



Diversity and biology of *Spirometra* tapeworms (Cestoda: Diphylobothriidea), zoonotic parasites of wildlife: A review

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ABSTRACT

Tapeworms of the genus *Spirometra* Faust, Campbell et Kellogg, 1929 have long been known as intestinal parasites of carnivores and their larvae (spargana) have been found in various vertebrates. Nevertheless, their species diversity, host associations and geographical distribution remain poorly understood. Molecular data clearly confirm the validity of the genus, which has been synonymised by several authors with *Diphylobothrium* Cobbold, 1858. Despite morphological similarities between the species of the two genera, they are not closely related and also differ in their life cycle. The present review provides a list of the species recognised as valid and additional genotypes that may represent other species, with a basic characterisation of each taxon and comments on their validity, the probable range of definitive and intermediate hosts, and their distribution. The existing taxonomic problems and the insufficient knowledge of the host specificity and distribution of *Spirometra* tapeworms can only be solved by combining molecular and morphological data, i.e. by comparing genetically characterised specimens with corresponding morphological vouchers (hologenophores). Further targeted sampling and surveys are required to clarify the distribution and host associations.

1. Introduction

Diphylobothriidean tapeworms are well-known parasites of wild animals, and their adults parasitise all groups of tetrapod vertebrates, including frogs (members of the family Cephalochlamydiae), reptiles (Scyphocephalidae), birds and mammals (Diphylobothriidae). Most species are reported from marine mammals (pinnipeds and cetaceans), but some members of the genera *Adenocephalus* Nybelin, 1931, *Dibothriocephalus* Lühe, 1899, *Diphylobothrium* Cobbold, 1883, and *Spirometra* Faust, Campbell et Kellogg, 1929 have zoonotic potential and are the main cause of widespread food-borne cestodosis (diphylobothriosis and sparganosis), with an estimated 20 million infected people worldwide. Mapping human hosts onto a phylogeny of broad tapeworms has shown that humans have been acquired several times as accidental hosts of broad tapeworms (Waeschenbach et al., 2017).

A better understanding of the epidemiology and distribution of broad tapeworms is hampered by difficulties in identifying both the adult tapeworms and the metacercodes (plerocercoids). Identification by morphology is problematic for several reasons, mainly because of the high intraspecific variation in most morphological characters, the different fixation methods and the usually poor quality of available

material. Host type and intensity of infection (parasite abundance) may also play an important role in the intraspecific variability of individual taxa (Andersen, 1972, 1973). As a result, a large number of taxa from the same hosts and regions have been described, but their validity is questionable (Kuchta and Scholz, 2017).

Scholz and Kuchta (2016) reviewed zoonotic broad tapeworms (members of *Diphylobothrium* and relatives) that use fish as intermediate hosts, while Kuchta et al. (2021) presented the first molecular phylogenetic hypothesis on the relationship of the species of *Spirometra*, whose members can cause life-threatening sparganosis. Species of *Spirometra* use terrestrial, mainly carnivorous mammals as definitive hosts and amphibians (frogs), reptiles (snakes) and mammals, rarely birds, but almost never fish (see Vettorazzi et al., 2023 and below), as their second intermediate hosts. Sparganosis is a disease of humans and animals caused by (i) ingestion of the first intermediate host (through drinking water with freshwater copepods infected with procercoids), (ii) ingestion of the second intermediate host (mainly snakes or frogs) infected with plerocercoids, or (iii) contact of an open wound with intermediate hosts (Waeschenbach et al., 2017; Kuchta et al., 2021). Occasionally, humans become infected with plerocercoids of *Spirometra*, which then develop into adults in the human intestine and cause spirometrosis

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(Kuchta et al., 2015, 2021).

Adult *Spirometra* tapeworms are morphologically similar to those of the genera *Dibothriocephalus* and *Diphyllobothrium*, which may even occur in the same definitive hosts (cats, dogs, foxes, etc.), making their identification even more difficult. Due to this morphological similarity and the occurrence in the same definitive hosts, some authors, including Schmidt (1986), have synonymised *Spirometra* with *Diphyllobothrium*. However, molecular data provided evidence that *Spirometra* is valid and not closely related to *Diphyllobothrium* and *Dibothriocephalus* (Waeschenbach et al., 2017).

In this review, we address the species diversity, distribution and biology of *Spirometra* species. The data are based on a critical review of the literature since 1819, when the first *Spirometra* species was described by Rudolphi (1819), and on the examination of extensive material of *Spirometra* tapeworms, including type specimens of several taxa from parasitological collections and specimens recently collected by numerous collaborators and kindly provided to the present authors (see Acknowledgements).

2. Systematics of *Spirometra* and species diversity

The tapeworms of the genus *Spirometra* are one of the most taxonomically complicated groups of tapeworms and their systematics and species identification are still a major challenge (Kuchta and Scholz, 2017). The general morphological uniformity of most taxa on the one hand and the high intraspecific, host-related variability on the other hand make it difficult to distinguish species based on morphology alone. In addition, many new species have been poorly described on the basis of limited and/or poorly fixed specimens (often from non-fresh hosts such as carcasses, roadkill and frozen hosts). These tapeworms are already decomposed, making their morphological identification impossible. Numerous authors also did not take into account the high degree of morphological variation and phenotypic plasticity of most taxa (see Iwata, 1934, 1972; Odening, 1985), and based their descriptions of 'new' taxa on variable morphological characters that were only examined on a few selected proglottids of an individual (Faust et al., 1929; Wardle et al., 1974).

Kuchta et al. (2021) gave a brief overview of the suitability of selected morphological and morphometric characters of the strobila, proglottids, uterine loops, ovary, testes, vitelline follicles, cirrus sac and external seminal vesicle for distinguishing individual species. However, most of these characteristics can vary even within a single specimen (Iwata, 1934, 1972). Consequently, morphologically different proglottids of the same specimen may correspond to different morphotypes (= 'species') described by Faust et al. (1929); these morphotypes are still used by some recent authors. Several authors placed great emphasis on the species of the definitive hosts, but it appears that the host specificity of *Spirometra* species at the definitive host level is not as strict as previously thought (Kuchta et al., 2021). In contrast, the geographical origin of individual specimens can play an important role in distinguishing some *Spirometra* species (Kuchta et al., 2021; Yamasaki et al., 2021, 2024).

The first tapeworm currently classified in *Spirometra* was *Dubium erinaceiropaei* Rudolphi, 1819, which was described from metacestodes (plerocercoids) found in a hedgehog (*Erinaceus europaeus* L.) in Europe. The original description was very superficial and did not allow this species to be adequately characterised. The type material is available (Kuchta et al., 2021), but plerocercoid form is not suitable for morphological identification to the species level. This species name has been widely used for plerocercoids and adults of *Spirometra* since the study by Faust et al. (1929), including isolates from humans on all continents except Antarctica (Daly, 1981). This was apparently a mistake for cases in Asia, where this European species does not occur (Kuchta et al., 2021; Yamasaki et al., 2021, 2024).

The first *Spirometra* tapeworm from Asia was *Ligula mansoni* Cobbold, 1883 described by Cobbold (1883) in China as a plerocercoid found at

autopsy of a man in Amony (now Xiamen). The first *Spirometra* from South America was *Dibothrium decipiens* Diesing, 1850 from various felids in Brazil, which was superficially described by Diesing (1850). All species described in the 19th century (see Scholz et al., 2019) were very superficially and incompletely characterised and it is impossible to compare these species with newly obtained material (Kuchta et al., 2021).

Spirometra plerocercoids with similar morphology, the adults of which were unknown for a long time, were later placed in the *Sparganum* Diesing, 1854 collective group proposed by Diesing (1854). The first link between plerocercoids of terrestrial vertebrates and adult tapeworms of carnivores was experimentally confirmed by Meggitt (1925) and Joyeux and Baer (1927), whereupon Faust et al. (1929) described six new species and proposed a new subgenus, *Spirometra*, in *Diphyllobothrium*, which was later elevated to the rank of a genus by Mueller (1937). Faust et al. (1929) designated *S. decipiens* as the type species of their new subgenus. However, when Mueller (1937) elevated this subgenus to the rank of a genus, he erroneously designated *S. erinaceiropaei* as the type species. This error was then adopted by all subsequent workers, including Kuchta and Scholz (2017). Therefore, the type species of the genus is *S. decipiens*, although Faust et al. (1929) mistook their specimens from China (most likely *S. mansoni*) for *S. decipiens* of Diesing (1850).

Schmidt (1986) synonymised *Spirometra* with *Diphyllobothrium*, but both Bray et al. (1994) and Kamo (1999) recognised *Spirometra* as valid, which was fully confirmed by molecular data. These data have shown that the two genera are not closely related (Waeschenbach et al., 2017; Fraija-Fernández et al., 2021). In the key to the genera of the Diphyllobothriidae, Bray et al. (1994) separated *Spirometra* from other diphyllobothriid genera by the structure of the male terminal genitalia, with the internal seminal vesicle forming the posterior part of the cirrus sac, which is separated as the external seminal vesicle in other diphyllobothriid genera such as *Diphyllobothrium* and *Dibothriocephalus*. The species of these two genera also differ in the appearance of the uterus, which in *Spirometra* is a simple spiral of a few closely spaced coils that widen to form a uterine pore anterior to the genital pore, whereas the uterus in most genera, including *Diphyllobothrium* and *Dibothriocephalus*, consists of several loops, which may be parallel or rosette-shaped in the last gravid proglottids and occupy most of the central space of the proglottids (Bray et al., 1994; Kamo 1999).

The most detailed taxonomic reports on *Spirometra* tapeworms, which included an examination of freshly fixed material from experimentally infected definitive hosts, were by Iwata (1934, 1972), Dubinina (1951), Mueller (1974) and Odening (1985). These authors came to the conclusion that it is almost impossible to distinguish individual *Spirometra* species based on morphological characteristics alone. Scholz et al. (2019) listed 49 nominal species of *Spirometra* that were originally described in several different genera (Daly, 1981; Kamo, 1999; Scholz et al., 2019).

Iwata (1972) synonymised all nominal taxa of *Spirometra* with *S. erinaceiropaei* being the only species of the genus, due to the morphological similarity of the individual taxa. Kamo (1999) recognised four species of *Spirometra* as valid, namely *S. erinaceiropaei*, *S. mansonioides* (Mueller, 1935), *S. pretoriensis* (Baer, 1924), and *S. theileri* (Baer, 1924). Kuchta and Scholz (2017) accepted this taxonomic view and also recognised only four valid species. Most recently, Kuchta et al. (2021) distinguished seven lineages corresponding to different species, most of which show a strong geographic pattern (see below). One of these lineages, '*Spirometra* sp. 1' from Asia, was recently described by Yamasaki et al. (2024) as a new species, *S. asiana* Yamasaki, Sugiyama et Morishima, 2024. All these lineages are listed below with notes on their morphology, host range and known distribution.

Recently, the complete mitochondrial genomes of several samples of *Spirometra* tapeworms have been sequenced, often with the stated aim of facilitating species identification of individual samples. Although mitogenomic data can be used for phylogenetic inference, their

suitability for routine species identification is questionable, especially when considering the high cost and research effort required to obtain these data and analyse them properly, compared to the much lower cost and time required for the 'golden standard' for genotyping *Spirometra* samples, i.e., sequencing of the *cox1* gene.

3. Life cycle and host associations

The life cycle of *Spirometra* tapeworms involves two intermediate hosts. The first host is freshwater copepods, which was first experimentally confirmed by Okumura (1919), who successfully infected *Mesocyclops leuckarti* (Claus) with *Spirometra* coradicia which contain an oncosphere (or hexacanth) and swim freely in the water. So far, planktonic copepods of the following genera of the family Cyclopidae have been confirmed as natural or experimental first intermediate hosts, namely *Cyclops*, *Diacyclops*, *Ectocyclops*, *Leptocyclops*, *Macrocyclus*, *Megacyclus*, *Mesocyclops*, *Microcyclops*, *Paracyclus* and *Thermocyclops* (Stephanson, 1985). The calanoid copepod *Calamoecia tasmanica* (Smith) (family Centropagidae) was also named as a suitable intermediate host (Stephanson, 1985). In contrast to the species of *Dibothriocephalus*, diaptomids (family Diaptomidae) are not suitable intermediate hosts for *Spirometra* tapeworms (Mueller, 1938).

Copepods harbour first-stage metacercariae called procercooids which have a caudal appendage (cercomer) with three pairs of embryonic hooks (Chervy, 2002). Depending on the water temperature, the development of the procercooids in the first intermediate host takes between 3 and 21 days (Okumura, 1919; Joyeux and Baer, 1927; Li, 1929; Mueller, 1938; Bearup, 1953; Opuni and Muller, 1974). The late nauplii and early copepodid stages are most susceptible to infection with coradicia, while adult copepods are rarely infected (Mueller, 1974).

