# Fish tapeworms (Cestoda) in the molecular era: achievements, gaps and prospects

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## Abstract

The tapeworms of fishes (Chondrichthyes and Actinopterygii) account one-third (1670 from around 5000) of the total tapeworm (Platyhelminthes: Cestoda) species diversity. In total 1186 species from 9 orders occur as adults in elasmobranchs (sharks, rays and chimaeras), and 484 species from 8 orders mature in ray-finned fishes (referred to here as teleosts). Teleost tapeworms are dominated by freshwater species (78%), but only 3% of elasmobranch tapeworms are known from freshwater rays of South America and Asia (Borneo). In the last 2 decades, vast progress has been made in understanding species diversity, host associations and interrelationships among fish tapeworms. In total, 172 new species have been described since 2017 (149 from elasmobranchs and 23 from teleosts; invalidly described taxa are not included, especially those from the Oriental region). Molecular data, however, largely limited to a few molecular markers (mainly 28S rDNA, but also 18S and *cox*1), are available for about 40% of fish tapeworm species. They allowed us to significantly improve our understanding of their interrelationships, including proposals of a new, more natural classification at the higher-taxonomy level (orders and families) as well as at the lower-taxonomy level (genera). In this review, we summarize the main advances and provide perspectives for future research.

## Introduction

Tapeworms (Cestoda) are parasitic flatworms (Platyhelminthes: Neodermata) that occur as adults almost exclusively in the intestinal tract of all major vertebrate groups, including elasmobranchs (Chondrichthyes: Holocephali and Elasmobranchii; here called elasmobranchs for simplicity) and ray-finned fishes (Actinopterygii; here called teleosts for simplicity). They are characterized by (1) the absence of a digestive tract (intestine), (2) the presence of hair-like structures called microtriches on their surface, (3) the anterior end of the body called the scolex and (4) a usually long, dorsoventrally flattened body (strobila) that contains multiple sets of genital organs (proglottids) in most groups (except for the earliest diverged orders called monozoic, i.e. with a single set of genital organs) (Khalil *et al.*, 1994; Caira and Jensen, 2017). Adult fish tapeworms vary in overall length from less than a millimetre up to 2 m (*Eubothrium crassum*), but their larvae (metacestodes) are usually much smaller (Williams and Jones, 1994; Chervy, 2002). 'Fish tapeworms' here refer to all tapeworms that mature in elasmobranchs and teleosts.

Caira and Jensen (2014) and Scholz and Kuchta (2017*a*) provided an overview of the current knowledge on elasmobranch and teleost tapeworms, respectively. Caira *et al.* (2014) provided evidence for the unexpected radiation of elasmobranch tapeworms and its importance in deciphering the evolutionary history of all tapeworms, and finally Caira and Jensen (2017) summarized updated information on all tapeworms in a comprehensive monograph. Data on nominal species of all tapeworms, including hosts, localities and authorities not listed herein, are available (and continually updated) in the freely available on-line Global Cestode Database (Caira *et al.*, 2022).

Here we briefly review the history of fish tapeworm research, focusing on the recent application of molecular tools, diversity of fish tapeworms, their systematics, host–parasite associations and distribution.

## Pre-molecular era

Research on tapeworms has a long tradition, mainly because some species infecting humans (such as the pork tapeworm *Taenia solium* and beef tapeworm *Taenia saginata* or the broad fish tapeworm *Dibothriocephalus latus*) were known since the Middle Ages and were already known to Linnaeus (1758). However, intensive research on tapeworms began much later, especially in the 20th century, with relatively few fish tapeworms described in the 18th and 19th centuries (Fig. 1).

The first fish tapeworm – larvae of trypanorhynchs (now *Tetrarhynchus argentinae*; see Southwell, 1929) – was recorded as early as in the 17th century by Redi (1684), who isolated its larvae from various organs of the herring smelt *Argentina sphyraena* and was probably the first helminthologist who studied fish tapeworms. The first adult fish tapeworm described was *Bothriocephalus scorpii* by Müller (1776) from the sculpin *Myoxocephalus scorpius* off
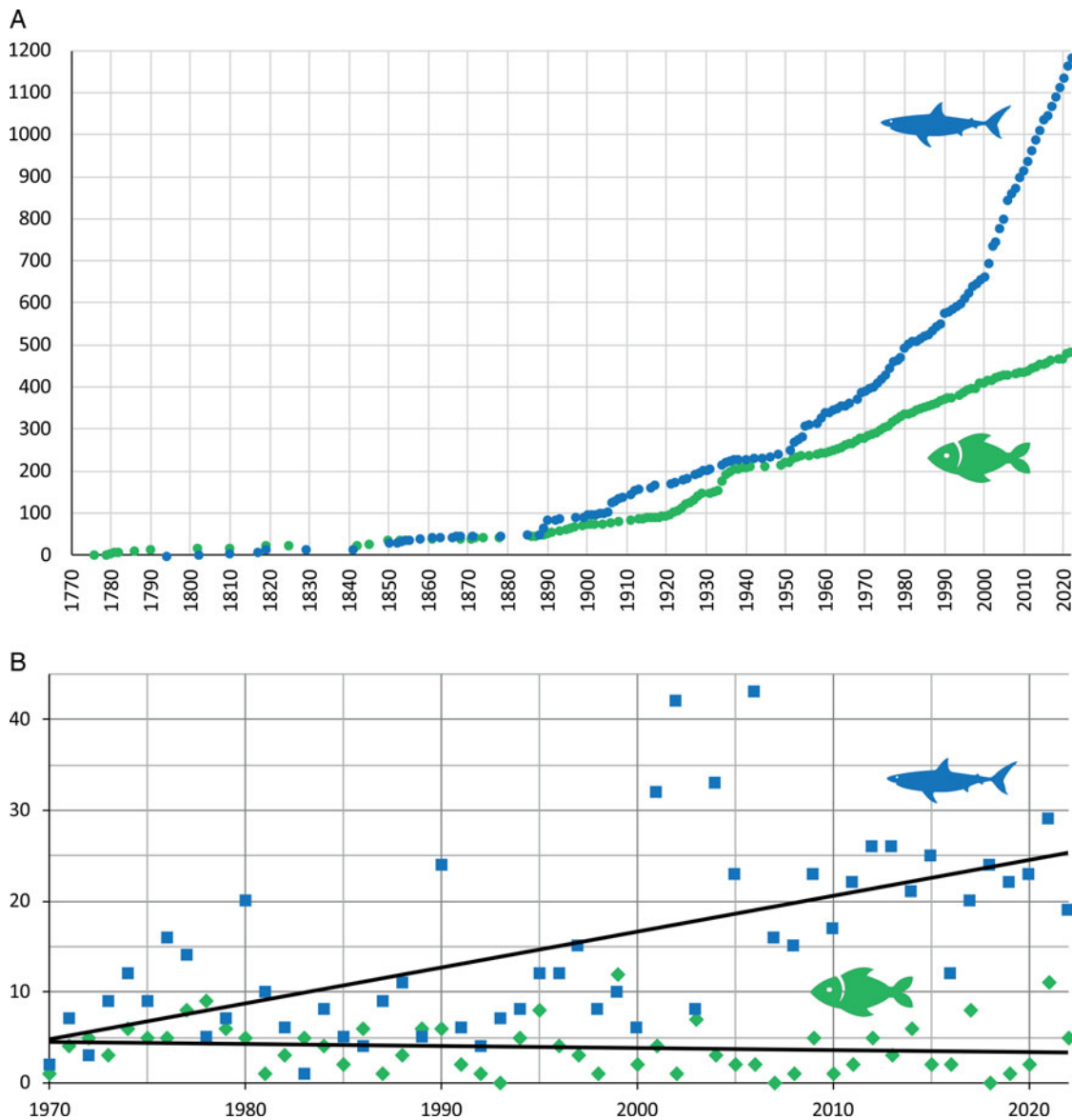
**Fig. 1.** Species diversity of fish tapeworms (elasmobranch tapeworms in blue, teleost tapeworms in green): (A) cumulative curve of species of fish tapeworms described since 1776; (B) numbers of species of fish tapeworms described every year since 1970; note steady or even slowly lowering rate of description of new species of teleost tapeworms within the last 50 years.

Denmark, followed by the description of the largest fish tapeworm *E. crassum* by Bloch (1779) from the Atlantic salmon *Salmo salar* in Germany. The first adult elasmobranch tapeworm was *Gilquinia squali*, described by Fabricius (1794) from the dogfish *Squalus acanthias* off Denmark (see Caira *et al.*, 2022).

Fish tapeworms have been most intensively studied in temperate regions, including Europe, the former USSR, Japan and North America (Dubinina, 1987; Williams and Jones, 1994; Hoffman, 1999). The life cycles of most pathogenic fish tapeworms were elucidated in the 20th century, but this almost exclusively involves freshwater taxa (mainly those of bothriocephalideans, caryophyllideans and proteocephalids [= Onchoproteocephalidea I; for simplicity and to avoid confusion, called thereafter as proteocephalideans]; see below). In contrast, little attention has been paid to the life cycles and ecology of marine fish tapeworms, mainly because of obstacles of laboratory experiments with marine animals (Jensen and Bullard, 2010). The first elasmobranch tapeworm life cycle elucidated was that of the trypanorhynch *Grillotia erinaceus*, which involves 2 intermediate hosts, copepods and fish (Ruszkowski, 1934).

The original concept of higher-level classification of tapeworms dates back to Van Beneden (1850) and van Beneden in Carus (1863), who recognized several groups that are now considered orders, such as Diphyllidea, Caryophyllidea or Tetraphyllidea, followed by the monographs of Wardle and McLeod (1952) and Yamaguti (1959) which set important milestones in terms of tapeworm systematics. Classification of cestodes at a higher taxonomic level was based mainly on the scolex morphology (Fig. 2) and the characteristics of the genital system (see Schmidt, 1986; Khalil *et al.*, 1994). The most important taxonomic categories are the orders and their delimitation was relatively uncontroversial (Wardle and McLeod, 1952; Yamaguti, 1959; Schmidt, 1986), with 14 orders recognized in the most comprehensive monograph published in the pre-molecular era (Khalil *et al.*, 1994).

