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Fossil constraints on the origin and evolution of Platyhelminthes are surprisingly concordant with modern molecular phylogenies

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ABSTRACT. Trace fossils preserved with fossil worm-shaped remains suggest the presence of free-living flatworms during the Ordovician at the latest and their occurrence in terrestrial environments during the Permian. The presence of hooks associated with acanthodian and placoderm fishes indicates the existence of parasitic monopisthocotyleans, with a simple life cycle, during the Devonian. The presence of eggs in shark coprolites suggests the occurrence of eucestode tapeworms, with complex life cycles, during the Permian, possibly even earlier in the Carboniferous. Fossil evidence for trematode flatworms, also with complex life cycles, is more recent, including diverse findings associated with bivalves, lizards, and coprolites of archosaurs in terrestrial environments between 126 and 76 Ma in the Cretaceous. Convincing evidence for gymnophallid trematodes in marine environments appears in the Eocene, with an earlier occurrence in Cretaceous freshwater environments. This chronological pattern of first appearance (Turbellarians > Monopisthocotylea > Cestoda > Trematoda) is surprisingly concordant with some recent molecular phylogenetic analyses. Further evidence to test these hypotheses could be obtained by conducting systematic screenings for resistant remains of platyhelminths such as hooks and eggs as well as characteristic traces such as trails or shell concretions preserved with their producers. Additional study and scrutiny are particularly needed for trace fossils attributed to free-living flatworms that are not associated with their producers. We make recommendations on how different constraints on flatworm evolution can be interpreted and used in future studies.

KEY WORDS. Cophylogeny, flatworms, fossil record, macroevolution.

INTRODUCTION

Flatworms are a diverse group of invertebrate animals with over 30000 described extant species (Caira and Littlewood 2013). Although most described flatworm species that exist today are members of the obligately parasitic Neodermata, the ancestral flatworm is inferred to have been free-living. All current free-living flatworms are contained within the paraphyletic "Turbellaria" (Collins 2017). The reported species numbers likely underestimate the diversity of both free-living and parasitic flatworms (Poulin and Morand 2000, Dobson et al. 2008, Curini-Galletti et al. 2020). Platyhelminths are of extreme societal and scientific importance as model organisms for the study of regeneration (Collins 2017, Vila-Farré et al. 2023), and because of their relevance for biomedicine and veterinary sciences as well as for conservation and evolutionary biology (Solà et al. 2015, Sluys 2019, van Straalen 2021, Mulvey et al. 2022).

The simple body plan of platyhelminths and their estimated phylogenetic position nested within Spiralia and Lophotrochozoa (Marlétaz et al. 2019) suggest that they are an ancient group of organisms. There has been considerable interest in what the ancestral flatworm might have looked like from both a neontological (Littlewood and Bray 2001, Baguñà and Riutort 2004b, Goodheart et al. 2023) and a paleontological perspective (De Baets et al. 2015, Budd and Jackson 2016, Tang et al. 2021); however, there is little doubt that it must have been free-living with a simple life cycle rather than a parasitic form with a complex life cycle.

Given their soft-bodied nature, comparatively small size and presence in habitats which hamper fossilization, it is not surprising that the flatworm fossil record is patchy and remains understudied (Kowalewski 1997, De Baets et al. 2021b, Littlewood and Donovan 2003). Only planarian tricladids, polyclads and neodermatans are among the flatworms to exhibit larger (> 1–2 mm) body sizes. All the other groups are collectively called "microturbellarians", reflecting their microscopic size and plesiomorphic adaptations to interstitial habitats (Laumer et al. 2015). Nevertheless, the latest reviews on the fossil record of platyhelminths show a better record than commonly assumed for neodermatan parasites (De Baets et al. 2015), resistant eggs of free-living rhabdocoels (Matsuoka and Ando 2021) or helminths more generally (De Baets et al. 2021a). Other sources reviewing the fossil record are over twenty years old (Poinar 2003). Currently available data suggest that several lineages are traceable to the Paleozoic based on trace fossils as well as resistant eggs and hooks (De Baets et al. 2015, 2021a).

Flatworms now exclude (xen)acoelomorphs (Ruiz-Trillo et al. 1999, Philippe et al. 2007, 2011). They consist of a monophyletic grouping of two clades, Catenulida and Rhabditophora, which are well-supported by molecular data (Egger et al. 2015, Laumer et al. 2015, Littlewood and Waeschenbach 2015). The sister groups Catenulida and Rhabditophora are each morphologically well-defined, but do not seem to share any known morphological apomorphies (Smith et al. 1986, Hooge 2001, Baguñà and Riutort 2004a, Larsson and Jondelius 2008). Although considerable progress has been made in the last decade, the internal phylogenetic relationships of Platyhelminthes are not yet fully resolved (Hahn et al. 2014, Egger et al. 2015, Laumer et al. 2015, Littlewood and Waeschenbach 2015, Kenny et al. 2019, Brabec et al. 2023, Caña-Bozada et al. 2023). Internal relationships are important for understanding constraints on the evolution of life history strategies and habitat shifts. Multiple flatworm lineages, including several turbellarian groups, developed symbiotic relationships (Jennings 1971, 1997, Rohde, 1997, Hoyal Cuthill et al. 2016, Blair et al. 2023), with at least nine inferred independent origins of parasitic relationships (Weinstein and Kuris 2016).

The relationships within the monophyletic Neodermata remain a particularly recalcitrant issue (Littlewood and Bray 2001, Littlewood 2006). Recent molecular phylogenetic analyses suggest a single origin of a parasitic lifestyle, with free-living Bothrioplanida as the closest relatives of the Neodermata (Egger et al. 2015, Laumer et al. 2015, Littlewood and Waeschenbach 2015). A previous popular hypothesis was that the initial appearance of ectoparasites with a simple life cycle was followed by the common origin of complex life cycles of trematodes and cestodes (Lockyer et al. 2003, Park et al. 2007, Hahn et al. 2014). Newer analyses question this hypothesis and find support for a scenario in which neodermatan lineages with a simple life cycle are not monophyletic (Justine 1998) and in which transitions between ectoparasitism with a simple life cycle and endoparasitism with a complex life cycle might have happened more than once (Brabec et al. 2023, Caña-Bozada et al. 2023, Zhang et al. 2024).

Another vexing issue is the scarcity of body fossils that can confidently be attributed to free-living turbellarians relative to members of Neodermata (De Baets et al. 2015). While relationships between some lineages of free-living flatworms are still debated, molecular phylogenetic analyses clearly suggest that free-living forms appeared before parasitic forms. Molecular phylogenetic analyses have also contributed to our understanding of habitat transitions between marine, freshwater, and (limno)terrestrial environments or of dispersal across environments (Van Steenkiste et al. 2013, Sluys 2019, van Straalen 2021, Okamura et al. 2022) in both turbellarians (Álvarez-Presas et al. 2008, Riutort et al. 2012, Benítez-Álvarez et al. 2020, Solà et al. 2022) and neodermatans (Badets et al. 2011, Brabec et al. 2015, Achatz et al. 2019, Fraija-Fernandez et al. 2021). While it is yet to be determined if the fossil record can provide suitable constraints on the age of all these transitions, such records would be the only direct evidence for the presence of flatworms in particular habitats at particular times (De Baets and Littlewood 2015). If no direct evidence is available for particular groups of platyhelminths, the fossil record of their close relatives could at least provide temporal constraints in other parts of the platyhelminth tree which might help to constrain the timing of these transitions. The fossil record of flatworms is often considered inappropriate for this task or deemed to be non-existent, but this is not entirely true – particularly when considering characteristic eggs and trace fossils associated with the remains of bodies of platyhelminths. The fossil record of helminth eggs can be at least as good as independently calibrated molecular divergence time estimates in eucestode tapeworms (De Baets et al. 2021a).

Here we review the fossil record and archeological finds of representatives of Platyhelminthes with a particular reference to constraining the earliest appearance of particular clades or the colonization of particular habitats or regions. We also evaluate how these fossil constraints on their evolution align with current phylogenetic hypotheses (Brabec et al. 2023) and make suggestions on the most fruitful directions to expand the application of fossils constraints when investigating flatworm evolution.

MATERIAL AND METHODS

We re-evaluated previously published findings including those listed in review articles (Poinar 2003, Gonçalves et al. 2003, Sianto et al. 2009 De Baets et al. 2015, 2021a, Ledger and Mitchell 2022). We also searched for new publications using Google Scholar and Web of Science with combinations of the keywords “fossil”, “flatworm” or “Platyhelminthes” and/or “paleoparasitology”. Only peer-reviewed articles, book chapters or review articles and additional references included in these sources were considered. To support our re-evaluations, we also sought references citing the original publications in Google Scholar containing expert opinions confirming or disagreeing with particular assignments.