The second intermediate hosts, which can include mammals, typically become infected by ingesting copepods carrying procercooids. However, direct penetration by procercooids through intact, unbroken skin, vagina or conjunctiva of mice and even human skin has been demonstrated experimentally (Li, 1929; Kobayashi, 1931; Mueller, 1966). Parenterally located plerocercoids, called spargana, develop in the second intermediate host, but can infect a wide range of paratenic hosts by predation, i.e., hosts without developing plerocercoids (Odening, 1976).

The development of plerocercoids in the second intermediate hosts can be extremely short, according to Mueller (1974) only 4.5 days, but plerocercoids can survive in these hosts for several months or even several years. Swartzwelder et al. (1964) reported a possible survival of plerocercoids in a patient from Louisiana up to 12 years and Mueller (1974) experimentally confirmed a survival of spargana transmitted between experimentally infected mice up to 16 years. Plerocercoids transplanted from mouse to mouse, or from mouse to monkey, also retained their infectivity for several years (Mueller, 1938). Successful transmission from host to host is only possible if the plerocercoids have an intact scolex (Mueller, 1938).

Transmission of spargana to other hosts is usually peroral, i.e. by predation, but direct penetration through the intact skin, vagina or eyes (conjunctiva) has also been observed in experimentally infected mice (Kobayashi, 1931). All groups of freshwater and terrestrial tetrapods, especially amphibians, reptiles and mammals, have been described as hosts of spargana, while birds are much less common. Some tetrapods such as cats, civets, dogs, foxes, hyenas, raccoon dogs, raccoons, servals and humans can serve both as second intermediate/paratenic hosts and as definitive hosts (Shipley, 1902; Baer and Fain, 1955; Harkema and Miller, 1964; Mueller, 1974).

Experimental infections of fish with procercooids injected into their body cavity failed. Small aquarium fish, catfish (*Ameiurus melas* [Rafinesque]), *Cnidogobius macrocephalus* [Valenciennes], *Silurus glanis* L.), mosquitofish (*Gambusia affinis* Baird et Girard), goldfish (*Carassius*

auratus [L.] and rainbow trout (*Oncorhynchus mykiss* [Walbaum]) were used unsuccessfully in laboratory experiments (Joyeux et al., 1934; Mueller, 1960; Odening and Bockhardt, 1982; Stephanson, 1985). However, Vettorazzi et al. (2023) reported a natural infection of the killifish *Austrolebias charrua* Costa et Cheffe (Cyprinodontiformes: Rivulidae) in Uruguay. The prevalence of infection was high (up to 58%), but the actual role of killifish in the life cycle of *Spirometra* tapeworms is not known. This recent report changes the paradigm that fish are never involved in the transmission of *Spirometra* tapeworms (Kuchta et al., 2015), but their role in the life cycle of *Spirometra* tapeworms appears to be very limited.

The definitive host becomes infected perorally by ingestion of second intermediate hosts or paratenic hosts harbouring plerocercoids (spargana). Ingested plerocercoids attach to the epithelium of the small intestine of their hosts and grow rapidly. The prepatent period is short and the first eggs have been found after two weeks in cats. Adult *Spirometra* tapeworms are relatively short-lived, especially compared to *Dibothriocephalus* species, but some adults can survive up to 3 years and 7 months, as observed by Mueller (1974) in *S. mansonioides* in cats. Berntzen and Mueller (1972) obtained adult *Spirometra* tapeworms, including egg-bearing (gravid) specimens, after culturing plerocercoids in various growth media.

The range of definitive hosts of *Spirometra* tapeworms is extremely broad, with representatives of the following tetrapod groups reported in the literature (see Supplementary Table S1 for a summary of host data). The most commonly reported definitive hosts of *Spirometra* tapeworms are cats and dogs, but no fewer than 67 mammalian species from 11 families, most commonly Felidae (28 spp.) and Canidae (19 spp.), but also Cercopithecidae (2 species in a single record), Didelphidae (2 spp.), Hominidae (1 sp.), Hyaenidae (2 spp.), Mephitidae (1 sp.), Mustelidae (4 spp.), Procyonidae (4 spp.), Sciuridae (1 species in a single record based on stool sample), and Viverridae (3 spp.) were also reported as final hosts of *Spirometra* spp. (Supplementary Table S1). The detection of adult *Spirometra serpentina* (Yamaguti, 1935) in the Chinese cobra *Naja atra* (Elapidae) in Taiwan by Yamaguti (1935) most likely represents postcyclic parasitism.

Mueller (1959, 1961) described in detail methods for the massive laboratory propagation of *S. mansonioides* from eggs to procercooids in copepods, to plerocercoids in mice and to adults in dogs, including *in vitro* breeding of plerocercoids. Okino et al. (2017) described a complete life cycle of *S. mansoni* using a triploid clone.

4. Survey of *Spirometra* species

This chapter contains basic information on species recognised as valid and additional genotypes representing different but not yet sufficiently characterised taxa, based on the recent studies by Kuchta et al. (2021), Yamasaki et al. (2024) and the present study (Fig. 1; Supplementary Fig. S1). For the list of nominal species, see Scholz et al. (2019) and for the invalidity of some recently used names, see below and supplementary data in Kuchta et al. (2021). For each taxon, data on definitive, second intermediate and paratenic hosts, geographical distribution and taxonomy as well as selected morphological characters are given. The taxa are listed in the chronological order of their first description. The acronyms of the parasitological collections are as follows: CMNPA – Canadian Museum of Nature Parasite Collection, Ottawa, Canada; IPCAS – Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic; NHMUK – Natural History Museum, London, UK; MHNG-PLAT – Natural History Museum, Geneva, Switzerland; MPM – Meguro Parasitological Museum, Tokyo, Japan; RMCA – Royal Museum of Central Africa, Tervuren, Belgium; USNM – Smithsonian National Museum of Natural History, Washington, D.C., USA; NMW – Natural History Museum, Vienna, Austria; ZMB – Zoological Museum, Berlin, Germany.

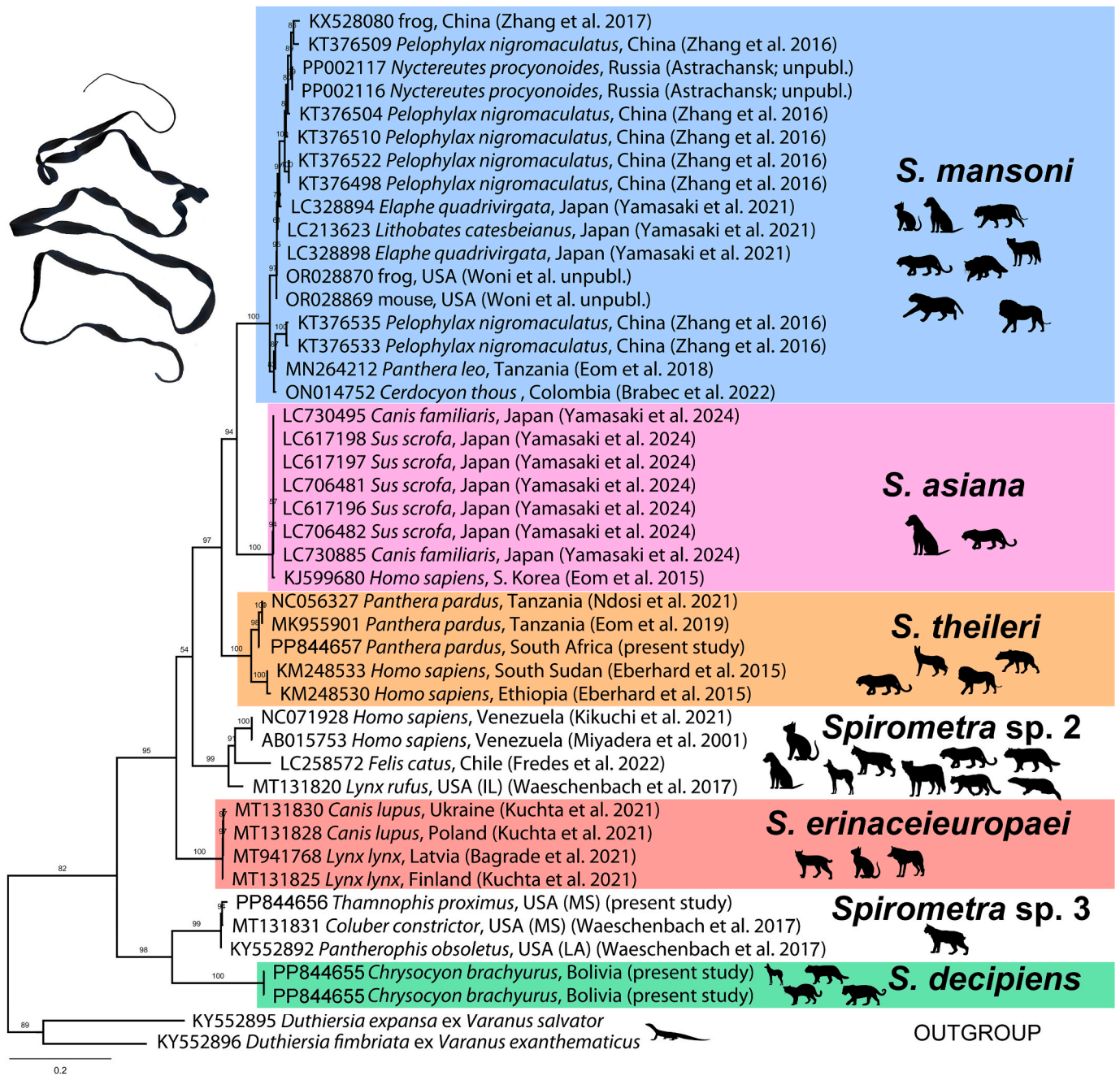


Fig. 1. Phylogenetic tree of the interrelationships of the genus *Spirometra* based on selected cytochrome c oxidase subunit I (*cox1*) gene data (long sequences), maximum likelihood. The branch length scale bar indicates number of substitutions per site. Colours highlight specimens of different species; samples without colour represent undescribed species. See [Supplementary Fig. 1](#) for more data based on larger dataset, but based on shorter sequences. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4.1. Species or lineages recognised as valid based on molecular data

***Spirometra erinaceiuropeae* (Rudolphi, 1819) Faust, Campbell et Kellogg, 1929** – ‘European lineage’ of [Kuchta et al. \(2021\) Figs. 2 and 3](#).

Synonyms: *Dubium erinaceiuropeae* Rudolphi, 1819; *Spirometra janickii* Furmaga, 1953; for other synonyms – see [Caira et al. \(2024\)](#).

Material examined: Specimens from *Canis lupus* L., Lubaczów, Poland, and Chernobyl, Ukraine (IPCAS C-110/1), *Lynx lynx* (L.), Kallasti, Finland (IPCAS C-110/2), *Felis catus* L. – experimental infection in Bologna, Italy (MHNG-PLAT-0045128); plerocercoids from *Erinaceus europaeus* L. (syntypes; ZMB-2246).

Type-host: European hedgehog *Erinaceus europaeus* (Eulipotyphla: Erinaceidae) – host of plerocercoids.

Definitive hosts (molecularly confirmed): wolf *Canis lupus* (Carnivora: Canidae); Eurasian lynx *Lynx lynx*; domestic cat *Felis catus* (both Carnivora: Felidae).

Intermediate (or paratenic) hosts (molecularly confirmed): Common racoon dog *Nyctereutes procyonoides* (Gray) (Carnivora: Canidae); European badger *Meles meles* (L.); Eurasian otter *Lutra lutra* (L.) (both Carnivora: Mustelidae); grass snake *Natrix natrix* (L.) (Squamata: Colubridae).

Type-locality: Europe (not specified more precisely — see Remarks).

Geographical distribution (molecularly confirmed): Europe (Belarus, Finland, Latvia, Poland, Ukraine).

Type-material: ZMB-2246 (see [Fig. 2D](#) in [Scholz et al., 2021](#)).

