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Fish-borne, zoonotic cestodes (*Diphyllobothrium* and relatives) in cold climates: A never-ending story of neglected and (re)-emergent parasites☆

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A B S T R A C T

Fish-borne cestodes capable of infecting humans are represented almost exclusively by so called broad tapeworms, i.e. members of the order Diphyllobothriidea. These large-sized human tapeworms have three host life-cycles, in which teleost fishes (except in the case of *Spirometra*) play a role of the second intermediate hosts and represent a source of human infection. Although the broad fish tapeworms (genera *Adenocephalus*, *Diphyllobothrium* and *Diplogonoporus*) have been recognized as human parasites for a long time, many aspects of their biology and epidemiology, including species composition of individual genera, their clinical relevance and geographical distribution have been noticeably understudied. The overriding obstacle preventing clarification of the diversity, origin and host-associations of diphyllobothriids is the poor state of systematics of the group. Even though diphyllobothriosis itself is not a life-threatening disease, it is considered the most important fish-borne zoonosis caused by a cestode with up to 20 million people estimated to be infected worldwide, with an affinity to colder climates including subarctic and arctic areas of the North and partly South Hemisphere. Moreover, several species seem to (re)-emerge in the most developed countries. Current (re)-emergence of diphyllobothriosis and the introduction of its agents into new geographical regions are mainly fuelled by: (i) increased preference of human societies to consume raw food, (ii) globalized trade with fish products, (iii) human migration. Dozens of nominal species have been described so far, but only 15 species currently recognized as valid have been reported to infect humans. Moreover, the validity of species described from Alaska, which have been reported from man (*Diphyllobothrium alascense*, *D. dalliae*, *D. ursi*) should be confirmed using molecular data. Yet, we still lack information about the intraspecific variability and species boundaries of the most important broad tapeworm species including those occurring in cold climates, such as *Diphyllobothrium latum*, *D. dendriticum* and *D. nihonkaiense*. Moreover, molecular data indicate paraphyly of the genus *Diphyllobothrium*, which may explain different host associations and morphology of species in distantly related lineages. For the first time in the literature, data on all human-infecting broad fish tapeworms, most of which occur in cold climates, are summarized, with focus on rare or uncommon species that were largely neglected in the literature or appeared in hardly accessible papers.

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Contents

1. Introduction

1.1. Aim and focus of the present paper

Diphyllobothriosis and its causative agents have been reviewed in several outstanding publications (e.g., von Bonsdorff, 1977; Dick, 2008; Dick et al., 2001). Recently, Kuchta et al. (2015a) and Scholz et al. (2009) summarized the basic information on broad fish tapeworms, with focus on the most notoriously known species such as *Diphyllobothrium latum*, *D. nihonkaiense*, *D. dendriticum* and *Adenocephalus pacificus* as well as *Diplogonoporus balaenopterae* (Fig. 1A–F). In contrast, the present paper is focused on rare and infrequent human infecting fish-borne cestodes, most of them having been reported from cold climates such as Alaska (USA) and Japan.

1.2. Broad fish tapeworms: brief history, basic characteristics and morphology

Tapeworms (Cestoda) of the order Diphyllobothriidea include species that can infect humans and cause diphyllobothriosis (or diplogonoporosis) by consuming raw or undercooked fish infected with metacestodes (plerocercoids). These cestodes are commonly called broad fish tapeworms and are the causative agents of the most frequent fish-borne human disease caused by cestodes (von Bonsdorff, 1977; Dick, 2008; Kuchta et al., 2015a; Scholz et al., 2009). The first broad fish tapeworm was described already by C. Linnaeus as *Taenia lata* Linnaeus, 1758 (now recognized as *Diphyllobothrium latum*) from humans and it is by far the most frequent causative agent of diphyllobothriosis (von Bonsdorff, 1977; Dick, 2008; Kuchta et al., 2015a). However, human cases were reported long time before the formal description of *D. latum* (see Kuchta et al., 2015a).

Broad fish tapeworms are usually large worms, with the maximum length reaching up to 20 m. von Bonsdorff (1964) reported a 42 years old Finnish man infected simultaneously with 16 specimens with a total length of 333 m. Their body is composed of a large number of proglottids containing one, rarely two, set(s) male and female genital organs within each proglottid (broad tapeworms are hermaphroditic as almost all other cestodes; they are capable of self-fertilization, even though cross-fertilization is also possible if two specimens mate). The anterior end (scolex) possesses paired, usually elongate and shallow attachment organs called bothria. Proglottids are filled with numerous vitelline follicles in its cortical layer; the follicles participate in formation of eggs and represent supply for developing embryo (oocyte). The tubular uterus usually forms several loops filled with numerous eggs in the central part of proglottids; the presence of dark eggs is the most striking morphological character even in live proglottids. The eggs are shelled, with an operculum on a narrower pole and do not contain fully developed embryo (six-hooked oncosphere or hexacanth), which is formed after expulsion of the eggs from gravid proglottids to the water. Detailed information on the morphology of diphyllobothriidean cestodes including broad fish tapeworms is provided by Andersen (1987); Delyamure et al. (1985); Hernández-Orts et al. (2015); Kuchta et al. (2013).

1.3. Life cycles and transmission

The first life cycle of diphyllobothriidean cestodes was elucidated by Janicki and Rosen (1917), who successfully infected planktonic copepods with coracidia (ciliated larvae containing oncospheres) of *D. latum* from Switzerland. These crustaceans serve as the first intermediate hosts and harbor larvae called procercoids in their body cavity. Freshwater fishes such as perch (*Perca* spp.), pike (*Esox*), pikeperch (*Sander*) and burbot (*Lota*) serve as the second intermediate hosts of broad tapeworms; they become infected after consuming copepods with procercoids. The definitive hosts also gets infection per-orally, i.e. by feeding second intermediate hosts harboring plerocercoids. Life cycles of only a few freshwater species have been completed and almost nothing is known about development and transmission of marine taxa, which impedes a more effective control of fish products as potential source of human infection (Kuchta et al., 2015a).

From the epidemiological point of view, site of infection of plerocercoids in fish body plays a key role. Whereas larvae localized in the muscles represent a high risk of human infections, plerocercoids localized in the body cavity, stomach wall or on the surface of internal organs are usually less important as a source of human infection. Unfortunately, microhabitat of infective larvae of numerous species, especially those maturing in marine mammals, is not well known.

1.4. Distribution and endemic regions

Even though diphyllobothriidean cestodes, such as *Diphyllobothrium stemmacephalum* and *Diplogonoporus balanopterae*, may have a nearly cosmopolitan distribution, most species occur in cold climates. However, areas with diphyllobothriosis are unevenly distributed on the globe, depending principally on eating habits of human population in individual regions. Over the last few decades, the number of human cases has declined dramatically in historical endemic areas such as Baltic countries and Finland, the River Danube delta, Russia (Karelia), Canada and northern USA (Great Lakes). In contrast, new cases have re-appeared in subalpine lakes, which were considered free of infection for decades (Dupouy-Camet and Peduzzi, 2004). A number of imported cases of 'exotic' cestodes, such as the Pacific seal tapeworm (*Adenocephalus pacificus*) in Europe and *Diphyllobothrium nihonkaiense* in Europe, western and eastern USA (California, North Carolina), China (Shanghai) and New Zealand have recently been confirmed using molecular markers (Kuchta et al., 2015a). Application of molecular tools, including Multiplex-PCR, has also enabled us to