RESULTS

Turbellarians

Multiple isolated body fossils have been attributed to tricladid or rhabdocoel turbellarians ranging from the Precambrian to the Quaternary. The oldest report of putative free-living flatworm fossils derives from the Precambrian (Allison 1975), although both the age and affinity of this specimen (Cloud et al. 1976, Eberlein and Lanphere 1988, Tweet et al. 2023) is questionable. We therefore advise against using this specimen to confidently constrain the presence of free-living flatworms.

Tang et al. (2021) compared the enigmatic ribbon-like fossil *Rugosusivitta* to flatworms, but they could not unequivocally assign it to Platyhelminthes. Peculiarly, although Tang et al. (2021) highlighted its larger size and obviously free-living mode of life, they compared it with derived parasitic tapeworms rather than their free-living relatives.

Poinar (2003, 2004) described an inclusion in Eocene Baltic amber as *Micropalaeosoma balticus* (Poinar, 2003) and interpreted it to be a rhabdocoel of the now defunct order Typhloplanoida and this finding was accepted by multiple authors (Knaust 2010, Van Steenkiste et al. 2010, De Baets et al. 2015, 2021a, Vila-Farré and Rink 2018, Worsaae et al. 2023). However, this amber inclusion has been plausibly re-interpreted as a pseudo inclusion by Szadziewski et al. (2018) making this taxon invalid. These authors reinterpreted the flatworm body with putative eggs as likely air bubbles on the surface of a 1.5 mm long ellipsoidal dent. This is in line with the lack of a digestive tract and its unnatural transparent preservation. As such, we suggest to not use this specimen as a calibration point.

The second-oldest report of body fossils from the Cenozoic attributed to free-living rhabdocoels and triclads are silicified remains from Miocene calcareous petroliferous nodules from a former lake environment in the Calico Mountains in California (Pierce 1960). These findings also need further scrutiny as the original publication only contains interpretative drawings and no photographs of the original specimens to corroborate these claims.

The oldest direct records that can be confidently attributed to free-living rhabdocoels are therefore eggs reported from Pleistocene to Holocene lake and sea deposits (Frey 1964, Harmsworth 1968, Kadota 1973, Van Geel et al. 1980, Haas 1996, Cocker et al. 2021, Matsuoka and Ando 2021). They are reminiscent of eggs of members of the rhabdocoel families Dalyelliidae, Polycystididae and Typhloplanidae (Matsuoka and Ando 2021). The oldest rhabdocoel eggs described so far derive from the Middle Pleistocene (250000 yrs BP [years Before Present]) of Lake Biwa in Japan (Kadota 1973). These eggs are of the *Gyratrix*-type and thus indicative of the presence of members of Polycystididae (Matsuoka and Ando 2021). Modern rhabdocoel representatives of the endosymbiotic Umagillidae and ectosymbiotic Temnocephalidae (Matsuoka and Ando 2021) as well as representatives of Tricladida (Kakui and Tsuyuki 2024) also produce characteristic egg capsules which could in principle be recovered from the sediment but are yet to be reported from the fossil record. Symbiotic fecampiids produce flash-shaped to long, tubular and spiral cocoons which typically contain two egg capsules attached to their hosts (mostly crustaceans) or hard marine substrates (e.g., rocks, wood, coral, rhizomes), but only modern specimens have been recovered so far (Handl and Bouchet 2007). As the exceptionally preserved body fossil record cannot be confidently identified before the Quaternary, there is a need to investigate the trace fossil record attributed to turbellarians (Fig. 1), particularly those associated with putative worm-like body fossils.

Knaust and colleagues recently attributed various trails to flatworm producers from the Ordovician (Knaust and Desrochers 2019) and the Triassic (Knaust 2010, 2021, Knaust and Costamagna 2012) which in some cases are still associated with a putative, but poorly preserved vermiform body outline. The latter are mostly preserved as calcitic casts of moulds but sometimes contain limonite mineralization around it, interpreted to represent a multilayered and complex body wall. In the best-preserved samples, the limonitic putative body wall is broken up by interpreted intercellular spaces and vacuoles filled by calcite. Some specimens are associated with complex calcareous spicules reminiscent of the spicular skeletons originating from the basal membrane known from modern marine rhabdocoel turbellarians such as *Florianella* and *Bertiliella* (Rieger and Sterrer 1975, Tyler and Hooge 2004). Superficially reminiscent spicules or small granular or crystalline bodies are known from most other flatworm orders as well as from other phyla including Xenacoelomorpha and Nemertea, but their composition, morphology, size and/or position seem to differ (Rieger and Sterrer 1975).

Various types of traces have been attributed to free-living flatworms (Knaust 2021), but only two types of traces (Fig. 1A, C) have clear modern analogues (Alessandrello et al. 1988, Knaust 2010). Horizontal creeping trails produced by minute vermiform organisms moving mucociliarily on or just beneath the seafloor were investigated by Collins et al. (2000). It might be difficult to unequivocally assign the mucociliary trails to particular lineages, but the size and morphology of associated worm-like body casts have been used to justify their assignment to platyhelminth orders or at least the phylum Platyhelminthes as opposed to other phyla or groups (Nemertea, sipunculid Annelida, Xenacoelomorpha). Such mucociliary trails from the Triassic were attributed to polyclads (Knaust 2010) based on their similarity to traces (Fig. 1A) produced by modern polyclad flatworms (Collins et al. 2000) as well the presence of spicules and vacuoles in the inferred body wall in associated putative body fossils. The size and appearance of the casts were used to assign similar traces from the Ordovician to free-living flatworms (Knaust and Desrochers 2019). Other traces at the Ordovician site have been attributed to members of Nemertea and Acoelomorpha based on their association with putative vermiform body fossils with different morphologies. The putative fossil nemerteans are more robust and elongate than turbellarians and display a pointed to rounded anterior end with structures consistent with the rhynchocoel, a fluid-filled coelomic cavity containing the proboscis, as well as a pointed anus indicative of a complete digestive system. The putative acoelomorph fossils have a flatter and rounder (discoidal) shape, which is consistent with the lack of a body cavity. A putative dark spot can be interpreted as a statocyst. Although they are no longer considered to belong to Platyhelminthes (Ruiz-Trillo et al. 1999, Baguñà and Riutort 2004), acoelomorphs share some characteristics with members of Nemertea and Platyhelminthes, including a ciliated epidermis, the presence of a statocyst, and a meiofaunal mode of life.

Age: The oldest marine trails associated with body fossils attributed to turbellarians derive from the Vauréal Formation of Anticosti Island, Canada (Knaust and Desrochers 2019). The studied units are assigned to the Katian allowing to assign an age at least as old as 445.2 ± 0.9 Ma (Mega-annum, i.e. unit of time equal to one million [10^6] years) according to GTS 2020 (Goldman et al. 2020).

Terricolichnus permicus Alessandrello, Pinna & Terruzi, 1988 trails from Permian and *Terricolichnus* sp. from the Triassic (Knaust 2010) have been attributed to planarian tricladids. They consist of a linear sequence of irregularly curved minute trails with impressions 0.5–1.0 mm long, 0.1 mm wide and in intervals of about 0.5–1.0 mm (Alessandrello et al. 1988, Knaust 2010). They are a few millimeters in length, straight to irregularly curved and often characterized by abrupt changes in directions consistent with the locomotion of peristaltic waves produced by myopodia going backward (Fig. 1B) to the direction of movement (Alessandrello et al. 1988) known from modern planarians (Pantin 1950, Froehlich 1955, Jones 1978, Minelli 1981). These traces from the Triassic (Knaust 2010) are sometimes associated with tiny sulphide aggregates interpreted as their producer's imprint, but the nature of these remains reveal no further anatomical details. The assignment of these traces to Tricladida seems reasonable based on our current state of knowledge, although experimental taphonomy might be needed for a more precise assignment and for better understanding the preservation mode of those traces. If the assignment is correct, it constrains terrestrial planarians as present by the Early Permian. The assignment of these traces to land planarians has been criticized by Ogren et al. (1999) who argued that (i) mucus trails cannot be preserved in the fossil record (although the opposite has been demonstrated; compare Collins et al. 2000) and that (ii) tracks resemble pressed tracks left by other animals with a higher body weight than land planarians. The more general argument that the