Representative DNA sequences: More than 300 sequences (mostly

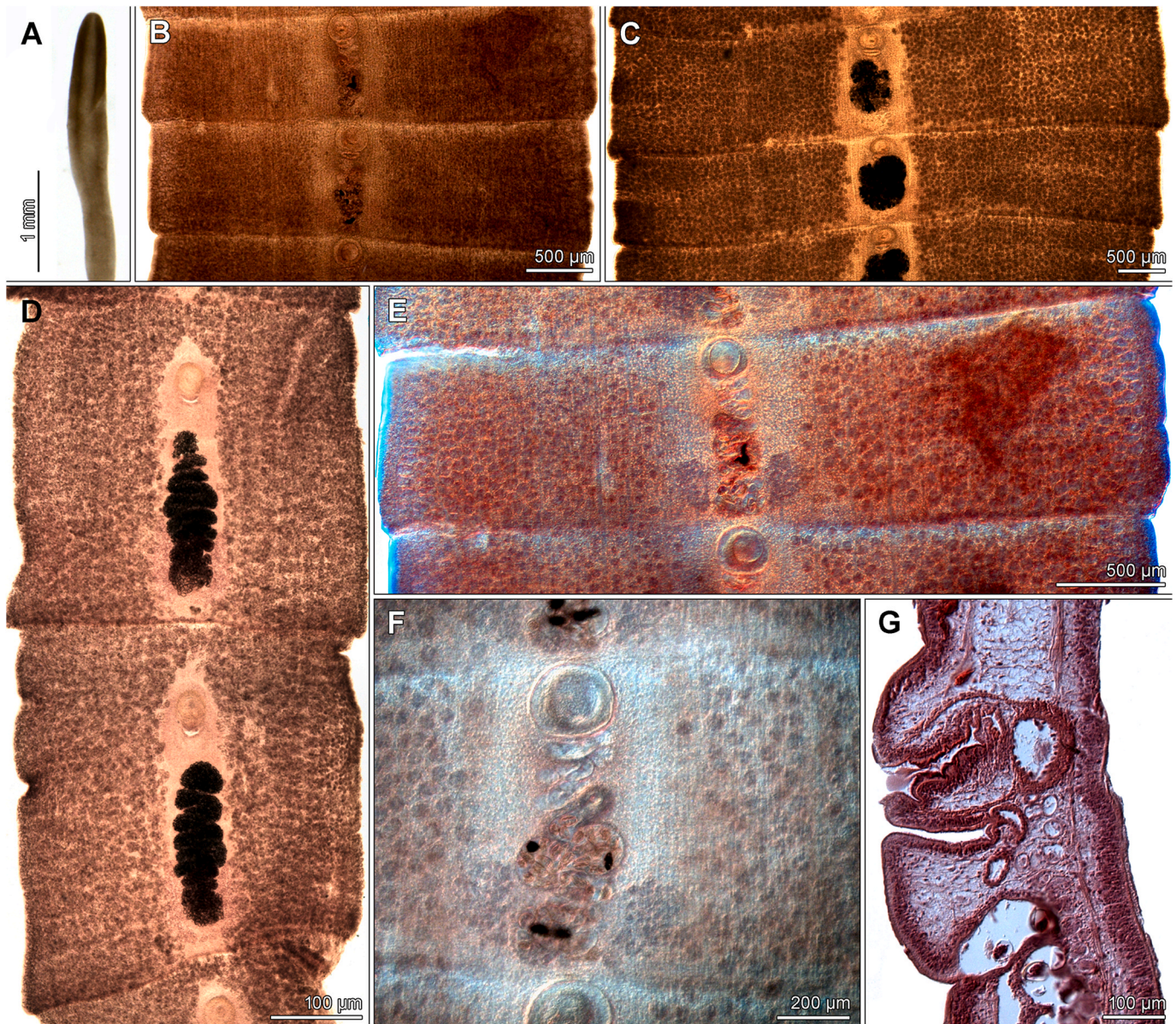


Fig. 2. Microphotographs of *Spirometra erinaceieuropaei* from *Canis lupus*. A – Scolex from Ukraine. B–F – Gravid and mature proglottids from Poland. G – Sagittal section of gravid proglottid from Poland.

cox1) (Kołodziej-Sobocińska et al., 2018, 2019; Kuchta et al., 2021; Čisovská Bazsalovicsová et al., 2022; Piekarska et al. unpublished; GenBank).

Selected morphological features: All specimens examined are fragmented, only specimens from the wolf and cat are suitable for morphological study. They are relatively small and about 5 mm wide. The uterus forms numerous loops without conspicuous enlargement of the last (distal) coils as in *S. decipiens* and the ovary is narrow in relation to the proglottid width (ratio <0.23 ; Fig. 3) compared to other species (ratio >0.24). *Spirometra erinaceieuropaei* also differs from *S. mansoni* in the ratio of the length to the width of the ovary (0.32–0.48 in the wolf tapeworm compared to 0.10–0.22 in the neotype of *S. mansoni*).

Remarks

This is the oldest available species name accepted by most authors (Schmidt, 1986; Bray et al., 1994; Kamo 1999; Kuchta et al., 2021; Yamasaki et al., 2024), but not the type species of the genus, as erroneously mentioned by most of the authors (see above). The original description of *S. erinaceieuropaei* was based on plerocercoids of the European hedgehog from an unspecified location in Europe, most likely in

the northern part of Central Europe (since 1810, C. A. Rudolphi worked in Berlin, the capital of the then province of Brandenburg-Prussia, later the Kingdom of Prussia, which extended to present-day Poland, Baltic states and Kaliningrad Oblast in Russia). Therefore, the Poland-Ukraine-Finland-Latvia strain/genotype was considered by Kuchta et al. (2021) to be the true *S. erinaceieuropaei*.

Another species, *Bothriocephalus felis* Creplin, 1825, was described from a cat in Greifswald (Germany), but due to the very superficial description based on two immature specimens, it is not possible to distinguish this worm from members of the genera *Dibothriocephalus*. Finally, *Spirometra janickii* Furmaga, 1953 was described by Furmaga (1953) from adult tapeworms of wolf and lynx in the Polish Białowieża Primeval Forest and from plerocercoids of the common shrew *Sorex araneus* L. and the fox *Vulpes vulpes*. The type material has been lost (R. Salamatina, pers. comm.), but the presence of material of *S. erinaceieuropaei* in the same area and in the same host allows us to synonymise *S. janickii* with this species (see Kuchta et al., 2021).

Spirometra tapeworms are also known from Italy and southern France, but no molecular data are available from this area. A re-

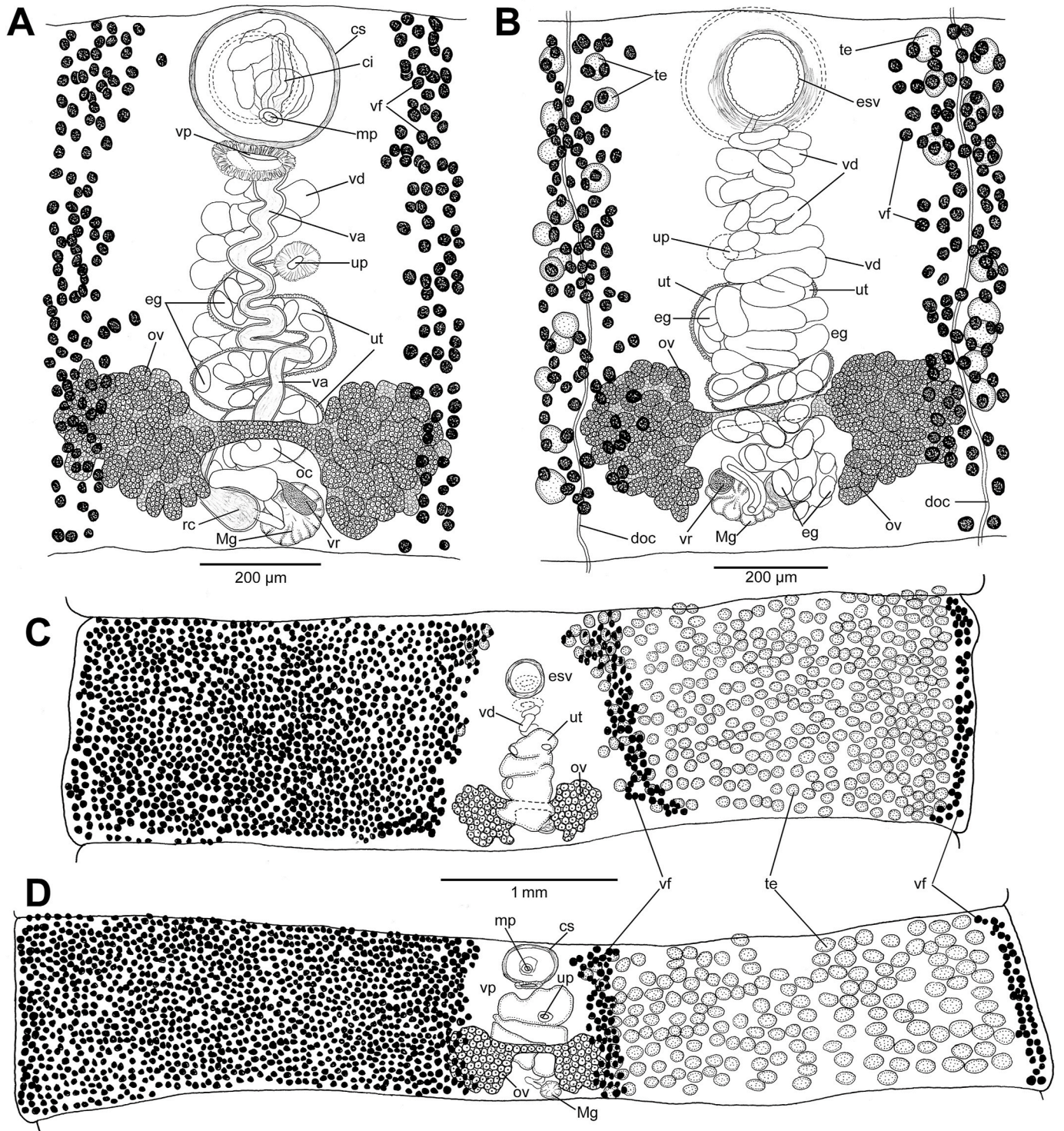


Fig. 3. Line drawings of *Spirometra erinaceieuropaei* from *Canis lupus*, Poland. A, B – ovarian region and terminal genitalia; ventral (A) and dorsal (B) view of the same proglottid. C, D – gravid proglottids; dorsal (C) and ventral (D) view; note the shape of the ovary, which is short, but with wide lateral wings. Vitelline follicles and testes illustrated in one side of proglottids only, except for lateral-most and median-most vitelline follicles. Abbreviations: ci – cirrus; cs – cirrus sac; doc – dorsal osmoregulatory canal; eg – eggs; esv – external seminal vesicle; mp – male genital pore; Mg – Mehlis’ gland; oc – oocapt; ov – ovary; rc – receptaculum seminis; te – testes; up – uterine pore; ut – uterus; va – vagina; vd – vas deferens; vf – vitelline follicles; vp – vaginal pore; vr – vitelline reservoir.

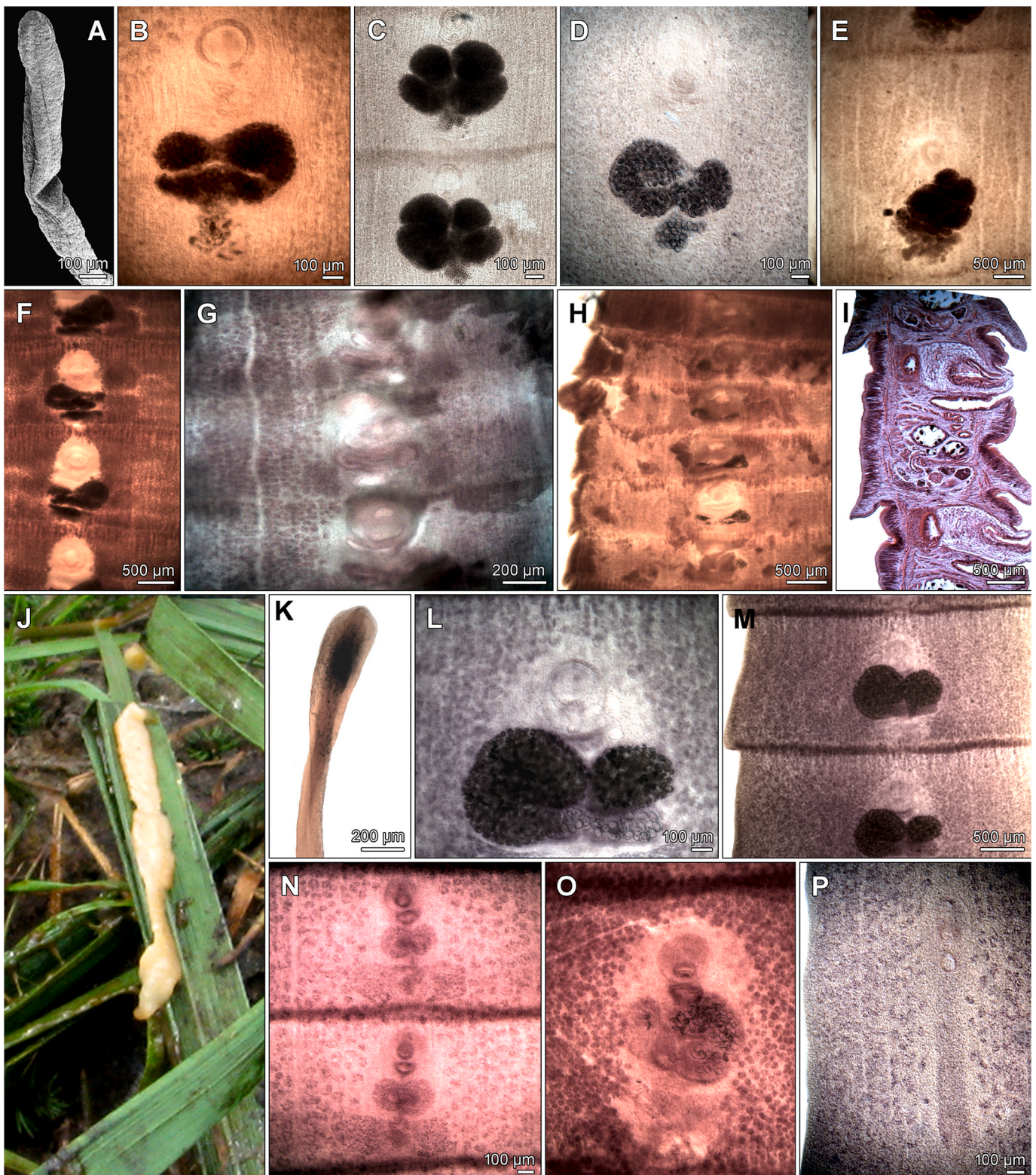


Fig. 4. Microphotographs of *Spirometra* spp. from North and South America. A–C – Scolex and gravid proglottids of *S. decipiens* syntype from *Puma concolor*, Brazil (NMW 2682, 2699). D, E – gravid proglottids of *S. decipiens* syntype from *Herpailurus yagouaroundi* (NMW 12781). F–J – Gravid proglottids and sagittal section of *S. decipiens* hologenophore from *Chrysocyon brachyurus*, Bolivia (USNM 1233899). K–O – Scolex and proglottids of *S. mansoni* syntype from *Felis catus*, USA (USNM 1333923). P – Immature proglottid of *Spirometra* sp. 2 hologenophore from *Lynx rufus*, USA Illinois (IPCAS C-987).