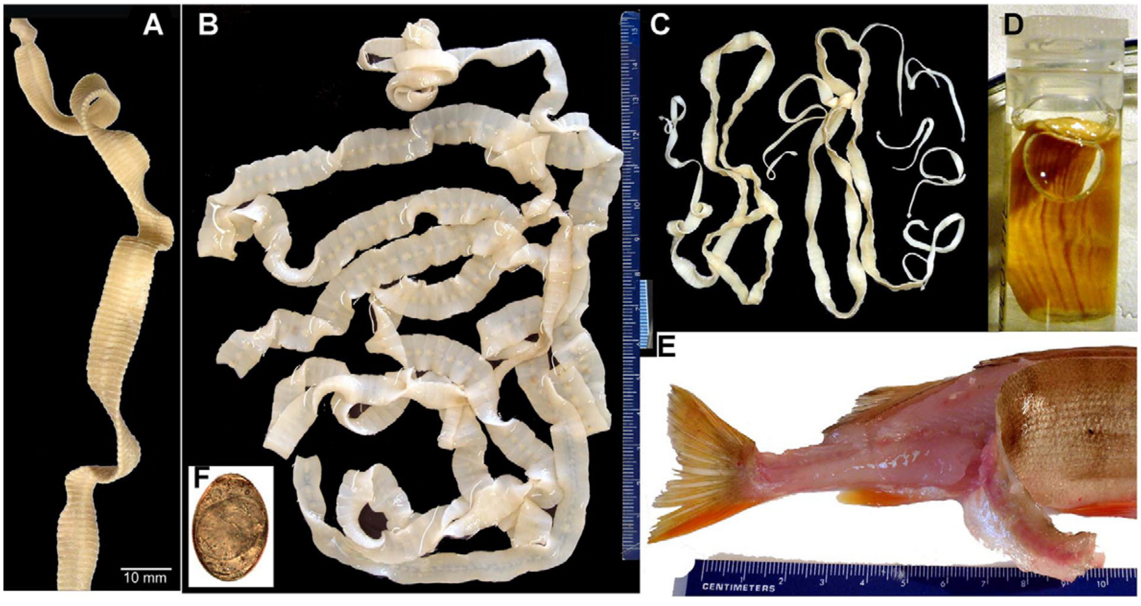

Fig. 1. A. *Diphyllobothrium dendriticum* from humans (modified from Kuchta et al., 2013). B, E, F. *Diphyllobothrium latum*. Adult from an experimental infection of a human volunteer (B); plerocercoids in the muscles of perch (*Perca fluviatilis*), Italy (E); fully embryonated eggs from a man (F). C. *Adenocephalus pacificus* from seal. D. *Diplogonoporus brauni* (=*Ligula interrupta*) from a man (type material).

reliably identify causative agents of human infection to the species level, which has changed our understanding of the actual distribution areas of several human-infecting species and documented (re)-emergence of some of them (see, e.g. Kuchta et al., 2013, 2015a, 2015b; Wicht et al., 2010).

1.5. Human disease: diagnostics, treatment and control

Diagnosis of human cases is usually based on the presence of operculate eggs or expelled parts of the strobila (chains of proglottids) in stool samples. The shape of proglottids and the median position of gonopores make their identification from other human tapeworms easy (proglottids of *Taenia* spp. have a different shape and the cirrus and vaginal pore are lateral). The eggs of diphyllobothriidean cestodes are relatively small and possess an operculum, thus superficially resembling those of some trematodes (Digenea). However, morphology-based identification of clinical samples to the species level is possible, mainly in the case of *A. pacificus* whose eggs are smaller than those of species of *Diphyllobothrium* and *Diplogonoporus* (see Hernández-Orts et al., 2015; Leštinová et al., 2016). In fact, reliable species identification of proglottids and eggs of most broad tapeworms is possible only using molecular tools, especially *cox*1 gene sequences (Kuchta et al., 2015a).

Treatment of infected patients is straightforward and a single dose of anthelminthic drug such as praziquantel is usually sufficient to expel cestodes from infected persons. The most effective and simple preventive measure to control the disease is avoiding consumption of raw fish, i.e. to eat fish that have been boiled, cooked or frozen before consuming (Kuchta et al., 2015a; Scholz et al., 2009).

2. Species capable of infecting humans

2.1. Notoriously known species

Out of 15 species of human-infecting diphyllobothriidean tapeworms, just four have been treated in detail in recent papers and reviews, namely *D. latum*, *D. nihonkaiense*, *D. dendriticum* and *A. pacificus* (see, e.g., Dick, 2008; Kuchta et al., 2015a, 2015b; Scholz et al., 2009). Therefore, only basic information about these notoriously known human-infecting species are provided herein; first intermediate hosts (always copepods of known life cycles) are not mentioned below.

2.1.1. *Diphyllobothrium latum* (Linnaeus, 1758) Lühe, 1910 (Fig. 1B, E, F)

Synonyms: *Taenia lata* Linnaeus, 1758; *Diphyllobothrium americanum* Hall et Wigdor, 1918; *D. tungussicum* Podyapolskaya et Gnedina, 1932; *D. skrjabini* Plotnikoff, 1933; see Delyamure et al. (1985) for other synonyms.

Definitive hosts (hosts to be verified marked with question mark): humans (type host), domestic dog, wild canids and felids (*Alopex lagopus*, *Canis latrans* (?), *C. lupus*, *Felis euptilura*, *F. silvestris*, *Lynx lynx* (?), *Nyctereutes procyonoides*, *Vulpes vulpes*), bears (?) (*Ursus arctos*, *U. americanus*), raccoons (?) (*Procyon lotor*), weasels (?) (*Gulo gulo*, *Lutra lutra*, *Martes martes*, *Martes zibellina*, *Meles meles*, *Neovison vison*), domestic cat (?), pig (?). Adults were obtained from experimentally infected golden hamster (*Mesocricetus auratus*).

Human infections: Estimates of a total of 10–20 million cases worldwide.

Second intermediate hosts: freshwater fishes, mainly pike (*Esox lucius*), perch (*Perca fluviatilis*), and burbot (*Lota lota*), less frequently ruff (*Gymnocephalus cernuus*), pikeperch (*Sander vitreum*), and yellow perch (*Perca flavescens*). In South America, naturalized wild and cultured salmonids such as rainbow trout (*Oncorhynchus mykiss*) have been reported as intermediate hosts of *D. latum* but these hosts need verification (Dick et al., 2001; Kuchta et al., 2015a).

Site of infection of plerocercoids: mostly free in the musculature.

Distribution: North America (Canada – Manitoba, Saskatchewan, the forested lakes of Ontario, Alberta, and USA – Lake Superior)) and Euro-Siberian bioregion (Scandinavia, Alpine lakes, River Danube basin, Russia).

Selected references: von Bonsdorff (1977); Dick (2008); Dick et al. (2001); Kuchta et al. (2015a); Scholz et al. (2009).

Remarks: This is the most frequent human fish-borne cestode, even though cases reported as *D. latum* from Japan and Korea, as well as many records from North America, were misidentified and belonged to other species, in particular *D. nihonkaiense* (see Choi et al., 2015; Kuchta et al., 2015a; Yamane et al., 1986). Records of *D. latum* from South America need confirmation. Three cases from humans have been confirmed from Chile, but they may represent imported cases (Mercado et al., 2010). Pigs may be unnatural hosts of *D. latum*. Given the possibility that reports of '*D. latum*' in felids has been confused with the related *Spirometra*, and given that cats are common hosts of *S. mansoni*, the report of *D. latum* in cats is highly suspect.

2.1.2. *Diphyllobothrium nihonkaiense* Yamane, Kamo, Bylund et Wikgren, 1986

Synonyms: *Diphyllobothrium giljacicum* Rutkevich, 1937 (?); *Diphyllobothrium klebanovskii* Muratov et Posokhov, 1988.

Definitive hosts: humans (type host), brown bear and grizzly bear (*Ursus arctos piscator*), American black bear (*U. americanus*), Asian black bear (*U. thibetanus*), wolf (*Canis lupus*), domestic dog (*Canis familiaris*), fox (*Vulpes vulpes*), rarely American mink (*Neovison vison*), pig (*Sus scrofa*); adults obtained from experimentally infected golden hamster (*Mesocricetus auratus*).

