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Kenneth De Baets
John Warren Huntley *Editors*

The Evolution and Fossil Record of Parasitism

Identification and Macroevolution of Parasites

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Editors

The Evolution and Fossil Record of Parasitism

Identification and Macroevolution of Parasites

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Foreword

The ‘fossil record’ and ‘parasites’ may seem strange bedfellows. Parasitism tends to be overlooked by palaeontologists even though it is one of the most successful ecological strategies and an important feature of the evolutionary history and palaeoecology of many groups. One measure of the importance of parasites is their diversity—they may account for more than 50% of all living species. Nonetheless, parasites are largely invisible today even if the same cannot be said of their effects. They are generally small and soft bodied, and certainly not strong candidates for fossilisation. However, their evolutionary history is intriguing and raises issues such as when parasitism originated and in which groups, how parasites coevolved with their hosts, how they impacted the ecology of ancient communities, and how interactions between parasite and host changed over time. The fossil record provides the only direct evidence of parasitism in the past, and it can contribute essential data to answering such questions.

Parasites, of their very nature, require exceptional conditions for fossilisation, and Konservat-Lagerstätten (conservation deposits) have proved important sources in recent decades. Malarial parasites and trypanosomatids, for example, have been discovered in the guts of biting insects in amber more than 100 million years old from the Cretaceous of Burma. Eggs and cysts of intestinal parasites are present in coprolites of late Palaeozoic elasmobranchs and Cretaceous dinosaurs, from aquatic and terrestrial settings, respectively. Giant flea-like insects have been found in Mesozoic lake sediments in Inner Mongolia and Liaoning Province in China. New examples of parasitism also continue to come to light in host fossils based on the galls, swellings and other malformations triggered by the parasite—but in this case the perpetrator is often difficult to identify and other factors may be at work.

Molecular data provide a major new line of evidence on the evolution of parasites, even though the nature of parasite genomes can present particular challenges. Gene sequences have allowed the phylogeny of different groups of parasites to be analysed where morphological data are limited. The phylogeny of the free-living relatives may also be informative. Phylogenies of parasites and of their host species, together with dates based on fossil occurrences, can yield estimates of divergence times (i.e. when they originated) based on molecular clocks. Such phylogenies reveal patterns of co-evolution and host switching. Fossils, however, are essential to calibrate clocks even though this is challenging due to the rare occurrence of parasites in the fossil record. Fossils may also provide more direct evidence of ancient parasite–host relationships. In rare cases they preserve associations that no longer persist, showing that initial hosts were different from those that are favoured today. The remarkable 430 million-year-old Silurian Herefordshire deposit in England, for example, which I have been investigating with colleagues for the last 25 years, has yielded a pentastomid crustacean which is clearly ectoparasitic on marine ostracods (examples are preserved attached to the ostracod carapace, and on eggs within it). Living pentastomids, in contrast, apart from a few exceptions that live on insects, are parasitic on terrestrial vertebrates where they invade the respiratory system.

A surprising range of parasites are represented in the fossil record but they have received relatively little attention to date, at least in terms of a major synthesis, an omission that is remedied here in grand style. The importance of parasitism is reflected in 25 contributions by more than 50 authors. All the important groups of parasites are reviewed: bacteria, protozoa, fungi, cnidarians, bivalves, gastropods, helminths, acanthocephalans, chelicerates, crustaceans and insects as well as fossil evidence on their impact on hosts: colonial organisms, crustaceans, trilobites, cephalopods, bivalves, echinoderms, vertebrates. The major issues covered include the ways in which parasites and their effects are fossilised, the evolution of host–parasite associations, the history of parasitism as recorded in the fossil record, and the utility of genomics and the molecular clock in revealing the course of host–parasite evolution. This welcome compilation will provide an indispensable platform for future work on this fascinating topic.

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Derek E. G. Briggs

Reconstructions of known and lesser known fossil parasites made especially for this volume by (c) Franz Anthony (http://franzanth.com/): Cambrian pentastomid *Heymonsicambria scandica* (upper left) described by Walossek and Müller (1994: https://doi.org/10.1017/S0263593300006295), developing roundworm *Ascarites priscus* (upper centre) from the Lower Cretaceous described by Poinar and Boucot (2006: https://doi.org/10.1017/S0031182006000138), Cretaceous copepod *Kabatarina pattersoni* (upper right) described by Cressey and Boxshall (1989: https://doi.org/10.2307/1485466), putative parasitic isopod *Urda rostrata* (middle center) from the Jurassic described by Nagler et al. (2017: https://doi.org/10.1186/s12862-017-0915-1), Late Cretaceous engorged tick *Deinocroton draculi* (middle left) described by Peñalver et al. (2017: https://doi.org/10.1038/s41467-017-01550-z), Eocene bird louse *Megamenopon rasnitsyni* (middle right) described by Wappler et al. (2004: https://doi.org/10.1098/rsbl.2003.0158), developing acanthocephalan (lower left) from the Upper Cretaceous described Cardia et al. (2019: https://doi.org/10.1590/0001-3765201920170848) early nematode *Palaeonema phyticum* (lower center) described by Poinar et al. (2008: https://doi.org/10.1163/156854108783360159) from the Lower Devonian, and developing tapeworm from the Permian described by Dentzien-Dias et al. (2013: https://doi.org/10.1371/journal.pone.0055007)

Preface

Over 50% of living organisms have been interpreted to be parasitic, and most organisms host at least one species of parasite during their life. Their historical reputation is not the best for obvious reasons. This is even worse in the fossil record where parasites and their traces are considered to be too scarce to be helpful. Although some reviews have been published in the last decades, these often involve works of archaeological remains or focus on particular groups or time intervals. The fossil record is often still ignored by parasitologists and palaeontologists alike and only briefly mentioned in works focusing on parasite evolution and ecology. We felt we wanted to change this by highlighting the importance of the fossil record in reconstruction of the evolution of parasitism. During a research stay of John in Erlangen, we decided this could best be done in the form of two volumes dedicated to the evolution and fossil record of parasitism. The first volume covers the palaeobiological constraints on the fossil record, while the second volume focuses on novel techniques as well as the merit of co-evolutionary and pathological information linked with parasitic disease. Furthermore, we do not only discuss the origin of modern groups of parasites but also groups which are now extinct. We hope you as a reader will learn about how one can study parasites in the fossil record as well as what they can tell us about the evolution of parasitism. This journey started when looking for particular authors to contribute to this work—special thanks goes to all of them in accepting, contributing, and bearing with us during this endeavour. Special thanks also to the reviewers as well as Franz Anthony who designed the accompanying illustration featuring some more and some lesser known fossil parasites. Despite being two parasite aficionados, we have learned a lot about the parasite fossil record and evolution during the preparation and editing of this book. These volumes demonstrate that a lot of progress has been made, but also highlight areas where there is still some work to be done. This is particularly true regarding the prevalence of parasites and gaining a better understanding of their taphonomy and temporal and spatial trends. At least some of these things might benefit from novel techniques such a computed tomography and genomics. Both of us have been working on parasites for about 10 years and had great fun and effort to bring these chapters together. We therefore hope you will enjoy the ride through the fossil record of various groups of parasites, the usefulness in finding them or their traces still associated with their hosts, as well as new techniques to further constrain their evolutionary history.

