Fossil constraints on the timescale of parasitic helminth evolution

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Abstract. The fossil record of parasitic helminths is often stated to be severely limited. Many studies have therefore used host constraints to constrain molecular divergence time estimates of helminths. Here we review direct fossil evidence for several of these parasitic lineages belong to various phyla (Acanthocephala, Annelida, Arthropoda, Nematoda, Nematomorpha, Pentastomida, Platyhelminthes). Our compilation shows that the fossil record of soft-bodied helminths is patchy, but more diverse than commonly assumed. The fossil record provides evidence that ectoparasitic helminths (e.g., worm-like pentastomid arthropods) have been around since the early Paleozoic, while endoparasitic helminths (cestodes) arose at least during, or possibly even before the late Paleozoic. Nematode lineages parasitizing terrestrial plant and animal hosts have been in existence at least since the Devonian and Triassic, respectively. All major phyla (Acanthocephala, Annelida, Platyhelminthes. Nematoda, Nematomorpha) had evolved endoparasitic lineages at least since the Mesozoic. Interestingly, although parasitism is considered derived within Metazoa, the oldest evidence for Nematoda and Platyhelminthes includes body fossils of parasitic representatives. Furthermore, the oldest fossil evidence of these parasitic lineages often falls within molecular divergence time estimates based on host co-evolution suggesting the fossil record of helminths themselves might be just as good or at least complementary (and less circular in justification) to calibration based on host associations. Data also provide evidence for obvious host switches or extinctions, which cautions against models of pure co-divergence where use of host calibrations to constrain divergence time estimates may be considered.

Keywords: parasitic worms, fossil record, molecular divergence estimates, host constraints

1 Introduction

Helminths are multicellular parasitic worms varied in size (Caira and Littlewood 2013) from the microscopic (200µm) to the enormously long (80 m). This polyphyletic grouping includes parasitic flatworms (flukes, tapeworms), nematodes and acanthocephalans (Rohde 2005). They can cause diseases in humans, livestock and wildlife (e.g., helminthiases). Some authors also include tongue worms (pentastomids: e.g., McAllister et al. 2010) or even parasitic annelids (e.g., Öktener 2005) when describing or listing helminths from particular regions. Although an artificial grouping, which contains a number of phylogenetically distantly related clades, the term 'helminths' is still used to describe a group of parasitic organisms sharing a similar form and lifestyle.

Despite their biomedical and economic importance, the deep time evolutionary history of parasitic worms remains poorly understood, which has been largely attributed to their meagre, or rather poorly explored, fossil record (Littlewood and Donovan 2003). As many helminths use vertebrate animal hosts or other hosts with a demonstrably better fossil record, it is helminth hosts that have been used to constrain helminth origins (by phylum) where a certain degree of host specificity might be assumed. With such approaches, some groups of nematodes and parasitic flatworms have been suggested as existing during the Cambrian – Ordovician (Littlewood 2006; Poinar 2011, 2015). In other cases, particularly where host-specificity is common, current biogeographic distribution patterns of host-parasite associations have been used to infer the temporal origin of the interaction (Borda et al. 2008; Verneau et al. 2009; Badets et al. 2011; Cuthill et al. 2016). Some of the most commonly used examples for host or biogeographic constraints include those made for the monogenean group Polystomatidae (Verneau et al. 2002, 2009; Badets et al. 2011; Héritier et al. 2015; Tinsley and Tinsley 2016). However, both approaches might involve circular reasoning (Kodandaramaiah 2011; De Baets et al. 2015, 2016; Warnock and Engelstädter 2020). Fossil associations are among the only direct sources of evidence for the existence of particular lineages in the geological past (De Baets & Littlewood, 2015). In addition, the fossil record can provide additional information on morphology, host association and/or life history.

The oldest known unambiguous fossil helminths are isolated remains of pentastomids which are known from the Cambrian-Ordovician (Klompmaker and Boxshall 2015). Older finds have been reported (Cong et al. 2017) although their phylogenetic assignment is poorly resolved and they are interpreted to be likely ectosymbiotic rather than ectoparasitic. There is also fossil evidence that nematodes already parasitized early land plants in the Early Devonian (Poinar et al. 2008) and monogeneans parasitized early gnathostomes in the Middle Devonian (Upeniece 2001, 2011). The first confidently identified evidence for intestinal helminths derives from the Permian (Dentzien-Dias et al. 2013) – although older Carboniferous finds have been reported (Zangerl and Case 1976). These finds suggest that the fossil record of helminths is more ancient than commonly perceived.

Here we review the fossil record of helminths with the aim of providing suitable minimum and maximum constraints for dating their origins and key host transitions during their evolution. The fossil record of particular group of helminths is reviewed at greater length in other publications (Poinar 2011, 2015; Maas 2013; Parry et al. 2014, 2019b; De Baets et al. 2015; Huntley and De Baets 2015; Herlyn 2020). We focus particularly on similarities and differences in the fossil record of helminths and in a phylogenetic context. For this purpose, we first briefly review the progress made in disentangling their phylogenetic position within the Metazoa since a major review on the topic (Zrzavý 2001).

2 Phylogenetic affinities and distribution of parasitic “helminths”

Since the early 1990s, the rapid accumulation of molecular sequence data has revolutionized our understanding of animal phylogeny and evolutionary history (Edgecombe et al. 2011). Bilaterian animals are now usually subdivided into three principal clades (Laumer et al. 2019): Deuterostomia, Ecdysozoa and Spiralia (including Lophotrochozoa), with the latter two groups forming the Protostomia. Protostomia contains the most animal phyla and body plans and likewise contains the highest diversity of groups that have evolved a parasitic lifestyle (Weinstein and Kuris 2016). A possible exception are Myxozoa – some of which are worm-like – now considered to be derived cnidarians (Okamura et al. 2015; see Okamura and Gruhl 2020). Various helminths are so divergent from their close relatives that they have previously been considered separate phyla. Examples include Acanthocephala and Pentastomida, which are now recognized as highly modified members of Rotifera in Syndermata (Struck et al. 2014; Sielaff et al. 2016; Herlyn 2020) and Crustacea in Euarthropoda (Sanders and Lee 2010; Oakley et al. 2012), respectively. In general, parasitic lineages have elevated rates of molecular sequence evolution, which often makes them hard to place robustly in phylogenies, where they often form long branches. Myzostomida are a key example, having been placed as close relatives of flatworms (Eeckhaut et al. 2000), rotifers (Zrzavý et al. 2001) and annelids (Bleidorn et al. 2009) based on different molecular datasets. More recent phylogenomic analyses (Weigert et al. 2014) have confirmed that myzostomids are modified annelids, but their precise phylogenetic position within the phylum remains uncertain.

Nematoda are closely related (sister) to Nematomorpha and are grouped together in the clade Nematoida. All recent phylogenetic studies, using sequence data from a variety of genes and species, place Nematoida and other Cycloneuralia (Scalidophora) together with Panarthropoda (Onychophora, Tardigrada and Arthropoda) in a clade named Ecdysozoa (characterized by a growth strategy involving periodic moulting of an external cuticle). Acoelomorpha are long since removed from the phylum Platyhelminthes which now consists of the paraphyletic “Turbellaria” and the parasitic Neodermata (Egger et al. 2015). The relative position of Platyhelminthes and Rotifera within the Metazoa is less well resolved

(Laumer et al. 2019), but they are usually assigned to Spiralia (Struck et al. 2014; Laumer et al. 2015; Marlétaz et al. 2019). The Spiralia also contain Lophotrochozoa including phyla as diverse as Cycliophora, Entoprocta, Mollusca, Nemertea, Annelida, Brachiopoda, Phoronida and Bryozoa. Most recent studies recover the mostly macrofaunal clade Lophotrochozoa as a sistergroup to a platyhelminth – gastrorich clade (Rouphozoa sensu Struck et al. 2014), both of which are sister to a clade populated by Gnathifera (Ghathostomulida, Micrognathozoa, Syndermata). The assignment of Chaetognatha as sistergroup to, or in a nested position within Gnathifera, is still debated (Laumer et al. 2019; Marlétaz et al. 2019).

Even within these phyla, parasitism may have evolved multiple times independently. Weinstein and Kuris (2016) reviewed incidences of parasitism in light of modern phylogenetics and suggested that parasitism might have evolved as many as 143 times in Arthropoda, 18 times in Nematoda, 13 times in Platyhelminthes, nine times in Annelida, seven times in Rotifera (= Syndermata), six times within Acoelomorpha, but only once in the Nematomorpha. These analyses, clearly suggest that parasitic helminths have evolved convergently. This might not only have resulted in similarities in morphology and ecology, but also in their preservation potential, which is largely restricted to sites of exceptional preservation (Konservation-Lagerstätten sensu Seilacher 1970; see De Baets et al. 2020 for a review).

3 Preservation potential

The fossil record of various groups of helminths, or the phyla they belong to, was recently reviewed by various authors (Poinar 2011, 2014, 2015; Maas 2013; Parry et al. 2014, 2019; De Baets et al. 2015; Klompmaker and Boxshall 2015; Herlyn 2020). To avoid repetition, we therefore focus here on the bearing of these fossils and alternatives for constraining date estimates of the origins and diversification of parasitic helminths.

As many helminths are small and soft-bodied their fossil record is quite patchy and largely restricted to rare finds in conservation traps (e.g., amber) or other sites of exceptional preservation (Littlewood and Donovan 2003; De Baets et al. 2020). Ectoparasitic forms often use attachment organs (suckers, hooks) and during fossilization might be transported away from their host making it hard to recognize their mode of life or association. Endoparasitic forms might not be discovered at all as they reside within their hosts; few have structures that are not likely decomposed along with the soft-tissues of their hosts. When body fossil evidence is found the often few remaining characters can make it difficult to assign them to particular lineages (Schram 1973; Muir et al. 2014). Additionally, due to convergent losses and gains of traits in the diversification of helminths, they can look quite different from their free-living ancestors and/or very similar to other extant clades of helminths (De Baets and Littlewood, 2015).

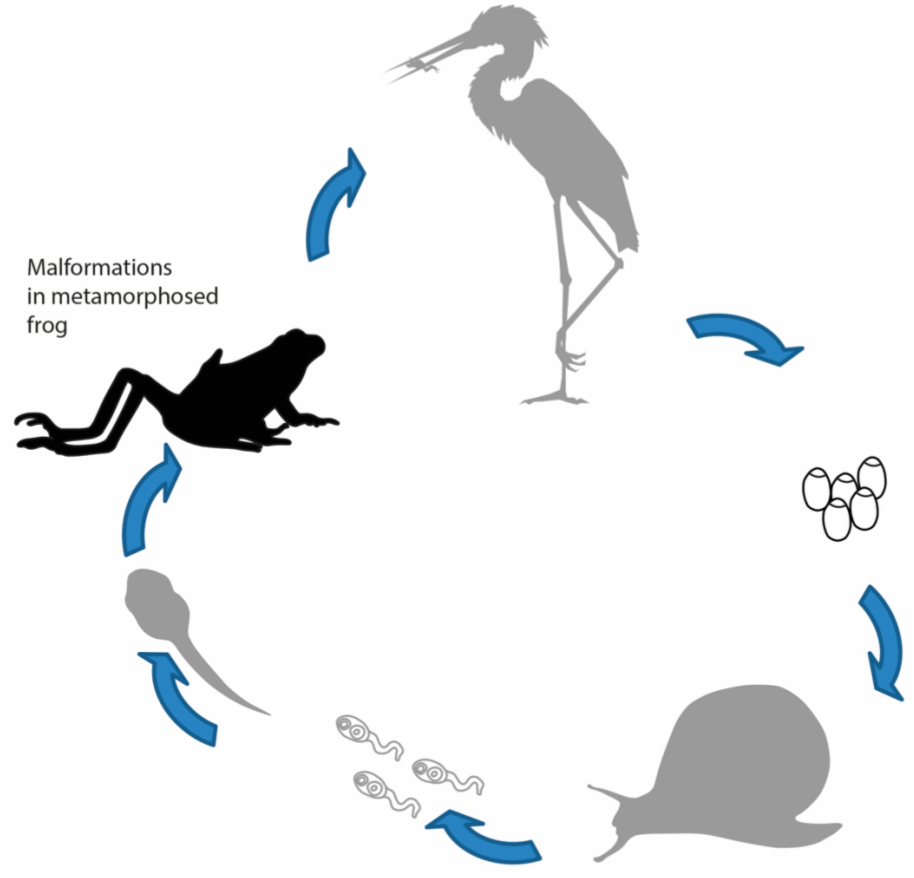

Figure 1. Life-cycle of the trematode *Ribeiroia ondatrae* marking stages which could be preferentially preserved in the fossil record (malformations in metamorphosed frog, eggs in coprolites).

Soft-body imprints or remains have become particularly known from nematodes, likely related to their resilient external cuticle – characteristic amongst both free-living and parasitic forms. Sclerotized or otherwise more resistant structures such as attachment organs, cocoons and eggs (Fig. 1) are considered to have a better preservation potential than body fossils (Littlewood and Donovan 2003). In particular, eggs of particular groups seem to have a high preservation potential – surviving various acid and base treatments (Dufour and Le Bailly 2013; Camacho et al. 2018). In the last decades new and impressive findings of parasite eggs have been particularly found with different techniques in subfossil (dessicated) to fossil (permineralized) coprolites. Coprolites are known to be a *Konservat-Lagerstätte* (Seilacher et al. 2001; Qvarnström et al. 2016), the bacteria content on feces induce early mineralization that allow the preservation of soft tissues in exquisite detail (e.g. muscles, parasite eggs, hair and feathers; Hollocher and Hollocher 2012; Chin in press). As most fossil coprolites are permineralized – they are commonly treated with HCl. Using such approaches nematode eggs have been recovered from material back to the Triassic (Da Silva et al. 2014; Hugot et al. 2014) with evidence of acanthocephalans and trematodes from the Cretaceous (Cardia et al. 2019a; Poinar and Boucot 2006). However, using such an approach might destroy particular remains. Additional, and including older, fossils have been discovered in coprolites using microscopic

(Zangerl and Case 1976) or thin section approaches (Dentzien-Dias et al. 2013, 2018; Francischini et al. 2018; see Fig. 2) – a common approach to study fossil coprolites (Chin 2002). The assignment of coprolites to their hosts is less straightforward than commonly assumed. It is often done based on composition, fossil content (providing clues to environment or diet), morphology and size. However, these methods are not flawless and identification is best achieved when they are still associated with their owner. Even if the coprolite producer can be identified, there is still a need to establish that putative parasitic remains are not simply present in the coprolite because the microorganism (or its host for that matter) is microbophagous (Poinar 2015) or coprophagous (Bajdek et al. 2016).

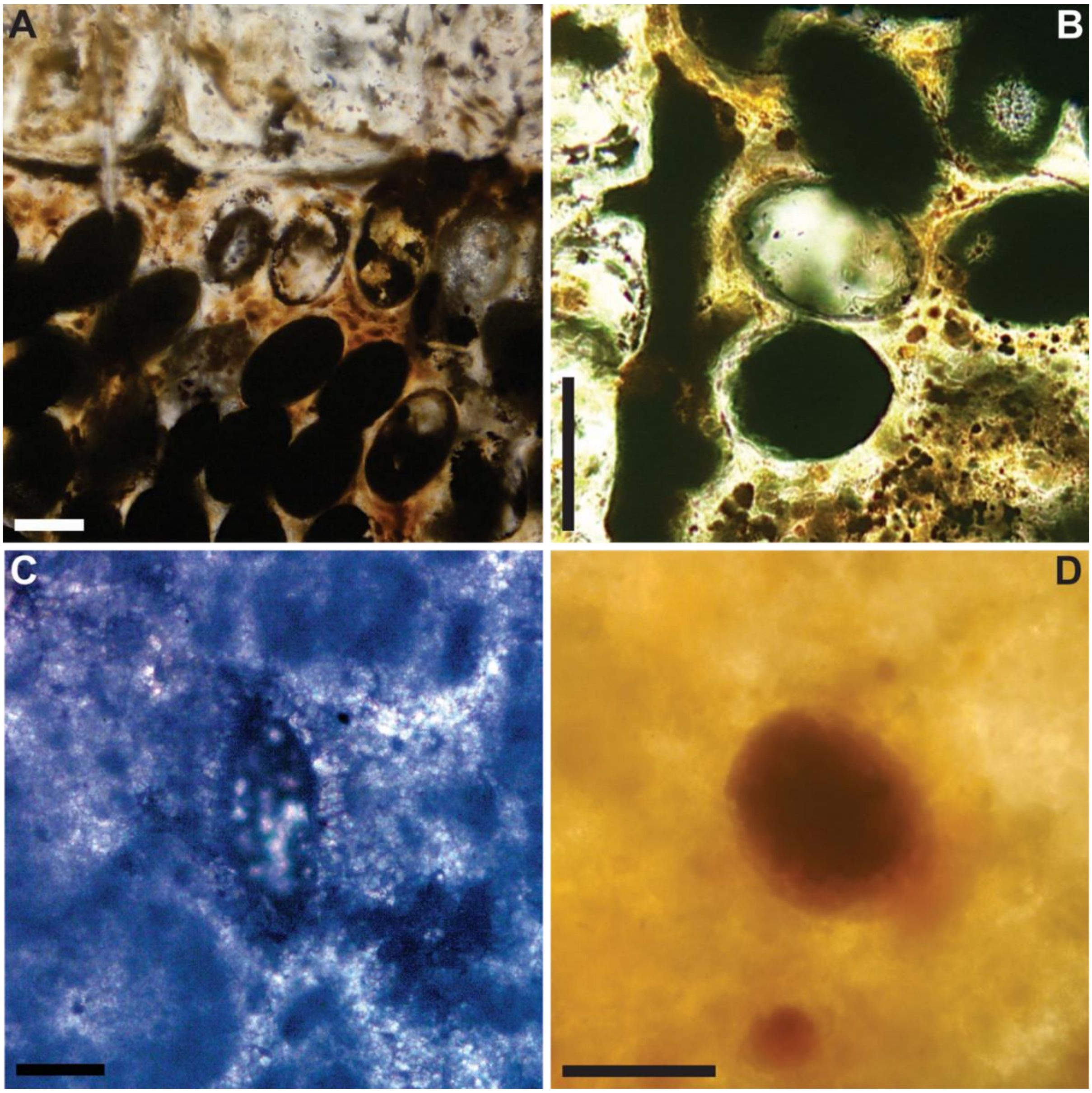

Figure 2. Parasites eggs found inside coprolite thin sections. A and B - Tapeworm eggs from a Permian shark coprolite (Dentzien-Dias et al. 2013); C - pinworm *Paleoxyuris cockburni* egg from a Triassic coprolite (Francischini et al. 2018); D - nematode egg with 65 µm long and 50 µm wide from a Miocene crocodile coprolite (Dentzien-Dias et al. 2018). Scale bars A: 75 µm, B-C:100 µm, D: 50 µm

Sclerotized hooks from helminth attachment organs have also been identified from fossil remains (Upeniece 2001; De Baets et al. 2015). The best evidence for this is a collection of 69 circlets of microscopic hooks – mostly still attached to their acanthodian and placoderm fish hosts in the Devonian Lode Formation (Upeniece 2001). Similar remains from acanthocephalan or cestode hooks have yet to be found, although the presence of their attachment organs have been interpreted to be present in remains of developing larvae within putative parasite eggs (Dentzien-Dias et al. 2013; Cardia et al., 2019a).