Human infections: more than 2000.

Second intermediate hosts: cherry salmon (*Oncorhynchus masou*), chum salmon (*O. keta*), pink salmon (*O. gorbuscha*), sockeye salmon (*Oncorhynchus nerka*), Japanese huchen (*Hucho perryi*), rarely whitespotted charr (*Salvelinus leucomaenis*) and taimen (*Hucho taimen*).

Site of infection of plerocercoids: free or encysted in the musculature.

Distribution: northern Pacific coast – Asia (Japan, China, Far East Russia, Korea) and western North America (Canada and North-West USA).

Selected references: Arizono et al. (2009); Awakura (1992); Catalano et al. (2015); Choi et al. (2015); Ho et al. (1979); Kamo (1978); Muratov (1990, 1993); Wicht et al. (2008a); Yamane and Shiwaku (2003); Yamane et al. (1986); Yamasaki (2012); Yera et al. (2006).

Remarks: The Japanese broad fish tapeworm is the second most frequent fish-borne cestode, even though almost all human cases of diphyllobothriosis in Japan were assigned to *D. latum*, but Kamo (1978) proposed to reconsider the taxonomic status of human-infecting tapeworms designated as *D. latum*. In 1986, Yamane et al. demonstrated morphological differences between *D. latum* from Finland and cestodes from Japan, for which they proposed a new species, *D. nihonkaiense*. Subsequent biochemical and genetic studies confirmed separate status of this Japanese species that has salmonid intermediate hosts, which further distinguishes it from *D. latum* (Arizono et al., 2009; Choi et al., 2015; Wicht et al., 2008a).

Diphyllobothrium klebanovskii was described from the lower Amur River basin in the Russian Far East (Muratov and Posokhov, 1988), but its synonymy with *D. nihonkaiense* was evidenced by Arizono et al. (2009). Dovgalev and Valovaya (1996) tentatively considered *D. giljacicum*, *D. luxi* (= probably synonym of *Adenocephalus pacificus* – see below) and *D. nihonkaiense* to be conspecific, but they did not provide any evidence.

For long time, all human cases were limited to Japan (more than 1700 cases in total – Yamane and Shiwaku, 2003; Yamasaki, 2012), but the tapeworm has recently been reported also from Korea (a total of 50 reported cases, with 36 samples sequenced – Choi et al., 2015), China and the Pacific coast of North America, i.e. Canada (British Columbia) and North-West USA. Imported cases of diphyllobothriosis caused by *D. nihonkaiense* have been recently confirmed in Europe (Czech Republic, France, Switzerland), USA (California, North Carolina, Pennsylvania), Asia (China) and Oceania (Hawaii, New Zealand) (see references above). Muratov (1990) reviewed human cases caused by *D. klebanovskii* (= *D. nihonkaiense*) in the Russian Far East.

2.1.3. *Diphyllobothrium dendriticum* (Nitzsch, 1824) Lühe, 1910 (Fig. 1A)

Synonyms: *Bothriocephalus dendriticus* Nitzsch, 1824; *Diphyllobothrium fissiceps* (Creplin, 1829); *D. cordiceps* (Leidy, 1872); *D. exile* (Linton, 1892); *Sparganum sebago* Ward, 1910; *D. minor* (Cholodkovsky, 1916); *D. canadense* Cooper, 1921; *D. strictum* (Talysin, 1932); *D. strictum* Neveu-Lemaire 1936; *D. obdoriense* Piotnikoff, 1933; *D. nenzi* Petrov, 1938; *D. laruei* Vergeer, 1942; *D. oblongatum* Thomas, 1946; *D. medium* Fahmy, 1954; *D. microcordiceps* Szidat et Soria, 1957; *D. norvegicum* Vik, 1957.

Definitive hosts: This cestode is a euryxenous parasite of birds and mammals. It has been found in 30 species of fish-eating birds from 9 families (Accipitridae, Alcidae, Corvidae, Gaviidae, Laridae, Pandionidae, Pelecanidae, Podicipedidae, and Sternidae), with the majority of the records from gulls (Laridae) [type host *Larus tridactylus*]. However, adults of *D. dendriticum* have been found also in mammals, mainly canids (foxes *Alopex lagopus* and *Vulpes vulpes*, domestic dog *Canis familiaris*) as well as in bears (grizzly *Ursus arctos*) and probably also in otters (*Lutra lutra*). Golden hamster (*Mesocricetus auratus*), golden mouse (*Ochrotomys nuttalli*) and rat (*Rattus norvegicus*) were proved to serve as suitable experimental hosts. Cestodes identified as *D. dendriticum* were also found once in *Hydromys chrysogaster* (Muridae) from Tasmania, but this record needs verification (Kuchta et al., 2013). Records of *D. dendriticum* from seals (*Pusa sibirica*, *Phoca hispida*) represent only accidental infections with plerocercoids (Kuchta and Scholz, 2016).

Human infections: about 1000 cases, most from the Lake Baikal region and Arctic and Subarctic North America (see Kuchta et al. (2013) for more data).

Second intermediate hosts: Plerocercoids have been reported from more than 50 species of 12 families of freshwater fish, but the principal hosts are salmonids including whitefish (*Coregonus* spp.) (Salmoniformes: Salmonidae).

Site of infection of plerocercoids: free (or encysted) in the viscera and body cavity, only rarely muscles.

Distribution: Holarctic (partly overlaps with *D. latum*, but *D. dendriticum* has a wider distribution, perhaps because of its bird definitive hosts; it tends to predominate in Arctic regions, but it is also found farther south than *D. latum*, in Wyoming, Montana, Great Lakes, etc.) and Patagonia (Argentina and Chile).

Selected references: Andersen et al. (1987); von Bonsdorff (1977); Chizhova and Gofman-Kadoshnikov (1968); Freeman and Jamieson (1972); Kuchta et al. (2013, 2015a); Leikina (1969); Rausch and Hilliard (1970); Vik (1957); Wicht et al. (2008b).

Remarks: *D. dendriticum* is the fourth most frequent causative agent of diphyllobothriosis in humans. Most of human cases have been reported from Lake Baikal area – Buryatia and Irkutsk (prevalence almost 30% in 1929 with around new 600 cases per year, but now just around 0.01%) and other parts of Siberia (Taymyr Peninsula, Nenetsia, Sverdlovsk, Tyumen, Yakutia, Yamalia). Only around 10 cases have been confirmed from the Arctic North America (Alaska, Nunavut and British Columbia), mostly from native Inuit populations.

Even though *D. dendriticum* is widely distributed in northern Europe, no autochthonous cases have been reported with the exception of few experimental self-infections in Norway and Finland (Vik, 1957 – he infected himself 11 times; Bylund and Wikgren, 1968 – 3 cases). There are 3 imported cases from the Czech Republic Switzerland (one patient seems to have become infected in Alaska) (Kuchta et al., 2013; Wicht et al., 2008b). Several volunteers infected themselves successfully by plerocercoids in Russia (Lake Baikal), USA (Maine) and Canada (Northwest Territories) (Andersen et al., 1987; Chizhova and Gofman-Kadoshnikov, 1968; Freeman and Jamieson, 1972), whereas other experimental infections of humans with *D. dentriticum* failed (Rausch and Hilliard, 1970).

This cestode has been previously neglected as a human parasite but recent data indicate that it may be relatively frequent (Kuchta et al., 2013).

