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Trematode diversity in freshwater fishes of the Globe I: 'Old World'

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Abstract In this paper, we review, continent by continent, the trematode fauna of freshwater fishes of the 'Old World', a vast area consisting of the Palaearctic, Ethiopian, Oriental and Australasian zoogeographical regions. Knowledge of this fauna is highly uneven and clearly incomplete for almost all regions, sometimes dramatically so. Although the biggest problem remains the completion of the 'first pass' of alpha taxonomy, there are in addition great problems relating to biogeography and elucidation of life-cycles. For the latter, molecular data, i.e. matching DNA sequences of larval stages and corresponding adults, may represent a powerful tool that should be used in future studies. Another challenging problem represents the existence of cryptic species and, in particular, considerable decrease of experts in taxonomy and life-cycles of trematodes.

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Introduction

Present knowledge of trematode diversity in freshwater fishes in the Palaearctic region is highly uneven and clearly incomplete. Moreover, comprehensive

checklists of trematodes are either unavailable or are outdated (e.g. Yamaguti, 1971; Bykhovskaya-Pavlovskaya & Kulakova, 1987; Khalil & Polling, 1997). The keys to the genera of trematodes (Gibson et al., 2002; Jones et al., 2005; Bray et al., 2008) do not contain lists of species and detailed information about geographical distribution of individual trematode groups.

The principal objective of the present contribution is to provide qualified estimates of species richness of fish trematodes and their nature in freshwaters of four zoogeographical regions, i.e. Palaearctic, Ethiopian, Oriental and Australasian regions. We also outline prospects for future studies on trematodes and thus hope to stimulate the research effort of a new generation of trematodologists. Due to serious gaps in available literature for several areas, as well as a steadily decreasing number of experts, it was not possible to provide exhaustive information on all zoogeographical regions. As a result, data summarised in this account are highly uneven and the trematode diversity may have been considerably underestimated. Where applicable, the names of contributors for particular regions appear near the headings of the respective sections. Estimates of trematode diversity are based on a literature search (Web of Science, Zoological Record, etc.), and especially records in the Host-Parasite Database of the Natural History Museum in London, UK (Gibson et al., 2005). Some information is presented as electronic supplementary material (Supplementary Tables S1–S4).

Palaearctic region

Background

Studies on trematodes of freshwater fishes have the longest tradition in Europe where also life-cycles of numerous species have been elucidated (see Yamaguti, 1975), but attention to their biology has waned due a decline in systematic studies. While molecular tools have provided an important stimulus to taxonomic studies and unravelling life-cycles, research effort has been limited to only a few groups of fish trematodes such as eye flukes (diplostomid metacercariae), and gorgoderids (Georgieva et al., 2013; Blasco-Costa et al., 2014; Faltýnková et al., 2014; Petkevičiūtė et al., 2015). Another problem is the absence of any recent and exhaustive 'all-Palaearctic' account.

Here we provide information separately for Europe (including the Mediterranean part), North-East Asia (largely covering the Siberian sub-region), southern Russian Far East (a large part of the Manchurian sub-region) and Japan (Table 1). To elucidate the current state of knowledge of trematodes occurring as adults in freshwater fishes in Europe, a database of a total of 8,202 host-parasite-locality (HPL) records in 30 countries from 281 papers published between 1912 and 2012 was compiled. The trematode species, locality (georeferenced when possible) and water body type were recorded. The data were gathered within the EU-funded project BioFresh (http://project.freshwaterbiodiversity.eu/).

Early studies in North-East Asia (Bauer, 1948; Petruschevskiy & Bauer, 1948) included surveys of fish parasites in the rivers Ob, Enisei, Lena, Kolyma and Anadyr (see Supplementary Table S1 for references). Long-term studies on fish trematodes have also been conducted in the rivers of Yakutia, Baikal Lake basin and Transbaikalia (e.g. Pronin et al., 2001; Odnokurtsev, 2010). The Kamchatka Peninsula and the northern part of the Okhotsk Sea basin are among the most studied regions (e.g. Atrashkevich et al., 2005; Boutorina et al., 2011; Supplementary Table S1).

South of the Russian Far East, i.e. Priamurye and Primorye, includes Primorsky and most of the Khabarovsky, Amursky and Sakhalinsky Regions of Russia. Fish parasites in this region have been studied for more than 80 years; more than 700 parasite species have been reported from fishes of 20 families (see bibliography and data in Supplementary Tables S1 and S2).

