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Constraining the Deep Origin of Parasitic Flatworms and Host-Interactions with Fossil Evidence

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Contents

1. Introduction	2
2. Assessment of the Flatworm Fossil Record	4
2.1 Devonian fossil hook circllets	5
2.2 Silurian blister pearls and calcareous concretions in bivalve shells	9
2.3 Permo-Carboniferous egg remains in shark coprolites	11
2.4 Cretaceous egg remains in terrestrial archosaur coprolites	13
2.5 Eocene shell pits in intermediate bivalve hosts	14
2.6 Eggs remains in a Pleistocene mammal coprolite	15
2.7 Holocene evidence for parasitic flatworms from ancient remains	15
2.8 Free-living flatworms	16
3. Interpolating or Extrapolating Extant Parasite—Host Relationships and the Assumption of Parasite—Host Coevolution	18
4. Molecular Clock Studies	21
5. Conclusions and Future Prospects	27
Acknowledgements	29
References	30

Abstract

Novel fossil discoveries have contributed to our understanding of the evolutionary appearance of parasitism in flatworms. Furthermore, genetic analyses with greater coverage have shifted our views on the coevolution of parasitic flatworms and their hosts. The putative record of parasitic flatworms is consistent with extant host

associations and so can be used to put constraints on the evolutionary origin of the parasites themselves. The future lies in new molecular clock analyses combined with additional discoveries of exceptionally preserved flatworms associated with hosts and coprolites. Besides direct evidence, the host fossil record and biogeography have the potential to constrain their evolutionary history, albeit with caution needed to avoid circularity, and a need for calibrations to be implemented in the most conservative way. This might result in imprecise, but accurate divergence estimates for the evolution of parasitic flatworms.

1. INTRODUCTION

Parasitic flatworms (Platyhelminthes: Neodermata) are a highly diverse group containing many parasites of biomedical, veterinary and economic importance (Olson and Tkach, 2005; Littlewood, 2006). Time constraints on the origin and evolution of parasitism in this group are still poorly resolved due to their patchy and largely overlooked fossil record (Littlewood and Donovan, 2003; Littlewood, 2006). The fossil record of parasitic flatworms is often disregarded by parasitologists (Combes, 2001; Littlewood, 2006; Verneau et al., 2009a; Badets et al., 2011) and evolutionary (paleo)biologists (Labandeira, 2002; Erwin et al., 2011; Wey-Fabrizius et al., 2013) alike. Most parasitologists have therefore focused on extrapolating or interpolating extant parasite–host associations to infer information on the evolution history of parasitic flatworms (Llewellyn, 1987; Brooks, 1989; Brooks and McLennan, 1993; Boeger and Kritsky, 1997; Hoberg, 1999; Hoberg et al., 1999; Littlewood et al., 1999a). Nevertheless, the last two decades have seen several new fossil discoveries, which have extended the record from certain lineages of parasitic flatworms deeper into the Cenozoic (Jouy-Avantin et al., 1999; Todd and Harper, 2011) or from the Cenozoic to the Mesozoic (Poinar and Boucot, 2006) or even the Paleozoic (Upeniec, 2001, 2011; Dentzien-Dias et al., 2013).

Furthermore, molecular analyses have considerably shifted our views on flatworm phylogeny (Lockyer et al., 2003a; Olson and Tkach, 2005; Littlewood, 2008; Perkins et al., 2010; Laumer and Giribet, 2014) with implications for older hypotheses of parasite–host coevolution. Due to the patchy fossil record, establishing the phylogeny of flatworms is particularly important for establishing a timeline for the group. Traditionally, Monogenea (ectoparasitic with simple life cycles) and Cestoda (endoparasitic with complex, trophically transmitted, life cycles) were often grouped based on morphological similarities of their larval stages (Bychowsky, 1937; Brooks,

1989), sometimes referred to as the cercomer theory (Lockyer et al., 2003a). However, most recent molecular-based analyses (Mollaret et al., 1997; Lockyer et al., 2003a; Park et al., 2007; Perkins et al., 2010; Wey-Fabrizius et al., 2013; Hahn et al., 2014; Egger et al., 2015) and those including alternative data such as microRNAs (Fromm et al., 2013) indicate a sister-group relationship between cestodes and trematodes (rather than between Monogenea and Cestoda) with one possible exception (Laumer and Giribet, 2014; Laumer et al., 2015), although no clear morphological characters support this arrangement. Interestingly, the monophyly of Monogenea i.e. the sister-group relationship between Monopisthocotylea and Polyopisthocotylea based on morphological data (Boeger and Kritsky, 2001), is not always supported by molecular phylogenetics (Mollaret et al., 1997; Justine, 1998; Lockyer et al., 2003a) either. Based on recent results employing mitogenomic data, primitive parasitic flatworms (Neodermata) were probably ectoparasitic with a simple life cycle on vertebrates (Park et al., 2007) and engaged in epithelial feeding (Perkins et al., 2010). Subsequently, it has been proposed they added an intermediate host to their life cycle, probably first a crustacean intermediate host in Cestoda and a mollusc intermediate host in Trematoda (Park et al., 2007) before switching to a blood diet (Perkins et al., 2010). This differs from previous hypotheses (Brooks, 1989; Littlewood et al., 1999a), where a sister-group relation between Monogenea and Cestoda, and between these taxa and Trematoda was postulated. This led to two now probably outdated hypotheses of interpreting the life cycle evolution of Neodermata (Park et al., 2007). One hypothesis (Littlewood et al., 1999a) suggested that proto-neodermatan first acquired an endoparasitic association with vertebrates and that independent adoptions of invertebrates by the Trematoda (molluscs) and Cestoda (crustaceans) as well as ectoparasitism in Monogenea were subsequent acquisitions (vertebrate first hypothesis). Another hypothesis (Cribb et al., 2001) suggested that the association of common ancestor of the Trematoda with molluscan hosts was primitive (acquiring its subsequent vertebrate hosts independently), and that the vertebrates were involved in the life cycle of the common ancestor of the Monogenea + Cestoda clade as independent initial hosts apart from that of trematodes, with the crustaceans as subsequent intermediate hosts adopted by the Cestoda groups after the ancestral cestode diverged from the monogeneans (mollusk first hypothesis).

The closest free-living relatives of helminths are also important in constraining divergence times in their evolutionary history (Littlewood et al., 1999b; Near, 2002; Littlewood, 2006). However, the phylogeny of

free-living flatworms has proven even more problematic (but see Littlewood and Waeschenbach, 2015 for a review of recent advances) and has been further complicated by the fact that some extant forms traditionally included in Platyhelminthes have been excluded from the phylum based on molecular analyses (Jondelius et al., 2002; Telford et al., 2003; Willems et al., 2006; Wallberg et al., 2007; Hejnol et al., 2009) such as the Acoela (Ruiz-Trillo et al., 1999; Mwinyi et al., 2010; Philippe et al., 2011) and *Xenoturbella* (Bourlat et al., 2003). Furthermore, platyhelminths have often been grouped in the Platyzoa (Cavalier-Smith, 1998) together with various other taxa including Acanthocephala, which have convergently evolved a parasitic lifestyle with larval stages and have been shown to be closely related with free-living Rotifera (Near, 2002; Weber et al., 2013). It remains unclear whether Platyzoa is a clade or an artificial grouping generated by systematic error and long-branch attraction artefacts (Edgecombe et al., 2011; Wey-Fabrizius et al., 2013; Struck et al., 2014), since subsequent studies have not only disagreed on the membership of the phyla, but also on the relationships within this grouping. This makes new fossil discoveries of parasitic flatworms not only relevant in constraining the evolutionary origin of flatworms, but also that of the Platyzoa as a whole.

Here we review the potential of fossil flatworm evidence with a view to using these data to constrain the timescale for the evolutionary history of this group and outline how they can be used to improve our understanding of the evolutionary radiation of the Neodermata. We consider whether these rare fossil finds are at least consistent with coevolution of parasitic flatworms and their hosts, as well as how fossil finds and other geological evidence in combination with molecular clock methodology can be best used to constrain the temporal framework for the evolution of parasitic flatworms. Such a temporal framework is a key to test evolutionary hypotheses regarding the origin and diversification of parasitism and its coincidence with certain biogeographic events, major environmental changes or key ecological or evolutionary events in the evolution of their hosts.

2. ASSESSMENT OF THE FLATWORM FOSSIL RECORD

Fossil evidence for parasitic flatworms can be derived from (1) rare exceptionally preserved body fossils, which can be isolated (Poinar and Boucot, 2006; Dentzien-Dias et al., 2013) or remain associated with their hosts (Upeniece, 2001, 2011) or (2) more commonly occur as characteristic

traces or skeletal pathologies in their (intermediate) hosts, which have the potential to be traced back in the fossil record (Ruiz and Lindberg, 1989; Ruiz, 1991; Ituarte et al., 2001, 2005; Huntley, 2007; Todd and Harper, 2011; Huntley and Scarponi, 2012; Huntley et al., 2014; Huntley and Scarponi, 2015; Huntley and De Baets, 2015). Parasite body fossils are scarce due to their small size, lack of hard parts and the residence within the host and/or isolation from their hosts (Conway Morris, 1981; Littlewood and Donovan, 2003; De Baets et al., 2011). The rarity of fossilized parasite–host associations and the fact that culprits of traces or pathologies in the skeletons of their hosts are often hard to identify can make it difficult to infer parasite–host associations from the fossil record. Nevertheless, it is the only direct evidence for the presence of such associations in the geological past.