## Onset of the molecular era

### Molecular phylogenetic studies

Molecular tools, particularly sequences of 18S rDNA, were used in tapeworms beginning in the late 1990s (Králová *et al.*, 1997;

**Fig. 2.** Scanning electron micrographs of scoleces of representatives of orders of fish tapeworms: (A) *Archigetes vadosus* (Caryophyllidea) from *Ictiobus bubalus*, USA; (B) *Diplocotyle olrikii* (Spathebothriidea) from *Myoxocephalus scorpius*, off Svalbard Archipelago, Norway; (C) *Haplobothrium globuliforme* (Haplobothriidea) from *Amia calva*, USA; (D) plerocercoid of *Dibothriocephalus latus* (Diphyllobothriidea) from *Perca fluviatilis*, Italy; (E) *Halysioncum reginae* (Diphyllidea) from *Pastinachus ater*, off Madagascar; (F) *Pterobothrium* sp. (Trypanorhyncha) from *Styracura schmardae*, off Belize; (G) *Kirstenella gordoni* (Bothriocephalidea) from *Heterobranchus bidorsalis*, Kenya; (H) plerocercoid of *Clistobothrium* sp. 3 of Caira *et al.* (2020*a*, 2020*b*) (Phyllobothriidea) from *Oncorhynchus gorbuscha*, off Alaska; (I) *Gangesia bengalensis* (Onchoproteocephalidea I – Proteocephalidae) from *Wallago attu*, India; (J) *Nippotaenia perccotti* (Nippotaeniidea) from *Perccottus glenii*, Slovakia; (K) *Ichthyolepis africana* (Cyclophyllidea: Dilepididae) from *Marcusenius macrolepidotus*, South Africa; (L) merocercoid of *Neogryporhynchus lasiopeius* (Cyclophyllidea: Gryporhynchidae) from *Tilapia sparrmanii*, Zimbabwe.

Liu *et al.*, 1997), but the study of Mariaux (1998) should be considered the starting point of the molecular phylogeny era in tapeworms, followed by studies of Olson and Caira (1999) and Kodedová *et al.* (2000), which included 16 and 33 species of fish tapeworms, respectively.

At the beginning of the 21st century, intensive efforts were made to verify the reliability of the existing classification of tapeworms. The initial studies, based primarily on partial 18S rDNA sequences, surprisingly identified the internally proglottized Spathebothriidea as the most basal 'true' tapeworms (Eucestoda) (Olson and Caira, 1999; Kodedová *et al.*, 2000). However, more comprehensive studies later confirmed the transition of cestode body plan from monozoy (Caryophyllidea) to polyzoy, i.e. the consequent evolution of strobilization and the formation of attachment organs on the scolex from simple bothria (bothriate groups) to sucker-like attachment organs (acetabulate groups) (Olson *et al.*, 2001).

Waeschenbach *et al.* (2007, 2012) and Caira *et al.* (2014) have provided the most robust phylogenetic dataset for all tapeworm orders to date. These studies confirmed unexpectedly high radiation of elasmobranch tapeworms (Caira *et al.*, 2014; Fig. 3; see section 'Remarkable achievements'). They also provided strong support for the previous ordinal classification of tapeworms, with only a few exceptions, such as the non-monophyly of the Pseudophyllidea (divided now into 2 unrelated orders, Bothriocephalidea and Diphyllobothriidea – Kuchta *et al.*, 2008*a*) and the existence of several independent lineages of elasmobranch tapeworms that merit elevation to the ordinal level (see below and Waeschenbach and Littlewood, 2017).
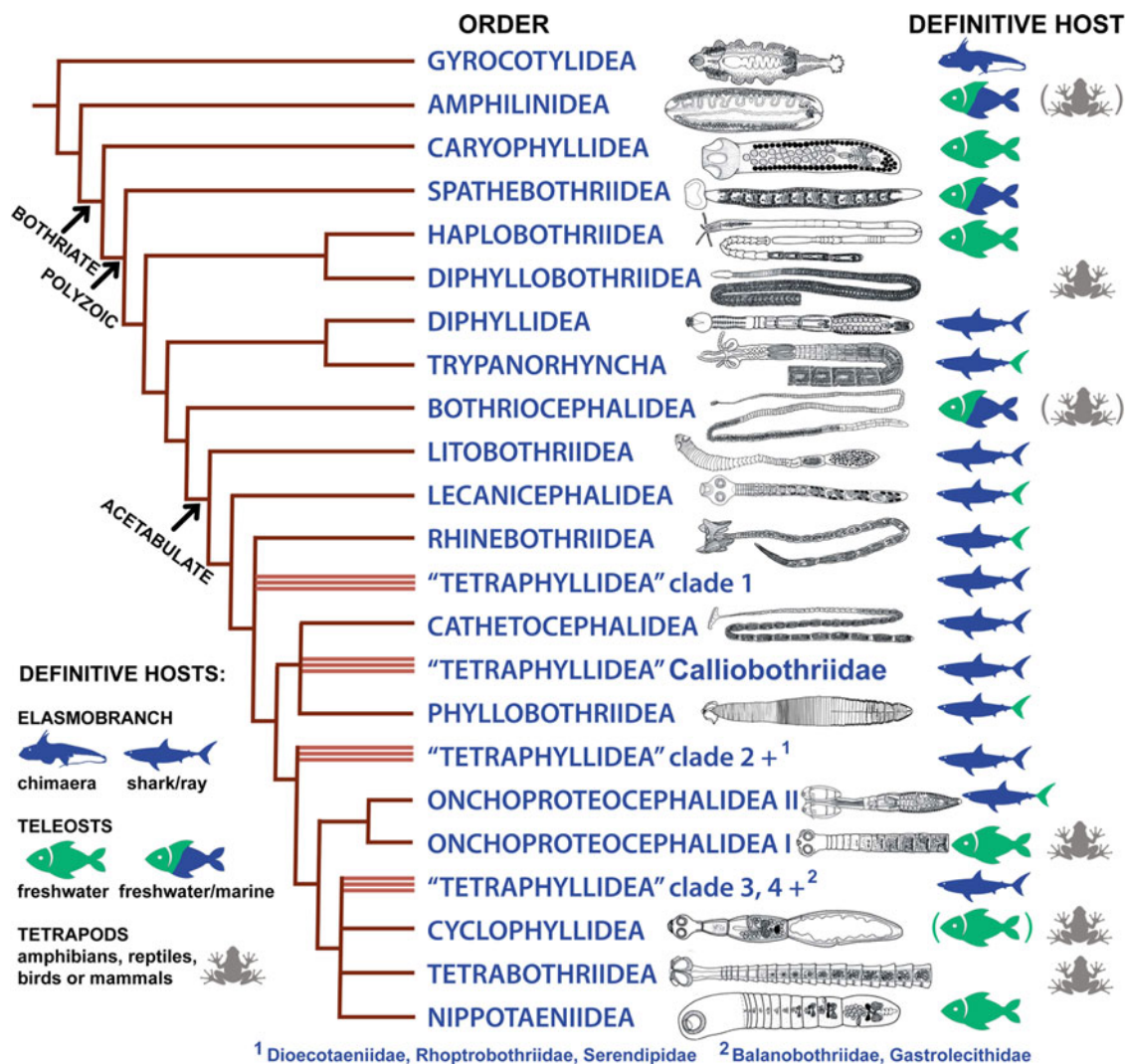
**Fig. 3.** Phylogenetic relationships of tapeworms (Cestoda); modified from Caira *et al*. (2014) and updated from Caira and Jensen (2017). A single species of adult cyclophyllideans was found in teleosts (host pictogram in parentheses). Freshwater hosts in green, marine hosts in blue (combined if tapeworms occur in both environments considering proportion of their species).

## Molecular markers used

The molecular markers used in studies of tapeworms depend on the taxonomic level studied. For higher level classification (ordinal and familiar), only partial 18S rDNA sequences were originally used, with the addition of partial 28S rDNA sequences as proposed by Olson *et al*. (2001). Domains D1–D3 of 28S rDNA have become the gold standard in most taxonomic and phylogenetic studies of fish tapeworms and a high number of their sequences are available, usually supplemented with other markers suitable for lower-level classification (genus and species levels), such as internal transcribed spacers (ITS-1, 5S rDNA, ITS-2) of the nuclear ribosomal DNA region. This region became popular some 15–20 years ago for taxonomic studies at the species level to discriminate closely related taxa. However, these markers can cause artefacts in some groups, such as Bothriocephalidea, Caryophyllidea and Diphyllobothriidea (Bouzid *et al*., 2008; Brabec *et al*., 2012, 2016), which partly concerns also some mitochondrial genes, especially the complete cytochrome *c* oxidase subunit I (*cox*1). The last marker is most commonly used in recent lower-level phylogenetic and population genetical studies of tapeworms. The most sequenced fish tapeworm to date is the invasive Asian fish tapeworm *Schyzocotyle acheilognathi* (syn. *Bothriocephalus acheilognathi*), with more than 100 sequences each of 18S, 28S and ITS. Details of currently available molecular markers of fish tapeworms can be found in the GenBank database and Table 1.