The trematode fauna of freshwater fishes of Japan is the best known because of sustained study (see Shimazu, 2003 for a review). Nevertheless, recent research has revealed previously unrecorded taxa and modified the taxonomic status of some known species (Supplementary Table S3). Information on the remaining areas of the Palaearctic, especially its southern part, is scarce and fragmentary, which impedes exhaustive and reliable overview of the fauna of fish trematodes of the region as a whole.

Trematode diversity in the Palaearctic region

Europe (*Anna Faltýnková*)

A total of 129 trematode species belonging to 53 genera of 22 families have been reported from

Table 1 Estimates of trematode diversity in freshwater fishes of the Old World expressed as the number of species/genera/families (see the text for sources of the data; metacercariae indicated by an asterisk)

Region/Country	Adult stage	Larval stage	Total	Most species-rich genera
Palaearctic Region: Europe	66/20/13	67/34/10	129/53/22	**Diplostomum* von Nordmann, 1832 (17 spp.); *Phyllodistomum* Braun, 1899 (10 spp.); *Asymphylodora* Looss, 1899 (8 spp.)
Palaearctic Region: North-East Asia	59/31/16	57/25/9	111/51/21	**Diplostomum* von Nordmann, 1832 (15 spp.); *Phyllodistomum* Braun, 1899 (10 spp.); *Allocreadium* Looss, 1900 (7 spp.)
Palaearctic Region: Southern Far East	75/24/15	67/23/10	137/42/20	**Diplostomum* von Nordmann, 1832 (18 spp.); *Phyllodistomum* Braun, 1899 (16 spp.); *Allocreadium* Looss, 1900 (11 spp.); *Sanguinicola* Plehn, 1905 (9 spp.)
Palaearctic Region: Japan	65/27/15	30/20/12	90/42/22	*Allocreadium* Looss, 1900 (13 spp.); *Genarchopsis* Ozaki, 1925 (7 spp.)
Ethiopian Region	67/34/20	35/20/8	102/54/28	**Diplostomum* von Nordmann, 1832 (8 spp.); *Allocreadium* Looss, 1900 (7 spp.); *Phyllodistomum* Braun, 1899 (6 spp.)
Oriental Region: India	217/81/33	49/20/10	268/104/36	*Allocreadium* Looss, 1900 (19 spp.); *Genarchopsis* Ozaki, 1925 (13 spp.); *Haplorchoides* Chen, 1949 (13 spp.)
Oriental Region: Bangladesh	45/27/16	7/5/3	51/31/18	*Allocreadium* Looss, 1900 (8 spp.); *Genarchopsis* Ozaki, 1925 (7 spp.)
Oriental Region: Vietnam	22/17/12	9/8/6	30/24/17	No genus with more than 2 species
Oriental Region: Philippines	6/5/5	23/15/5	27/19/9	**Stictodora* Looss, 1899 (4 spp.)
Australasian Region	31/24/11	12/10/7	40/31/16	No genus with more than 2 species

freshwater fishes; of these, 66 (51%) species of 20 genera and 13 families use fishes as definitive hosts (Table 1; Supplementary Table S2). The fish hosts belong to 111 species of 64 genera and 18 families, i.e. 19% of Europe's fish species. The most intensely studied groups are cyprinid (55% of HPL records), percid (17%) and salmonid (9%) fishes. According to the types of water body, 46% of the HPL records originated from lakes, 44% from rivers, 4% from coastal brackish ecosystems and 1% from ponds (5% unspecified).

The most frequently recorded trematode families are the Allocreadiidae Looss, 1902 (35% of the HPL records), Opecoelidae Ozaki, 1925 (20%) and Gorgoderidae Looss, 1899 (16%). The distribution of taxonomic diversity of the adult trematodes in fishes is uneven, with seven genera represented by a single species and two species-rich genera, *Phyllodistomum* Braun, 1899 (ten species) and *Asymphylodora* Looss, 1899 (eight species).

The genus *Phyllodistomum* is common in Europe, but its taxonomy is not resolved. Principle obstacles are the great variation of characters within species and the lack of useful diagnostic characters (Petkevičiūtė et al., 2015). In Europe there are records of *Phyllodistomum angulatum* von Linstow, 1907, *P. conostomum* (Olsson, 1876), *P. dogieli* Pigulewski, 1953, *P. elongatum* Nybelin, 1926, *P. folium* (Olfers, 1816), *P. macrocotyle* (Lühe, 1909), *P. megalorchis* Nybelin, 1926, *P. pseudofolium* Nybelin, 1926, *P. simile* Nybelin, 1926, and *P. umblae* (Fabricius, 1780). However, the diversity may be lower because Bakke (1985) synonymised *P. conostomum* with *P. umblae* and Petkevičiūtė et al. (2015) considered *P. elongatum* and *P. simile* synonyms of *P. folium* and assumed that *P. dogieli* is a synonym of *P. macrocotyle*.

