Broad tapeworms (Diphyllobothriidae), parasites of wildlife and humans: Recent progress and future challenges

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A B S T R A C T

Tapeworms of the family Diphyllobothriidae, commonly known as broad tapeworms, are predominantly large-bodied parasites of wildlife capable of infecting humans as their natural or accidental host. Diphyllobothriosis caused by adults of the genera *Dibothriocephalus*, *Adenocephalus* and *Diphyllobothrium* is usually not a life-threatening disease. Sparganosis, in contrast, is caused by larvae (plerocercoids) of species of *Spirometra* and can have serious health consequences, exceptionally leading to host's death in the case of generalised sparganosis caused by '*Sparganum proliferum*'. While most of the definitive wildlife hosts of broad tapeworms are recruited from marine and terrestrial mammal taxa (mainly carnivores and cetaceans), only a few diphyllobothriideans mature in fish-eating birds. In this review, we provide an overview the recent progress in our understanding of the diversity, phylogenetic relationships and distribution of broad tapeworms achieved over the last decade and outline the prospects of future research. The multigene family-wide phylogeny of the order published in 2017 allowed to propose an updated classification of the group, including new generic assignment of the most important causative agents of human diphyllobothriosis, i.e., *Dibothriocephalus latus* and *D. nihonkaiensis*. Genomic data of selected representatives have also begun to accumulate, promising future developments in understanding the biology of this particular group of parasites. The list of nominal species of taxonomically most complicated genus *Spirometra* as well as host-parasite list of 37 species of broad tapeworms parasitising marine mammals (pinnipeds and cetaceans) are also provided.

1. Introduction

Broad tapeworms (members of the family Diphyllobothriidae of the order Diphyllobothriidea) are notorious for their impact on public health, especially species formerly placed in genus *Diphyllobothrium* (now *Dibothriocephalus*; see Waeschenbach et al., 2017); to prevent any confusion, the genus name of *Diphyllobothrium* will be abbreviated to *Diph.* and *Dibothriocephalus* to *Dibo.* throughout the text), and species of *Spirometra*, whose larvae called sparganum can cause human sparganosis (Daly, 1981; Kuchta et al., 2015; Kuchta and Scholz, 2017). However, vast majority of broad tapeworm species parasitise as adults in wildlife, especially in marine and terrestrial mammals. They are among the largest tapeworms on the Earth (Fig. 1), with some specimens from sperm whale reaching up to 30 m in length (Yurakhno, 1992; Yurakhno and Maltsev, 1997).

The family Diphyllobothriidae contains the well-known and most species-rich genus *Diphyllobothrium* (and *Dibothriocephalus*) housing more than 60 nominal species appearing in the literature since 1758, when the first species, *Taenia lata*, was described by Linnaeus (1758). After decades of being neglected, broad tapeworms now attract growing attention thanks to the increasing number of reports of human cases but also thanks to considerable advancement achieved by application of

molecular methods in diagnosis and epidemiological studies. Several review articles of book chapters on broad tapeworms have been published recently, but most of them focused mainly on human-infecting taxa (Dick, 2008; Scholz et al., 2009; Kuchta et al., 2015; Scholz and Kuchta, 2016). In the present review, historical data are briefly reviewed, some of recent achievements pinpointed and key questions for future research highlighted, with the focus on broad tapeworms occurring in wildlife.

2. A brief excursion to history

Broad tapeworms were among the first helminths to be recognised as human parasites because of their large size, with the body reaching up to several metres (Figs. 1 and 2). Long co-existence of broad tapeworms with humans is evidenced by archeoparasitological data from mummies and coprolites, which showed the presence of eggs of diphyllobothriid tapeworms at least since the early Neolithic period in Europe and South America (Mitchell, 2013). In 1592, two Swiss physicians, Thaddeus Dunus in Lucarno and somewhat later Gaspard Wolphius in Zurich described in a recognisable form tapeworms now known as the broad fish tapeworm (*Dibothriocephalus latus*; see Grove, 1990). However, these researchers did not recognise the differences

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Fig. 1. Microphotographs of diphyllobothriid tapeworms. A – *Adenocephalus pacificus* from *Callorhinus ursinus*, St. Paul Island, Alaska; fixed with hot water by T. Kuzmina. B – *Dibothriocephalus latus* spontaneously shed from experimentally infected man; fixed by R. Kuchta. C – *Pyramicocephalus phocarum* from *Erignathus barbatus*, Saint Lawrence Island, Alaska; fixed after relaxation by R. Rausch (MSBP 16648). D – *Dibothriocephalus alasensis* from *Canis familiaris*, Chevak, Alaska, 28 June 1958; fixed after relaxation by R. Rausch; type series (MSBP 17496). E – *Dibothriocephalus dalliae* from *C. familiaris* experimentally infected with plerocercoids from *Dallia pectoralis*, Gene Lake, Alaska, 12 March 1958; fixed after relaxation by R. Rausch; type series (MSBP 17092). F – *Plicobothrium globicephalae* from *Orcinus orca*, Newfoundland, Canada; inset: detail of the scolex; 'cold' (= in room temperature) fixation, museum sample (CMNPA 1999-0009). G – *Diphyllobothrium cordatum* (larger), *Diphyllobothrium lanceolatum* and *Diphyllobothrium schistochilos* (smaller) from *E. barbatus*; Greenland, 5 May 1916, "Crocker Land Expedition"; 'cold' fixation (SNM). H – *Diphyllobothrium cordatum* from *E. barbatus*, Greenland; 24 July 1890; decomposed material; museum sample (SNM). I – *Diphyllobothrium scotium* from *Hydrurga leptonyx*, Antarctica; type material (NMS Z.1921.1.43.1501). J – *Diphyllobothrium hians* from *Monachus monachus*; captured in Austria; collected by K.M. Diesing; type material (NMW 2684). K – *Spirometra decipiens* from *Puma concolor*, Brazil; collected by J. Natterer; type material (NMW 2682). Acronyms of museum collections: CMNPA – Canadian Museum of Nature, Parasitology Collection, Ottawa, Ontario, Canada; MSBP – Museum of Southwestern Biology, Division of Parasitology, University of New Mexico, Albuquerque, New Mexico, U.S.A.; NMS – National Museum of Scotland, Edinburgh, Scotland, U.K.; NMW – Das Naturhistorische Museum Wien, Vienna, Austria; SNM – Swedish Museum of Natural History, Stockholm, Sweden.

between this tapeworm and human-infecting *Taenia saginata* and *T. solium*. As a result, all large-sized human tapeworms were collectively called as '*Lumbricus latus*'. The first person who undoubtedly recognised these two groups and called them as *species prima* (= *Dibotriocephalus*) and *species secunda* (= *Taenia*) was another Swiss, Felix Platter (Platerus) in Basel in 1602 (see Grove, 1990).

Confusion in differentiation of human tapeworms continued throughout the following two centuries. The first illustration of broad fish tapeworm (lacking a scolex) was provided by Nicholas Andry in 1718, but the scolex was first illustrated by Bonnet in 1750 (Grove, 1990). Finally, Linnaeus (1758) named the broad fish tapeworm as *Taenia lata*. In the same book, he also described another diphyllobothrid cestodes, *Fasciola intestinorum* (now *Ligula intestinalis*), which was found as a larva (plerocercoid) in fish. A few years later, Müller (1776) described adults of *Taenia solida* (now *Schistocephalus solidus*) as the first diphyllobothriid species found in birds.

