# Chapter 11
# The History of Insect Parasitism and the Mid-Mesozoic Parasitoid Revolution

**Conrad C. Labandeira and Longfeng Li**

**Abstract** Insect parasites and parasitoids are a major component of terrestrial food webs. For parasitoids, categorization is whether feeding activity is located inside or outside its host, if the host is immobilized or allowed to grow, and if the feeding is done by one or many conspecific or heterospecific individuals, and other features. Fossil evidence for parasitism and parasitoidism consists of taxonomic affiliation, morphology, gut contents, coprolites, tissue damage and trace fossils. Ten hemimetabolous and holometabolous orders of insects developed the parasite condition whereas seven orders of holometabolous insects evolved the parasitoid life habit. Modern terrestrial food webs are important for understanding the Mid Mesozoic Parasitoid Revolution. The MMPR began in late Early Jurassic (Phase 1), in which bottom-to-top regulation of terrestrial food webs dominated by inefficient clades of predators were replaced by top-to-bottom control by trophically more efficient parasitoid clades. The MMPR became consolidated in Phase 2 by the end of the Early Cretaceous. These clades later expanded (phases 3 and 4) as parasitoids became significant ecological elements in terrestrial food webs. Bottom-to-top food webs explained by the resource concentration hypothesis characterize pre-MMPR time. During phases 1 and 2 of MMPR (Middle Jurassic to Early Cretaceous), a shift

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K. De Baets, J. W. Huntley (eds.), *The Evolution and Fossil Record of Parasitism*,
Topics in Geobiology 49, https://doi.org/10.1007/978-3-030-42484-8_11

ensued toward top-to-down food webs, explained by the trophic cascade hypothesis, exemplified by hymenopteran parasitoid clades Stephanoidea and Evanioidea. Clade-specific innovations spurring the MMPR included long, flexible ovipositors (wasps), host seeking, triungulin and planidium larvae (mantispids, beetles, twisted-wing parasites, flies), and extrudable, telescoped ovipositors (flies). After the MMPR, in phases 3 and 4 (Late Cretaceous to Recent), parasitoids increased in taxonomic diversity, becoming integrated into food webs that continue to the present day.

**Keywords** Food webs · Idiobiont · Koinobiont · Ovipositor drill · Telescoped ovipositor · Triungulin larvae

> It seems clear that the ancestral hymenopteran and dipteran parasitoids found themselves in a relatively unexploited adaptive zone. The resultant adaptive radiation onto different host species, possibly occurring simultaneously with the adaptive radiation of the modern insect orders, is responsible for the huge number of species we observe today. (H.C.J. Godfray 1994)

> … parasites [and parasitoids] strongly affect food web structure. Indeed, they disproportionately dominate food web links. … yet some parasites [parasitoids] have population dynamic impacts that are hugely disproportionate to their small size … recognition of parasite [parasitoid] links may have important consequences for ecosystem stability because they can increase connectance and nestedness. (Lafferty et al. 2006, insertions ours to conform with modern terminology)

## 11.1 Introduction

One of the enduring features of continental ecosystems during and since the mid Mesozoic has been the ecological expansion of insect parasitism in general and the emergence of the insect parasitoid guild in particular. This underappreciated fact only recently has been recognized (Labandeira 2002, 2015; Li et al. 2018a), given the increasingly important role that insect (Freeland and Boulton 1992; Mills 1994; Lafferty et al. 2006; Dunne et al. 2013) and other (Kuris et al. 2008; Hughes et al. 2011a) parasitoids play in the trophic structure of modern terrestrial ecosystems. For example, one of the best-studied systems has been the leaf miner–parasitoid community in Central America, which spotlights the importance of top-to-bottom parasitoid regulation of leaf-mining herbivores in local food webs (Memmott et al. 1994, 2000). According to the fossil record, parasitism—in the broad sense that includes parasitoidism (Lafferty et al. 2006)—began in the marine realm, evolving at least 136 times across 15 of the conventionally recognized 43 phyla ranging from Cnidaria to Arthropoda (Weinstein and Kuris 2016). Of these phyla, it is Arthropoda, both marine and continental, that had the most numerous independent originations of parasitism, constituting about 64% of total originations. It is in the continental realm that encompasses terrestrial and freshwater ecosystems where known cases of parasitism expand dramatically. The parasitoid guild in continental ecosystems is represented by at least 84 separate originations among 10 orders of insects, amounting to 10% of all described insect species (Gaston 1991; Weinstein and Kuris 2016). Considering only parasitoids, rather than the broader category that would include inquilines, parasites and cleptoparasitoids, there are 68,000 out of 850,000 described insect species, or about 8% of the total, that are obligately parasitoid species (Gaston 1991; Godfray 1994). The majority of insect parasitoids are typically small, inconspicuous wasps of Hymenoptera (sawflies, wasps, ants and bees), constituting about 75% of the total, and Diptera (true flies) account for another 20% (Eggleton and Belshaw 1992). The remaining 5% is scattered among lineages of Neuroptera (lacewings and antlions), Coleoptera (beetles), Strepsiptera (twisted-wing parasites), Trichoptera (caddisflies) and Lepidoptera (moths and butterflies) (Askew 1971; Eggleton and Belshaw 1992; Godfray 1994). However, because of their inconspicuousness, rarity and frequent fidelity to a single host, there is significant underreporting of parasitoid taxa in local, community-level assessments. This under-representation especially is true for apocritan wasps (LaSalle and Gauld 1991) and tachinid Diptera (Crosskey 1980; also see Stireman III 2005). Given these and other recent updates and trends in species descriptions, it is probable that up to 25% of insect species have parasite or parasitoid life habits (Godfray 1994), and that 20% of insect species are solely parasitoids (Hochberg and Hawkins 1992).