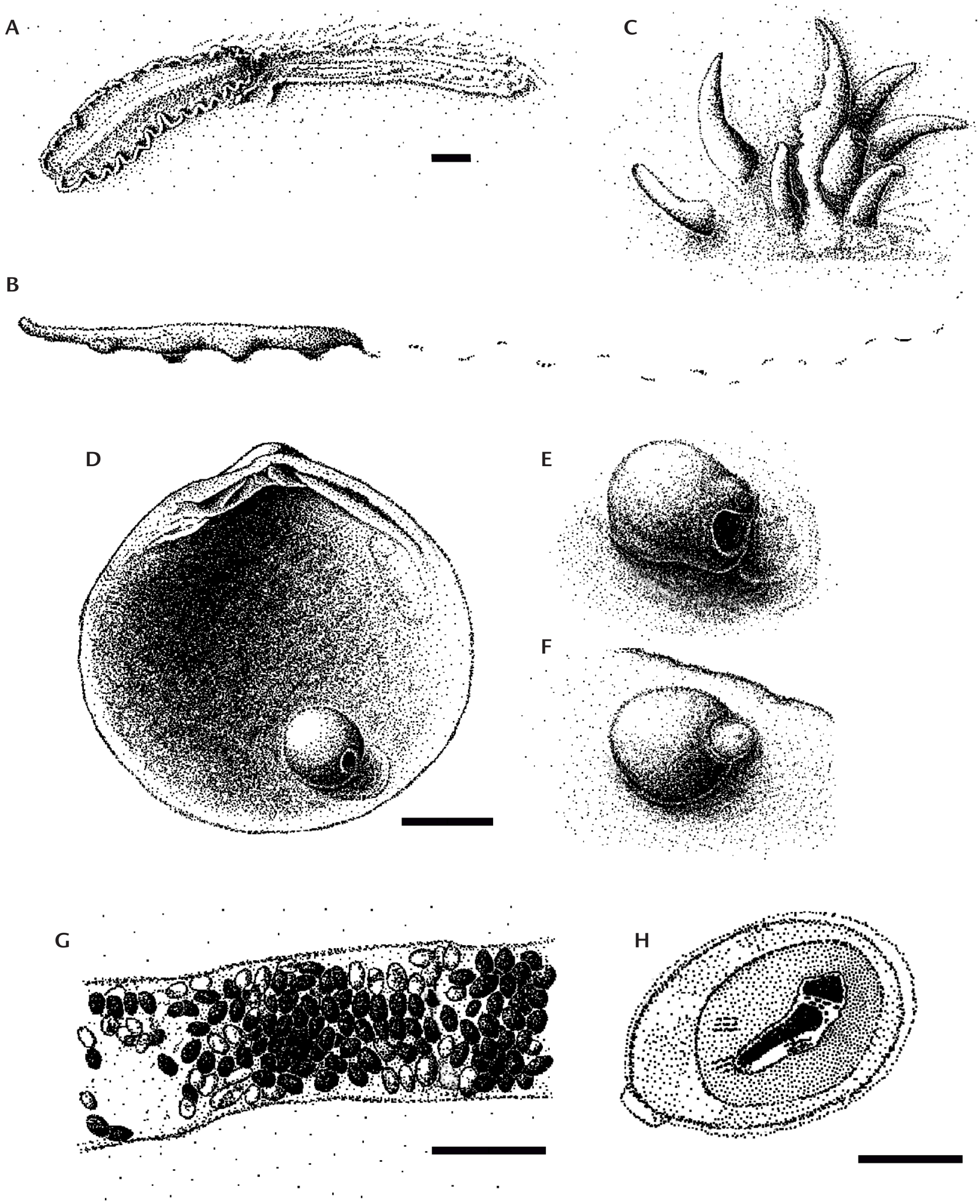

Figure 1. Examples of characteristic traces or structures attributed to representatives of Platyhelminthes which can be preserved in the fossil record. (A) Modern marine polyclad producing a mucociliary trail (drawing based on Collins et al. 2000); (B) Modern planarian producing a mucociliary trail (drawing based on Pantin 1950); (C) Circlet of hooks attributed to monopisthocotylean neodermatans associated with Devonian gnathostome fish (drawing based on Upeniece 2001); (D–F) Igloo-shaped concretions attributed to gymnophallid trematodes in a fossil bivalve (drawing based on Rogers et al. 2018) and a modern bivalve (drawing based on Ituarte et al. 2005); (G, H) eggs attributed to eucestode neodermatans in a Permian coprolite (drawings based on Dentzien-Dias et al. 2013). Scale bars: A = 5.0 mm, D = 0.5 mm, G = 1.0 mm, H = 50 µm.

tracks were produced by other mucus-ciliary movements is harder to dismiss (Collins et al. 2000, Ogren et al. 1999). Similar traces have occasionally also been attributed to or compared with arthropod tracks (Buatois et al. 2017, Ronchi and Santi 2003). The Permian and Triassic trails assigned to *T. permicus* are remarkably similar to observations (Fig. 1B) of modern planarian triclads of *Rhynchodemus* (Pantin 1950) and *Microplana* (Minelli 1981). Given the peculiarities of their movement, a triclad nature of these trails seems most likely.

Age: The oldest trails of *T. permicus* were found on a grey-green siltstone slab from the Lower Permian of Pre-Alps in Lombardy and interpreted to be produced by land planarians (Alessandrello et al. 1988). The siltstone slab was initially attributed to the Collio Formation which is now bounded by radiometric ages yielding a minimum age of 279.8 ± 1.1 Ma for these traces (Marchetti et al. 2015a, Schaltegger and Brack 2007). However, the holotype of *T. permicus* derives from the former Orobic Collio Formation in the Scioc valley (Ronchi and Santi 2003) and these units are now assigned to the Pizzo del Diavolo Formation considered to be of Kungurian age (Marchetti et al. 2015b). As the precise position within the Pizzo del Diavolo Formation is unknown, we suggest using the conservative minimum age of the top of the Kungurian, which is 274.4 ± 0.4 Ma according to GTS 2020 (Henderson et al. 2020).

Older trace fossils, such as *Curvolithus* from the Precambrian and Cambrian (Webby 1970, Buatois et al. 1998, Seilacher et al. 2003, 2005), have been suggested to be produced by larger free-living flatworms. However, they lack association with putative body fossils, have no obvious modern analogue, and are also not consistent with the supposedly small size of early branching lineages of modern free-living flatworms (Laumer and Giribet 2014, Laumer et al. 2015). Such traces could have been produced by a variety of infaunal carnivores including gastropod molluscs and nemerteans in addition to free-living flatworms (Buatois et al. 1998, Baucon et al. 2015). Additional constraints are needed to confidently attribute these Precambrian to Cambrian trails and other ichnofossils, particularly those not found in association with body fossils, to a flatworm producer and they should therefore not be used to constrain the flatworm molecular clock divergence time estimates.

Neodermata

Counterintuitively, the fossil record of derived parasitic neodermatans is more diverse and older (De Baets et al. 2015, 2021a) than those of their turbellarian relatives (compare Table 1, Figs 1, 2), which relates to their record of resistant eggs, hooks and pathologies preserved with their skeletonized hosts.

Upeniece and colleagues described over 69 circlets of hooks, at least 29 still associated with placoderms and acanthodian fishes (Upeniece 2001, 2011, De Baets et al. 2015, 2021a, Leung 2017, 2021), which were considered the earliest record of ectoparasitic neodermatans with a simple life cycle. No formal phylogenetic analyses were performed, but their circular arrangement of the bilateral symmetric hooks (Fig. 1C), traces of cuticular discs, their position as well as the maximum number of associations of up to 16 hooks speak for their assignment to Monopisthocotylea. So far, no additional reports of hooks attributable to Monopisthocotylea have been published, which could relate to the exceptional preservation, preparation biases and/or a lack of interest. Cuticular hooks attributable to cestodes – their potential sister lineage (Brabec et al. 2023) – have been interpreted as present in a tapeworm egg containing a putative developing larva in a proglottid (Dentzien-Dias et al. 2013, De Baets et al. 2015, 2021a).

Age: The circlets of hooks attributable to Monopisthocotylea derive from the Lode Formation which was traditionally assigned to the early Frasnian (Upeniece 2001). However, the Lode Formation is currently assigned to the Upper Givetian. This corresponds to 378.9 ± 1.2 Ma which is the minimum age assigned to the Givetian-Frasnian boundary according to GTS 2020 (Becker et al. 2020).

Tapeworm eggs have few defining characters and could potentially be confused with those of other helminths (Zangerl and Case 1976). In the Permian, the assignment of eggs associated with tapeworms in a spiral coprolite is supported by a putative developing embryo in one of the eggs (Fig. 1G) as well as assortment of eggs (Fig. 1H) in proglottids (De Baets et al. 2015, Dentzien-Dias et al. 2013). The latter speaks for their assignment to eucestode tapeworms.

Age: The coprolite containing the eggs interpreted to be associated with proglottids derives from the upper member of the Rio do Rasto Formation (Paraná Basin, southern Brazil). The vertebrate fauna suggests a Guadalupian (Late Wordian – Capitanian) age (Dentzien-Dias et al. 2013) which yields a minimum age of 259.5 ± 0.4 Ma defined by the Guadalupian-Lopingian boundary in GTS 2020 (Henderson et al. 2020).

Older eggs in a cololite associated with the shark genus *Cobelodus* have a surface structure and size consistent with modern tapeworm eggs (Zangerl and Case 1976), but their more precise assignment needs further investigation (De Baets et al. 2015, 2021a).