examination of extensive material of *Joyeux and Baer (1927)* (deposited in the MHNG), who analysed material from cats experimentally infected with plerocercoids of the grass snake in Bologna (Italy), suggests a possible conspecificity with *S. erinaceiropaei* based on the relative size of the ovary. It appears that *Spirometra ranarum* (Gastaldi, 1854), described in an Italian green frog (*Pelophylax esculentus* [L.]) in Turin (Italy), may also be conspecific with *S. erinaceiropaei*, but this should be verified by molecular data.

Molecular data confirm that *S. erinaceiropaei* occurs only in Central and Eastern Europe and has a relatively low genetic variability (Čisovská Bazsalovicsová et al., 2022). However, this species name has often been erroneously applied to specimens of *Spirometra* from all over the world (Kamo 1999). The recently described species *S. asiatica* from Korea and Japan was also misidentified as *S. erinaceiropaei* by Korean authors (see Kuchta et al., 2021; Yamasaki et al., 2021, 2024).

***Spirometra decipiens* (Diesing, 1850) Faust, Campbell et Kellogg, 1929** – type species Fig. 4.

Synonyms: *Dibothrium decipiens* Diesing, 1850; *Sparganum proliferum* of Miyadera et al. (2001), Schauer et al. (2016), Arrabal et al. (2020); *Spirometra decipiens* species complex 2 (South American lineage) of Kuchta et al. (2021).

Material examined: Type specimens (syntypes) of Diesing (1850) from *Panthera onca* (L.) (NMW 2681, USNM 1368664), *Puma concolor* (L.) (NMW 2682, 2699) and *Herpailurus yagouaroundi* (Geoffroy) (NMW 12781), Brazil; vouchers from *Chrysocyon brachyurus* (Illiger), Bolivia (USNM 1233899).

Type-host: Not explicitly stated in the original description by Diesing (1850), but certainly a South American felid (syntypes are from big cats); the first listed was the puma *P. concolor* (see Diesing, 1850, 1856; Caira et al., 2024 for a complete list of original hosts).

Definitive hosts (confirmed molecularly): ocelot *Leopardus pardalis* (L.); Geoffroy's cat *Leopardus geoffroyi* (d'Orbigny et Gervais) in Brazil (Carnivora: Felidae); maned wolf *Chrysocyon brachyurus* (Carnivora: Canidae) in Bolivia (USNM 1233899; examined by the present authors).

Intermediate (or paratenic) hosts (confirmed molecularly): Patagonia green racer *Philodryas patagoniensis* (Girard) (Squamata: Colubridae) in Uruguay.

Type-locality: Brazil (not further specified, but refers to the expeditions of the Austrian naturalist Johann Natterer into the rainforests of Brazil between 1817 and 1835).

Distribution and records: South America (Bolivia, Brazil, Uruguay).

Type-material: NMW 2621, 2622, 2624, 2681, 2682, 2699, 12779–12781, 12783, 12801, 12841, USNM 1368664.

Representative DNA sequences: Molecular data are available for several isolates from South American felids, a canid and a snake (Almeida et al., 2016; Armúa-Fernández et al., 2021; Trindade et al. unpublished; GenBank; present study). Škerfíková et al. (2006) obtained an ITS2 sequence (DQ386133) allegedly from the type material of *S. decipiens*, but this sequence was not of a *Spirometra* species and probably represents contamination.

Selected morphological features: All the specimens examined, including the type specimens, were decomposed because they came from dead hosts or from fresh faeces, as in the case of the specimen from the maned wolf (USNM 1233899). The tapeworms are relatively large and wide (up to 6 mm). The most characteristic feature of *S. decipiens* observed in the type specimens is the shape of the uterus, which consists of a few loops, with the conspicuous terminal (distalmost) C-shaped loop filled with numerous eggs (Fig. 4). The same feature was used by Mueller (1935, 1974) to distinguish *S. mansonioides*, described from North America, from other *Spirometra* species. The ovary of *S. decipiens* is relatively wider in relation to the proglottid width than in *S. erinaceiropaei*, but similar to that of *S. mansoni*.

Remarks

This is the type species of *Spirometra* (see Faust et al., 1929) and the first species described from the New World (Brazil). Diesing (1850)

briefly described *Spirometra decipiens* as *Dibothrium decipiens* from several South American felids from Brazil and the Vienna zoo. The same author (Diesing, 1856) provided further data on this species, including colour illustrations (see Caira et al., 2024). Diesing (1850) listed *Bothriocephalus felis* from a cat in Germany as a senior synonym of *D. decipiens*, but the tapeworms used for the description of *D. decipiens* were most likely only from large Brazilian felids collected by J. Natterer between 1817 and 1835; this material is still deposited in NMW. Therefore, *S. decipiens* is considered a typical species of these large cats in South America, which was also assumed by Ariola (1900) or Schmidt and Martin (1978).

A unique form of the uterus of *S. decipiens* was first described by Lühe (1899) and later by Schmidt and Martin (1978), who examined the type material of Diesing. Schmidt and Martin (1978) considered this shape of the uterine coils to be a useful feature for recognising *S. decipiens*. The present study based on Diesing's type material (1850) confirmed that the uterus forms a conspicuous, C-shaped terminal loop (Fig. 4B, C). A similar shape of the uterus was found by Mueller (1935) in specimens from a cat in the United States, which he described as the new species *S. mansonioides* (Fig. 4L, M).

Kuchta et al. (2021) recognised two lineages of *Spirometra* tapeworms from South America, designated as *S. decipiens* species complex 1 and 2. The molecularly characterised specimens of complex 1 appear to have a 'normal' shape of the uterus consisting of several loops of similar size (Arrabal et al., 2020; Fredes et al., 2022). Therefore, they are not considered conspecific with the 'true' *S. decipiens*, although they occur in the same big cat species that harbour *S. decipiens*, such as ocelot and puma.

Molecular data also suggest that complex 2 may consist of two different lineages: (i) tapeworms from North America (morphological data for the only confirmed specimen from *Lynx rufus* [Schreber] in Wisconsin are not available) (see below), and (ii) specimens from South

Table 1

List of nominal species of *Spirometra* described from South America.

Species	Authority	Type host or first listed host	Distribution (country)
<i>Dibothrium decipiens</i>	Diesing, 1850	<i>Felis catus</i> ^a	Brazil
<i>Ligula reptans</i>	Diesing, 1850	<i>Saimiri sciureus</i> (plerocercoids) ^b	Brazil
<i>Dibothrium serratum</i>	Diesing, 1850	<i>Cerdocyon thous</i> ^c <i>Canis familiaris</i>	Brazil
<i>Bothriocephalus didelphidis</i> ^d	Ariola, 1900	<i>Didelphis aurita</i> ^d	Brazil (São Paulo)
<i>Bothriocephalus longicollis</i>	Parodi et Widakowich, 1917	<i>Panthera onca</i> , <i>Puma yagouaroundi</i> ^e	Argentina (ZOO)
<i>Diphyllobothrium bresslaui</i>	Baer, 1927	<i>Didelphis aurita</i>	Brazil (Rio de Janeiro)
<i>Diphyllobothrium gracile</i>	Baer, 1927	<i>Leopardus wiedii</i> ^f	Brazil (Teresópolis)
<i>Diphyllobothrium trinitatie</i>	Cameron, 1936	<i>Procyon cancrivora</i> ^g	Suriname, Trinidad
<i>Diphyllobothrium urichi</i>	Cameron, 1936	<i>Leopardus pardalis</i> ^h	Trinidad

^a First listed host (as synonym of *Bothriocephalus felis* Creplin 1825); first listed South American host is *Felis onca* (= *Panthera onca*).

^b First listed host (as *Callithrix sciurea*), subcutaneous follicle.

^c First listed host (as *Canis azarae*), intestine.

^d Reported as *Didelphys azarae* collected by Lutz; later misspelled as "didelphidys" by Ariola (1900).

^e Reported as *Felis onca* and *Felis yagouaroundi*, respectively.

^f Reported as *Felis (Oncoides) macrura* which is most probably misspelled *Felis macroura*, a synonym of *Leopardus wiedii*.

^g Reported as *Procyon carnivora*.

^h Reported as *Felis pardalis*.

America, including the definitive hosts reported by Diesing (1850), i.e. 'true' *S. decipiens*; unfortunately, the available material for morphological studies is very limited and of poor quality.

The tapeworms of *Chrysocyon brachyurus*, which were found as worm fragments on grass from the faeces of a maned wolf on October 15, 2013

in Los Fierros, Noel Kempff National Park, Bolivia, collected by Louise Emmons, were examined by the present authors. The incomplete tapeworm of only gravid proglottids is contracted, but the enlarged terminal loops typical of *S. decipiens* are present (Fig. 4F, G). In addition, unpublished sequences of tapeworms from Geoffroy's cat in Brazil

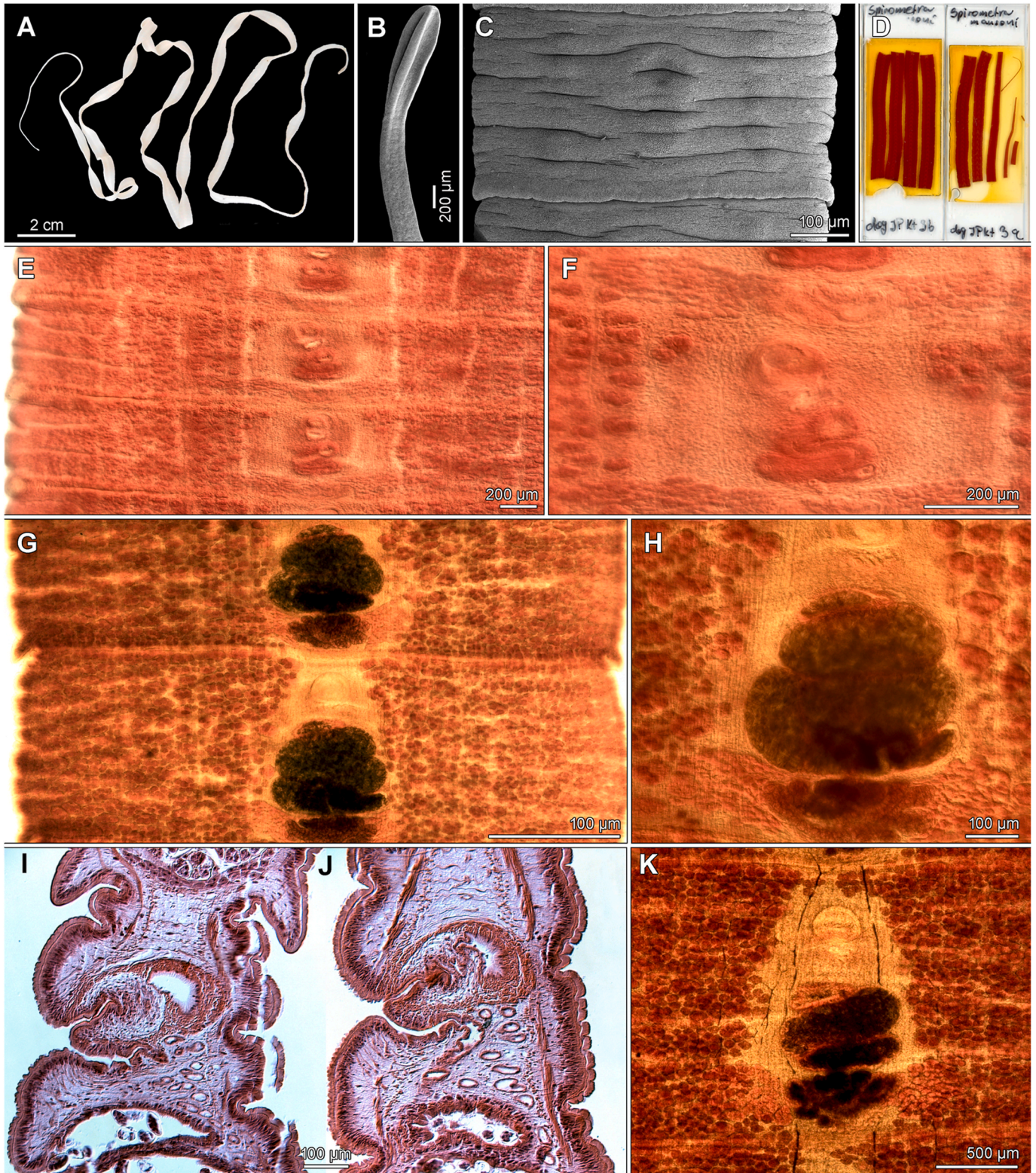


Fig. 5. Microphotographs of *Spirometra mansoni* neotype from experimentally infected dog *Canis familiaris*, Japan. A – Whole unstained neotype. B, C – SEM photo of scolex and gravid proglottid. D – Whole mounts with part of neotype. E, F – Mature proglottids. G, H, K – Gravid proglottids. I, J – Sagittal section of gravid proglottid.