The second species-rich genus, *Asymphylodora*, is common in the Holarctic (Bray, 2008). Skrjabin (1955) reported 11 species from Europe, but *Asymphylodora exspinosa* (Hausmann, 1897) and *A. ferruginosa* (von Linstow, 1877) were considered synonyms of *A. tincae* by Dawes (1946). The eight species recorded in the database are *Asymphylodora demeli* Markowski, 1935, *A. imitans* (Mühling, 1898),

A. kubanicum (Issaitschikov, 1923), *A. markewitschi* Kulakovskaya, 1947, *A. parasquamosa* Kulakova, 1972, *A. pontica* Chernyshenko, 1949, *A. progenetica* Serkova & Bykhovsky, 1940, and *A. tincae*.

The genus *Diplostomum* von Nordmann, 1832 (Diplostomidae Poirier, 1886) includes metacercariae of 17 species that parasitise predominantly in the eye lens of freshwater fishes in Europe, with cyprinids serving as the most common second intermediate hosts. Detailed data on larval stages of trematodes in European freshwater fishes are presented by Faltýnková et al. (2016, this issue).

North-East Asia (*Tamara E. Boutorina*)

The trematode fauna of freshwater fishes of North Asia includes 111 species (Table 1) of which nearly half are represented by metacercariae (Pugachev, 2003). The number of trematodes is much lower (62 spp.) in the northeastern part of this region, i.e. in Yakutia, Priokhotye, Kamchatka and Chukotka and 17 species represent larval stages of diplostomids, strigeids and echinostomatids.

The northern part of the Okhotsk Sea basin exhibits a high degree of endemism of fishes (Fedorov et al., 2003) and a mix of marine/brackish and freshwater species. A total of 40 species of trematodes, including 30 freshwater species, were found in fishes of the mouth of the River Tauy (Atrashkevich et al., 2005); 18 species are represented by metacercariae of the families Strigeidae Railliet, 1919 and Diplostomidae, whereas most species represented by adults (six species) are allocreadiids. From 24 trematode species found in anadromous salmonids from the Rivers Tauy, Yama and Giziga, only six species were freshwater (four allocreadiids and two gorgoderids) (Pospekhov et al., 2014). In freshwater fishes of the River Okhota basin, 18 species of trematodes belonging to Allocreadiidae Looss, 1902 (six species), Gorgoderidae Looss, 1899 (six spp.), Azygiidae Lühe, 1909 (two spp.), Monorchiidae Odhner, 1911 (two spp.) and Opecoelidae Ozaki, 1925 (two spp.) have been found.

Only six of 15 species of trematodes in Chukotka are freshwater, five of which are in the Allocreadiidae (see Pugachev, 1984). Out of 48 species of trematodes found in fishes of the Kamchatka Peninsula, only 17 species (35%) are freshwater, with only five species in adult stage; most trematodes are represented by metacercariae of diplostomids (ten spp.) and strigeids (two spp.) (Pugachev, 1984; Supplementary Table S1).

A total of 42 species of trematodes were registered in fishes and lampreys from the Republic of Sacha (Yakutia); fishes serve as second intermediate hosts for 19 species and they are definitive hosts for 20 freshwater species (Boutorina & Reznik, 2015). Adult worms belong to four freshwater families, i.e. Allocreadiidae (seven spp.), Gorgoderidae (six spp.), Azygiidae (two spp.) and Monorchiidae (one spp.); one family, Opecoelidae (four spp.), includes both marine and freshwater parasites.

Southern Russian Far East (*Vladimir V. Besprozvannykh*, *Alexey V. Ermolenko* & *Marina B. Shedko*)

A total of 137 trematode species of 20 families has been recorded from the southern Russian Far East (Table 1; see Supplementary Tables S1 and S3 for references and species lists, respectively). Of these, 63 species were found in freshwater fishes from the mainstream of the River Amur and its northern tributaries, 44 species in the River Ussuri, 61 species in the Khanka Lake basin, 69 species in rivers of southern Primorye, 17 species in rivers of the eastern coast of Primorye, and 12 species in rivers of the Sakhalin Island (Supplementary Table S3).

Trematodes were found in fishes of 19 families, with the highest number of species (42 adults and 60 larvae) in cyprinids, which also represent the most species-rich family in the Far East and include most ecological groups. Eleven species represented by adults and 17 species represented by metacercariae infect the Chinese sleeper, *Perccottus glenii* Dybowski, the single member of the family Odontobutidae. These trematodes were all found in fish captured in the rivers and their life-cycles are probably completed in fresh water (Besprozvannykh et al., 2015a, b).