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Chapter 1
Parasites of Fossil Vertebrates: What We Know and What Can We Expect from the Fossil Record?

Tommy L. F. Leung

Abstract Parasites are ubiquitous in extant ecosystems and vertebrate animals often harbour rich parasite communities. However, the geological record of parasites is extremely sparse as their very nature means they are rarely fossilised. The few fossil parasites which have been described have provided interesting insights into the evolution of various parasite taxa, and the development of technology such as high-resolution computed tomography has made detecting signs of parasitism in the fossil record more practical. In this chapter, I will provide an overview of vertebrate-infecting macroparasites which have been described from fossils, and compare those fossil forms with their extant counterparts. I will also discuss what those fossils can tell us about the evolution of parasitism and the ecology of their hosts, the type of parasite fossils which may be associated with fossil vertebrates, and suggest some future research directions which combine aspects of palaeontology, ecology, and parasitology.

Keywords Parasitism · Parasites · Parasite communities · Helminths · Arthropods · Amber · Coprolite · Palaeoecology

1.1 Introduction

Parasites are ubiquitous in extant ecosystems, many of them play important ecosystem roles and form key parts of many food webs (Lafferty et al. 2006; Hatcher and Dunn 2011). As a life-style, parasitism has evolved independently multiple times in many disparate groups of organisms (Poulin and Morand 2004; Poulin 2007; Weinstein and Kuris 2016), and extant vertebrates are host to rich communities of

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parasites, both on their external surfaces as well as their various internal organs and tissues. These parasites vary in their taxonomy, life-cycle, infection site, and the effects that they have on their hosts. Many parasites are specialised to live on a specific part of the host's body, and the body of a vertebrate animal can be thought of as a collection of microhabitats, each inhabited by one or more specific parasite species (Loker and Hofkin 2015).

Despite their abundance in many extant ecosystems, parasites are exceedingly rare in the fossil record as most parasites are not conducive to being preserved as fossils. Many of them are small and have soft bodies, or do not leave traces of their presences on the host tissue in a way which will be fossilised (De Baets et al. 2021b). Additionally, most palaeontological studies are not focused on looking for traces of parasitism, so it is also possible that many fossil parasites are being overlooked (Littlewood and Donovan 2003). As such, little is known about the effects they have on their hosts or the ecological roles they played in various palaeoenvironments. However, there are a small collection of studies which have found evidence of parasites from fossil vertebrates (Boucot and Poinar 2011; De Baets and Littlewood 2015; Leung 2017). These studies provide vital glimpses into the evolution of parasitism throughout Earth's history.

The potential for detecting the signs of parasitism or parasites themselves in fossil samples has increased in recent years with technology such as computed tomography which allows well-preserved specimens to be examined for finer, microscopic details (e.g. Siveter et al. 2015; Robin et al. 2016; Poinar et al. 2017; Peñalver et al. 2017). However, an important step in furthering the study of fossil parasites is for palaeontologists to be aware of and recognise the potential for fossilised parasites. As such, any prospective palaeoparasitologists needs to be aware of what to expect and what to look for when it comes to potential fossil parasites. Since vertebrate taxa have relatively large body sizes and are host to a variety of different parasites, fossil vertebrates and their associated remains are great potential sources of parasite fossils. So how would a prospective parasite palaeontologist know what to look for when it comes to fossil parasites? How can they recognise a parasite when they see one? This is where having a general idea of the likely parasite community of a given fossil vertebrate taxa would be helpful, and there are methods for inferring potential parasites of extinct vertebrate taxa and anticipate their association with well-preserved vertebrate fossils.

The aim of this chapter is to provide an overview of vertebrate-infecting parasites which have been described from the fossil record, how they compare with their equivalents found in extant vertebrates, and how we can combine concepts and techniques from palaeontology and ecological parasitology to further develop research into this field. This chapter will be covering the types of macroparasites which have been found from fossil vertebrates that are pre-Pleistocene in age. For each group, I will provide (1) some background on the biology and ecology of their extant taxa, (2) what groups can be expected to host such parasites, (3) what types of fossils can be expect from such parasites, and (4) future research directions.

1.1.1 Cestodes (Tapeworms)

There are approximately 6000 described species of cestodes (Stunkard 1983). Better known as tapeworms, cestodes are found in all major groups of extant vertebrates (Littlewood et al. 2015). They have a complex life-cycle that is deeply linked with predator-prey relationships (see Mackiewicz 1988 for details). The adult cestode lives in the intestine of a vertebrate animals where it produces eggs via sexual reproduction. These eggs are released into the environment where they are ingested by an animal which functions as the intermediate host where the larva can grow and develop. This intermediate host is usually an arthropod, though for some families of cestodes, the intermediate host is a vertebrate animal, and may involve sequentially infecting two or more intermediate hosts. The life-cycle is completed when the infected intermediate host is eaten by the definitive vertebrate host (Mackiewicz 1988).

Being soft-bodied internal parasites, adult cestodes are not readily fossilised (Littlewood and Donovan 2003). The only known fossils for cestodes come in the form of their fossilised eggs (Zangerl and Case 1976; Dentzien-Dias et al. 2013; De Baets et al. 2015). While the sclerotized hooks on the cestode's scolex, the attachment organ anterior of the parasite, can potentially be fossilised under the right conditions, and putative fossils of such hooks in fossil cestode eggs have been reported by Dentzien-Dias et al. (2013). While Upeniece (2011) and De Baets et al. (2015) have suggested some fossil hook circlets associated with Devonian placoderm and acanthodians fossils might be cestode hooks, such fossilised hooks would be situated deep within the host's body and are unlikely to be found from an external examination of a fossil specimen. Upeniece (2001, 2011) has previously documented microscopic hooks present on placoderm fossils and suggested they might be cestode or monogenean hooks. Based on the arrangements of the hooks and where they were distributed on the placoderm, Leung (2017) suggested that it is more likely that they belong to monogeneans (see also De Baets et al. 2015, 2021a)—a group of ectoparasitic flatworms that will be discussed later in this chapter.

So far, there have been two published examples of fossilised cestode eggs, both of them from elasmobranch hosts (Zangerl and Case 1976; Dentzien-Dias et al. 2013), however, given the taxonomic range of extant vertebrates that act as definitive hosts for cestodes (Littlewood et al. 2015), there is a strong possibility that fossilised cestode eggs may be present in the coprolites or lower gastrointestinal tract of fossil vertebrates other than elasmobranchs. The findings of fossilised cestode eggs in elasmobranch coprolites supports molecular phylogeny studies which points to a very long coevolutionary history between elasmobranchs and many cestode lineages (Olson et al. 2010; Caira and Jensen 2014; Caira et al. 2014). Indeed a significant number of extant cestode species (28%) parasitise elasmobranch hosts (Littlewood et al. 2015), and the lineages that infect tetrapod and teleost hosts are nested within elasmobranch-infecting lineages (Caira et al. 2014). Fossils of cestode eggs can provide additional insight into when cestodes began colonising non-elasmobranch hosts, and act as useful calibration points for molecular phylogeny studies (De Baets et al. 2021a). Given fossils of other helminth eggs have previously been found as inclusions in coprolites (e.g. Poinar and Boucot 2006; Hugot et al. 2014; Chin 2021), the coprolites of many other vertebrates should be similarly examined for the presence of cestode eggs in a manner comparable to what has been achieved with subfossils and other archaeological remains (Gonçalves et al. 2003).