Other types of evidence involve characteristic trace fossils and pathologies left in their hosts (Huntley et al. 2020), although they are hard to tie to particular parasite taxa with much phylogenetic precision. In some cases, various phylogenetically distantly related modern or now extinct groups with similar behavior could have led to similar structures. More confidence is gained when characteristic parasitic remains or at least signs of in-situ infestation are associated with these structures. Such evidence is however comparatively rare and in some cases, the host structure might be unsuitable for preservation (e.g., early decay of isopod parasite within decapod pathologies: Klompmaker et al. 2017).

4 Time constraints on the origin of eumetazoan helminths

The fossil record can only provide meaningful hard minimum time constraints on the timing of divergences of a clade. Various authors have used records of near-relatives to place soft maxima on the existence of a certain clade at a certain time. This is typically based “on the understanding that they could have been there but are not based on the existence of facies preserving their near relatives, among which are at least some ecological analogues” (Benton et al., 2015). In the case of Eumetazoa a meaningful maximum constraint would be the maximum age of the Lantian biota (Benton et al., 2015). This together with Doushantuo Formation represent the oldest Konservät-Lagerstätten which have yielded putative eumetazoans in similar preservations which have yielded eumetazoans in younger formations. Consequently, a soft-maximum of 636.1 Ma (Condon et al., 2005) time constraint on the origin of free-living eumetazoan clades may be inferred. As parasitism is a derived condition within the various eumetazoan lineages discussed herein, so the origins of parasitic helminths could only arise after the first appearance of Eumetazoa.

Eumetazoan origins considerably predate putative nematoid remains (Muir et al. 2014), with possible traces from the Ediacaran to Ordovician (Balinski et al. 2013) or borings found in Cambrian-Ordovician trilobites (Babcock 2007) reminiscent of possible nematode borings in foraminifers (Sliter 1971; Hope and Tchesunov 1999). These traces even predate the Ediacaran fossils where *Dickinsonia* has occasionally been superficially compared with the annelid *Spinther* (Wade 1972; Conway Morris 1981) associated as ectoparasites or commensals with modern sponges (Rouse and Pleijel 2003; Rouse 2005). However, *Dickinsonia* shows no annelid characters and is now mostly considered a more early divergent metazoan (Sperling and Vinther 2010; Bobrovskiy et al. 2018) if indeed a metazoan at all (Brasier and Antcliffe 2008). Considering its comparatively large size it is also difficult to consider it parasitic as no larger-sized suitable host has so far been found (De Baets & Littlewood 2015). More importantly, *Dickinsonia* has been found associated with trace fossils attesting to its free-living mode of life (e.g., Sperling and Vinther 2010).

In the following, we discuss possible time constraints on the origin of particular helminths in their phylogenetic and host context (see Fig. 3). We provide details for some possible calibrations, largely following the guidelines by Parham et al. (2012). However, most helminth fossils have not been included in formal phylogenetic analyses. We therefore list the characters which have been used, or could be used, to justify their inclusion within a particular clade.

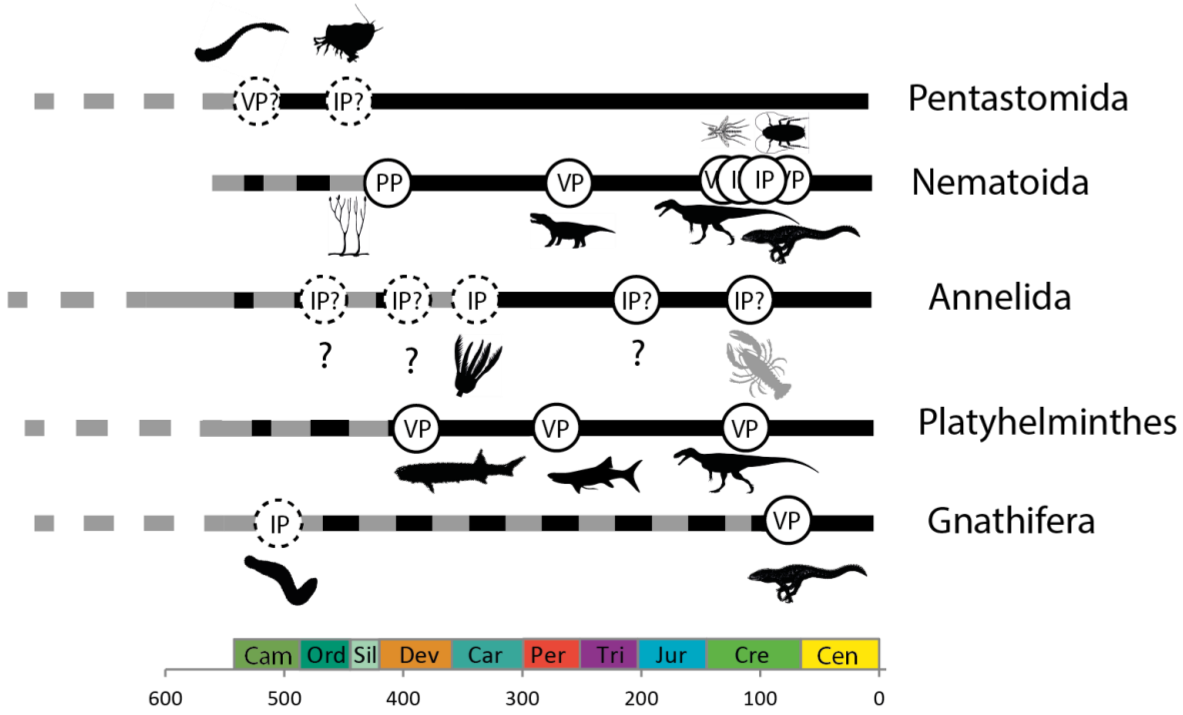

Figure 3. A timeline of clades evolving parasitic worms. The phyla or larger clades to which they belong are listed on the right. See Figure 5 for explanations of abbreviations.

7.4.1 Fossil record of parasitic annelids

The fossil record of Annelida was recently reviewed by Parry et al. (2014, 2019b). The fossil record of free-living annelids can be traced back to the early Cambrian at least (Morris and Peel 2008; Han et al. 2019), but are resolved as members of annelid stem lineage. The earliest fossil jaw elements or scolecodonts taken to represent crown-group annelids probably are as old as the Tremadocian (Hints and Nõlvak 2006), but even older soft-body remains of crown group annelids from the early Cambrian were recently described (Chen et al. 2020).

Node. Total group Annelida

Fossil taxon. *Ipoliknus avitus, Adelochaeta sinensis* and at least two unnamed species

Fossil evidence. 6 carbonaceous compression fossils (Han et al. 2019).

Phylogenetic assignment. Both *Ipoliknus* and *Adelochaeta* possess biramous parapodia with capillary chaetae, constraining them to the annelid total group. *Ipoliknus avitus* is resolved as the deepest lineage in the annelid stem group in analysis only considering extinct taxa (Han et al. 2019) as well as a more comprehensive analysis of most annelid lineages and their close relatives (Parry et al. 2019a).

Min age. 515.5 Ma. The fossils are derived from the early Cambrian Chengjiang Biota from the Maotianshan Shales of southwest China. The maximum age of the Chengjiang Biota has been constrained to 518.03±0.69/0.71 Ma using CA-ID-TIMS U-Pb geochronology, whereas the minimum age is constrained by correlation with the *Antatlasia gutta-pluviae* Zone to an age of 517.0±1.5 Ma (Yang et al. 2018). This minimum age is slightly older than minimum age based on the *Nevadella* trilobite zone for the Sirius Passet Lagerstätte (Harper et al. 2019) which has previously been considered to yield the oldest annelids (Morris and Peel 2008).

Node. Crown group Annelida

Fossil taxon. *Dannychaeta tucolus* Chen et al. 2020

Fossil evidence. 21 carbonaceous compression fossils

Phylogenetic assignment. *Dannychaeta tucolus* shares morphological features with extant Magelonidae, including a flattened prostomium, ventrolateral palps that attach near the mouth opening and a sessile, tubicolous lifestyle (Chen et al. 2020). Phylogenetic analysis recovers this genus as a member of stem group Magelonidae, and it is therefore a member of crown Annelida.

Min age. 514 Ma. The fossils derive from the Hongjingshao Member of the Canglangpu Formation which is Cambrian Stage 3 in age, and younger than the Chengjiang Biota (Zeng et al. 2014; Chen et al. 2020).

Annelid fossils of a similar age to those found in Chengjiang have been found in the early Cambrian Sirius Passet Lagerstätte (Conway Morris and Peel 2008). Two species are currently described from this deposit, namely *Phragmochaeta canicularis* (Conway Morris and Peel 2008) and *Pygocirrus butyricampum* (Vinther et al. 2011). Although annelid fossils are more abundant at this site than Chengjiang the age of Sirius Passet is less tightly constrained. This deposit is constrained to the middle to late Cambrian Stage 3 based on its correlation with the *Nevadella* trilobite Zone (Harper et al. 2019). According to GTS 2016 (Ogg et al. 2016), this would yield a minimum age of 515 Ma but the site may be as old as 518 Ma and so this uncertainty encompasses the age of the Chengjiang Lagerstätten (Yang et al. 2018).

Previously, the annelid crown node has been calibrated based on the age of the oldest scolecodonts (Benton et al. 2015), the jaws of eunicidan polychaetes, which first appear unambiguously in the Tremadocian (Hints and Nõlvak 2006). Eunicida is deeply nested within annelids however (Weigert et al. 2014; Parry et al. 2019a) and so this calibration was always a conservative estimate for the age of the annelid crown group. The above age for the annelid crown node may also be slightly too conservative if the identification of sipunculans from the Chengjiang Biota is correct (Huang et al. 2004) as Sipuncula is recovered as an ingroup annelid taxon in phylogenomic analyses (Weigert et al. 2014). However, no additional sipunculan specimens from the Cambrian have been positively identified (nor are unambiguous sipunculans known from younger deposits) and so the occurrence of this taxon in the Cambrian requires confirmation. *Pygocirrus butyricampum* from Sirius Passet could also conceivably be the oldest crown group annelid, but the phylogenetic position of this taxon is poorly constrained and it is typically resolved in a polytomy with the annelid crown node (Parry et al. 2019a).

All of the fossil annelids known from the Cambrian either have morphological features indicating an epibenthic lifestyle or live in dwelling tubes and so are demonstrably free living and not parasitic. So far, fossil evidence for only four lineages of parasitic annelids has been identified: Branchiobdellida, Myzostomida, Oenonidae and Spionidae. Other groups of annelid parasites have no known fossil record.

Two eunicidan polychaete families that share a prionognath type jaw apparatus are parasitic (Paxton 2009). The family Oenonidae contains species that spend part of their lifecycle as endoparasites of polychaetes, echiurans and bivalves (Hernández-Alcántara and Solís-Weiss 1998). The majority of oenonids parasitize other polychaetes, although some species are thought to be exclusively free-living. This may be a consequence of the parasitic phase of these species not having been recognized however, and all oenonids may in fact share a parasitic lifestyle (Poulin 2001). The Histriobdellidae share a similar jaw architecture and live as commensals on crustaceans, but their close relationship to Oenonidae and other prionognath eunicidans is not universally accepted (Paxton 2009); some authors consider them as close relatives of the Dorvilleidae (Tzetlin 1980). Currently there is no phylogenetic analysis that integrates the diversity of fossil polychaete jaws with extant taxa, although phylogenetic hypotheses of relationships are shown in Paxton (2009) and Parry et al. (2019b).

The prionognath jaw apparatus first appears in the Middle Ordovician (Hints and Eriksson 2007; Paxton 2009), indicating that the oenonid total group had diverged from Lumbrineridae, their sister group (Struck et al. 2015). Jaws that appear more similar to extant oenonids occur in the Silurian (Mierzejewski 1984), with species that are Mesozoic (Jurassic, upper Oxfordian) being assigned to the extant genus *Arabella* (Szaniawski and Gazdzicki 1978), suggesting that the crown group of Oenonidae is at least Oxfordian in age.

Node. Total group Oenonidae

Fossil evidence. Isolated scolecodont finds

Phylogenetic justification. No explicit phylogenetic analysis has been undertaken for polychaete groups known from isolated scolecodonts. Atraktoprionidae fossils have jaw apparatuses that are of the prionognath type, a type of jaw apparatus that is characteristic of oenonids (Paxton 2009).

Host. *unknown*

Min age. 458.4 Ma. The earliest finds of these taxa are reported from the Ordovician of Estonia and surrounding regions. Several finds derive loose glacial erratic boulders which are hard to date as their original provenance and stratigraphic context is not precisely known (Hints 1998). Some finds like *Atraktoprion* sp. A might at least range into the local Uhaku stage (Hints 2000) which would correlate with the top of the Middle Ordovician yielding an age of 458.4 Ma according to GTS 2016 (Ogg et al. 2016).

Node. Crown group Oenonidae

Phylogenetic justification. Mesozoic fossils have been assigned to the extant genus *Arabella* based on the morphology of jaw elements and apparatus architecture (Szaniawski and Gazdzicki 1978)

Host. unknown

Min age. The specimens derive from a borehole and have been attributed to the upper Oxfordian (Szaniawski and Gazdzicki 1978). This would correspond with a minimum age of 157.3 Ma according to GTS 2016 (Ogg et al. 2016).

The body plan of Myzostomida is unique among annelids due to their mode of life, but several traits place them in the Annelida, including the presence of parapodia with chaetae (Lanterbecq et al. 2008). Recent myzostomids are associated with echinoderm hosts – chiefly crinoids and to a lesser degree asteroids and ophiuroids (Summers and Rouse 2014). Myzostomid lifestyles range from forms stealing food from their host´s food grooves (kleptoparasitic) to consuming host tissue directly (true parasites). Most described species live freely on the exterior of their hosts as adults (although starting life on the host within cysts), while some taxa permanently reside in galls (hard), cysts (soft), or within their host's mouth, digestive system, coelom, or gonads (Summers and Rouse 2014). Typically, galls are expected to have good preservation potential in the fossil record (Welch 1976). A variety of galls in fossil echinoderms – particularly in crinoids - have been attributed to myzostomids (Cameron 1969; Warn 1974; Radwańska and Radwański 2005). However, only pathologies observed in Carboniferous and Jurassic crinoid arms (Hess, 2010; Welch, 1976) represent galls which are similar to those produced by extant myzostomids (Jangoux 1987; but see Eeckhaut 1998). So far, no identifiable remains of myzostomids have been identified from such galls which is not surprising as myzostomes have no hard parts other than five pairs of small chitinous hooks (Welch 1976). Other swellings are of uncertain affinity (Ausich and Simms 1999). Eeckhaut (1998) described the first galls induced by myzostomids on extant crinoid stalks, but these look quite different from previous fossils galls on Paleozoic crinoid stems attributed to myzostomids. In some cases, other types of swellings are associated with phosphatic tubes or rings attributed to *Phosphannulus* – an organism of uncertain affinity. The composition, microstructure and morphology of these tubes and rings rules out an affinity with myzostomids (Welch 1976). Additionally, myzostomids build true galls (Summers and Rouse 2014), penetrating from the outside with the host crinoid reacting with the production of a swelling. *Phosphannulus* are found attached to the outside of crinoid stems and may be subsequently overgrown, a feature not found in association with myzostomids. Although their affinities are unclear, some *Phosphannulus* might have at least been facultative parasites as they were seemingly able to tap in the axial canal of the crinoid when attached (Welch 1976).

Node. Myzostomida

Fossil evidence. Figured gall on the arm of crinoid

Host. unidentified crinoid

Min age. 303.4 Ma. The specimen derives from the Seminole Formation of Tulsa County (Okhlahoma). It is attributed to the Missourian (Welch 1976) which is correlated with the Kasimovian – this upper limit of this stage yields a minimum age of 303.4 Ma according to GTS 2016 (Ogg et al. 2016).

Phylogenetic assignment. The galls target the arms and are similar in form and morphology to those caused by extant myzostomids.

Spionid annelids have also been implicated in a variety of pathologies (Cameron 1969) and are usually treated together with parasites by the damage they cause in shellfish and other invertebrates (Martin and Britayev 1998). Spionidae characteristically bore hard substrates, including bivalves shells (Martin and Britayev 1998) and are facultative parasites at best (Huntley 2007). Mud blisters caused by some taxa (e.g., *Polydora*) indicate that they can also affect living bivalves. The oldest confident occurrences of spionid trace fossils derive from the Miocene although candidate trace fossils might be as old as the Silurian (Cameron 1969). Cameron (1967) attributed soft-tissues remains found within a burrow within a bivalve to Spionidae as far back as the Devonian, although the understanding of the preservation of this specimen, and therefore also its phylogenetic affinity, are in need of revision (Blake and Evans 1972; Parry et al. 2014). The bivalve did not show evidence for an *in vivo* response.

Node. Spionidae

Phylogenetic justification. Cameron (1967) interpreted external structures such as a prostomium, anterior tentacle-like palps, peristomial cirri, parapodia, and dorsal cirri of the parapodia. Its habit together with its residence within a bivalve shell would speak for its assignment to the Spionidae. Nevertheless, the worm is not associated with a U-tube or mud blister attributed to be characteristic for *in situ* damage of most of this group (Blake and Evans 1972; Huntley 2007).