2.1 Devonian fossil hook circlets

Circlets of fossil hooks described from the Devonian of Latvia (Upeniece, 1996, 1998, 1999, 2001, 2011) are the oldest potential body fossil evidence for parasitic flatworms. Upeniece (2001, 2011) discovered about 77 circlets, which were mostly attached or closely associated with fossil gnathostomes (16 juveniles of the antiarch placoderm *Asterolepis ornata*; 27 specimens of the acanthodian *Lodeacanthus gaujicus*; Figures 1(b, c, e, f)). However, one isolated circlet was found close to a specimen of a clam shrimp (Figure 1(g)) and two other circlets were found associated with another crustacean arthropod (Mysidacea; Figure 1(e)), but the hooks are too large to indicate parasitism based on the size of the crustaceans.

The location of these remains in fossils of their vertebrate hosts (Figure 1(b) and (c)) and their similarity to the hooks of parasitic helminths, strongly suggest a parasitic nature (Upeniece, 2011). In acanthodians (*L. gaujicus*), they are associated with the gill regions, near the fin spines, and in the abdominal region near the scapula (Figure 1(d) and (f)), while in placoderms (*A. ornata*) their location is not so well determined (see Figure 1(a)). The length of infested fishes varies between 1 and 4 cm (Figure 1(a) and (d)). Several of them were infested with 2–9 parasites (7 hook circlets can be counted in the specimen figured in Figure 1(b)). Most authors agree that they are the remains of parasitic helminths, although their exact affinity remains the subject of debate (Upeniece, 2001; Littlewood and Donovan, 2003; Upeniece, 2011). These are reminiscent of hooks which are used by Neodermata (Monogenea, Cestoda) and Acanthocephala to attach themselves to their hosts. Differences in morphology and their location on the host body (Upeniece, 2011) might even indicate that they belong to different groups

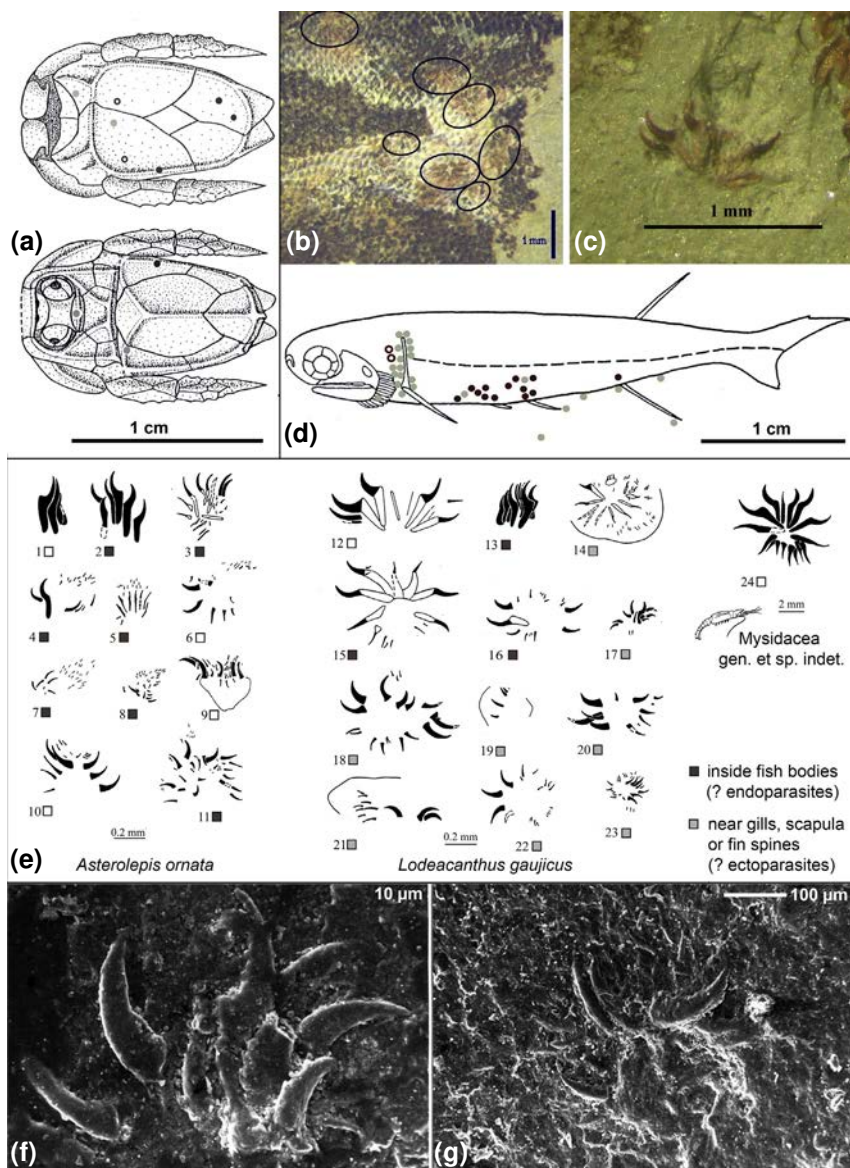


Figure 1 Fossil helminth remains in Middle Devonian gnathostomes (Upeniece, 2001, 2011) (Modified from Upeniece (2011) unless otherwise stated.): (a) Locations where helminth remains were found on juveniles of the placoderm *Asterolepis ornata*. (b) Multiple fossil circllets of parasitic helminth hooks (marked with ellipses in (a)) found inside the acanthodian *Lodeacanthus gaujicus*, LDM 270/18c (Upeniece, 2001, Pl. 3, Figure 2); (c) Close-up on the hook circllet found associated with *L. gaujicus*, specimen LDM 270/33; (d) Locations where helminth remains were found in juvenile and adults of the

of parasites (Upeniece, 2001), including ectoparasites (e.g. monogeneans) and endoparasites (e.g. cestodes and acanthocephalans).

The circular arrangement of the bilaterally symmetrically located hooks, traces of cuticular disc as well as the maximum number of 16 hooks, which is characteristic for early divergent monogeneans (Boeger and Kritsky, 1993), indicates that at least some of them represent Monogenea (Combes, 2001; Upeniece, 2011), although the larvae of Cestoda can also have radially arranged chitinous hooks for attachment. The hooks are also considerably larger (length: 0.02–0.40 mm) than those of extant flatworms, but this does not necessarily rule out a monogenean affinity. Poulin (2005), for example, could demonstrate an evolutionary trend towards decreasing body size in extant ectoparasitic Monogenea, while this was less clear for derived endoparasitic flatworms (Digenea). Interestingly, Upeniece (2011) observed that small-sized acanthodians possessed small hook systems, while larger acanthodians exhibited the greatest range in size of the hook systems. These might indicate that parasites might have spent all their life in one host, which might further corroborate a similarity to early divergent parasitic flatworms. The lack of fossilized soft body parts, with the exception of traces of the disc outline, further hampers a more precise taxonomic assignment. Upeniece (1999, 2011) suggested that at least two morphological groups are presented in both species of fish: hooks with a ‘handle’ and hooks without a ‘handle’. She noticed that the hooks with ‘handles’ typically occur in the abdominal region of acanthodians and placoderms, suggestive of a close affinity with endoparasites such as Acanthocephala or Cestoda. The elongated tube-like body of acanthocephalans typically possesses a thorny proboscis, which is an anterior retractile organ bearing a large number of hooks (Bush et al., 2001). This holdfast organ is only fully evaginated after death and resembles the ‘introvert’ of Rotatoria, Priapulida, Kinorhyncha and Nematomorpha larvae (Taraschewski, 2005). Larval forms of Cestoda typically bear hooks, present even in basal extant Cestoda like Gyrocotylidae (Xylander, 2005) and Amphilinidea (typically 10), which can be retained in the adult forms

acanthodian *L. gaujicus*; (e) Schematic drawing of circlets of fossil hooks (*Modified from Upeniece (1999).*) found in juveniles of placoderm fish *A. ornata* (No 1–11), in juveniles and adults of acanthodian *L. gaujicus* (No 12–23), and in/on crustacean Mysidacea (No 24); (f) Fossil hooks found in juvenile acanthodian body near the scapula (see also Figure 1(e), No. 17), LDM 270/4a; (g) fossil hooks found near a clam shrimp. All specimens derive from the Middle Devonian, Liepa (Lode) pit. Dark grey circles, squares – possible endoparasites; Light grey circles, squares – possible ectoparasites.

such as in Amphilinidea (Rohde, 2005). Derived Cestoda have a specialized attachment device (the scolex) that has a highly variable morphology and may have hooks: Diphyllidea typically possesses a scolex bearing a dorsal and ventral set of apical hooks (Caira and Reyda, 2005), some Cyclophyllidea have a dome-shaped structure at the end of the scolex, the rostellum, which may be armed with hooks arranged in one or more circles (Bush et al., 2001), while others like Trypanorhyncha can have a scolex with four retractable tentacles bearing hooks (Caira and Reyda, 2005). Most authors agree that the fossil circlets of hooks probably belong to platyzoan helminths (Upeniec, 2001, 2011; Poinar, 2003), although we cannot entirely exclude the possibility that they belong to a now-extinct lineage of parasites. A reinvestigation of these attachment structures with particular focus on taphonomy, their composition (element analysis) and the three-dimensional structure using computer tomography can be particularly useful for disentangling phylogenetic affinity as it did for the elements of the now-extinct conodonts (Purnell and Donoghue, 1997; 2005; Goudemand et al., 2011; Murdock et al., 2013). Whatever the exact taxonomic affinity of the parasite hook circlets, they remain the oldest direct evidence for the presence of helminth—gnathostome and helminth—vertebrate association in the fossil record (Boucot and Poinar, 2010).