1.1.2 Trematodes (Flukes)

There are 18,000 described species of trematodes (Cribb et al. 2001). Like cestodes, trematodes are also internal parasites of vertebrates and have complex life-cycles (Cribb et al. 2003; Galaktionov and Dobrovolskij 2003). While most species have adult stages that live in the gastrointestinal tract of their definitive vertebrate host, there are some families of trematodes that have evolved to occupy other parts of the host's body such as the circulatory system, eyes, lungs, liver, bladder, and the connective tissue and muscles (Cribb et al. 2003; Poulin 2005). Additionally, extant trematodes in the Digenea group (which represents over 99.9% of all known living species) have an asexual reproduction stage (Cribb et al. 2003; Galaktionov and Dobrovolskij 2003) which results in the production of vast number of mobile larval stages which infect the next host in the life-cycle. Depending on the family, this is either a second intermediate host where they encyst, or the vertebrate definitive host where they will develop into sexually mature adults. This asexual reproduction stage in the intermediate host is absent in most other parasitic worms, and in most extant trematodes, asexual reproduction occurs in a mollusc host, which is usually a gastropod in most families (Cribb et al. 2003; Galaktionov and Dobrovolskij 2003). As with other parasitic worms, adult trematodes are soft-bodied internal parasites that do not usually fossilise even under the most ideal preservation conditions. However, they do produce environmentally resistant eggs that can potentially be fossilised with coprolites. So far, there has been one published example of fossilised trematode eggs, reported from dinosaur coprolites dating from the Early Cretaceous (Poinar and Boucot 2006). Given that trematodes are known from all major extant vertebrate groups (Cribb et al. 2003; Galaktionov and Dobrovolskij 2003; Littlewood et al. 2015), and that eggs from various lineages of trematode have been reported in more recent quaternary fossils and subfossil coprolites (e.g. Jouy-Avantin et al. 1999; Le Bailly and Bouchet 2010; Wood et al. 2013) examination of older coprolite samples may yield more trematode egg fossils.

A recent fossil find indicates that amber can preserve the larval stage of trematodes along with their host. Recently, Poinar et al. (2017) reported finding what appears to be the metacercaria stage of a trematode from a lizard preserved in Myanmar amber dated to the Early Cretaceous. The size and position of the fossil metacercaria is strikingly similar to that of some extant trematodes which use lizards (particularly Anoles) as the second intermediate host in their life-cycle (Poinar et al. 2017). This fossil provides some very useful insight into the evolutionary history of these trematodes, and its similarity in general morphology, host type, and host site to some extant trematodes indicates that the complex life-cycle of trematodes seen in extant taxa have existed since at least the Cretaceous.

Aside from their eggs and larval stages preserved *in situ* with their host in amber, larval trematodes may also leave other type of traces in the fossil record. The larval stages of some trematodes, namely those in the Gymnophallidae family, also infect bivalves as a part of their life-cycles and their presence can induce pitting, igloo-shaped concretions (e.g. Ituarte et al. 2005) and/or pearl formation in the shell which are more readily fossilised (e.g. Ruiz and Lindberg 1989; Ozanne and Harries 2002; see Huntley and De Baets 2015; Huntley et al. 2021). While shell pitting in bivalves can also be caused by other non-trematode factors (Leung 2017), the igloo-shaped concretions produced by gymnophallid larvae are quite distinct and is considered to be a reliable indicator of that particular trematode lineage (Huntley and De Baets 2015). A recent study places definitive evidence for the presence of igloo-shaped concretions in the Cretaceous (Rogers et al. 2018), and while similar traces have been found on the shells of Silurian bivalves (Liljedahl 1985), Huntley and De Baets (2015) cautioned against interpreting those as being caused by gymnophallid trematodes. Similarly, the presence of “blister pearls” (often represented as pits in steinkerns) of Early Devonian ammonoids might have been caused by parasites (De Baets et al. 2011), there is no conclusive evidence that they were caused by trematodes (De Baets et al. 2015). So while trematodes can leave potential trace fossils, fossilised eggs in coprolites or larval stages preserved in the intermediate hosts provide more definitive information on the likely lineage or taxonomic identity of the fossil trematode. Since trematodes are common in extant vertebrates with 18,000 known extant species, fossils can give insight into how and when they became so diverse and successful (De Baets et al. 2021a).

1.1.3 Nematodes (Roundworms)

Nematodes (commonly known as roundworms) are one of the most diverse and abundant animal phyla on earth, they inhabit a wide variety of ecological niches including parasitism (Poinar 1983). For the purpose of this chapter, I will be focusing on nematodes that infected fossil vertebrates, but for an extensive and detailed overview of parasitic nematodes in the fossil record, readers are referred to (De Baets et al. 2021a; Poinar 2015).

Parasitism has independently evolved at least 15 times in different nematode lineages, parasitising invertebrates, vertebrates, and plant hosts (Blaxter and Koutsovoulos 2015). Based on molecular phylogeny, nematodes have evolved to parasitise vertebrate animals on four separate occasions, and that they had arisen from arthropod-infecting taxa (Blaxter et al. 1998). A more recent molecular phylogenetic study proposed that Ascaridoidea—a diverse superfamily of nematodes found in all major vertebrate groups—has a common ancestor dating back to the Early Carboniferous (Li et al. 2018). Ascaridoidea is a particularly important group of vertebrate parasites, containing over 800 known species, many of which are widely recognised and studied because of their medical and economic importance (Anderson 2000). Much like cestodes and trematodes discussed above, the adult stage living in the gastrointestinal tract is very unlikely to become fossilised. However the environmentally-resistant eggs produced by the adult parasite can be preserved as inclusions in coprolites (e.g. Da Silva et al. 2014), survive treatment with strong acids and/or bases (e.g. Brinkkemper and van Haaster 2012; Dufour and Le Bailly 2013), and serve as a reliable indicator of the parasite's presence. Fossilised ascarid nematode eggs have so far been found in archosaur coprolites from the Early Cretaceous to Late Cretaceous (Poinar and Boucot 2006; Cardia et al. 2018, 2019a) and cynodont coprolites from Middle Triassic (Da Silva et al. 2014). Given the ubiquity of parasitic nematodes in extant vertebrate hosts (Anderson 2000), the presence of fossilised nematode eggs in the coprolites of phylogenetically distant groups as archosaurs and synapsids, and the result by Li et al. (2018) which proposed ascaridoids had originated in terrestrial hosts during the Early Carboniferous—close to the period when tetrapods began diversifying into various terrestrial habitats (Dunne et al. 2018)—it can be expected that most extinct vertebrate groups were host to ascaridoid nematodes, and their fossilised eggs may be present as inclusions in coprolites originating from many different tetrapods.