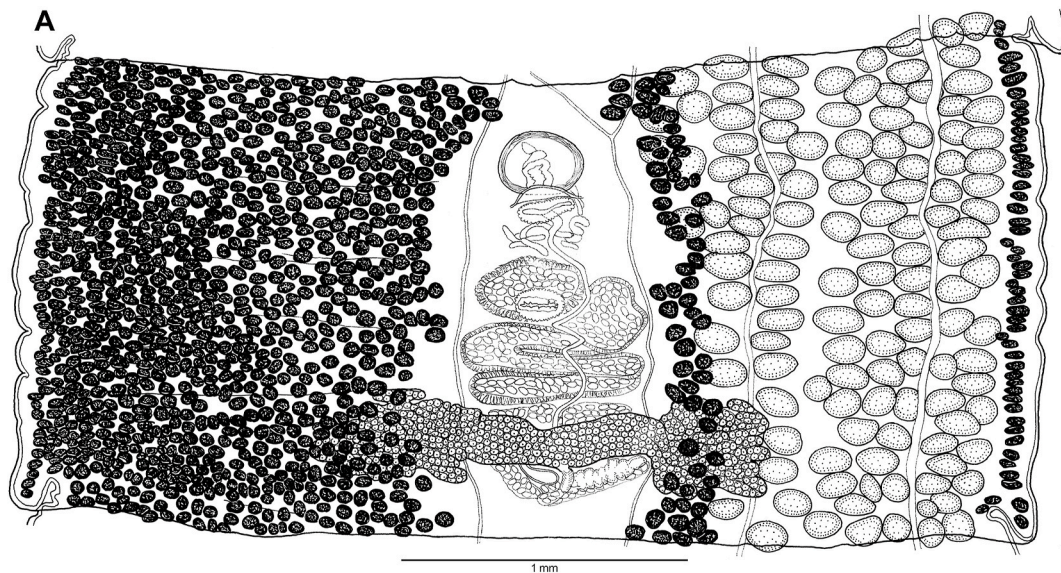


Fig. 6. Line drawing of gravid proglottid of the neotype of *Spirometra mansoni* from *Canis familiaris*, Japan (IPCAS C-988), ventral view; note the shape of the ovary, which is long, with narrow lateral wings. Vitelline follicles and testes illustrated in one side of proglottids only, except for lateral-most and median-most vitelline follicles.

(OR351540, OR351541) are designated in GenBank as *S. mansonoides*, possibly reflecting the shape of the uterus typical of this species. Based on the data discussed above, the tapeworms of *Spirometra decipiens* complex 2 (South American lineage) are considered to represent *S. decipiens*.

In addition, there are eight other nominal species that have been described from South America and still need to be verified (Table 1). They have been described mainly from Brazil, but the descriptions are incomplete and type material is not available or is of low quality (only histological sections and dark pieces of strobila are available), such as *S. bresslaui* and *S. gracilis* (MHNG-PLAT Nos. 56105; 56129) or *S. trinitatis* and *S. urichi* (CMNPA 1995-0151/1995-0160; 1995-0143/1995-0150).

Spirometra mansoni (Cobbold, 1882) Faust, Campbell et Kellogg, 1929 Figs. 5 and 6.

Synonyms: *Bothriocephalus marginatus* Kreff, 1871; *Bothriocephalus liguloides* Leuckart, 1886; *Dibothrium tangalangi* MacCallum, 1921; *Sparganum phillipiense* Tubangui, 1924; *Diphyllobothrium* (*Spirometra*) *houghtoni* Faust, Campbell et Kellogg, 1929; *Diphyllobothrium* (*Spirometra*) *okumurai* Faust, Campbell et Kellogg, 1929; *Diphyllobothrium fausti* Vialli, 1931; *Ligula ranarum* of Meggitt (1924); *Diphyllobothrium* (*Spirometra*) *decipiens* of Faust et al. (1929); *Diphyllobothrium* (*Spirometra*) *erinacei* of Faust et al. (1929); *Spirometra decipiens* of Jeon et al. (2015); *Spirometra ranarum* of Eom et al. (2018) and Jeon et al. (2018).

Material examined: Neotype from experimentally infected *Canis familiaris* in Japan by T. Okino (IPCAS C-988; vouchers IPCAS C-242; Fig. 6); vouchers from *Felis catus* in Laos (IPCAS C-950/1).

Type-host: Human *Homo sapiens* L. (Primates: Hominidae).

Additional definitive hosts (molecularly confirmed): Domestic cat *Felis catus* in Australia, Laos and South Korea; jungle cat *Felis chaus* Schreber in Iran; Amur leopard *Panthera pardus orientalis* (Schreber) in Russian Far East; tiger *Panthera tigris* (L.) in China; leopard cat *Prionailurus bengalensis* Kerr in China; wild cat *Felis silvestris* Schreber in Iran; lion *Panthera leo* (L.) in Tanzania (all Carnivora: Felidae); crab-eating fox *Cerdocyon thous* (L.) in Colombia; domestic dog *Canis familiaris* in Australia, India, Indonesia, Japan, Laos (both Carnivora: Canidae).

Intermediate (or paratenic) hosts (confirmed molecularly): Many amphibians, reptiles and mammals, including humans (see Kuchta et al., 2021).

Type-locality: Amoy (now Xiamen), China.

Geographical distribution and records: Worldwide distribution, with most records from Asia (China, India, Indonesia, Iran, Japan, Korea, Laos, Myanmar, Thailand, Vietnam) and Australia, rarely from Africa (Tanzania, Mauritius), Europe (Romania), Oceania (New Zealand), North and South America (USA, Colombia – Jeon et al., 2016 (see Fig. 1).

Type-material: Does not exist; therefore, neotype of *S. mansoni* is designated (IPCAS C-988).

Representative DNA sequences: Too numerous to list separately (see Kuchta et al., 2021; Brabec et al., 2022; Yamasaki et al., 2024; present study).

Selected morphological features: Heat-fixed specimens are relatively small, up to 5 mm wide (Fig. 5A). The uterus consists of several loops. Compared to *S. erinacei* (17–23% and 0.32–0.42) and *S. asiana* (24–32% and 0.42–0.59), the ovary of *S. mansoni* is relatively wider (about 40–50% of the proglottid width) and narrower (ratio length/width of ovary 0.10–0.26) (Fig. 6). The eggs of *S. mansoni* are smaller (55–72 × 32–42 μm; mean 58 × 36 μm of the neotype) than those of *S. asiana* (74–80 μm × 33–41 μm wide), but similar to those of *S. erinacei* (54–59 × 38–43 μm) (see Yamasaki et al., 2024; present study).

Remarks

This species was described as a larva found at autopsy of a man in Amoy (now Xiamen, China), and it is the first taxon described in Asia. Almost all specimens from China and other Asian countries are considered conspecific with *S. mansoni* based on molecular data. This is by far the most common and widespread species of *Spirometra*, which has probably also been introduced to Africa, Australia and Oceania, south-eastern Europe (Romania) and North and South America (Jeon et al., 2016; Kuchta et al., 2021; Brabec et al. 2023). It is also the most important pathogen causing sparganosis and spirometrosis in humans (Kuchta et al., 2021). Jeon et al. (2015) misidentified specimens of *S. mansoni* from Korea as *S. decipiens*, which is endemic to the Americas (see above). Jeon et al. (2016) and Eom et al. (2018) also misidentified *S. mansoni* from Myanmar and Tanzania as *S. ranarum*, a species of uncertain taxonomic status known only from Europe (see below).

In general, high genetic diversity, moderate genetic differentiation and low genetic exchange between geographical populations in China have been observed (Xu et al., 2022).

Spirometra theileri (Baer, 1924); Opuni et Muller, 1974 Fig. 7.

Synonyms: *Sparganum baxteri* Sambon, 1907 (?); *Diphyllobothrium*

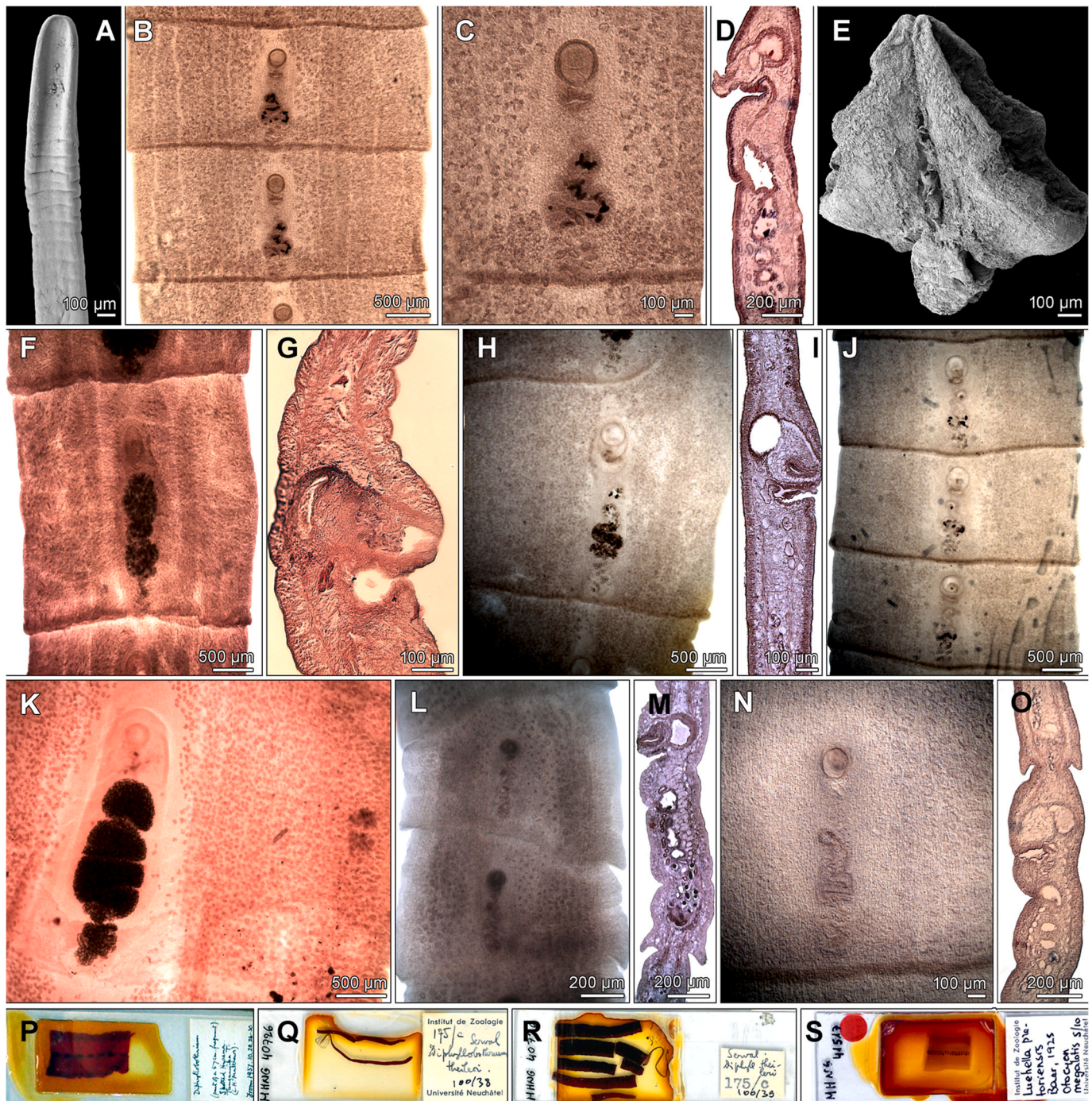


Fig. 7. Microphotographs of *Spirometra* spp. and *Dibothrium folium* from Africa. **A–D** – Scolex, proglottids and sagittal section of *S. theileri* from *Panthera leo*, DR Congo material of **Baer (1959)** (RMCA 32316). **E** – Scolex of *D. folium*, type specimen (NMW No. 2616). **F, G** – Gravid proglottid and sagittal section of hologenophore from *Panthera pardus*, South Africa (IPCAS C-986). **H, I** – Gravid proglottid and sagittal section from *P. pardus*, Siera Leone (NHMUK 1924.6.12.116). **J** – Gravid proglottid from *P. pardus*, DR Congo (NHMUK 1934.12.18.51). **K, P** – Gravid proglottid and mounted specimen from *Crocota crocuta*, Tanzania (NHMUK 1937.10.20.26–30). **L, M** – Gravid proglottid and sagittal section from *P. leo* (RMCA 32316). **N, O** – Gravid proglottid and sagittal section from *P. pardus*, DR Congo (1934.12.18.51–54). **Q, R** – Syntype slides of *Diphyllobothrium theileri* from *Leptailurus serval*, South Africa (MHNG-PLAT 40726). **S** – Syntype slide of *Lueheella pretoriensis* from *Otocyon megalotis*, South Africa (MHNG-PLAT 41517).