As a result of the complex geological history of this region in the alluvium period, its trematode fauna in freshwater fishes has a mixed character, with species of the six faunal complexes: boreal plain, boreal piedmont, Pacific piedmont, Arctic freshwater, Chinese plain and Indian plain (Ermolenko, 1992).

Japan (*Takeshi Shimazu*)

At present, 52 identified and 13 unidentified species of adult digeneans of 26 genera (plus one unidentified

genus) in 15 families (plus one trematode unidentified to the family level) are known from Japan (Table 1; Supplementary Table S4; see also Supplementary file S1 for a complete bibliography). Molecular data have also been used to validate some nominal species, uncover cryptic diversity and resolve biogeographical questions, such as recently in the genus *Genarchopsis* Ozaki, 1925 (Urabe et al., 2013; Shimazu, 2015a).

Some names of known trematode species had to be changed due to the priority of specific names of cercariae over those of adults, such as *Allogenarchopsis problematica* (Faust, 1924) (syns *Cercaria problematica* Faust, 1924; *Genarchopsis yaritanago* Shimazu, Urabe & Grygier, 2011) (see Urabe & Shimazu, 2013). *Isoparorchis eurytremum* (Kobayashi, 1915) (Isoparorchiidae) in *Silurus asotus* Linnaeus and *S. biwaensis* Tomoda has long been treated as a synonym of either *I. trisimilitubis* Southwell, 1913 or *I. hypselobagri* (Billet, 1898), but Shimazu et al. (2014) have demonstrated that *I. eurytremum* is valid and that *Cercaria introverta* Faust, 1924 is its larva (see also Shimazu, 2015b).

Urabe et al. (2007) reported metacercariae and adults of *Parabucephalopsis parasiluri* Wang, 1985 and *Prosorhynchoides ozakii* (Nagaty, 1937) (Bucephalidae), both probably introduced with their first intermediate host *Limnoperna fortunei* (Dunker) (Mytilidae) from China as a contaminant of edible corbiculid bivalves in the 1990s (Baba et al., 2012; Shimazu, 2014). A series of papers that review all groups of digeneans from freshwater fishes in Japan has been, or will be, published by T. Shimazu (Supplementary Table S4).

Palaearctic region: general conclusions and summary

The diversity of trematodes of freshwater fishes in the Palaearctic region is probably the best known globally, but considerable gaps in our knowledge still exist for some parts of this region. Fish trematodes have been studied most intensively in Europe. However, the proportion of fishes serving as definitive hosts of trematodes (19% of the total number of freshwater fishes in Europe) is rather low.

The most remarkable feature of almost the entire North-East Asian region, except for Yakutia, is the predominance of marine and anadromous fishes and their trematodes. The trematode fauna of the southern Russian Far East is characterised by its mixed composition, i.e. its formation from several faunal complexes, and focal distribution because the trematode fauna of the same fish species may differ up to 100% even in two neighbouring tributaries of the same river. The trematode fauna of Japanese freshwater fishes is well known and includes several endemic species, but some species have also been recorded in Far East Russia, Korea, China and Vietnam.

Extensive gaps in the present knowledge exist for the eastern part of the Mediterranean subregion, but these largely arid countries certainly do not host a rich fauna of freshwater fishes and thus their trematode faunas are probably depauperate. Fish trematodes in China are insufficiently known internationally because most reports have been published in Chinese, are difficult to get, and often lack adequate comparison of new taxa with those already known from the other regions (e.g. Zhang et al., 1999). However, future studies using morphological and molecular data may reveal interesting patterns in the composition of the fauna of fish trematodes from this area because China falls in both Palaearctic and Oriental zoogeographical regions.

Ethiopian Region (*Nico J. Smit*)

Background

Freshwater systems in Africa cover a surface area of almost 30,000 km^2 (Van As et al., 2012) and collectively these freshwater bodies form 12 major freshwater habitat types ranging from closed basins, small lakes, floodplains and swamps to large tropical rivers, and contains almost 3,000 fish species, i.e. 25% of the world's 13,000 freshwater fish species (Lévêque et al., 2008). Species belonging to 48 of the world's 170 freshwater fish families are known from Africa, but the fauna is dominated by cichlids and cyprinids (Lévêque et al., 2008).