Another group of parasitic nematodes commonly found in the gastrointestinal tract of extant vertebrates are the Oxyurida—also known as "pinworms". Pinworms are found in the hindgut of many different invertebrate and vertebrate animals and are usually associated with hosts that have hindgut bacterial fermentation because of their bacterivorous diet (Adamson 1994). Fossils of pinworm eggs have been found in the coprolites attributed to therapsid cynodonts from the Middle Triassic (Hugot et al. 2014; Francischini et al. 2018), and given the taxonomic breadth of extant pinworm hosts, it can be expected that pinworm eggs may be present in coprolites of a wide range of terrestrial vertebrates. Various aspects of these pinworm biology also means they can provide valuable insight on the ecology and biology of their host. Francischini et al. (2018) pointed out that pinworm egg inclusions were found in "cylindrical" type coprolites, which were traditionally considered to be produced by carnivorous or omnivorous therapsids. However, the presences of the pinworm egg fossils overturn such an interpretation, as their presence implies that the originator of those coprolites included substantial amount of plant matter in their diet (Francischini et al. 2018). Also mentioned above, pinworms are restricted to infecting animals that use their hindgut as a site for bacterial fermentation, furthermore their eggs have limited dispersal ability and mostly rely upon social grooming or local contamination for transmission (Adamson 1994). Therefore, the very presence of fossilised pinworm eggs in coprolites can provide at least three key insights on the diet (mostly plant matter), physiology (hindgut fermentation) and behaviour (living in social groups or colonies) of the host taxa which may not be evident from examining the fossil of the host alone.

While all the known whole body fossils of animal-infecting parasitic nematodes have so far been from amber fossils of insect-infecting taxa (Poinar 2015), those fossils may nevertheless provide insight into nematodes that do infected fossil vertebrates. Some vertebrate-infecting nematodes with complex life-cycles are phylogenetically affiliated with and may have evolved from insect-infected lineages (Blaxter and Koutsovoulos 2015). Furthermore, many vertebrate-infecting nematodes use insects and other arthropods as intermediate hosts (Anderson 2000), thus much like the fossilised trematode metacercariae described by Poinar et al. (2017), some amber fossils may contain insects (and other small animals) which hosted the larval stage of vertebrate-infecting nematodes. Furthermore, some biting insects can act as vectors for parasitic nematodes—another superfamily of nematodes that commonly parasitises tetrapod vertebrates are the Filarioidea. Also known as filarials, the adult stage lives in the lymphatic or cardiovascular system of their vertebrate host, producing larval stages known as microfilarials which use blood-feeding arthropods as vectors to transmit to new hosts (Anderson 2000). Presently, there are three known species of filarials which have been described from fossils, all of which have been placed in the *Cascofilaria* genus; *C. baltica* which was found associated with a blackfly in Eocene age Baltic amber, *C. dominicana* which was found associated with a female mosquito in Dominican amber, and *C. parvus* which was also found associated with a mosquito host (Poinar 2015). The morphology of those fossil microfilarials resemble extant filarial species that infect mammals and amphibians (Poinar 2015). It is worth pointing out that there is some evidence to suggest human-infecting (and other mammal-infecting) filarial worms might have originated from bird-infecting filarials about 17–25 million years ago (Suh et al. 2016; Suh 2021), which overlaps with the age of Dominican amber which have preserved remains of tropical birds including their feathers and egg shells (Poinar 2010). Thus, parasites which are found in biting insects that are preserved in such amber deposits can provide vital insight into the origin and evolution of vector-transmitted parasites such as filarial nematodes.

1.1.4 Acanthocephalans (Thorny-Headed Worms)

Acanthocephalans, commonly known as thorny-headed worms, are a group of internal parasites with complex life cycles. There are about 1150 known living species, and all major groups of extant vertebrates have been found to host acanthocephalans, with the adult stage of this parasite living in the gastrointestinal tract of various vertebrate animals including fish, amphibians, reptiles, mammals, and birds (Kennedy 2006). The adult worm anchors itself to the gut wall of the vertebrate host using an eversible proboscis which is covered with hooks and spines (Miller and Dunagan 1985).

The typical life cycle of acanthocephalan involves two hosts, with the adult living in a vertebrate host, producing eggs which are released into the environment, and an arthropod intermediate host which become infected by acanthocephalan larvae when they ingest the parasite's eggs (Kennedy 2006). However, many species also incorporate additional vertebrates to act as paratenic (transport host) (e.g. Sinisalo and Valtonen 2003; Médoc et al. 2011)—the acanthocephalan larvae do not undergo further development in those hosts, however paratenic hosts can help the parasite complete its life-cycle as they serve as a bridge between arthropods and the acanthocephalan's final host, which are often macropredatory vertebrates which do not usually prey upon small arthropods (Nickol 1985; Kennedy 2006).

The adult stages of acanthocephalans are soft bodied and thus unlikely to be preserved as fossils, and while theoretically the hooks on the proboscis may potentially become fossilised under ideal circumstances, much like what has been discussed above for tapeworms, flukes, and roundworms, the stage most likely to be found as fossils would be eggs embedded in coprolites produced by their vertebrate hosts (Herlyn 2021).

Presently, the oldest known fossil example of acanthocephalans are fossilised eggs which were found as inclusions in coprolites that have been attributed to Late Cretaceous crocodyliformes (Cardia et al. 2019b). Much like the fossil pinworm eggs discussed above, they provide us with some interesting insight into the ecology of their host, since the presence of acanthocephalan eggs indicates the crocodyliformes that produced the coprolite had either consumed arthropods and/or vertebrate animals. This allows us to conclude that the coprolites most likely originated from one of the species of carnivorous (or at least omnivorous) crocodyliformes that had been found in that formation.

Furthermore fossils of acanthocephalans may also provide information on the evolution of Acanthocephala as a whole and their pattern of host-usage (Herlyn 2021). Presently, Acanthocephala is divided into four distinct classes, and each of those classes infect different suite of vertebrate animals from different environments as their final hosts (Verweyen et al. 2011). Finding evidence of acanthocephalan infection in fossil vertebrates, especially in lineages that left no living relatives, may help shed light how these parasites had evolved to infect the type of hosts that they do today.

1.1.5 Monogeneans

Monogeneans are a major group of parasitic flatworms which mostly live as ectoparasite of fish, with approximately 3000–4000 described species (Whittington 1998). Being soft-bodied animals they are highly unlikely leave behind fossils, however their attachment organ—the haptor—has microscopic, scleritised hooks which can potentially be fossilised under certain conditions (Littlewood and Donovan 2003). Fossilised monogenean hooks have previously been found associated with placoderms and acanthodians (Upeniece 2001, 2011), and their positioning on the fins, gill region, and abdomen of the host is comparable to that of extant monogeneans (Whittington 1998). Given their presence on those two phylogenetic distinct groups of extinct fish and the wide range of extant fish lineages that host monogeneans, it can be expected that most fossil fish from the Devonian period onward would have been parasitised by monogeneans.

1.1.6 Parasitic Copepods

Aside from monogeneans, one of the most commonly found ectoparasites of extant fishes are parasitic copepods (Boxshall 2005; Klompmaker and Boxshall 2015). Parasitic copepods make up approximately one-third of all known extant copepod diversity (Humes 1994; Ho 2001), and many of them are parasites of fish (Boxshall 2005) that attach themselves to the skin, gills, fins, or eyes of their hosts (Kearn 2004). Some parasitic copepods have highly derived morphology and are not easily recognisable as crustaceans, and some are considered as "mesoparasites" because the adult stages live partially embedded within the host's internal organ, while the rest of the body (usually the reproductive organs) protrude into the external environment (Kearn 2004).