Host. Bivalve *Cornellites flabellum*

Min age. The fossil assemblage derives from a small quarry north of Morrisville where the middle part of the Cardiff shale member of the marine Marcellus Formation is exposed (Cameron 1967). This member correlates with the upper part of the Marcellus Formation (Oatna Creek Member) at other localities which are considered to represent the upper part of the *hemisiatus* conodont zone of the Givetian (Brett et al. 2011). The upper boundary of the zone would yield a minimum age of 387.3 Ma according to GTS 2016 (Ogg et al. 2016).

Clitellata can be confidently traced back to the Triassic based on characteristic cocoons (Manum et al. 1991, 1994; Bomfleur et al. 2012, 2015; McLoughlin et al. 2016). The most likely producers of these cocoons are considered true leeches and branchiobdellids (Manum et al. 1991; Bomfleur et al. 2015). Clitellate cocoons sometimes function as conservation traps for other remains including nematodes or ciliates (Bomfleur et al. 2015). In one case, they contain spermatozoa, which suggest branchiobdellids could have produced these coccoons at least since the Eocene and that this group had a significantly different geographic range in the past. This group is usually considered as ectoparasitic of, or at least ectosymbiotic with, crayfish – although they show a variety of relationships ranging from symbiotic, commensal to parasitic (Skelton et al. 2013). More precise evidence is necessary to tie older Triassic cocoons to Branchiobdellids as they could also belong to Hirudinae. True leeches might occur in the Upper Jurassic (Kozur 1970; Shcherbakov et al. 2020), but this specimen is rather considered a carnivorous then a parasitic species.

Node. *Total group Hirudinae*

Phylogenetic justification. Characteristic cocoons are only produced by true leeches (Euhirudinae) and branchiobdellids. They may also provide the oldest evidence for clitellata as a whole (Parry et al. 2014), but a putative oligochaete has recently been described from the Lower Triassic (Shcherbakov et al. 2020).

Min age. 201.4 Ma. The earliest finds are attributed to the Rhaetian (Bomfleur, Mörs, Ferraguti, Reguero Marcelo, et al., 2015; Manum et al., 1991), which would yield a minimum age for this group of 201.4 Ma according to GTS 2016 (Ogg et al., 2016).

Node. Total group Branchiobdellida

Host. Unknown, but modern representatives are mostly leech-like ectoparasites of crayfish (Govedich et al. 2010).

Phylogenetic justification. Annelid sperm described from inclusions in cocoons from the Eocene of Antarctica possess characteristic elongate acrosomes and helical marginal fibres of branchiobdellidan spermatozoans (Bomfleur et al. 2015).

Min age. 47.8 Ma. The Cucullaea I Allomember of the La Meseta Formation has been considered Ypresian (Montes et al. 2013), early Eocene, based on Strontium isotopes stratigraphy (Ivany et al. 2008) as well as mammal biostratigraphy (Reguero et al. 2013). The age of the Ypresian-Lutetian boundary tabulated in GTS 2016 (Ogg et al., 2016) can therefore be used as a conservative minimum constraint.

7.4.2 Fossil record of parasitic pentastomids

Pentastomids, or tongue worms, have traditionally been considered to be a separate phylum, but they are now considered crustaceans (Klompmaker and Boxshall 2015) – most likely the sister group of Branchiura (Oakley et al., 2012; Regier et al., 2010; Sanders & Lee, 2010; but see Haug et al. 2020). So far no crown-group Branchiura have been reported from the fossil record. Dzik (2008) assigned the enigmatic Cyclida (Carboniferous – Triassic) to Branchiura, but these are free-living (Schram et al. 1997) and their affinities with modern Branchiura is unlikely (Haug et al. 2020).

The fossil record of Pentastomida has been reviewed by various authors (Castellani et al. 2011; Klompmaker and Boxshall 2015). Various isolated fossils from the Cambrian-Ordovician have been identified as pentastomids (Walossek and Müller 1994; Walossek et al. 1994; Waloszek et al. 2005; Castellani et al. 2011), and due to their morphology these early forms have been interpreted as being parasitic. They represent the oldest direct evidence for ectoparasitic "worms" in the fossil record. Their hosts are still debated (De Baets et al. 2015). Most authors suspect they were parasitizing early vertebrates (Walossek and Müller 1994; Sanders and Lee 2010), but no direct associations are known. Their hosts must have been different from current hosts as present day lineages were not around at the time of the early fossil pentastomids (De Baets et al. 2015). A recent discovery interpreted as a pentastomid (but see Haug et al. 2020) makes interpretations of early life histories even more problematic as these fossils are interpreted as larval and attached to ostracods - a host relationship so far not observed in present day associations (Siveter et al. 2015).

Node. Total Group Ichthyostraca

Fossil Taxon. *Boeckelericambria pelturae* Walossek and Müller 1994

Fossil evidence. Isolated phosphatic remains of larvae in calcareous nodules

Phylogenetic justification. The diagnostic synapomorphy of a head of *Boeckelericambria pelturae* with two pairs of grasping hooks (Walossek and Müller 1994) as well as a cladistic analysis (Almeida and Christoffersen 1999) place this species as a stem-group pentastomid. If we accept pentastomida to be the sister group of Branchiura, *B. penturae* must therefore also constrain the first appearance of Ichthyostraca (Wolfe et al. 2016; but see Haug et al. 2020).

Host. Unknown – possibly a conodont or other early vertebrates (based on circumstantial evidence).

Hard minimum. 497 Ma. The Orsten fossils derive from the *Agnostus pisiformis* zone in the Cambrian Alum Shale, which is now considered to represent the upper boundary of the Cambrian series 3 (Nielsen et al. 2014). The minimum age of the uppermost stage of the Cambrian 3 series therefore yields 497 Ma according to GTS 2016 (Ogg et al. 2016).

7.4.3 Fossil record of parasitic platyhelminths

Transitions from free-living to parasitism amongst the Platyhelminthes may have evolved at least 9 times (Weinstein and Kuris 2016), but only the divergence of the Neodermata can be reasonably constrained by fossil evidence (De Baets et al. 2015). Neodermata are a monophyletic group comprising exclusively obligate parasites (Fig. 4). Present day associations include the use of vertebrates as definitive hosts. The internal phylogeny is still debated, but most authors consider ectoparasitic monogeneans as the earliest diverging lineage while cestode and trematodes are considered sister groups in most molecular analyses (Lockyer et al. 2003; Park et al. 2007; Egger et al. 2015). The oldest fossils of Neodermata include circlets of hooks found on early jawed fishes (Upeniece 2001, 2011; De Baets et al. 2015). Their appearance, particularly the arrangement of hooks and association with putative sucker discs, are consistent with their identification as monogeneans (De Baets et al. 2015; Leung 2017). Their location near gills and abdominal near fin spines, would also be consistent with an ectoparasitic mode of life. The larger size of hooks when compared to extant taxa is consistent with a trend towards smaller size within monogeneans over time (Poulin, 2005).

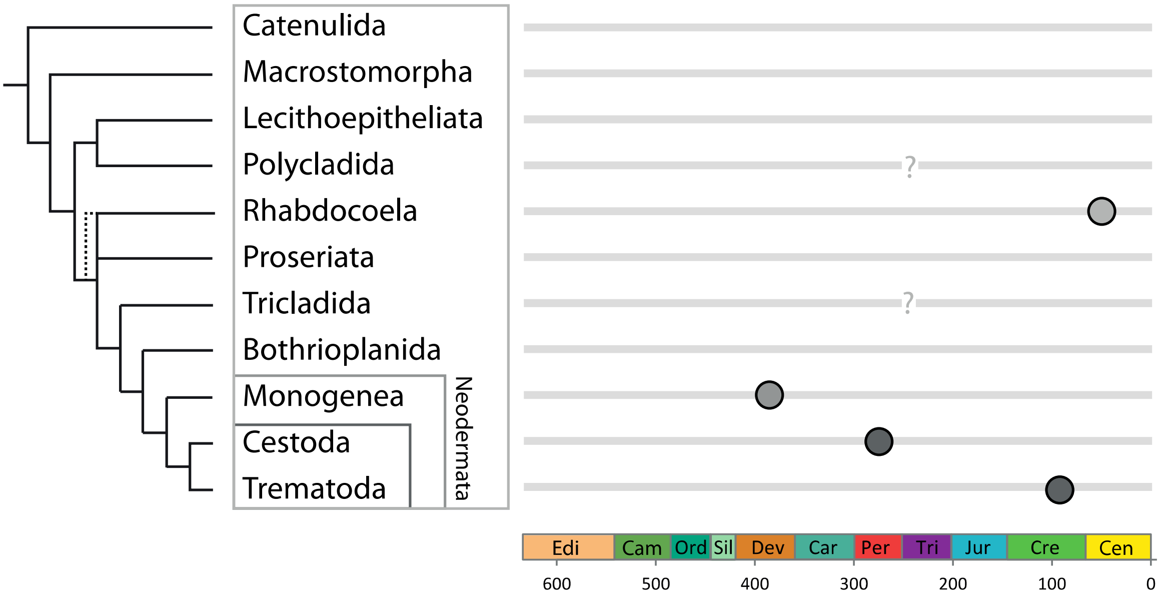

Figure 4. Flatworm body fossils plotted against phylogenetic structure of Platyhelminthes (Egger et al. 2015). Flatworm fossil assignment follow De Baets et al. (2015) unless otherwise discussed.

Node. Neodermata

Fossil evidence. Over 69 circlets of hooks, at least 29 still associated with their fish hosts in position suggestive of ectoparasitism (Upeniece 2001, 2011)

Phylogenetic justification. No formal phylogenetic analysis on the attachment organs was performed. However, the circular arrangement of the bilateral symmetric hooks, traces of cuticular disc as well the maximum number of 16 hooks strongly suggests their assignment as monogenean platyhelminths (Upeniece 2011; De Baets et al. 2015; Leung 2017).

Host. mostly attached to the acanthodian *Lodeacanthus gajicus* (24) and some (5) also associated with juveniles of the placoderm *Asterolepis ornata* (Upeniece 2001, 2011).

Minimum age. 382.7 Ma. The formation containing the finds was initially assigned to the Early Frasnian (Upeniece 2001), but currently the Lode Formation is assigned to the Upper Givetian (Lukševičs et al. 2012, 2014). This corresponds with 382.7 Ma corresponding to the minimum age assigned to the Givetian-Frasnian boundary according to GTS 2016 (Ogg et al., 2016).

Most phylogenetic analyses resolve a sister relationship between Trematoda and Cestoda (Lockyer et al. 2003; Park et al. 2007; Egger et al. 2015), both groups with complex life cycles, although some rare phylogenomic analyses suggest otherwise (Laumer et al. 2014, 2015). Cestodes can be confidently traced back to the Permian (Dentzien-Dias et al. 2013) with fossil remains yielding cestode-like eggs based on morphology and size, the presence of a developing larva with familiar cestode-like hooks and the arrangement of eggs in proglottids. Older finds of eggs within shark coprolites have been attributed to cestodes (Zangerl and Case 1976), but this identification is less convincing and in need of reinvestigation (De Baets et al. 2015). Either way, these finds represent the oldest convincing evidence for endoparasitic helminths in the fossil record (but see Upeniece 2011 for putative earlier finds) and also overlap with divergence time estimates for trypanorhynch tapeworms (Olson et al. 2010).

Node. Eucestoda

Fossil evidence. Eggs in Permian coprolites (Dentzien-Dias et al. 2013)

Phylogenetic justification. No formal phylogenetic analysis was performed. However, the size and morphology of the eggs (ovoid, smooth shelled, with operculum, among others), their interpretation of hooks within one of them as well as their association in protoglottidia (Dentzien-Dias et al. 2013) speak for the assignment to Eucestoda.

Host. Shark based on spiral coprolite morphology (reflecting the spiral valve morphology of the shark intestine).

Minimum age. 259.8 Ma. The coprolite containing the fossil evidence derives from the upper member of the Rio do Rasto Formation. The vertebrate fauna suggests a Guadalupian (Late Wordian – Capitanian) age (Cisneros et al. 2012; Dentzien-Dias et al. 2012; Dias-Da-Silva 2012) which yields a minimum age of 259.8 Ma defined by the Guadalupian-Lopingian boundary (Ogg et al., 2016).

Although eggs of some lineages of Trematoda such as Dicrocoeliidae (Dufour & Le Bailly, 2013) are considered quite resistant – trematodes have so far only been found in a Cretaceous coprolite (Poinar and Boucot 2006) and Middle Pleistocene to younger coprolites (Jouy-Avantin et al. 1999). Most evidence in the fossil record derives from characteristic pathologies these helminths cause in their hosts (De Baets et al. 2015; Huntley and De Baets 2015). Research has focused particularly on characteristic pits and igloo-shaped concretions caused today by gymnophallid trematodes in their bivalve hosts (Ruiz and Lindberg 1989; Ituarte et al. 2001, 2005; Huntley and De Baets 2015). These structures allow tracing back the origin of trematodes to the Eocene (Todd and Harper 2011) and the Cretaceous (Rogers et al. 2018), respectively. However, other trematodes or even distantly related taxa could potentially cause similar pathologies. Superficially similar igloo-shaped pathologies in bivalves (Liljedahl 1985) have been observed as far back as the Silurian. The only fossil vertebrate pathology attributed to a trematode was found in Burmese amber (Poinar et al. 2017). Remains of a lizard trapped in resin contained a cyst which could be convincingly compared to similar metacercarian cysts found in extant lizards. Due to the sister-group relationship between

Cestoda and Trematoda, the first appearance of trematodes can be at least constrained to the Permian. If cestodes and monogeneans would be sister taxa, as in some morphological (Brooks, 1989) and less commonly molecular analyses (Laumer et al. 2015), trematodes and cestodes could be constrained to the Devonian as inferred from the first appearance of monogeneans in the fossil record.

The ancient record of parasitic flatworms is quite remarkable since the body fossil record of confidently identifiable free-living flatworms (the paraphyletic 'Turbellaria') start considerably later. Trace fossils associated with soft-body impressions of Permian-to-Triassic age have been attributed to polyclad and triclad flatworms (Knaust 2010). Earlier Ordovician trace fossils associated with worm could potentially be attributable to free-living 'Turbellaria', but this assignment awaits further scrutiny (Knaust and Desrochers 2019). The oldest confidently identified body fossil of a free-living flatworm is that of a rhabdocoel flatworm from Baltic amber (Poinar 2003a). Rhabdocoela separated even earlier from the lineage leading to the obligate parasitic flatworms (Neodermata) than triclad flatworms (Egger et al. 2015). This establishes the record of more derived Neodermata to be seemingly more ancient and relatively more common than that of their free-living relatives.

Acoelomorpha are now assigned to their own clade (Xenacoelomorpha) together with Xenoturbellida and no longer considered platyhelminths (Philippe et al. 2011; Ruiz-Trilloand Paps 2016). Xenacoelomorpha are now considered simplified relatives of the Ambulacraria (Philippe et al. 2019). To our knowledge, there is no fossil record of parasitic acoelomorphs. Some drop-shaped structure in X-ray analyses of the Early Hunsrück Slate, considered of early Emsian age (De Baets et al. 2013), have been interpreted as acoelomorph remains (Fauchald et al. 1988) – but this interpretation (Knaust and Desrochers 2019) and several other of Stürmer's interpretations based on such X-ray analyses have been proven to be erroneous (as reviewed in Otto 1999, 2000). Based on trace fossils associated with body fossil remains – acoelomorphs have potentially been traced back the Late Ordovician (Knaust and Desrochers 2019), although these comparisons are hard to verify and await further scrutiny.

7.4.4 Fossil record of parasitic nematodes

Molecular phylogenetic analyses have shown that parasitism of plants and animals has arisen at least 15 times independently in nematodes (Blaxter and Koutsovoulos 2015). The sampling coverage of enigmatic nematode lineages is slowly improving (Leduc and Zhao 2019; Leduc et al. 2018), but as long as not all extant families have been molecularly sampled, the independent origins of parasitism might be more numerous (Sudhaus 2008, 2010; Weinstein and Kuris 2016). The fossil record can so far not constrain all of these transitions, but it can place multiple constraints on the origin of parasitism throughout the nematode tree. The fossil record of parasitic nematodes has recently been reviewed by Poinar (2015), who also reviewed the fossil record of nematodes in general with a focus on amber deposits (Poinar 2011, 2014). In the meantime, various new discoveries of parasitic nematodes have been made in Triassic to Cretaceous coprolites (Da Silva et al. 2014; Hugot et al. 2014; Cardia et al. 2018; Francischini et al. 2018) and in Miocene coprolites (Dentzien-Dias et al. 2018).

We herein map fossil finds in the phylogeny (Fig. 5) to demonstrate that several constraints on nematode evolution may be derived from the fossil record.

Based on trace fossils suggestive of free-living nematodes, and therefore also their sister-group Nematomorpha, Nematoda must have been around at least since the Late Ordovician (Knaust and Desrochers 2019). Older sinusoidal trace fossils have been reported from the Early Ordovician (Balinski et al. 2013) and even the Cambrian-Ediacaran (Parry et al. 2017). Such sinusoidal trace fossils are caused by the specific movement of vermiform animals (possibly nematodes) in waves as their body wall comprises only longitudinal muscles but no ring muscles - an apomorphy for Nematoida (Maas 2013). Confident assignment to Nematoda remains difficult however, as distantly related forms with similar behavior could potentially also have created such burrows (Metz 1987; Collins et al. 2000; Seilacher 2007). One can be more confident when such traces are associated with worm-like body fossil remains (Knaust 2010; Knaust and Desrochers 2019), but even then it is quite difficult to identify the particular lineages of nematodes that created these traces. Many nematodes lack rich distinguishing external features, which makes them even more difficult to identify in a fossil state, particularly when poorly preserved (Schram 1973; Muir et al. 2014). This is ably illustrated by putative carboniferous nematode remains (Størmer 1963) that have now been re-identified as scorpion spines (Poinar 2011). Well-preserved compression or impression fossils have been attributed to free-living nematodes since the Carboniferous. Schram (1973, 1979) described various specimens of a putative nematode *Nevamermis mackeei*, considering it to be the remains of a free-living form with affinities to modern species of Chromadorida which have comparable cuticular ornamentation and structures possibly identifiable as papillae or cirri (an opinion shared by Poinar 2011). However, these characters are plesiomorphic for Nematoda and are not necessarily helpful for their taxonomic assignment (Maas 2013). According to Poinar (2014), no other fossil nematodes could so far be attributed to Chromadorida.