Historically, a major issue regarding macroevolutionary patterns in parasite and especially parasitoid insects has been whether diet specialization, as opposed to consumption of an eclectic spectrum of food, has been a pathway for increased diversification (Rainford and Mayhew 2015). One early test of these two contending hypotheses was sister clade comparisons of lineages in which one clade possessed a non-parasitoid diet and its sister clade engaged in an exclusively parasitoid diet (Wiegmann et al. 1993). The question posed by the authors of that study was whether the parasitoid life habit (see below for a definition) was an evolutionary dead end involving specialization, or rather a key innovation that led to expansive speciation (Wiegmann et al. 1993). The authors found, of 15 clades examined, that 6 were significantly more diverse and 9 less diverse than their saprophage or predator sister clades, leading to the conclusion that a parasitic or parasitoid life style does not result in increased diversification rates and may very well be an evolutionary dead end. However, the “push of the past” phenomenon, whereby clades that persist for a significant length of deep time typically experience high levels of early diversification but subsequently have substantially decreased levels (Budd and Mann 2018), is a relevant consideration. The push-of-the-past phenomenon may indicate that currently depauperate parasitoid clades have experienced elevated speciation levels in the past. Nevertheless, this seeming paradox of elevated specialization and evolution of a highly restricted life habit yielding a dramatic increase in speciosity (Drake 2003) was retested by Rainford and Mayhew (2015) by employing a different approach, methodology and analyses (details are provided in Rainford and Mayhew 2015). The results of Rainford and Mayhew (2015) indicated that there are well-characterized bouts of diversification of parasitoidism involving parasitoid wasps (Rainford and Mayhew 2015), where the bulk of parasitoidism, approximately 75%, resides (Eggleton and Belshaw 1992). Contributing to this pre-eminence of hymenopteran parasitoids is that about 85% of insect parasitoids have an adult female as the host-seeking stage (Eggleton and Belshaw 1992). By contrast, the relatively rare life-habit of ectoparasitism (defined below) was identified as an ecological dead end for insect diversification, occurring prominently in the Phthiraptera (lice). Importantly, the majority of these parasitoid and ectoparasite lineages (Rainford and Mayhew 2015), whether or not they led to specialized dead ends or elevated diversification of taxa, originated during the Middle Jurassic to Early Cretaceous (Labandeira 2002). During the mid Mesozoic, the diversification of parasitoid taxa, compared to the slowly evolving ectoparasite taxa, likely was linked to the presence of complete metamorphosis (holometabolous development) as a major key innovation (Rainford et al. 2014), rather than any clade-specific transformation.

This contribution is organized into two sections. The first section is a review of the biology and fossil history of insect parasitism and parasitoidism. The review includes relevant definitions of a parasite and parasitoid and their relationship to predation, the several types of parasitoidism, the kinds of evidence for demonstrating all three feeding behaviors in the fossil record, their evolutionary biology, and an extended exploration of their fossil record. In the second section, the Mid Mesozoic Parasitoid Revolution (MMPR) is proposed as a major biological event in terrestrial food-web history. As the MMPR is the principal emphasis of this report, evidence for the MMPR is provided from the fossil record and modern studies of terrestrial food webs, indicating that ecological communities were transformed during this prolonged event. This transformational change started from resource-driven control of consumers that emphasized bottom–up links in which photosynthesis was regulated by the availability of plant resources for their herbivore consumers. Later, a shift toward parasitoid-driven control of consumers focused on top–down, more efficient regulation. Four fossil biotas from each of the time intervals—before, during and after the MMPR—illustrate this trophic transformation of food webs by the dramatic increase of parasitoid groups in the mid Mesozoic. Last, the diversification events of two lineages of wasp parasitoids, Stephanoidea and Evanioidea, are examined to understand the role of hymenopteran parasitoids during the early phases of the MMPR. The contribution concludes by an assessment of the role that trophic specialization provided in launching the MMPR and the consequences of this major ecological event.

## 11.2 Defining the Insect Consumption of Animals

The terms predation and parasitism are well established in the paleobiological and entomological literature. The indelicately pronounced term, parasitoidism, has been a more recent term and formalized concept, and has received a considerable amount of scrutiny, particularly in the older literature (Clausen 1940; Askew 1971). In the earlier literature, the term parasitism was used confusingly to mean the traditional parasitism of insects that often feed on a variety of integumental tissues or less commonly in internal tissues of large animals, often vertebrates, whose hosts remain alive after attack, as well as true parasitoids that consume and eventually kill their considerably larger hosts. In this contribution, a distinction is made between these three, very different life habits and consideration is made of parasitism and parasitoidism as trophically distinctive feeding modes (Frank and Gillett-Kaufman 2006; Labandeira 2002).

A recurring issue that informs the definition of parasitism is whether herbivory, in the broadest sense of the interaction, a form of parasitism (Windsor 1998; Eggleton and Gaston 1990). Efforts also have been made to circumscribe a special type of herbivory that occurs in concealed plant tissues, such as leaf mines or galls, as parasitism (Janzen 1975; Price 1980). Whether the broader or the narrower version of herbivory is considered as parasitism, it would render moot much of the specialized trophic biology of animal–animal interaction inherent in true parasitism. Moreover, if parasites are defined as species that exploit other free-living species (Windsor 1998), then minimally about half of all species are parasites (May 1988; Bush et al. 2001), or parasites probably outnumber free-living species by a factor of 4 (May 1992). Such an inordinate broadening of the definition of parasitism would provide sustenance to the claim that parasitism is a confounding concept (Araújo et al. 2003). Historically, herbivory has been considered as a fundamental trophic interaction limited to plants as the consumed organisms (Ings et al. 2009), whereas parasitism—as well as predation and parasitoidism—have considered animals as the consumed organisms. That distinction is retained herein.