Despite their ubiquity among extant fishes, there is currently only one documented example of a parasitic copepod in fossil fish (although some pathologies in fossil fish have been attributed to copepods, see Klompmaker and Boxshall 2015 for discussion), which was found within the gill chamber of an Early Cretaceous fish (Cressey and Patterson 1973). It was later described and named *Kabatarina pattersoni* and assigned to an extant family of parasitic copepod; Dichelesthiidae (Cressey and Boxshall 1989). This discovery raises two key points; (1) there may be extant parasitic copepod families that have had long histories and have relatives in the fossil record which have similar morphologies to their extant counterparts, and (2) well-preserved fish fossils presents opportunities for finding fossils of parasitic copepods (and indeed other parasites). This is a possibility which should be explored using micoCT scans, and much like monogeneans, given the ubiquity of parasitic copepods among extant fish (Kabata 1982), it can be expected that many extinct fish taxa would be host to parasitic copepods.

1.1.7 Parasitic Isopods

Parasitism has evolved in many crustacean taxa and aside from copepods, another group with many parasitic representatives are the isopods. Within Isopoda, there are three major groups of parasites: the Cymothoidae which are mostly ectoparasites of fish (Smit et al. 2014); Gnathiidae which are specialised ectoparasitic blood-feeders with a multi-stage developmental cycle (Smit and Davies 2004), and Epicaridea which are highly-derived parasites of crustaceans (Williams and Boyko 2012). Of those groups, the cymothoids and gnathiids are the two families which parasitise vertebrate hosts, mostly ray-finned fishes (Smit and Davies 2004; Smit et al. 2014).

A few recent studies on molecular phylogeny and fossils of parasitic isopods have provided some insight into the origin and evolution of parasitism in isopods. Smit et al. (2014) have suggested that based on the presence of fossil evidence for bopyrid (a very speciose family within Epicaridea) isopods in the Jurassic (Boucot and Poinar 2011; Klompmaker et al. 2014), fish-parasitising cymothoids most likely originated during the same time since the two group share a close common ancestry. This is supported by the recent discovery of some Middle to Late Jurassic fish fossils which are fossilised with isopods attached to their body (Haug et al. 2021; Nagler et al. 2016, 2017).

But as mentioned above, apart from the external body surfaces, cymothoids are also known to live in other parts of the host body such as the buccal cavity, gill chambers, and body cavity (Smit et al. 2014). A recent molecular phylogeny study indicates that the shift between living on the body surface and living in the buccal cavity or gill chambers might have independently occurred a number of times within the cymothoids (Hata et al. 2017). Furthermore, colonisation of the host body cavity has independently evolved in two separate lineages of cymothoids (Hata et al. 2017). Therefore, we should also expect that aside from being present on the skin and fins of fossil fish, there is also a possibility that some might be obscured within the host's mouth, gill chambers, and abdominal cavity, much like the parasitic copepod (Cressey and Patterson 1973) from the gill chamber of an Early Cretaceous fish fossil. As mentioned in relation to that example, microCT and similar techniques can potentially be used to examine well-preserved fish fossils for the presence of parasitic isopods (Nagler et al. 2017). While they are mainly parasites of teleost fish, cymothoids have also been documented from some elasmobranchs (Williams et al. 2010), and two disparate groups of extant marine reptiles—snakes (Saravanakumar et al. 2012) and turtles (Júnior et al. 2015). In the case of turtles, they were found around parts of the body that have thinner tissue and are more vascularized such as eyelids (Júnior et al. 2015). Given their capacity to infect those two extant marine reptile groups, it is possible that some Jurassic and Cretaceous marine reptiles may have also served as viable hosts for these parasitic isopods, thus expanding the range of potential hosts in the fossil record which may have hosted cymothoids.

However, a note of caution in regards to interpreting fossils of isopods as parasites when they are found in association with larger animals. Marine isopods are opportunistic feeders that frequently scavenge on vertebrate carcasses, and fossils of their scavenging activities have previously been found (Wilson et al. 2011; Klompmaker and Boxshall 2015; Robin et al. 2019). Thus before concluding any fossils of vertebrate-isopod association as a case of parasitism, one must ensure there is evidence to indicate that the host was alive and engaged in extended interaction with the isopod(s) when they became fossilised. Another possible method of establishing whether a fossil isopod was parasitic is by comparing its functional morphology and with that extant parasitic isopods, as parasitic species have specialised feeding and attachment structures that distinguish them from their free-living relatives (e.g. Nagler and Haug 2016).

1.1.8 Pentastomids (Tongue Worms)

Aside from copepods and isopods, another group of parasitic crustaceans which are known from fossils are the pentastomids. Also known as "tongue worms" due to the shape of the adult stage, the taxonomic affinity of pentastomids had been an enigma until they were finally recognised as highly-derived crustaceans (Lavrov et al. 2004). Extant pentastomids are respiratory tract parasites of tetrapods, mostly reptiles (Riley 1986), but the oldest known fossils of pentastomids are larval stages dating back from the Late Cambrian (Walossek and Müller 1994; Walossek et al. 1994; Klompmaker and Boxshall 2015), over 100 million years before the appearance of tetrapods, therefore it is unclear what those pentastomids parasitised (assuming that they were parasites at all). It has been suggested that those early pentastomids might have been parasites of basal chordates and led a more simple life-cycle than extant pentastomida (Sanders and Lee 2010), living in the gill cavities of their hosts (Walossek and Müller 1994).

A more recently described fossil suggests that the original hosts for pentastomids were in fact crustaceans (Siveter et al. 2015) and that they colonised vertebrate hosts much later in their evolutionary history. *Invavita piratica* lived during the mid-Silurian period and unlike the isolate larval microfossils found by Walossek and Müller (1994), the *I. piratica* specimen was interpreted as an adult which was found attached to its host—an ostracod (Siveter et al. 2015). This indicates that pentastomids might have originated as ectoparasites of crustaceans and incorporated vertebrates host and became internal parasites much later in their evolutionary history (but see Haug et al. 2021). So how and when did this switch in host and mode of parasitism occur?

Leung (2017) suggested it might have occurred through a process of "upward incorporation" (Parker et al. 2015)—the original crustacean host of pentastomids may have also been prey for the jawed fish that began appearing in the ocean during that period (Friedman and Sallan 2012; Klug et al. 2017), and what might have begun as an way of surviving their host's predation by transferring to the vertebrate predator subsequently became an obligate part of their life-cycle. In this scenario, as tetrapods evolved from those jawed fish and began colonising terrestrial biomes, the pentastomids coevolved with them, by which point they had evolved to live as internal parasites which allow them to survive in hosts which lived in terrestrial biomes. Further fossils of pentastomids can test the validity of this hypothesis, as well as provide more insights into how and when pentastomids transitioned from being ectoparasites of crustaceans to endoparasites of tetrapods, and how this might relate to the colonisation of land by tetrapods.