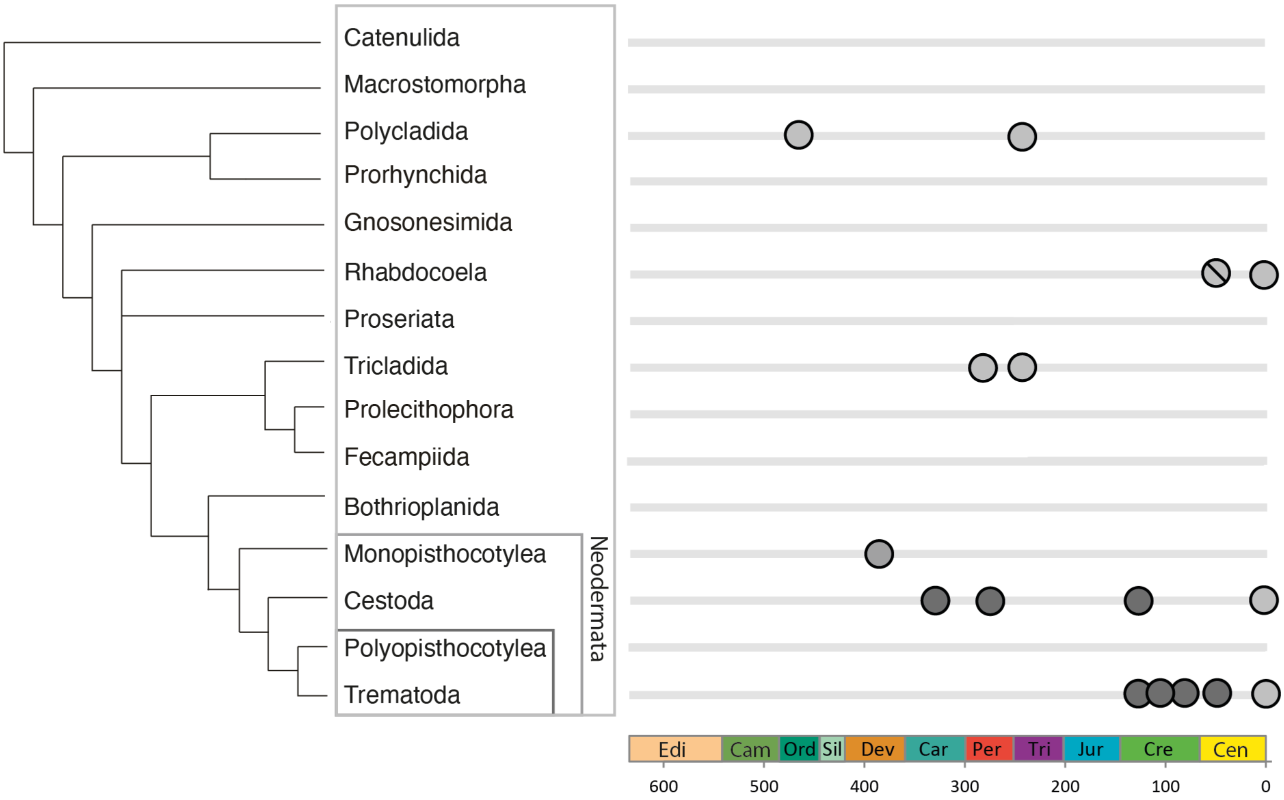

Figure 2. Stratigraphic occurrence of fossil evidence for particular orders of Platyhelminthes. Phylogeny follows Littlewood and Waeschenbach (2015) with the exception of Neodermata which follows Brabec et al. (2023). See Table 1 and text for further details of each find.

Table 1. Fossil finds attributed to particular groups of Platyhelminthes. More details can be found in text.

Node	Min. Age (Ma)	Stratigraphy, Stage, Country	Coll.	Environment	Support	Reference
Platyhelminthes (free-living turbellarians)	444.0	Vauréal Fm., Katian, Canada	MfN	Marine	Characteristic trails	Knaust and Desrochers (2019)
Tricladida	274.4	Pizzo del Diavolo Fm., Kungurian, Italy	MNHN	Freshwater	Characteristic trails	Alessandrello et al. (1988)
Monopisthocotylea	377.7	Lode Fm., Givetian, Latvia	LDM	Marginal marine	Circlets with up to 16 hooks	Upeniece (2001)
Cestoda	304.8	Stark Shale Mb., Kasimovian, USA	PF	Marine	Egg with similar surface ornamentation and size	Zangerl and Case (1976)
Eucestoda	259.1	Rio do Rasto Fm., Wordian-Capitanian, Brazil	UFRGS	Freshwater	Egg arranged in proglottids	Dentzien-Dias et al. (2013)
Trematoda	120.2	La Huérguina Fm., Barremian, Spain	MUPA	Freshwater	Egg with operculum	Barrios-de Pedro et al. (2020)
Gymnophallidae	75.22	Judith River Fm., Campanian, USA	UC	Freshwater	Characteristic igloo-shaped concretion	Rogers et al. (2018)
Gymnophallidae	52.93	London Clay Fm., Ypresian, England	NHM	Marine	Characteristic pit with raised rime	Todd and Harper (2011)

Age: The older eggs assigned to cestodes derive from excrements still lodged within the intestine of its producer the shark *Cobelodus aculeatus* (Cope, 1894). The fossil association derives from the Stark Shale member of the Dennis Formation near Forth Calhoun, Nebraska (Zangerl and Case 1976). It is assigned to the Missourian North American regional substage which largely corresponds to the Kasimovian (Falcon-Lang et al. 2011, Rosscoe and Barrick 2013). Conodont microfossils from this unit derive from the *Idiognathus confragus* zone (Heckel et al. 2011, Heckel 2013, Barrick et al. 2022) which would have a minimum age of 304.8 Ma according to GTS 2020 (Aretz et al. 2020).

An additional fossil egg was attributed to cestodes in a Cretaceous archosaur (?theropod) coprolite of Bernissart (Belgium) where it was associated with a putative trematode egg and amoeboid cyst (Poinar and Boucot 2006).

Age: See age discussed for the trematode egg found within the same coprolite.

Recently, a difficult to place isolated structure in Myanmar amber was interpreted as a cestode tentacle (rostellum). It has some characteristics which at first glance seem most consistent with its assignment to trypanorhynch tapeworms (Palm et al. 2009) that parasitize marine elasmobranchs (mainly sharks and rays). However, the tentacle is longer, and the hooks are different and inconsistently shaped from those that can be confidently assigned to any modern lineage of Trypanorhyncha. The structure also has similarities to extinct armored worm-like paleoscolecid ecdysozoans not recovered from the Post-Silurian fossil record (Harvey et al. 2010, Wills et al. 2012), but this was also the time their main preservational windows closed (Wendruff et al. 2020, Whitaker et al. 2020). The taphonomic scenario to explain how to detach such structures which are firmly embedded within a scolex (Beveridge et al. 2014) is highly speculative and unlikely. More complete material, preferably still associated with its host remains, is necessary to confirm its precise assignment, mode of life as well as its host affinities. Irrespective of their assignment and host affinity, they further underline that structures similar to a cestode scolex and its hooks could be more widely preserved in the fossil record than currently known.

Age: See age discussed for the swelling in an agamid lizard attributed to trematodes

Trematodes

Various fossils indicate that trematodes were present in terrestrial environments in the Cretaceous (Okamura et al. 2022). However, the oldest is an egg from a bump-head lace morphotype of a fish coprolite derived from Las Hoyas Lagerstätte (Cuenca, Spain) which was compared with the eggs of members of the modern family Opisthorchiidae and attributed to Digenea (Barrios-de Pedro et al. 2020).

Age: The oldest egg (MUPA-LH-SnG11-Tr) attributed to the digenetic trematodes derives from the Las Hoyas locality, which is interpreted to be deposited in a freshwater wetland environment. Las Hoyas located within La Huérguina Formation is attributed to the latest Barremian based on the combination of charophyte and ostracod content (Schudack and Schudack 2009, Vicente and Martín-Closas 2013, Fregenal-Martínez et al. 2017). A conservative minimum age for the egg is therefore the Barremian-Aptian boundary coinciding with the start of magnetochron M0r which was placed at 121.4 ± 0.6 Ma according to GTS 2020 (Gale et al. 2020). However, the start of magnetochron M0r has now been redated to 120.29 ± 0.09 Ma (Li et al. 2023).

A second egg attributable to trematodes was reported from a slightly younger archosaur coprolite (Poinar and Boucot 2006) but could not be assigned further.

Age: The fossil-bearing Wealden-facies of the Sainte-Barbe Clays Formation in the Bernissart pit can now be more precisely dated as Late Barremian to Early Aptian in age (MCT4) based on the combination of palynology and chemostratigraphy (Yans et al. 2006, 2012, Schnyder et al. 2009), corresponding with the upper part of magnetochron M1n, M0r and the basal part of M0n. This yielded an approximate minimum age for these strata of 120.6 Ma, the age assigned to the base of the *Leupoldina cabri* biozone which is correlated to postdate the upper part of MCT4 corresponding with M0n (Schnyder et al. 2009) in GTS 2020 (Gale et al. 2020). However, a recent redating of magnetochron M0r resulted in an age of 119.40 ± 0.12 Ma assigned to the base of *L. cabri* Zone (Li et al. 2023).