2.1.4. Adenocephalus pacificus Nybelin, 1931 (Fig. 1C)

Synonyms: *Bothriocephalus* sp. of Stiles and Hassall (1899); *B. macrophallus* von Linstow, 1905, pro parte; *Diphyllobothrium glaciale* (Cholodkovsky, 1915); *Adenocephalus septentrionalis* Nybelin, 1931; *D. arctocephali* Drummond, 1937; *D. arctocephalinum* Johnston, 1937; *D. krotovi* Delyamure, 1955; *D. pacificum* (Nybelin, 1931) Margolis, 1956; *D. atlanticum* Delyamure and Parukhin, 1968.

Definitive hosts: 9 species of fur seals and sea lions (Pinnipedia: Otariidae), including Juan Fernández fur seal *Arctocephalus philippii* (misidentified as *A. australis*) (type host); accidental hosts: domestic dog (*Canis familiaris*) and black-backed jackal (*Canis mesomelas*).

Human infections: nearly 1000 cases, with great majority in Peru, rarely in Chile and Equador, 6 cases in Japan, 10 cases probably in the Sakhalin Island, Russia, and 5 in Spain.

Second intermediate hosts: plerocercoids were found in 21 species of marine fishes of 12 families including 1 shark (for details, see Kuchta et al., 2015b).

Site of infection of plerocercoids: encysted in the body cavity and on the surface of internal organs (see Kuchta et al., 2015b).

Distribution: Cosmopolitan (Arctic and Temperate North Pacific, Southern Ocean and Temperate South America, Temperate South Africa and Australia). However, the human cases have been reported almost exclusively from the Pacific coast of South America.

Selected references: Baer et al. (1967); Hernández-Orts et al. (2015); Kuchta et al. (2014, 2015b); Pastor-Valle et al. (2014).

Remarks: This species has been recently redescribed by Hernández-Orts et al. (2015) who also proposed resurrection of the genus *Adenocephalus* Nybelin, 1931, with *A. pacificus* as its type and only species, based on molecular data and unique morphological traits. Kuchta et al. (2015b) reviewed available literary data on human cases and provided information about geographical distribution of the parasite in human population and revised the spectrum of second intermediate hosts. Even though the great majority of human cases is limited to Peru, there are some, yet still occasional, cases of infection from Ecuador and Chile and outside South America with six cases in Japan, but without molecular evidence.

Marine fishes are the source of human infection, but their precise species composition and distribution are insufficiently known (Kuchta et al., 2015b). Recently, 4 human cases have been reported from Spain (Kuchta et al., 2014; Pastor-Valle et al., 2014), but their origin remains unknown. Import of marine fishes from endemic areas in South America on ice, i.e. not frozen, may have represented the source of human infections in Europe.

Rutkevich (1937) described *Diphyllobothrium luxi* from 10 natives at the Sakhalin Island, Russia, but this species is most probably conspecific with *A. pacificus* (see Kuchta et al., 2015b).

2.2. Neglected and/or poorly known human-infecting species

The validity of some of the species listed below requires confirmation but material suitable for genotyping is usually missing. Most of them are confined in their geographical distribution to cold or temperate climates. The key role in detecting broad fish tapeworms in humans and unravelling their species diversity and biology was played byR. L. Rausch in Alaska (see below for references to his pivotal papers). In Japan, a similarly important role was played by H. Kamo (see references below).

2.2.1. Diphyllobothrium alascense Rausch et Williamson, 1958

Definitive hosts: domestic dog (*Canis familiaris*) (type host), humans (?).

Human infections: only one doubtful record.

Second intermediate hosts: burbot (*Lota lota*), boreal smelt (*Osmerus mordax*).

Site of infection of plerocercoids: lumen of the stomach.

Distribution: North America (western Alaska).

Selected references: Adams and Rausch (1997); Hilliard (1960, 1972); Rausch and Adams (2000); Rausch and Hilliard (1970); Rausch and Williamson (1958); Rausch et al. (1967).

Remarks: This species was described from tapeworms found in 10 sled-dogs at the village of Chevak in the Yukon-Kuskokwim Delta by Rausch and Williamson (1958) and later also reported from the Hooper Bay by Rausch et al. (1967). Prevalence of infection was 13%, maximum intensity of infection was 109 tapeworms, but only 19 were mature (Rausch and Adams, 2000). This cestode was 'tentatively' identified as *D. alascence* by Rausch et al. (1967) in clinical sample from a man after anthelminthic treatment.

According to Rausch and Adams (2000), *D. alascense* most closely resembles in its morphology *D. cordatum*, a cestode of pinnipeds, especially common in the bearded seal, *Erignathus barbatus*, in northern seas (see below). Records from harbor seal in Levelock (Kvichak River) by Dailey and Fallace (1989); Margolis and Dailey (1972) and Rausch and Hilliard (1970) thus seem to have been misidentified (Rausch and Adams, 2000).

Plerocercoids are small-sized (length 0.7–1.5 mm) and are located only in the lumen of the stomach of burbot and boreal smelt; dogs are readily infected after consuming burbot. Overall prevalence in burbot was higher than 50% (Rausch and Adams, 2000). The eggs have a thick, pitted shell and the coracidium is able to survive even in seawater (Hilliard, 1960).

2.2.2. Diphyllobothrium cameroni Rausch, 1969

Definitive host: Hawaiian monk seal (*Neomonachus schauinslandi*) (type host).

Human infections: two doubtful records.

Second intermediate hosts: unknown.

Site of infection of plerocercoids: unknown.

Distribution: Pacific Ocean (endemic to Hawaii).

Selected references: Andersen (1987); Kamo et al. (1982, 1986); Rausch (1969).

Remarks: This species was described from the endemic Hawaiian monk seal in Hawaii and has been reported only by Andersen (1987) since its original description except for a doubtful record from a man in Japan. Kamo et al. (1982) identified tapeworms expelled from a 57 years old Japanese seaman as *D. cameroni* but this identification based only on proglottids needs verification because of some discrepancies between these cestodes and those of *D. cameroni* in morphometric characteristics such as diameters of the seminal vesicle and the size of the eggs. Kamo et al. (1986) reported cestodes from other Japanese seamen and identified one them as *D. cameroni*, even though its internal anatomy resembled more that of the morphologically similar *D. hians* (see Andersen, 1987). Maejima et al. (1989, 1991) re-studied these cestodes from Japanese seamen, with focus on their egg morphology and excretory system.

Since there is not any convincing evidence that *D. cameroni* can actually infect humans, it should not be considered as a human parasite.

2.2.3. *Diphyllobothrium cordatum* (Leuckart, 1863) Meggitt, 1924

Definitive hosts: bearded seal (*Erignathus barbatus*), harp seal (*Pagophilus groenlandicus*), harbor seal (*Phoca vitulina*), probably also walrus (*Odobenus rosmarus*); occasionally domestic dog (*Canis familiaris*). A woman harbored adult tapeworms and was listed first in the original description; it is thus considered as a type species (see Remarks).

Human infections: only human case was reported by Leuckart (1863) and some supposedly caused by *D. cordatum* reported by Kolpakova (1933; cited in Verhinskii, 1964) and Rausch et al. (1967).

Second intermediate hosts: unknown.

Site of infection of plerocercoids: unknown.

Distribution: Arctic and circumboreal.

Selected references: Andersen (1987); Delyamure et al. (1985); Kolpakova (1933), Leuckart (1863); Rausch (2005); Rausch and Adams (2000); Rausch et al. (1967).

Remarks: The only reliable human record of *D. cordatum* is that of Leuckart (1863) from western Greenland (70°N). He described a tapeworm voided from a woman in Godhavn (North Greenland) during her fifth pregnancy. Leuckart's (1863) description of *D. cordatum* seems to have been based on material of two species, i.e. a single fully mature cestode from a Greenland woman and about 20 much smaller, not fully mature specimens of different morphology from 5 dogs, all collected at Godhavn, in western Greenland.