### *11.2.1 Predation*

Predation is a type of trophic interaction of a consumer that requires multiple prey items throughout its lifetime and always results in death of its prey (Morris 1998). Such a definition excludes consumption of multiple organisms that do not result in their individual deaths, nor is predation the prolonged consumption of a single organism (a host) that eventually results in its death. Consequently, distinctions are made between prey and host. Prey is the term that applies to an organism that is killed quickly by a consumer involved in predation. By contrast, a host, unlike prey, is defined as a temporally prolonged food resource used by a parasite or parasitoid. One type of host is an organism that is not killed by its consumer after a brief encounter, which involves minor consumption such as a blood-feeding mosquito on a vertebrate host. Such a relationship is parasitism. A second type of host is an organism that is killed only after a prolonged process of consumption, such as a wasp larva feeding internally on an herbivorous caterpillar. Such an interaction is parasitoidism.

### *11.2.2 Parasitism*

Parasitism is an intimate trophic interaction between a consumer and its' typically much larger host that does not result in death of the host (Morris 1998). Parasitism does not include herbivory, for reasons mentioned above, because one fundamental difference of a food web is based on the trophic interactions of the consumption of plants versus the consumption of animals. Thus, the exclusion of herbivory from parasitism makes good ecological sense. An alternative view is that parasitism is a perplexing concept difficult to define owing to conceptual difficulties in separating parasitism from herbivory and from the insensible trophic gradations among commensalism, mutualism and symbiosis (Araújo et al. 2003)—a view that is not taken here.

### *11.2.3 Parasitoidism*

Parasitoidism is a trophic interaction whereby a free-living adult has a dispersive stage whose parasitic larva gradually consumes and eventually obligately kills its host from within or without upon the parasitoid emerging as an adult (Gauld and Bolton 1988; Morris 1998). The feeding behavior of parasitoids can be considered intermediate between that of a predator and a parasite (Knutson and Berg 1966). Although a parasitoid does kill its host, analogous to a predator killing its prey, it also feeds and has life habits like that of a parasite, existing in intimate association and extracting in incremental fashion nutrition from its host (Askew 1971). The definition of what constitutes a parasitoid has undergone many changes in the century-long history of the concept. These shifts in definition are probably why there are several categories of parasitoids.

### *11.2.4 Parasitoidism: A History of the Term*

Reutter (1913) was the first to coin the term parasitoid, which he defined, insightfully, as a feeding behavior intermediate between predation and parasitism. The term was redefined by Waage and Greathead (1986), who detailed the parasitoid life history as follows.

> Adult female parasitoids are free-living, feed on nectar, pollen or as predators and forage actively for their arthropod hosts on plants and other substrates. Usually, on locating a host, the female lays one or more eggs on or in it, and the ensuing larvae consume the host tissue, killing the host in the process.

By contrast, Eggleton and Gaston (1990) mentioned that Price (1984) offered a more unambiguous definition based on a circumscribed definition of parasitoid life-history patterns.

> A species of insect that requires and eats only one animal in its life span by living parasitically as a larva on a host; but the adult is free-living and may ultimately kill many hosts by leaving eggs or larvae near or on the host that consume the host.

A few years later Gauld and Bolton (1988) provided a more succinct definition with a greater economy of words.

> Parasitoids are insects whose larvae develop by feeding on or within an arthropod host, and this host individual is almost always killed by the developing parasitoid larva.

Finally, the definition by Eggleton and Gaston (1990) is presented, which is a minor elaboration of Gauld and Bolton's (1988) formulation. However, the definition was borrowed mostly from Kuris (1974).

> A parasitoid is an organism which develops on or in another single ("host") organism, extracts nourishment from it, and kills it as a direct or indirect result of that development.

These definitions vary in scope, with emphases placed variously on the larval or adult stages. The more restrictive definition is that of Gauld and Bolton (1988), for which Eggleton and Gaston (1990) references the deep understanding of hymenopteran biology by the authors. The less circumscribed definitions of the first two quotes are not as inclusive and probably exclude clades such as Strepsiptera. Strepsiptera do not kill their hosts, but rather castrate them, but in any event, a genetic death is the result. (Consequently, strepsipterans are considered herein as parasitoids.) More to the point, the first three definitions would exclude organisms other than insects, an unsound restriction that would disallow mermithinid nematodes (Poinar Jr 2003) and ophiocordycipitacean fungi (Hughes et al. 2011a; Evans et al. 2011), which clearly are non-insectan parasitoids, often on insects. However, the last definition of Eggleton and Gaston (1990) would encompass non-insectan taxa, including the myriad of phyla with parasitoid taxa in the marine realm (Weinstein and Kuris 2016). Because the definitions of trophic groups such as herbivore, parasite and predator are functional descriptions, the simple, functional definition immediately above by Eggleton and Gaston (1990) is proposed for a parasitoid, with minor exceptions, based on an earlier meaning by Kuris (1974). Such an ecumenical definition would include mermithid nematodes and ophiocordycipitacean fungi mentioned above and probably hemiepiphytic plants that ultimately kill their host plants (Putz and Holbrook 1989).