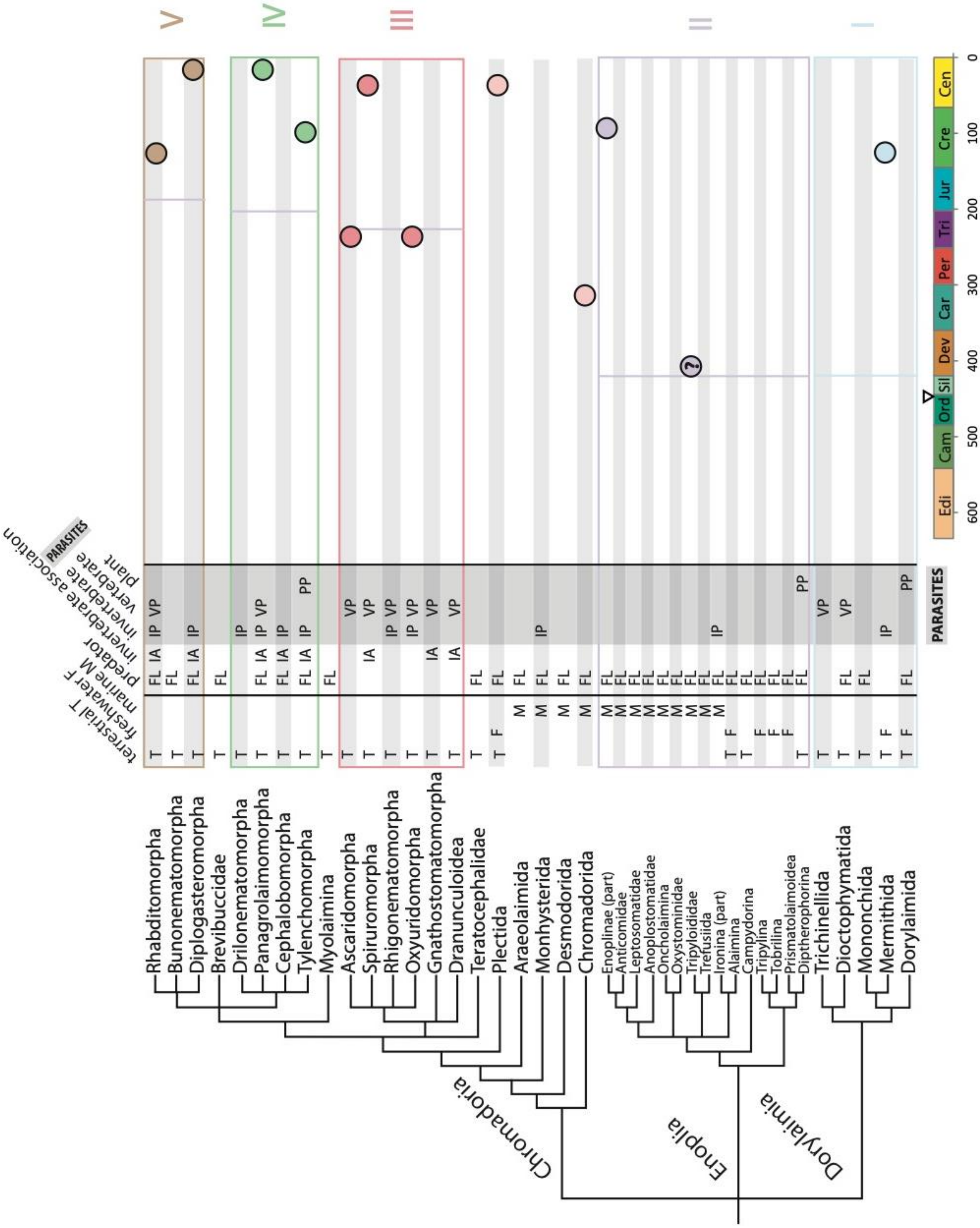

Figure 5. Nematode fossils plotted against phylogenetic structure of Nematoda based on nuclear small subunit ribosomal RNA analyses and interpretation of taxon relationships derived from morphology and origins of particular types of parasitism (Blaxter and Koutsovoulos 2015). Nematode fossil – assignments follow Poinar (2011, 2014, 2015) unless otherwise discussed.

Node. Nematoida

Fossil evidence. Trace fossils associated with worm-like fossils (Knaust and Desrochers 2019)

Phylogenetic justification. The sinusoidal trace associated with worm-like body fossils suggest a nematode or at least a nematoid caused these traces

Minimum age. The rocks of the Vaureal Formation have been assigned to the Late Katian (Knaust and Desrochers 2019), which yield a minimum age of 445.2 Ma according to GTS 2016 (Ogg et al. 2016).

Additional free-living nematode remains include the Jurassic *Eophasma jurasicum* (Arduini et al. 1983), the Early Cretaceous *Captivonema cretacea* (Manum et al. 1994) and the Late Cretaceous *Palaeoenoploides alessandrellianus* (Mattavelli and Bracchi 2008). These have been assigned to their own families (Eophasmidae, Captivonematidae, Palaeoenoploididae) which in turn have been attributed to modern orders (Desmoscolecida, Plectida and Enoplida, respectively; Poinar 2011). However, their assignment to modern lineages (Poinar 2011) is based on limited and possibly plesiomorphic traits (e.g., small size, finely annulated cuticle and dense coating of prominent irregularly distributed setae in *Captivonema*; coarsely annulated cuticle in *Eophasma*). The second oldest fossil attributed to the order Plectida is *Oligoplectus succini* derived from Baltic amber (Poinar 2014).

The oldest confidently identified nematode body fossils derives from the Early Devonian (Poinar et al. 2008; Maas 2013). These specimens are associated with the early land plant, *Aglaophyton major* (Poinar et al. 2008), and are considered the earliest evidence for plant parasitic/pathogenic nematodes (Poinar 2011, 2015). The fossils placed in their own family (Paleonematidae) have also been assigned tentatively to Enoplida (Poinar 2011).

Node. Crown-group Nematoda

Fossil Taxon. *Palaeonema phyticum* Poinar et al. 2008

Fossil Evidence. Up to 500 nematodes and eggs from substomatal chambers and intercellular spaces of early land plants (Poinar et al. 2008)

Host. *Aglaophyton major*

Phylogenetic justification. The body fossils are well-preserved revealing fine morphological details such as buccal cavity, surface ornamentation, pharynx, ovaries, tail and various other features (Poinar et al. 2008) which allows them to be placed unequivocally within Nematoda (Maas 2013). They were assigned to their own family based on the presence of transverse cuticular striations and structure of pharynx and buccal cavity, but could be assigned tentatively to Enoplia due to inconspicuous lips, a buccal cavity divided in two sections, presence of teeth (two visible, probably three) in the buccal cavity, didelphic and reflexed ovaries, spiral amphidial apertures and a cylindrical pharynx it shares with members of Tripyloididae (Poinar et al. 2008).

Minimum age. 407.6 Ma. The relationship of the radiometric dating of the Milton of Noth Andesite (Parry et al. 2011) with the Rhynie chert is still disputed (Mark et al. 2013; Parry et al. 2013). Therefore, it is more conservative to use the age of the Pragian-Emsian boundary (407.6 Ma according to GTS 2016: Ogg et al. 2016) based on the constraints of spore assemblages of Windyfield and stratigraphically underlying Rhynie chert (Parry et al. 2011).

Cretaceous Burmese amber provides the first evidence for mycetophagous nematodes in the form of fungal-feeding *Cretaciaphelenchoides burmensis* which Poinar (2011) assigned to the Aphelenchoididae; this is also considered the oldest evidence for the order Tylenchomorpha in the fossil record (Poinar 2015).

Node. Tylenchomorpha

Fossil Taxon. *Cretaciaphelenchoides burmensis* Poinar 2011

Fossil evidence. Worm body associated with host in Burmese amber

Host. Crane fly (*Gonomyia*)

Phylogenetic justification. Poinar (2011) assigned it to Thelasmotidae based on its morphology, dimensions and host association. He suspects it is closely related to *Cephalobellus*.

Minimum age. Biostratigraphic evidence suggest a late Albian to early Cenomanian age for Burmese amber. Recently, dated zircons suggest a minimum age of 98.17 Ma (Shi et al. 2012).

The oldest record for nematodes exploiting other animals can be traced back to the Mesozoic with evidence of eggs found in a herbivore coprolite from the Triassic (Da Silva et al. 2014). The coprolite is usually assigned to a cynodont (Hugot et al., 2014) – although identifying its owner is not straightforward (Francischini et al. 2018). This coprolite contains eggs attributed to Ascarididae (Ascaridoidea, Ascarida) (Da Silva et al. 2014) and overlap in time with the molecular clock divergence time estimates of Ascaridoidea (Li et al. 2018) based on the host fossil records. This suggests, in some cases at least, the fossil record may have value in constraining the initial radiation of terrestrial parasites.

Eggs attributed to Ascaridomorpha are also known from a Lower Cretaceous coprolite (*Ascarites gerus*, *A. priscus*) attributed to a theropod dinosaur from Belgium (Poinar and Boucot 2006) and Upper Cretaceous coprolites (*Bauruascaris adamantinensis*, *B. cretacicus*) attributed to Crocodyliformes from Brazil (Cardia et al. 2018, 2019b). Younger eggs from the Upper Cretaceous Adamantina Formation (Campanian-Maastrichtian) were attributed to Heterocheilidae (Cardia et al. 2019b) – their minimum age (Castro et al. 2018) falls just outside the divergence times estimated by Li et al. (2018) for the crown-group of this lineage.

Node. Ascaridomorpha

Fossil Taxon. *Ascarites rufferi* Da Silva et al. 2014

Host. Inferred to be a cynodont based on circumstantial evidence

Fossil Evidence. Egg derived from an Upper Triassic Coprolite.

Phylogenetic Justification. No formal phylogenetic analysis was performed but possession of a round, mammillated surface suggests the assignment of eggs to Ascaridae (Da Silva et al. 2014).

Minimum age. 236 Ma. Coprolites from the formation which is assignable to the Dinodontosaurus Assemblage Zone (Da Silva et al. 2014). This is can be assigned a minimum age with age derived from zircons from the overlying formation and consistent with the correlation of this Formation with the Chañares Formation (Francischini et al. 2018).

These Triassic coprolites attributed to cynodonts also contained eggs assigned to Oxyuridomorpha (Hugot et al. 2014) which represent the oldest eggs assigned to Ascaridae.

Node. Oxyuridomorpha

Fossil Taxon. *Paleoxyuris cockburni* Hugot et al. 2014

Fossil Evidence. Egg from in Triassic coprolites

Host. Cynodont? (see Ascaridomorpha)

Phylogenetic Justification. The size, shape and presence of a polar cap speak for the assignment of fossil eggs to the family Heteroxynematidae (Hugot et al. 2014)

Minimum age. 236 Ma. See Ascaridomorpha.

Based on modern host associations and fossil record, oxyurids might have parasitized invertebrates before vertebrates (Poinar 2015). The oldest direct evidence for oxyurids parasitizing invertebrates, however, is *Paleothelastoma tipulae* found associated with the crane fly *Gonomyia* found in Burmese Amber (Poinar 2011). This species was compared with Thelastomatidae parasitizing modern crane flies.

Various other lineages of parasitic nematodes or at least containing parasitic representatives (Mermithidae, Heterorhabtidae, Cosmocercidae, Allantonematidae) are now known from Cretaceous to Cenozoic amber (Poinar 2015); in various cases these are still associated with their arthropod hosts (Poinar 2011). This does not necessarily mean parasitism of invertebrates started later, but probably rather reflects a preservation and/or collection bias associated with later deposits.

Mermithidae have been reported from various amber deposits (Poinar 2011). The oldest fossils which have been assigned to this group (Poinar et al. 1994) derive from Lebanese amber now attributed to the Barremian (Maksoud et al. 2017). Mermithids are reminiscent in size and shape to nematomorphs, but have a smooth outer cuticle as opposed to prominences observed in the cuticle of nematomorphs (Poinar and Buckley 2006).

Node. Mermithida

Fossil Taxon. *Cretacimermis libani* Poinar et al. 1994

Phylogenetic justification. The characteristic of the final molt occurring in the host, the absence of cross fibers in the cuticle, the lack of a tail projection on the postparasitic cuticle as well as the host family speak for their similarity to the extant *Heleidomermis* and their assignment to Mermithidae (Poinar et al. 1994). The specimen was interpreted to be moulting in post-parasitic late ontogenetic stage which is rare, but also observed in some extant mermithidae parasitizing chironomid and biting midges (Poinar 2011).

Fossil Evidence. Body fossil coiled in abdominal cavity of host in Lebanese Amber.

Host. Midge (Chironimidae)

Minimum age. 126.3 Ma. The age of the Lebanese amber has been pushed back to the Barremian (e.g., Maksoud et al. 2017). These authors argued that amber from middle to late Barremian was reworked from older Early Barremian strata. We conservatively use the age of the Barremian – Aptian boundary as the minimum age until the reworking hypothesis is more generally accepted and it is better established that all amber with inclusions can be confidently attributed to the early Barremian.

The earliest evidence for parasitic Rhabditida or Rhabditomorpha (Heterorhabditidae) are the Cretaceous *Proheterorhabdites burmanicu*s parasitizing a rove beetle found in Burmese Amber (Poinar 2011). Free-living forms (*Vetus libani*) initially unattributed on the family level, first attributed to the same family (Poinar 2011) but later attributed to a closely related family Rhabditidae prove the earliest evidence for the order Rhabditida (Poinar 2014). The latter are slightly older as they can be traced back to the Barremian as they were reported from Lebanese amber.

Node. Heterorhabditidae

Taxon. *Proheterorhabdites burmanicu*s Poinar 2011

Host. Rove beetle (Staphylinidae)

Phylogenetic justification. Their size, ensheathing cuticle with longitudinal striations and small terminal tooth align these fossils interpreted as third-stage juvenile with heterorhabditids (Poinar 2011). The presence of bacterial cells in the body cavity similar in size to that of modern representatives also strengthens this interpretation (Poinar 2015).

Minimum age. 98.17 Ma. See Tylenchomorpha for justification.

Juveniles of the parasitic *Palaeocosmocerca burmanicum* adjacent to a snail in Burmese amber are considered the oldest fossil evidence of family Cosmoceridae (Poinar 2011)

Node. Cosmocercidae

Taxon. *Palaeocosmocerca burmanicum* Poinar 2011

Fossil Evidence. Worm bodies associated with putative host in Burmese Amber

Host. Unidentified snail

Phylogenetic Justification. The morphological characteristics of the second-stage juveniles (offset lips, flat head, constricted anterior portion of the pharynx) and dimensions of pre-infective stages are similar to extant Cosmocercidae – particularly *Cosmocercoides dukae* (Poinar 2011)

Minimum age. 98.17 Ma. See Tylenchomorpha for justification

Howardula helenoschini from Baltic amber, considered to belong to Allantonematidae (Poinar 2003b), provides the oldest evidence for the presence of animal parasitism in Tylenchomorpha (Poinar 2011, 2015). Other evidence for the presence of this order in the fossil record is *Paleoiotonchium dominicanum* parasitizing a fungus gnat in Dominican amber and a population of *Oligaphelenchoides atrebora* from Mexican amber (Poinar 2011). The former might represent the oldest fossil evidence for the presence of separate life cycles between fungal gnats and fungi in Iotonchidae (Poinar 2011). The latter consist of eggs, juvenile and adults, together with fungal hyphae, providing further evidence for mycophagy in the family Aphelenchoididae (Poinar 2015).

Direct evidence for filariid nematodes goes back to Baltic amber and Dominican amber (Poinar 2015). Their size, shape and ornamentation speak for their identification as filariid nematodes. Horizontal transfers of retroposons suggest that at some time filariids were likely parasitizing tropical birds rather than mammals, thus constraining them to a time interval which at least partially overlaps with the age estimates of Dominican amber (Suh et al. 2016; Suh 2020). In addition to filarial remains, also tropical bird remains (Poinar et al. 2007) have been reported from Dominican amber, suggesting they at least were present at the same time in the same region.

Node. Filarioidea

Fossil Taxon. *Cascofilaria baltica* Poinar 2011

Fossil evidence. Microfilaria associated with its female blackfly intermediate host (see Poinar 2012)

Host. Female blackfly (Simuliidae)

Phylogenetic Justification. Their dimension, morphology and number speak for its identification as filarial nematodes. Due to its body size and morphology with rounded heads and pointed tails, they have been compared with modern *Onchocerca* and *Spendidofilaria* infecting modern mammals and birds, respectively (Poinar 2011)

Minimum age. 34.7 Ma. The age of Baltic amber is still debated. The age of the richest amber-bearing deposits deriving from the Prussian Formation have been attributed to the Late Eocene microfaunistically (Kaplan et al. 1977). However, Ritzkowski (1997) inferred a middle Eocene for the lower layer of the Prussian Formation based on glauconitic dating of its host sediment. However, this reassignment is not generally accepted (Perkovsky et al. 2007). We hereby conservatively use the 34.7 Ma based on Kaplan et al. (1977) which is younger than the minimum age estimate of 43.1 Ma by Ritzkowski (1997).

A summary of this exercise (see Fig. 5) illustrates that constraints are available for parasitic lineages or at least free-living relatives assigned to all major nematode clades (I-IV) proposed by Blaxter et al. (1998). Clade II can possible be traced back to the Early Devonian, Clade III to the Upper Triassic, Clades I, IV and V at least to the Cretaceous. Pending reinvestigations and new discoveries, fossil evidence for additional orders can potentially be traced back to the Mesozoic or even Paleozoic.

7.4.5 Fossil record of nematomorphs

Adult nematomorphs are free-living in marine or freshwater, while larvae are parasitic on terrestrial or marine arthropods (Hanelt et al. 2005). The oldest confidently identified crown-group hairworm derives from Cretaceous amber (Poinar and Buckley 2006), which is considerably later than the inferred origin based on the fossil record of their sister-group Nematoda. The host of the oldest specimen is unknown, but other finds have been found associated with cockroaches (Poinar 1999). Younger finds derive from Eocene brown coal deposits (Voigt 1938) and Dominican amber (Poinar 1999) which is now usually dated to the Miocene (Iturralde-Vinent and MacPhee 1996; Iturralde-Vinent 2001). All forms so far reported have been attributed to the Gordoidea – parasites of terrestrial arthropods. They are reminiscent of mermithid nematodes, which have, however, a smooth outer cuticular layer. No fossil forms have so far been attributed to the nectonematids, a group which exclusively parasitizes marine invertebrates.