Age: The finds of the Lode Formation were described initially as Early Frasnian, Upper Devonian (Upeniec, 2001), although most authors now assign this to the Upper Givetian, Middle Devonian (Mark-Kurik et al., 1999; Jurina and Raskatova, 2012; Lukševičs et al., 2012; Mark-Kurik and Põldvere, 2012; Lukševičs et al., 2014). This corresponds with at least 381.9 Ma, the minimum age assigned to the Givetian—Frasnian boundary (382.7 Ma $\pm$ 0.8 Myr: Becker et al., 2012). It is common practice in geological and paleontological studies to use Ma for ‘Million years ago’, while XX Myr is often used to refer to a duration of XX million years.

Lukševičs et al. (2009) attributed various skeletal pathologies from Middle (Givetian) to Upper Devonian (Frasnian, Famennian) gnathostomes to cestode and trematode infestations. However, the characteristics of these (Lukševičs et al., 2009) and other pathologies like skin lesions (Petit, 2010; Petit and Khalloufi, 2012) are insufficient to attribute them to particular group of parasites confidently, or even rule out potential other causes. Interestingly, they also overlap temporally with the presence of blister pearls in Devonian ammonoids (Rakociński, 2012), which might also have been caused by parasitic flatworms, although no conclusive evidence for a parasitic flatworm infestation was found (De Baets et al., 2011, 2013, 2015).

2.2 Silurian blister pearls and calcareous concretions in bivalve shells

As (blister) pearls and volcano- to igloo-shaped concretions can be induced by intermediate stages of parasitic flatworms (Götting, 1974, 1979; Lauckner, 1983; Campbell, 1985; Ituarte et al., 2001, 2005), their first occurrence in the Silurian (Kříž, 1979; Liljedahl, 1985, 1994; De Baets et al., 2011) might already indicate the presence of derived parasitic flatworms in the Silurian. Pearls and blisters can, however, be caused by a variety of irritants, including other parasites, shell burrowing organisms and inorganic particles (Götting, 1974; Lauckner, 1983). The earliest known fossil blister pearls from the Silurian (Kříž, 1979; Liljedahl, 1985, 1994) and earliest known free pearls from Triassic (Kutassy, 1937; Conway Morris, 1981; Combes, 2001; Geyer et al., 2005; Rouse, 2005; Boucot and Poinar, 2010) are therefore not characteristic for parasitism unless parasitic remains can be found inside of them (De Baets et al., 2011). This is not straightforward since it has been demonstrated that the remains of soft-bodied helminths can be destroyed during the pearl formation process (Lauckner, 1983). However, other pathologies are believed to be more characteristic for particular lineages of parasitic flatworms such as Gymnophallidae including shell pits (Ruiz and Lindberg, 1989; Ruiz, 1991; Huntley, 2007; Todd and Harper, 2011, Figure 1(e); Huntley and Scarponi, 2012; Huntley et al., 2014; Huntley and Scarponi, 2015; Huntley and De Baets, 2015) and volcano- to igloo-shaped calcareous concretions (Campbell, 1985; Ituarte et al., 2001, 2005; Figure 2(a–c); Huntley and De Baets, 2015). Ituarte et al. (2001, 2005) demonstrated a link between igloo-shaped concretions and gymnophallid digenean flatworms, which these authors traced back to 6400 years in the Holocene. Superficially, similar igloo-shaped concretions have, however, also been reported from the Upper Silurian (Liljedahl, 1985, 1994; Figure 2(d)), but the Paleozoic occurrence of this structure is not consistent with extant host associations of Gymnophallidae, which typically have shorebirds (Charadriiformes) as final hosts (Ching, 1995), although some forms also infest humans as final hosts (Lee and Chai, 2001). The earliest fossils that can be confidently assigned to extant lineages of charadriiform birds are stem-group representative of Alcidae from the Upper Eocene of North America (Mayr, 2011), although older charadriiform-like fossils have been reported from the Lower Eocene of Denmark (Bertelli et al., 2010, 2013). Molecular clock estimates usually place the origin of shorebirds in the Cretaceous (Paton et al., 2003; Baker et al., 2007), although this might be based on the incorrect

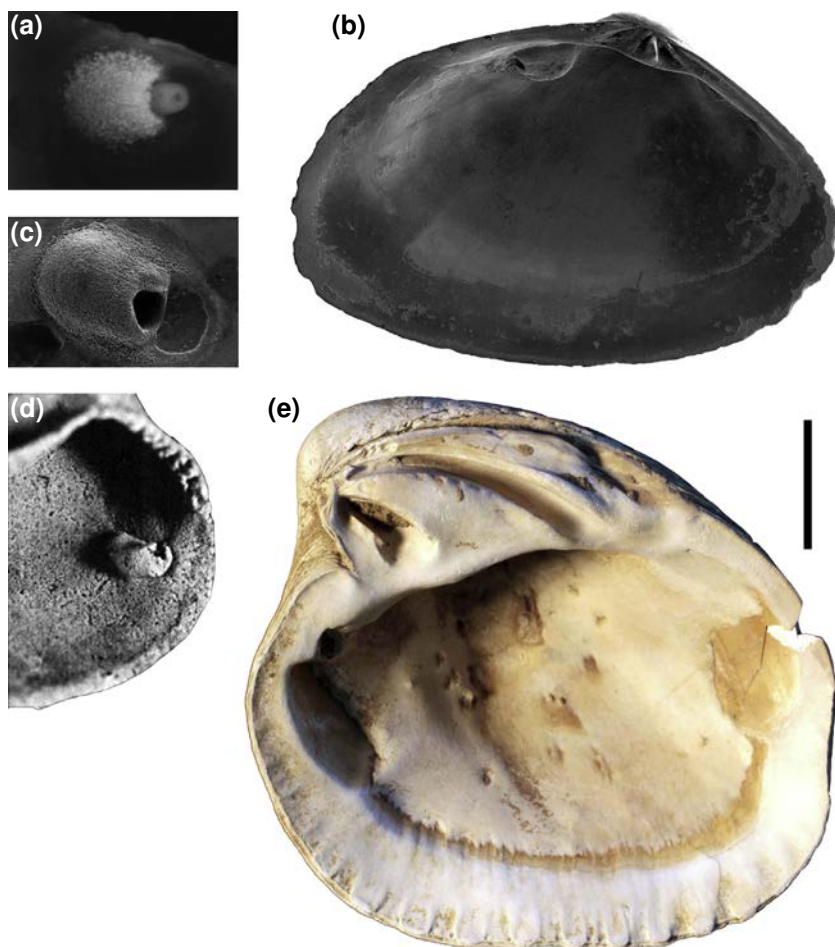


Figure 2 Shell structures (igloo-shaped concretions, shell pits) which have been linked with gymnophallid trematodes (Digenea) in extant and fossil bivalves. (a) Metacercaria lodged in live position into an igloo-shaped calcareous covering of *Gaimardia trapesina* (MLP 5659) from Beagle Channel in Ushuaia; note the noncalcified area around the anterior end of the larva (photo: Cristian Ituarte; refigured from Ituarte *et al.* (2005).); (b) Scanning electron micrograph of a left valve of *Cyamiomactra* sp. from a Holocene sample of Río Varela (Tierra del Fuego) showing a single igloo-shaped covering just below the anterodorsal margin (Photo: Cristián Ituarte; refigured from Ituarte *et al.* (2005).); (c) Upper view of an igloo-shaped covering in *G. trapesina* (MLP 5659) from Beagle Channel in Ushuaia showing the non-calcified area in front of the igloo opening (Photo: Cristian Ituarte; refigured from Ituarte *et al.* (2005).); (d) Igloo-shaped concretion found close to posterior adductor muscle scar in the Silurian bivalve *Nuculodonta gotlandica* (SGU Type 1030) from the Halla Formation of Gotland (Modified from Liljedahl (1994).); (e) Interior of right valve of *Venericor clarendonensis* (NHMUK PI TB 14236) from the Eocene (subdivision B2 of the London Clay) with irregular shell deformations and shell pits interpreted to have been produced in response to digenean trematode infestation. Photo courtesy of Jon Todd; compare Todd and Harper (2011).

placement of fossil taxa (Dyke and Van Tuinen, 2004; Thomas et al., 2004; Mayr, 2011) and/or other methodological artefacts (cf. Ksepka et al., 2014). The appearance of shorebirds in the Cretaceous or Early Paleogene suggests that the Paleozoic structures were probably caused by a different group of parasites or even epizoa (Liljedahl, 1985, 1994) with similar behaviour, although we cannot rule out the possibility that gymnophallids, or closely related (now potentially extinct) taxa or their ancestors, had different life cycles and host associations in the past. Shell pits have so far been traced back only to the Eocene (Ruiz and Lindberg, 1989; Todd and Harper, 2011; Huntley and De Baets, 2015), which is more or less consistent with the presence of gymnophallid–shorebird associations (Figure 2).

Age: The Silurian occurrence of an igloo-shaped concretion was found in the silicified Möllboss 1 fauna from the Halla Formation (previously Halla Beds) of Gotland (Liljedahl, 1985, 1994). Jeppsson et al. (2006) correlated Möllboss 1 with the *parvus* graptolite biozone and the *Ozarkodina bohemica longa* conodont subzone 2 as defined by Calner and Jeppsson (2003). The top of the *Pristiograptus dubius parvus* – *Gothograptus nassa* graptolite biozone has been dated to 428.18 ± 0.4796 Myr, yielded an minimum age of 427.7 Ma (Melchin et al., 2012). This is consistent with U–Pb age of 428.45 ± 0.35 Myr obtained by Cramer et al. (2012) for the Grötlingbo bentonite at the nearby locality Hörsne 3, which has been correlated with Möllboss 1 (Jeppsson et al., 2006) and probably accounts for some of the silicification of the strata there (Mikael Calner, personal communication 2014).