## *11.2.5 Types of Parasitoidism*

Parasitoidism represents a complex interplay of ecological and behavioral phenomena. These phenomena can be categorized in many ways, some of which are binary contrasts and others that are terms for singular, distinctive types of parasitoidism. The major types of parasitoid relationships in common usage are detailed below.

### 11.2.5.1 Ectoparasitoidism Versus Endoparasitoidism

Parasitoids that develop within the body and feed on the internal tissues of their host are endoparasitoids. Ectoparasitoids, by contrast, live on the external surface of their host although often their mouthparts are buried into deeper subcutaneous tissues. Complexities to these two contrasting definitions are parasitoids which include species that spend part of their development as endoparasitoids and the other part as ectoparasitoids (Godfray 1994), or parasitoids that have their bodies partly located deep in host internal tissue and partly exposed to the surface (Cook 2014).

#### 11.2.5.2 Koinobiont Parasitoidism Versus Idiobiont Parasitoidism

Koinobiont parasitoids initially immobilize but continually allow their host to grow. After a parasitoid oviposits an egg on its host, a koinobiont parasitoid allows its host to develop to maturity while simultaneously feeding on it. Koinobiont development of the host frequently is promoted by endoparasitoidism. By contrast, after initial oviposition, an idiobiont parasitoid prevents further development of its host while feeding on it, resulting subsequently in limited host resources (Haeselbarth 1979). Idiobiont development of its host is frequently fostered by ectoparasitoidism.

#### 11.2.5.3 Solitary Versus Gregarious Parasitoidism

Solitary parasitoids are those that feed alone on a host without other parasitoid accompaniment (Mackauer and Chau 2001). Gregarious parasitoids, by contrast, feed on a host in multiple numbers, ranging from two to thousands such that typically one parasitoid individual remains after all conspecifics have died (Mackauer and Chau 2001). Generally, solitary versus gregarious parasitoidism is a property of the particular parasitoid species and is regulated by complex hormonal interactions with the host and other potential colonizing parasitoids.

#### 11.2.5.4 Superparasitoidism Versus Multiparasitoidism

Superparasitoidism is a condition whereby multiple eggs, typically many, are oviposited on or in the same host individual by a female of the same parasitoid species (Fisher 1961; Mackauer and Chau 2001). However, if a second parasitoid species lays eggs in addition to the first parasitoid species, multiparasitoidism is the result (Fisher 1961). In either situation, monospecific or heterospecific competition ensues among the parasitoid larvae for limited resources of the host. Superparasitoidism sometimes is accompanied by the oviposition of a single polyembryonic egg that produces multiple, genetically identical larvae that number from tens to thousands of individuals (Silvestri 1906). Unlike gregarious parasitism, multiple, often many, individuals survive to complete their development on the same host.

#### 11.2.5.5 Hyperparasitoidism

Primary parasitoids have a simple relationship between a host and its parasitoid. Secondary parasitoids, or hyperparasitoids, are facultative or obligate parasitoids of a primary parasitoid on the same source host. Tertiary parasitoids have been documented (Godfray 1994; Frank and Gillett-Kaufman 2006), and up to five levels of hyperparasitoidism can occur in the case of oak galls that involve ichneumon wasps (Askew 1961). Facultative hyperparasitoids are situations where a parasitoid can attack either a host or the parasitoid of that host, as opposed to an obligate hyperparasitoid that can only attack a parasitoid of the host (Godfray 1994). Obligate hyperparasitoids exhibit very high host specificity (Schär and Vorburger 2013). The concept of hyperparasitoidism is inextricably linked to hyperparasitism in the older biological literature, where the two life histories were not distinguished. The French naturalist Maria Sibylla Merian (1647–1717) was probably the first person to recognize hyperparasitoidism (as hyperparasitism), as illustrated in her drawings (Todd 2011). The concept later was recognized in verse in 1733 by the English writer Jonathan Swift, who undoubtedly borrowed the idea from earlier authors.

#### 11.2.5.6 Egg Parasitoidism, Larval Parasitoidism, Pupal Parasitoidism and Adult Parasitoidism

Parasitoids of holometabolous insects can attack any of the four major developmental stages, or any two of adjacent stages of the egg, multiple instars of the larva, pupa and adult. Frequently parasitoids are not only species specific but also target particular developmental instars, such as egg parasitoids (Malyshev 1968; Huber 1986; Whitfield 1998), larval parasitoids (Askew 1971; Weinstein and Austin 1991; Whitfield 2003), pupal parasitoids (Clausen 1940; Quevillon and Hughes 2018) and adult parasitoids (Askew 1971; Whitfield 1998, 2003), although it is the earlier stages that are most often attacked. For hemimetabolous insect hosts, parasitoids attack their eggs (Muldrew 1953; Greathead 1963; Brown 1973); nymphs, if terrestrial (Eggleton and Belshaw 1992; Cook 2014); naiads, if aquatic (Clausen 1940; Askew 1971); or adults (DeBach 1964; Kirkpatrick 1947; Elzinga 1977; Cook 2014), although there is little somatic differentiation between nymphal and their conspecific adult instars. Parasitoids of egg, pupal and adult stages of their hosts typically are idiobionts, as are those parasitoids of larvae whose sting causes permanent paralysis (Gauld and Bolton 1988; Godfray 1994). Koinobiont parasitoids are those that attack the egg–larval and larval–pupal instar couplets or are parasitoids of adjacent larval instars, and do not paralyze their hosts. A special category is an egg parasitoid, which often is a miniscule insect that deposits typically very small eggs on the surface or in the interstitial tissues of a much larger host egg. Other egg parasitoids oviposit in an egg sac containing multiple eggs, in which the hatched parasitoid larva either slowly consumes nutritive tissues of the egg that eventually starves and kills the embryo, or alternatively successively consumes eggs within an egg sac (Askew 1971; Vetter et al. 2012).