## Mitogenomics (mtDNA) and next-generation sequencing (NGS)

In contrast to the Cyclophyllidea and Diphyllobothriidea, which may parasitize humans, very few data are available on mitochondrial genomes of fish tapeworms. To date, very few mitochondrial genomes of fish tapeworms are available. Waeschenbach *et al*. (2012) used large fragments of mtDNA (more than 4000 bp) together with 18S and 28S rDNA to reconstruct the relationships of 23 tapeworm species from all 18 orders. Brabec *et al*. (2016) characterized complete mitochondrial genomes and nuclear rRNA operons of 8 geographically distinct isolates of the bothriocephalidean *S. acheilognathi*, representing the parasite's global diversity spanning 4 continents. These authors also demonstrated the limited utility of nuclear rRNA sequences, including ITS, which likely misled previous phylogenetic and population genetic studies of *S. acheilognathi* because of the presence of considerable intragenomic sequence variation (i.e. the presence of multiple paralogous sequences of these genomic loci within an individual) within the rDNA and ITS, as well as the other rRNA operon loci

**Table 1.** Number of DNA sequences of tapeworms, including species parasitizing fish, i.e. teleosts and elasmobranchs (data as of 31 May 2022)

| Marker | No. of sequences | No. of species | Most sequenced fish tapeworms | Order |
|---|---|---|---|---|
| 18S rDNA | 2003 | ~470 | *Schyzocotyle acheilognathi* (119) | Bothriocephalidea |
| | | | *Neobothriocephalus aspinosus* (26) | Bothriocephalidea |
| | | | *Tentacularia coryphaenae*[a] (22) | Trypanorhyncha |
| 28S rDNA | 2924 | ~640 | *Proteocephalus ambloplitis* (130) | Onchoproteocephalidea I |
| | | | *S. acheilognathi* (130) | Bothriocephalidea |
| | | | *Wenyonia virilis* (23) | Caryophyllidea |
| Ef 1-α | 233 | ~22 | No multiple sequences per species | |
| 16S rDNA | 1162 | ~220 | *P. ambloplitis* (322) | Onchoproteocephalidea I |
| | | | *Caryophyllaeus laticeps* (9) | Caryophyllidea |
| | | | *Rhinebothrium* sp. 1[a] (8) | Rhinebothriidea |
| ITS-1 + 2 | 2486 | ~200 | *S. acheilognathi* (110) | Bothriocephalidea |
| | | | *Atractolytocestus huronensis* (20) | Caryophyllidea |
| | | | *Atractolytocestus sagittatus* (19) | Caryophyllidea |
| *cox*1 | 8684 | ~340 | *A. huronensis* (47) | Caryophyllidea |
| | | | *S. acheilognathi* (39) | Bothriocephalidea |
| | | | *Bothriocephalus cuspidatus* (36) | Bothriocephalidea |

[a]Elasmobranch tapeworms.

of *S. acheilognathi* (Brabec *et al.*, 2016). In addition, Brabec *et al.* (2018) developed a set of 15 polymorphic microsatellite markers for future population genetic and phylogeographic studies of *S. acheilognathi*. Moreover, Li *et al.* (2017) sequenced mito-chondrial genomes of 3 caryophyllidean tapeworms and *S. acheilognathi*. A comparative analysis of 54 cestode mitogenomes of 52 species, which included 40 cyclophyllideans (16 species of *Taenia* and 9 species of *Echinococcus*), revealed that *Atractolytocestus huronensis* had the longest mitogenome of all tapeworms (15 130 bp long) and that mitogenomes of all 3 caryophyllideans sequenced (*A. huronensis*, *Breviscolex orientalis* and *Khawia sinensis*) had the lowest A–T content (58.6–65.6%) of all cestodes (Li *et al.*, 2017). An unpublished sequence of the mitogenome of another caryophyllidean, *Caryophyllaeus brachycollis* from China, is deposited in the GenBase database (KT028770).

In the case of elasmobranch tapeworms, Trevisan *et al.* (2019) sequenced the mitogenome of *Anindobothrium anacolum* and *Rhinebothrium reydai*. Trevisan *et al.* (2021) obtained complete mtDNA sequences of 86 specimens from 5 orders. At that time, these data nearly doubled the mtDNA dataset available for ces-todes and an expansion of the representation of the cestode orders by about 1/3. The complete mtDNA of fish tapeworms is around 13 500 bp long and contains 12 protein-coding genes, 22 tRNA (trn) genes and 2 rRNA genes, following the pattern of flatworms (Brabec *et al.*, 2016; Trevisan *et al.*, 2021).

NGS data are scarce for fish tapeworms (e.g. Brabec *et al.*, 2016, 2018; Trevisan *et al.*, 2019, 2021). To date, there are only 6 transcrip-tomes, all diphyllobothriideans that use fish as intermediate hosts (*Dibothriocephalus dendriticus*, *D. latus*, *D. nihonkaiensis*, *Ligula intestinalis*, *Schistocephalus solidus*, and *Spirometra mansoni*), and 3 published genomes for *D. latus*, *S. solidus* and *S. mansoni* com-pared with at least 13 available genomes for cyclophyllideans (International Helminth Genomes Consortium, 2019). However, new high-throughput data are currently being generated for several fish tapeworms (J. N. Caira, University of Connecticut, Storrs, USA; J. Brabec, Biology Centre CAS, České Budějovice, Czech Republic, personal communication, 2022).

## Remarkable achievements

### Species diversity

The last 2 decades have seen unprecedented progress in the study of the diversity of fish tapeworms (Caira *et al.*, 2017*a*). Several monographs have been published on individual elasmobranch tapeworm orders, namely Trypanorhyncha – Palm (2004), Lecanicephalidea – Jensen (2005), Diphyllidea – Tyler (2006) and Phyllobothriidea – Ruhnke (2011). Caira and Jensen (2014) and Scholz and Kuchta (2017*a*) presented concise reviews ('digest') of elasmobranch and teleost tapeworms, respectively, but the major achievements were summarized in a monograph by Caira and Jensen (2017) that provides detailed information on all cestode orders.

Another milestone is the establishment of the Global Cestode Database (www.tapewormdb.uconn.edu; Caira *et al.*, 2022), which contains taxonomic and nomenclatural data on most of the described cestode species with their original hosts and localities, availability of type material and in most cases also with their ori-ginal descriptions and images. To date (as of 1 June 2022), there are 12 790 records, including 1334 nominal generic names (804 valid) and 11 456 nominal species names (3400 valid species have been included to date, representing 68% of ~5000 known valid tapeworm species, with the fish tapeworm orders almost fully represented – Caira and Jensen, 2017; Caira *et al.*, 2022). Moreover, the database also contains extensive literature, particu-larly original descriptions of new species that are available elec-tronically (a total of 4779 papers and monographs is available online in the Global Cestode Database).

Since 2000, the pace of descriptions of new cestode taxa from fish has accelerated, with an increase of 527 new species that represent almost 1/2 of known species of elasmobranch tape-worms and 75 new species of teleost tapeworms, as shown by comparing the data of Caira and Jensen (2017) with the current status (Fig. 1, Table 2). The highest increase in species richness since 2017 is seen in the Rhinebothriidea (38 new species, includ-ing 15 spp. of *Rhinebothrium*), Phyllobothriidea (37 new species,

**Table 2.** Number of valid species of tapeworms in 2022

| | Total species | Fish speciesᵃ | % | Fresh water | Marine | Genera | Genera in fish |
|---|---|---|---|---|---|---|---|
| **Teleosts** | | | | | | | |
| Amphilinidea | **8** (8) | **7** (7) | 88 | 6 | 1 | 6 | 6 |
| Bothriocephalidea | **135** (131) | **131** (129) | 97 | 42 | 89 | 49 | 49 |
| Caryophyllidea | **130** (117) | **130** (117) | 100 | 117 | 0 | 44 | 44 |
| Cyclophyllidea | **>3000** (0) | **1** (0) | 0 | 1 | 0 | 437 | 1 |
| Haplobothriidea | **2** (2) | **2** (2) | 100 | 2 | 0 | 1 | 1 |
| Nippotaeniidea | **6** (6) | **6** (6) | 100 | 6 | 0 | 1 | 1 |
| Onchoproteocephalidea I | **334** (318) | **201** (194) | 60 | 201 | 0 | 73 | 59 |
| Spathebothriidea | **6** (6) | **6** (6) | 100 | 3 | 3 | 6 | 5 |
| Total | **>3621** | **484** | 13 | 378 | 93 | 617 | 166 |
| Freshwater species | | | | **78%** | | | |
| **Elasmobranchs** | | | | | | | |
| Cathetocephalidea | **6** (6) | **6** (6) | 100 | 0 | 6 | 3 | 3 |
| Diphyllidea | **59** (59) | **59** (59) | 100 | 0 | 59 | 6 | 6 |
| Gyrocotylidea | **12** (10) | **12** (10) | 100 | 0 | 12 | 1 | 1 |
| Lecanicephalidea | **94** (90) | **94** (90) | 100 | 3 | 91 | 29 | 29 |
| Litobothriidea | **9** (9) | **9** (9) | 100 | 0 | 9 | 1 | 1 |
| Onchoproteocephalidea II | **271** (246) | **271** (246) | 100 | 18 | 253 | 12 | 12 |
| Phyllobothriidea | **111** (69) | **111** (69) | 100 | 1 | 110 | 21 | 21 |
| Rhinebothriidea | **175** (136) | **175** (136) | 100 | 15 | 160 | 24 | 24 |
| Trypanorhyncha | **337** (315) | **337** (315) | 100 | 2 | 335 | 84 | 84 |
| 'Tetraphyllidea' relicts | **119** (104) | **119** (104) | 100 | 0 | 123 | 84 | 84 |
| Total | **1193** | **1189** | 100 | 39 | 1158 | 265 | 265 |
| Freshwater species | | | | **3%** | | | |
| All tapeworms | **>4814** | **1632** | **34** | **417** | **1251** | **882** | **431** |

Numbers from Caira and Jensen (2017) in parentheses. Total numbers in bold.
ᵃIncluding orders using fish as final (definitive) host, with the exception of Diphyllobothriidea (71 spp.) and Tetrabothriidea (70 spp.).

including 7 spp. of *Scyphophyllidium*), Onchoproteocephalidea II (22 new species, including 15 spp. of *Acanthobothrium*), Trypanorhyncha (20 new spp.), 'Tetraphyllidea' (19 new spp.), Caryophyllidea (13 new spp.) and Onchoproteocephalidea I (12 new spp.) (Caira *et al.*, 2022).