The placement of exclusively parasitic Nematomorpha as sister to Nematoda in molecular analyses raises the interesting question whether the common ancestor of nematodes and nematomorph was also parasitic. However, it is clear that although parasitism arose multiple times in nematodes, the earliest divergent lineages are free-living and lineages parasitizing arthropods similar to nematomorphs like mermithidae are derived (Blaxter and Koutsovoulos 2015). This suggests stem-nematomorphs were likely free-living and may look quite different from crown-group nematomorphs.

The diversity of Cycloneuralia in the Cambrian fossil record might suggest an even earlier origin (Maas 2013). Some free-living forms of Palaeoscolecidae even closely resemble some Nematomorpha (Xianguang and Bergström 1994), but they are usually interpreted as being early offshoots of the lineage towards Priapulida (Harvey et al. 2010). *Shergoldana australensis* from the Cambrian of Queensland resembles nematomorph larvae to some degree (Maas et al. 2007), and probably also lived in the meiofauna, similar to kinorhynch cycloneuralians (Nagler and Haug 2015).

The oldest constraints on the origin of Ecdysozoa are arthropod trace fossils (Benton et al. 2015).

Node. Gordioida.

Fossil Taxon. *Cretachordodes burmitis* Poinar and Buckley 2006

Fossil evidence. Isolated body fossil

Fossil Host. Unknown – possibly a cockroach based on circumstantial evidence (Poinar and Buckley 2006).

Phylogenetic Justification. No formal phylogenetic analysis has been performed, but surface ornamentation, dimensions, coiling after death speak for the assignment of these body fossils to Gordioida (Poinar and Buckley 2006).

Minimum age. 98.17 Ma. See Tylenchomorpha (Nematoda) for justification.

7.4.6 Fossil record of Syndermata

Weinstein and Kuris (2016) considered that parasitism might have evolved at least nine times independently in Rotifera (= Syndermata). However, earlier reports (May 1989) considered the ectoparasitic *Seison* and Acanthocephala to be independent transitions which is probably not the case (Sielaff et al. 2016). The fossil record of Pararotatoria (Acanthocephala + Seisonidae), which are now considered derived rotifers (syndermatans), is rare. Until recently, the oldest fossil constraint for their presence was that of their closely relatives – bdelloid rotifers in Dominican amber (Poinar and Ricci 1992; Waggoner and Poinar 1993). Other more distant relatives have become known from older non-marine Eocene deposits from South Australia (Southcott and Lange 1971). Dominican amber has traditionally been dated to the Eocene to Oligocene, but is currently attributed to the Miocene (Iturralde-Vinent and MacPhee 1996; Iturralde-Vinent 2001). New discoveries of acanthocephalan eggs from Upper Cretaceous crocodyliform coprolites push back this record considerably (Cardia et al. 2019a). However, estimates based on host relationships might place the origin of this group considerably earlier as far back as the Cambrian (Conway Morris and Crompton 1982; Sielaff 2016; Herlyn 2020). Enigmatic hook-like fossils from the Cambrian have been attributed to Acanthocephala (Qian and Yin 1984; Amin 2013), but their size and morphology make this assignment unlikely (see Herlyn 2020).

The age of the gnathiferan crown group is complicated by the phylogenetic position of chaetognaths, which have historically been difficult to place in animal phylogeny. Chaetognaths have recently been argued to belong either within, or as the sister taxon of gnathifera (Laumer et al. 2019; Marlétaz et al. 2019) based on phylogenomic analyses. Furthermore, macrofossils with morphological similarities with both chaetognaths and other gnathiferans have been identified from the middle Cambrian Burgess Shale (Caron and Cheung 2019; Vinther and Parry 2019) further bolstering the hypothesis that chaetognaths and gnathiferans are closely related.

The oldest evidence for chaetognaths are protoconodonts, identified as the remains of their grasping spines (Bengtson 1983; Szaniawski 2002; Vannier et al. 2007), which can at least be traced back to the Fortunian (Yang et al. 2016; Kouchinsky et al. 2017). The grasping spines of chaetognaths have been argued to be homologous with the jaw apparatus of gnathiferans (Vinther and Parry 2019). These fossils therefore provide a minimum age for the split between chaetognaths and their sister taxon, which may be all other gnathiferan phyla (e.g., some analyses in Laumer et al. 2019), a clade of rotifers and gnathostomulids (Marlétaz et al., 2019) or Rotifera (Vinther and Parry 2019).

Ectoparasitic, or at least ectosymbiotic, relationships were likely present since the Cambrian (Cong et al. 2017) in forms which are by some considered as possible gnathiferans (Vinther and Parry 2019).

Node. Total Group Gnathifera

Fossil taxon. *Protohertzina anabarica*

Phylogenetic justification. No formal analysis incorporating protoconodonts has been performed, but based on microstructural and gross morphological similarities, protoconodonts have been assigned to the total group of chaetognaths (Bengtson 1983; Szaniawski 2002; Vannier et al. 2007) and would therefore be crown group gnathiferans.

Hard minimum. The oldest protoconodonts assigned to *Protohertzina anabarica* (Bengtson 1983) derive from the middle Fortunian Anabarites trisulcatus – Protohertzina anabarica assemblage zone or its correlatives (Yang et al. 2016; Kouchinsky et al. 2017). This would yield a minimum age of 532.7 Ma according to GTS 2016 (Ogg et al. 2016).

Node. **Archiacanthocephala**

Fossil evidence. Unnamed remains of acanthor larvae (Cardia et al. 2019a)

Host taxon. Probably a crocodyliform archosaur (Crocodyliformes) based on the characteristics of the coprolite (Cardia et al. 2019a), but this is probably only a false or facultative host based on modern host-parasite relationships (Herlyn 2020).

Phylogenetic justification. No formal phylogenetic analysis was performed, but egg size, their elliptical shape and structures wrapped by three concentric, thick shells suggests their identification as acanthocephalan eggs containing remains of acanthor larvae (Cardia et al. 2019a). These thick-shelled eggs are most similar in size and morphology to other described archiacanthocephala eggs from recent ancient remains and lack a fourth layer present in extant forms. The latter might however be a preservational artefact as this layer is usually poorly present or absent in ancient remains (compare Herlyn 2020).

Hard minimum. 69.9 Ma. The coprolites derive from the Adamantina Formation. The age of the Adamantina Formation is still debated (Castro et al. 2018). The youngest analyses place it formation between 87.7 Ma in the Coniacian (Castro et al. 2018) to early Maastrichtian

(Gobbo-Rodrigues et al. 1999) yielding a minimum age of 69.9 Ma according to GTS 2016 (Ogg et al. 2016).

7.5 Discussion

In some case, confidently identified fossil remains of free-living relatives are more ancient (e.g., annelids) than those of parasitic representatives. In other cases, remains of parasitic helminths are considerably older than those confidently attributable to their closest free-living relatives. Putative free-living Ordovician nematodes have been reported (Muir et al. 2014; Knaust and Desrochers 2019), but confident assignment to Nematoda is unclear. Helminth eggs seems to be more readily preserved in the coprolites of sharks (Dentzien-Dias et al. 2013; De Baets et al. 2015), archosaurs (Poinar and Boucot 2006; Cardia et al. 2018, 2019a, 2019b) or synapsids (Da Silva et al. 2014; Hugot et al. 2014) with age depending on the clade investigated.

At least the rare cases where divergence time estimates based on host-constraints can be compared with those of fossil helminths recovered from these hosts (Fig. 6) suggest that additional evidence from Paleozoic Lagerstätten or coprolites might be useful to constrain the macroecolutionary and macroecological history of worm parasites (Dentzien-Dias et al. 2013; Da Silva et al. 2014; Cardia et al. 2018, 2019b). Such examples concern estimates of crown-group eucestode flatworms (Olson et al. 2010) and stem-group ascaridoid nematodes (Li et al. 2018). The minimum age of eggs attributed to Heterocheilidae (Cardia et al. 2018, 2019b) are slightly younger than the molecular divergence estimate (Li et al. 2018). However, the age of this Lagerstätte is still uncertain (Castro et al. 2018) with older estimates overlapping with these divergence time estimates. Furthermore, it might also be just a matter of time before similar eggs are recovered from older vertebrate coprolites.

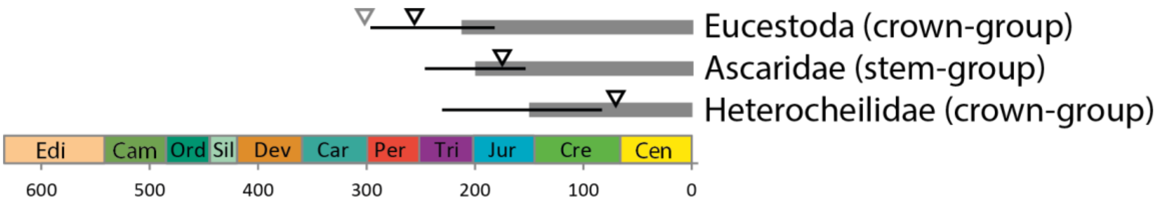

Figure 6. Minimum age of fossil attributable to particular parasitic helminth lineages (Dentzien-Dias et al. 2013; Da Silva et al. 2014; Cardia et al. 2019b) plotted in relationship with available molecular clock divergence estimates based on their hosts (Olson et al. 2010; Li et al. 2018). More details can be found in the text.

In other cases, remains have been recovered from extinct hosts which are phylogenetically placed in between extant hosts suggesting their record might still be consistent (De Baets et al. 2015) with a deep evolutionary origin of these parasites in their common ancestor (e.g., oxyurid nematode in cynodont coprolites, monogenean flatworms attached to fossil acanthodians). In yet other cases, fossil helminth remains are recovered from extinct hosts which are only distantly related to extant hosts suggesting host relationships which are no longer recovered nor predicted from extant host relationships (e.g., putative pentastomid attached to ostracod, gnathiferan ectosymbionts attached to scalidophorans). This suggests caution in considering modern evidence alone when constraining the evolution of past parasites and inferring ancient parasite-host relationships (De Baets and Littlewood 2015; Warnock and Engelstädter 2020). However, novel methods are currently being developed which might be able to deal with changes in host repertoire (Braga et al. 2019). Fossil finds and their known host associations should be considered when available and further finds might provide crucial information in the context of unravelling the evolutionary history of helminth parasitism.

7.6 Conclusions

The fossil record of soft-bodied helminths is patchy, but more diverse as commonly assumed. This summary provides evidence that ectoparasitic helminths in various lineages have existed since the early Paleozoic, while endoparasitic helminths arose during, or before the late Paleozoic. Lineages parasitizing terrestrial plant and animal hosts have been in existence at least since the Devonian and Triassic, respectively. All major helminth phyla had evolved endoparasitic lineages at least since the Mesozoic. Data also provide evidence for obvious host switches or extinctions, which cautions against models relying solely on co-divergence where use of host calibrations to constrain divergence time estimates may be considered. In some cases, the fossil record of parasitic helminths is better than that of their free-living relatives, yielding constraints on the age of their free-living sister-groups. In at least some cases (Eucestoda, stem-Ascarida), the earliest fossil evidence for particular lineages falls within the divergence time estimates based on host constraints. The fossil record also provides direct evidence for certain modern or now extinct host associations (e.g., pentastomida on ostracods, gnathifera attached to scalidophora).

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References

Almeida, W. O., & Christoffersen, M. L. (1999). A Cladistic Approach to Relationships in Pentastomida. The Journal of Parasitology, 85(4), 695-704. https://doi.org/10.2307/3285745

Amin, O. M. (2013). Classification of the acanthocephala. *Folia Parasitologica, 60*(4), 273-305. https://doi.org/10.14411/fp.2013.031

Arduini, P., Pinna, G., & Teruzzi, G. (1983). *Eophasma jurassicum* n. g. n. sp., a new fossil nematode of the Sinemurian of Osteno in Lombardy. Atti della Società italiana di scienze naturali e del museo civico di storia naturale di Milano, 124(1-2), 61-64.

Ausich, W. I., & Simms, M. J. (1999). Ecology and Ecological Interactions. In C. E. Brett, H. Hess, M. J. Simms, & W. I. Ausich (Eds.), *Fossil Crinoids* (pp. 55-60). Cambridge: Cambridge University Press.

Babcock, L. E. (2007). Role of malformations in elucidating trilobite paleobiology: a historical synthesis. In D. G. Mikulic, E. Landing, & J. Kluessendorf (Eds.), *Fabulous Fossils–300 Years of Worldwide Research on Trilobites* (pp. 3-19). New York: The State Education Department.

Badets, M., Whittington, I., Lalubin, F., Allienne, J. F., Maspimby, J. L., Bentz, S., Du Preez, L. H., Barton, D., Hasegawa, H., Tandon, V., Imkongwapang, R., Ohler, A., Combes, C., & Verneau, O. (2011). Correlating early evolution of parasitic platyhelminths to Gondwana breakup. *Systematic Biology, 60*(6), 762-781. https://doi.org/10.1093/sysbio/syr078

Bajdek, P., Qvarnström, M., Owocki, K., Sulej, T., Sennikov, A. G., Golubev, V. K., & Niedźwiedzki, G. (2016). Microbiota and food residues including possible evidence of pre-mammalian hair in Upper Permian coprolites from Russia. *Lethaia, 49*(4), 455-477. https://doi.org/10.1111/let.12156

Balinski, A., Sun, Y., & Dzik, J. (2013). Traces of marine nematodes from 470 million years old Early Ordovician rocks in China. *Nematology, 15*, 567-574. https://doi.org/10.1163/15685411-00002702

Bengtson, S. (1983). The early history of the Conodonta. *Fossils and Strata, 15*, 5-19.

Benton, M. J., Donoghue, P. C., Asher, R. J., Friedman, M., Near, T. J., & Vinther, J. (2015). Constraints on the timescale of animal evolutionary history. *Palaeontologia Electronica, 18.1.1FC*, 1-106.

Blake, J., & Evans, J. (1972). *Polydora* and related genera (Polychaeta: Spionidae) as borers in mollusk shells and other calcareous substrates. *Veliger, 15*, 235-249.

Blaxter, M., & Koutsovoulos, G. (2015). The evolution of parasitism in Nematoda. *Parasitology, 142 Suppl 1*, S26-39. https://doi.org/10.1017/S0031182014000791

Blaxter, M. L., Ley, P., Garey, J. R., Liu, L. X., Scheldeman, P., Vierstraete, A., Vanfleteren, J. R., Mackey, L. Y., Dorris, M., Frisse, L. M., Vida, J. T., & Thomas, W. K. (1998). A molecular evolutionary framework for the phylum Nematoda. *Nature, 392*, 71-75. https://doi.org/10.1038/32160

Bleidorn, C., Podsiadlowski, L., Zhong, M., Eeckhaut, I., Hartmann, S., Halanych, K. M., & Tiedemann, R. (2009). On the phylogenetic position of Myzostomida: can 77 genes get it wrong? *BMC Evolutionary Biology, 9*(1), 150. https://doi.org/10.1186/1471-2148-9-150

Bobrovskiy, I., Hope, J. M., Ivantsov, A., Nettersheim, B. J., Hallmann, C., & Brocks, J. J. (2018). Ancient steroids establish the Ediacaran fossil *Dickinsonia* as one of the earliest animals. *Science, 361*(6408), 1246-1249. https://doi.org/10.1126/science.aat7228

Bomfleur, B., Kerp, H., Taylor, T. N., Moestrup, Ø., & Taylor, E. L. (2012). Triassic leech cocoon from Antarctica contains fossil bell animal. *Proceedings of the National Academy of Sciences, 109*(51), 20971-20974. https://doi.org/10.1073/pnas.1218879109

Bomfleur, B., Mörs, T., Ferraguti, M., Reguero, M. A., & McLoughlin, S. (2015). Fossilized spermatozoa preserved in a 50-Myr-old annelid cocoon from Antarctica. *Biology Letters, 11*(7), 20150431. https://doi.org/10.1098/rsbl.2015.0431

Borda, E., Oceguera-Figueroa, A., & Siddall, M. E. (2008). On the classification, evolution and biogeography of terrestrial haemadipsoid leeches (Hirudinida: Arhynchobdellida: Hirudiniformes). *Molecular Phylogenetics and Evolution, 46*(1), 142-154. https://doi.org/10.1016/j.ympev.2007.09.006

Braga, M. P., Landis, M., Nylin, S., Janz, N., & Ronquist, F. (2020). Bayesian inference of ancestral host-parasite interactions under a phylogenetic model of host repertoire evolution. *Systematic Biology,* syaa019. https://doi.org/10.1093/sysbio/syaa019

Brasier, M. D., & Antcliffe, J. B. (2008). *Dickinsonia* from Ediacara: A new look at morphology and body construction. *Palaeogeography, Palaeoclimatology, Palaeoecology, 270*(3–4), 311-323. http://doi.org/10.1016/j.palaeo.2008.07.018

Brett, C. E., Baird, G. C., Bartholomew, A. J., DeSantis, M. K., & Ver Straeten, C. A. (2011). Sequence stratigraphy and a revised sea-level curve for the Middle Devonian of eastern North America. *Palaeogeography, Palaeoclimatology, Palaeoecology, 304*(1), 21-53. https://doi.org/10.1016/j.palaeo.2010.10.009

Brooks, D. R. (1989). The Phylogeny of the Cercomeria (Platyhelminthes: Rhabdocoela) and General Evolutionary Principles. *The Journal of Parasitology, 75*(4), 606-616.

Caira, J. N., & Littlewood, D. T. J. (2013). Worms, Platyhelminthes. In S. A. Levin (Ed.), *Encyclopedia of Biodiversity, 2nd Edition, volume 7* (pp. 437-469). Waltham MA: Academic Press.