Kolpakova (1933) reported frequent occurrence (prevalence 41–64%) of broad tapeworms identified as *D. latum* and *D. cordatum* in Sacha Region (Yakutia, Russia), with the maximum intensity of infection as many as 256 cestodes. Rausch et al. (1967) found scolices of tapeworms possibly belonging to *D. cordatum* in a man (lower Kuskokwim River, Alaska), but this record was not mentioned in Rausch's later paper re-describing *D. cordatum* – see Rausch (2005). This identification thus needs verification.

2.2.4. *Diphyllobothrium dalliae* Rausch, 1956

Definitive hosts: Arctic fox (*Alopex lagopus*), domestic dog (*Canis familiaris*); experimentally in glaucous-winged gull (*Larus glaucescens*) [type host].

Human infections: not known precisely.

Second intermediate hosts: Alaska blackfish (*Dallia pectoralis*), dolly varden (*Salvelinus malma*).

Site of infection of plerocercoids: free in the body cavity.

Distribution: North America (Western Alaska – St. Matthew Island, St. Lawrence Island, Chevak, Mt. Village, Tanunak), north-eastern Siberia (Lavrentiya Bay, Chukotsk Peninsula).

Selected references: Hilliard (1959, 1960); Rausch (1956); Rausch and Hilliard (1970); Rausch and Williamson (1958); Rausch et al. (1967); Zhukov (1963).

Remarks: Rausch and Hilliard (1970) considered this species to be a relatively common parasite of humans, dog, Arctic fox and gulls in the western Alaska, where Alaska blackfish was frequently eaten raw by the Eskimos (Yupiks). According to Rausch et al. (1967), it was probably the most frequent diphyllobothriid in sled-dogs from Alaska, which were fed upon blackfish in winter (). It was also found in Arctic fox from the St. Matthew and St. Lawrence Islands. Plerocercoids, but no adults, were recorded in eastern Siberia (Zhukov, 1963).

The plerocercoids of *D. dalliae* are resistant to cold and may survive for 24 h at −6 °C in a blackfish averaging 17 g (Hilliard, 1959). Morphology of the eggs and coracidia were studied in detail by Hilliard (1960). The prevalence in fish intermediate hosts around the type locality was up to 84% (45 blackfish examined), with mean intensity of 3.7 plerocercoids per fish. Zhukov (1963) reported prevalence 90% in *D. pectoralis* and 6% in *S. malma* from Lavrentiya Bay in the Chukotsk Peninsula (Russia). In contrast, examination of blackfish from other areas in Alaska such as Hooper Bay (Rausch and Williamson, 1958) or Anchorage (24 specimens from 4 lakes examined by the junior author) were unsuccessful.

2.2.5. *Diphyllobothrium elegans* (Krabbe, 1865) Meggitt, 1924

Definitive hosts: hooded seal (*Cystophora cristata*) [type host], harbor seal (*Phoca vitulina*); probably also Mediterranean monk seal (*Monachus monachus*).

Human infections: one doubtful record.

Second intermediate hosts: unknown.

Site of infection of plerocercoids: unknown.

Distribution: Arctic and circumboreal.

Selected references: Andersen (1987); Delyamure et al. (1985); Kamo (1999); Kamo et al. (1986).

Remarks: This species was originally described from hooded seal in Greenland and later reported from several other hosts and regions, but these records need verification. The only human case was reported by Kamo et al. (1986) from a Japanese seaman, but tapeworms expelled from this patient were identified as *D. elegans* only tentatively. Interestingly, the same author (Kamo, 1999) and Yamane and Shiwaku (2003) did not list this species among human parasites in the reviews of human diphyllobothriids. It remains questionable whether this species is capable of infecting humans, but is included here for completeness.

2.2.6. *Diphyllobothrium hians* (Diesing, 1850) Meggitt, 1924

Definitive hosts: Mediterranean monk seal (*Monachus monachus*) [type host]; reported also from the hooded seal (*Cystophora cristata*) (?), bearded seal (*Erignathus barbatus*) (?), ringed seal (*Pusa hispida*) (?) and harbor seal (*Phoca vitulina*) (?).

Human infections: two cases reported by Kamo et al. (1986, 1988).

Second intermediate host: unknown.

Site of infection of plerocercoids: unknown.

Distribution: Mediterranean and circumboreal.

References: Kamo et al. (1986, 1988); Yamane and Shiwaku (2003).

Remarks: This species was described from the Mediterranean monk seal and later reported from several other seals from the Arctic and Subarctic coast of Europe (Andersen, 1987; Delyamure et al., 1985; Markowski, 1952a). However, these identifications from other than type hosts are doubtful because these specimens differ in their morphology from that of the type material of Diesing (1850).

Kamo et al. (1986) reported tapeworms tentatively identified as *D. hians* from a 27 years old Japanese seaman. The same authors reported the “first” case of *D. hians* from 29 years old Japanese seaman based on re-description of *D. hians* by Markowski (1952a). The latter case is considered to represent the only reliable record of this cestode (Kamo, 1999; Scholz et al., 2009; Yamane and Shiwaku, 2003), but verification of species identification is pending.

2.2.7. *Diphyllobothrium lanceolatum* (Krabbe, 1865) Meggitt, 1924

Definitive hosts: bearded seal (*Erignathus barbatus*) [type host], ribbon seal (*Histriophoca fasciata*), harp seal (*Pagophilus groenlandicus*), ringed seal (*Pusa hispida*), harbor seal (*Phoca vitulina*); reported also from the Mediterranean monk seal (*Monachus monachus*) (?); occasionally in domestic dog (*Canis familiaris*).

Human infections: only a single plerocercoid found in man.

Second intermediate host: sardine cisco (*Coregonus sardinella*).

Site of infection of plerocercoids: free in the body cavity.

Distribution: Arctic and circumboreal.

Selected references: Andersen (1987); Delyamure et al. (1985); Krabbe (1865); Maltsev (1998); Markowski (1952a); Rausch and Hilliard (1970); Yurakhno and Maltsev (1993).

Remarks: This species was described by Krabbe (1865) from bearded seal in Greenland and it is easily distinguishable from all but one (*D. schistochilos* Germanos, 1895) species of the genus by lanceolate shape of the body. *Diphyllobothrium schistochilos* is much smaller and has a restricted distribution area (occurs only in the European part of the Arctic – Maltsev, 1998).

The only human case, which is quite doubtful and needs verification, was reported by Rausch and Hilliard (1970). These authors found *D. lanceolatum* in 7 dogs from the Hooper Bay and Kotzebue and assumed this cestode may be capable of developing also in humans. In the same study, they found three well-developed strobilae of *D. dalliae* and 52 plerocercoids and early-stage strobilae of diphyllobothriids, among which was a single plerocercoid identified as *D. lanceolatum*, in a resident of Chevak after his treatment with quinacrine. Rausch and Hilliard (1970) also reported plerocercoids of *D. lanceolatum* from the body cavity of a whitefish, *Coregonus sardinella*, from a brackish lagoon near Point Barrow, Alaska.

Considering that the only human infection assigned to *D. lanceolatum* is uncertain, and it was represented only by a plerocercoid rather than a strobilate tapeworm, this species should no longer be listed as a human parasite.

2.2.8. *Diphyllobothrium orcini* Hatsushika et Shirouzu, 1990

Definitive host: killer whale (*Orcinus orca*) [type host].

Human infections: 2 cases in Japan.

Second intermediate host: unknown.

Site of infection of plerocercoids: unknown.

Distribution: Pacific Ocean (Japan).

Selected references: Hatsushika and Shirouzu (1990); Kifune et al. (2000); Nakazawa et al. (1992).