Numerous species of broad tapeworms were described in the 19th century from mammals and, much less frequently, birds, such as the human-infecting *Dibothriocephalus dendriticus* (Nitzsch, 1824), *Dibothriocephalus ditremus* (Creplin, 1825) from birds, *Diphyllobothrium stemmacephalum* Cobbold, 1858 (type species of the genus) from dolphins, and '*Diphyllobothrium*' *tetrapterum* (von Siebold, 1848) from seals. The first documented case of human diphyllobothriosis outside Europe was likely caused by the Japanese broad tapeworm, now *Dibothriocephalus nihonkaiensis* (Yamane, Kamo, Bylund and Wikgren, 1986), and was described in the traditional Japanese medical book

'Shinsen-Yamainosoushi' published in 1850 (see Yamane et al., 1998).

In 1854, Diesing (1854) established the genus *Sparganum* as a collective group to house larvae (plerocercoids) of broad tapeworms with similar morphological features. Subsequently, immature forms of diphyllobothriids were placed provisionally in this genus until the corresponding adult form was found. The first human case of sparganosis was reported as early as in 1596 (see Qiu and Qiu, 2009), but the first scientifically documented human case was that of Patrick Manson in 1881 (Cobbold, 1883). When studying lymphatic filariosis caused by the nematode *Wuchereria bancrofti* in Xiamen, China, Manson carried out a secret (in the night) autopsy of a 34-year-old man with elephantiasis. Manson found adult filariae, but also dozen ribbon-like worms in the retroperitoneal adipose tissue and pleural cavity. He sent these specimens to Cobbold in London who named them *Ligula mansoni* Cobbold (1883), but they were later renamed as *Bothriocephalus liguloides* Leuckart, 1886 and finally *Spirometra mansoni* by Faust et al. (1929).

In the 20th century, research on broad tapeworms was quite intensive, especially in North America (pivotal papers by Justus F. Mueller on *Spirometra* and Robert L. Rausch's accounts on species of '*Diphyllobothrium*' mainly from North America) and former Soviet Union (Siberia and Far East of Russia by several authors) (Delyamure et al., 1985). From the latter country, as many as 1,725 studies on diphyllobothriids were published in Russia between 1950 and 1972 (Rosenberg, 1977). Noteworthy are also numerous studies from Scandinavia, e.g., K. Andersen, B. von Bonsdorff, G. Bylund, O. Halvorsen, R. Vik and others
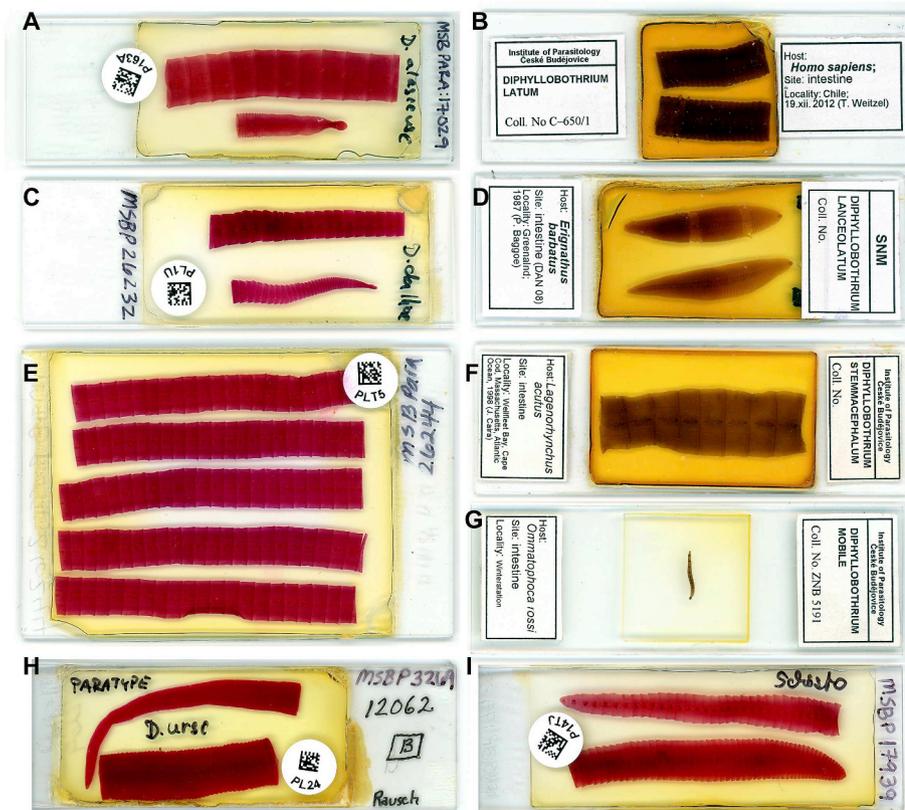
Fig. 2. Microphotographs of permanent slides of diphyllobothriid tapeworms. A – *Dibothriocephalus alasensis* from *Canis familiaris*, Hooper Bay, Alaska, March 18, 1958; fixed after relaxation by R. Rausch (MSBP 17029). B – *Dibothriocephalus latus* from *Homo sapiens*, Chile, 19 November 2012; contracted clinical sample fixed with 'cold' fixative by T. Weitzel. C – *Dibothriocephalus dalliae* from *C. familiaris*, Alaska, 5 November 1970; fixed after relaxation by R. Rausch (MSBP 26232). D – *Diphyllobothrium lanceolatum* from *Erignathus barbatus*, Greenland, 7 October 1987; collected by P. Baagoe (SNM). E – *Dibothriocephalus* cf. *nihonkaiensis* from *Homo sapiens*, Newtok, Alaska, 26 March 1967; fixed after relaxation by R. Rausch (MSBP 26244). F – *Diphyllobothrium stemmacephalum* from *Lagenorhynchus acutus*, Wellfleet Bay, Cape Cod, Massachusetts, 1998; collected by J.N. Caira. G – *Diphyllobothrium mobile* from *Ommatophoca rossii*, Antarctica, 11 August 1901, Deutsche Südpolar-Expedition; collected by E. Dagobert von Drygalski (ZNB 5188). H – *Dibothriocephalus ursi* from *Ursus arctos middendorfi*, Karluk Lake, Kodiak Island, 9 October 1952; fixed after relaxation by R. Rausch; paratype (MSBP 3269). I – *Schistocephalus* sp. from *C. familiaris*, Newtok, Alaska, 4 April 1958; fixed after relaxation by R. Rausch (MSBP 17939). Acronyms of museum collections: MSBP – Museum of Southwestern Biology, Division of Parasitology, University of New Mexico, Albuquerque, New Mexico, U.S.A.; SNM – Swedish Museum of Natural History, Stockholm, Sweden; ZNB – Zoologische Museum Berlin, Berlin, Germany.