Camacho, M., Araújo, A., Morrow, J., Buikstra, J., & Reinhard, K. (2018). Recovering parasites from mummies and coprolites: an epidemiological approach. *Parasites & Vectors, 11*(1), 248. https://doi.org/10.1186/s13071-018-2729-4

Cameron, B. (1967). Fossilization of an Ancient(Devonian) Soft-Bodied Worm. *Science, 155*(3767), 1246-1248. https://doi.org/10.1126/science.155.3767.1246

Cameron, B. (1969). Paleozoic shell-Boring Annelids and their Trace Fossils. *American Zoologist, 9*(3), 689-703. https://doi.org/10.1093/icb/9.3.689

Cardia, D. F. F., Bertini, R. J., Camossi, L. G., & Letizio, L. A. (2018). The first record of Ascaridoidea eggs discovered in Crocodyliformes hosts from the Upper Cretaceous of Brazil. *Revista Brasileira de Paleontologia, 21*(3), 238-244. http://dx.doi.org/10.4072/rbp.2018.3.04

Cardia, D. F. F., Bertini, R. J., Camossi, L. G., & Letizio, L. A. (2019a). First record of Acanthocephala parasites eggs in coprolites preliminary assigned to Crocodyliformes from the Adamantina Formation (Bauru Group, Upper Cretaceous), São Paulo, Brazil. *Anais da Academia Brasileira de Ciencias, 91*(Suppl. 2), e20170848. https://doi.org/10.1590/0001-3765201920170848

Cardia, D. F. F., Bertini, R. J., Camossi, L. G., & Letizio, L. A. (2019b). Two new species of ascaridoid nematodes in Brazilian Crocodylomorpha from the Upper Cretaceous. *Parasitology International, 72*, 101947. https://doi.org/10.1016/j.parint.2019.101947

Caron, J.-B., & Cheung, B. (2019). Amiskwia is a large Cambrian gnathiferan with complex gnathostomulid-like jaws. *Communications Biology, 2*(1), 164. https://doi.org/10.1038/s42003-019-0388-4

Castellani, C., Maas, A., Waloszek, D., & Haug, J. T. (2011). New pentastomids from the Late Cambrian of Sweden - deeper insight of the ontogeny of fossil tongue worms. *Palaeontographica Abteilung A, 293*(4-6), 95-145.

Castro, M. C., Goin Francisco, J., Ortiz-Jaureguizar, E., Vieytes, E. C., Tsukui, K., Ramezani, J., Batezelli, A., Marsola, J. C. A., Langer, M. C. (2018). Late Cretaceous mammal from Brazil and the first radioisotopic age for the Bauru Group. *Royal Society Open Science, 5*(5), 180482. https://doi.org/10.1098/rsos.180482

Chen, H., Parry, L. A., Vinther, J., Zhai, D., Hou, X., & Ma, X. (2020). A Cambrian crown annelid reconciles phylogenomics and the fossil record. Nature. https://doi.org/10.1038/s41586-020-2384-8

Chin, K. (2002). Analyses of coprolites produced by carnivorous vertebrates. *Paleontological Society Papers, 8*, 43-50. https://doi.org/10.1017/S1089332600001042

Cisneros, J. C., Abdala, F., Atayman-Güven, S., Rubidge, B. S., Şengör, A. M. C., & Schultz, C. L. (2012). Carnivorous dinocephalian from the Middle Permian of Brazil and tetrapod dispersal in Pangaea. *Proceedings of the National Academy of Sciences, 109*(5), 1584-1588. https://doi.org/10.1073/pnas.1115975109

Collins, A. G., Lipps, J. H., & Valentine, J. W. (2000). Modern Mucociliary Creeping Trails and the Bodyplans of Neoproterozoic Trace-Makers. *Paleobiology, 26*(1), 47-55. https://doi.org/10.2307/2666060

Condon, D., Zhu, M., Bowring, S., Wang, W., Yang, A., & Jin, Y. (2005). U-Pb Ages from the Neoproterozoic Doushantuo Formation, China. *Science, 308*(5718), 95-98. https://doi.org/10.1126/science.1107765

Cong, P., Ma, X., Williams, M., Siveter, D. J., Siveter, D. J., Gabbott, S. E., Zhai, D., Goral, T., Edgecombe, G. D., & Hou, X. (2017). Host-specific infestation in early Cambrian worms. *Nature Ecology & Evolution, 1*(10), 1465-1469. https://doi.org/10.1038/s41559-017-0278-4

Conway Morris, S. (1981). Parasites and the fossil record. *Parasitology, 83*(3), 489-509. https://doi.org/10.1017/S0031182000067020

Conway Morris, S., & Crompton, D. W. T. (1982). The origins and evolution of the Acanthocephala. Biological Reviews of the Cambridge Philosophical Society, 57(1), 85-115. https://doi.org/10.1111/j.1469-185X.1982.tb00365.x

Conway Morris, S., & Peel, J. S. (2008). The earliest annelids: Lower Cambrian polychaetes from the Sirius Passet Lagerstätte, Peary Land, North Greenland. Acta Palaeontologica Polonica, 53(1), 137-149. http://dx.doi.org/10.4202/app.2008.0110

Cuthill, H. J. F., Sewell, K. B., Cannon, L. R. G., Charleston, M. A., Lawler, S., Littlewood, D. T. J., Olson, P. D., & Blair, D. (2016). Australian spiny mountain crayfish and their temnocephalan ectosymbionts: an ancient association on the edge of coextinction? *Proceedings of the Royal Society of London B: Biological Sciences, 283*(1831). https://doi.org/10.1098/rspb.2016.0585

Da Silva, P. A., Borba, V. H., Dutra, J. M. F., Leles, D., Da-Rosa, A. A. S., Ferreira, L. F., & Araujo, A. (2014). A new ascarid species in cynodont coprolite dated of 240 million years. *Anais da Academia Brasileira de Ciencias, 86*, 265-270. https://doi.org/10.1590/0001-3765201320130036

De Baets, K., Klug, C., Korn, D., Bartels, C., & Poschmann, M. (2013). Emsian Ammonoidea and the age of the Hunsrück Slate (Rhenish Mountains, Western Germany). Palaeontographica A, 299(1-6), 1-113.

De Baets, K., Antonelli, A., & Donoghue, P. C. J. (2016). Tectonic blocks and molecular clocks. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 371*(1699). https://doi.org/10.1098/rstb.2016.0098

De Baets, K., Dentzien-Dias, P., Upeniece, I., Verneau, O., & Donoghue, P. C. J. (2015). Constraining the Deep Origin of Parasitic Flatworms and Host-Interactions with Fossil Evidence. *Advances in Parasitology, 90*, 93-135. http://doi.org/10.1016/bs.apar.2015.06.002

De Baets, K., & Littlewood, D. T. J. (2015). The Importance of Fossils in Understanding the Evolution of Parasites and Their Vectors. *Advances in Parasitology, 90*, 1-51. http://doi.org/10.1016/bs.apar.2015.07.001

De Baets, K., Huntley, J. W., Klompmaker, A. A., Schiffbauer, J. D., & Muscente, A. D. (2020). The fossil record of parasitism: Its extent and taphonomic constraints. Topics in Geobiology 50.

Dentzien-Dias, P., Carrillo-Briceño, J. D., Francischini, H., & Sánchez, R. (2018). Paleoecological and taphonomical aspects of the Late Miocene vertebrate coprolites (Urumaco Formation) of Venezuela. *Palaeogeography, Palaeoclimatology, Palaeoecology, 490*, 590-603. https://doi.org/10.1016/j.palaeo.2017.11.048

Dentzien-Dias, P. C., de Figueiredo, A. E. Q., Horn, B., Cisneros, J. C., & Schultz, C. L. (2012). Paleobiology of a unique vertebrate coprolites concentration from Rio do Rasto Formation (Middle/Upper Permian), Paraná Basin, Brazil. *Journal of South American Earth Sciences, 40*(0), 53-62. http://doi.org/10.1016/j.jsames.2012.09.008

Dentzien-Dias, P. C., Poinar, G., Jr., de Figueiredo, A. E. Q., Pacheco, A. C. L., Horn, B. L. D., & Schultz, C. L. (2013). Tapeworm Eggs in a 270 Million-Year-Old Shark Coprolite. *PLoS ONE, 8*(1), e55007. https://doi.org/10.1371/journal.pone.0055007

Dias-Da-Silva, S. (2012). Middle–Late Permian tetrapods from the Rio do Rasto Formation, Southern Brazil: a biostratigraphic reassessment. *Lethaia, 45*(1), 109-120. https://doi.org/10.1111/j.1502-3931.2011.00263.x

Dufour, B., & Le Bailly, M. (2013). Testing new parasite egg extraction methods in paleoparasitology and an attempt at quantification. *International Journal of Paleopathology, 3*(3), 199-203. https://doi.org/10.1016/j.ijpp.2013.03.008

Dzik, J. (2008). Gill structure and relationships of the Triassic cycloid crustaceans. *Journal of Morphology, 269*(12), 1501-1519. https://doi.org/10.1002/jmor.10663

Edgecombe, G., Giribet, G., Dunn, C. W., Hejnol, A., Kristensen, R. M., Neves, R. C., Rouse, G. W., Worsaae, K., & Sørensen, M. V. (2011). Higher-level metazoan relationships: recent progress and remaining questions. *Organisms Diversity & Evolution, 11*(2), 151-172. https://doi.org/10.1007/s13127-011-0044-4

Eeckhaut, I. (1998). Mycomyzostoma calcidicola gen. et sp. nov., the First Extant Parasitic Myzostome Infesting Crinoid Stalks, with a Nomenclatural Appendix by M. J. Grygier. *Species Diversity, 3*(1), 89-103. https://doi.org/10.12782/specdiv.3.89

Eeckhaut, I., McHugh, D., Mardulyn, P., Tiedemann, R., Monteyne, D., Jangoux, M., & Milinkovitch, M. (2000). Myzostomida: a link between trochozoans and flatworms? *Proceedings of the Royal Society B-Biological Sciences, 267*(1451), 1383-1392. https://doi.org/10.1098/rspb.2000.1154

Egger, B., Lapraz, F., Tomiczek, B., Müller, S., Dessimoz, C., Girstmair, J., Škunca, N., Rawlinson, K. A., Cameron, C. B., Beli, E., Todaro, M A., Gammoudi, M., Noreña, C., Telford, M. J. A (2015). A Transcriptomic-Phylogenomic Analysis of the Evolutionary Relationships of Flatworms. *Current Biology, 25*(10), 1347-1353. https://doi.org/10.1016/j.cub.2015.03.034

Fauchald, K., Stürmer, W., & Yochelson, E. L. (1988). Two worm-like organisms from the Hunsrück slate (Lower Devonian), southern Germany. *Paläontologische Zeitschrift, 62*(3), 205-215. https://doi.org/10.1007/BF02989493

Francischini, H., Dentzien-Dias, P., & Schultz, C. L. (2018). A fresh look at ancient dungs: the Brazilian Triassic coprolites revisited. *Lethaia, 51*(3), 389-405. https://doi.org/10.1111/let.12251

Gobbo-Rodrigues, S. R., Petri, S., & Bertini, R. J. (1999). Ocorrências de ostrácodes na formação Adamantina do grupo Bauru, cretáceo superior da Bacia do Paraná, e possibilidades de correlação com depósitos isócronos argentinos. Parte II- Família Limnocytheridae. *Anais da Academia Brasileira de Ciencias, 71*(1), 147-148.

Govedich, F. R., Bain, B. A., Moser, W. E., Gelder, S. R., Davies, R. W., & Brinkhurst, R. O. (2010). Annelida (Clitellata): Oligochaeta, Branchiobdellida, Hirudinida, and Acanthobdellida. In Ecology and classification of North American freshwater invertebrates (pp. 385-436). Academic Press.

Han, J., Conway Morris, S., Cuthill, H. J. F., & Shu, D. (2019). Sclerite-bearing annelids from the lower Cambrian of South China. *Scientific Reports, 9*(1), 4955. https://doi.org/10.1038/s41598-019-40841-x

Hanelt, B., Thomas, F., & Schmidt-Rhaesa, A. (2005). Biology of the Phylum Nematomorpha. In J. R. Baker, R. Muller, & D. Rollinson (Eds.), *Advances in Parasitology* (Vol. 59, pp. 243-305): Academic Press.

Harper, D. A. T., Hammarlund, E. U., Topper, T. P., Nielsen, A. T., Rasmussen, J. A., Park, T.-Y. S., & Smith, M. P. (2019). The Sirius Passet Lagerstätte of North Greenland: a remote window on the Cambrian Explosion. *Journal of the Geological Society*, jgs2019-2043. https://doi.org/10.1144/jgs2019-043

Harvey, T. H. P., Dong, X., & Donoghue, P. C. J. (2010). Are palaeoscolecids ancestral ecdysozoans? *Evolution & Development, 12*(2), 177-200. https://doi.org/10.1111/j.1525-142X.2010.00403.x

Haug, J. T., Haug, C., Nagler, C. (2020). Evolutionary history of crustaceans as parasites. In Topics in Geobiology 50. Springer, Cham.

Héritier, L., Badets, M., Du Preez, L. H., Aisien, M. S. O., Lixian, F., Combes, C., & Verneau, O. (2015). Evolutionary processes involved in the diversification of chelonian and mammal polystomatid parasites (Platyhelminthes, Monogenea, Polystomatidae) revealed by palaeoecology of their hosts. *Molecular Phylogenetics and Evolution, 92*, 1-10. http://doi.org/10.1016/j.ympev.2015.05.026

Herlyn, H. (2020). Thorny-headed Worms(Acanthocephala): Jaw-less Members of Jaw-bearing Worms that Parasitize Jawed Arthropods and Jaw-bearing Vertebrates. In Topics in Geobiology 49. Springer, Cham.

Hernández-Alcántara, P., & Solís-Weiss, V. (1998). Parasitism among polychaetes: a rare case illustrated by a new species: *Labrorostratus zaragozensis*, n. sp.(Oenonidae) found in the Gulf of California, Mexico. *The Journal of parasitology, 84*(5), 978-982.

Hess, H. (2010). Myzostome Deformation on Arms of the Early Jurassic Crinoid *Balanocrinus gracilis* (Charlesworth). *Journal of Paleontology, 84*(6), 1031-1034. https://doi.org/10.1666/10-036.1

Hints, O. (1998). Late Viruan [Caradoc] polychaete jaws from North Estonia and the St. Petersburg region. *Acta Palaeontologica Polonica, 43*(3), 471-516.

Hints, O. (2000). Ordovician eunicid polychaetes of Estonia and surrounding areas: review of their distribution and diversification. *Review of Palaeobotany and Palynology, 113*(1-3), 41-55.

Hints, O., & Eriksson, M. (2007). Diversification and biogeography of scolecodont-bearing polychaetes in the Ordovician. *Palaeogeography Palaeoclimatology Palaeoecology, 245*, 95-114. https://doi.org/10.1016/j.palaeo.2006.02.029

Hints, O., & Nõlvak, J. (2006). Early Ordovician scolecodonts and chitinozoans from Tallinn, North Estonia. *Review of Palaeobotany and Palynology, 139*(1), 189-209. https://doi.org/10.1016/j.revpalbo.2006.01.004

Hollocher, K., & Hollocher, T. C. (2012). Early process in the fossilization of terrestrial feces to coprolites, and microstructure preservation: New Mexico Museum of Natural History and Science, Bulletin 57, 79-91.

Hope, W. D., & Tchesunov, A. V. (1999). Smithsoninema inaequale n.g. and n.sp. (Nematoda, Leptolaimidae) Inhabiting the Test of a Foraminiferan. *Invertebrate Biology, 118*(2), 95-108. https://doi.org/10.2307/3227052

Huang, D.-Y., Chen, J.-Y., Vannier, J., & Saiz Salinas, J. I. (2004). Early Cambrian sipunculan worms from southwest China. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 271*(1549), 1671-1676. https://doi.org/10.1098/rspb.2004.2774

Hugot, J.-P., Gardner, S., Borba, V., Araujo, P., Leles, D., Stock Da-Rosa, A., Dutra, J., Ferreira, L. F., & Araujo, A. (2014). Discovery of a 240 million year old nematode parasite egg in a cynodont coprolite sheds light on the early origin of nematode parasites in vertebrates. *Parasites & Vectors, 7*(1), 486. https://doi.org/10.1186/s13071-014-0486-6

Huntley, J. W. (2007). Towards establishing a modern baseline for paleopathology: Trace-producing parasites in a bivalve host. *Journal of Shellfish Research, 26*(1), 253-259. https://doi.org/10.2983/0730-8000(2007)26[253:TEAMBF]2.0.CO;2

Huntley, J. W., & De Baets, K. (2015). Trace Fossil Evidence of Trematode—Bivalve Parasite—Host Interactions in Deep Time. *Advances in Parasitology, 90*, 201-231. https://doi.org/10.1016/bs.apar.2015.05.004

Ituarte, C., Cremonte, F., & Zelaya, D. G. (2005). Parasite-mediated shell alterations in Recent and Holocene sub-Antarctic bivalves: the parasite as modeler of host reaction. *Invertebrate Biology, 124*(3), 220-229. https://doi.org/10.1111/j.1744-7410.2005.00021.x

Ituarte, C. F., Cremonte, F., & Deferrari, G. (2001). Mantle-shell complex reactions elicited by digenean metacercariae in *Gaimardia trapesina* (Bivalvia : Gaimardiidae) from the Southwestern Atlantic Ocean and Magellan Strait. *Diseases of Aquatic Organisms, 48*(1), 47-56. https://doi.org/10.3354/dao048047

Iturralde-Vinent, M. A. (2001). Geology of the amber-bearing deposits of the greater Antilles. *Carribean Journal of Science, 37*(3-4), 141-166.

Iturralde-Vinent, M. A., & MacPhee, R. D. E. (1996). Age and Paleogeographical Origin of Dominican Amber. *Science, 273*(5283), 1850-1852. https://doi.org/10.1126/science.273.5283.1850

Ivany, L. C., Lohmann, K. C., Hasiuk, F., Blake, D. B., Glass, A., Aronson, R. B., & Moody, R. M. (2008). Eocene climate record of a high southern latitude continental shelf: Seymour Island, Antarctica. *Geological Society of America Bulletin, 120*(5-6), 659-678. https://doi.org/10.1130/B26269.1

Jangoux, M. (1987). Diseases of Echinodermata. 111. Agents metazoans (Annelida to Pisces). *Dis. Aquat. Org, 3*, 59-83.