1.1.9 Ticks

There is abundant evidence for non-avian dinosaurs, pterosaurs, and non-mammalian synapsids being covered in fine integumentary features (Dhouailly et al. 2017)—which seems to be an ideal niche for ectoparasitic arthropods. Ticks are common ectoparasites of terrestrial vertebrates (Klompen et al. 1996), and while molecular phylogeny analysis placed the origin of ticks to the late Carboniferous (Mans et al. 2012), the oldest confidently identified fossil ticks are from the Cretaceous (e.g. Poinar and Buckley 2008; Estrada-Peña and de la Fuente 2018; Dunlop 2021).

Fossil ticks are usually found in isolation from host material, however, their morphology resembles that of extant ticks closely enough to infer their parasitic, hematophagous life-style, in some case can even be identified to extant genera (e.g. *Amblyomma birmitum*—Chitimia-Dobler et al. 2017). While only a few fossils of ticks have been described, they are likely to have been blood-feeding ectoparasites of many extinct terrestrial vertebrate taxa. This is supported by fossils that indicate such ticks were also hosts for vector-borne pathogens which are similar to those that infect extant vertebrates (Poinar 2019). A molecular phylogeny study found the divergence of hard and soft ticks to have occurred during the Early Permian, which indicates a Carboniferous origin for ticks (Mans et al. 2012). This was also during an important period in the evolution and diversification of terrestrial vertebrates and amniote animals (Clack 2002), therefore it is possible that ticks coevolved with terrestrial tetrapods.

Recent discoveries of dinosaur body parts or even entire hatchlings with intact plumage in amber (Xing et al. 2016, 2017) presented exceptional opportunities to investigate potential dinosaur ectoparasites such as ticks. Such amber fossils not only preserve the parasite in detail, but also *in situ* with host material, thus providing direct evidence for their parasite-host relationships. As an illustrative example, recently some tick fossils were described by Peñalver et al. (2017) from Middle Cretaceous Burmese amber. The ticks were found in association with loosely vaned pennaceous feathers which are found on penneraptoran dinosaurs, but not crown birds (Peñalver et al. 2017), thus providing unequivocal evidence of ectoparasites on non-avian theropod dinosaurs. Furthermore, some of the fossil ticks have morphology which indicates they belonged to families that no longer exist, such as *Deinocroton draculi* which was assigned to the family Deinocrotonidae (Peñalver et al. 2017). This indicates that there are families of ticks which have become co-extinct with their hosts, indeed this should be expected as many extant parasite groups had lineages that have become extinct with their hosts during various extinction events, indeed the potential co-extinction of parasites with their endangered hosts has recently emerged as a key issue in conservation biology (e.g. Campião et al. 2015; Strona 2015; Thompson et al. 2018).

1.1.10 Ectoparasitic Insects (Fleas and Lice)

While insects originated in the Devonian (Misof et al. 2014), evidence for insect feeding on the blood of vertebrates did not appear until the mid-Mesozoic (Lukashevich and Mostovski 2003). Nagler and Haug (2015) provided an extensive review on fossils of parasitic insects including those that are ectoparasites of vertebrates. There are at least seven orders of insects that have evolved to associate with vertebrates with their relationships ranging from commensalism to parasitism, with some feeding non-invasively on host secretion to those that actively feed on host tissue such as integumentary growth or blood (Waage 1979). It is worth noting that the major groups of ectoparasitic insects are usually associated with hosts that have integumentary features, it is possible that the evolution of integumentary structures in synapsids and dinosaurs might have provided suitable environments for the diversification of many ectoparasitic insect groups (Leung 2017), in a manner comparable to how angiosperm plants had coevolved with many herbivorous and pollinator insects (Labandeira et al. 1994; Grimaldi 1999). Of those, the insect orders that have evolved to parasitise vertebrates, the most successful groups are the lice (orders Phthiraptera) and the fleas (order Siphonaptera), both of which are composed wholly of ectoparasitic species, and both are common parasites of birds and mammals.

But while homeothermic terrestrial vertebrates had been interpreted to exist at least since the Triassic (Padian and Sues 2015), as mentioned above, both lice and fleas only began appearing in the fossil record after the K-Pg mass extinction event. Zhu et al. (2015) found that fleas diversified on mammals before they also colonised birds. A recent study on the molecular phylogeny of lice indicates that they radiated on birds and mammals after the K-Pg event, of which one lineage was exclusive to birds, and that the rapid diversification of birds and mammals after K-Pg was associated with the evolutionary radiation of their lice (Johnson et al. 2018). At the same time, another recent study indicates that there was a K-Pg mass extinction of stem birds, subsequently followed by a radiation of crown birds (Field et al. 2018). Together, these provide evidence that modern lice and fleas diversified alongside lineages of birds and mammals that survived the K-Pg extinction event. Much like other fossil insects, amber would be the most promising material to investigate for ectoparasitic insects, especially amber fossils that include some integumentary material or parts of the body from a potential host, as discussed above in relation to fossil ticks.

1.2 A Note of Caution Regarding Fossil Parasites

As discussed above, despite their diversity and abundance on extant birds and mammals, truly definitive fossils of lice and fleas did not appear until the Early Eocene (Wappler et al. 2004) and Miocene (Dittmar et al. 2015) respectively. While there have been some reports of “giant Jurassic fleas” from the mid-Mesozoic (Gao et al. 2012), their status as fleas or even as ectoparasites appears questionable. Dittmar et al. (2015, 2016) have pointed out a number of problems with the interpretation of those fossil insects as hematophagous ectoparasites. Indeed, that seems to be a recurring problem in the literature on various fossil insects which have been interpreted as having a parasitic life-style based on nothing more than conjecture (as discussed in Leung 2017). For example, the Strashilidae, a family of Jurassic insects, was initially interpreted as ectoparasites of pterosaurs or dinosaurs based on the morphology of mouthpart and hindlimbs (Ponomarenko 1976). This assumption was carried over in subsequent published studies on this family of insects (Rasnitsyn 1992; Vršanský et al. 2010) until newer fossil specimens led to a re-evaluation of its lifestyle and revealed it to be a sexually dimorphic aquatic insect (Huang et al.

2013). Furthermore, the morphological traits that were initially cited by Rasnitsyn (1992) as adaptations for parasitism—sucking mouthparts and prominent hindlimbs—are also found in a wide range of non-parasitic insects and should not be considered as definitive diagnostic features for ectoparasitism (Leung 2017). Similarly, the fossil larvae of Jurassic dipteran *Qiyia jurassica* was interpreted by Chen et al. (2014) as a hematophagous ectoparasite of aquatic amphibians on the basis of its sucking mouthpart and thoracic suckers, yet as Leung (2017) pointed out, the characteristics that Chen et al. (2014) interpreted as parasitic adaptations are also found on many non-parasitic freshwater insects. Most importantly, none of those fossils insects that have been interpreted as ectoparasites were ever found in association with their postulated hosts or host material. Misattribution of parasitism to extinct taxa is still an ongoing issue in the palaeontological literature. For example, Ponomarenko (1976) described the Early Cretaceous insect *Saurophthirus* as a kind of stem flea that lived on pterosaurs on the basis of a single fossil. But as Dittmar et al. (2015) and Zhu et al. (2015) pointed out, that interpretation is highly questionable and inconsistent with what is known about the morphology and phylogeny of crown fleas (Dittmar et al. 2016). Despite that, recently published studies on *Saurophthirus* has taken the "pterosaur ectoparasite" interpretation at face value, so much so that every aspect of its morphology has been interpreted by some workers as that of a hematophagous pterosaur ectoparasite (Rasnitsyn and Strelnikova 2017; Shcherbakov 2017) even though (1) no Saurophthiridae fossils have ever been found in association with pterosaur fossil material, (2) their morphological traits are also found on insects with non-parasitic life-styles, and (3) multiple aspects of the *Saurophthirus* fossil contradict this hypothesis (Rasnitsyn and Strelnikova 2018).