(see von Bonsdorff, 1977), North America (e.g. T. Dick, T.V.M. Cameron, H.E. Essex, T.B. Magath, L. Margolis, T. Vergeer, R.A. Wardle) and Japanese researchers (e.g., E. Eguchi, H. Kamo and Y. Yamane). However, attention paid to broad tapeworms sharply declined in the last decades of the 20th century.

Life cycles of only a few broad tapeworms are known currently. The source of human infection with broad fish tapeworm was first identified by the Finnish researcher H. D. Spöring, in 1747. He noticed that people who lived on the banks of rivers, rapids and lakes with abundant fish suffered from the tapeworm infections more than human populations living in other localities. In 1881, M. Braun experimentally infected dogs and three medical students with plerocercoids from pike; later, he found a large number of eggs of *D. latus* in students' stool. However, the full three-host life cycle that includes also copepods as the first intermediate host was completely elucidated by Janicki and Rosen (1917) in Switzerland for *Dibo. latus* and just 2 years later by Okumura (1919) in Japan for *S. mansoni* (= *S. erinaceieuropaei*). Another breakpoint in our knowledge of the biology of broad tapeworms was made by Gnezdilov (1957) in former Soviet Union who discovered that golden hamsters could be easily infected with plerocercoids of the genus *Dibothriocephalus* to produce adult worms in the laboratory. In contrast, attempts to culture broad tapeworms *in vitro* have not been successful with exception of almost whole life-cycle of *Schistocephalus solidus* and *Spirometra mansonoides* (Berntzen and Mueller, 1972; Mueller, 1974; Jakobsen et al., 2012).

3. Diversity, phylogenetic relationships and updated classification

Considerable contribution to the present knowledge of the diversity and morphology of broad tapeworms has been made, among others, by Delyamure et al. (1985), Yurakhno (1992), Kamo (1999), to mention just a few (see Kuchta and Scholz, 2017 for more data). Remarkable advancement has been made also recently, mainly thanks to application of methods of integrative taxonomy including generation of molecular data, which proved critical for differentiation of morphologically similar taxa. Kuchta and Scholz (2017) presented a list of 58 species in 13 genera of broad tapeworms recognised as valid (see Table 1).

Waeschenbach et al. (2017) provided a robust phylogenetic hypothesis of interrelationships of diphyllobothriidean cestodes, using 30 representative species of the whole order and on two ribosomal plus two mitochondrial genes. They confirmed that the genus *Diphyllobothrium* is polyphyletic and includes closely unrelated taxa of independent evolutionary origin. As a result, the most important human-infecting species were placed in the resurrected genus *Dibothriocephalus* Lühe, 1899 (in total 7 species – see Table 1). 'True' *Diphyllobothrium* including the type species *D. stemmacephalum* comprises only 7 species from pinnipeds, including *Diplogonoporus balaenopterae*, type species of *Diplogonoporus*, which is invalidated (for diplogonadic forms, separate genera should not be proposed because the number of genital complexes may vary even within the strobila of a single worm (Hernández-Orts et al., 2017). Non-monopyletic '*Diphyllobothrium*' provisionally comprises 20 species (8 characterised molecularly) that do not form a monophyletic assemblage; these species are considered as *incertae sedis* (Waeschenbach et al., 2017).

4. Host associations and life cycles

Tapeworms of the order Diphyllobothriidea are peculiar among all other tapeworm orders but one (Cyclophyllidea) cestode orders in successful colonising all major tetrapod groups. Molecular data revealed that the main lineages corresponding to three families recognised by Kuchta et al. (2008) reflect the evolutionary history of their tetrapod definitive hosts and the complexity of parasites' life-cycles (Waeschenbach et al., 2017). Species of the most speciose and relatively more derived lineage of the order, the Diphyllobothriidae, parasitise mammals including humans and, to a lesser extent, birds as definitive hosts. Earliest diverging groups of diphyllobothriids (*Spirometra* and

Table 1
List of genera of diphyllobothriid tapeworms with numbers of their species, definitive hosts and habitats.

genus	spp.	definitive host	habitat	reference
Adenocephalus	1	**M**[a]: Otariidae, (Canidae, Hominidae)	marine	Hernández-Orts et al. (2015)
Baylisia	2	**M**: Phocidae	marine	Kuchta and Scholz (2017)
Baylisiella	1	**M**: Phocidae	marine	Kuchta and Scholz (2017)
Dibothriocephalus	7	**M**: Canidae, Felidae, Hominidae, Ursidae, (Muridae, Mustelidae); **A**[b] Accipitridae, Alcidae, Anatidae, Ardeidae, Corvidae, Gaviidae, Laridae, Pandionidae, Pelecanidae, Phalacrocoracidae, Podicipedidae, Sternidae	terrestrial	Waeschenbach et al. (2017)
Diphyllobothrium	7	**M**: Balaenidae, Balaenopteridae, Delphinidae, Eschrichtiidae, Monodontidae, Phocoenidae, Ziphiidae	marine	Waeschenbach et al. (2017)
'*Diphyllobothrium*'	20	**M**: Otariidae, Phocidae, (Mustelidae); **A**: Spheniscidae	marine	Waeschenbach et al. (2017)
Flexobothrium	1	**M**: Phocidae	marine	Kuchta and Scholz (2017)
Glandicephalus	2	**M**: Phocidae	marine	Kuchta and Scholz (2017)
Ligula	5	**A**: Anatidae, Laridae, Podicipedidae and many others[c]	terrestrial	Dubinina (1980)
Plicobothrium	1	**M**: Delphinidae	marine	Kuchta and Scholz (2017)
Pyramicocephalus	1	**M**: Phocidae, (Mustelidae)	marine	Kuchta and Scholz (2017)
Schistocephalus	5	**A**: Anatidae, Laridae and many others[c]	terrestrial	Dubinina (1980)
Spirometra	4	**M**: Canidae, Felidae, Herpestidae, Hyaenidae, Mephitidae, Mustelidae, Viverridae, Procyonidae, (Didelphidae)	terrestrial	Kuchta and Scholz (2017)
Tetragonoporus	1	**M**: Physeteridae	marine	Kuchta and Scholz (2017)
Total	**58**			

[a] Mammalia.
[b] Aves.
[c] 80 species of fish-eating birds (e.g., Dubinina, 1980a).

Schistocephalus) colonised freshwater-terrestrial ecosystems followed by radiation in marine mammals (pinnipeds and cetaceans – '*Diphyllobothrium*' *Adenocephalus*, etc.). In contrast, species of the most recently diverging groups (*Ligula* and *Dibothriocephalus*) use terrestrial mammals and fish-eating birds as their definitive hosts and larvae developed in freshwater environment (Waeschenbach et al., 2017).

The life cycles of the Diphyllobothriidae are always connected with aquatic environment (freshwater or marine), because the first larva (coracidium) is aquatic and needs to pass to the first aquatic intermediate host – a copepod. Two intermediate hosts are involved: copepods as first intermediate hosts and vertebrates as second intermediate hosts (Janicki and Rosen, 1917; Okumura, 1919; Kamo et al., 1973; Dubinina, 1980; Hatsushika et al., 1981). The second intermediate hosts (with the exception of the genus *Spirometra*) are freshwater or brackishwater fish (Dubinina, 1980; Kuchta et al., 2015; Kuchta and Scholz, 2017). In contrast, the life cycle of species of *Spirometra* includes a wide spectrum of amphibians, reptiles, birds or mammals as second intermediate hosts, but never fish (see chapter 7 below).