Jouy-Avantin, F., Combes, C., Lumley, H., Miskovsky, J. C., & Moné, H. (1999). Helminth Eggs in Animal Coprolites from a Middle Pleistocene Site in Europe. *The Journal of Parasitology, 85*(2), 376-379. https://doi.org/10.2307/3285652

Kaplan, A., Grigelis, A., Strelnikova, N., & Glikman, L. (1977). Stratigraphy and correlation of Palaeogene deposits of South-Western cis-Baltic region. *Sovetskaâ Geologiâ, 4*, 30-43.

Klompmaker, A. A., & Boxshall, G. A. (2015). Fossil Crustaceans as Parasites and Hosts. *Advances in Parasitology, 90*, 233-289. https://doi.org/10.1016/bs.apar.2015.06.001

Knaust, D. (2010). Remarkably preserved benthic organisms and their traces from a Middle Triassic (Muschelkalk) mud flat. *Lethaia, 43*(3), 344-356. ttps://doi.org/10.1111/j.1502-3931.2009.00196.x

Knaust, D., & Desrochers, A. (2019). Exceptionally preserved soft-bodied assemblage in Ordovician carbonates of Anticosti Island, eastern Canada. *Gondwana Research, 71*, 117-128. https://doi.org/10.1016/j.gr.2019.01.016

Kodandaramaiah, U. (2011). Tectonic calibrations in molecular dating. *Current Zoology, 57*(1), 116-124. https://doi.org/10.1093/czoolo/57.1.116

Kouchinsky, A., Bengtson, S., Landing, E., Steiner, M., Vendrasco, M., & Ziegler, K. (2017). Terreneuvian stratigraphy and faunas from the Anabar Uplift, Siberia. *Acta Palaeontologica Polonica, 62*(2), 311-440. https://doi.org/10.4202/app.00289.2016

Kozur, H. (1970). Fossile Hirudinea aus dem Oberjura von Bayern. Lethaia, 3(3), 225-232. https://doi.org/10.1111/j.1502-3931.1970.tb01267.x

Lanterbecq, D., Bleidorn, C., Michel, S., & Eeckhaut, I. (2008). Locomotion and fine structure of parapodia in *Myzostoma cirriferum* (Myzostomida). *Zoomorphology, 127*. http://doi.org/10.1007/s00435-007-0052-2

Laumer, C. E., Bekkouche, N., Kerbl, A., Goetz, F., Neves, R. C., & Sørensen, M. V. (2015). Spiralian phylogeny informs the evolution of microscopic lineages. *Current Biology, 25*. http://doi.org/10.1016/j.cub.2015.06.068

Laumer, C. E., Fernández, R., Lemer, S., Combosch, D., Kocot, K. M., Riesgo, A., Andrade, S. C. S., Sterrer, W., Sørensen, M. V., & Giribet, G. (2019). Revisiting metazoan phylogeny with genomic sampling of all phyla. *Proceedings of the Royal Society B: Biological Sciences, 286*(1906), 20190831. http://doi.org/10.1098/rspb.2019.0831

Laumer, C. E., & Giribet, G. (2014). Inclusive taxon sampling suggests a single, stepwise origin of ectolecithality in Platyhelminthes. *Biological Journal of the Linnean Society, 111*(3), 570-588. http://doi.org/10.1111/bij.12236

Laumer, C. E., Hejnol, A., & Giribet, G. (2015). Nuclear genomic signals of the 'microturbellarian' roots of platyhelminth evolutionary innovation. eLife, 4:e05503. https://doi.org/10.7554/eLife.05503.001

Leduc, D., & Zhao, Z. Q. (2019). Phylogenetic position of the parasitic nematode Trophomera (Nematoda, Benthimermithidae): A molecular analysis. *Molecular Phylogenetics and Evolution, 132*, 177-182. https://doi.org/10.1016/j.ympev.2018.12.005

Leduc, D., Zhao, Z. Q., Verdon, V., & Xu, Y. (2018). Phylogenetic position of the enigmatic deep-sea nematode order Rhaptothyreida: A molecular analysis. *Molecular Phylogenetics and Evolution, 122*, 29-36. https://doi.org/10.1016/j.ympev.2018.01.018

Leung, T. L. (2017). Fossils of parasites: what can the fossil record tell us about the evolution of parasitism? *Biological Reviews of the Cambridge Philosophical Society, 92*(1), 410-430. http://doi.org/10.1111/brv.12238

Li, L., Lu, L., Nadler, S. A., Gibson, D. I., Zhang, L. P., Chen, H. X., . . . Guo, Y. N. (2018). Molecular Phylogeny and Dating Reveal a Terrestrial Origin in the Early Carboniferous for Ascaridoid Nematodes. *Systematic Biology*. http://doi.org/10.1093/sysbio/syy018

Liljedahl, L. (1985). Ecological aspects of a silicified bivalve fauna from the Silurian of Gotland. Lethaia, 18(1), 53-66. https://doi.org/10.1111/j.1502-3931.1985.tb00684.x

Littlewood, D. T. J. (2006). The evolution of parasitism in flatworms. In A. G. Maule & N. J. Marks (Eds.), *Parasitic Flatworms: Molecular Biology, Biochemistry, Immunology and Physiology* (pp. 1-36).

Littlewood, D. T. J., & Donovan, S. K. (2003). Fossil parasites: A case of identity. *Geology Today, 19*(4), 136-142. https://doi.org/10.1046/j.1365-2451.2003.00406.x

Lockyer, A. E., Olson, P. D., & Littlewood, D. T. J. (2003). Utility of complete large and small subunit rRNA genes in resolving the phylogeny of the Neodermata (Platyhelminthes): implications and a review of the cercomer theory. *Biological Journal of the Linnean Society, 78*(2), 155-171. https://doi.org/10.1046/j.1095-8312.2003.00141.x

Lukševičs, E., Stinkulis, Ģ., Mūrnieks, A., & Popovs, K. (2012). Geological evolution of the Baltic Artesian Basin. In A. Delina, A. Kalvans, T. Saks, U. Bethers, & V. Vircavs (Eds.), *Highlights of groundwater research in the Baltic Artesian Basin* (pp. 7-52): University of Latvia.

Lukševičs, E., Stinkulis, Ģ., Saks, T., Popovs, K., & Jātnieks, J. (2014). The Devonian Stratigraphic Succession and Evolution of the Baltic Sedimentary Basin. In R. Rocha, J. Pais, J. C. Kullberg, & S. Finney (Eds.), *STRATI 2013* (pp. 539-541): Springer International Publishing.

Maas, A. (2013). Gastrotricha, Cycloneuralia and Gnathifera: the fossil record. *Handbook of Zoology. Gastrotricha, Cycloneuralia and Gnathifera, 1*, 11-28.

Maas, A., Waloszek, D., Haug, J. T., & Muller, K. J. (2007). A possible larval roundworm from the Cambrian'Orsten'and its bearing on the phylogeny of Cycloneuralia. *Memoirs of the Association of Australasian Palaeontologists*(34), 499.

Maksoud, S., Azar, D., Granier, B., & Gèze, R. (2017). New data on the age of the Lower Cretaceous amber outcrops of Lebanon. *Palaeoworld, 26*(2), 331-338. https://doi.org/10.1016/j.palwor.2016.03.003

Manum, S. B., Bose, M. N., & Sawyer, R. T. (1991). Clitellate cocoons in freshwater deposits since the Triassic. *Zoologica Scripta, 20*, 347-366. http://doi.org/10.1111/j.1463-6409.1991.tb00300.x

Manum, S. B., Bose, M. N., Sayer, R. T., & Boström, S. (1994). A nematode (Captivonema cretacea gen. et sp. n.) preserved in a clitellate cocoon wall from the Early Cretaceous. *Zoologica Scripta, 23*(1), 27-31. http://doi.org/10.1111/j.1463-6409.1994.tb00370.x

Mark, D. F., Rice, C. M., & Trewin, N. H. (2013). Discussion on 'A high-precision U–Pb age constraint on the Rhynie Chert Konservat-Lagerstätte: time scale and other implications': Journal, Vol. 168, 863–872. *Journal of the Geological Society, 170*(4), 701-703. http://doi.org/10.1144/jgs2011-110

Marlétaz, F., Peijnenburg, K. T. C. A., Goto, T., Satoh, N., & Rokhsar, D. S. (2019). A New Spiralian Phylogeny Places the Enigmatic Arrow Worms among Gnathiferans. *Current Biology, 29*(2), 312-318.e313. https://doi.org/10.1016/j.cub.2018.11.042

Martin, D., & Britayev, T. A. (1998). Symbiotic polychaetes: review of known species. *Oceanography and marine biology: an annual review, 36*, 217-340.

Mattavelli, A., & Bracchi, G. (2008). Palaeoenoploides alessandrellianus n. gen. n. sp: a Late Cenomanian 'roundworm' from the Upper Cretaceous of Lebanon (Nematoda: Enoplidae). *Atti della Società italiana di scienze naturali e del museo civico di storia naturale di Milano, 149*(2), 179-194.

May, L. (1989). Epizoic and parasitic rotifers. *Hydrobiologia*, 186(1), 59-67. https://doi.org/10.1007/978-94-009-0465-1_8

McAllister, C., Bursey, C., & Freed, P. (2010). Helminth parasites (Cestoidea, Nematoda, Pentastomida) of selected herpetofauna from Cameroon, West Africa. *Acta Parasitologica, 55*(1), 90-93. https://doi.org/10.2478/s11686-010-0014-6

McLoughlin, S., Bomfleur, B., Mörs, T., & Reguero, M. (2016). Fossil clitellate annelid cocoons and their microbiological inclusions from the Eocene of Seymour Island, Antarctica. *Palaeontologia Electronica, 19.1.11A*, 1-27. palaeo-electronica.org/content/2016/1448-eocene-annelid-cocoons

Metz, R. (1987). Sinusoidal Trail Formed by a Recent Biting Midge (Family Ceratopogonidae): Trace Fossil Implications. *Journal of Paleontology, 61*(2), 312-314. https://doi.org/10.1017/S0022336000028481

Mierzejewski, P. (1984). *Synclinophora synclinalis* Eisenack—the oldest Arabellid polychaete. *Review of Palaeobotany and Palynology, 43*(1-3), 285-292. https://doi.org/10.1016/0034-6667(84)90037-X

Montes, M., Nozal, F., Santillana, S., Marenssi, S., & Olivero, E. (2013). Mapa Geológico de la isla Marambio (Seymour) Escala 1: 20.000. *Serie Cartográfica Geocientífica Antártica*.

Muir, L. A., Ng, T.-W., Li, X.-F., Zhang, Y.-D., & Lin, J.-P. (2014). Palaeoscolecidan worms and a possible nematode from the Early Ordovician of South China. *Palaeoworld, 23*(1), 15-24. http://doi.org/10.1016/j.palwor.2013.06.003

Nagler, C., & Haug, J. T. (2015). From Fossil Parasitoids to Vectors: Insects as Parasites and Hosts. *Advances in Parasitology, 90*, 137-200. http://doi.org/10.1016/bs.apar.2015.09.003

Nielsen, A. T., Weidner, T., Terfelt, F., & Høyberget, M. (2014). Upper Cambrian (Furongian) biostratigraphy in Scandinavia revisited: definition of superzones. *GFF, 136*(1), 193-197. http://doi.org/10.1080/11035897.2013.878748

Oakley, T. H., Wolfe, J. M., Lindgren, A. R., & Zaharoff, A. K. (2012). Phylotranscriptomics to Bring the Understudied into the Fold: Monophyletic Ostracoda, Fossil Placement and Pancrustacean Phylogeny. *Molecular Biology and Evolution*. http://doi.org/10.1093/molbev/mss216

Ogg, J. G., Ogg, G., & Gradstein, F. M. (2016). *A concise geologic time scale: 2016*. Amsterdam: Elsevier.

Okamura, B., Gruhl, A., & Bartholomew, J. L. (2015). An introduction to myxozoan evolution, ecology and development. In *Myxozoan evolution, ecology and development* (pp. 1-20): Springer.

Okamura, B., & Gruhl, A. (2020). Evolution, Origins and Diversification of Parasitic Cnidarians. In Topics in Geobiology 49. Cham, Springer.

Öktener, A. (2005). A checklist of parasitic helminths reported from sixty-five species of marine fish from Turkey including two new records of monogeneans. Zootaxa, 1063(1), 33-52. https://doi.org/10.11646/zootaxa.1063.1.2

Olson, P. D., Caira, J. N., Jensen, K., Overstreet, R. M., Palm, H. W., & Beveridge, I. (2010). Evolution of the trypanorhynch tapeworms: parasite phylogeny supports independent lineages of sharks and rays. *International Journal for Parasitology, 40*(2), 223-242. http://doi.org/10.1016/j.ijpara.2009.07.012

Otto, M. (1999). The problem of fossil interpretation. *Lethaia, 32*(2), 140-142. http://doi.org/10.1111/j.1502-3931.1999.tb00532.x

Otto, M. (2000). Supposed soft tissue preservation in the Hunsrückschiefer (Lower Devonian, Rheinisches Schiefergebirge): the example of brachiopods. *Paläontologische Zeitschrift, 74*(1-2), 79-89. http://doi.org/10.1007/BF02987954

Parham, J. F., Donoghue, P. C. J., Bell, C. J., Calway, T. D., Head, J. J., Holroyd, P. A., . . . Benton, M. J. (2012). Best Practices for Justifying Fossil Calibrations. *Systematic Biology, 61*(2), 346-359. http://doi.org/10.1093/sysbio/syr107

Park, J. K., Kim, K. H., Kang, S., Kim, W., Eom, K. S., & Littlewood, D. T. J. (2007). A common origin of complex life cycles in parasitic flatworms: evidence from the complete mitochondrial genome of Microcotyle sebastis (Monogenea : Platyhelminthes). *BMC Evolutionary Biology, 7*, 11. http://doi.org/10.1186/1471-2148-7-11

Parry, L., Tanner, A., & Vinther, J. (2014). The Origin of Annelids. *Palaeontology, 57*, 1091-1103. http://doi.org/10.1111/pala.12129

Parry, L. A., Edgecombe, G. D., Sykes, D., & Vinther, J. (2019). Jaw elements in *Plumulites bengtsoni* confirm that machaeridians are extinct armoured scaleworms. *Proceedings of the Royal Society B: Biological Sciences, 286*(1907), 20191247. http://doi.org/10.1098/rspb.2019.1247

Parry, L. A., Eriksson, M., & Vinther, J. (2019). The Annelid Fossil Record. In G. Purschke, M. Böggemann, & W. Westheide (Eds.), *Handbook of Zoology. Annelida. Volume 1: Annelida Basal Groups and Pleistoannelida, Sedentaria I.* (pp. 69–88). Berlin: DeGruyter.

Parry, S. F., Noble, S. R., Crowley, Q. G., & Wellman, C. H. (2011). A high-precision U–Pb age constraint on the Rhynie Chert Konservat-Lagerstätte: time scale and other implications. *Journal of the Geological Society, 168*(4), 863-872. http://doi.org/10.1144/0016-76492010-043

Parry, S. F., Noble, S. R., Crowley, Q. G., & Wellman, C. H. (2013). Reply to Discussion on 'A high-precision U–Pb age constraint on the Rhynie Chert Konservat-Lagerstätte: time scale and other implications': Journal, 168, 863–872. *Journal of the Geological Society, 170*(4), 703-706. http://doi.org/10.1144/jgs2012-089

Parry, L. A., Boggiani, P. C., Condon, D. J., Garwood, R. J., Leme, J. D. M., McIlroy, D., Brasier, M. D., Trindade, R., Campanha, G. A. C., Pacheco, M. L. A. F., Diniz, C. Q. C., & Liu, A. G. Mírian L. A. F. Pacheco, (2017). Ichnological evidence for meiofaunal bilaterians from the terminal Ediacaran and earliest Cambrian of Brazil. Nature Ecology & Evolution, 1(10), 1455-1464. https://doi.org/10.1038/s41559-017-0301-9

Paxton, H. (2009). Phylogeny of Eunicida (Annelida) based on morphology of jaws. *2009, 2*, 241-264. http://doi.org/10.11646/zoosymposia.2.1.18

Perkovsky, E., Rasnitsyn, A., Vlaskin, A., & Taraschuk, M. (2007). A comparative analysis of the Baltic and Rovno amber arthropod faunas: representative samples. *African Invertebrates, 48*(1), 229-245.

Philippe, H., Brinkmann, H., Copley, R. R., Moroz, L. L., Nakano, H., Poustka, A. J., Wallberg, A., Peterson, K. J., & Telford, M. J. (2011). Acoelomorph flatworms are deuterostomes related to *Xenoturbella*. *Nature, 470*(7333), 255-258. https://doi.org/10.1038/nature09676

Poinar, G. (1999). *Paleochordodes protus* n.g., n.sp. (Nematomorpha, Chordodidae), Parasites of a Fossil Cockroach, with a Critical Examination of Other Fossil Hairworms and Helminths of Extant Cockroaches (Insecta: Blattaria). *Invertebrate Biology, 118*(2), 109-115. https://doi.org/10.2307/3227053

Poinar, G. (2003a). A rhabdocoel turbellarian (Platyhelminthes, Typhloplanoida) in Baltic amber with a review of fossil and sub-fossil platyhelminths. *Invertebrate Biology, 122*(4), 308-312. https://doi.org/10.1111/j.1744-7410.2003.tb00095.x

Poinar, G. (2003b). Fossil evidence of phorid parasitism (Diptera: Phoridae) by allantonematid nematodes (Tylenchida: Allantonematidae). *Parasitology*, 127(6), 589. https://doi.org/10.1017/s0031182003004141

Poinar, G., & Boucot, A. J. (2006). Evidence of intestinal parasites of dinosaurs. *Parasitology, 133*(02), 245-249. http://doi.org/10.1017/S0031182006000138

Poinar, G., Kerp, H., & Hass, H. (2008). *Palaeonema phyticum* gen. n., sp. n. (Nematoda: Palaeonematidae fam. n.), a Devonian nematode associated with early land plants. *Nematology, 10*(1), 9-14. http://doi.org/10.1163/156854108783360159

Poinar, G., Philbrick, K. A., Cohn, M. J., Turner, R. T., Iwaniec, U. T., & Wunderlich, J. (2017). X-ray microcomputed tomography reveals putative trematode metacercaria in a 100 million year-old lizard (Squamata: Agamidae). *Cretaceous Research, 80*, 27-30. https://doi.org/10.1016/j.cretres.2017.07.017

Poinar, G. O. (2011). *The evolutionary history of nematodes: as revealed in stone, amber and mummies* (Vol. 9). Netherlands: Brill.