Currently, nearly 1200 species of elasmobranch tapeworms and nearly 500 species of teleost tapeworms are recognized as valid (Fig. 4, Table 2; Caira *et al.*, 2022). Elasmobranch diversity hot spots are indeed restricted to regions where recent sampling has occurred, with tropical marine regions predominating (Caira and Jensen, 2017). For teleost tapeworms, the main hot spot of diversity is South American fresh water, i.e. the Amazon and Paraná river basins (de Chambrier *et al.*, 2017), where 7 new species have been described since 2017 (Alves *et al.*, 2020, 2021), but there are still many undescribed taxa (unpublished data). Another hot spot is North America, especially the southern USA, where 10 new caryophyllidean species have been described since 2017 (Scholz and Oros, 2017). In contrast, very few new species have been described from other regions, including the Afrotropical region (3 new spp.), and only 2 valid species from the Oriental region (Scholz and de Chambrier, 2012; Scholz *et al.*, 2022a).

Molecular tools also allowed us to discover cryptic species diversity in some groups, such as caryophyllideans of the genus *Paracaryophyllaeus* in loaches (Cobitoidei) in the Palaearctic region and *Bothriocephalus* in the Nearctic region (Scholz *et al.*, 2014; Choudhury and Scholz, 2020). However, the number of cryptic species of fish tapeworms discovered is rather low, most likely due to the predominant use of 28S rDNA sequences and the small number of specimens studied, which prevents the discovery of genetically similar but distinct taxa.

Taxonomic revisions of fish tapeworms in the Oriental region have shown that the actual number of valid species is much lower. Our recent studies of freshwater teleost tapeworms, based on new material from Bangladesh, Cambodia, India, Indonesia and Vietnam, have substantially reduced the number of valid species of teleost tapeworms in this region, where dozens of species and many 'new' genera have been inadequately and often invalidly described (*nomina nuda* or *species inquirendae*), mostly based on only 1 or 2 poorly fixed specimens found in a few teleost species, such as catfishes *Clarias batrachus*, *Heteropneustes fossilis*, *Wallago attu*, *Sperata seenghala*, snakeheads *Channa* spp. and zig-zag eels *Mastacembelus* spp. (Kuchta and Scholz, 2007, 2017a). Similarly, Ash *et al.* (2011a, 2011b) recognized only 9 of 78 caryophyllidean species described from *C. batrachus* and *H. fossilis*, or only 4 of 48 species of proteocephalideans described from *W. attu* and *S. seenghala* (Ash *et al.*, 2012, 2015). A similar situation also occurs in bothriocephalideans, where at least 80 species (57 since 2000) from 7 genera (*Apicobothrium*, *Circumoncobothrium*, *Mastalobothrium*, *Polyonchobothrium*, *Probothriocephalus*, *Ptychobothrium* and *Senga*) have been described very superficially and often in violation of the International Code of Zoological Nomenclature (Ride *et al.*,
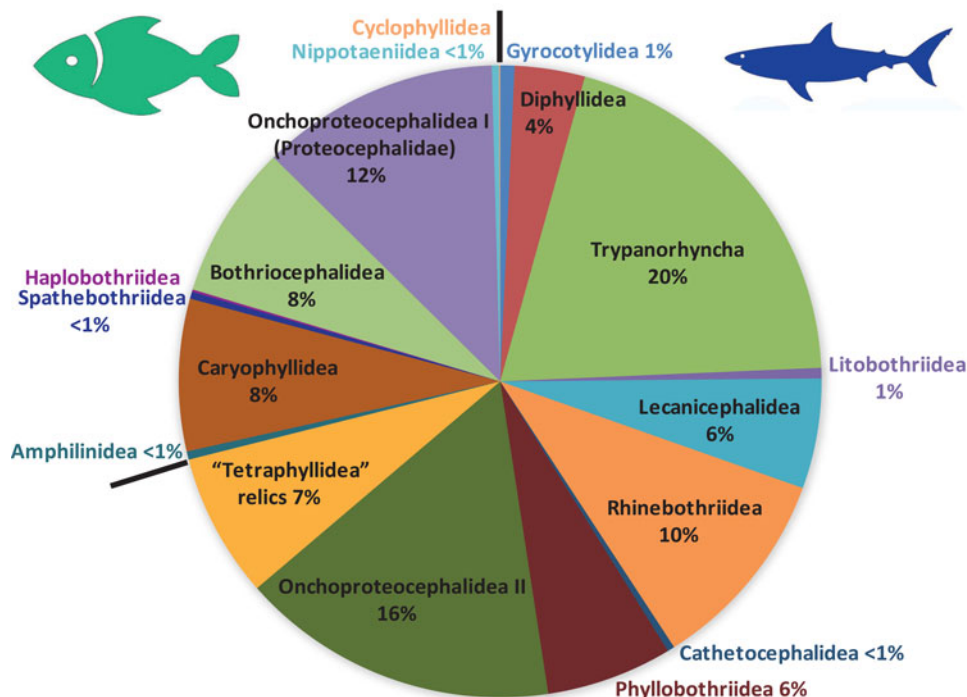
**Fig. 4.** Pie chart documenting species diversity of fish tapeworms, i.e. proportion of species numbers of individual orders of fish tapeworms.

1999) from a single host species, the zig-zag eel *Mastacembelus armatus*, in India and southeast Asia. The first and probably only valid species (and genus) from *M. armatus* was described by Johri (1956) as *Senga lucknowensis* (see Kuchta and Scholz, 2007; Kuchta *et al.*, 2008*b*). The situation is even worse for the notorious genus *Senga* (and its synonyms), where no less than 152 (!) species have been described from 36 species of snakeheads and zig-zag eels in India, Pakistan and other southeast Asian countries. Provisionally, only 14 species are considered valid (Kuchta and Scholz, 2007, 2017*a*; Caira *et al.*, 2022), but the actual number of valid taxa may be even lower. A similar situation exists for *S. acheilognathi*, where 24 species from 5 genera are considered synonyms (see Kuchta *et al.*, 2008*b*, 2018). Moreover, all these taxonomic changes proposed more than 10 years ago are constantly ignored by local authors who continue to describe 'new' taxa, including genera, from the same host species. The same problem, but to a somewhat lesser extent, exists also with the elasmobranch tapeworms of the Oriental region. Editors of scientific journals are strongly urged to avoid publishing these invalid and scientifically unsound descriptions of 'new' taxa, which only pollute the literature.

### Phylogenetic interrelationships and new classification

Recent collaborative efforts of cestodologists have allowed us to greatly improve our understanding of the interrelationships between all groups of tapeworms and their evolutionary history. New molecular phylogenetic data have confirmed the crucial role of fish tapeworms in the evolution of all tapeworms and also led to major changes in their higher classification. These new data revealed (or confirmed) the following:

(1) *Transition from monozoy to polyzoy in cestode evolution and consecutive development of the scolex* from simple attachment organs to bothriate structures (1, 2 or 4 attachment grooves), followed by the development of acetabulate attachment organs (usually with 4 suckers or bothridia) (Fig. 3; Olson *et al.*, 2001; Waeschenbach *et al.*, 2007, 2012; Caira *et al.*, 2014). New data collected in the last 2 decades suggest the

evolutionary scenario that the non-strobilate orders (Gyrocotylidea, Amphilinidea and Caryophyllidea) form the basal lineages of cestodes followed by the bothriate orders, while the acetabulate orders are the most derived (Fig. 3; Caira *et al.*, 2014).

(2) *Non-monophyly of fish tapeworms*, i.e. independent, repeated colonization of elasmobranchs and teleosts with different, distantly related lineages of cestodes during their evolution (Caira *et al.*, 2014). Molecular data confirmed at least 8 colonizations of freshwater environments (Fig. 3). Chimaeras, as members of an apparently relict vertebrate group, were most likely colonized by tapeworm progenitor represented recently only by gyrocotylideans (Kuchta *et al.*, 2017; Barčák *et al.*, 2021). However, chimaeras also harbour, albeit rarely, derived tapeworms, namely *Prochristianella clarkeae* (broad host range) (Trypanorhyncha) and *Chimaerocestos prudhoei* (specific) (Phyllobothriidea).

In contrast, further colonization of elasmobranchs (rays and sharks) originally occurred in more recently diverging groups, such as trypanorhynchs and diphyllideans, but surprisingly after the colonization of marine and even freshwater teleosts (Amphilinidea, Caryophyllidea, Spathebothriidea) and probably also tetrapods (Diphyllobothriidea) and ancient freshwater bowfin fishes (Haplobothriidea) (Caira *et al.*, 2014) (Fig. 3). However, the interrelationships between the individual orders (especially the basal ones) are not well supported by any available molecular data (Waeschenbach and Littlewood, 2017). Furthermore, reliable dating of individual colonization events is problematic because fossils of flatworms, including parasitic Neodermata, are completely lacking. However, it is assumed that the Neodermata must have parasitized the stem group Gnathostomata between the Cambrian and Ordovician (Littlewood, 2006).

(3) Probably most surprising is the *extraordinary diversity of elasmobranch tapeworms* (Caira and Jensen, 2014, 2017; Caira *et al.*, 2014), which belong to 8 orders and at least 9

other independent lineages that may represent new independent orders (Fig. 3).