theileri **Baer, 1924**; *Lueheella pretoriensis* **Baer, 1924** (?); *Spirometra pretoriensis* (**Baer, 1924**) **Wardle, McLeod et Stewart, 1947** (?); *Spirometra* Africa II of **Opuni and Muller, 1974**); *Spirometra* sp. of **Eberhard et al. (2015)**; *Spirometra folium* of **Kuchta et al. (2021)**.

Material examined: Syntypes of *S. theileri* from *Leptailurus serval* (Schreber) and *Felis lybica cafra* Desmarest, South Africa (MHNG-PLAT 40724–26, 56111–12, 56218, 56143, 56145); syntypes of *S. pretoriensis*

from *Otocyon megalotis* (Desmarest), South Africa (MHNG-PLAT 41517–18, 56137, 60952); hologenophore from *Panthera pardus pardus*, Mpumalanga Province, South Africa, collected by Sonia Dumendiak ((SAF48a – IPCAS C-986); vouchers of uncertain taxonomic position: from *Crocota crocuta* (Erleben), Tanzania (NHMUK 1937.10.20.26–30), from *Panthera leo* (L.), DR Congo (NHMUK 1967.11.27.51–55, RMCA 32316); from *P. p. pardus*, Sierra Leone (NHMUK 1924.6.12.116) and DR

Congo (1934.12.18.51–54); specimens (in poor condition) from *Caracal caracal* (Schreber), Prague Zoo (IPCAS C-109).

Type-host: Serval *Leptailurus serval* (as *Zibethailurus serval*) – first listed, Southern African wildcat *Felis lybica cafra*.

Definitive hosts (molecularly confirmed): Leopard *Panthera pardus*; lion *Panthera leo* (Carnivora: Felidae); spotted hyena *Crocuta crocuta* (Carnivora: Hyaenidae).

Intermediate (or paratenic) hosts (molecularly confirmed): Human *Homo sapiens* (Primates: Hominidae) (Eberhard et al., 2015); most probably also other mammals such as desert warthog *Phacochoerus aethiopicus* (Pallas) or spotted hyena (see Opuni and Muller 1974).

Type-locality: Moovilei (first listed) and Bridgewater, Rustenburg, South Africa.

Distribution and records: Africa (Chad [?], DR Congo, Ethiopia, Kenya, Sierra Leone, South Africa, South Sudan, Sudan, Tanzania) (Eberhard et al., 2015; Kuchta et al., 2021); potentially also in other African countries (see Supplementary Table S1).

Type-material: Syntypes in MHNG (see above for collection numbers).

Representative DNA sequences: Eberhard et al. (2015); Eom et al. (2019); Ndosi et al. (2020, 2021); present study.

Selected morphological features: All specimens examined were decomposed because they came from dead hosts. The tapeworms of the spotted hyena are relatively large and wide (up to 13 mm), similar to the syntypes of *S. pretoriensis* which are up to 10 mm wide, as also reported by Graber (1981). The uterus of *S. theileri* forms several loops, and the ovary is relatively long and narrow, similar to the Palaearctic species.

Remarks

The first *Spirometra* species described from Africa is *Dibothrium folium* Diesing, 1850 from *Ichneumia albicauda* (Cuvier) (Carnivora: Herpestidae). This was the reason why Kuchta et al. (2021) referred to the African isolates of *Spirometra* as *S. folium*. However, a recent study of the type of this species (NMW 2616) and Diesing's (1856) drawings of *D. folium* has shown that it is not a species of *Spirometra*. Although the type material is in poor condition (the worm is very dark and its anatomy is not recognisable), it has a broad, arrow-shaped scolex (Fig. 7E), which is never present in *Spirometra* species. In contrast, a similar lanceolate scolex is typical of species of *Duthiersia* Perrier (1873) from varanid lizards, which also occur in Africa, or some *Diphyllobothrium* species (see Kuchta and Scholz, 2017; Waeschenbach et al., 2017).

As *D. folium* has never been described since its first description, it is not possible to reliably identify this taxon to genus level and it is considered a *nomen dubium*. Based on the ITS2 sequence of the type specimen of *D. folium* (DQ386134) obtained by Škeříková et al. (2006), it is identical to *Diphyllobothrium cordatum* (Leuckart, 1863). However, later attempts to obtain other sequences from this specimen failed (unpublished data).

The second species of *Spirometra* described from Africa is *Sparganum baxteri* Sambon, 1907. A 15 cm long plerocercoid was removed from an abscess on the thigh of a Maasai in British Central Africa (now Malawi). The plerocercoid showed numerous irregular transverse folds and a pronounced longitudinal furrow on the ventral surface. The anterior end was 2–5 mm wide, and the scolex was completely invaginated (Sambon, 1907). It is possible that this plerocercoid corresponds to some adult *Spirometra* species described from African carnivores such as *S. theileri* (see Opuni and Muller 1974), but this taxon is provisionally considered to be a *species inquirenda*. Plerocercoids isolated from humans in South Sudan and Ethiopia were molecularly characterised by Eberhard et al. (2015) and all seven isolates are closely related to other sequenced tapeworms from Africa, here named *S. theileri* (Fig. 1).

Baer (1924) described two species of Diphyllobothriidea from carnivores in South Africa, namely *Lueheella pretoriensis* Baer, 1924 (as the type and only species of the new genus *Lueheella*, which was never recognised as valid) and *Diphyllobothrium theileri* Baer, 1924. Both species were then placed in *Spirometra* by Wardle et al. (1974) and Opuni and Muller (1974), respectively. However, the available molecular data from several adult tapeworms of carnivores and plerocercoids of humans

throughout Africa confirmed the presence of a single genotype more similar in size to *S. theileri* than to *S. pretoriensis*.

Spirometra theileri was described from the serval and the Southern African wildcat, both hosts near Rustenburg, South Africa (Baer, 1924, 1925). Later, Baer and Fain (1955) and Baer (1959) reported *S. theileri* in lion, leopard and serval, both from the DR Congo. Material from lion in the DR Congo (RMCA 32316; Fig. 7L, M) was examined by the present authors, and its morphology is fully consistent with the description of *S. theileri* and the hologenophore of the sequenced material from leopard from South Africa (IPCAS C-986; Fig. 7F, G). Graber (1981) found *S. theileri* in Chad in *F. lybica*, *Acinonyx jubatus* (Schreber), *Canis aureus* (most likely *Lupulella mesomelas* [Schreber], as *C. aureus* does not occur in Africa) and *Panthera pardus*.

Spirometra pretoriensis was described from an incomplete and highly contracted specimen (no scolex present) from the bat-eared fox and then reported from spotted hyena and African wild dog in Ethiopia and Zambia (Graber, 1981). The morphology of this species is poorly known, but it has a more massive, much broader strobila (>70 cm long and up to 10 mm wide) than *S. theileri* (total length <35 cm, maximum width of 3.5 mm; Graber, 1981). Odening (1985) mentioned that the configuration of the uterus of *S. pretoriensis* is similar to that of *S. mansonioides* (and *S. decipiens*), but the type material is highly contracted and not suitable for morphological description. In contrast, the type material of *S. theileri* contains a scolex and the strobilar morphology corresponds to that of the sequenced specimens from leopard for which hologenophores (morphological vouchers) are available (Fig. 1). In addition, tapeworms identified as *S. theileri* have been repeatedly reported from African carnivores (Round, 1968; Graber, 1981).

Only recently, several tapeworms of leopard, spotted hyena and lion in Tanzania were characterised molecularly and morphologically as *S. theileri* (Eom et al., 2019; Ndosi et al., 2020). These tapeworms included relatively smaller tapeworms in a leopard (45 cm long and probably 6.0–6.5 mm wide; the original values, i.e. 0.60–0.65 mm, are apparently erroneous) and much larger specimens in a spotted hyena (135 cm × 10 mm), but both specimens are genetically identical and belong to the same species, for which the name *S. theileri* is proposed to maintain taxonomic stability.

Tapeworms from the leopard recently collected by S. Dumendiak in South Africa (present study) are genetically indistinguishable from tapeworms found in various felids in Tanzania and are tentatively identified as *S. theileri*. In addition, Eom et al. (2018) reported a large tapeworm (75 × 1.2 cm) from a lion; this specimen, identified as *S. ranarum*, is genetically identical to *S. mansoni*. Ndosi et al. (2020) found tapeworms in leopard that were 45 cm long and 0.9 cm wide; they were misidentified as *S. erinaceieuropaei*, but actually belong to *S. asiana*. However, this sequence is very short, which casts doubt on the correct identification.

In summary, the species identity of *Spirometra* tapeworms in Africa is uncertain and future research based on matching molecularly characterised specimens with their morphological vouchers (hologenophores) is highly desirable. Currently, *S. theileri* is thought to be the species that occurs as adults in African carnivores, while its plerocercoids can infect humans and cause sparganosis (Opuni and Muller, 1974; Eberhard et al., 2015). If future research proves the existence of other species, *S. baxteri* could be a candidate for the designation of tapeworms that parasitise humans.

Spirometra asiana Yamasaki, Sugiyama et Morishima, 2024.

Synonyms: *Spirometra erinaceieuropaei* of Eom et al. (2015), Jeon et al. (2015), Kudo et al. (2017); *Spirometra* Type II of Yamasaki et al. (2021); *Spirometra* sp. 1 of Kuchta et al. (2021).

Material examined: not available.

Type-host: Domestic dog *Canis familiaris* (Carnivora: Canidae).

Additional definitive host (molecularly confirmed): Domestic cat *Felis catus* (South Korea; experimental host); leopard *Panthera pardus pardus* (?) (Tanzania) (Carnivora: Felidae – Ndosi et al., 2020).

Intermediate (or paratenic) hosts (molecularly confirmed): Japanese boar *Sus scrofa leucomystax* Temminck (Japan) (Artiodactyla: Suidae); human *Homo sapiens* (Japan, Korea).

Type-locality: Yasakacho Takauchi, Hamada City, Japan.

Geographical distribution: East Asia (Japan, Korea), Africa (?) (Tanzania).

Type-material: Meguro Parasitological Museum, Tokyo, Japan (MPM 21893 – holotype, MPM 21894a, b – paratypes).

Representative DNA sequences: Jeon et al. (2015), Kudo et al. (2017), Ndosi et al. (2020) – as *S. erinaceiueuropaei*, Yamasaki et al. (2024).

Selected morphological features: Only two adult specimens are available (Jeon et al., 2015; Yamasaki et al., 2024); they are relatively large worms (holotype 2.43 m long) and about 8 mm wide. The uterus forms numerous loops and the ovary is relatively wide (ovary length/width ratio 0.42–0.59) and narrow (ovary width is 24–32% of the proglottid width), resembling the ovary of *S. erinaceiueuropaei*. The eggs are larger than those of *S. mansoni* and *S. erinaceiueuropaei* (74–80 µm long and 33–41 µm wide; average 77 × 33 µm).

Remarks

This is the best characterised species, which is genetically distinct from the widespread *S. mansoni* (see Yamasaki et al., 2024). It was recently described by Yamasaki et al. (2024) using adult cestodes from dogs and plerocercoids from wild boars in Japan. These tapeworms belong to the second, rare Asian lineage recognised by Kuchta et al. (2021) and Yamasaki et al. (2021).