2.3 Permo-Carboniferous egg remains in shark coprolites

The earliest confident record of parasitic flatworms with complex parasite life cycles are eggs attributed to Cestoda from the Rio do Rasto Formation (Dentzien-Dias et al., 2013), which has been assigned to the Middle to Late Permian (Holz et al., 2010). The eggs were obtained from a coprolite (Figure 3(a)), which was isolated from its host and forms part of a set of more than 800 coprolites of different shapes and sizes found in a geographically restricted area (Dentzien-Dias et al., 2012, 2013). It was identified as a shark coprolite by its spiral structure and fossil content (Dentzien-Dias et al., 2012, 2013). The eggs occur in a cluster (Figure 3(b)) and are ovoid, smooth shelled and with a small operculum (polar swelling) suggesting that they are nonerupted eggs (Figure 3(c) and (d)). Most eggs are filled with pyrite and one egg is suggestive of containing a developing larva (Figure 3(c) and (d)). The eggs vary little in size within the cluster, ranging from 145 to 155 μm in length and 88–100 μm in width. The morphological features

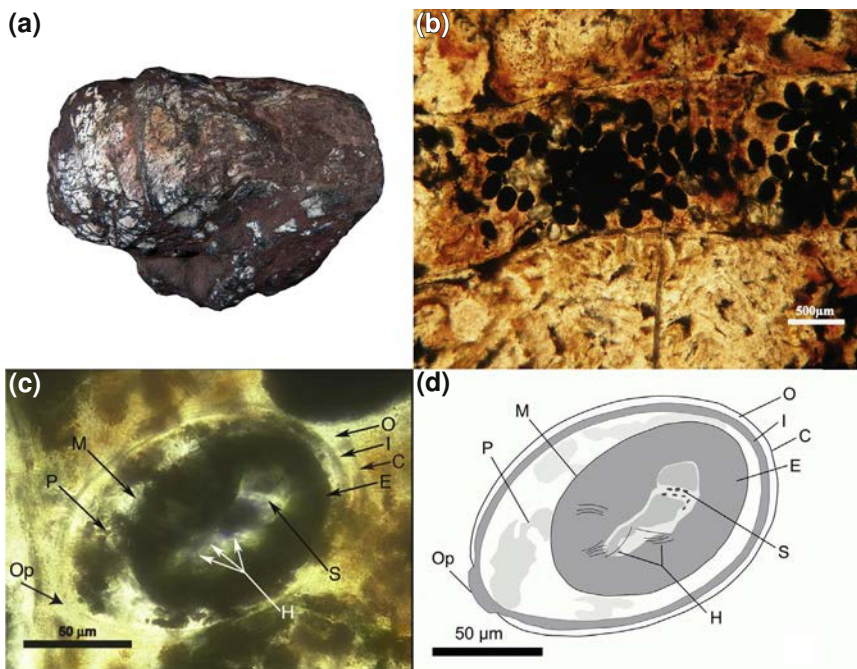


Figure 3 Fossil evidence for the presence of derived parasitic flatworms (Cestoda) in the Middle Permian (*Modified from Dentzien-Dias et al. (2013).*): (a) Picture of the spiral heteropolar coprolite from the Rio do Rasto Formation, which has yielded the cestode eggs, before destructive thin section analysis; (b) Thin section of the coprolite part containing parasite eggs clustered in; (c) Cestode egg with a developing embryophore. (d) Partial reconstruction of egg in (c) with interpretations of the observed structures. Abbreviations: C = capsule or shell; E = embryophore (ochosphere); H = putative developing hooklets; I = inner envelope; M = oncospherical membrane; O = outer envelope; P = putative polar thickening; Op = operculum; S = somatic cells.

of these eggs (operculum, egg shape and size: Figure 3(c) and (d)) as well as their deposition together in an elongate arrangement (Figure 3(b)), which is typical of modern tapeworm eggs deposited in mature segments or proglottids, corroborates their cestode affinity.

Age: The coprolite derives from the upper member of the Rio do Rasto Formation, which has also yielded a variety of vertebrate faunas (Dentzien-Dias et al., 2012). The locality is located near Posto Queimado, where vertebrate faunas indicate a Guadalupian (Late Wordian—Capitanian) age (Cisneros et al., 2012; Dias-Da-Silva, 2012). The coprolite should therefore be older than the Guadalupian (Capitanian)—Lopingian (Wuchiapingian) boundary dated to at least 259.4 Ma (259.8 ± 0.4 Myr: Henderson et al., 2012).

Older reports of potential cestode eggs (Zangerl and Case, 1976; Combes, 2001) within a Carboniferous coprolite are still controversial (Boucot, 1990; Poinar, 2003; Dentzien-Dias et al., 2013). Strictly speaking, this coprolite should be called a cololite as the fossilized faecal remains were found lodged within its producer (Hunt et al., 2012). Boucot (1990) considered the report as fairly speculative as the urea-rich environment of the dead shark would probably lead to the rapid decomposition of such eggs, but the latest discovery of cestode eggs in a Permian shark coprolite (Dentzien-Dias et al., 2013) illustrate that their interpretation as helminth eggs cannot be excluded. However, further analyses of the morphology and the arrangement of these spherical bodies are necessary to confirm their assignment to cestodes (Zangerl and Case, 1976; Combes, 2001) or other parasitic helminths.

Age: The *Cobelodus aculeatus* specimen with the putative cestode eggs derives from the Stark Shale, the core black shale member of the Dennis Formation of the Missouri Series, near Fort Calhoun, Nebraska. It was assigned to the Westphalian D by Zangerl and Case (1976) without any information corroborating this assignment. The Missouri series form part of the local Missourian stage, which largely corresponds with the Kasimovian (Falcon-Lang et al., 2011), which also includes the Stark Shale (Rosscoe, 2008; Rosscoe and Barrick, 2013). An age older than the Kasimovian—Gzhelian boundary (303.6 Ma according to the 2012 Geological Timescale: Davydov et al., 2012) can therefore be used as minimum constraint. Pending reinvestigation of this fossil, it could extend range of cestode eggs in shark coprolites by an additional 40 Myr.

2.4 Cretaceous egg remains in terrestrial archosaur coprolites

The oldest fossil evidence for Trematoda is an egg which was recovered from an Early Cretaceous isolated terrestrial vertebrate coprolite found near Bernisart in Belgium (Poinar and Boucot, 2006). The producers of these coprolites (and therefore also hosts of the parasites) are still debated (Chin et al., 1998; Baele et al., 2012). Both Bertrand (1903) and Poinar and Boucot (2006) presented arguments that they could have been produced by theropod dinosaurs (as opposed to crocodiles). However, theropod coprolites are rare (Hone and Rauhut, 2010), particularly when compared with coprolites of aquatic vertebrates (Chin, 2002) such as crocodylians in contemporary deposits (Hunt et al., 2012). Their seemingly precise assignment to ‘*Megalosaurus*’ *dunkeri* is therefore questionable, as it is based on the co-occurrence of a single metatarsal in the same deposits. This metatarsal was originally assigned to *M. dunkeri*

(now *Altispinax dunkeni*), but its morphology is only sufficient to assign it to theropods at best (Pascal Godefroid, personal communication 2014). Nevertheless, it remains the oldest evidence for trematodes in terrestrial predatory archosaurs (Poinar and Boucot, 2006).

Age: The fossil-bearing strata are now more precisely dated to be of Late Barremian to Early Aptian age (Yans et al., 2005; Schnyder et al., 2009; Yans et al., 2012), corresponding with the upper part of magnetochron M1n, M0r and the basal part of M0n. This yields an approximate minimum age for these strata of 125.93 Ma, the age attributed to the top of magnetochron M0r by Ogg (2012), or a more conservative age of 125.7 Ma, the age assigned to the base of the Tethyan *Deshayesites deshayesi* ammonoid biozone (Schnyder et al., 2009) by Ogg et al. (2012).

2.5 Eocene shell pits in intermediate bivalve hosts

The oldest evidence for the presence of Gymnophallidae might lie in the Eocene in the form of characteristic shell pits found in their intermediate bivalve hosts (Ruiz and Lindberg, 1989, Figure 2(e), Todd and Harper, 2011). These characteristic pits have been reported throughout the Cenozoic from the Eocene to the Holocene (Johannessen, 1973; Ruiz and Lindberg, 1989; Ruiz, 1991; Huntley, 2007; Todd and Harper, 2011; Huntley and Scarponi, 2012, 2015; Huntley et al., 2014; Huntley and De Baets, 2015). These pits have been commonly linked with Gymnophallidae (Ruiz and Lindberg, 1989; Todd and Harper, 2011), although superficially similar structures might also be caused by other digenetic trematodes such as Lepocreadiidae (Ituarte et al., 2001; see review by Huntley and De Baets, 2015).

Age: The oldest precisely dated shells (*Venericor clarendonensis*) with pits derive from subdivision B2 of the London Clay, Eocene (Todd and Harper, 2011). Berggren and Aubry (1996) assigned this unit to upper calcareous nannofossil zone NP11, which corresponds with a minimum age of 53.9 Ma according to the 2012 Geological Timescale (Vandenberghe et al., 2012).