So far, no additional eggs from the Mesozoic could be confidently assigned to trematodes, but Matsuoka and Ando (2021) suggested that some taxa of organic-walled acritarch microfossils could potentially represent trematode egg capsules.

A swelling in an agamid lizard preserved in Myanmar amber was also compared and interpreted as an encysted trematode metacercaria using computed tomography (Poinar et al. 2017).

Age: Myanmar amber is at least 98.79 ± 0.62 Ma old (Shi et al. 2012).

Gymnophallid lineages of trematodes produce characteristic pit and igloo-structures (Figs 1D–F, 3) which have been confidently traced back to the Eocene (Todd and Harper 2011, Huntley and De Baets 2015) and Cretaceous (Rogers et al. 2018, Huntley et al. 2021), respectively. The oldest igloo-structures from the Maastrichtian of the USA reminiscent of structures produced by modern gymnophallids complete the Cretaceous record of trematodes (Rogers et al. 2018).

Age: Distinctive igloo-shaped traces attributable to a trematode have been found on the freshwater bivalve belonging to *Sphaerium* in the fluvial and lacustrine facies of the Coal Ridge Member of the Judith River Formation of Montana. The coal ridge member is well constrained through radiometric ages between 76.32 and 75.22 Ma (Rogers et al. 2016, Ramezani et al. 2022).

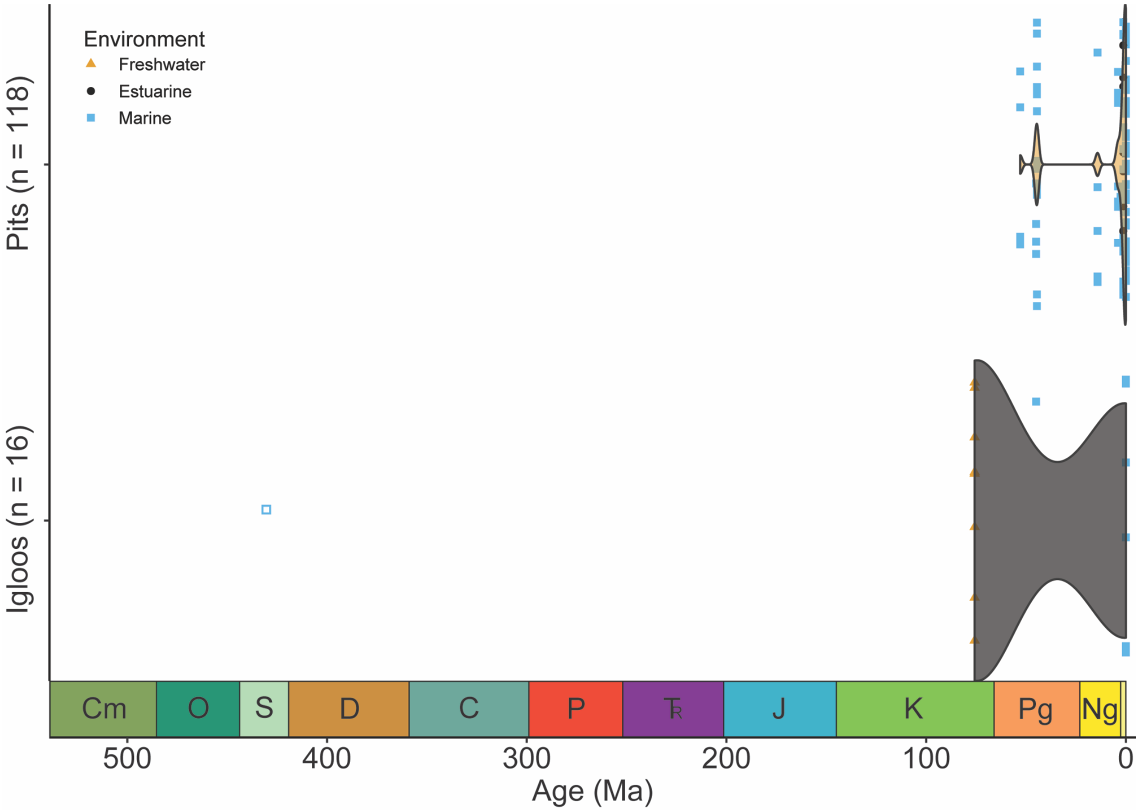

Figure 3. Summary of the stratigraphic occurrence of characteristic igloo-shaped and pit-shaped structures attributed to gymnophallid trematodes. Question mark refers to a superficially similar igloo structure discussed in text which is superficially similar but lacks diagnostic characters to make it clearly assignable to trematodes. See text for further details.

The Cretaceous igloo-like structures might therefore indicate the presence of representatives of Gymnophallidae by 75 Ma in freshwater environments at the latest (Rogers et al. 2018) and pre-date the appearance and fossil record of their modern shorebird hosts (Ruiz and Lindberg 1989, Černý and Natale 2022). The latest molecular divergence time estimate places the origin of shorebirds in the Paleocene (Černý and Natale 2022). Interestingly, the London Clay Formation which yielded the oldest known pits confidently assignable to trematodes also yielded fossils of shorebirds (Mayr and Kitchener 2023). Both of these traces have modern analogues (Huntley and De Baets 2015, Huntley et al. 2021) and have been comparatively well-studied in Gymnophallidae (Ituarte et al. 2001 2005, Cremonte and Ituarte 2003, Huntley 2007).

The absence of reports of pits from older deposits might relate to the lack of systematic screening of suitable materials (e.g., well-preserved sediment-free inner valves) but internal moulds or rare silicified shells might provide suitable conditions for discovery of both shell concretions and pearl-like structures as far back as the Paleozoic (Liljedahl 1985, De Baets et al. 2011).

Age: The oldest precisely dated shells – *Venericor clarendonensis* (Wood, 1871) – with trematode pits derive from subdivision B2 of the London Clay Formation (Todd and Harper 2011). This part of the London Clay Formation (Berggren and Aubry 1996) was dated to the upper calcareous nannofossil zone NP 11 (Ypresian, Early Eocene), which corresponds to a minimum age of 52.930 Ma assigned to its top in GTS 2020 correlated with the base of magnetochron C24n.1n (Speijer et al. 2020).

Archeological finds

Eggs of neodermatans have been repeatedly reported from the Quaternary (see Table 2, Fig. 4). Dicrocoeliidae can be dated back to at least 550000 yrs BP in a coprolite attributed to a carnivorous mammal (Jouy-Avantin et al. 1999), Anoplocephalidae to 16985 yrs BP in rodent coprolites (Beltrame et al. 2012) and Hymenolepididae and Taeniidae

Table 2. Earliest archaeological finds of parasitic Platyhelminthes families from Pleistocene (c. 2.58 Ma–11.7 Ka) and Holocene (< 11.7 Ka), in chronological order. Taxonomy follows the National Center for Biotechnology Information (NCBI) database. All Holocene finds except for Euphrates Cave (ID:7) are associated with human habitation. If an age range given, earliest age provided; site ID corresponds to Fig. 4; where applicable, review articles given in square brackets; yrs BP, years Before Present; NS, not specified.