Plerocercoids (spargana) of this species were found by Jeon et al. (2015) and Kudo et al. (2017) in 35 individuals from Korea and one patient from Japan, respectively. All specimens were misidentified as *S. erinaceiueuropaei* by Jeon et al. (2015) and Eom et al. (2015) as well as in other studies by these authors. Recently, Ndosi et al. (2020) confirmed a single case of *S. asiana* (misidentified as *S. erinaceiueuropaei*) in a leopard in Africa. The validity of this record should be checked as the sequence is short and does not match well with the regions covered by other sequences.

Spirometra sp. 2 (American lineage) Fig. 4.

Synonym: *Spirometra decipiens* complex 1 of Kuchta et al. (2021) and Vettorazzi et al. (2023).

Material examined: Only one immature piece (hologenophore) from *Lynx rufus*, USA (Illinois) (IPCAS C-987).

Definitive host (molecularly confirmed): Domestic cat *Canis familiaris* in Uruguay; crab-eating fox *Cerdocyon thous* in Brazil and Uruguay; domestic cat *Felis catus* in Brazil and Chile; lesser grison *Galictis cuja* (Molina) in Brazil; Geoffroy's cat *Leopardus geoffroyi* in Brazil; pampa cat *Leopardus munoai* (Ximénez) in Uruguay; ocelot *Leopardus pardalis* in Argentina; pampas fox *Lycalopex gymnocercus* (Fischer) in Argentina; hoary fox *Lycalopex vetulus* (Lund) in Brazil; bobcat *Lynx rufus* in USA; puma *Puma concolor* in Argentina.

Intermediate (or paratenic) hosts (molecularly confirmed): Human *Homo sapiens* in Venezuela; *Crotalus* sp. in Brazil; *Philodryas patagoniensis* in Uruguay; *Didelphis albiventris* in Brazil, Uruguay; *Austrolebias charrua* in Uruguay.

Geographical distribution: South America (Argentina, Brazil, Chile, Uruguay, Venezuela), North America (USA – Illinois).

Representative DNA sequences: Miyadera et al. (2001), Petriugh et al. (2015), Almeida et al. (2016), Arrabal et al. (2020), Armúa-Fernández et al. (2021), Kuchta et al. (2021), Fredes et al. (2022), Kikuchi et al. (2021), Vettorazzi et al. (2023); Trindade et al. unpublished – see the Genbank database).

Selected morphological features: The uterus is similar in appearance to the Palaearctic species, i.e. it lacks the conspicuously enlarged C-shaped distal loops typical of *S. decipiens* (Fig. 4).

Remarks

Kuchta et al. (2021) found two different lineages of *Spirometra* tapeworms in North and South America and named them *S. decipiens* complex 1 and *S. decipiens* complex 2. Tapeworms of complex 1 form a

relatively well-supported lineage between the European *S. erinaceiueuropaei* and the predominantly Palaearctic *S. mansoni* and *S. asiana* (Fig. 1). This complex 1 consists of specimens of various South American carnivores (adults) and plerocercoids of reptiles and humans, including the enigmatic *Sparganum proliferum* (Arrabal et al., 2020). Vettorazzi et al. (2023) have also indicated the rivulid killifish *Austrolebias charrua* as paratenic host of this tapeworm, which is the first report of *Spirometra* plerocercoids in fish.

Spirometra sp. 3 (North American lineage) Fig. 4

Synonym: *Spirometra decipiens* complex 2 (North American lineage) of Kuchta et al. (2021).

Possible synonym: *Spirometra mansonoides* (Mueller, 1935) Mueller, 1936.

Material examined: syntypes of *S. mansonoides* from *Felis catus* L., USA (USNM 1333923).

Definitive host (molecularly confirmed): Bobcat *Lynx rufus* in USA (Wisconsin) (Carnivora: Felidae).

Intermediate (or paratenic) hosts (molecularly confirmed): Eastern racer *Coluber constrictor* (L.) in USA (Mississippi); western rat snake *Pantherophis obsoletus* (Say in James) in USA (Louisiana); *Thamnophis proximus* in USA (Mississippi) (Squamata: Colubridae); meerkat *Suricata suricatta* (Schreber) in USA (South Carolina zoo) (Carnivora: Herpestidae).

Geographical distribution: USA (Louisiana, Mississippi, South Carolina, Wisconsin).

Representative DNA sequences: Waeschenbach et al. (2015), McHale et al. (2020).

Remarks

Tapeworms of the part of the former *S. decipiens* complex 2 from large cats in South America, including Brazil, where *S. decipiens* was described by Diesing (1850), are considered to be 'true' *S. decipiens* (see above) and the second lineage from reptiles and bobcats from North America form an independent lineage (possibly a separate species). In contrast, it remains an open question whether the tapeworms of the other North American lineage (*S. decipiens* complex 2) actually belong to *S. mansonoides*, which was described in a domestic cat in New York State (see below; Fig. 1).

4.2. Species of unclear taxonomic status

Spirometra ranarum (Gastaldi, 1854) Faust, Campbell et Kellogg, 1929.

Synonym: *Ligula ranarum* Gastaldi, 1854.

Remarks

This little-known species of uncertain taxonomic status was described by Gastaldi (1854) on the basis of plerocercoids found in the green frog *Pelophylax esculentus* (L.) from northern Italy (Turin). Meggitt (1924) reported this species, including experimentally obtained adults, from Asia (Myanmar) (MHNG-PLAT 56230; examined by the present authors). This obvious misidentification with *S. mansoni* was later repeated by Faust et al. (1929) in the identification of specimens from China. Molecular data on '*S. ranarum*' were presented by Eom et al. (2018), Jeon et al. (2018) and Ndosi et al. (2020) for isolates from Korea, Myanmar and Tanzania, but all tapeworms actually belong to *S. mansoni* based on the molecular data (see Kuchta et al., 2021).

Molecular data on *S. ranarum* from southern Europe (Italy and France) are not available to confirm the validity of this species, which could be conspecific with the European *S. erinaceiueuropaei* or with the cosmopolitan *S. mansoni*, which was molecularly confirmed in ranid frogs (*Pelophylax* spp.) from the Danube Delta in Romania (Kuchta et al., 2021).

Spirometra raillieti (Rätz, 1913) Wardle, McLeod et Stephanson, 1985

Synonym: *Sparganum raillieti* Rätz, 1913.

Remarks

The systematic status of this species, described from plerocercoids of domestic pigs (*Sus scrofa* L.) in Hungary and Serbia, is unclear as it has never been reported since its first description and no molecular data on *Spirometra* from Hungary are available to confirm the validity of this poorly characterised species. [Kotlán \(1923\)](#) obtained adult tapeworms from experimentally infected dogs, but was unable to become infected himself. The geographically closest record of *Spirometra* tapeworms comes from Romania, where the presence of *S. mansoni* in green frogs (*Pelophylax* spp.) was confirmed by molecular data ([Kuchta et al., 2021](#)).

Spirometra mansonioides ([Mueller, 1935](#)) Mueller, 1936 Fig. 4K–O.
Synonym: *Diphyllobothrium mansonioides* [Mueller \(1935\)](#).

Remarks

This species was described by [Mueller \(1935\)](#) as *Diphyllobothrium mansonioides*, based on adult tapeworms found in domestic cat near Syracuse, New York, USA. The type material was examined by the present authors (USNM 1333923). Morphologically, *S. mansonioides* differs from most *Spirometra* species (mainly *S. asiana*, *S. erinaceieuropaei*, *S. mansoni* and *S. theileri*) in that the uterus consists of two large terminal loops and forms a typical C-shaped terminal part of the uterus ([Fig. 4](#)). However, this type of uterus is also present in *S. decipiens* (see [Lühe 1899](#); [Schmidt and Martin 1978](#); [Mueller 1935, 1974](#); present study). According to [Marucci and Mueller \(1972\)](#), the plerocercoids of *S. mansonioides* are more delicate and fragile than those of other *Spirometra* species. However, no molecular data on *S. mansonioides* are available, which makes a clear characterisation of this species impossible.

The available sequences of *Spirometra* tapeworms from the USA include two lineages designated by [Kuchta et al. \(2021\)](#) as ‘*S. decipiens* complex 1’ (=‘true’ *S. decipiens*; see above) from the bobcat in Illinois, and ‘*S. decipiens* complex 2’ from snakes in Mississippi, and the meerkat in a zoo in South Carolina. Molecular data on tapeworms from the region where the type locality is located (Syracuse, New York) are needed to clarify the taxonomic status and confirm the validity of *S. mansonioides*.

Bothriocephalus maculatus Leuckart, 1848.

Remarks

It is likely that this species is related to the genus *Spirometra*. However, it was only briefly described by [Leuckart \(1848\)](#), using material from an imported “leopard” (probably *Panthera pardus*) of unknown

origin. It is therefore not possible to identify this species. Due to this incomplete description, this species is considered a *species inquirenda*.

5. Geographical distribution

Spirometra tapeworms are distributed worldwide and have been reported from all continents except Antarctica, including some isolated islands such as Guam, Hawaii, Madagascar, Mauritius, New Zealand and Puerto Rico ([Daly, 1981](#); [Scholz et al., 2019](#)) ([Fig. 8](#); [Supplementary Table S1](#)). Most records come from South and East Asia, but relatively many also from South America. Only a few records have been published from Africa and some from the USA thanks to the numerous studies by J. F. Mueller ([Supplementary Table S1](#)). However, it is difficult to provide more precise information on the occurrence of individual species, as most published reports cannot be reliably assigned to any of these species, with the exception of specimens that have been sequenced (see [Supplementary Table S1](#)). The main reasons for the lack of reliable species identification are discussed in Chapter 2. In addition, the geographical separation of individual species may be questionable, as *Spirometra* tapeworms may also have been spread throughout the world by domestic dogs and cats ([Mueller, 1974](#); [Odening, 1979](#); [Daly, 1981](#)). For example, *Spirometra* may have been introduced to Australia with the arrival of placental mammals (Eutheria), possibly also through human activities ([Stephanson 1985](#)).

Despite the obstacles mentioned above, it is obvious that most records of *Spirometra* tapeworms originate from subtropical and tropical latitudes with warmer climates ([Fig. 8](#)). In this respect, *Spirometra* tapeworms differ from *Dibothriocephalus* tapeworms, which are more common in colder climates, i.e. in temperate zones, including the Arctic ([Scholz et al., 2019](#)). In addition, a certain geographical pattern can be observed in the distribution of the individual species that have been genetically characterised ([Kuchta et al., 2021](#); [Yamasaki et al., 2024](#)). In short, most species appear to have a rather limited geographical distribution (see [Fig. 3](#) in [Kuchta et al., 2021](#); further details are given in a review of individual valid species – Chapter 4 – and in a review of the fauna of individual continents below): (i) *S. erinaceieuropaei* is possibly endemic to Europe, as there are no reliable records of this species outside Europe supported by molecular data; (ii) *S. theileri* is probably endemic to Africa; (iii) *S. decipiens* and *Spirometra* sp. 2 and 3 (American lineage 2) are possibly endemic to the Americas; (iv) the recently described

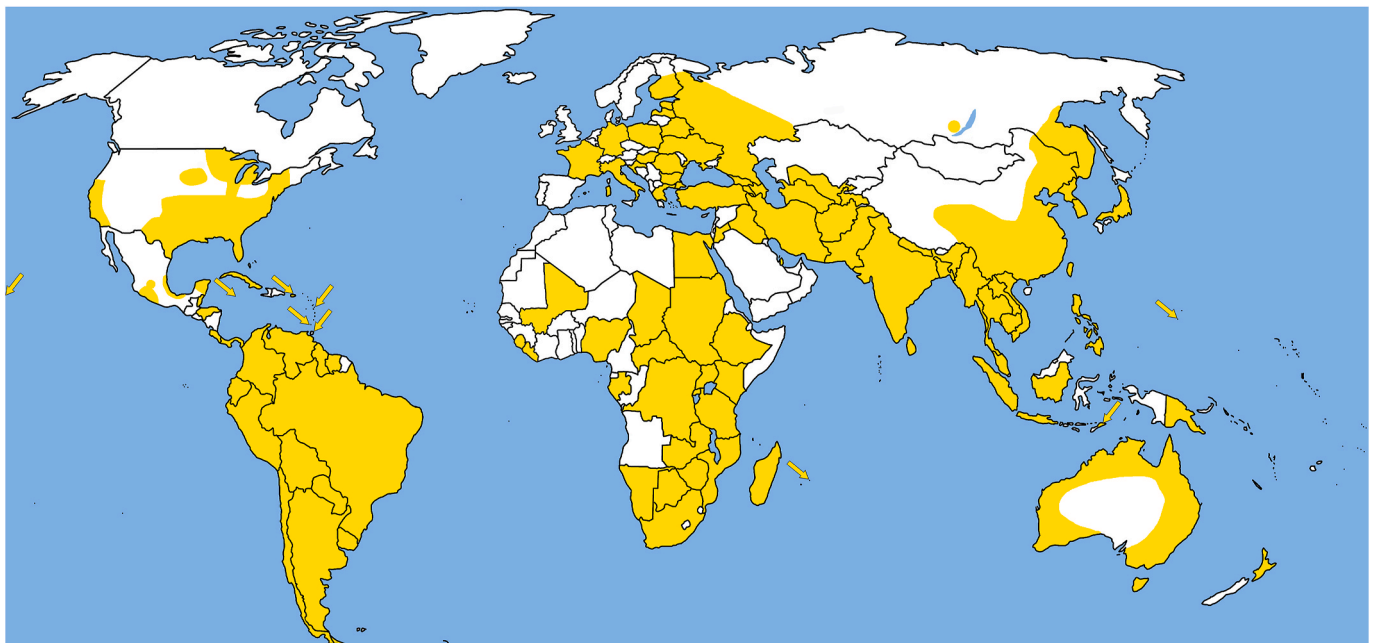


Fig. 8. Map of the distribution of *Spirometra* spp. in the world (in yellow). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

S. asiana has been found in Japan and Korea; Ndotsi et al. (2020) have reported the alleged occurrence of this species in Africa (Tanzania) but this record needs to be verified. In contrast, the most widespread *S. mansoni*, by far the most commonly reported in humans, has a wide geographical distribution (Eurasia, Australia and Africa), with a recent molecularly confirmed case from Colombia (Brabec et al., 2022).