Further support could come from the distribution of volcano-shaped (Campbell, 1985) to igloo-shaped calcareous concretions (Ituarte et al., 2001, 2005), which have been traced back to at least 6240 ± 70 years BP in the Holocene (Ituarte et al., 2005). Despite a certain degree of variability in these structures in extant bivalves, they are believed to be characteristic for gymnophallid trematodes (Campbell, 1985; Ituarte et al., 2001, 2005). Studies on pathology have focused on invertebrate intermediate hosts (Ruiz and Lindberg, 1989; Ituarte et al., 2001, 2005; Huntley, 2007; Huntley and Scarponi, 2012; Huntley et al., 2014; Huntley and De Baets,

2015), although some pathologies in vertebrate intermediate hosts have also been linked with parasitic flatworms. The best examples are probably the teratological limb malformations in North American amphibians, which have been linked with the trematode *Ribeiroia* on several occasions (Johnson et al., 2001, 2002; Stopper et al., 2002; Johnson and Sutherland, 2003; Johnson and Chase, 2004; Koprivnikar et al., 2012) and could potentially be found in the fossil record (cf. Fröbisch et al., 2014). Nevertheless, limb malformations — including supernumerary limbs and bone bridges — can have various other causes, meaning their interpretation is not always straightforward (Blaustein and Johnson, 2003; Lunde and Johnson, 2012).

2.6 Eggs remains in a Pleistocene mammal coprolite

The oldest Quaternary flatworm evidence is derived from an isolated Middle Pleistocene mammal coprolite (Jouy-Avantin et al., 1999), which these authors attributed to Ursidae based on its morphology and associated fossil finds. The morphology of the eggs (asymmetrical shell, the brown colour and the presence of an operculum) is characteristic of dicrocoelid flatworms, which makes this the oldest direct evidence for the presence of dicrocoelid flatworms (Digenea: Dicrocoelidae). They could not be assigned to a particular genus, although their dimensions are reminiscent of *Dicrocoelium* and *Eurythrema* based on egg measurements.

Age: The coprolite (H13 HEN5 1526) derives from an archeological layer at the Caune de l'Arago cave (Tautavel, Pyrénées-Orientales, France) and could be dated to a minimum age of 550,000 years BP (Jouy-Avantin et al., 1999) during a cold and dry climatic period (Lumley et al., 1984).

2.7 Holocene evidence for parasitic flatworms from ancient remains

Other Quaternary parasitic flatworm fossils and subfossils derive from the Holocene, mostly from archeological sites (see Gonçalves et al., 2003 for a review, Searcey et al., 2013; Araújo et al., 2014; Beltrame et al., 2014), with possible ages up 6368 years BP for Trematoda and ages up to 10,000 years BP for Cestoda. They can provide upper constraints for the earliest appearance of various taxa of Cestoda and Trematoda, including genera and species. The age assignment used in archeological publications can be a bit confusing. Before Present (BP) stands for a timescale, which starts at the 1st of January 1950 reflecting the fact that radiocarbon dating became practicable around that time and also antedates large-scale nuclear weapons testing altering the global ratio of carbon isotopes (Taylor,

1985). Archeological publications often use BC (Before Christ) and AD (Anno Domini). Hundred years BP is 100 years before 1950 (i.e. the year AD 1850). At ages older than about 0.5 Ma, the difference between BP and AD becomes negligible. We herein use the dates mentioned in the original publications to avoid confusion. Note that age assignment might change or differ according to the dating methods used (Iles, 1980). We recommend using the most conservative age estimates using reliable methods.

Remains of the Cestoda *Diphyllobothrium pacificum* can be traced back to about 10,000–4000 BP according to Reinhard (1992), although the exact evidence for such an age were not discussed in this paper. The record of anoplocephalid cestodes can be traced back to at least 8920 ± 200 years BP based on eggs founds in coprolites attributed to humans (Fugassa et al., 2010). Anoplocephalid remains which could be more specifically determined as *Monoecocestus* can be found in rodent coprolites dated as old as 6700 ± 70 years BP (Sardella et al., 2010). The earliest reports of *Hymenolepis* were dated approximately from 4000 to 2000 years BC (Gonçalves et al., 2003) and *Taenia* eggs from an Egyptian mummy attributed to about 3200 years BC (Reyman et al., 1977). According to Gonçalves et al. (2003), trematodes (*Fasciola* as well as Opisthorchioidea) can be traced back to at least 5400 ± 40 to 5230 ± 40 years BP (Roever-Bonnet et al., 1979), *Microcoelium* can be traced back to 3384–3370 BC (Dommelier Espejo, 2001), *Schistosoma* can be traced back to 3200 years BC based on the discovery of *Schistosoma haematobium* antigen in the shin tissue of an Egyptian predynasty mummy (Deelder et al., 1990) and *Schistosoma* ova in another contemporary mummy (Reyman et al., 1977), and as *Clonorchis sinensis* could be traced back to a mummy from Chu Dynasty (475–221 years BC) with an age of at least 2171 years BP (Wen-yuan et al., 1984). Eggs of *S. haematobium* were one of the earliest to be discovered in Egyptian mummies.

Recently, ancient DNA of echinostomatid trematodes was extracted from coprolites of the extinct ratite bird *Megalapteryx* from New Zealand (Wood et al., 2013), which might range from about 6368 years BP to the 694 ± 30 years BP, coincident with the time of their extinction (Wood et al., 2012).

2.8 Free-living flatworms

The body fossil record of free-living flatworms is also of little help as it is poorer or even more patchy than the fossil record of parasitic flatworms (Poinar, 2003). The oldest free-living flatworm body fossils derive from

Eocene Baltic amber (Poinar, 2003) and calcareous nodules of Miocene age (Pierce, 1960; Poinar, 2003), and those of flatworm egg capsules from Quaternary lake sediments (Frey, 1964; Harmsworth, 1968; Gray, 1988). These fossils considerably post-dated divergence time estimates for free-living flatworms derived from molecular clock studies. Older molecular clock studies place the origin of (free-living) Platyhelminthes deep in the Precambrian (Hausdorf, 2000; Otsuka and Sugaya, 2003), but more recent relaxed molecular clock studies place their origins between the latest Precambrian (Ediacaran) and the early Cambrian (Douzery et al., 2004; Peterson et al., 2004, 2008; Erwin et al., 2011). Some Ediacaran fossils have occasionally been related to free-living flatworms (Allison, 1975; Palij et al., 1979; Fedonkin, 1985), although they cannot be confidently assigned to the phylum (Conway Morris, 1981; Labandeira, 2002; Erwin et al., 2011). Even *Dickinsonia* was assigned to flatworms at one point (Palij et al., 1979; Conway Morris, 1981). The taxonomic position of *Dickinsonia* has been heavily debated (Retallack, 2007; Brasier and Antcliffe, 2008) and this taxon is often interpreted as one of the earliest divergent metazoans (Xingliang and Reitner, 2006; Sperling and Vinther, 2010). Various Permian to Triassic trace fossils have also been attributed to turbellarians including Polycladida and Tricladida (Alessandrello et al., 1988; Knaust, 2010). The assignment of trace fossils to this phylum is also problematic as various worm-like groups with similar ecology and mode of locomotion could also have produced these traces (Seilacher, 2007). *Curvolithus* has also been attributed to flatworms (Seilacher, 2007), but could also have been produced by other taxa with similar behaviour (Buatois et al., 1998). Further studies of traces produced by extant forms as well as fossil traces associated with body fossils are therefore important to confidently assign them to the phylum (Collins et al., 2000; Knaust, 2010).

The oldest parasitic flatworm fossils are therefore not only important for putting constraints on free-living flatworms, but also on the presence of Platyzoa in the fossil record, a group currently containing both parasites (Platyhelminthes, Acanthocephala) and free-living taxa (Wey-Fabrizius et al., 2013). The assignment of Cambrian fossils (cambroclaves) to the Acanthocephala as suggested by some authors (Qian and Yin, 1984), which has also been followed in some recent classifications (Amin, 2013), is highly questionable and widely rejected (Conway Morris et al., 1997; Elicki and Wotte, 2003; Kouchinsky et al., 2012). These problematic Cambrian organisms can be classified as Lophotrochozoa at best (Kouchinsky et al., 2012); Compare Conway Morris and Crompton (1982) and Near (2002) for further speculations and hypotheses on the origin and evolution of parasitism towards

the rise of the Acanthocephala. Furthermore, the oldest accepted record of Rotifera, the free-living relatives of Acanthocephala, derives from Dominican amber deposits (Waggoner and Poinar, 1993), which is now more confidently dated to the Miocene (Iturralde-Vinent and MacPhee, 1996; Iturralde-Vinent, 2001). The oldest confidently assigned Acanthocephala remains have been reported from archeological sites (Gonçalves et al., 2003); some dating back to 9500 years BC according to Fry and Hall (1969). Considering that multiple authors (Upeniece, 2001, 2011; Littlewood and Donovan, 2003) have suggested that the Middle Devonian hook circlets might belong to a platyzoan helminth, a putative reinvestigation of these fossils could be used to constrain the evolutionary history of this entire group. Many studies on extant flatworms have focused on the hook elements of particular groups (Vignon and Sasal, 2010; Vignon, 2011) or taxa (Shinn et al., 2003). Information and illustrations of these helminth structures can also be found in comprehensive systematic treatments: Yamaguti (1959), Schmidt (1986) and Khalil et al. (1994) for Cestoda; Yamaguti (1963a) for Monogenea and Yamaguti (1963b) and Golvan (1969) for Acanthocephala.

