Nearctic region, proteocephalids in the Neotropical region and bothriocephalideans in marine teleosts. Existing taxonomic problems also impede a more reliable assessment of cestode diversity and their associations with fish hosts; these problems are caused, among other reasons, by the
inedquent quality of cestode material used for systematic studies and the absence of molecular data for numerous groups of tapeworms of fishes. Therefore, appropriate methods of integrative taxonomy and phylogenetic systems including proper fixation (hot fixative) of freshly collected cestodes should be applied. This will make it possible to present a more robust hypothesis about the actual diversity of fish cestodes, their interrelationships, and their evolution leading to a more natural classification. Continuing decline of funding of systematic research poses a serious threat to faster progress in unravelling key questions related to cestode diversity and biology, and their role in aquatic ecosystems. More intensive international collaboration and formation of a new generation of cestodologists are also urgently needed to overcome the existing obstacles. Last but not least, much more attention should be paid to life cycle studies because, as stated by Poulin et al. (2016) for marine parasites, “Our ignorance of the life cycles of marine parasites has implications for our understanding of their roles in ecosystems and their transmission pathways.”

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