Adults of *Dibo. dendriticus* and *Dibo. ditremus* have been reported from fish-eating birds (Markowski, 1949; Delyamure et al., 1985; Kuchta et al., 2013). The spectrum of these hosts is rather wide, but they are primarily core water birds (clade Aequornithes), less frequently members of the orders Anseriformes, Charadriiformes and Podicipediformes, whereas records from the Accipitriformes, Gruiformes and Passeriformes are considered accidental (Delyamure et al., 1985). Only one species, *Diph. scoticum* (Rennie et Reid, 1912) was reported to parasitise penguins, along with its typical definitive hosts, seals (Kuchta and Scholz, 2017).

Most species of *Ligula* and *Schistocephalus* are euryxenous at the level of definitive hosts, with adults of these genera having been reported from almost 80 species of fish-eating birds (Dubinina, 1980). For example, *S. solidus* has been reported from as many as 42 species in eight bird orders (Vik, 1954). In contrast, three-spined sticklebacks (*Gasterosteus aculeatus*) serve as the only second intermediate host species of this tapeworm: plerocercoids continue to grow for an unusually long time (several months), and nearly reach sexual maturity in the fish host. In the definitive host, adults of *S. solidus* survive only few days, producing high numbers of eggs meanwhile (Dubinina, 1980). However, gravid adults of *Ligula* and *Schistocephalus* were occasionally (accidently?) as well as after experimental infection found also from mammals as dogs and cats (Rausch et al., 1967; Dubinina, 1980; Fig. 2I).

5. Broad tapeworms and human-infections (diphyllobothriosis and sparganosis)

Humans get infected mainly by terrestrial species of the genera *Dibothriocephalus* and *Spirometra* (Figs. 1 and 2), but also by a few species that normally mature in marine mammals such as *Adenocephalus pacificus* and *Diph. balaenopterae*. Scholz and Kuchta (2016) critically reviewed records of 19 species of broad tapeworms (except for species of *Spirometra*) previously reported from humans. They found many of the records of human cases doubtful, accidental or apparently erroneous, and concluded that only the following six species can be considered genuine human parasites (all confirmed with molecular techniques): *A. pacificus*, *Dibo. dendriticus*, *Dibo. latus*, *Dibo. nihonkaiensis*, *Diph. balaenopterae* and *Diph. stemmacephalum*. The remaining 13 species should not be considered typical human parasites because they have been reported from humans only rarely and their identification based on morphological characters only (Scholz and Kuchta, 2016).

Waeschenbach et al. (2017) provided evidence that human parasitism evolved on minimum of four independent occasions within the broad tapeworm clade. Two of those lineages include tapeworms living in freshwater/terrestrial habitats (species of *Spirometra* and *Dibothriocephalus*) and two in marine habitats (*A. pacificus* and *Diph. balaenopterae* with *Diph. stemmacephalum*). The origin of most of the human infections with broad tapeworms is likely zoonotic, i.e. the parasites of wildlife infecting humans accidently (Waeschenbach et al., 2017). Humans likely represent the principal definitive hosts only for *Dibo. latus* and, probably, *Dibo. nihonkaiensis*; the former species has the ability to grow faster in humans compared to other experimental hosts (dogs, cats, wolves, foxes, etc. Essex and Magath, 1931; Andersen, 1975; von Bonsdorff, 1977).

Humans are usually infected with euryxenous species, e.g., *Dibo. dendriticus*, *Dibo. nihonkaiensis*, *Dibo. latus*, *A. pacificus*, *Diph. balaenopterae*, *Diph. stemmacephalum*, whereas reports of human cases caused by presumably stenoxenous or oioxenous species ('*Diph.*' *scoticum*, '*Diph.*' cf. *cameroni* and '*Diph.*' cf. *hians*) are rare and validity of *Dibo. alascencesis*, *Dibo. daliae* and *Dibo. ursi* reported exclusively from Alaska by R. Rausch needs verification (Scholz and Kuchta, 2016; Waeschenbach et al., 2017) (Figs. 1 and 2). Numerous unverified or questionable records further bias reliable assessment of the actual host spectrum of broad tapeworms including those parasitising humans. In addition, definitive hosts of broad tapeworms are often predators and may thus represent postcyclic or incidental hosts.

Broad tapeworms of terrestrial and marine mammals are seemingly capable of better survival in the environment of human intestines compared to species occurring in birds such as *Dibo. ditremus* that is likely incapable of infecting humans (Waeschenbach et al., 2017). Therefore, it was probable that ecological rather than evolutionary factors played a key role in the origin of broad tapeworms infections in humans, i.e., consumption of raw or poorly cooked fish in the case of species of *Adenocephalus*, *Dibothriocephalus* and *Diphyllobothrium*, and amphibians, snakes or mammals in the case of *Spirometra* (Waeschenbach et al., 2017).

Based on habitat, diphyllobothriids can be divided into two ecological groups: (i) parasites of marine mammals (confirmed from 32 species of phocids and 28 species of cetaceans) that are relatively narrowly host specific (37 species – see Supplementary Table 1), and (ii) parasites of terrestrial mammals (mainly canids and felids), less frequently fish-eating birds, both displaying lower levels of host specificity (euryxeny; 21 species). The majority of the members of the terrestrial group (i.e., species of the genera *Dibothriocephalus*, *Ligula* and *Schistocephalus*) use freshwater and anadromous teleosts as second intermediate hosts, whereas species of *Spirometra* use tetrapods, mainly amphibians and reptiles, but never fish as second intermediate hosts (Mueller, 1974; Daly, 1981; Kuchta and Scholz, 2017).

A better knowledge of the host associations and geographical distribution of causative agents of human diphyllobothriosis (Fig. 3) is impeded by erroneous diagnosis (numerous misidentifications with *Spirometra*) and the existence of doubtful or erroneous records, especially from the subtropical and tropical regions, including Ethiopia (Abere et al., 2013), India (Ramana et al., 2011; Sasikala et al., 2018), Nigeria (Umar, 2009; Alayande et al., 2013), or Pakistan (Kuntz, 1960).

6. Broad tapeworms in wildlife

Marine mammals are hosts of almost 2/3 (64%) of diphyllobothriids, i.e., 37 of a total number of 58 known species of broad tapeworms (Kuchta and Scholz, 2017; Supplementary Table 1). They infect mainly pinnipeds (reported from 17 of 19 species of the Phocidae and 15 of 16 species of the Otariidae), but also cetaceans (reported from 7 of 13 species of the Mysticeti and 21 of 55 species of the Odonoceti – Supplementary Table 1). Pinnipeds or seals (Phocidae and Otariidae) serve as definitive hosts for 30 diphyllobothriid species (52% of broad tapeworm diversity). Out of these, phocids host a much richer (28 species) fauna compared to otariids with only four species, *A. pacificus* being the only species specific to eared seals. Cetaceans of the families Balaenidae, Balaenopteridae, Delphinidae, Eschrichtiidae, Monodontidae, Phocoenidae, Physeteridae and Ziphiidae host nine broad tapeworm species (Supplementary Table 1).