3. INTERPOLATING OR EXTRAPOLATING EXTANT PARASITE—HOST RELATIONSHIPS AND THE ASSUMPTION OF PARASITE—HOST COEVOLUTION

Analysis of the range of current parasite—host associations has often been used to infer the evolutionary origin of parasitic organisms (Littlewood and Donovan, 2003). With the exception of highly derived taxa, parasitic flatworms do not parasitize hagfishes or lampreys (Littlewood, 2006). This may suggest that parasitic flatworms evolved in basal gnathostomes (Littlewood, 2006), which would lie somewhere around the Cambrian—Ordovician based on the host fossil record (Friedman and Sallan, 2012; Donoghue and Keating, 2014). This considerably predates the oldest generally accepted fossil evidence for parasitic flatworms, but the fossil record indicates that other groups like pentastomids, which parasitize vertebrates today and might have done in the past, were already around at this time (Walossek and Müller, 1994; Walossek et al., 1994; Maas and Waloszek, 2001; Waloszek et al., 2005; Sanders and Lee, 2010; Castellani et al., 2011). If we map the fossils of parasitic flatworms on their host phylogenies (Figure 4), they are at least consistent with extant parasitic flatworm—host associations, which is not the case for all parasites (Figure 5). Pentastomids mainly parasitize terrestrial vertebrates today (Christoffersen and De Assis,

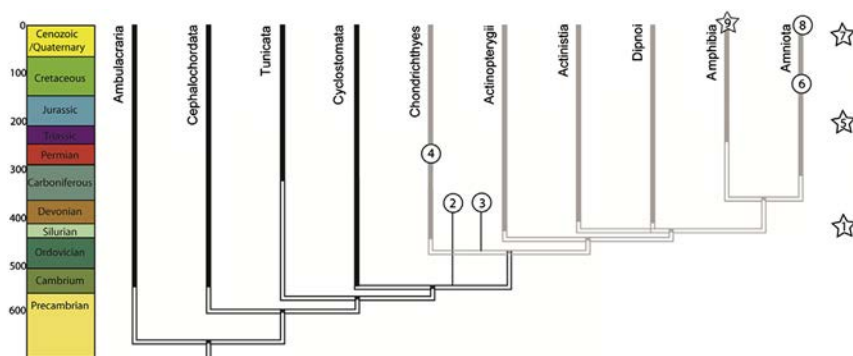


Figure 4 Fossil finds of putative flatworm fossils discussed in the text mapped on their host phylogeny, which was modified from Donoghue and Smith (2003) and Rowe (2004) taking into account new phylogenetic hypotheses summarized in Donoghue and Keating (2014).

2013), but in the Cambrian–Ordovician (Walossek and Müller, 1994; Walossek et al., 1994; Waloszek et al., 2005; Castellani et al., 2011), they are found in marine deposits and there were no terrestrial vertebrates to serve as hosts at this time. Their morphology indicates a parasitic lifestyle, but the

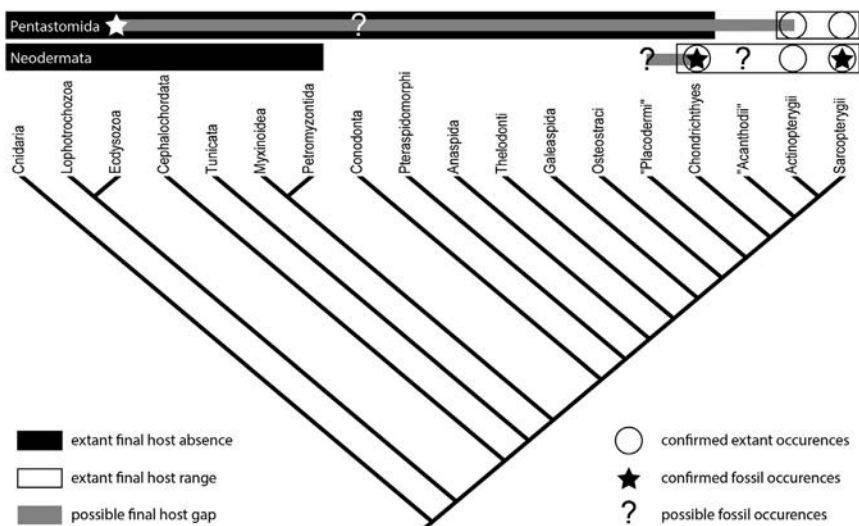


Figure 5 Comparisons of the consistency between extant and fossil host ranges of parasitic flatworms and pentastomids. Host phylogeny was modified from Goudemand et al. (2011). Note that the host gap would be considerably greater if the position of conodonts would be more basal as postulated by some authors (Blieck et al., 2010; Turner et al., 2010). Recent discoveries of Silurian pentastomids associated with ostracods even further extend the host gap between fossil and extant pentastomids (Siveter et al., 2015).

exact host of these marine forms is still unknown as they were not found directly associated with their hosts. Some have suggested their hosts might have been conodonts (Walossek and Müller, 1994), of which tooth-like remains have been commonly found in these deposits. Interestingly, the Cambrian–Ordovician fossil pentastomids resemble larvae of modern forms that can infest fish, making it conceivable that these small pentastomids represent adults that spent their entire life cycle on small fish-like vertebrates (Sanders and Lee, 2010). The range of the host gap between Cambrian and extant pentastomids (Figure 5) might therefore depend on the systematic position of conodonts, which is still debated. Most authors agree that conodonts are chordates, probably either stem- or crown-vertebrates (Blieck et al., 2010; Turner et al., 2010; Goudemand et al., 2011; Murdock et al., 2013; Donoghue and Keating, 2014). Interestingly, putative pentastomid remains were recently also reported from ostracods within the Silurian Herefordshire Lagerstätte (Siveter et al., 2015), which further increases the host gap between extant and fossil pentastomids. This might suggest that invertebrates might have been the initial hosts in the marine realm, if ostracods are the final hosts as suggested by these authors and if no host switching occurred between the Cambrian and the Silurian. However, pentastomid–host associations from the Cambrian and Ordovician lagerstätten would be necessary to further test this hypothesis.

Thus, it is not always possible to precisely constrain parasite–host associations in the fossil record. This is not only the case for isolated remains of parasites not directly attached to their hosts (Castellani et al., 2011), but also for parasite remains found in isolated coprolites not confidently assignable to precise host taxa (Jouy-Avantin et al., 1999; Poinar and Boucot, 2006; Dentzien-Dias et al., 2013).

Fossils of potential hosts might be common or present in the same layers, although without direct evidence for a parasitic relationship (attached or found within well-preserved body fossils of their hosts), appointing a potential host remains within the realm of speculation. In the case of intermediate hosts, where the fossil evidence is often pathologies or traces, it is hard to be certain of the identity of the culprits since various organisms with similar behaviour can produce similar traces. Furthermore, it might also be hard to identify the final host without finding remains of the putative parasite associated with them. Predator–prey relationships might provide a clue (Ruiz and Lindberg, 1989; De Baets et al., 2011), but direct evidence for predation from one taxon on another is rare in the fossil record too (Brett and Walker, 2002; Walker and Brett, 2002). Nevertheless, age in itself might

be sufficient to rule out certain hosts if they had not yet evolved, they must have had different intermediate and/or final hosts at that time. Although the hosts of Cambrian–Ordovician pentastomids remain speculative, hosts assignable to taxa they currently parasitize were not around yet, so they must have had additional parasite–host associations in the past which are now extinct.

4. MOLECULAR CLOCK STUDIES

Molecular clock (timetree) methods for calibrating phylogenies have the potential to be useful to discriminate evolutionary scenarios in parasite evolution or host–parasite associations (Hypša, 2006). However, molecular clocks still need to be calibrated to obtain absolute age estimates, which is not that straightforward among parasite groups with a patchy fossil record. Thus, a cophylogenetic approach has been used (Hafner et al., 1994; Page et al., 1998; Light and Hafner, 2007), which may in turn provide a robust evolutionary timescale for apparent cospeciating symbiotic species when the timescale of the host lineage is (comparably) well constrained (Moran et al., 1993, 1995). Due to the lack of well-preserved specimens in parasitic flatworms, most molecular clock studies have relied on the host fossil record to inform divergence estimates (Verneau et al., 2002, 2009a,b; Olson et al., 2010; Badets et al., 2011; Héritier et al., 2015). More rarely biogeography (focusing on vicariance events) has been invoked to constrain molecular clock estimates of parasitic flatworms (Zietara and Lumme, 2002; Waltari et al., 2007; Badets et al., 2011; Martínez-Aquino et al., 2014). Only one study (Perkins, 2010) used the parasitic flatworm fossil record as a calibration, although it relied on the Upper Devonian and Carboniferous putative flatworm fossils, whose taxonomic assignment to Monogenea and Cestoda, respectively, is still debated (as discussed above). Other studies have relied on molecular substitution rates derived from other studies (Despres et al., 1992; Zietara et al., 2002; Huyse and Volckaert, 2005), which is even more problematic (Papadopolou et al., 2010; Hipsley and Müller, 2014).

The best practice for using fossils for molecular clock calibration has been discussed and reviewed extensively (Donoghue and Benton, 2007; Benton et al., 2009; Parham et al., 2012). Most authors agree that the fossil specimens can only directly provide a well-justified minimum constraint for the origin of some particular lineages. According to Parham et al. (2012),

fossil calibrations are well justified if the following criteria are fulfilled: (1) listing of museum numbers of specimen(s) that demonstrate all the relevant characters and provenance data, (2) availability of apomorphy-based diagnoses of the specimen(s) or an explicit, up-to-date, phylogenetic analysis that includes the specimen(s), (3) explicit statements on the reconciliation of morphological and molecular data sets, (4) specification of the locality and stratigraphic level (to the best current knowledge) from which the calibrating fossils are derived, (5) reference to a published radioisotopic age and/or numeric timescale with details on its selection. Divergence time estimation is not possible with minimum constraints alone, as the substitution rate is variable and unknown; therefore, at least one point calibration or maximum constraint is required to calculate the substitution rate and absolute divergence times (Warnock et al., 2012).