Age (yrs BP)	Site	Site ID (Map)	Family	Taxonomic unit identified	Source	Type of find	Putative host	Reference
Pleistocene								
550 000	Caune de l'Arago Cave, France	a	Dicrocoeliidae	Dicrocoeliidae	Coprolites	Parasite eggs	Carnivorous mammal	Jouy-Avantin et al. (1999)
16 985[1]	Cueva Huenul 1, Argentina	b	Anoplocephalidae	*Viscachataenia quadrata*	Coprolites	Parasite eggs	Rodent	Beltrame et al. (2012)
12 680[2]	Cueva del Milodón, Chile	c	Hymenolepididae	Hymenolepididae	Coprolites	Parasite eggs	*Mylodon darwini* (Darwin's ground sloth)	Oyarzún-Ruiz et al. (2021)
			Taeniidae	Taeniidae				
Holocene								
10 421[3]	Cerro Casa de Piedra 7, Argentina	1	Anoplocephalidae	Anoplocephalidae	Coprolites	Parasite eggs	Human	Fugassa et al. (2010)
			Hymenolepididae	*Rodentolepis* sp.				
10 049	East Chia Sabz, Iran	2	Taeniidae	Taeniidae	Sediment from skeletal remains	Parasite eggs	Canid	Paknezhad et al. (2017)
10 000[4]	Coast, Peru	3	Diphyllobothriidae	*Adenocephalus pacificus*	Mummified remains	NS	Human	Reinhard and Barnum (1991) in: Reinhard (1992)
9 549[5]	Shillourokambos, Cyprus	4	Fasciolidae	*Fasciola hepatica*	Sediment from skeletal remains	Parasite eggs	Human	Harter-Lailheugue et al. (2005)
8 949	Zamostye 1,2, Russia	5	Diplostomidae	*Alaria alata*	Coprolites	Parasite eggs	Canid	Engovatova and Khrustalev (1996) in: Slepchenko and Reinhard (2018)
			Opisthorchiidae	*Opisthorchis felineus*				
7 849	Atacama, Chile	6	Troglotrematidae	*Paragonimus* sp.	Coprolites	Parasite eggs	Human	Hall (1976) in: Horne (1985)
7 315[6]	Euphrates Cave, New Zealand	7	Notocotylidae	Notocotylidae	Coprolites	DNA trace	Moa	Boast et al. (2018)
7 26[9]7	La Draga, Spain	8	Dicrocoeliidae	*Dicrocoelium dendriticum*	Sediment from occupational layers	DNA trace	Ruminant	Maicher et al. (2017)
			Paramphistomidae	*Paramphistomum*				
6 500[8]	Tell Zeidan, Syria	9	Schistosomatidae	*Schistosoma* sp.	Sediment from skeletal remains	Parasite eggs	Human	Anastasiou et al. (2014)
5 125	Zürich-Parkhaus-Opéra, Switzerland	10	Echinostomatidae	*Echinostoma*	Sediment from occupational layers	Parasite eggs	Mammal or bird	Maicher et al. (2019)
3 059	Tarapacá-40, Chile	11	Dipylidiidae	*Dipylidium caninum*	Mummified remains	Parasite eggs	Human	Ramirez et al. (2021)
1 726[9]	Chehrabad Salt Mine, Iran	12	Davaineidae	*Fuhrmannetta malakartis*	Coprolites	DNA trace	Bird	Askari et al. (2022)
1 600[10]	St Lawrence Island, USA	13	Heterophyidae	*Cryptocotyle lingua*	Mummified remains	Parasite Eggs	Human[5]	Zimmerman and Smith (1975)
449	Sapgyo, South Korea	14	Gymnophallidae	*Gymnophalloides seoi*	Mummified remains	Parasite Eggs	Human	Shin et al. (2012)

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[1] Based on calibrated radiocarbon age estimates for stratigraphic unit VII of Cueva Huenul 1 in Tietze et al. (2019): 13 844 ± 75 yrs BP (16 390 – 16 985 cal yrs BP).

[2] Earliest radiocarbon age estimate for Cueva del Milodón from Borrero et al. (1999): 12 552 ± 128 yrs BP.

[3] Based on calibrated radiocarbon age estimates for archaeological layer XVI of CCP7 in Velázquez et al. (2014): 8 920 ± 200 yrs BP (9 495 – 10 421 cal yrs BP).

[4] Due to the lack of further details associated with this finding, the next earliest finding of Diphyllobothriidae was from Shillourokambos sediment sample (see the next row), reported in Le Bailly and Bouchet (2013).

[5] The PhD thesis by the first author (Harter 2003) provides an earlier date for the burial containing remains of Taeniidae and Fasciolidae (10 449 BP or 8 500 BC).

[6] Based on the earliest calibrated radiocarbon age estimates for Euphrates Cave in Wood et al. (2012): 6 368 ± 31 yrs BP; 7 315 – 7 165 cal yrs BP. Wood et al. 2013 also found a DNA trace of a sister family to Notocotylidae in coprolites of similar age deposited by extinct New Zealand moa.

[7] Another find of dicrocoeliid eggs close in age was obtained from sediment from a domestic context, Leipzig-Zwenkau, Germany, 7 208 yrs BP (5 259 yrs BC) reported in Le Bailly and Bouchet (2010).

[8] Schmidt et al. 1992 reported 'schistosome-like' eggs – but without the characteristic operculum – in dung balls of *Nothrotheriops shastensis* (Shasta ground sloth) from Rampart Cave, Arizona, USA, radiocarbon dated at 10 500 ± 180 yrs BP.

[9] The earliest date corresponds to the establishment of Sassanid Empire (224–651 AD), Askari et al. (2018).

[10] Considered to be a case of 'false parasitism': an incidental finding of a parasite in a species that is not normally part of its lifecycle. In this case, the human was thought to have consumed fish infected by *Cryptocotyle lingua*.

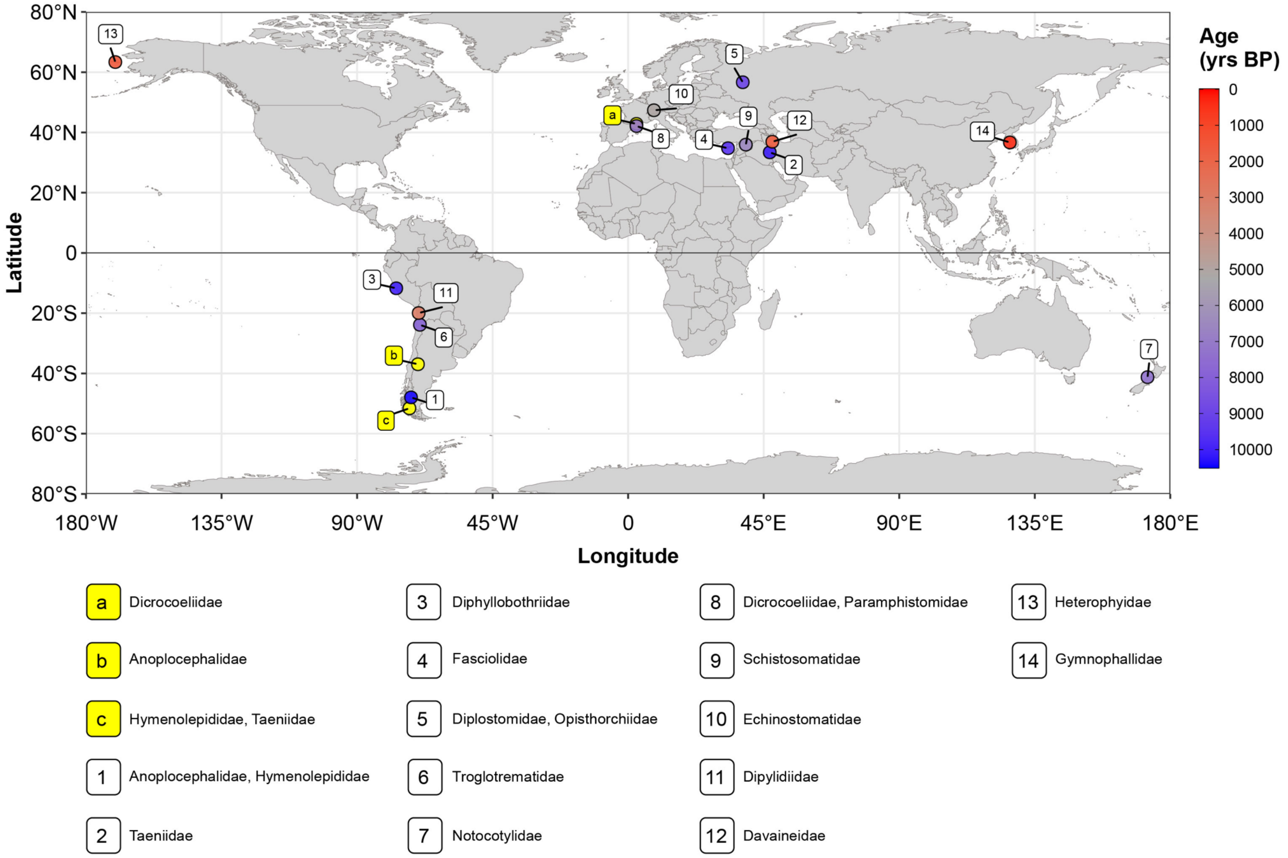

Figure 4. Earliest direct archaeological finds of families of parasitic platyhelminths from Pleistocene (c. 2.58 Ma – 11.7 Ka, yellow labels) and Holocene (< 11.7 Ka, white labels). Sites numbered in chronological order; age in years Before Present (yrs BP); age scale bar pertains to Holocene finds. See Table 2 for further details of each find.

to 12680 yrs BP in ground sloth coprolites (Oyarzún-Ruiz et al. 2021). Findings of these families also represent some of the oldest eggs reported from archeological sites with eggs of Anoplocephalidae and Hymenolepididae reported from human remains dated at 10421 yrs BP (Fugassa et al. 2010) and eggs of Taeniidae associated with dog remains at 10049 yrs BP (Paknezhad et al. 2017). The oldest members of Dicrocoeliidae attributable to a modern genus and species are based on DNA traces associated with sediments from occupational layers dated at 7269 yrs BP (Maicher et al. 2017). Various other families are found in the Holocene record ranging from Diphyllobothridae (Reinhard and Barnum 1991, Reinhard 1992), Fasciolidae (Harter-Lailheugue et al. 2005), Diplostomatidae and Opisthorchiidae (Engovatova and Khrustalev 1996, Slepchenko and Reinhard 2018), Troglotrematidae (Hall 1976, Horne 1985), Notocotylidae (Boast et al. 2018, Wood et al. 2013 also found a DNA trace of a sister family to Notocotylidae of similar age), Paramphistomatidae (Maicher et al. 2017), Schistosomatidae (Anastasiou et al. 2014), Echinostomatidae (Maicher et al. 2019), Dipylidiidae (Ramirez et al. 2021), Davaneidae (Askari et al. 2022), Heterophyidae (Zimmerman and Smith 1975), to Gymnophallidae (Shin et al. 2012). The oldest find of a modern genus and species is *Viscachataenia quadrata* reported from rodent coprolites from the Cueva Huenel 1 in Argentina dated to 16985 yrs BP (Beltrame et al. 2012). Although the characteristic igloo-like structures attributable to members of Gymnophallidae (Leung 2021) can be traced from the Cretaceous (Rogers et al. 2018) to the Quaternary (Huntley and De Baets 2015, Ituarte et al. 2005), finds of their eggs in the archaeological record attributable to a modern genus and species *Gymnophalloides seoi* Lee, Chai & Hong, 1993, can only be traced back to 449 yrs BP so far (Shin et al. 2012).