This should not be taken as a discouragement against searching for parasitic insects in the fossil record, but rather, a call for a more critical appraisal of fossil material and cultivating interdisciplinary research between palaeontologists, parasitologists and researchers from various other relevant fields. The lack of true fossil fleas and lice prior to the Cenozoic actually raises some intriguing questions about whether insects lived as ectoparasites of terrestrial homeotherms prior to the K-Pg extinction event, and if so (1) were they of the same order as those of extant ectoparasites, or did they belong to entirely different or potentially extinct groups? (2) Or perhaps the ectoparasitism niche was occupied by some other type of arthropods, and if so (3) what were the dominant ectoparasites of terrestrial homeotherms such as dinosaurs and mammals during the Mesozoic?

1.3 Framework for Inferring Parasite Communities of Extinct Vertebrate Groups

Based on fossil parasites which have been described thus far, it seems that most extinct vertebrates, at least those from the Mesozoic to recent, have similar or comparable parasites to their extant relatives (De Baets et al. 2015). While fossil parasites are rare and difficult to find, it is possible to anticipate the potential presence of certain parasite taxa in fossil taxa of vertebrates, based on the kind of parasites which are found on their extant relatives or modern ecological equivalents. This can be done by applying two concepts taken from palaeontology and ecology respectively: Extant Phylogenetic Bracketing and Ecological Fitting.

Extant Phylogenetic Bracketing (EPB; Bryant and Russell 1992; Witmer 1995) is often used for inferring the potential presence of certain soft tissues in extinct taxa, however, it can also be applied in a manner to inferring the potential parasite communities of extinct taxa. For example based on the ubiquity of tapeworms in extant vertebrates, it is possible to infer that many extinct fossil taxa bracketed within Vertebrata would had served as definitive hosts to the adult tapeworms (see Fig. 1.1). Similar, for monogeneans discussed above, since they are found in all extant groups of jawed fish and fossils of their hooks have been found on two wholly extinct groups (placoderms and acanthodians), it is possible to infer that many extinct taxa of fish could have potentially hosted monogeneans. By applying the EPB framework to parasite communities of fossil taxa, this would allow us to use their closest living relatives as a rough guide to the potential composition of their parasite communities.

But what if the extinct taxa are morphologically and ecologically very different from their closest living relatives (for example sphenacodontid synapsids, large theropod dinosaurs, sauropod dinosaurs, sauropterygians)? That is where the concept of “Ecological Fitting” (Agosta and Klemens 2008) would be useful. The term was coined by Janzen (1985) to describe an organism that is able to live and persist in a

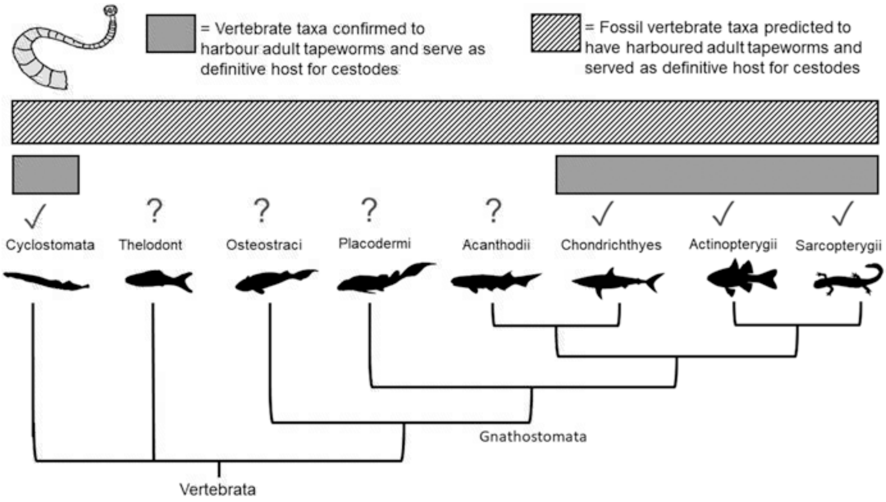


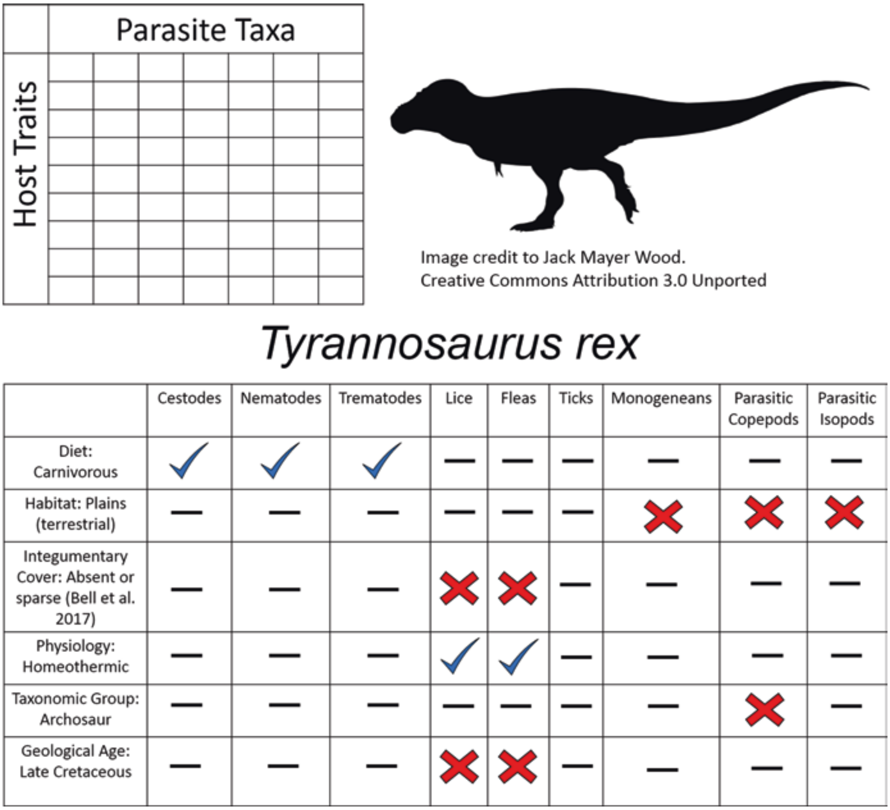
Fig. 1.1 An example of applying Extinct Phylogenetic Bracketing to fossil host taxa. Here, the focal parasites are the adult stage of cestodes (tapeworms). By looking at the extant groups which are known to act as definitive hosts for cestodes, it can be inferred that some wholly extinct vertebrate taxa may have also hosted adult cestodes in their gastrointestinal tract. Silhouette of the different hosts are from PhyloPic (http://phylopic.org/)

novel environment as a result of adaptations that have evolved under a different set of circumstances. As applied to parasites, it means some parasites may be found in host groups with which they did not have a long co-evolutionary history, and that taxonomically different hosts may share similar parasites because they share similar ecological niche and acquire similar parasite communities as a result of being exposed to a similar suite of infective stages (Hoberg and Brooks 2008).