In contrast to the known high diversity of freshwater fish hosts, the low number of identified adult trematodes of Africa shows a clear paucity of research on this group of parasites. Studies on the diversity of freshwater fish trematodes started at the turn of the 20th Century when A. Looss published a series of papers from 1896 to 1907 on the parasitic fauna of Egypt (see Khalil & Polling, 1997). Khalil (1971) was

the first to quantify the number of known trematodes from Africa and reported a total of 43 species. Twenty-six years later, Khalil & Polling (1997) recorded a total of 62 species in 37 genera from 20 families, equating to almost one new species being described per year since 1971. Unfortunately, the species discovery rate over the following years dropped drastically. To the author's knowledge, only adult trematodes of five species and metacercariae of four species of *Diplostomum*, including one new genus, *Malawitrema* Bray & Hendrix, 2007, have since been added to the fauna of trematodes (see Supplementary Table S1 for references).

Trematode diversity in the Ethiopian region

Currently, there are 20 digenean families reported from 59 African freshwater fish species belonging to 30 genera and 20 families (Table 1). Almost 65% of these host species harbour only a single trematode species. The sharptooth catfish, *Clarias gariepinus* (Bürchell), is thus exceptional in having 12 species of seven families represented by adults (Allocreadiidae Looss, 1902; Aporocotylidae Odhner, 1912; Cephalogonimidae Looss, 1899; Gorgoderidae Looss, 1899; Opisthorchiidae Looss, 1899; Paramphistomidae Fischoeder, 1901; and Plagiorchiidae Lühe, 1901) and clinostomid and diplostomid metacercariae of five species (Mashego & Saayman, 1989; Chibwana & Nkwengulila, 2010).

The case of *C. gariepinus* suggests that the current low number of freshwater fish trematodes known from Africa is not due to a naturally low diversity, but rather a lack of dedicated studies. The distribution of the currently known trematode species over the continent is a further testimony to this as there are no records of these parasites from almost 40% of African countries. The countries with the highest number of species, i.e. Egypt (22 spp.), Sudan (19 spp.) and Ghana (17 spp.), benefited from several research visits by international experts to the respective countries.

Despite the presently low number of known species, the African trematode fauna exhibits high taxonomic diversity with more than 50% of the 20 families being represented by one or two species. Most species are from four families: Allocreadiidae (nine spp.), Cephalogonimidae, Cryptogonimidae Ward, 1917 and Gorgoderidae (all with eight spp. each). One of the most interesting components of the fauna is the plagiorchiid genus *Heterorchis* Baylis, 1915, three species of which are found in African lungfishes.

Due to the lack of large-scale surveys it is difficult to comment on the host specificity of the currently known African freshwater fish trematodes, but some trends can be observed. All eight cephalogonimids (representing two genera) reported from Africa parasitise only catfishes (ten species from four genera) and both species of *Nematobothrium* van Beneden, 1858 (Didymozoidae) have only been recorded from seven cyprinids of the genus *Labeo* Cuvier, indicating at least some degree of host specificity. In contrast, the four paramphistomids currently known from Africa have been recorded from 17 species of cichlid, citharinid, clariid, distichodontid, mochokid and mormyrid fishes.

The most species-rich genera of adult trematodes are *Allocreadium* Looss, 1900 (seven spp.) and *Phyllodistomum* (six spp.). If larvae unidentified to the species level, including those recently detected using molecular markers (Chibwana et al., 2013; Locke et al., 2015), are not considered, metacercariae of a total of 35 species in 20 genera from eight families have been reported from African freshwater fishes (Khalil & Polling, 1997; Zhokhov, 2014). The highest number of species with metacercariae reported (11) are the clinostomids, with *Clinostomum* Leidy, 1856 accounting for five species, whereas the highest number of genera (7) represent heterophyids (Khalil & Polling, 1997).

Conclusions and summary

Although African researchers have not described large numbers of new trematodes recently, work on this important group of parasites did not come to a complete halt. The focus has rather been on morphological aspects of known species, documenting new hosts and localities, ecological aspects of the parasites, and new records and species represented by metacercariae (see Supplementary Table S1 for references).

One of the more recent exciting developments in African fish parasitology are the first publications using molecular techniques and specifically genetic barcoding to study the diversity of trematodes (Chibwana et al., 2013; Locke et al., 2015). Hopefully, these initiatives will stimulate a new generation of African scientists focusing on freshwater fish parasites and

more specifically to work on the neglected trematode faunas.

Oriental Region (*Tomáš Scholz, Anna Faltýnková & Anindo Choudhury*)

Background

Even though systematic research on fish trematodes started in some countries of this region at the end of the 19th and the first third of the 20th Century (Billet, 1898; Tubangui, 1931), the present knowledge of trematode diversity is poor and the quality and reliability of many published data are questionable. This is valid mainly for the Indian subcontinent and surrounding areas because of the existence of a high number of inadequately described or misidentified taxa (Arthur & Ahmed, 2002; our unpublished observations). With few exceptions, type- or voucher specimens of species described from this region are not available for scrutiny. In fact, many species are considered by specialists as synonyms, *species inquirendae* or *nomina nuda*.