DISCUSSION

Given what we currently know about the appearance of metazoan phyla in the fossil record (Slater and Bohlin 2022) and the nested position of Platyhelminthes within Spiralia or Lophotrochozoa (Marlétaz et al. 2019, Drábková et al. 2022, Liao et al. 2023), a late Precambrian to Cambrian appearance seems likely. Deep Precambrian (pre-Ediacaran) estimates of metazoans based on molecular clock analyses (Cunningham et al. 2017, Anderson et al. 2023) are hard to bridge with the diverse fossil evidence (Slater and Bohlin 2022) and could be explained by various biases in such molecular divergence approaches rather than by large-scale taphonomic biases (Budd and Mann 2020, 2023). The oldest trace fossil evidence associated with putative body fossils places free-living flatworms in the marine environment in the late Ordovician at the latest (Knaust and Desrochers 2019, Knaust 2021). As they leave no resistant mouth parts and do not have a resistant cuticle, it is perhaps not so surprising. Also, early branching flatworms are considered to be quite small (Laumer et al. 2015). Recent molecular analyses suggest a single transition from marine to freshwater environments in Tricladida, which might be one of the oldest among soil invertebrates; however, a calibrated time-tree is missing (Sluys 2019, van Straalen 2021). Subsequently, freshwater forms colonized the land although some forms re-invaded freshwater environments. Trace fossil evidence suggests planarians to be present in freshwater environments at the latest in the early Permian (Alessandrello et al. 1988, Knaust 2010). These trace fossils suggest that Tricladida was present in Eurasia when the supercontinent Pangea was assembled and before the break-up of Gondwana.

The oldest fossils assignable to flatworms are trace fossils attributed to turbellarians in the Ordovician and are followed by the first evidence of ectoparasitic neodermatans assignable to Monopisthocotylea associated with acanthodian and placoderm hosts in the Devonian. Fossils attributable to endoparasitic neodermatans with complex life cycles appear later in the Carboniferous and Permian in the form of tapeworm eggs associated with shark body fossils or coprolites. Evidence for endoparasitic trematodes in vertebrates appears considerably later in the Cretaceous fossil record. Trematodes and cestodes have been reported to co-occur in Cretaceous archosaur coprolites but older coprolites only yielded tapeworms, which seems to suggest that the lack of trematodes might be a genuine pattern rather than an artefact. At the moment there is no comprehensive study on the relationship between structure and preservation potential of egg capsules for trematodes and cestodes. Lineages in both groups have eggs that can survive aggressive palynomorph preparations. It has also been suggested that quinone tanning (sclerotization) of eggs in their ancestors may have been a pre-adaptation to colonize the gut and survive acids and digestive enzymes (Llewellyn 1965, Zamparo 2001) which could contribute to their preservation in the fossil record. The transmission strategy in parasites might also play a role in the degree of tanning (and therefore preservation potential) as demonstrated by up to six independent losses in trematodes and one loss of quinone tanning within Cestoda. However, the structure and preservation potential needs further study in an up-to-date and more comprehensive phylogenetic framework. Acetolysis experiments have shown the complete destruction of eggs of the nematode *Ascaris lumbricoides* Linnaeus, 1758 and the trematode *Schistosoma japonicum* Katsurada, 1904, many destroyed eggs of the cestode *Taenia pisiformis* Bloch, 1780, but a relative increase in egg number of the trematode *Clonorchis sinensis* Cobbold, 1875 (Reinhard et al. 1986).

So, there is no straightforward difference in the range of possible structures and preservations of egg capsules between cestodes and trematodes which could further relate to their reproductive strategies (Smyth and Clegg 1959, Shinn 1993, Wharton 1983). Understanding the difference in preservation potential is also complicated by the packaging of eggs in proglottids in eucestodes which would be the functional equivalent of changing a quinone-tanned eggshell for a keratinized eggshell (Zamparo 2001) and could further improve their preservation potential. The earlier appearance of cestodes in the fossil record needs to be further corroborated by recovery of additional positive identification of (isolated) tapeworm eggs in comprehensive sampling of pre-Cretaceous coprolites which are negative for trematode eggs.

This relative order of appearance is most consistent with the hypotheses resulting from some new molecular phylogenetic analyses placing the divergence of Monopisthocotylea from the rest of Neodermata before the divergence of Cestoda from a clade of Trematoda and Polyopisthocotylea (Fig. 5). Using the fossil record to confirm this hypothesis needs further support by extending the fossil record of resistant hooks of Monopisthocotylea beyond the single Devonian site and by additional sampling of Pre-Cretaceous coprolites for helminth eggs as the discovery of older trematode eggs could potentially turn this pattern around. Eggs of members of Monopisthocotylea or Polyopisthocotylea have so far not been reported in the fossil record even though many of them are also be expected to be tanned/sclerotized and resistant with some rare exceptions (Llewellyn 1965, Fried and Stromberg 1971, Ramalingam 1973b, Guraya and Parshad 1988, Cable et al. 1997, Kearn et al. 1999, Zamparo 2001, Kearn 2005). So far, no fossil findings can be attributed to Polyopisthocotylea. In the case of clamps, this may relate to differences in composition as these are stabilized by dityrosine as opposed to keratin in hook sclerites and hamuli (Lyons 1966, Ramalingam 1973a). However, differences in stabilization need to be further investigated in a phylogenetic context and the presence of polyopisthocotyleans in coelacanths (*Latimeria*) and lungfishes has been used to argue for their latest origin at the split of Actinopterygia-Sarcopterygia (De Baets et al. 2015, Verneau et al. 2009). However, so far there is no direct evidence for the latter claim and latest analyses suggest both host switching and parasite extinction might have played a larger role in the evolution of Polyopisthocotylea than commonly assumed (Mulvey et al. 2022, Verneau et al. 2023).

Other new analyses inferring a sister-group relationship between a clade of Monopisthocotylea and Cestoda on the one hand and a clade of Polyopisthocotylea and Trematoda on the other hand would indicate a large gap in the stratigraphic record lacking fossils – also called ghost lineage – of the latter clade (Fig. 5). The latter merits discussing – in addition to the preservation potential of their eggs – an older igloo-like structure in a Silurian bivalve (Liljedahl 1985) and potentially relating it to a trematode producer (Huntley and De Baets 2015). However, the difference in morphology and the large temporal gap with the igloo-type structures confidently assignable to gymnophallid trematodes as well as the absence of their final tetrapod hosts speak for their assignment to a trace-maker with a similar behaviour but different phylogenetic assignment (Huntley and De Baets 2015).

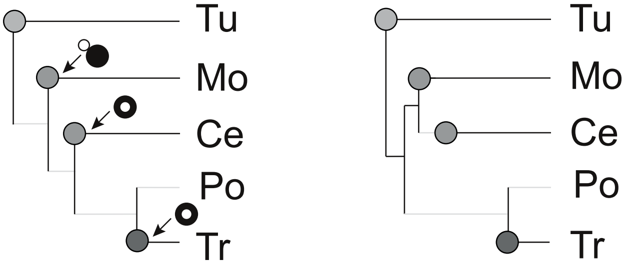

Figure 5. Alternative topologies obtained for Neodermata in analyses of Brabec et al. (2023). Circles indicate the oldest fossil record for particular groups (differently coloured circles reflect those for early to later branching groups in Fig. 2). Light gray tree branches reflect lacking fossil record, black bars reflect present fossil record. Circle within circle refers to origin of endoparasitism and smaller circle attached to larger circle refers to origin of ectoparasitism based on fossil record. See Table 1 and discussion in text for further details of the oldest finds. Note the different stratigraphic range and distribution of ghost lineages depending on the topology.