#### 11.2.5.7 Cleptoparasitoidism

Cleptoparasitoidism is a rare life style in which a parasitoid absconds a vital resource such as food that results in the death of the host after it is deprived of the supply (Frank and Gillett-Kaufman 2006; Dehon et al. 2017). Food resources can include foliage, galls, insects or other provisions intended for the host (Eggleton and Belshaw 1992). A related concept is social parasitism, which is a special type of parasitism constituting a relationship between two species such that one species is dependent parasitically on the other (Brandt et al. 2005; Smith et al. 2007).

An example is a social parasite that benefits from brood care and access to resources that are managed by and benefits the host colony. Social parasitism occurs among a broad variety of insects in which the hosts and the parasites often are closely related, in some cases forming a sympatric species pair. By contrast, inquilines are animals that exploit the living space, such as a termite or ant nest, resulting in a commensal relationship in which one member benefits and the other member derives a reward or is not harmed (Malyshev 1968). Inquilism often is a precursor to social parasitism, which in turn may be a precursor to cleptoparasitoidism (Askew 1971).

## 11.3 The Evidence: Distinguishing Predation, Parasitism and Parasitoidism

Several types of evidence are important for detecting the presence of predation, parasitism and parasitoidism in the fossil record (Fig. 11.1). Some of this evidence is associated with particular techniques, such as synchrotron X-ray microtomography (van de Camp et al. 2018), or time-of flight secondary-ion mass spectrometry

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**Fig. 11.1** (continued) New York State (Shear et al. 1989). (**c**) Vertebrate coprolite containing remains of a cockroach, including wings (w), legs (l) and ovipositor (o) from the Middle Pennsylvanian Mazon Creek locality of Illinois (FMNH PE 54114). (**d**) From the same locality as (**c**) is the insect *Protdiamphipnoa woodwardi* Brongniart (Cnemidolestodea: Cnemidolestidae), with prominent forewing eyespots (Carpenter 1971). (**e**) The enigmatic flea or flea-like insect *Strashila incredibilis* Rasnitsyn (?Siphonaptera: Saurophthiridae), from the Late Jurassic of Transbaikalia, Russia, exhibiting aptery, chelate hind tarsus and piercing-and-sucking mouthparts (Rasnitsyn 1992). (**f**) The parasitoid ensign wasp *Leptephialtites caudatus* Rasnitsyn (Hymenoptera: Ephialtitidae) from the Late Jurassic of Karatau, Kazakhstan, with elongate ovipositor (o) and ovipositor valves (ov) (Rasnitsyn 1975). (**g**) The digger wasp *Angarosphex beiboziensis* Hong (Hymenoptera: Angarosphecidae) from the Jurassic–Cretaceous boundary of China, exhibiting abdominal banding indicating a Batesian model (Hong 1984). (**h**) The peculiar chewing louse *Saurodectes vrsanskyi* Rasnitsyn & Zherikhin (?Phthiraptera: Saurodectidae) from the Early Cretaceous of Transbaikalia, Russia (Rasnitsyn and Zherikhin 1999) Note gut contents. (**i**) Gut contents of the middle Eocene bat *Palaeochiropteryx tupaiodon* Revilliod (Chiroptera: Palaeochiropterygidae) from Messel, Germany, containing butterfly scales and other insect fragments (Richter and Storch 1980). Approximate length of scale at right is 90 μm. (**j**) Robber fly (Diptera: Asilidae) from the middle Eocene of Colorado, USA (USNM501477), displaying raptorial forelegs and mouthparts of a single, dagger-like stylet (arrow). (**k**) The egg (nit) of an undetermined sucking louse (Phthiraptera: Anoplura) on a mammalian hair shaft, from middle Eocene Baltic amber of Germany (Voigt 1952). (**l**) *Palaeopsylla klebsiana* Dampf (Siphonaptera: Hystrichopsyllidae), a mammal-parasitizing flea from the same provenance as (**k**), showing socketed antennae, head comb and maxillary lever–stylet complex typical of fleas (Dampf 1910). (**m**) The seed *Tectocarya rhenana* (Cornaceae), with exit hole of a seed predator, from the early Miocene of Germany (Schmidt et al. 1958). (**n**) A bee cell (Hymenoptera: Stenotritidae) from the Pleistocene of South Australia, with a small exit hole of a probable parasitoid (Houston 1987). All subfigures are redraw from original images or are camera lucida drawings of specimens from the Field Museum of Natural History in Chicago (FMNH) or the National Museum of Natural History in Washington, DC (USNM). Scale bars: solid, 1.0 cm; striped, 0.1 cm. (Reproduced, with permission of the Paleontological Society, from Fig. 2 of Labandeira 2002)