It would therefore be more appropriate to use the oldest estimate (95% confidence maximum) for the origin of the total group from a robust molecular clock analysis as the maximum, and the oldest fossil assignable with confidence to the crown group (as the minimum), to constrain the evolutionary history of the host (and the parasite). For example, if the origin of parasitic flatworms occurred during the early evolution of gnathostomes as suggested by Littlewood (2006), this would mean they originated between the Cambrian (643 Ma: oldest confidence intervals of Erwin et al., 2011 for this node) and the earliest well-dated fossils that can be confidently assigned to crown-group gnathostomes deriving from Ordovician (~ 421.8 Ma: Benton et al., 2009; Donoghue and Keating, 2014). Alternatively, the entire 95% confidence posterior interval (from robust molecular clock studies) for diverging host clades could be used as priors on the clade ages in the parasites.

A more conservative and less circular approach would be to use the latest robust relaxed molecular clock estimates for the origin of their free-living ancestors (744 Ma: oldest confidence of Erwin et al., 2011 for this node) and the earliest certain appearance of parasitic flatworms in the fossil record, which would be only Permian (>259.4 Ma as discussed above). This would yield quite large confidence intervals (cf. Warnock et al., 2012 for Parasitiformes), but such estimates would be more honest and accurate (closer to reality) than seemingly precise estimates which are arguably inaccurate, since the origin of parasitism falls outside the calibration interval a priori (Warnock et al., 2011). Furthermore, reinvestigation of putative flatworm trace or body fossils from Upper Silurian (>427.7 Ma) or Middle Devonian (>381.9 Ma) deposits might further narrow this

time interval in the future. The fossil record also provides constraints on the origin of Cestoda in shark hosts (Dentzien-Dias et al., 2013) and Trematoda in archosaur hosts (Poinar and Boucot, 2006). Furthermore, the fossil record provides upper constraints on the origin of Gymnophallidae in the form of characteristic pathologies, dicrocoelid flatworms derived from eggs in coprolites as well as several genera and even species from archeological sites (e.g. *Dicrocoelium*, *Diphyllbothrium*, *Fasciola*, *Monoecocestus*, *Schistosoma*, *Taenia*).

The oldest fossil evidence for schistosomes are antigens deriving from a 3200 BC Egyptian mummy, but the origin of this group is believed to be considerably older based on the evolutionary history of their intermediate or final hosts (Lawton et al., 2011). Davis (1993) suggested that the genus *Schistosoma* arose before the breakup of the supercontinent Gondwana over 150 Ma based on the distribution of their snail hosts and that ancestors of Asian schistosomes were carried to Asia via India after it separated from Africa. More recent studies (Snyder and Loker, 2000) have suggested a younger, ancestral Asian origin somewhere in the Miocene, which might indicate that schistosomes only colonized Africa around 15–20 Ma (Lawton et al., 2011). Performing a robust molecular clock analysis using dates of fossil *Schistosoma* and their hosts might be a more formal way to test these hypotheses. In some cases, additional historical dates might become available to constrain certain nodes such as the possible slave transport of *Schistosoma mansoni* to South America (Lockyer et al., 2003b), which is so far not contradicted by finds of older remains of *S. mansoni* in archeological sites of South America (Gonçalves et al., 2003). Direct dating of samples yielding ancient DNA (Wood et al., 2013) might also provide additional constraints in such studies. However, a recent study by Mello et al. (2014) has demonstrated that the assignment of calibration information to deeper phylogenetic nodes is more effective in obtaining more precise and accurate divergence time estimates compared to analyses involving calibration at the shallowest node.

Most authors agree that multiple, well-justified calibrations are the best approach to obtain the most robust and accurate molecular clock estimates (Warnock et al., 2011; Parham et al., 2012). Note that careful a priori selection of suitable calibration points cannot be replaced by using as a posteriori cross-validation procedures (Near et al., 2005; Andújar et al., 2014) as these only verify consistency (Clarke et al., 2011). In some cases, multiple inaccurate calibrations might be consistent, which can result in erroneous rejection of more reasonable calibrations. Furthermore, consistent calibrations may be

redundant by definition, since they fail to correct for changes in rate variation (Clarke et al., 2011; Warnock et al., 2015). Furthermore, calibration should be implemented in the most conservative way, which might result in less precise, but ultimately more accurate divergence estimates (Warnock et al., 2012).

In the absence of a suitable fossil record, one could resort to the use of biogeographic events or calibrations related only to the host fossil record. Nevertheless, both methods also have their problems and add an additional component of circularity to calibration procedures depending on the hypotheses being tested (Hipsley and Müller, 2014). Biogeographic calibrations as they are currently implemented are problematic (Goswami and Upchurch, 2010; Kodandaramaiah, 2011; De Baets and Donoghue, 2012; Hipsley and Müller, 2014), and they should be implemented more conservatively. It should be established when a certain barrier, causal to a given speciation event, actually occurred (De Baets and Donoghue, 2012; Warnock, 2014).

Most importantly, there remains an assumption that biogeographic distributions have not changed significantly in geological time, making it harder to establish whether biogeographic barriers were coincident with speciation events, and introduce an aspects of circularity (Crisp et al., 2011). Having taxon-area relationships consistent or inconsistent with biogeographic events, does not necessarily mean that these clades diversified at the same time as these events, because older events might have led to similar distributions (pseudo-congruence) or younger events might have altered their distributions (pseudo-incongruence; see Donoghue and Moore, 2003). Even for some of the classical examples of groups with current distributions congruent with vicariance, such as onychophorans and cichlids, studies have demonstrated that divergence might predate (Murienne et al., 2014) or postdate (Friedman et al., 2013) the continental break-up of supercontinents, respectively.

Using the fossil record of hosts also introduces an aspect of circularity in addition to other considerations related with fossil calibrations (Donoghue and Benton, 2007; Parham et al., 2012) as discussed above. It assumes that the current parasite–host associations did not markedly change through geological time, which is not necessarily true, particularly in groups which are estimated to range several hundred million years into the past (e.g. the pentastomid example we discussed above). Using hosts also leads to circular reasoning when employing them to investigate hypotheses of parasite–host coevolution. In highly host-specific lineages with simple life cycles like the

Polystomatidae (Figure 6), it might work well, but for groups with common host switches and/or complex life cycles this approach might be less suitable. The most conservative way to implement them would be to use the oldest reliable estimate for the origin of this group as a maximum and the oldest from well-attributable fossil to this lineage as a minimum. Polystomatid flatworms are one of the most host-specific groups of parasitic flatworms and their direct life cycle that involves a short free-living aquatic larval stage (which means they are probably only passively disseminated by their hosts), have made them an ideal model to test the use of constraints from biogeography and the host fossil record (Bentz et al., 2001, 2006; Verneau et al., 2002, 2009a,b; Badets et al., 2011). Verneau et al. (2002) used 425 Ma to calibrate the split between Actinopterygii and Sarcopterygii (Figure 6), although this event must have happened at the latest by about 419 Ma (Zhu et al., 2009). However, it would be more conservative to use the oldest robust estimate from relaxed molecular clock studies for the separation of actinopterygian from sarcopterygians and the earliest fossil confidently assigned to either tetrapods or lungfishes to constrain this node (Badets et al., 2011). The oldest stem-group lungfish is generally considered to be *Diabolepis* (Friedman, 2007; Qiao and Zhu, 2009), while one of the oldest ingroup lungfishes might be *Westollrhynchus* (Qiao and Zhu, 2009). Badets et al. (2011) also suggested that some dates might be consistent with the break-up of the supercontinent Gondwana, although this needs to be further tested with additional sampling.

Taxon sampling can play a large role in tree reconstruction and interpretation with respect to biogeography (Trewick and Gibb, 2010) or host switching (Hafner and Page, 1995). In the case of lineages or parasite–host associations, which have been around for many hundreds of millions of years, host range changes and extinction might contribute significantly to missing taxa, making it hard to infer past biogeographical distribution or parasite–host associations, from extant data alone. There is at least some evidence that extinction might also have played a role in parasitic flatworms and other helminths over longer timescales as several parasite–host associations documented in the (sub)fossil record are now evidently extinct (Upeniece, 2001, 2011; Poinar and Boucot, 2006; Wood et al., 2013). Furthermore, molecular studies with greater taxonomic coverage have particularly focused on biomedically or economically important taxa such as Schistosomatidae (Lockyer et al., 2003b; Orélis-Ribeiro et al., 2014) or particular lineages with a high host specificity such as Polystomatidae (Bentz et al., 2001, 2006; Badets et al., 2011, 2013; Héritier et al., 2015). To better