Poinar, G. O. (2014). Palaeontology of nematodes. In A. Schmidt-Rhaesa (Ed.), *Handbook of Zoology: Gastroricha, Cycloneuralia and Gnathifera* (Vol. 2: Nematoda, pp. 173-178).

Poinar, G. O. (2015). The Geological Record of Parasitic Nematode Evolution. *Advances in Parasitology, 90*, 53-92. http://doi.org/10.1016/bs.apar.2015.03.002

Poinar, G. O., & Ricci, C. (1992). Bdelloid rotifers in Dominican amber: Evidence for parthenogenetic continuity. *Experientia, 48*(4), 408-410. http://doi.org/10.1007/bf01923444

Poinar, G., Acra, A., & Acra, F. (1994). Earliest fossil nematode (Mermithidae) in Cretaceous Lebanese amber. *Fundamental and Applied Nematology, 17*(5), 475-477.

Poinar, G., & Buckley, R. (2006). Nematode (Nematoda: Mermithidae) and hairworm (Nematomorpha: Chordodidae) parasites in Early Cretaceous amber. *Journal of Invertebrate Pathology, 93*(1), 36-41. http://doi.org/10.1016/j.jip.2006.04.006

Poinar, G., Voisin, C., & Voisin, J. F. (2007). Bird eggshell in Dominican amber. *Palaeontology, 50*(6), 1381-1383. http://doi.org/10.1111/j.1475-4983.2007.00713.x

Poinar, G. O. (2012). New fossil nematodes in Dominican and Baltic amber. *Nematology, 14*(4), 483-488. http://doi.org/10.1163/156854111X612199

Poulin, R. (2001). Body size and segmentation patterns in free-living and parasitic polychaetes. *Canadian Journal of Zoology, 79*(5), 741-745. http://doi.org/10.1139/z01-033

Poulin, R. (2005). Evolutionary trends in body size of parasitic flatworms. *Biological Journal of the Linnean Society, 85*(2), 181-189. http://doi.org/10.1111/j.1095-8312.2005.00481.x

Qian, Y., & Yin, G. (1984). Zhijinitae and its stratigraphical significance. *Acta Palaeontologica Sinica, 23*, 216-223.

Qvarnström, M., Niedźwiedzki, G., & Žigaitė, Ž. (2016). Vertebrate coprolites (fossil faeces): an underexplored Konservat-Lagerstätte. Earth-Science Reviews, 162, 44-57. https://doi.org/10.1016/j.earscirev.2016.08.014

Radwańska, U., & Radwańska, A. (2005). Myzostomid and copepod infestation of Jurassic echinoderms: A general approach, some new occurrences, and/or re-interpretation of previous reports. *Acta Geologica Polonica, 55*(2), 109-130.

Regier, J. C., Shultz, J. W., Zwick, A., Hussey, A., Ball, B., Wetzer, R., Martin, J. W., & Cunningham, C. W. (2010). Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. *Nature, 463*(7284), 1079-1083. https://doi.org/10.1038/nature08742

Reguero, M., Goin, F., Hospitaleche, C. A., Marenssi, S., & Dutra, T. (2013). Late Cretaceous/Paleogene Stratigraphy in the James Ross Basin. In *Late Cretaceous/Paleogene West Antarctica Terrestrial Biota and its Intercontinental Affinities* (pp. 19-25): Springer.

Ritzkowski, S. (1997). K-ar-altersbestimmungen der bernsteinführenden sedimente des samlandes (paläogen, bezirk kaliningrad). *Metalla (Sonderheft), 66*, 19-23.

Rogers, R. R., Curry Rogers, K. A., Bagley, B. C., Goodin, J. J., Hartman, J. H., Thole, J. T., & Zatoń, M. (2018). Pushing the record of trematode parasitism of bivalves upstream and back to the Cretaceous. *Geology*, 46 (5), 431-434. https://doi.org/10.1130/G40035.1

Rohde, K. (2005). Definitions, and adaptations to a parasitic way of life. In K. Rohde (Ed.), *Marine Parasitology* (pp. 1-6). Oxon: CSIRO.

Rouse, G. W. (2005). Polychaeta (Bristle Worms). In K. Rohde (Ed.), *Marine Parasitology* (pp. 193-196). Oxon: CABI Publishing.

Rouse, G. W., & Pleijel, F. (2003). Problems in polychaete systematics. *Hydrobiologia, 496*(1), 175-189. https://doi.org/10.1023/A:1026188630116

Ruiz, G. M., & Lindberg, D. R. (1989). A fossil record for trematodes: extent and potential uses. *Lethaia, 22*(4), 431-438. https://doi.org/10.1111/j.1502-3931.1989.tb01447.x

Ruiz-Trillo, I., & Paps, J. (2016). Acoelomorpha: earliest branching bilaterians or deuterostomes? *Organisms Diversity & Evolution, 16*(2), 391-399. https://doi.org/10.1007/s13127-015-0239-1

Sanders, K. L., & Lee, M. S. Y. (2010). Arthropod molecular divergence times and the Cambrian origin of pentastomids. *Systematics and Biodiversity, 8*(1), 63-74. https://doi.org/10.1080/14772000903562012

Schram, F. R. (1973). Pseudocoelomates and a Nemertine from the Illinois Pennsylvanian. *Journal of Paleontology, 47*(5), 985-989. https://doi.org/10.2307/1303083

Schram, F. R., Vonk, R., & Cees, H. J. H. (1997). Mazon Creek Cycloidea. *Journal of Paleontology, 71*(2), 261-284. https://doi.org/10.1017/S0022336000039172

Seilacher, A. (1970). Begriff und bedeutung der Fossil-Lagerstätten. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1970, 34-39.

Seilacher, A. (2007). *Trace fossil analysis*: Springer.

Seilacher, A., Marshall, C., Skinner, H. C. W., & Tsuihiji, T. (2001). A fresh look at sideritic "coprolites". *Paleobiology*, 27(1), 7-13. https://doi.org/10.1666/0094-8373(2001)027%3C0007:AFLASC%3E2.0.CO;2

Shcherbakov, D. E., Timm, T., Tzetlin, A. B., Vinn, O., & Zhuravlev, A. Y. (2020). A probable oligochaete from an Early Triassic Lagerstätte of the southern Cis-Urals and its evolutionary implications. *Acta Palaeontologica Polonica*, 65(2), 219-233. https://doi.org/10.4202/app.00704.2019

Shi, G., Grimaldi, D. A., Harlow, G. E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., & Li, X. (2012). Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretaceous Research, 37*(0), 155-163. https://doi.org/10.1016/j.cretres.2012.03.014

Sielaff, M., Schmidt, H., Struck, T. H., Rosenkranz, D., Mark Welch, D. B., Hankeln, T., & Herlyn, H. (2016). Phylogeny of Syndermata (syn. Rotifera): Mitochondrial gene order verifies epizoic Seisonidea as sister to endoparasitic Acanthocephala within monophyletic Hemirotifera. *Molecular Phylogenetics and Evolution, 96*, 79-92. http://doi.org/10.1016/j.ympev.2015.11.017

Siveter, D. J., Briggs, D. E., Siveter, D. J., & Sutton, M. D. (2015). A 425-million-year-old silurian pentastomid parasitic on ostracods. *Current Biology, 25*(12), 1632-1637. https://doi.org/10.1016/j.cub.2015.04.035

Skelton, J., Farrell, K. J., Creed, R. P., Williams, B. W., Ames, C., Helms, B. S., Stoekel, J., & Brown, B. L. (2013). Servants, scoundrels, and hitchhikers: current understanding of the complex interactions between crayfish and their ectosymbiotic worms (Branchiobdellida). Freshwater Science, 32(4), 1345-1357. https://doi.org/10.1899/12-198.1

Sliter, W. V. (1971). Predation on benthic foraminifers. *The Journal of Foraminiferal Research, 1*(1), 20-28. https://doi.org/10.2113/gsjfr.1.1.20

Southcott, R. V., & Lange, R. T. (1971). Acarine and other microfossils from the Maslin Eocene, South Australia. Records of the South Australian Museum, 16, 1–21.

Sperling, E. A., & Vinther, J. (2010). A placozoan affinity for *Dickinsonia* and the evolution of late Proterozoic metazoan feeding modes. *Evolution & Development, 12*(2), 201-209. https://doi.org/10.1111/j.1525-142X.2010.00404.x

Størmer, L. (1963). *Gigantoscorpio willsi*, a new scorpion from the Lower Carboniferous of Scotland and its associated preying microorganisms. *Skrifter Utgitt av det Norske Videnskaps-Akademi i Oslo. Mathematisk-Naturvidenskabelig Klasse*, 8, 1-171.

Struck, T. H., Golombek, A., Weigert, A., Franke, F. A., Westheide, W., Purschke, G., Bleidorn, C., & Halanych, K. M. (2015). The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology, 25*, 1993-1999. https://doi.org/10.1016/j.cub.2015.06.007

Struck, T. H., Wey-Fabrizius, A. R., Golombek, A., Hering, L., Weigert, A., Bleidorn, C., Klebow, S., Iakovenko, N., Hausdorf, B., Petersen, M., Kück, P., Herlyn, H., & Hankeln, T. (2014). Platyzoan paraphyly based on phylogenomic data supports a non-coelomate ancestry of Spiralia. *Molecular Biology and Evolution*. https://doi.org/10.1093/molbev/msu143

Sudhaus, W. (2008). Evolution of insect parasitism in rhabditid and diplogastrid nematodes. In S. E. Makarov & R. N. Dimitrijevic (Eds.), *Advances in Arachnology and Developmental Biology: Papers Dedicated to Professor Bozidar P.M. Curcic* (pp. 143-161). Belgrade: Institute of Zoology.

Sudhaus, W. (2010). Preadaptive plateau in Rhabditida (Nematoda) allow the repeated evolution of zooparasites, with an outlook on evolution of life cycles with Spiroascarida. *Palaeodiversity, 3*(supplement), 117-130.

Suh, A., Witt, C. C., Menger, J., Sadanandan, K. R., Podsiadlowski, L., Gerth, M., Weigert, A., McGuire, J. A., Rheindt, F. E. (2016). Ancient horizontal transfers of retrotransposons between birds and ancestors of human pathogenic nematodes. *Nature Communications, 7*(1), 11396. https://doi.org/10.1038/ncomms11396

Suh, A. (2020). Horizontal Transfer of Transposons as Genomic Fossils of Host-Parasite Interactions. In Topics in Geobiology 50. Cham, Springer.

Summers, M. M., & Rouse, G. W. (2014). Phylogeny of Myzostomida (Annelida) and their relationships with echinoderm hosts. *BMC Evolutionary Biology, 14*(1), 170. https://doi.org/10.1186/s12862-014-0170-7

Szaniawski, H. (2002). New evidence for the protoconodont origin of chaetognaths. *Acta Palaeontologica Polonica, 47*(3), 405–419.

Szaniawski, H., & Gazdzicki, A. (1978). A reconstruction of three Jurassic polychaete jaw apparatuses. *Acta Palaeontologica Polonica, 23*(1), 5-29.

Tinsley, R. C., & Tinsley, M. C. (2016). Tracing ancient evolutionary divergence in parasites. *Parasitology, 143*(14), 1902-1916. https://doi.org/10.1017/s0031182016001347

Todd, J. A., & Harper, E. M. (2011). Stereotypic boring behaviour inferred from the earliest known octopod feeding traces: Early Eocene, southern England. *Lethaia, 44*(2), 214-222. https://doi.org/10.1111/j.1502-3931.2010.00237.x

Tzetlin, A. (1980). Ophryotrocha schubravyi sp. n. and the problem of evolution of the mouth parts in the Eunicemorpha (Polychaeta). *Zoologichesky Zhurnal, 59*(5), 666-676.

Upeniece, I. (2001). The unique fossil assemblage from the Lode Quarry (Upper Devonian, Latvia). *Fossil Record, 4*(1), 101-119. http://doi.org/10.1002/mmng.20010040108

Upeniece, I. (2011). *Palaeoecology and Juvenile Individuals of the Devonian Placoderm and Acanthodian Fishes from Lode Site, Latvia.* (Unpublished Doctoral Thesis). University of Latvia, Riga.

Vannier, J., Steiner, M., Renvoisé, E., Hu, S. X., & Casanova, J. P. (2007). Early Cambrian origin of modern food webs: evidence from predator arrow worms. *Proceedings of the Royal Society B: Biological Sciences, 274*(1610), 627-633. https://doi.org/10.1098/rspb.2006.3761

Verneau, O., Bentz, S., Sinnappah, N. D., Preez, L. d., Whittington, I., & Combes, C. (2002). A view of early vertebrate evolution inferred from the phylogeny of polystome parasites (Monogenea: Polystomatidae). *Proceedings of the Royal Society B-Biological Sciences, 269*(1490), 535-543.

Verneau, O., Du Preez, L., & Badets, M. (2009). Lessons from parasitic flatworms about evolution and historical biogeography of their vertebrate hosts. *Comptes Rendus Biologies, 332*(2-3), 149-158.

Vinther, J., Eibye-Jacobsen, D., & Harper, D. A. (2011). An Early Cambrian stem polychaete with pygidial cirri. Biology Letters, 7(6), 929-932.

Vinther, J., & Parry, L. A. (2019). Bilateral Jaw Elements in *Amiskwia sagittiformis* Bridge the Morphological Gap between Gnathiferans and Chaetognaths. *Current Biology, 29*(5), 881-888.e881. https://doi.org/10.1016/j.cub.2019.01.052

Voigt, E. (1938). Ein fossiler Saitenwurm (*Gordius tenuifibrosus* n. sp.) aus der eozänen Braunkohle des Geiseltales. Nova Acta Leopoldina, N.F. 5, 351-360.

Wade, M. (1972). *Dickinsonia*: polychaete worms from the late Precambrian Ediacara fauna, South Australia. *Memoirs of the Queensland Museum, 16*(2), 171-190.

Waggoner, B. M., & Poinar, G. O., Jr. (1993). Fossil habrotrochid rotifers in Dominican amber. *Experientia, 49*(4), 354-357. https://doi.org/10.1007/BF01923421

Walossek, D., & Müller, K. J. (1994). Pentastomid Parasites from the Lower Paleozoic of Sweden. *Transactions of the Royal Society of Edinburgh-Earth Sciences, 85*, 1-37. https://doi.org/10.1017/S0263593300006295

Walossek, D., Repetski, J. E., & Muller, K. J. (1994). An exceptionally preserved parasitic arthropod, *Heymonsicambria taylori* n.sp. (Arthropoda incertae sedis: Pentastomida), from Cambrian-Ordovician boundary beds of Newfoundland, Canada. *Canadian Journal of Earth Sciences, 31*(11), 1664-1671. https://doi.org/10.1139/e94-149

Waloszek, D., Repetski, J. E., & Maas, A. (2005). A new Late Cambrian pentastomid and a review of the relationships of this parasitic group. *Transactions of the Royal Society of Edinburgh-Earth Sciences, 96*, 163-176. http://doi.org/10.1017/S0263593300001280

Warn, J. M. (1974). Presumed Myzostomid Infestation of an Ordovician Crinoid. *Journal of Paleontology, 48*(3), 506-513.

Warnock, R., & Engelstädter, J. (2020). The molecular clock as a tool for understanding host-parasite evolution. In Topics in Geobiology 50. Cham, Springer.

Weigert, A., Helm, C., Meyer, M., Nickel, B., Arendt, D., Hausdorf, B., Santos, S. R., Halanych, K. M., Purschke, G., Bleidorn, C., & Struck, T. H. (2014). Illuminating the base of the annelid tree using transcriptomics. *Molecular Biology and Evolution, 31*(6), 1391-1401. https://doi.org/10.1093/molbev/msu080

Weinstein, S. B., & Kuris, A. M. (2016). Independent origins of parasitism in Animalia. *Biology Letters, 12*(7). https://doi.org/10.1098/rsbl.2016.0324

Welch, J. R. (1976). *Phosphannulus* on Paleozoic crinoid stems. *Journal of Paleontology, 50*(2), 218-225.

Wolfe, J. M., Daley, A. C., Legg, D. A., & Edgecombe, G. D. (2016). Fossil calibrations for the arthropod Tree of Life. *Earth-Science Reviews, 160*, 43-110. https://doi.org/10.1016/j.earscirev.2016.06.008

Xianguang, H. O. U., & Bergström, J. A. N. (1994). Palaeoscolecid worms may be nematomorphs rather than annelids. *Lethaia, 27*(1), 11-17. https://doi.org/10.1111/j.1502-3931.1994.tb01548.x

Yang, B., Steiner, M., Zhu, M., Li, G., Liu, J., & Liu, P. (2016). Transitional Ediacaran–Cambrian small skeletal fossil assemblages from South China and Kazakhstan: Implications for chronostratigraphy and metazoan evolution. *Precambrian Research, 285*, 202-215. https://doi.org/10.1016/j.precamres.2016.09.016

Yang, C., Li, X.-H., Zhu, M., Condon, D. J., & Chen, J. (2018). Geochronological constraint on the Cambrian Chengjiang biota, South China. *Journal of the Geological Society, 175*(4), 659-666. https://doi.org/10.1144/jgs2017-103

Zangerl, R., & Case, G. R. (1976). *Cobelodus aculeatus* (Cope), an anacanthous shark from Pennsylvanian black shales of North America. *Palaeontographica, Abteilung A, 154*(4-6), 107-157.

Zeng, H., Zhao, F., Yin, Z., Li, G., & Zhu, M. (2014). A Chengjiang-type fossil assemblage from the Hongjingshao formation (Cambrian stage 3) at Chenggong, Kunming, Yunnan. *Chinese science bulletin*, 59(25), 3169-3175. https://doi.org/10.1007/s11434-014-0419-y

Zrzavý, J. (2001). The interrelationships of metazoan parasites: a review of phylum-and higher-level hypotheses from recent morphological and molecular phylogenetic analyses. *Folia Parasitologica, 48*(2), 81-103.

Zrzavý, J., Hypša, V., & Tietz, D. F. (2001). Myzostomida are not annelids: molecular and morphological support for a clade of animals with anterior sperm flagella. *Cladistics, 17*(2), 170-198. https://doi.org/10.1006/clad.2000.0148