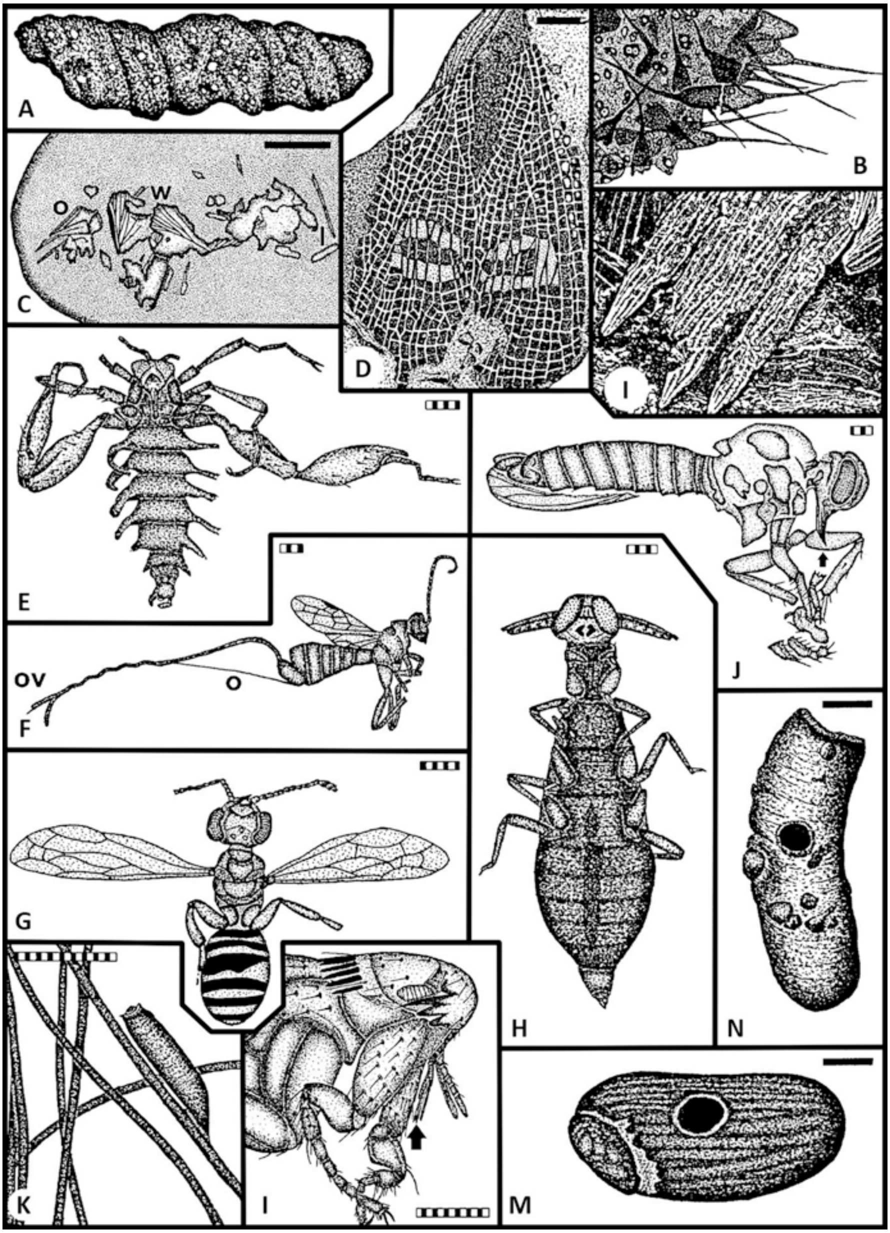


**Fig. 11.1** Evidence from taxonomic affiliation (**f**, **h**, **j**–**l**), structural and functional attributes (**b**, **e**, **f**, **h**, **j**, **l**), organismic damage (**m**, **n**), gut contents (**i**), coprolites (**a**, **c**), and predation avoidance (**d**, **g**) for insect predation, parasitism and parasitoidism in the fossil record. Examples are predation (**a**–**d**, **g**, **i**, **j**, **m**), parasitism (**e**, **h**, **k**, **l**) and parasitoidism (**f**, **n**). (**a**) A coprolite containing early land-plant spores from the Early Devonian of Wales (Edwards et al. 1995). (**b**) A fossil spider spinneret, showing a cluster of attached and detached spigots, from the Middle Devonian of Gilboa,

(Greenwalt et al. 2013; Greenwalt 2021), that allows for assignment of these insect fossils, respectively, to parasitoid and parasite life habits. The evidence is highly variable and consists of modern and fossil molecular data, broadly construed (Nagler and Haug 2015), but also includes morphological and interaction-related features of the fossil organisms themselves or their taxonomic affiliations (Fig. 11.1f, h, j–l) (De Baets and Littlewood 2015; Leung 2017). Functional features also are important (Fig. 11.1b, e, f, h, j, l), as are damage to organisms (Fig. 11.1m, n), gut contents (Fig. 11.1h), coprolites (Fig. 11.1a, c), and predator avoidance traits (Fig. 11.1d, g) (Labandeira 2002). Evidence of parasitism is seen in Fig. 11.1e, h, k, l; evidence of parasitoidism is seen in Fig. 11.1f, n.

### *11.3.1 Biomolecular Data*

Within the deep-time context of the insect fossil record, study of biomolecules has two basic applications for understanding the occurrence of predation and especially parasitism and parasitoidism. The first approach involves understanding of the feeding habits and other host relationships of the fossil parasite containing the ingested biomolecule such as blood (Greenwalt 2021; Greenwalt et al. 2013; Yao et al. 2014). In a complementary sense, identification of the ingested biomolecule itself is necessary for specification of the host taxon (De Baets and Littlewood 2015). Identification of both parasite and host is still is in their infancy (De Baets and Littlewood 2015); but characterization of certain biomolecules, such as fossil keratin, shows considerable promise (Wappler et al. 2004; Briggs and Summons 2014).