Infection rate in seals can be extraordinarily high, with prevalence reaching up to 100% (Kuzmina et al., 2015, 2018) and with extremely high intensity of infections, especially in Antarctic seals. For example, the Weddell seal (*Leptonychotes weddellii*) is a host of 7 diphyllobothriid species and the mean intensity reported by Yurakhno and Maltsev (1997) reaching an estimated 1,300,000 tapeworms per host (based on examination of 28 individuals). The most heavily infected seal harboured as many as 3,600,000 specimens of *D. mobile*, but majority of specimens were juvenile (Yurakhno and Maltsev, 1997). The leopard seal (*Hydrurga leptonyx*) was also found heavily infected with four diphyllobothriid species, with *Diph. quadratum* and *Diph. scoticum* being the most abundant (mean intensity of 180,000 specimens per seal; 60 of 67 seals examined were infected). The highest intensity of infection was recorded in a one-year-old *H. leptonyx* with 1,600,000 individuals of
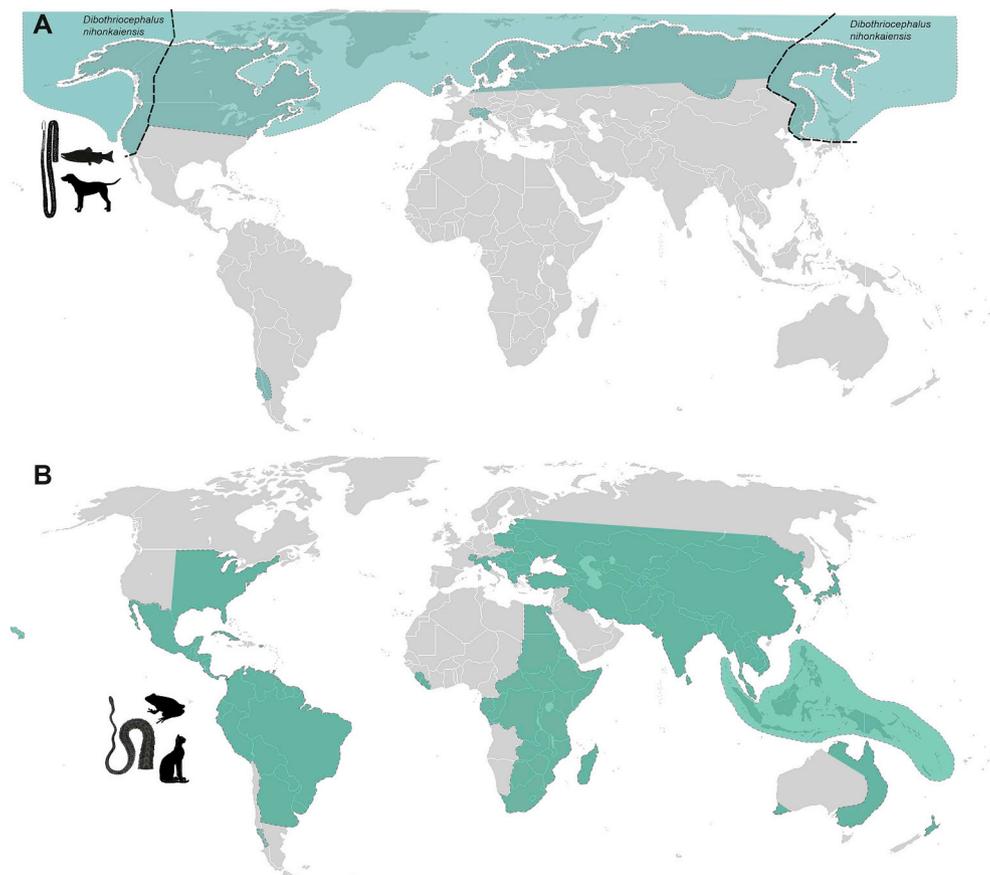
Fig. 3. Distribution of two genera of diphyllobothriid tapeworms from wildlife and man. A – *Dibothriocephalus* spp., B – *Spirometra* spp. Based on available literature data by countries except for some large countries where occurrence was estimated based on data available (Russia, China, etc.).

Diph. quadratum (see Yurakhno and Maltsev, 1997).

Intensity of infection of seals (Phocidae) in the Northern hemisphere, compared to the seals in the Southern hemisphere, is generally much lower, but still remains relatively high. Nearly every single bearded seal (*Erignathus barbatus*) is usually infected with diphyllobothriids and the maximum intensity of 50,000 individuals of *Diph. lanceolatum* and *Diph. schistochilos* has been reported (Delyamure and Popov, 1975; Delyamure et al., 1976; Fiscus et al., 1976; Shulman and Popov, 1982; Schaeffner et al., 2018) (Fig. 1G). Even the endemic Hawaiian monk seal, *Neomonachus schauinslandi*, is heavily infected with as many as three species of broad tapeworms with prevalence of 78% (282 seals examined – Reif et al., 2006). However, great majority of broad tapeworms found in these heavily infected pinnipeds are juvenile or immature. For example, Kuzmina et al. (2015) found that 70% of 14,660 tapeworms of three species in 756 northern fur seals (*Callorhinus ursinus*) were immature.

Cetaceans are also common hosts of diphyllobothriids with nine species reported including the type species *Diph. stemmacephalum* (Supplementary Table 1). The infection rates, however, reach much lower levels compared to pinnipeds, with common prevalence being about 10% and intensity of infection much lower than that in seals (Brattey and Stenson, 1995; Herreras et al., 1997; Gibson et al., 1998; Krivokhizhyn, 2000; Kleinertz et al., 2014). High prevalence (52%; 25 hosts examined) of diphyllobothriid eggs, most likely a species of *Tetragonoporus*, was found in the sperm whale (*Physeter macrocephalus*) in the Mediterranean Sea (Hermosilla et al., 2018).

Terrestrial species of broad tapeworm genera such as *Spirometra* or *Dibothriocephalus* are not able to mature in pinnipeds or cetaceans and only plerocercoids of *Dib. dendriticus* and *Schistocephalus solidus* have been rarely found in seals from Lake Baikal and Baltic Sea, most likely representing accidental infections (Pronin and Zhaltsanova, 1999; Sinisalo et al., 2003). However, several previous checklists erroneously listed as many as eight pinnipeds and cetaceans as definitive hosts of the human broad fish tapeworm *Dibo. latus* (see Felix, 2013). Broad tapeworms of terrestrial vertebrates are represented by 21 species of four genera, *Dibothriocephalus*, *Ligula*, *Schistocephalus* and *Spirometra* (36% of all known diphyllobothriids). They infect significantly wider spectrum of hosts and generally exhibit far lower host specificity compared to marine species (see above). Members of the genera *Dibothriocephalus* and *Spirometra* are typical parasites of carnivores (several unrelated families), occasionally of fish-eating birds (some species of *Dibothriocephalus*).