(4) *The taxonomic significance of some previously used traditional morphological characters has been questioned.* The position of the internal longitudinal musculature relative to the reproductive organs used in higher classification of Caryophyllidea and Proteocephalidae (Onchoproteocephalidea I) is not congruent with molecular data (de Chambrier *et al.*, 2004, 2015; Brabec *et al.*, 2012; Scholz *et al.*, 2021*a*). It is therefore obvious that this apparently homoplastic character is not suitable to define (sub)families. Also, the shape of the scolex seems to represent a homoplastic character that does not reflect the interrelationships at the level of families and even genera of some groups, such as bothriocephalideans, lecanicephalideans, proteocephalideans and 'tetraphyllideans' (Brabec *et al.*, 2015; de Chambrier *et al.*, 2015; Jensen *et al.*, 2016; Caira et al., 2017*b*).

(5) New molecular phylogenetic data have led to *significant changes in the classification and nomenclature of fish tapeworms* at different taxonomic levels (ordinal, familial and generic). At the ordinal level, not all groups deserved changes and their ordinal status has been confirmed (see below). In contrast, taxonomic changes were made in some groups, based on the presence of independent lineages of fish tapeworms that deserve to be elevated to ordinal or subordinal rank (Fig. 3; Caira *et al.*, 2014; Caira and Jensen, 2017).

### Monozoic groups

The 2 most basal groups (orders) of tapeworms, namely the **Gyrocotylidea** (spiral intestine of the chimaeras) and the **Amphilinidea** (body cavities of freshwater and marine teleosts, including sturgeons, and turtles), called Cestodaria and sometimes classified as a subclass (Schmidt, 1986), have a 10-hooked lycophore larva (decacanth) and a non-proglottized body without scolex, and have been considered sister groups to all other 'true' tapeworms (Eucestoda), which have a 6-hooked larva called a hexacanth (Conn and Świderski, 2008). However, the available molecular data do not support the monophyly of the 'Cestodaria', as the Gyrocotylidea most likely forms a sister group to all other tapeworms, including the Amphilinidea (Waeschenbach *et al.*, 2012; Caira *et al.*, 2014). However, the interrelationships of these most basal tapeworms are not yet sufficiently resolved (Waeschenbach *et al.*, 2012; Caira and Jensen, 2017).

**Caryophyllidea** (parasites of cypriniform and siluriform teleosts, intestines, exclusively freshwater). Scholz *et al.* (2021*a*) presented the most comprehensive multi-gene molecular phylogeny of this group, encompassing ~50 and 75% of the known species and genus diversity, respectively (Scholz and Oros, 2017). Phylogenetic reconstructions provided high support for 3 major lineages that were only partially consistent with previously recognized families. In contrast, host association and biogeographical distribution play key roles in circumscribing the 3 well-supported clades revealed by molecular data (Scholz *et al.*, 2021*a*). The most basal caryophyllideans seem to be species of *Balanotaenia* from catfishes in Australasia and/or *Lytocestoides tanganyikae* from cichlids in Africa (Scholz *et al.*, 2021*a*).

### Polyzoic bothriate groups

**Spathebothriidea** (parasites of marine and freshwater teleosts including sturgeons) are a small group with a relatively low host specificity. Phylogenetic interrelationships have been studied by Kuchta *et al.* (2014), and the most basal species seems to be the marine *Spathebothrium simplex* with a simple scolex without specialized attachment organs.

**Pseudophyllidea** (parasites of a wide range of vertebrates; share the presence of bothria as attachment organs). Based on molecular, morphological and ecological evidence, the long recognized order Pseudophyllidea proposed by Carus (1863) was suppressed by Kuchta *et al.* (2008*a*) and 2 new, not closely related orders, Diphyllobothriidea and Bothriocephalidea, were proposed (see below).

**Diphyllobothriidea**, so-called 'broad tapeworms' (parasites of marine, freshwater and terrestrial tetrapods; teleosts usually serve as a second-intermediate host; formerly part of the Pseudophyllidea). The molecular interrelationships of more than 30 of 70 known species have been studied using multigene and mitogenome analyses (Waeschenbach *et al.*, 2017; Fraija-Fernández *et al.*, 2021). Three major lineages were recognized that correspond well to the 3 recognized families that include parasites of frogs (the most basal lineage), reptiles and the most derived group with parasites of birds and mammals, including humans (causing diphyllobothriosis or sparganosis). Humans were found to have been accidental hosts at least 4 times during the diphyllobothriidean evolution (Waeschenbach *et al.*, 2017). Fraija-Fernández *et al.* (2021) sequenced the complete mitochondrial genome (mtDNA) of 13 representatives and added nodal resolution to major branches (families) of the order.

**Diphyllidea** (parasites of marine batoids and rarely of sharks). This small group of small tapeworms was revised and the sequences of 31 of 59 recognized species were analysed. Based on molecular and morphological evidence, 4 new genera were proposed, with *Halysioncum* to be the most basal genus (Caira *et al.*, 2013, 2017*c*; Abbott and Caira, 2014).

**Trypanorhyncha** (most species-rich order of elasmobranch tapeworms; larvae in invertebrates and teleosts; with 2 species, *Paroncomegas araya* and *Paroncomegas baeri*, specific parasites of freshwater stingrays in South America). Two robust molecular phylogenetic studies based on extensive datasets (66 of 335 known species) have been published (Palm *et al.*, 2009; Olson *et al.*, 2010). Two new, well-supported suborders (lineages) have been erected, Trypanobatoida and Trypanoselachoida, which parasitize primarily rays and sharks, respectively (Olson *et al.*, 2010). The interrelationships of this species-rich order are not yet adequately understood, because available molecular data represent only about one-fifth of the known taxa (Beveridge *et al.*, 2017).

**Bothriocephalidea** (parasites of marine and freshwater teleosts and rarely of amphibians; formerly part of the Pseudophyllidea). Brabec *et al.* (2015) evaluated the interrelationships of this order using multi-gene molecular phylogenetic analyses that included 59 of 135 recognized species, covering 70% of recognized genera. The order proved to be monophyletic, but 3 of 4 recognized families appeared non-monophyletic. Only the family Bothriocephalidae is monophyletic, and forms the most derived lineage of the order which comprises a single freshwater clade and several marine clades (including the most species-rich and polyphyletic genus *Bothriocephalus*). Biogeographical patterns within the freshwater clade indicate that monophyletic lineages have evolved in Africa and North America (Brabec *et al.*, 2015). The most basal genera seem to be fresh water (*Marsipometra* and/or *Bathybothrium*) or marine (*Abothrium* or *Parabothrium*) (Brabec *et al.*, 2015).

### Polyzoic acetabulate groups

**Litobothriidea** (small group in 1 genus; parasitize exclusively pelagic sharks). With one exception (enigmatic *Litobothrium aenigmaticum*), all possess a scolex consisting of a single apical sucker followed by a series of pseudosegments, part of which is cruciform (Caira *et al.*, 2017*d*). In contrast, the scolex of *L. aenigmaticum* consists of a simple dome-shaped scolex proper and an

extended cephalic peduncle housing 4 distinct tissue types (Caira et al., 2017d). The order Lithobothriidea is considered a sister taxon to all acetabulate tapeworms (Fig. 3; Caira and Jensen, 2014; Caira et al., 2014, 2017d).

**Lecanicephalidea** (parasites of elasmobranchs, mainly rays; with only a few freshwater species). Jensen et al. (2016) presented the first assessment of the phylogenetic interrelationships of the order and confirmed its monophyly. However, 61 species representing 22 of the 25 valid genera were found to have an apparent conflict between scolex morphology and proglottid anatomy, complicating the assignment of many of these genera to families. Proglottid anatomy was found to be much more conserved and informative of phylogenetic relationships than scolex morphology, and genera lacking apical structures (such as the Paraberrapecidae) were confirmed to be the earliest diverging lineages (Jensen et al., 2016). The order is divided into 8 families based on molecular data (Jensen et al., 2016, 2017).

**Rhinebothriidea** (formerly part of the Tetraphyllidea; parasites of elasmobranchs, with 15 known species in freshwater rays). The order was erected by Healy et al. (2009) based on molecular data and is characterized by the possession of a scolex consisting of 4 bothridia borne on stalks. Ruhnke et al. (2015, 2017) proposed 4 families of the order and erected several new genera. The order contains the second most species-rich genus of elasmobranch tapeworms, *Rhinebothrium*, with 63 valid species, including 11 species from freshwater rays in South America that form a monophyletic group with species parasitizing potamotrygonid stingrays (Reyda and Marques, 2011), and 2 species from freshwater whipray in Borneo (Healy, 2006) that are not closely related to the Neotropical taxa (Ruhnke et al., 2017). Moreover, 1 *Anindobothrium* species from Amazonian potamotrygonids and *Sungaicestus kinabatanganensis* from Bornean giant freshwater whipray have been recently discovered (Ruhnke et al., 2017, Trevisan et al., 2017). Rhinebothriideans adapted to a freshwater environment at least 4 times, with the most basal species appearing to be new genus 11 *sensu* Ruhnke et al. (2015) (Ruhnke et al., 2017).

**Cathetocephalidea** (formerly part of the Tetraphyllidea; parasites of pelagic sharks). This is a very small but peculiar order characterized by a scolex consisting of an anterior globose or transversely extended region and a posterior rugose base with or without a papillary band (Caira and Jensen, 2014). Caira et al. (2014) found this small order deeply nested among the acetabulate orders of cestodes. *Sanguilevator yearsleyi* from the broadfin shark *Lamiopsis tephrodes* off Borneo has a unique scolex with internal chambers and channels that appear to sequester host blood cells, making it possibly the only known tapeworm species that ingests blood (Caira et al., 2005).