Remarks: This species was described from a killer whale collected from the Kii Peninsula, Honshu, Japan by Hatsushika and Shirouzu (1990). Two years later, Nakazawa et al. (1992) reported one strobila without scolex assigned to *D. orcini* expelled from 39 years old man from Yokohama in Japan. The second human case was reported by Kifune et al. (2000) from 25 years old man from Kasuga in Japan. *Diphyllobothrium orcini* is morphologically similar to *D. polyrugosum* Delyamure and Skriabin, 1966 described also from killer whale in Russia, but molecular data that would confirm separate status of both species are not available.

2.2.9. Diphyllobothrium scoticum (Rennie et Reid, 1912) Meggitt, 1924

Definitive host: leopard seal (*Hydrurga leptonyx*) [type host].

Human infections: only a single case in Japan.

Second intermediate host: unknown.

Site of infection of plerocercoids: unknown.

Distribution: Antarctic.

References: Fukumoto et al. (1988); Markowski (1952b); Yurakhno and Maltsev (1994).

Remarks: The only human case was reported from a 30 year old Japanese seaman from Fukuoka Prefecture in Japan after his treatment with bithionol. The specimen expelled was without scolex, but the presence of the terminal part of the uterus forming a thick-walled pocket filled with eggs indicated that it was *D. scoticum*. The patient reported eating raw euphausiid crustaceans on the voyage to the Antarctic Ocean, but his infection with procercoids (first-stage larva – see Chervy, 2002) from the first intermediate host is doubtful. Eating of raw fish, not admitted explicitly by this patient, seems to be a more plausible explanation of his apparently accidental infection in the Antarctic.

2.2.10. Diphyllobothrium stemmacephalum Cobbold, 1858 – type species

Synonyms: *Diphyllobothrium ponticum* Delyamure, 1971; *D. yonagoense* Yamane, Kamo, Yazaki, Fukumoto et Maejima, 1981.

Definitive hosts: dolphins – harbor porpoise (*Phocoena phocoena*) [type host], bottle-nosed dolphin (*Tursiops truncatus*), Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), short-beaked common dolphin (*Delphinus delphis*), long-beaked common dolphin (*Delphinus capensis*), Risso's dolphin (*Grampus griseus*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*).

Human infections: Twenty-four cases have been reported (23 from Japan, 1 from Korea).

Second intermediate host: unknown.

Site of infection of plerocercoids: unknown.

Geographical distribution: North hemisphere.

Selected references: Andersen (1987); Fukumoto et al. (1992); Kamo et al. (1977, 1982); Lee et al. (1988); Maejima et al. (1983); Sunagawa (1965); Yamane et al. (1981, 1998); Yamasaki et al. (2016).

Remarks: Cobbold (1858) described this species from harbor porpoise off Scotland as the type species of his new genus *Diphyllobothrium*. The first human case caused by this species, but assigned to *D. latum*, was reported in 1965 from 29 years old Japanese in Okinawa, Japan (Sunagawa, 1965). Cestodes were reported as "the abnormal proglottids of *Diphyllobothrium latum* with a single or double sets of reproductive organs" by Koga and Iwata (1967), but Kamo et al. (1977) suggested the presence of a new species of diphyllobothriid expelled from humans tentatively named 'Koga-Okamura type'. These cestodes were then described as *Diphyllobothrium yonagoense* by Yamane et al. (1981).

However, Andersen (1987) synonymized *D. yonagoense* with *D. stemmacephalum* based on a morphological study of both species. So far, 23 human cases have been reported from Japan (mainly from the Honshu and Kyushu Islands) and one case from South Korea (Lee et al., 1988). All but 2 cases were detected after expulsion of tapeworms from patients and human infections were generally asymptomatic.

2.2.11. Diphyllobothrium ursi Rausch, 1954

Synonym: *Diphyllobothrium gonodo* Yamaguti, 1942 (?)

Definitive hosts: bears (*Ursus arctos middendorffi* [type host], *Ursus americanus*), occasionally humans; experimentaly in gull (*Larus glaucescens*).

Human infections: 11 cases.

Second intermediate host: sockeye salmon (*Oncorhynchus nerka*).

Site of infection of plerocercoids: encysted on the serous membrane of the stomach.

Distribution: North America – Canada (British Columbia), USA (Alaska).

Selected references: Ching (1984); Hilliard (1960); Margolis (1957); Kuchta et al. (2013); Rausch (1954); Rausch and Hilliard (1970); Yamasaki et al. (2012a).

Remarks: This species is a common parasite of bears in the northern part of North America. This large cestode (up to 11 m long) differs from *D. latum* in having a larger, more massive scolex (Rausch, 1954). Plerocercoids of *D. ursi* are well adapted to low temperatures and survived longer at −12 °C than the remaining 10 tested species of *Diphyllobothrium* in experiments of Hilliard (1959).

According to Rausch and Hilliard (1970), *D. ursi* may be a junior synonym of *D. gondo* Yamaguti, 1942, but detailed comparison of both species that would include molecular data is necessary. Andersen et al. (1987) synonymized *D. ursi* with *D. dendriticum* and Yamasaki et al. (2012a), who sequenced samples of holotype and paratype of *D. ursi*, found that *D. ursi* is most closely related to this species. In another molecular phylogenetic analysis based on *cox*1 sequences, Chilean isolates identified as *D. dendriticum* formed a distinct lineage with *D. ursi* apart from the remaining representatives of *D. dendriticum* (see Kuchta et al., 2013). However, it was not possible to provide convincing evidence that tapeworms from Chile were in fact misdiagnosed *D. ursi* or that *D. ursi* represents a large form of *D. dendriticum* from bears.

2.2.12. Diplogonoporus balanopterae Lönnberg, 1892 (Fig. 1D)

Synonyms: *Krabbea grandis* Blanchard, 1894; *Diplogonoporus fukuokaensis* Kamo et Miyazaki, 1970.

Definitive hosts: whales – sei whale (*Balaenoptera borealis*) [type host], common mink whale (*Balaenoptera acutorostrata*), blue whale (*B. musculus*), fin whale (*B. physalus*), humpback whale (*Megaptera novaeangliae*); reported also from domestic dog (*Canis familiaris*) and cat (*Felis catus*).

Human infections: 268 cases.

Second intermediate host: probably Japanese anchovy (*Engraulis japonica*), Japanese sardine (*Sardinops melanostictus*) and skipjack tuna (*Katsuwonus pelamis*).

Site of infection of plerocercoids: unknown.

Distribution: cosmopolitan.

Selected references: Arizono et al. (2008); Chung et al. (1995); Clavel et al. (1997); Eguchi and Takagi (1924); Kamo et al. (1971); Kino et al. (2002); Kuchta et al. (2015a); Pastor-Valle et al. (2014); Rausch (1964); Wilhelm, 1958; Yamane and Shiwaku (2003); Yamasaki et al. (2012b).

Remarks: Lönnberg (1892) described *Diplogonoporus balaenopterae* from sei whale in Norway and proposed a new genus, *Diplogonoporus*, to accommodate this new species. Just two years later, Ijima and Kurimoto (1894) reported tapeworms identified as *Bothriocephalus* sp. from 28 years old Japanese in Nagasaki Prefecture, Japan. This is in fact the first reported human case of diplogonoporiosis caused by *D. balaenopterae*. However, Blanchard (1894) described these cestodes as a new species *Krabbea grandis* of a new genus, *Krabbea* Blanchard, 1894. Additional species, which is apparently conspecific with *D. balaenopterae*, was described from a Japanese man as *Diplogonoporus fukuokaensis* Kamo and Miyazaki, 1970.

The life cycle of *D. balaenopterae* is partly known. Kamo et al. (1972, 1973) experimentally infected copepods (*Oithona nana*) and fish (only in Japanese). Japanese anchovy, Japanese sardine and skipjack tuna are suspected to be the most likely sources of infection in humans (Kino et al., 2002; Kuchta et al., 2015a).