It seems unlikely that fossil species and genera described from the Paleozoic and Mesozoic represent modern species or genera. Also, modern families could not be confidently traced back beyond the Quaternary with the exception of Gymnophallidae (De Baets et al. 2015, 2021a, Leung 2017). This begs the question of how far back we can trace modern species, genera, or other families in the Quaternary (Fig. 4). Many families can be traced back within the Holocene and some as far back as the Pleistocene with the oldest egg capsules of dicrocoeliid trematodes and polycystidid turbellarians dated to at least 550,000 and 250,000 yrs BP, respectively.

Future perspectives

Currently, the oldest most reliable age for parasitic flatworms is provided by circlets of resistant hooks and eggs. More resistant remains need further systematic screening to potentially fill the gaps (compare Fig. 6). In the case of free-living flatworms, the oldest evidence comprises trace fossils indicative of mucociliary motion associated with putative body fossils.

Trace fossils attributed to free-living flatworms and other mucociliary motion might need further scrutiny, particularly those not associated with body fossils. Meiofaunal sites where trace fossils are occasionally associated with resistant body parts or outlines might help in this endeavor (Knaust 2007, 2010, Knaust and Desrochers 2019). Even if the internal structure is mostly destroyed due to early-diagenetic processes, their morphology and size can still be used to recognize higher-order taxa and as fingerprints to link a trace maker to a distinct meiobenthic trace fossil (Knaust 2007). Simple traces could potentially be produced by vermiform organisms belonging to a range of animal phyla. However, new mathematical approaches enable to identify previously unrecognized signatures left by trace makers (e.g., deviation angle series of self-crossing traces) allowing to more confidently assign them to their known modern (or fossil) producers (Wang and Rahman 2023). In addition, the association of trace fossils with characteristic spicules and a more comprehensive understanding of the distribution of such behavior or spicules in an up-to-date phylogenetic context (Rieger and Sterrer 1975, Knaust 2010) would also be helpful to more robustly assign them to modern lineages.

Structures Clades	Sclerotized hooks	Resistant cuticle	Resistant egg capsules	Calcareous spicules	Clusters of eggs	Characteristic host damage	Characteristic trails
Polycladida			?	●			●
Tricladida			?				●
Rhabdocoela	?		●	○			
Monopisthocotylea	●		?				
Polyopisthocotylea	?		?				
Cestoda	●		●*		●	●	
Trematoda			●			●	
Nematoda		●	●			●	

Figure 6. Table highlighting the possible (hollow circles) and realized (filled circles) preservation potential of structures in the fossil record modified and mainly expanded from these references (Rieger and Sterrer 1975, Littlewood and Donovan 2003, Knaust 2010, De Baets et al. 2021a, 2021b). In-depth discussion of these points and associated references can be found in the main text. Question marks relate to a structure likely having increased preservation potential but further documentation is needed. Asterisks refers to packaging of eggs may further increase resistance of egg capsules.

The preservation potential of the smallest flatworm representatives, namely the microturbellarians, is poorly known. Many groups of microturbellarians, including macrostomorphs, gnosonesimids, rhabdocoels, and proseriates, have sclerotized parts in their atrial organs or feeding structures that can be beautifully preserved for SEM (Damborenea et al. 2007) or as permanent whole mounts (Schockaert 1996), while dissolving the weak tissues with harsh chemicals. Indeed, these sclerotized parts in microturbellarians range from hooks/spines/girdles/stylets or cirri armed with tiny spines in the male copulatory organ (Artois and Schockaert 2003, Smith III et al. 2020), to hooks or denticles in the kalyptorhynch proboscis (Uyeno and Kier 2010). Some rhabdocoel groups have sclerotized bursal appendages, thickened basal membranes, bursal spines or sclerotized channels guarding the female system (Artois and Schockaert 2005, Van Steenkiste and Leander 2018). However, whether these structures can be recovered in fossil samples and would be recognized as such needs to be further explored. The preservation potential of catenulids, the earliest diverging major lineage of flatworms (Laumer et al. 2015), is likely limited due to the combination of their small size and a simple anatomy lacking hard parts (Van Steenkiste et al. 2023).

More resistant platyhelminth eggs in coprolites, palynomorph preparations or sediment samples remain a largely untapped resource with great potential. To our knowledge no comprehensive comparative studies on the preservation potential of eggs across different lineages of flatworms have been performed. Various lineages produce sclerotized/tanned egg capsules which increases their preservation potential (Guraya and Parshad 1988, Shinn 1993, Zamparo 2001) including Tricladida (Huggins and Waite 1993), Polycladida (Ishida and Teshirogi 1986), Rhabdocoela (Breckenridge and Nathanael 1988) and Neodermata (Smyth and Clegg 1959, Kearn et al. 1999, Ramalingam 1973b). Eggs capsules of at least some lineages of rhabdocoel microturbellarians including Dalyelliidae, Polycystididae (*Gyratrix*) and Typhloplanidae (Haas 1996, Warner 1989, Matsuoka and Ando 2021) as well as parasitic cestodes such as *Diphyllobothrium* and trematodes such as *Dicroelium* or *Clonorchis* are well-known to be more resistant to palynological preparations (Reinhard et al. 1986, Shumilovskikh and van Geel 2020) and have been recovered from fossil samples older than 250000 yrs BP.

Eggs of parasitic flatworms are often considered less resistant than those of nematodes (Brinkkemper and van Haaster 2012, Dufour and Le Bailly 2013) which might explain why nematodes have been recovered more often from Mesozoic coprolites (Hugot et al. 2014, Cardia et al. 2019, Nonsrirach et al. 2023) and sedimentary samples in the archeological record (Morrow et al. 2016). However, the oldest and the only helminth eggs recovered from Paleozoic coprolites can be attributed to tapeworms (Zangerl and Case 1976, Dentzien-Dias et al. 2013, Chin 2021). Isolated eggs of cestodes and trematodes co-occur in at least some Cretaceous coprolite samples (Poinar and Boucot 2006), but confidently identified trematode eggs have so far not been recovered from coprolites positive for nematode or cestode helminths before the Cretaceous. Sampling effort as well as preservation factors could play a role in this pattern. If the archeological record is an indicator, eggs of nematodes are more common than those of cestodes and trematodes, but whether this relates to their different preservation potential or other factors remains unresolved. Isolated trematode or cestode eggs in sediment samples could potentially also be confused with turbellarian eggs (Matsuoka and Ando 2021). The better body fossil record of nematodes is not so surprising due to their resistant cuticle (Littlewood and Donovan 2003, Poinar 2011, Maas 2012, De Baets et al. 2021b, 2023, Luo et al. 2023). Also, nematode eggs seem to be more resistant compared to those of trematodes when subjected to hard acids and bases (Brinkkemper and van Haaster 2012, Dufour and Le Bailly 2013, but see Reinhard et al. 1986).

Despite their patchiness, fossil remains of flatworms (particularly when combined with fossil evidence from outgroups) can remain valuable for calibrating molecular divergence estimates. At least the age of some fossil constraints (e.g., eucestode tapeworms) are as good as those of independently calibrated molecular divergence estimates as their ages fall within or even pre-date confidence limits of previous divergence time estimates (De Baets et al. 2021a). Based on poor fossil records in some groups, biogeographic calibrations have been suggested as an alternative to fossil constraints (Zietara and Lumme 2002, Scarpa et al. 2015, Sluys 2019). However, the consistency of such hypotheses with modern distributions should be independently and robustly tested before using them as potential calibrations (Upchurch 2008, Kodandaramaiah 2011). When inherent assumptions and attendant errors are properly considered, calibrations derived from geological events are not necessarily more precise or easier to codify than those of the fossil record and should be seen as complementary rather than competing approaches (De Baets et al. 2016). The same can be said for host calibrations in the case of symbiotic lineages (Olson et al. 2010, Badets et al. 2011, Hoyal Cuthill et al. 2016), which should likely only be used if there is a strong independent support for a high degree of co-divergence and host specificity, but a low degree of host switching or extinction in this part of the trees (Warnock and Engelstädter 2021, Mulvey et al. 2022). (Co-)evolutionary history is likely more complex as revealed by traditional models with host switching as well as extinction playing a larger role and codivergence a smaller role than traditionally thought (e.g., Araujo et al. 2015, Brooks and Boeger 2019). Various new methods have been developed to help with reconstructing and testing this complex history (Braga et al. 2020, Warnock and Engelstädter 2021, Dismukes et al. 2022, Mulvey et al. 2022).

Whatever the calibrations used, constraints on their assumptions should be explicitly discussed and rigidly tested independently in a non-circular way. For instance, biogeographic or host calibration should not be used to test related biogeographic or host hypotheses, respectively; trace fossils should not be used to reconstruct the evolution of locomotion behavior but rather in sensitivity analyses. A better understanding of the flatworm fossil record as well as the modern phylogenetic placement of preservable structures (hooks, eggs, spicules) therefore remains crucial for constraining the timing of the origin and evolution of Platyhelminthes as well as their co-phylogeny with their hosts.

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