**Phyllobothriidea** (formerly part of the Tetraphyllidea; parasites of elasmobranchs; 1 species in fresh water). Based on their molecular phylogenetic analyses, Caira et al. (2014) elevated the family Phyllobothriidae to ordinal status. Caira et al. (2021a, 2021b) provided the most comprehensive phylogenetic analysis of this order; their dataset included species from 15 of the 18 genera, as well as 3 new genera. Members of the order have simple, undivided bothridia, each bearing an apical sucker. The most species-rich genus is now *Scyphophyllidium* with 45 species, as 6 genera have been synonymized with this genus, and the most basal genus appears to be *Clistobothrium* (Caira et al., 2020a, 2021). Surprisingly, 1 species of *Scyphophyllidium*, originally described as *Anindobothrium guariticus* and later transferred to *Nandocestus*, was described from freshwater potamotrygonid stingrays in South America (Caira et al., 2021a).

**Onchoproteocephalidea** (a highly controversial order consisting of members of the long recognized order Proteocephalidea parasitizing freshwater teleosts and tetrapods – Onchoproteocephalidea I,

and taxa of the former 'tetraphyllidean' family Onchobothriidae from elasmobranchs – Onchoproteocephalidea II). Caira et al. (2014) proposed this new order based on molecular data, but no morphological, biological or ecological synapomorphies for the order have been identified to characterize this rather heterogeneous assemblage of tapeworms.

Tapeworms of the former order **Proteocephalidea** (Onchoproteocephalidea I) are parasites of freshwater teleosts (60% of species) and some tetrapods (amphibians, reptiles and 1 in mammals) that are currently placed in a single family, Proteocephalidae (see de Chambrier et al., 2017). The most comprehensive phylogenetic study included more than 100 of 334 now recognized species from 54 genera (80% of all recognized genera) (de Chambrier et al., 2015). The results confirmed the origin of proteocephalideans in the Old World with the most basal groups appearing in catfishes (Gangesiinae) or reptiles (Acanthotaeniinae), with more recent dispersal followed by radiation in teleosts, particularly pimelodid catfishes in South America. Most of the subfamilies and species-rich genera proved to be non-monophyletic, requiring a profound systematic reorganization of this cestode group, abandoning the traditional subfamily system (de Chambrier et al., 2015, 2017).

**Onchoproteocephalidea II** of Caira and Jensen (2017) consists of hooked cestodes parasitizing rays and sharks. They encompass the most species-rich genus of elasmobranch tapeworms *Acanthobothrium* with 211 valid species (Caira et al., 2022; Van der Spuy et al., 2022), including 11 species described from giant freshwater whipray in Borneo and potamotrygonid stingrays in South America (Fyler and Caira, 2006; Caira et al., 2022). Moreover, all 7 species of *Potamotrygonocestus* with unique acetabula and unipronged hooks are specific parasites of potamotrygonid stingrays in South America (Marques et al., 2003) and may represent elasmobranch tapeworms most closely related to proteocephalideans (Caira et al., 2017e).

**Nippotaeniidea** (small group, exclusive in freshwater teleosts). They have only been found in freshwater gobiids (Perciformes) and osmeroids (Osmeriformes) in the Palaearctic region and New Zealand (Scholz et al., 2017a). They are closely related to the Tetrabothriidea, Cyclophyllidea (both groups parasitize tetrapods) and some tetraphyllidean relics, but their relationships are still not clearly resolved (Caira et al., 2014; Waeschenbach and Littlewood, 2017).

**Cyclophyllidea** (mature in tetrapods; 1 species has recently been described from freshwater teleosts). This is the most species-rich order, comprising over 3000 species (more than 60% of tapeworm diversity) that are parasites of tetrapods, especially birds and mammals, including humans (Mariaux et al., 2017). However, adults had never been found in bony fishes until Scholz et al. (2020) described the dilepidid *Ichthyolepis africana* in 6 species of elephantfishes (Mormyriformes) across Africa. The new species belongs to the dilepidid lineage consisting of tapeworms of African swifts (Apodidae) (Scholz et al., 2020).

**'Tetraphyllidea' relics.** This group tentatively includes more than 100 species of acetabulate elasmobranch tapeworms with highly diverse morphologies that form at least 9 independent lineages of acetabulate tapeworms that may represent new orders (Caira et al., 2017b) (Fig. 3). Recently, numerous morphological and molecular data have been added to these groups, including descriptions of new genera such as *Ambitalveolus* (Eudy et al., 2019; Caira et al., 2021; Caira and Jensen, 2021, 2022; Jensen et al., 2021; Sadeghi Kamachali and Haseli, 2022; Stephan and Caira, 2022).

(6) Several genera of fish tapeworms, including taxa of medical and veterinary importance, were found to be non-monophyletic, resulting in nomenclatural changes at the

genus level. For example, the bothriocephalidean genus *Schyzocotyle* was resurrected by Brabec *et al.* (2015) to accommodate the important fish pathogen and invasive Asian fish tapeworm *S. acheilognathi* (see Scholz *et al.*, 2012; Kuchta *et al.*, 2018).

A molecular phylogenetic study by Waeschenbach *et al.* (2017) resulted in several taxonomic changes in the genera containing human-infecting broad tapeworms (Diphyllobothriidea), especially resurrection of the genus *Dibothriocephalus* that accommodates freshwater and terrestrial species, including human parasites, such as *D. latus*, *D. nihonkaiensis* and *D. dendriticus*, and the genus *Adenocephalus* with the Pacific broad tapeworm that infects humans on the Pacific coast of South America, with marine teleosts serving as a source of human infections (Kuchta *et al.*, 2015), and the synonymy of *Diplogonoporus* (including parasites of humans) with *Diphyllobothrium* by Waeschenbach *et al.* (2017).

## Host associations

As noted above, both elasmobranchs and teleosts were independently colonized several times during the evolution of tapeworms, including the most basal gyrocotylideans, amphilinideans and caryophyllideans, but also recently by divergent acetabulate groups such as nippotaeniideans (Caira *et al.*, 2014; Fig. 3). In elasmobranchs, the next colonization event after the establishment of gyrocotylidean–holocephalan association occurred much later, most likely by ancestors of the recent Trypanorhyncha and Diphyllidea, which expanded in both sharks and rays (Caira *et al.*, 2014, 2017c; Beveridge *et al.*, 2017). Using a relaxed molecular clock model calibrated by host fossil data, the Trypanobatoida of rays was estimated to have diversified around the Jurassic–Cretaceous boundary, whereas the Trypanoselachoida of sharks was estimated to have diversified later, in the mid-Cretaceous (Olson *et al.*, 2010).

Teleosts have also been colonized independently several times (Fig. 3). Tapeworms occur in their most basal groups, i.e. the 2 orders of the most basal superorder Chondrostei, namely Polypteriformes and Acipenseriformes (proteocephalideans, bothriocephalideans and amphilinideans – Kuchta *et al.*, 2012; de Chambrier *et al.*, 2017; Scholz and Kuchta, 2017b). Fishes of both orders of another ancient superorder Neopterygii (orders Amiiformes and Lepisosteiformes) have also been colonized by relatively derived proteocephalidean tapeworms, and bowfin (*Amia calva*) also by haplobothriideans (Brabec *et al.*, 2015; Scholz *et al.*, 2022a, 2022b). Adult tapeworms also occur in the most basal superorder Teleostei, as in the Osteoglossiformes (2 amphilinideans in *Arapaima gigas*), Elopiformes (bothriocephalideans) and Anguilliformes (1 proteocephalidean and 2 bothriocephalideans) (de Chambrier *et al.*, 2017; Kuchta and Scholz, 2017a; Scholz and Kuchta, 2017b). With the exception of amphilinideans, all of the above-mentioned tapeworms belong to more derived groups, so their colonization of ancient fish groups was apparently the result of host switching.

Bothriocephalideans have spread in marine and freshwater teleosts, with a few taxa switching to amphibians (Kuchta and Scholz, 2017a). Further colonization of freshwater teleosts has occurred much later by members of acetabulate tapeworms (Fig. 3), particularly proteocephalideans, which have adapted to an extraordinarily wide range of distantly related orders, including basal ray-finned species such as the Polypteriformes, Amiiformes and Lepisosteiformes, as well as the recently divergent orders Centrarchiformes, Cichliformes, Gobiiformes and 'Perciformes', but also other vertebrate groups (de Chambrier *et al.*, 2017).

Species of 4 orders (Caryophyllidea, Haplobothriidea, Onchoproteocephalidea I and Nippotaeniidea) live exclusively in fresh water. In the Spathebothriidea, the most basal extant species (*S. simplex*) is a parasite of marine snailfish, while the most basal bothriocephalideans may occur in freshwater hosts (see above; Brabec *et al.*, 2015). Interestingly, the number of marine species among teleost tapeworms accounts only for 22% of known species (Scholz and Kuchta, 2017a; Table 1).

There are 1200 described species of elasmobranch fishes (Last *et al.*, 2016), of which an estimated 40% have been examined for tapeworms from which almost 1200 species have been described (Table 2; Caira *et al.*, 2017a). Nearly all elasmobranch species examined for parasites harbour at least 1 tapeworm species (Caira *et al.*, 2001), but each elasmobranch species may harbour an average of 6 tapeworm species, 4 of which have strict host specificity (Randhawa and Poulin, 2010). In addition, it is estimated that there are at least 3600 undescribed tapeworm species from 'known' elasmobranchs (Randhawa and Poulin, 2010; Caira *et al.*, 2017a). Most species of elasmobranch tapeworms were described after 1986 (Fig. 1; Randhawa and Poulin, 2019).

The number of known teleosts is much higher, with at least 35 000 described species (10 000 in fresh water and 15 000–20 000 marine) (Reis *et al.*, 2016). To date, only a small number of them has been examined for parasites. A large sample of more than 8000 freshwater teleosts of at least 300 species from 5 bioregions revealed an overall prevalence of 16%, with the highest species diversity in the Neotropical realm (Kuchta and Scholz, 2017a).