Using molecular markers, Arizono et al. (2008) and Yamasaki et al. (2012b) provided evidence that tapeworms from whales and humans are conspecific. Until now, a total of nearly 300 human cases of diplogonoporiosis have been reported, which great majority of reports from Japan, where it is the second most common fish-borne cestode after *D. nihonkaiense*, with about 11% of reported cases of human infections caused by broad fish tapeworms (Yamane and Shiwaku, 2003; Yamasaki, 2012). In 1996, as many as 46 cases have been reported only from Shizuoka Prefecture (Kino et al., 2002). Since most human cases were diagnosed in June and July, juvenile Japanese anchovy captured in spring and eaten raw is assumed to have been source of human infection (Kino et al., 2002).

Only a very few records of diplogonoporiosis are known out of Japan, with 4 cases in Spain (Clavel et al., 1997; Pastor-Valle et al., 2014), 1 case from a Chilean seaman (Wilhelm, 1958) and 1 from Korea (Chung et al., 1995). The cestode has been reported twice from dogs in Chile and Alaska (Rausch, 1964; Wilhelm, 1958), but diplogonoporic tapeworms from seal, otters and mink represent another species of the genus, *D. tetrapterus* (von Siebold, 1848), which has not been found in humans (Kuzmina et al., 2015; Rausch, 1964). The complete mitochondrial genome of *D. balaenopterae* is available (Yamasaki et al., 2012).

2.2.13. Ligula intestinalis (Linnaeus, 1758) Gmelin, 1790 and Ligula interrupta Rudolphi, 1810

Synonyms: see Dubinina (1980).

Definitive hosts: numerous fish-eating birds, primarily gulls (Laridae), less frequently fish-eating species of ducks (*Bucephalus* and *Mergus*) and geese (*Podiceps*).

Human infections: two doubtful cases from Romania.

Second intermediate host: numerous cyprinid fishes (for detailed information, see Dubinina, 1980).

Site of infection of plerocercoids: free in the body cavity.

Distribution: cosmopolitan.

Selected references: Bouzid et al. (2008); Dubinina (1980); Joyeux and Baer (1929); Leon (1907, 1908, 1910); Štefka et al. (2009).

Remarks: Leon (1907, 1908, 1910) described two unusual diphyllobothriid plerocercoids found in men from Romania. One with doubled genital organs as *Diplogonoporus brauni* Leon, 1907 reported 2 times and the second with single organs in every proglottid as *Braunia jassyensis* Leon, 1908. Joyeux and Baer (1929), who critically examined rare species of human tapeworms, considered *D. brauni* to represent merely a plerocercoid of the genus *Digramma* Cholodkovsky, 1914 (= syn. of *Ligula* – see Kuchta et al., 2008) and Dubinina (1980) considered *B. jassyensis* as a synonym of *Ligula intestinalis*. Both findings represent unusual, probably accidental records of parasites of fish-eating birds in humans.

Using molecular markers including microsatellites, Bouzid et al. (2008) and Štefka et al. (2009) demonstrated the existence of several lineages of ligulid tapeworms, which most probably represent separate species differing from each other in the spectrum of fish intermediate hosts and geographical distribution. They also supported invalidation of *Digramma* proposed by Kuchta et al. (2008), because its type species, *D. interrupta*, appeared among several lineages of the *L. intestinalis* species complex.

Since both human cases reported one century ago from Romania were apparently represented by plerocercoids, i.e. larval stages, and not by sexually mature cestodes, species of *Ligula* should not be considered as human parasites.

2.2.14. Pyramicocephalus phocarum (Fabricius, 1780) Monticelli, 1890

Synonyms: *Taenia phocarum* Fabricius, 1780; *Pyramicocephalus anthocephalus* (Rudolphi, 1810) Monticelli, 1890; see Delyamure et al. (1985) for other synonyms.

Definitive host: bearded seal (*Erignathus barbatus*) (type host).

Human infections: no particular case found in the literature (see Remarks).

Second intermediate hosts: several groups of marine fishes and burbot (*Lota lota*) – see Remarks.

Site of infection of plerocercoids: body cavity and internal organs

Distribution: Arctic and circumboreal.

Selected references: Delyamure et al. (1985); Markowski (1952a); Rausch and Adams (2000); Rausch et al. (1967).

Remarks: This is a common parasite of bearded seal, *Erignathus barbatus*, and other phocid seals; several marine fishes serve as second intermediate hosts (Delyamure et al., 1985; Rausch and Adams, 2000). *Pyramicocephalus phocarum* appeared repeatedly in the checklists of human parasites (Ashford and Crewe, 2003; Coombs and Crompton, 1991) and humans were also listed among its definitive hosts in the literature (Delyamure et al., 1985; Schmidt, 1986). However, the present authors were unable to find any reliable report of this seal tapeworm from humans. Moreover, Rausch et al. (1967) and Rausch and Adams (2000) reported unsuccessful attempts to infect two human volunteers with plerocercoids from burbot, which can migrate to the sea. Since there is no convincing evidence that this cestode can infect human beings, it is not considered as a potential human parasite by the present authors.

2.2.15. Schistocephalus solidus (Müller, 1776) Steenstrup, 1857

Synonyms: *Taenia solida* Müller, 1776; *Taenia gasterostei* Fabricius, 1780; *Schistocephalus dimorphus* Creplin, 1829; see Dubinina (1980) for exhaustive list of synonyms.

Definitive hosts: fish-eating birds (Laridae, Sternidae, *Mergus*, *Bucephala*, Ciconiiformes, Podicipedidae, Alcidae, Procellariformes); birds of other groups such as Charadridae and corvids can swallow individual plerocercoids which have left the body cavity of sticklebacks and thus become infected.

Human infections: 2 cases from Alaska.

Second intermediate host: three-spined stickleback (*Gasterosteus aculeatus*).

Site of infection of plerocercoids: body cavity.

Distribution: northern part of the Holarctic region, especially near sea coast.

Selected references: Dubinina (1980); Rausch et al. (1967).

Remarks: Similarly as species of *Ligula*, adults of the genus *Schistocephalus* Creplin, 1829 exhibit very low host specificity at the level of the definitive host. This species has been reported from as many as 42 species of birds of 8 orders (Vik, 1954); adults spend a very short time (several days only) in the definitive host, because their plerocercoids almost reach sexual maturity in the second intermediate host and definitive host is only needed for production of eggs and oviposition (Dubinina, 1980).

This species has been reported twice from men in Chevak, Alaska (Rausch et al., 1967), but both cases seem to have represented accidental infection with plerocercoids. Therefore, this cestode is not considered to be a true human-infecting species.

3. Discussion

3.1. Gaps and challenges

Even though broad fish tapeworms are known for a long time, there are considerable gaps in our knowledge of numerous aspects of their biology, epidemiology and distribution. Some of the obstacles that complicate a more effective control of the human disease caused by these large-sized tapeworms are briefly discussed below.

Species delimitation is a key requirement for a reliable identification, which is considerably complicated by quite uniform morphology of most diphyllobothriidean cestodes, especially proglottids and their internal organs. A high degree of intraspecific, often host-related variability of many taxa also makes definition of species boundaries difficult or virtually impossible. As a result, the actual species diversity of broad fish tapeworms is corroborated insufficiently.

Problems with species delimitation based on morphological characteristics have also resulted in the high number of doubtful records that should be verified using molecular tools if ethanol-fixed material is available. This is valid for numerous records of human infections including several rare species that normally occur in marine (whales, seals) or terrestrial (bears) mammals.