This is broadly comparable to convergent evolution, where phylogenetically disparate taxa evolve similar adaptations under similar circumstances. In this case, such adaptations might have also predisposed them to being infected by similar parasites. For example, various studies have found associations between an animal's diet and the composition of its parasite fauna (Poulin and Morand 2004). Many parasites use trophic transmission, where the parasite is transmitted via the consumption of the infective stage in prey items as a mean of completing their life-cycles (Lafferty 1999), thus diet has a direct influence on the composition of their internal parasites. Indeed, parasites can be used to infer the diet of an animal and in contrast to stomach content, which can only provide a brief snapshot of what the animal had recently consumed, the presence of a parasite species is a lasting indicator of an animal's diet (e.g. Valtonen et al. 2010). In regards to fossil parasites of extinct vertebrate hosts, this line of inference can be inverted. The likely diet of a fossil animal might help us infer what kind of internal parasites we can expect to find associated with it.

In some cases, the presence of parasite larvae in prey species which are consumed by many different types of predators can facilitate host switch across phylogenetically distant taxa. For example, *Corynosoma australes* is an acanthocephalan commonly found in the gastrointestinal tract of pinnipeds, but they have also successfully parasitised Magellanic penguins (*Spheniscus magellanicus*) (Hernández-Orts et al. 2017). Despite being from completely separate branches of amniotes, due to the overlap in diet in both sea lions and penguins (in this case, fish), the latter acquired a parasite which would usually complete its life-cycle in a marine mammal host. Indeed, it seems that over long evolutionary time, endoparasitic helminths are particularly apt at switching between phylogenetically distant vertebrate definitive hosts and host-switching appear to be a common feature in their evolution (Poulin and Morand 2004). Therefore, extant species occupying the same ecological niche may provide a general approximation of the type of parasites that infect phylogenetically distant taxa that once occupied the same niche. For example, many of the marine reptiles that lived during the Mesozoic filled similar ecological niches to those occupied by extant marine mammals (Kelley and Motani 2015), and given that some of those extinct marine reptiles such as ichthyosaurs and plesiosaurs might have also been at least partially homeothermic (Bernard et al. 2010), there is a strong possibility that they shared similar parasite communities to some modern cetaceans.

Thus based on what is known about the ecology and host types of extant parasites, one can use information on the diet, habitat, morphology, physiology, phylogeny, and geological age of a given fossil taxon to infer what type of parasites were potentially included in (or conversely, excluded from) its parasite community (see



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Tyrannosaurus rex

	Cestodes	Nematodes	Trematodes	Lice	Fleas	Ticks	Monogeneans	Parasitic Copepods	Parasitic Isopods
Diet: Carnivorous	✓	✓	✓	—	—	—	—	—	—
Habitat: Plains (terrestrial)	—	—	—	—	—	—	✗	✗	✗
Integumentary Cover: Absent or sparse (Bell et al. 2017)	—	—	—	✗	✗	—	—	—	—
Physiology: Homeothermic	—	—	—	✓	✓	—	—	—	—
Taxonomic Group: Archosaur	—	—	—	—	—	—	—	✗	—
Geological Age: Late Cretaceous	—	—	—	✗	✗	—	—	—	—

Fig. 1.2 A method for using host characteristics to infer the potential parasite community of a fossil taxa. Here *Tyrannosaurus rex* is used as an example, and the parasite taxa represented are based on the groups discussed in this chapter. Each row represents a given host characteristic, while each column represents a different parasite taxon. Check mark denotes that the characteristic predisposes the host to being infected with that given parasite type. Dash denotes the characteristic having neutral or no effect on the likelihood of harbouring such parasite type. Cross denotes the characteristic would exclude such parasite taxa as having occurred on/in the host. A single cross associated with any of the host characteristics will conclusively exclude the existence of said parasite taxon from the host taxon, even if other characteristics may theoretically predispose the host to it

Fig. 1.2). The focal host taxa can be as broad as an entire class or as narrow as a single species. The same also applies to the parasite taxa being examined which can be as broad as different phyla or as specific as different families within a given order (for example, comparing different families of animal-infecting nematodes which have different life-cycles and transmission pathways).

Through a combination of EPB and Ecological Fitting, one can deduce a list of potential parasites which are likely to have associated with a given extinct vertebrate taxa, and based on that, guide potential searches for fossils of said parasites whether they be in amber, coprolite, or compression fossils. Amber is an exceptional material that can preserve many organisms intact and in some cases, in their original ecological context (Poinar 1992), including some parasite-host relationships as shown through the examples discussed in this chapter. However, researchers must be mindful that amber is subjected to preservation biases (e.g. De Baets et al. 2021b; Kraemer et al. 2018), which provides an incomplete picture of the range of interactions which existed in a given palaeoenvironment. For coprolites, given the range of palaeoecology information that can be derived from studying the coprolites of vertebrates (Chin 2002, 2021; Bajdek et al. 2016), it would be advisable for researchers to also be on the lookout for fossils of parasite propagules while investigating such material.

1.4 Future Research Directions and Further Questions

Fossils can provide vital insights into the evolution of parasitism (De Baets and Littlewood 2015; De Baets et al. 2021b). Based on molecular phylogeny and fossils of parasites, it seems that major events in the history of parasite groups were often associated with diversification and extinction events of their vertebrate host taxa. Future fossil discoveries can address some key questions about evolution of parasites which are found on vertebrate hosts, and can in turn be used to help calibrate molecular studies on the phylogeny of various parasite groups. Many different taxa have independently evolved some kind of parasitic life style and often the parasitic representatives have heavily derived morphology that differ very significantly from their closest living non-parasitic relatives. Fossil parasites might provide insight into the transition between free-living and parasitism, both in terms of changes in their morphology and pattern of host or resource usage.

There are some fossil parasites that were discovered or described incidentally such as the case of Zangerl and Case (1976), where microfossils of what appears to be cestode eggs were found amidst the coprolitic material associated with the lower intestinal tract of a Carboniferous elasmobranch. Re-examination of older specimens using more recent technology such as microCT scans and other techniques (e.g., Maas 2013) may yield further discoveries. At the same time, microfossils of parasite materials such as helminth eggs or monogenean hooks may become inadvertently dislodged or destroyed during some preparation processes, thus any prospective palaeoparasitologists should make use of preparation and analysis methods that minimise disruption of the original material.

When examining, describing, and identifying potential fossil parasites, the study by Poinar et al. (2017) on the trematode metacercaria embedded in the leg of an amber-preserved lizard can be considered as an example of “best practice”. The fossil they described was of the type of deposit/material (in this case,