The prevalence and intensity of infection with diphyllobothriids in terrestrial mammals are very variable and differ across localities/regions studied; majority of records comes from colder latitudes (Fig. 3). Dogs and cats are infected with species of *Dibothriocephalus* with the prevalence ranging from 2 to 50% (Rausch and Hilliard, 1970; Salb et al., 2008; Schurer et al., 2013). Muratov (1993) provided comprehensive data on the prevalence of *Dib. nihonkaiensis* (as *Diphyllobothrium klebanovskii*) in the Russian Far East based on a survey of 2,198 terrestrial mammals of 18 species. He found that the brown bear (*Ursus arctos*) and black bear (*Selenarctos tibetanus*) were most heavily infected (prevalence up to 50%) with the intensity of infection up to 538 tapeworms per brown bear individual. The prevalence and intensity of infection were much lower in other mammals such as wolf, domestic dog, American mink or domestic pig, prevalence not reaching more than 2% with intensity of infection 1 or 2 tapeworms per host.

Species of *Spirometra* occur in warmer latitudes (Fig. 3) than species of *Dibothriocephalus*. Dogs are also infected with Spirometra but with lower infection rates compared to cats (Mueller, 1974; Daly, 1981). Prevalence of infection in dogs varied from 0.6% (500 examined hosts) in Thailand to 44% (34) in Laos (Rojekittikhun et al., 2013; Otake Sato et al., 2017) and in cats from 1% in New Jersey, U.S.A. and 13% (55) in Laos to 40% in China (116) up to 61% in New South Wales, Australia (146) (Mueller, 1974; Ryan, 1976; Scholz et al., 2003; Hong et al., 2016). Some mammals such as raccoons or man (see below) may serve as second intermediate as well as definitive hosts of species of *Spirometra* (Mueller, 1974; Daly, 1981).

7. *Spirometra* & sparganosis: current problems and prospects

Species of the genus *Spirometra* have been recognised as intestinal parasites of carnivores for a long time, but still remain unsatisfactorily known (Daly, 1981; Kuchta and Scholz, 2017). Despite numerous attempts to clarify their taxonomy, host specificity and geographical distribution (Faust et al., 1929; Wardle et al., 1974), the genus remains one of the most complicated groups of tapeworms. Iwata (1934, 1972), Mueller (1974) and Odening (1985) concluded that it is almost impossible to distinguish some of nearly 50 nominal species of *Spirometra* based on morphological characteristics only (Table 2). In the last revision of the family, Kamo (1999) recognised only four species as valid; Kuchta and Scholz (2017) accepted this taxonomic view. Our preliminary molecular data (LSU and *cox*1) comparisons of isolates of *Spirometra* from several biogeographical regions indicate that the actual species diversity of the genus is higher and different than assumed by previous authors including Kamo (1999) and Kuchta and Scholz (2017). Taxonomy of this genus should thus be regarded as in its infancy thanks to the numerous problems with species circumscription and distinguishing remain to be resolved using methods of integrative taxonomy applied to newly collected and properly processed material (Kuchta and Scholz, 2017).

Unfortunately, general uniformity of most species, their high intraspecific variability and lack of agreement among investigators as to species circumscription has led to confusion about the classification of *Spirometra* (Mueller, 1974; Daly, 1981; Kuchta and Scholz, 2017). Moreover, most of the available material was obtained from host examined long time *post mortem* or even from decomposed carcasses, which may have caused significant morphological changes (Hernández-Orts et al., 2015). Live tapeworms obtained from experimentally infected hosts were usually fixed under pressure or following their relaxation in saline or tap water, which may have also led to unnatural changes in worms' morphology and anatomy. As a result, morphological and biometrical data in some species descriptions may be misleading or even erroneous, which seriously impedes reliable species identification of individual taxa.

Similarly, most clinical samples of larval stages (plerocercoids called 'sparganum'; plural 'spargana') were not characterised molecularly and were described under four different names (Table 2). In many cases, no voucher material has been preserved for many records to confirm identification. Poorly resolved taxonomy and classification of the genus have also led to apparently erroneous reports, such as repeated identification of isolates from southeastern Asia as the South American species *S. decipiens* and the European *S. ranarum* in Myanmar (Jeon et al., 2015, 2018). Cosmopolitan distribution of the type species, *S. erinaceieuropaei*, is also questionable and should be confirmed by a critical study of isolates from throughout the world, mainly from Europe. This species was described from Europe and its occurrence may be limited.

Another serious limitation that has considerably contributed to the existing deplorable situation in the taxonomy of *Spirometra* is very poor morphological description of the type species, *S. erinaceieuropaei*, originally based on larvae (plerocercoids) from a European hedgehog (*Erinaceus europaeus*) from an unknown locality in Europe. It is desirable to obtain presumably conspecific adults and larvae from Europe for a detailed morphological and molecular characterisation of the type species and its differentiation from other congeneric species (Odening and Bockhardt, 1982; Qiu and Qiu, 2009; Kuchta and Scholz, 2017). However, adults of *Spirometra* are reported from Europe very rarely and prevalence of infection of carnivorans with adults is apparently very low and restricted to a few localities such as Białowieża National Park in Poland, Belarus, Lithuania, Ukraine or Bulgaria (Odening, 1985; Kornyushin et al., 2011; Kołodziej-Sobocińska and Miniuk, 2018).

Table 2
Nominal species of *Spirometra* (adults in grey frame, plerocercoids not highlighted).