In total 101 proteocephalidean species from 81 catfish species have been reported in South America, representing an average of 1.2 proteocephalidean species per host species (Alves *et al.*, 2017; present data). Catfishes are probably the most suitable teleost group in which new tapeworms are to be discovered, but the known species diversity is still very low when compared to the diversity of elasmobranch tapeworms. The diversity of catfishes in South America alone is much higher than the total diversity of elasmobranchs in the whole world (estimated at 1915 spp. by Reis *et al.*, 2016). When extrapolated to the currently recognized species of proteocephalideans, the total diversity of proteocephalideans in South American siluriforms could reach 2400 species. However, this is almost certainly overestimation because proteocephalideans are mainly found in members of a single family Pimelodidae, and 85 proteocephalideans have been reported from 38 pimelodid species, i.e. 2.2 tapeworm species per host. Considering the existence of at least 113 pimepodid species (based on Froese and Pauly, 2022), there could be at least 250 proteocephalidean species just in fishes of this single family alone. In contrast, species diversity of proteocephalideans in other catfishes is much lower (they occur in only another 8 families). Overall, rough estimates of proteocephalidean diversity in South America vary between 1000 and 2000 species, suggesting that we have described only 5–10% of the freshwater teleost tapeworms of South America.

The prevalence and diversity of tapeworms in marine teleosts is low and also varies among different ocean depths. The shelf, epipelagic (up to 200 m) and mesopelagic fauna (up to 1000 m) is relatively poor, whereas the cestode fauna of deep-sea teleosts appears to be much richer. Kuchta and Scholz (2007) reported that only 4 of 500 teleosts of 37 species from 11 sites in the epipelagic Atlantic Ocean off Scotland were infected with only 2 species of adult tapeworms. In contrast, 20 of 286 teleosts from 42 species in the deep sea off the Outer Hebrides were infected with 5 species of bothriocephalideans (Kuchta and Scholz, 2007).

Among marine teleosts, only the family Centrolophidae (Scombriformes) represents a 'hot spot' of tapeworm diversity. To date, 16 bothriocephalid species have been reported from 9

centrolophid species, corresponding to 1.8 tapeworm species per host species. Considering the existence of 32 species of centrolophids (Froese and Pauly, 2022), there could be as many as 57 species of bothriocephalid tapeworms.

Caira and Jensen (2014, 2017) reviewed all groups of elasmobranch tapeworms, which are generally strictly host-specific (oioxenous; strict specialists), with the exception of Trypanorhyncha, where strict host specificity at the species level is not the general pattern (Palm, 2004; Caira and Jensen, 2014). A remarkable case of suprageneric specialist or even low generalist (euryxeny) has also been reported for some species of *Rhinebothrium* by Golzarianpour *et al.* (2021). In general, tapeworms are parasites of all groups of elasmobranchs (with the greatest diversity in rays), including recent freshwater lineages in South America and Southeast Asia (Caira and Jensen, 2014, 2017).

Scholz and Kuchta (2017a) found no general patterns in host use at the level of definitive hosts of teleost tapeworms, as they are found in distantly related fish groups, particularly proteocephalideans (see above). They parasitize mainly fishes of 3 teleost orders, namely Siluriformes, Cypriniformes and 'Perciformes' (=*sensu lato*). More than 60% of teleost tapeworms are specialists (Scholz and Kuchta, 2017a). Extremely low host specificity (euryxenous; high generalists) was rarely observed (8%), mainly among bothriocephalideans, including the most opportunistic helminth, *S. acheilognathi*, which has been reported from more than 300 freshwater actinopterygian species as well as axolotls, snakes and birds (Kuchta *et al.*, 2018).

Kuchta *et al.* (2020) critically revised tapeworms of cypriniform fishes known in Europe and North America and found that their host specificity is more strict than previously hypothesized by Scholz and Kuchta (2017a), primarily due to the predominance of highly specific caryophyllideans in Nearctic catostomids (Uhrovič *et al.*, 2021a, 2021b, 2022).

## Life cycles

The life cycles and transmission patterns of fish tapeworms, including marine taxa, are poorly understood (Williams and Jones, 1994; Beveridge, 2001; Poulin *et al.*, 2016). To date, at least 1 complete cycle is known for representatives of only 11 of the 18 tapeworm orders (Table 3). Life cycles are best known in 2 freshwater groups, proteocephalideans and caryophyllideans (Table 3). In elasmobranch tapeworms, life cycles are clarified only for a few species of the Trypanorhyncha and Rhinebothriidea. The first-intermediate hosts are mainly copepods (confirmed in 7 orders), less frequently amphipods or crayfish (Amphlinidea, Spathebothriidea) or oligochaetes (Caryophyllidea). The second-intermediate host is not required in fish tapeworms of at least 6 orders, but may be involved in at least 7 orders, with teleost fish (including the cyclophyllidean family Gryporhynchidae) or rarely crustaceans and cephalopods serving as second-intermediate hosts (Table 3). Tetrapods, including humans, may also serve as intermediate or accidental hosts in some taxa of the Cyclophyllidea (Mesocestoidae, Taeniidae) and in the Diphyllobothriidea (*Spirometra*).

The main obstacles to studying life cycles are the lack of diagnostic features in larval stages and the difficulty of maintaining experimental hosts in the laboratory, particularly marine invertebrates and fish. The application of DNA sequencing allowed the assignment of different ontogenetic stages of tapeworms, which helped to elucidate their development (Aznar *et al.*, 2007; Jensen and Bullard, 2010; Caira *et al.*, 2020b). For example, Caira *et al.* (2020b) confirmed molecularly the systematic position of well-known larvae infecting marine mammals tentatively designated as *Monorygma grimaldii* and *Phyllobothrium delphini*, as well as several larvae from marine teleosts that are molecularly related to the phyllobothriidean genus *Clistobothrium*.

Recently, Appy *et al.* (2019) experimentally investigated the life cycle of *Rhinebothrium urobatidium* (Rhinebothriidea) from the round stingray *Urobatis halleri* off California and found that the copepod *Tigriopus californicus* (Harpacticoidea) and gobies (*Clevelandia ios*) serve as the first- and second-intermediate hosts, respectively. This is the first completed life cycle of a rhinebothriidean tapeworm and the fourth known cycle of elasmobranch tapeworms (Table 3).

## Zoogeographical distribution

The biogeographical data collected in the last 2 decades also made it possible to significantly expand the distributional ranges of many fish tapeworms. The distributional ranges of marine tapeworms are more extensive compared to those of freshwater taxa and even span most of the globe. Overall, tropical and subtropical areas are richest in elasmobranchs (Naylor *et al.*, 2012a, 2012b) as well as their tapeworms (Caira and Jensen, 2014, 2017; Randhawa and Poulin, 2019). However, for some species of trypanorhynchs or phyllobothriideans, a near cosmopolitan distribution including Arctic areas has been demonstrated (Palm *et al.*, 2007; Beveridge *et al.*, 2017; Caira and Jensen, 2017).

The distribution of teleost tapeworms differs markedly from one another, with no obvious general pattern (see Scholz and Kuchta, 2017a). However, individual lineages are generally restricted to a single continent or biogeographical region (Amphilinidea, Bothriocephalidea, Caryophyllidea, Nippotaeniidea and Proteocephalidae). Particularly little is known about the distribution of 'deep-sea' fish tapeworms (Kuchta *et al.*, 2008b; Klimpel *et al.*, 2009; Brabec *et al.*, 2015). Most tapeworms of freshwater teleosts (and those of freshwater rays) have much more restricted distributions, usually confined to 1, at most 2, zoogeographical regions. Teleost tapeworms are more diverse in the temperate zones of the Northern Hemisphere, i.e. Nearctic and Palaearctic regions, than in the tropics, with the exception of proteocephalideans in the Neotropical region, where they account for up to 95% of all tapeworm species (with the exception of 2 amphilinideans and 4 bothriocephalideans) (Scholz and Kuchta, 2017a). Caryophyllideans dominate in the Nearctic region, along with proteocephalideans also in the Ethiopian and Palaearctic realms.

Unnatural distributions as a result of human activities are exhibited by invasive species that include caryophyllideans (*A. huronensis*, *Khawia japonica*, *K. sinensis*), bothriocephalideans (*S. acheilognathi*) and nippotaeniideans (*Nippotaenia perccotti*) (Scholz and Kuchta, 2017a). Caryophyllideans and *S. acheilognathi* have been introduced to Europe, North America, Australia and Africa probably from East Asia by infected carps (*Cyprinus carpio* and *Ctenopharyngodon idella*) (Oros *et al.*, 2004, 2009; Scholz *et al.*, 2015, 2018a; Kuchta *et al.*, 2018), but *N. perccotti* was introduced relatively recently from Asia to Central and Eastern Europe by the invasive Chinese sleeper *Perccottus glenii* (Mierzejewska *et al.*, 2012; Kvach *et al.*, 2013).