However, literature search made it possible to provide rough estimates of trematode diversity in a limited number of countries/areas of the Oriental region. Therefore, data presented below undoubtedly do not give a complete picture of the true diversity in this region, which is rich in freshwater fishes, especially cypriniforms and siluriforms (Lévêque et al., 2008).

Trematode diversity in the Oriental Region

The richest fauna of trematodes has been revealed in India, with adult trematodes of 117 species from 47 genera and 18 families reported by Mehra (1980), Srivastava (1982) and cross-referencing from published papers by one of us (AC). The species-rich families were Opecoelidae (24 species), Bucephalidae (15) and Maseniidae (11), but information for allocreadiids was incomplete. The species-rich genera were *Bucephalus* Baer, 1827 (nine spp.), *Eucreadium* Dayal, 1950 (eight spp.) and *Phyllodistomum* (eight spp.). Metacercariae of the following families were reported from freshwater fishes in India: Acanthocolpidae Lühe, 1906, Bucephalidae Poche, 1907, Clinostomidae Lühe, 1901, Cryptogonimidae, Diplostomidae and Heterophyidae Leiper, 1909 (see Mehra, 1980; Srivastava, 1982).

Data compiled by Gibson et al. (2005) have revealed much higher numbers of trematodes reported in freshwater fishes from India than those listed in Mehra (1980) and Srivastava (1982) and found by cross-referencing from published papers: 220 trematode species (both adults and metacercariae) of 98 genera and 35 families. New additions based on a Web of Science search increase the total number of fish trematodes in freshwaters in India to 268 species of 104 genera and 36 families (Table 1). These high numbers must be regarded with caution as many descriptions are difficult to evaluate, often based on apparently decomposed or poorly fixed specimens, many of the trematodes have never been found since their original description, and no reference material including types is known to exist for a large number of species described in recent decades. Based on the senior author's experience with fish tapeworms [instead of the 59 species of 15 genera of three families of caryophyllideans from *Clarias batrachus* (Linnaeus) only eight species of five genera from a single family were recognised; see Ash et al. (2011)], many species may be invalid and the actual number of fish trematodes reported from India is likely considerably lower.

Arthur & Ahmed (2002) listed adult trematodes of 45 species from 27 genera in 16 families and metacercariae of seven species from five genera in three families found in freshwater fishes of Bangladesh. The most species-rich genera were *Allocreadium* and *Genarchopsis* with adults of eight and seven species, respectively. The authors pointed out that trematode fauna of teleosts in Bangladesh is poorly known and many apparent misidentifications have been made. In addition, parasites have been reported from only 85 of the 528 species of marine and freshwater fishes of Bangladesh, the latter including 213 species of teleosts (Arthur & Ahmed, 2002).

Data on trematodes of freshwater fishes in Vietnam, Cambodia, Laos and Thailand are scarce, except for a number of studies on metacercariae of causative agents of human fish-borne trematodoses, i.e. small liver flukes *Opisthorchis viverrini* (Poirrier, 1886) and *Clonorchis sinensis* (Cobbold, 1875), and small intestinal flukes, especially species of the heterophyid genera *Haplorchis* Looss, 1899, *Centrocestus* Looss, 1899 and *Stellantchasmus* Onji & Nishio, 1916) (see Chai et al., 2005 for a review and Supplementary Table S1 for other references).

The fauna of freshwater fishes of Vietnam is poorly known as are their trematodes. Arthur & Te (2006) listed adult trematodes of only 22 species from 17 genera in 12 families and metacercariae of nine species of eight genera in six families, which is only about one fifth of the total number of named trematodes found in marine and freshwater fishes of Vietnam (151 spp.). Scholz (1991a, b) reported metacercariae of 14 species (but only eight identified to species level; five of these from the family Heterophyidae) and adults of only five species from fishes in Laos. With the exception of a few studies (e.g. Sirikanchana, 1982; see Supplementary Table S1), data on trematodes of freshwater fish in neighbouring Thailand are also limited mainly to studies focused on opisthorchiid and heterophyid metacercariae (Supplementary Table S1).