5.1. Africa

The first species named from Africa is ‘*Spirometra*’ *folium*, but it is in fact not a species of *Spirometra* (see above). Several other species have been described from Africa (see Scholz and Kuchta, 2019), such as *Sparganum baxteri*, *Spirometra pretoriensis* and *Spirometra theileri* (see Sambon, 1907; Baer, 1924, 1925); the last species is the most common and considered valid (see above).

Spirometra tapeworms have been reported in about 40 records from the following countries, including human cases (Supplementary Table S1; Fig. 8): Central African Republic, Chad, DR Congo, Egypt, Ethiopia, Gabon, Kenya, Liberia, Madagascar, Mali, Mozambique, Namibia, Nigeria, Republic of Congo, Rwanda, Sierra Leone, South Africa, South Sudan, Sudan, Tanzania, Zambia and Zimbabwe. However, molecular data on *Spirometra* tapeworms in Africa are scarce and genetically characterised specimens are only available for two, possibly three species from the following countries: Ethiopia (*S. theileri*), Mauritius (*S. mansoni*), South Africa (*S. theileri*), South Sudan (*S. theileri*) and Tanzania (*S. theileri*, *S. asiana* (?) and *S. mansoni*) (Eberhard et al., 2015; Ndotsi et al., 2020; Kuchta et al., 2021; present study).

The definitive host of *Spirometra* tapeworms in Africa is mainly the spotted hyena, but they are also frequently reported from lions and leopards (Nelson et al., 1965; Engh et al., 2003; Berentsen et al., 2012; Kavana et al., 2015; Ndotsi et al., 2020). Plerocercoids are known from mammals such as desert warthog, the spotted hyena, but also from humans with sparganosis. Opuni and Muller (1974) experimentally infected dogs with plerocercoids of *Phacochoerus aethiopicus* and obtained adults identified as *S. theileri* (material not available). They maintained the entire life cycle in England, where they infected several mammals that served as a second intermediate or paratenic host (rodents, rhesus monkeys). However, they were unable to infect amphibians and reptiles, which are commonly used as second intermediate hosts of *S. erinaceiropaei* or *S. mansoni*.

5.2. Asia

In Asia, two *Spirometra* species have been confirmed by molecular data, with the widespread, probably cosmopolitan *S. mansoni* dominating; most records come from East (China, Japan) and Southeast Asia (Laos, Thailand and Vietnam). There are reports from the following countries: Azerbaijan, Bangladesh, China, Georgia, India, Indonesia, Iran, Iraq, Japan, Jordan, Malaysia, Philippines, Russia, South Korea, Sri Lanka, Tajikistan, Thailand, Turkmenistan, Uzbekistan and Vietnam (see Supplementary Table S1).

Molecular evidence for the occurrence of *S. mansoni* is available from the following 11 countries (see Supplementary Table S1): Cambodia, China, India, Indonesia, Iran, Laos, Japan, Myanmar, South Korea, Thailand and Vietnam. The second Asian lineage of *Spirometra* (see Kuchta et al., 2021) was recently described as *S. asiana* by Yamasaki et al. (2024) from Japan and South Korea. The report by Ndotsi et al. (2020) of *S. asiana* (misidentified as *S. erinaceiropaei*) in a leopard in Africa should be confirmed.

5.3. Australia and Oceania

Spirometra tapeworms are widely distributed in Australia, with the exception of the central part of the country, and are common in introduced placental mammals. The prevalence of adults can be high (up to 60%) in cats and foxes, but much lower in dogs (Stephanson 1985).

Spirometra tapeworms have also been reported from isolated islands such as Guam, Hawaii, New Zealand, Papua New Guinea and Tasmania (Supplementary Table S1). However, molecular data from this zoogeographical region are sparse and confirm the presence of the widespread *S. mansoni* in dogs and cats from Melbourne (Waeschenbach et al., 2017), a cat from Manawatu, New Zealand (Ugarte et al., 2005 – erroneously as *S. erinaceiropaei*), as well as plerocercoids from the Australian green tree frog *Ranoidea caerulea* (White) imported to Europe (Fischer et al., 2010), and the lowland copperhead *Austrelaps superba* (Günther) in Victoria (Kuchta et al., 2021).

5.4. Europe

Several species have been described from Europe, but their validity is questionable. *Spirometra* tapeworms, especially plerocercoids from second intermediate hosts, including humans, have been reported from 17 countries (Kuchta et al., 2021, Fig. 8). Currently, the presence of only two species, *S. erinaceiropaei* and *S. mansoni*, has been confirmed based on molecular data (Kuchta et al., 2021). Molecular data confirmed that *S. erinaceiropaei* occurs in Central and Eastern Europe and has relatively low genetic variability (Čisovská Bazsalovicsová et al., 2022).

However, this species name has often been erroneously applied to specimens of *Spirometra* from around the world, including the recently described *S. asiatica* from Korea and Japan, which was also misidentified as *S. erinaceiropaei* by Korean authors (see Kuchta et al., 2021; Yamasaki et al., 2021, 2024). The cosmopolitan *S. mansoni* was recently found as a plerocercoid in green frogs in Romania, but the species identity of *Spirometra* tapeworms reported from the Mediterranean and the Balkans is still unclear (Kuchta et al., 2021).

The systematic status of *Spirometra ranarum*, described as a larva from an Italian frog (but erroneously reported by several authors from Africa and Asia), and *Spirometra raillieti* (Rátz, 1913), described as a larva from domestic pigs in Hungary and Serbia, is unclear, as no molecular data are available to confirm the validity of these poorly known and insufficiently characterised species (see above).

5.5. North America (including Central America and the Caribbean)

Spirometra tapeworms have been found in Belize, Canada, the Cayman Islands, Costa Rica, Cuba, Grenada, Honduras, Mexico, the Netherlands Antilles, Puerto Rico and in 24 states of the USA (Supplementary Table S1), but molecular evidence is only available for specimens from two different genetic lineages corresponding to *Spirometra* sp. 2 and sp. 3 (=‘*S. decipiens* species complex 1 and 2’). *Spirometra* sp. 2 occurs mainly in South America, but a single specimen from a bobcat in Illinois (USA) genetically corresponds to South American isolates of *Spirometra* sp. 2 (Fig. 1).

The specimens of *Spirometra* sp. 3 (North American lineage) could represent a separate species of the tapeworms of the same lineage (*S. mansonioides*?) found in North and South America, but the available data are too limited to make a reliable decision. Because *S. mansonioides* has been described from the northeastern United States, it is desirable to collect new material from near the type locality (Syracuse, New York) to clarify the validity and phylogenetic relationships of this previously repeatedly reported but poorly characterised species with an unknown host range and geographical distribution. For the most widespread *Spirometra* species, *S. mansoni*, there is no reliable (molecularly characterised) evidence from North America.

5.6. South America

Several species assigned to *Spirometra* have been described from South America, but the validity and taxonomic status of most of them are uncertain (Table 1). *Spirometra* tapeworms with different names have been found in Argentina, Bolivia, Brazil, Chile, Colombia, Ecuador, Panama, Paraguay, Peru, Suriname, Trinidad, Uruguay and Venezuela

(Supplementary Table S1). However, only specimens from Argentina, Bolivia, Brazil, Colombia, Uruguay and Venezuela were sequenced (Vettorazzi et al., 2023).

Currently, tapeworms of three different lineages (= putative species) have been found in South America, most likely corresponding to three different species: (i) *S. decipiens* (= '*S. decipiens* species complex 2 South American lineage'), which is a typical parasite of felids in South America and was recently also found in rivulid fish in Uruguay by Vettorazzi et al. (2023); (ii) *Spirometra* sp. 2 (= '*S. decipiens* species complex 1') commonly reported from a wide range of wild felids as well as domestic cats and dogs in South America, but also one isolate from bobcat from USA (Illinois); and (iii) the widespread *S. mansoni*, recently found in crab-eating fox from Colombia by Brabec et al. (2022) (Fig. 1; Supplementary Fig. 1).

6. Conclusions and prospects

With a little exaggeration, one can say that the taxonomy of *Spirometra* should start from scratch due to the lack of reliable morphological data associated with genetically characterised specimens. A radical approach would be to consider any species described from spargana as *species inquirenda* or even *nomina dubia*, unless there is irrefutable molecular or life cycle evidence that a particular sparganum is associated with a properly known/described adult tapeworm.

The recent description of *S. asiana* by Yamasaki et al. (2024) should serve as a guide for what future taxonomic accounts should look like, i.e. individual species should be characterised based on properly fixed fresh material of tapeworms suitable for molecular and morphological description.

Molecular data indicate the presence of at least seven different *Spirometra* lineages, but it is possible that additional species will be recognised based on the sequencing of new samples, especially from South America and Africa. The available data suggest broad host specificity of most species at the definitive and intermediate host level, but much more information is needed before a more reliable conclusion can be drawn. With the exception of the cosmopolitan *S. mansoni*, the other species appear to have a rather limited geographical distribution, mostly restricted to a single continent.

Fixation is an important factor that can significantly influence morphology of the samples. To obtain comparable samples suitable for morphological studies, heat-fixation is strongly recommended: a near-boiled 4% formaldehyde solution (formalin), provided that a piece of tissue from the same sample is simultaneously fixed in 96–99% molecular ethanol for sequencing, or killing with a near-boiled saline solution (0.9% NaCl) followed by preservation of the entire sample in 70–80% molecular ethanol (Chervy, 2024).

The traditional practice of relaxing diphylobothriidean tapeworms in saline or even in water, or fixing them under strong pressure, must be avoided, as these methods cause artificial changes in morphology (Kuchta and Scholz, 2017; Chervy, 2024). However, most *Spirometra* tapeworms are obtained from dead or frozen definitive hosts, making the specimens unsuitable for reliable morphological examination. Nevertheless, molecular data can be obtained from these samples.

The morphological differences between individual *Spirometra* species do not appear to be very great. Therefore, genotyping will remain unavoidable for the identification of adult tapeworms and plerocercoids, including clinical samples of human sparganosis or spirometosis. Despite the obstacles in accessing fresh material, new species should never be described on the basis of limited and/or poorly fixed specimens, as this makes it impossible to distinguish between intraspecific morphological and morphometric variation and interspecific differences (Iwata 1934, 1972; Kuchta and Scholz 2017; Kuchta et al., 2021).

In terms of nomenclature, it is advisable to use already established names of *Spirometra*, provided that new, properly fixed material is collected from type hosts near type localities of a given taxon. Otherwise, new names should be proposed for putatively new species when

there is no link to previously described taxa, i.e. when there is no correspondence with the definitive hosts and locality of the original description.

Despite great efforts in recent decades, the most enigmatic 'species', *Sparganum proliferum*, described from Japan and causing fatal infections in humans, has still not been identified, partly because most clinical samples have been previously fixed in formalin, making their molecular characterisation impossible, with the exception of one sample from Venezuela (Miyadera et al., 2001; Kikuchi et al., 2021). All clinical staff, physicians and veterinarians are strongly advised to fix all samples of *Spirometra* tapeworms in molecular ethanol to allow genotyping of the samples and subsequent species identification.

CRedit authorship contribution statement

Roman Kuchta: Writing – review & editing, Visualization, Investigation, Data curation, Conceptualization. **Anna J. Phillips:** Writing – review & editing, Investigation. **Tomáš Scholz:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ijppaw.2024.100947>.

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