## Tapeworms as fish pathogens and causative agents of human fish-borne zoonoses

There are relatively few fish tapeworms that can be transmitted to humans. The eggs of invasive *S. acheilognathi* have been detected once in the stool of a human, but most likely as an incidental infection (Yera *et al.*, 2013). Moreover, some trypanorhynch larvae such as *Hepatoxylon trichiuri* and *Nybelinia surmenicola* have been reported (as accidental pseudoparasites) in 4 cases, apparently after accidentally ingesting an infected second-intermediate host (Heinz, 1954; Grimmo and Buckley, 1961; Ikikuchi *et al.*, 1981; Fripp and Mason, 1983). In fact, only the larvae (plerocercoids) of a few fish diphyllobothriideans (mainly *D.*

**Table 3.** Survey of life cycles by tapeworm orders

| Order | First-intermediate host (IH 1) | Second-intermediate host (IH 2) | Species number[a] | Remarks |
|---|---|---|---|---|
| Gyrocotylidea | ? | ? | 0 | Egg and larva known. Is there any IH? |
| Amphilinidea | Amphipods, crayfish | – | 2 | Studied sturgeon and turtle species |
| Caryophyllidea | Oligochaetes | – | 20 | Progenesis possible (*Archigetes*) |
| Haplobothriidea | Copepods | Teleosts | 1 | |
| Diphyllobothriidea | Copepods | Teleosts, (tetrapods) | 16 | Studied mainly human-infecting species; Cephalochlamydidae (most basal group) uses only IH 1 |
| Spathebothriidea | Amphipods | – | 2 | Progenesis possible |
| Diphyllidea | ? | (Teleosts, shrimps) | 0 | Larvae in teleosts; molecularly confirmed (Bray and Olson, 2004) |
| Trypanorhyncha | Copepods | Teleosts, shrimps, cephalopods | 3 | Additional paratenic hosts included; IH 2 known for many species |
| Bothriocephalidea | Copepods | (Teleosts) | 10 | IH 2 known only for *Triaenophorus* |
| Litobothriidea | ? | ? | 0 | |
| Lecanicephalidea | ? | ? | 0 | |
| Rhinebothriidea | Copepods | Teleosts, (molluscs) | 1 | Recently elucidated cycle (Appy et al., 2019); larvae in molluscs; molecularly identified[b] |
| Cathetocephalidea | ? | ? | 0 | |
| Phyllobothriidea | ? | Teleosts, cetaceans | | Larvae in teleosts; molecularly confirmed[b] |
| Onchoproteocephalidea I | Copepods | – | 22 | Teleosts may serve as paratenic hosts |
| Onchoproteocephalidea II | ? | (Teleosts) | | Larvae in teleosts; molecularly confirmed[b] |
| Nippotaeniidea | Copepods | – | 1 | |
| Tetrabothriidea | ? | (Teleosts?) | 0 | Teleosts are predicted, but not confirmed as IH 2 |
| Cyclophyllidea | Invertebrates, vertebrates | (Invertebrates, vertebrates) | 140 | Mostly IH 1; teleosts as IH 2 in the family Gryporhynchidae |
| 'Tetraphyllidea' relicts | ? | (Teleosts, molluscs) | 0 | Larvae in molluscs and teleosts molecularly confirmed[b] |

?, no cycle known.
[a]Number of species with known complete life cycle.
[b]Jensen and Bullard (2010).

*latus, D. nihonkaiensis* and *Adenocephalus pacificus*) can cause the disease called diphyllobothriosis in humans (see Scholz and Kuchta, 2016; Scholz *et al.*, 2019; Králová-Hromadová *et al.*, 2021).

There are also relatively few cestodes, especially their larvae (metacestodes), that are actually pathogenic to fish (Williams and Jones, 1994; Dick *et al.*, 2006; Scholz *et al.*, 2021*b*, 2021*c*). Plerocercoids of species of *Dibothriocephalus* are commonly found in the viscera and musculature of freshwater and marine teleosts, especially salmonids, including those in aquaculture, and can adversely affect heavily infected fish (Williams and Jones, 1994; Scholz *et al.*, 2021*b*). Plerocercoids of *Proteocephalus ambloplitis* in North American centrarchids and larvae of trypanorhynch tapeworms in marine teleosts may also pose a threat to local fish populations because of their pathogenicity (Williams and Jones, 1994).

Invasive parasites are a major threat to biodiversity and non-native parasites introduced to new regions can also negatively affect the health of cultured fish in newly colonized regions. Parasites introduced into new areas with their non-native hosts alter natural host–parasite interactions, which can lead to the emergence of disease in native species (Šimková *et al.*, 2019). Most invasive tapeworms are found in cyprinids, particularly common carp, which have contributed to the spread of several successful invaders among tapeworms (see above).

## Unresolved problems and prospects of future research

Despite vast progress over the past 2 decades, it is evident that only a small fraction of the global cestode diversity, including fish tapeworms, has been adequately described. The following obstacles should be overcome in future research to better characterize the true diversity of extant tapeworms in elasmobranchs and teleosts:

(1) *Limited accessibility of potential fish hosts*. Serious barriers include restrictions related to the availability of less common or protected hosts, and restrictions on the export of biological samples based on the Nagoya Protocol (Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from their Utilization to the Convention on Biological Diversity), which seriously impair or even prevent any international collaboration in research. Limited accessibility to biological samples, both hosts and their parasites, can have negative consequences for the

advancement of biodiversity studies, especially in countries with the strictest Nagoya Protocol regulations.

(2) *Methodological obstacles*. A seemingly very trivial issue, proper processing of tapeworm samples, remains one of the major obstacles in tapeworm studies. The unfortunate practice of studying long dead, non-fresh or frozen fish hosts, and the use of inappropriate fixation or inadequate processing (flattening, relaxation or use of fixatives in the case of teleost tapeworms, lack of ethanol-fixed vouchers for molecular studies, etc.), as well as headless and/or fragmented specimens, lead to poor and incomplete morphological descriptions of new taxa, including where internal structures are often misinterpreted or not adequately characterized (Oros *et al*., 2010; Scholz *et al*., 2018*b*). It is strongly recommended to collect only complete tapeworms with the scolex from freshly killed fish after they have been gently cleaned in saline and fixed in hot fixative (for teleost tapeworms), including preservation of molecular vouchers, i.e. hologenophores/paragenophores (Pleijel *et al*., 2008; Scholz *et al*., 2018*b*).

(3) *Correct host identification*. Host taxonomy and nomenclature are constantly changing (especially for elasmobranchs with over 300 new species described in the last 20 years), which can complicate their correct identification and thus assessment of the range of cestode host specificity. It is strongly recommended that tapeworm hosts always be adequately documented by photographs and tissue samples for DNA genotyping for each infected host should be deposited (Caira and Jensen, 2014; Scholz *et al*., 2018*b*).

(4) *Taxonomic crisis*. The recent biodiversity crisis is accompanied by a taxonomic crisis, i.e. a continuous loss of taxonomic expertise, including limited funding of taxonomic studies. Factors that have led to this crisis include unfavourable evaluation of taxonomy by other scientists, insufficient funding, declining effort to properly identify specimens in biodiversity studies, methods of global diversity assessment, penalization of large, long-term work and faunal surveys and bureaucratic obstacles that hinder fieldwork (Löbl, 2018).

(5) *International collaborations*. The exceptional achievements of the international cestode consortium of the projects funded by NSF-PBI (Caira and Jensen, 2017) are strong evidence of the need for international scientific collaboration in future studies on fish tapeworms. The greater the number of authors per study, the higher its quality, suggesting that more collaborations between taxonomists and experts from other fields are needed to produce more comprehensive species characterizations (Poulin and Presswell, 2016).

Our understanding of tapeworm evolution and phylogenetic relationships has improved considerably, especially for fish tapeworms. However, several important questions still remain unanswered, in part because of the lack of resolution of tapeworm relationships at the order level, such as in the so-called 'Tetraphyllidea relicts', whose members represent at least 9 independent lineages that may be established as new orders (see above; Fig. 3). The prevailing practice of deriving taxonomic conclusions and proposals for new classification, even at the ordinal level, from single-gene phylogenies (especially short sequences of the 28S rRNA gene) is somewhat problematic because phylogenies of cestodes based on a single marker, including mitochondrial genes, may not capture their evolutionary history (Trevisan *et al*., 2021).

A serious problem is also the limited suitability of some of the molecular markers widely used so far, especially ITS, since its paralogues have been detected in some species of the Caryophyllidea, Bothriocephalidea and Diphyllobothriidea (Bouzid *et al*., 2008; Králová-Hromadová *et al*., 2010, 2012; Bazsalovicsová *et al*., 2011; Brabec *et al*., 2016). The situation is particularly unfavourable with respect to the use of common molecular markers in caryophyllideans, one of the most basal groups of all cestodes. Brabec *et al*. (2012) evaluated the utility of 2 nuclear and 2 mitochondrial molecular markers (ssrDNA and lsrDNA, nad3 and cox1) for estimating caryophyllidean interrelationships. They found that these markers did not contain sufficient phylogenetic signal. Moreover, Brabec *et al*. (2012) detected multiple *trn*K + *nad*3 + *trn*S + *trn*W + *cox*1 haplotypes within individuals, suggesting gene exchange between the mitochondrial and nuclear genomes. The presence of such nuclear paralogues (i.e. numts) makes the search for informative markers to estimate their evolution unusually problematic, especially compared to other major tapeworm lineages (Brabec *et al*., 2012).

Multigene phylogenies are largely absent in fish tapeworms, with exception of phylogenetic studies on individual orders (see Waeschenbach and Littlewood, 2017), which were based on sequences of 2 nuclear and 2 mitochondrial gene sequences. Phylogenomic approaches have not been applied at all, even to the most 'problematic' groups with poor resolve position within the cestode tree, such as the Gyrocotylidea, Amphilinidea, Onchoproteocephalidea and 'Tetraphyllidea-like' lineages. Trevisan *et al*. (2021) call for a comprehensive evidence framework to be conducted in tapeworm phylogeny studies and consider the characterization of the new mitochondrial genomes a good step to provide a valuable resource for future studies on the evolutionary relationships of tapeworms. Another problem with some groups, particularly Trypanorhyncha, is the insufficient representation of the sequenced taxa to cover most of the diversity of a given group (Beveridge *et al*., 2017).

More molecular data are of course also needed for a better understanding of the actual host associations of fish tapeworms and their geographical distribution, including deciphering the most plausible scenario of colonization of individual fish groups by tapeworms and colonization of individual zoogeographical regions. Last but not least, molecular tools should be increasingly used in ecologically oriented research of fish tapeworms and in studies of their life cycles. The eDNA metabarcoding of ontogenetic stages of fish tapeworms also represents a promising tool that should be increasingly used in ecological and epidemiological studies and in screening the occurrence and species diversity of tapeworms in aquatic ecosystems. It is evident that quite good progress has been made in cestodology, but much remains to be unravelled and many interesting evolutionary and ecological questions to be answered.

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