Trematode fauna of fishes of the Philippines is dominated by marine and brackish species (more than two thirds of taxa); that of freshwater fishes is composed of metacercariae of 23 species, especially heterophyids (ten spp. in six genera), from 15 genera and five families, whereas adult trematodes of only six species from five genera and five families have been reported by Arthur & Lumanlan-Mayo (1997). Almost no information is available on trematodes of freshwater fishes of Indonesia, except for metacercariae of *Clinostomum complanatum* (Rudolphi, 1819) characterised by ITS sequences (Riauwaty et al., 2012) and a report of *Orientocreadium* sp. by Davy & Graham (1979). The trematode fauna of freshwater fishes in Malaysia has also been poorly studied as evidenced by the reports of only five identified and two innominate digenean species (Lim & Furtado, 1984; Bu & Seng, 1997).

Life-cycles of fish trematodes in the Oriental region are poorly known and were studied only by a few researchers, e.g. by C. C. Velasquez in the Philippines and R. Madhavi in India (see Arthur & Lumanlan-Mayo, 1997 and Supplementary Table S1 for references).

Conclusions and summary

The present knowledge of the fauna of trematodes parasitising freshwater teleosts in the Oriental region is fragmentary and suffers from unreliability of many published records and unavailability of reference specimens, especially in the Indian subcontinent. It is thus impossible to assess the species diversity, degree of endemism and host-associations of trematodes in this region. Molecular data on fish trematodes from the Oriental Region are almost completely lacking, except for few exceptions (Shimazu et al., 2014; Athokpam & Tandon, 2015). It is a major challenge for a new generation of taxonomists to critically revise Oriental taxa, especially those from India and neighbouring countries, using properly fixed material evaluated by the methods of modern taxonomy and phylogenetic systematics.

Australasian Region (*Thomas H. Cribb*)

Background

Australia's reputation as the driest continent (other than Antarctica) is reflected by a depauperate fauna of just over 300 freshwater fish species (Allen et al., 2003). Most of the species are secondary freshwater taxa; the most highly radiated freshwater fish families in Australia (e.g. Eleotridae, Melanotaeniidae, Plotosidae and Terapontidae) have close marine relatives. The fauna is, however, not without distinctive components. Among these are the lungfish *Neoceratodus forsteri* (Krefft), two species of osteoglossiforms, and the salamanderfish (Lepidogalaxiidae); there is also a rich fauna of galaxiids in southern Australia. An important aspect of the fauna is what it lacks; there are no characids, cichlids, cyprinids, poeciliids or salmonids.

Low numbers of trematode species partly reflect limited study. The first two named species, *Isoparorchis tandani* Johnston, 1927 and *Tandanicola bancrofti* Johnston, 1927, were reported only in 1927 (Johnston, 1927). Most reports relate to studies on the eastern Australian coast and a smaller number relate to species from the inland Murray-Darling drainage. There are no reports from Tasmania, Western Australia or the Northern Territory and just two from Victoria (Cribb, 1986). No species has been described for the fauna since Gibson et al. (1990).

Trematode diversity in the Australasian Region

The fauna of adult trematodes of Australian fishes comprises 31 identified species. These relate to 11 families and have been reported from 34 species of 14 families of fishes. The nature of the fauna is

immediately highlighted by its taxonomic diversity; the 31 known species relate to 24 genera and no genus is reported with more than two species (Table 1).

Numerous species have evidently relatively recent marine origins. Among these, the single reported hemiurid and several of the numerous reported haploporids (the single richest family), plus a single atractotrematid, are possibly transmitted in the sea and only enter freshwater transitorily (see Supplementary Table S1 for references). Haploporids and atractotrematids are known only from mugilids which, with the exception of *Trachystoma petard* (Castelnau), migrate freely between freshwater and the sea. Species of several other families (Derogenidae Nicoll, 1910, Opecoelidae, Tandanicolidae Johnston, 1927, and Transversotrematidae Witenberg, 1944) are known or thought to be transmitted in freshwater, but have close marine relatives; there are even both marine and freshwater species of several genera.

Among the most distinctive components of the fauna are species of two genera of Aephnidiogenidae Yamaguti, 1934, *Stegodexame* Macfarlane, 1951 and *Tetracerasta* Watson, 1984. These infect anguillids (Watson, 1984) and percichthyids (Cribb, 1988), and species of both genera are transmitted in freshwater (Watson, 1984). A species of *Stegodexame* was first reported in New Zealand (MacFarlane, 1951) and recently from New Caledonia (Moravec & Justine, 2007). These genera have no clearly close marine counterparts although the family is highly radiated in the sea (Bray & Cribb, 2012).