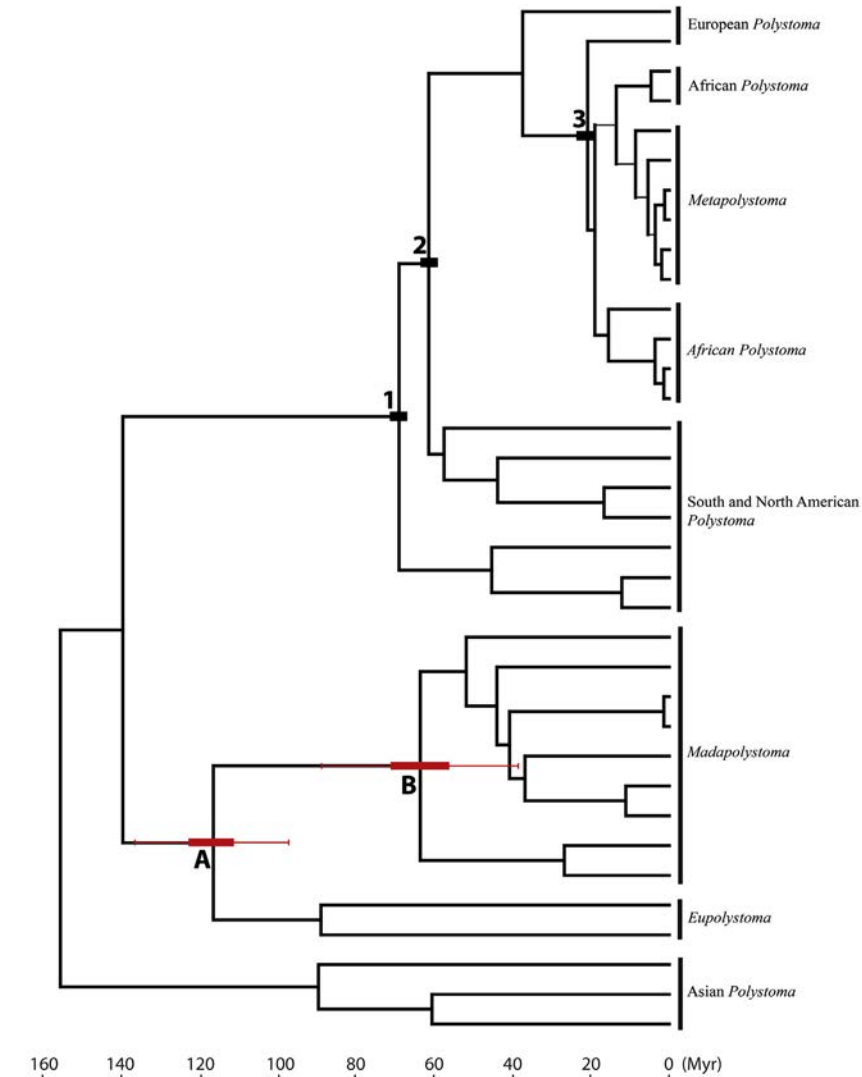


Figure 6 Ultrametric tree of neobatrachian polystomes inferred from MULTIDIVTIME (Modified after Verneau et al. (2009b)). Calibration points (black rectangles, nodes 1–3) were deduced from historical biogeographical scenarios suggested by Bentz et al. (2001, 2006) and Badets et al. (2011). The divergence of the lineage associating *Metapolystoma*, Eurasian and African *Polystoma* from their closest South and North American relatives (nodes 1 and 2) was constrained between 65 and 56 Myr, reflecting vertebrate exchanges between the two Americas in the Paleocene (Gayet et al., 1992) and possible dispersal to Eurasia via Beringia. The divergence between the European *Polystoma* species (i.e. *Polystoma gallieni*) and the lineage grouping *Metapolystoma* and African *Polystoma* was constrained between 25 and 5 Myr, reflecting the

understand the evolutionary history using molecular methods, it is essential to sample as many distinct lineages of parasites as possible as well as their free-living relatives, focusing particularly on evolutionary important taxa which have putative fossil records (e.g. Gymnophallidae, basal Monogenea, Cestoda) or reliable geological constraints derived from biogeography or the evolutionary history of their hosts.

When no appropriate constraints are available, relative rates of uncalibrated molecular clocks can be used to test the support or reject the temporal congruence of parallel distributions or parasite–host evolution (Loader et al., 2007; Hibbett and Matheny, 2009; Loss-Oliveira et al., 2012). Nevertheless, it should be kept in mind when interpreting the results that the rate of molecular evolution might be significantly different between parasites and hosts (Page et al., 1998) or within and between lineages of parasites and/or hosts (Thomas et al., 2006, 2010; Bromham, 2009), which can bias the results of such studies (Hipsley and Müller, 2014). Furthermore, novel probabilistic approaches make it possible to incorporate in biogeographic inference, estimates of the divergence time of lineages as well as external sources of evidence such as climate, geography, their fossil record or ecological tolerance (Sanmartín, 2012).

5. CONCLUSIONS AND FUTURE PROSPECTS

The earliest fossil evidence for the presence of helminths falls in the Middle Devonian in the form of hooks, some of which are most reminiscent of extant Monogenea, although some could also belong to Acanthocephala or more derived flatworms (Cestoda). The oldest secure record of parasitic flatworms with complex parasite life cycles lies in the Permian which can be confidently assigned to cestodes, although the presence of

hypothesized ages of dispersal routes between Eurasia and Africa (Rage, 1988; Bentz et al., 2001). Finally, the root prior was set at 160 Ma (sd $\pm$ 5 Myr), corresponding to an initial divergence separating Asian and Australian polystomes from all other neobatrachian polystomes (Badets et al., 2011), hypothetically corresponding to a separation of the western and eastern components of Gondwanaland. Divergence time estimates (see Verneau et al., 2009b) are reported for two nodes that are relevant for understanding the origin of the new Malagasy genus, i.e. *Madapolystoma* (see Du Preez et al., 2010). According to Verneau et al. (2009b), *Madapolystoma* would have diverged from *Eupolystoma* about 116 Ma (node A) and the first crown divergence in *Madapolystoma* (node B) would have occurred about 63 Ma.

igloo-shaped concretions reminiscent of those caused by gymnophallid trematodes in extant bivalves might already indicate the presence of derived parasitic flatworms with complex parasite life cycles in the Late Silurian (>428 Ma). These Silurian occurrences are, however, not consistent with evolutionary history of current gymnophallid hosts (shorebirds), which are believed to have appeared somewhere between the Cretaceous and Eocene. Characteristic pits in bivalves shells indicative for the presence of digenetic trematodes (Gymnophallidae) appear already in the Eocene (Ruiz and Lindberg, 1989; Todd and Harper, 2011; Huntley and De Baets, 2015), which is more or less consistent with the presence of their final host in the fossil record. The first evidence for terrestrial parasitic flatworms and trematodes was found in the form of eggs within a Lower Cretaceous coprolite (Poinar and Boucot, 2006), which can be confidently attributed to archosaurs (potentially theropod dinosaurs or crocodylians). The earliest evidence for dicroelid trematodes (Jouy-Avantin et al., 1999) falls at about 0.55 Ma in the Middle Pleistocene. Various extant genera and species have been described from younger archeological sites (Gonçalves et al., 2003; Araújo et al., 2014). Several putative flatworm fossils need additional study to confidently assign them to a certain lineage of flatworms including platyzoan helminth hooks in Middle Devonian gnathostomes, putative cestode eggs in a Carboniferous shark coprolite and eggs in a Cretaceous archosaur coprolite. Remarkably, the fossil record of parasitic flatworms is considerably better than that of free-living flatworms (Poinar, 2003) and Platyzoa in general (Conway Morris and Crompton, 1982; Wey-Fabrizius et al., 2013) and it could therefore be used to constrain the evolutionary origin of flatworms and other Platyzoa. Only rarely have studies been performed to assess the evolution of these structures over larger scales; e.g. see Malmberg (1990) for Monogenea, which is a rather controversial study for different reasons (Gusev, 1992). A comparative analysis of hook elements of acanthocephalans and parasitic flatworms (Monogenea, Cestoda) in a new molecular phylogenetic framework would therefore be in order to more confidently assign the fossil hook circlets to a certain clade or phylum. Furthermore, the study of eggs as well as hook circlets, which is now largely done with destructive methods and in two dimensions, would benefit from CT-scanning technologies to characterize their 3D-morphology and structure in a nondestructive way and potentially reveal additional details or fossils which otherwise might be destroyed by the sample preparation process (e.g. thin-sectioning, chemical sample preparation, resedimentation procedures).

Fossil evidence can only provide minimum time constraints and is not available for all lineages of parasitic flatworms. Interpolations based on parasite–host associations or biogeographic events can potentially be used to supplement fossil constraints. However, circularity in testing hypotheses should be avoided and caution should be taken when multiple host-switching events are suspected. Before using such calibrations it should be at least verified if this hypothesis is robust to a wider sampling of extant and extinct taxa as well as the evolutionary history of their hosts, where the sampling and fossil record might be comparatively better. We therefore advise implementing such calibrations in the most conservative way. For calibrations based on the evolutionary history of parasites or their hosts, this would correspond with using the oldest estimate based on relaxed molecular clock estimates as maximum and the oldest well-attributable fossils of the parasite or its host as a minimum; for calibrations based on biogeographic events, this would correspond to the using the oldest age of the oldest geological event that could have influenced the distribution of the parasites and their hosts as a maximum and the youngest age of the geological events that could have influenced their distribution as a minimum.

Several recent discoveries indicate that exceptionally preserved gnathostomes or their coprolites might yield additional finds of parasitic flatworm fossils, particularly their attachment organs or their eggs (Littlewood and Donovan, 2003; Poinar and Boucot, 2006; Dentzien-Dias et al., 2013), which can be characteristic for certain lineages. Novel methods like experimental decay studies or computer tomography might provide additional insights into the phylogeny, 3D-morphology and ecology of such fossils. The future of constraining the evolutionary history of Platyzoa and parasitic flatworms lies in molecular clock methodology by combining information from the geological record (particularly body fossils or eggs) and molecular sequences with the fewest assumptions. Characteristic pathologies might also put constraints on the evolutionary history of parasitic flatworm, although this still needs to be further studied in extant and fossil hosts to establish a robust relationship with a particular lineage of parasites (Campbell, 1985; Ituarte et al., 2001, 2005).

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