	Genus	Species	Authority	Hosts	Distribution
1.	*Dubium*	*erinaceieuropaei*	Rudolphi, 1819	*Erinaceus europaeus*	Europe (Germany)
2.	*Bothriocephalus*	*felis*	Creplin, 1825	*Felis catus*	Europe (Germany?)
3.	*Bothriocephalus*	*maculatus*	Leuckart, 1848	*Panthera pardus*	imported from Africa or Asia
4.	*Dibothrium*	*decipiens*	Diesing, 1850	*Panthera onca* and other felids	South America (Brazil)
5.	*Dibothrium*	*serratum*	Diesing, 1850	*Cerdocyon thous, Canis familiaris*	South America (Brazil)
6.	*Ligula*	*reptans*	Diesing, 1850	*Saimiri sciureus*	South America (Brazil)
7.	*Dibothrium*	*folium*	Diesing, 1850	*Ichneumia albicauda*	Africa (Sudan)
8.	*Sparganum*	*affine*	Diesing, 1854	*Lissotriton* sp.	Europe (?)
9.	*Sparganum*	*mygales moschatae*	Diesing, 1854	*Melogale moschata*	Asia (China?)
10.	*Sparganum*	*falconis*	Diesing, 1854	*Falconis* sp.	not known
11.	*Sparganum*	*strigis accipitrinae*	Diesing, 1854	*Asio flammeus*	not known
12.	*Sparganum*	*lanii pomerani*	Diesing, 1854	*Schetba rufa*	Africa (Madagascar?)
13.	*Sparganum*	*ardeae coerolae*	Diesing, 1854	*Egretta caerulea*	South America (?)
14.	*Ligula*	*ranarum*	Gastaldi,1854	*Pelophylax esculentus*	Europe (Italy)
15.	*Dibothrium*	*sulcatum*	Molin, 1858	*Panthera pardus*	Europe (Italy – zoo?)
16.	*Sparganum*	*ellipticum*	Molin, 1858	*Martes foina*	Europe (Italy)
17.	*Sparganum*	*lanceolatum*	Molin, 1860	*Erinaceus europaeus*	Europe (Italy)
18.	*Ligula*	*pancerii*	Polonio, 1860	*Natrix natrix*	Europe (Italy)
19.	*Bothriocephalus*	*marginatus*	Krefft, 1871	*Macropus* sp.	Australia (Queensland)
20.	*Ligula*	*mansoni*	Cobbold, 1882	*Homo sapiens*	Asia (China)
21.	*Bothriocephalus*	*liguloides*	Leuckart, 1886	*Homo sapiens*	Asia (Japan)
22.	*Bothriocephalus*	*didelphidis**	Ariola, 1900	*Didelphis aurita*	South America (Brazil)
23.	*Bothriocephalus*	*ratticola*	von Linstow, 1904	*Rattus rattus*	Asia (Singapore)
24.	*Plerocercoides*	*prolifer*	Ijima, 1905	*Homo sapiens*	Asia (Japan)
25.	*Sparganum*	*baxteri*	Sambon, 1907	*Homo sapiens*	Africa (Central African Republic)
26.	*Sparganum*	*raillieti*	Rátz, 1913	*Sus scfrofa*	Europe (Hungary)
27.	*Bothriocephalus*	*longicollis*	Parodi et Widakowich, 1917	*Panthera onca, Puma yagouaroundi*	South America (Argentina – zoo)
28.	*Dibothrium*	*tangalongi*	MacCallum, 1921	*Viverra tangalunga*	Asia (Indonesia – Borneo)
29.	*Sparganum*	*philippinensis*	Tubangui, 1924	*Paradoxurus hermaphroditus*	Asia (Philippines)
30.	*Lueheella*	*pretoriensis*	Baer, 1924	*Otocyon megalotis*	Africa (South Africa)
31.	*Diphyllobothrium*	*theileri*	Baer, 1924	*Leptailurus serva, Felis silvestris cafra*	Africa (South Africa)
32.	*Diphyllobothrium*	*bresslaui*	Baer, 1927	*Didelphis marsupialis*	South America (Brazil)
33.	*Diphyllobothrium*	*gracile*	Baer, 1927	*Felis macrura*	South America (Brazil)
34.	*Diphyllobothrium*	*houghtoni*	Faust Campbell et Kellogg, 1929	*Homo sapiens*	Asia (China)
35.	*Diphyllobothrium*	*okumurai*	Faust Campbell et Kellogg, 1929	*Canis familiaris*	Asia (China)
36.	*Diphyllobothrium*	*fausti*	Vialli, 1931	*Erinaceus amurensis*	Asia (China)
37.	*Diphyllobothrium*	*mansonoides*	Mueller, 1935	*Felis catus*	North America (USA)
38.	*Diphyllobothrium*	*serpentis*	Yamaguti, 1935	*Naja naja arta*	South America (Argentina)
39.	*Sparganum*	*canis*	Fernandez et Vogelsang, 1935	*Canis familiaris*	South America (Venezuela)
40.	*Diphyllobothrium*	*trinitatis*	Cameron, 1936	*Procyon cancrivorus*	North America (Trinidad)
41.	*Diphyllobothrium*	*urichi*	Cameron, 1936	*Leopardus pardalis*	North America (Trinidad)
42.	*Sparganum*	*okapiae*	Fain, 1948	*Okapia johnstoni*	Africa (Congo)
43.	*Sparganum*	*ameiva*	Vogelsang et Gallo, 1949	*Ameiva ameiva*	South America (Venezuela)
44.	*Sparganum*	*fernandezi*	Vogelsang et Gallo, 1949	*Capra hircus*	South America (Venezuela)
45.	*Spirometra*	*janickii*	Furmaga, 1953	*Lynx lynx; Canis lupus*	Europe (Poland)
46.	*Sparganum*	*cuniculi*	Lizcano Herrera, 1958	*Oryctolagus cuniculus*	Europe (Spain)

Molecular data on *Spirometra* have been collected intensively, but nearly exclusively for isolates from China and Korea, including complete characterisation of a total number of eight mitochondrial genomes (Zhang et al., 2017). While the available mitochondrial sequence-based comparisons document only very low levels of genetic differentiation within the Asian isolates (Eom et al., 2015; Jeon et al., 2015; Zhang et al., 2015, 2016, 2017), the relatively sporadic (and mostly highly fragmentary) sequence data on *Spirometra* from remaining regions suggest there is far greater diversification among geographically distant (and presumably individual species-level) taxa (Almeida et al., 2016; Eberhard et al., 2015; Petrigh et al., 2015; Waeschenbach et al., 2017). Based on this simple observation, one could expect that any sequence data of isolates from under-sampled geographical localities (Europe, Africa, the Americas) will allow to obtain far greater insights into the taxonomical richness of the genus.

The life cycle is known only partially for a few species of *Spirometra* (Daly, 1981; Kuchta and Scholz, 2017). Planktonic crustaceans (copepods) serve as the first and a wide range of tetrapods as the second intermediate or paratenic hosts. Identification of spargana from these hosts to the species level using morphological tools is impossible. The larvae are most commonly found in frogs and reptiles that serve as source of infections of mammals (Magnino et al., 2009; Oda et al., 2016). They may also occur in a spectrum of wild mammals such as badgers, baboons, feral swines, macaques, monotremes, raccoons, but also in cats and dogs and other domestic animals (Keeling et al., 1993; Nobrega-Lee et al., 2007; Stief and Enge, 2011; Woldemeskel, 2014). As many as 128 spargana have been found in a single badger (*Meles meles*) in the Białowieża Primeval Forest in Poland (Kołodziej-Sobocińska et al., 2014). It is of special interest that some of the above-listed mammals may serve as both intermediate/paratenic and definitive hosts – raccoons, foxes, hyenas, etc. (Daly, 1981; Buergelt et al., 1984; Bengtson and Rogers, 2001; Bauchet et al., 2013).

Species of *Spirometra* are distributed around the globe, throughout much of the tropics and subtropics, but also in part of Europe and Americas (Daly, 1981; Kuchta et al., 2015; Fig. 3). The prevalence of infection in the definitive as well as intermediate hosts seems to be usually very low (around 1.5% in South America – Oda et al., 2016). Exceptions include some endemic areas in Asia (e.g., in China prevalence up to 40% – Hong et al., 2016) or few studies from Serbia reporting prevalence in pigs up to 57% and from Russia in grass snake (*Natrix natrix*) up o 100% (Dubinina, 1951; Rukavina et al., 1957; Ryzhenko, 1969).

Whereas adults of *Spirometra* hardly cause any pathology, the penetration and migration of plerocercoids through tissues of intermediate and incidental hosts typically result in clinical manifestations (Daly, 1981). Adults of *Spirometra* are capable of maturing in the human intestine, causing rather rare disease spirometrosis, usually lacking any clinical symptoms (Lee et al., 1984; Wang et al., 2012; Le et al., 2017). In contrast, spargana often cause serious disease in humans and other vertebrates (mammals) called sparganosis (Daly, 1981; Bauchet et al., 2013). More than 1,600 human cases have been reported globally so far, with the number of patients recently increasing in endemic areas, especially in China and South East Asia (Liu et al., 2015). Larvae are usually located in the subcutaneous tissue and muscles of the host or alternatively invade other internal organs (Liu et al., 2015; Kuchta et al., 2015). In rare cases, sparganosis may result in fatalities, manifesting mostly as a so-called proliferative sparganosis caused by closely uncharacterised taxonomic entity called *Sparganum proliferum* (Moulinier et al., 1982; Kuchta et al., 2015). Fatal proliferative sparganosis was also reported from domestic cats in North America (Buergelt et al., 1984; Woldemeskel, 2014) and dog in Europe (Stief and Enge, 2011).