The other major use of biomolecular data relevant for inferring predation, parasitism and parasitoidism in the fossil record is the production of phylogenies (De Baets and Littlewood 2015; Nagler and Haug 2015; Warnock and Engelstädter 2021). The influence of molecular phylogenies of insects—particularly those of fossil-calibrated cladistic studies of predator, parasite and parasitoid groups—has provided considerable assistance in inferring the predatory, parasitic or parasitoidic life habits of many insect lineages (Pohl and Beutel 2005; Winterton et al. 2007; Bologna et al. 2008; Heraty et al. 2013; Winkler et al. 2015; Peters et al. 2017; Gillung et al. 2018). In addition, such studies are a principal basis for understanding the inter-relationships among predator and especially parasite and parasitoid lineages and their relationships to sister clades (Grimaldi and Engel 2005a).

### *11.3.2 Taxonomic Affiliation*

The insect fossil record consists of evidence for predatory, parasitic and parasitoidic interactions based on taxonomic similarity to their recent relatives (Boucot and Poinar Jr 2010; Leung 2017). For example, bee cleptoparasitism was found in the fossil record of a late Paleocene (60 Ma) site from Menat, France (Martins et al.

2018). The cleptoparasite was identified based on distinctive features of its wing that are affiliated with modern cleptoparasite bees. Similarly, modern Strepsiptera (twisted-wing parasites) are endoparasitoids that have distinctive features, including extreme sexual dimorphism between males and females and high levels of morphological specialization between immatures and adults (Askew 1971; Kathirithamby 2009). Three species of fossil Strepsiptera were found in 21 million-year-old Dominican Amber (Kathirithamby and Grimaldi 1993) that display the same distinctive features as their extant strepsipteran relatives, indicating that the same parasitoid relationships have survived approximately 21 million years.

Amber provides a wealth of morphological, and indirectly behavioral, detail occasionally revealing the consuming predator and its consumed prey item, often *in flagrante delicto* (Labandeira 2014a). Examples include a dance fly with a nonbiting midge clutched by its forelegs and an insect larva consuming a scuttle fly's head (Grimaldi 1996; Janzen 2002). As for parasitism, there are several occurrences of modern-aspect Paleogene fleas attributable to a modern clade (Poinar Jr 2015). Older, Late Jurassic to Early Cretaceous stem-group lineages have been attributed to modern Siphonaptera (Gao et al. 2012, 2014) based on several common, structural features (but see Dittmar et al. 2016; Leung 2021). Mesozoic evidence for parasitoids also occurs in amber, but is qualitatively different by providing more detail of external insect structure (Labandeira 2014a). Poinar (2013) shows several such examples of parasitoids that involve insects.

### 11.3.3 Structural and Functional Attributes

Structural evidence historically has been the standard mode for inferring the presence of parasitism or parasitoidism in the fossil record. Many examples illustrate body structures, especially mouthparts, attachment devices and ovipositors, of a particular larva or adult that indicate a parasite or parasitoid life habit during the later Mesozoic and Cenozoic (Leung 2017). Body structures strongly implicating parasitoidism include those from Coleoptera (Engel 2005a; Poinar Jr 2009), Diptera (Rocha et al. 2015; Zhang et al. 2016) and Hymenoptera (Barling et al. 2013; Spasojevic et al. 2017). Of special note is synchrotron X-ray microtomography (Labandeira 2014a), that has been used for documenting parasitoid interactions with their hosts caught in the act (van de Kamp et al. 2018). In that study (van de Kamp et al. 2018) 55 parasitoidization events were three-dimensionally imaged that recorded four species of hymenopteran endoparasitoids in a dipteran pupal host.

The life habits of predators, parasites and parasitoids frequently can be deduced from their functional morphology (Leung 2017). The fossil record provides considerable evidence for predation, such as silk-producing spigots in a Devonian insectivorous spider likely used for trapping of prey items (Fig. 11.1b). The fossil record also provides evidence, such as wing eyespots of a cnemidolestid archaeorthopteran (Fig. 11.1d), evidently a potential prey item, to deflect attention and avoid consumption by a potential predator. The presence of a long drilling ovipositor (Fig. 11.1f) is strong evidence for parasitoidism.

Evidence for social parasitism is available from a rove beetle, *Cretotrichopsenius burmiticus*, (Coleoptera: Staphylinidae) from Myanmar amber (99 Ma). These beetles were assigned to the subfamily Aleocharinae and consisted of a horseshoe crab or "limuloid" larval ecomorph with associated structural features that indicated termitophily and nest parasitism (Cai et al. 2017). Many specialized structures of this aleocharine beetle have a mimetic body form of a termite worker caste that allowed accommodation within termite society, probably Mastotermitidae or Kalotermitidae. Notably, evidence for social parasitism was provided by another aleocharine rove beetle from the same deposit, *Mesosymbion compactus* (Yamamoto et al. 2016), which possessed a similar limuloid habitus and other structural features that are associated with termitophily.

### *11.3.4 Host Tissue Damage*

Physical evidence for parasitism can take many forms, including indirect and direct evidence for parasites and parasitoids on a variety of arthropod and vertebrate hosts (Boucot and Poinar Jr 2010; De Baets and Littlewood 2015; Dunlop 2021; Poinar 2021). One previously unrecorded type of paleopathological evidence is punctures in the osteoderms of armadillos from the late Miocene of the Pampas, in Argentina (Tomassini et al. 2016). Osteoderms occur occasionally in mammals and are particularly common in edentates that include Pleistocene glyptodonts and modern armadillos. In these mammals, osteoderms are osseous or keratinous deposits that form plates, scales or other flat structures embedded in the integument. Osteoderms from the extinct armadillo *Ciasicotatus ameghinoi* (Cingulata: Dasypodidae) bear punctures, sometimes clustered, that indicate feeding by the jigger flea *Tunga* (Siphonaptera: Tungidae) when the host was still alive.