Interestingly, many doubtful records from humans (e.g., *D. cameroni*, *D. elegans* or *D. hians*) are from Japanese seamen almost exclusively from the Kyushu Island in Japan (Tables 1, 2). One of just two records of *D. orcini* is also from Kyushu, whereas the other from Honshu. It is obvious that great popularity of eating raw or undercooked fish and their products in Japan considerably contributes to an extraordinarily high number of human infections with fish-borne parasites including broad fish tapeworms in this country.

Due to insufficiently resolved systematics, i.e. uncertainties in species delimitation and validity of individual taxa, it is also impossible to provide reliable data on the spectrum of definitive hosts and geographical distribution of individual cestode species. A big challenge represents unravelling the origin of South American (Chilean) populations of broad fish tapeworms, because they probably colonized native and imported fish hosts quite recently (Torres et al., 2012; Kuchta et al., 2013).

Table 1
Survey of human-infecting species of diphyllobothriidean cestodes.

Species	Host	Second inter-mediate host	Distribution	No. cases	Env.
A. pacificus	Seals	Unknown	Cosmopolitan	1000	M
Dh. alascense	Dog	Burbot, smelt	Alaska	1	A
Dh. cameroni	Monk seal	Unknown	Off Hawaii	1 doubtful	M
Dh. cordatum	Seals	Unknown	Arctic and circumboreal	1	M
Dh. dalliae	Fox, dog	Alaska blackfish	Alaska	"common"	FW
Dh. dendriticum	Birds, mammals	Salmonids	Holarctic, South America	~1000	FW
Dh. cf. *elegans*	Seals	Unknown	Arctic and circumboreal	1 doubtful	M
Dh. hians	Seals	Unknown	Mediterranean, circumboreal	2 doubtful	M
Dh. lanceolatum	Seals	Sardine cisco	Circumpolar	1 doubtful	M
Dh. latum	Man	Perch, pike	Holarctic, South America	~20 million	FW
Dh. nihonkaiense	Bear, fox	Pacific salmonids	Off North Pacific	~2000	A
Dh. orcini	Killer whale	Unknown	Pacific Ocean, Japan	2	M
Dh. scoticum	Leopard seal	Unknown	Antarctic	1 doubtful	M
Dh. stemmacephalum	Dolphins	Unknown	North hemisphere	24	M
Dh. ursi	Bear	Sockeye salmon	Alaska, West Canada	11	A
Dl. balaenopterae	Whales	Unknown	cosmopolitan	~270	M
Ligula/Digramma	Fish-eating birds	Cyprinids	cosmopolitan	2 doubtful	FW
P. phocarum	Seals	Marine fish	circumpolar	1 doubtful	M
S. solidus	Fish-eating birds	Stickleback	circumpolar	2	FW

A. – *Adenocephalus*; *Dh.* – *Diphyllobothrium*; *Dl.* – *Diplogonoporus*; *P.* – *Pyramicocephalus*; *S.* – *Schistocephalus*; monk seal – Hawaiian monk seal; stickleback – three-spined stickleback; Host – principal definitive host; No. cases – estimated number of cases; Env. – environment; A – anadromous; FW – freshwater; M – marine.

It is acknowledged that diagnosis of human cases is generally easy and straightforward as is treatment of patients. However, control of this fish-borne parasitosis is generally not effective enough, partly because of our limited knowledge of life cycles of most species, their transmission patterns and actual distribution.

3.2. Opportunities

Steadily increasing popularity of consumption of raw or poorly cooked fish represents a challenge in our effort to control fish-borne diseases globally. (Re)-emergence of diphyllobothriosis in some regions, including those with good medical care and high hygienic standards, demonstrates that this human disease is not directly related to poverty or poor socio-economic conditions as it is the case of many other parasitic diseases.

Considerable progress has been achieved thanks to methods of molecular taxonomy, i.e. application of genetic (molecular) markers in genotyping clinical samples. At present, genetic characterization of tapeworms from human infections as well as from non-human hosts is inevitable to obtain reliable information about species identity, which helps overcome obstacles caused by problematic morphology-based identification as discussed above.

International collaborative effort is another important opportunity to advance our understanding of the biology and epidemiology of broad fish tapeworms. Such a collaborative effort is necessary to facilitate future studies on the epidemiology, life cycles, distribution and host-associations of the causative agents of human diphyllobothriosis and related diseases.

Complex life-cycles of broad fish tapeworms are completed in aquatic environment and thus are largely controlled by numerous abiotic factors related to temperature and water quality. The present climate change thus represents another opportunity to assess its impact on the life cycles of these parasites, their transmission and distribution, especially in temperate and cold climates.

Table 2
Distribution of species of diphyllobothriidean cestodes reported from humans.

Region	Species reported from humans	Imported species
Pacific coast of North America	*D. alascense*, *D. cordatum*[a], *D. dalliae*, *D. dendriticum*, *D. lanceolatum*[a], *D. nihonkaiense*, *D. ursi*, *S. solidus*	Unknown
North America (except Pacific coast)	*D. dendriticum*, *D. latum*	*D. nihonkaiense*
South America	*A. pacificus*, *D. dendriticum*[a], *D. latum*	*D. nihonkaiense*
Asia except Japan	*D. balaenopterae*, *D. dendriticum*[a], *D. latum*, *D. nihonkaiense*	
Japan	*A. pacificus*, *D. balaenopterae*, *D. cameroni*, *D. dendriticum*, *D. elegans*, *D. hians*, *D. nihonkaiense*, *D. orcini*, *D. scoticum*, *D. stemmacephalum*	*D. latum*
Europe	*D. dendriticum*[a], *D. latum*	*A. pacificus*, *D. dendriticum*[a], *D. nihonkaiense*
Africa	None	*D. latum*[a], *D. nihonkaiense*
Australia	None	*D. latum*[a], *D. nihonkaiense*

[a] Doubtful or unclear records.

3.3. Limitations and obstacles

Broad fish tapeworms are well known causative agents of human disease, but our knowledge of their biology and epidemiology is still insufficient due to several limitations and obstacles. One of the major obstacles to get deeper knowledge of broad fish tapeworms is the fact that this disease, which is actually not life-threatening, attracts little attention from physicians (Kuchta et al., 2015a). Since clinical signs of diphyllobothriosis are usually mild, only little attention is paid to proper fixation of samples and species identification in diagnostic laboratories. Especially improper processing of clinical samples, which are usually fixed with formalin or AFA (= a mixture of acetic acid, formalin and ethanol), is a serious obstacle that impedes molecular characterisation of samples, which is in fact the only way how to identify reliably proglottids and eggs in human stool, even though egg morphology may be sufficient for species identification (Leštinová et al., 2016).

A more effective control of this fish-borne disease is complicated by the rapidly increasing popularity of eating raw fish, mainly salmonids, but also smoked, dried or fermented fish products. It is thus unrealistic to expect considerable changes in the present trend, i.e. increase of human cases even in non-endemic areas. Eradication of this parasitic disease is also impeded by global trade with fresh fish transported on ice and tourism. Food-safety measures should include veterinary inspection of fish products before their importation to decrease the risk of human infection with plerocercoids of broad fish tapeworms.

3.4. Concluding remarks and future trends

Our understanding of many aspects of the species diversity, biology, epidemiology, host-associations, evolutionary history and distribution of broad fish tapeworms is still rather limited, partly due to the fact that the human disease caused by these large-sized cestodes is not considered to be serious and life-threatening. However, recent application of molecular methods, i.e. genotyping of clinical samples, has provided us a powerful tool that makes it possible to identify reliably causative agents of human disease. This has also consequences for a better understanding of transmission of individual species, their geographical distribution and life cycles. It is highly recommended to always fix at least part of clinical samples (as well as larvae in fish intermediate hosts if found during veterinary inspection) in molecular-graded ethanol for molecular characterization. The most effective measure to control this fish-borne helminthosis is to simply avoid meals from raw or poorly cooked fish and their products, which is, however, a fashion trend last years.

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