The Gorgoderidae is represented by three species. One, *Phyllodistomum magnificum* Cribb, 1987, is thought to use a sphaeriid bivalve as first intermediate host (Cribb, 1987a) and to belong to an essentially global radiation of such species (Cutmore et al., 2013; Petkevičiūtė et al., 2013). The two other species belong to *Pseudophyllodistomum* Cribb, 1987, species of which infect corbiculid bivalves and occur only in Australia and parts of Asia (Cribb, 1987b; Urabe et al., 2015).

The Isoparorchiidae provides one of the best understood biogeographical stories for the fauna. The single giant species (reaching over three cm) present in Australia, *I. tandani*, infects the swim bladder of the plotosid catfish *Tandanus tandanus* (Mitchell). Shimazu et al. (2014) have shown that the species is unique to Australia, but part of a complex of species occurs in siluriforms in Asia and Australia.

The Aporocotylidae has two known species. *Plethorchis acanthus* Martin, 1975 infects a catadromous mugilid, *Mugil cephalus* Linnaeus. The life-cycle remains unknown, but Lester et al. (2009) inferred that transmission occurs in freshwater. *Paracardicoloides yamagutii* Martin, 1974 infects anguillid eels; the same species is thought to occur in eels in New Zealand (Hine, 1978). Nolan & Cribb (2004) showed that the intermediate host is a tateid gastropod.

One interesting component of the fauna is the Cladorchiidae Fischoeder, 1901, given that *Bancroftrema neoceratodi* Angel, 1966 is known only from the Australian lungfish (Angel, 1966). However, the two other species of Cladorchiidae, *Australotrema brisbanensis* Khalil, 1981 and *Pretestis australianus* Angel & Manter, 1970, are reported from much less distinctive fishes, a freshwater mugilid and a melanotaeniid, respectively (Angel & Manter, 1970; Khalil, 1981); one of these genera also has a species in an Australian freshwater turtle (Ferguson et al., 2001). The origin, relationships and the direction of possible host-switching of these species can only be speculated on at present.

A significant aspect of the trematode fauna of Australian fishes is what it lacks. Two families frequently reported in freshwater fishes elsewhere are the Allocreadiidae and the Heterophyidae. Although neither has been reported from Australia, species of both have been observed by the author. Important trematode taxa of freshwater fishes elsewhere so far entirely unknown from the fauna are bucephalids, lissorchiids, macroderoidids and opisthorchiids.

There has been no sustained effort to characterise the use of Australian freshwater fishes as hosts for metacercariae. Seven families (none with more than three species) and 12 species have been reported. Three of the species also have fishes as definitive hosts. The remainder infect birds. References to these reports are incorporated in the Supplementary Table S1.

Conclusions and summary

Undoubtedly, there remain many more species to be reported from the Australasian region, but it seems unlikely that the present mean ratio of almost one species of trematode per fish species will be

maintained for the fauna of the whole given that there are so many small species in which trematode richness can be expected to be low. Overall, despite the limited range of hosts, the Australian freshwater fish trematode fauna presents an intriguing array of taxa from forms clearly recently derived from the sea, to Australasian and globally distributed freshwater taxa; a few enigmatic groups may be endemic to the Australia/New Zealand region.

We note that although it doubtless has a key role in the interpretation of the Australian fauna, nothing at all is known of trematode fauna of the giant island to Australia's north, New Guinea, and little more is known of the fauna of Indonesian freshwater fishes. Thus, although a small part of the global freshwater fish trematode fauna, Australia and nearby regions certainly play their part in our continuing global ignorance.

Summary and prospects

Research on trematodes of freshwater fishes in the Old World has a long tradition and an admirable amount of data have been accumulated by our predecessors, especially in Europe and the former USSR. However, there are still serious gaps in our knowledge of trematode diversity in fishes of every region considered here. The current decrease in the number of taxonomists, lower attention paid to systematic studies in general, decline in funding of faunal surveys and taxonomic studies as well as difficulties to obtain new material of trematodes for molecular studies in some regions, all hamper progress in this field.

Utility of molecular tools in systematic studies, if used together with morphological and life-cycle data, has been proven. Molecular tools have also revealed the existence of species complexes in some trematode groups, which makes a better understanding of true diversity even more complicated. Molecular markers can also help in elucidating life-cycles of trematodes by matching individual developmental stages, but a considerable decline in studies on the life-cycles can be observed globally in the last decades (Scholz & Choudhury, 2014). Some recent studies using genetic markers have challenged previous data on life-cycles of fish trematodes and new studies are pending even in presumably well-known groups and regions (Petkevičiūtė et al., 2015). Last but not least, international collaborative efforts should be encouraged to unravel general patterns in host-associations, zoogeography, life-cycles of these parasites and their evolution (Cribb et al., 2003).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with animals performed by any of the authors.

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