Spargana may cause rapid growth in hypophysectomised or thyroidectomised rats, and exert an ameliorative effect in the diabetic rat (Mueller, 1974; Odening, 1985). The growth response is due to a protein that is synthesised and released by plerocercoids in the host called 'sparganum growth factor' (SGF) or 'plerocercoid growth factor' (PGF). It is transported by the blood and interacts with growth hormone receptors (Phares, 1996). This activity is not yet well understood, but it illustrates the clear impact of larvae of *Spirometra* on the second intermediate, paratenic or accidental host.

8. Genomics of broad tapeworms

Broad tapeworms have found a few of their representatives in a noteworthy position of being involved in high-throughput sequencing efforts during the recently established era of genomics. Presumably thanks to the fact that the family incorporates human parasites (as well as a long-time appreciated laboratory model), three representatives of the broad tapeworms were included within the genome sequencing project run by the 50 Helminth Genomes Initiative (Coghlan et al., 2018). While not reaching comparable levels of attention to the flagship human-infecting tapeworm species (*Echinococcus* and *Taenia*), the sequencing effort resulted in gathering notable amounts of high-throughput sequence data and their assemblies into the following draft genomes in various state of completeness: *Dibothriocephaus latus* and *Schistocephalus solidus* (Coghlan et al., 2018) and *Spirometra erinaceieuropaei* (Bennett et al., 2014). The laboratory model *S. solidus* represents the most advanced genome assembly of the three at the moment, according to various genome completeness assessment measures, e.g. BUSCO (Simão et al., 2015). All of the data are publicly available from the WormBase ParaSite portal (http://parasite.wormbase.org; (Howe et al., 2017).

Schistocephalus solidus genome sequencing further benefited from independent *de novo* transcriptome sequencing undertaken by Hébert et al. (2016). In their effort, Hébert et al. (2016) generated high-throughput sequence data (more than 290,000 transcript assemblies, 10,285 high-confidence unique genes) from three developmental stages of the parasite allowing them to validate the gene prediction models previously generated based solely on the genomic sequence by the 50 Helminth Genomes Initiative. Hébert et al. (2016) then followed with careful comparisons of the relative gene expression levels of the three developmental stages, finding striking differences between gene expression patterns illustrative of the biological processes characteristic to the individual life cycle stages.

The adult worm transcriptome was found significantly enriched for reproduction-related genes, including energy metabolism genes exclusively upregulated in specific tissues, e.g., the elevated production of glyceraldehyde-3-phosphate dehydrogenase in testes as opposed to the remaining body tissues. Endocytosis-related genes were also found upregulated in the adult worm tissues. Even more interestingly, two broadly specified groups of genes lacking homology to any known genes (i.e., without functional annotation or resemblance to other parasitic helminths deposited in public sequence repositories) were found both specific and among the most differentially upregulated in either the adult or the infective plerocercoid stages. These two facts make those pools of genes notably peculiar to the parasite, potentially representing evolutionary novelties linked to the unique life histories of the parasite, and thus, the most attractive points of attention of future research (Hébert et al., 2016).

Aside of the above mentioned sequencing efforts, there has been only a single additional transcriptomic resource devoted to a broad tapeworm: an expressed sequence tags (EST) database derived from plerocercoids of *S. erinaceieuropaei* naturally infecting snakes. While the dedicated SpiroESTdb (Kim et al., 2012) database can be no longer accessed online, the EST data consisting of a total of 5,634 ESTs corresponding to 1,787 unique ESTs are available in GenBank (Kim et al., 2014). Similar to the situation in *S. solidus*, 443 ETSs of *Spirometra* did not match any of the sequences deposited in public databases based on similarity searches (at the time of the publication), potentially rendering those genes *Spirometra* lineage-specific. The EST data of Kim et al. (2014) were also directly compared to the gene models of *S.*

erinaceieuropaei derived from an independent parasite tissue source (Bennett et al., 2014). Reminiscent of *S. solidus*, all of the ESTs by Kim et al. (2014) had a significant match within the draft genome and conversely, the gene models of Bennett et al. (2014) predicted 73% of the ESTs, demonstrating the utility of the gene prediction tools employed.

Altogether, the high-throughput sequence data generated recently from an essential, broadly accessible pool of data to benefit from in future explorations into various aspects of parasitic flatworms' biology. Appealing examples from research on taeniid tapeworm models already exist, e.g., the survey of tapeworm nervous system components by Koziol et al. (2016) and Preza et al. (2018) demonstrating the conservation and/or loss of individual neurotransmitters within this evolutionary lineage. Given the relative state of the genome assembly as well as the availability (and manageability) of its life cycle in the laboratory, *S. solidus* might be the first among the broad tapeworms to join the established taeniid models and allow for further validating various biological phenomena studied in cestodes. While the life cycle of *S. erinaceieuropaei* has also been successfully established as a laboratory model (Okino et al., 2017), we suspect its sustainable maintenance would be too complicated by the requirement to keep the parasite's definitive host in the animal husbandry and thus, unfortunately, hindering developments in functional research on this human pathogen.

9. Conclusions and prospects

Broad tapeworms represent a peculiar group of cestodes because of the large size of most of their species and ability to colonise all major groups of tetrapods including humans. After a long period of being neglected, this group of predominantly parasites of wildlife began to regain some attention by the scientific community driven, in part, by the increasing number of human case reports from developed countries caused by the popularity of consuming raw meat. While benefiting from the application of recent molecular methods, most of the attention remains devoted to broad tapeworm taxa of medical importance, leaving the wildlife parasite majority neglected. Reliable estimates of human cases are still missing to allow assessment of the actual effect of broad tapeworms on human and wildlife health. Genomic data could be utilised for design of future tools for diagnosis and epidemiological surveys, including environmental DNA screenings for presence of life cycle stages of broad tapeworms in the environment. Several basic questions remain to be adequately addressed within this group: species composition of the genus *Spirometra*; ability of individual species to cause human sparganosis or spirometrosis; current occurrence and geographical distribution of causative agents of human disease; or explanation of the recent outbreak of diphyllobothriosis in Alpine lakes. Previous data on broad tapeworms of wildlife are only of limited use thanks to the general unavailability of samples suitable for DNA sequencing and the poor quality of material for morphological descriptions. Future surveys should focus on the diverse tapeworm fauna of marine, often endangered host species, as well as adult life cycle stages of *Spirometra* in terrestrial mammals and their larvae in second intermediate, paratenic or accidental hosts.

Conflicts of interest

There is no conflict of interest in submitted manuscript titled "Broad tapeworms (Diphyllobothriidae), parasites of wildlife and humans: recent progress and future challenges".

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijppaw.2019.02.001.

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