One mode of evidence involving tissue damage is the rare emergence of a parasitoid from its host, as revealed in 44 million-year-old middle Eocene Baltic Amber (Leung 2017). From this deposit Poinar Jr and Miller (2002) document a parasitoid wasp larva, identified as an extinct genus of the subfamily Neoneurinae (Hymenoptera: Braconidae), exiting the abdomen of its host, a species of the garden ant *Lasius* (Hymenoptera: Formicidae). Both host and parasitoid were alive during this episode, as the ant displays contorted body features in response to a stimulus while the wasp larva began to secrete silk for its pupal case. Both behavioral features occurred immediately before their demise. This relationship, typical of certain braconid wasps attacking *Lasius* ants today, is an interaction that has been pushed back to the middle Eocene, demonstrating the antiquity of some highly specific parasitoid–ant host interactions. Other types of evidence are more difficult to acquire; for example, host tissues occasionally are altered such as a small puparium of a strepsipteran parasitoid ensconced within the body of a stingless bee (Boucot and Poinar Jr 2010).

### *11.3.5 Plant–Insect Interactions*

Plant–insect interactions also can reveal the presence of parasitoids, recording the identities of the plant host, often the insect herbivore, but rarely the insect parasitoid. The parasitoid often remains unidentifiable because of the lack of distinctive features of the parasitoid entry hole, the induction of anomalous host behavior resulting in atypical plant damage, or exit holes. For example, the galler damage type DT83 (Labandeira et al. 2007b, page 13) has features consistent with a gall midge (Diptera: Cecidomyiidae) gall, occurring on plant morphotype TY46 (Euphorbiaceae) from early Eocene Laguna del Hunco, Argentina. However, this gall individual contains six, undistinctive, circular, parasitoid exit holes of varying diameters that are unidentifiable to a culprit taxon. Similarly, although often considered a plant–insect interaction, an example of predation occurs in a seed with a circular exit hole (Fig. 11.1m), but lacks sufficient characters to identify the seed predator, such as a seed bug (Lattin 1999).

Leaf mines also can record the presence of parasitoid behavior from oviposition scars (Krassilov 2008a). As leaf miners are concealed herbivores, an adult parasitoid must penetrate through or otherwise pierce foliar tissue with their ovipositor to deposit an egg on or in the larval host or mine. Evidence for ovipositor piercings or larval entry holes does occur on fossil leaf mines. These penetrations often are termed “cut-outs” (Krassilov 2008a), or alternatively “predation holes” (Krassilov 2008b), some of which may be linear oviposition scars adjacent the leaf mine from ovipositing parasitoids.

Another type of evidence reveals the presence of a parasitoid, in this case a fungus, in a series of distinctive, successive, bilaterally symmetrical holes adjacent major veins found on the undersides of dicotyledonous leaves in humid, tropical environments (Harper and Krings 2021). Such features are the “death grips” of a zombie ant, such as the carpenter ant *Camponotus*, as it dies following zombification by the parasitoid fungus *Ophiocordyceps* (Hypocreales: Ophiocordycipitaceae), a widespread plant–fungus–ant interaction across the modern tropics (Hughes et al. 2011a). Such distinctive evidence also has been found on a dicot leaf from the 48 million-year-old Messel Formation in central–west Germany (Hughes et al. 2011b). This occurrence indicates that the parasitoid association has been present since the early Eocene, and probably originated in the Cretaceous (Sung et al. 2007), during the initial diversification of the parasitoid fungus clade. As in the case of plant galls caused by mites and insects, the infected zombie ant and its characteristic leaf damage is considered the extended phenotype of the parasitoid fungus (Hughes 2014).

### *11.3.6 Gut Contents*

Gut contents in insects assume a variety of forms, ranging from solid contents such as pollen and indigestible plant-tissue fragments in guts of insects (Krassilov et al. 1997; Rasnitsyn and Krassilov 2000), to shaft fragments of bird feathers and vertebrate blood (Wappler et al. 2004; Greenwalt et al. 2013; Greenwalt 2021) in parasites and parasitoids. The 48 million-year-old Messel Formation of Germany preserves gut contents spectacularly well, an example of which are butterfly scales in the gut of the bat *Palaeochiropteryx tupaiodon* (Fig. 11.1i) described by Richter and Storch (1980). Another instance is the chewing louse *Saurodectes vrsanskyi* (?Phthiraptera: Saurodectidae) that shows fluidized gut contents consisting of likely secreted dermal fluids or blood (Fig. 11.1h). For parasites, the detection of blood in gut contents is especially important (Greenwalt 2021).

Four studies have used the gut contents in a louse, a bug, a flea and a mosquito to indicate the presence of parasitism and reveal the specific diets of these parasites. First, a bird louse (Phthiriaptera: Amblycera: Menoponidae), with mandibulate mouthparts typical for this clade, was discovered among a well-preserved middle Eocene (44 Ma) biota at Eckfeld, Germany (Wappler et al. 2004). The presence of remains of keratinous scales from feather shaft bases in the gut of the louse, detected by light-microscope imaging, securely indicated an ectoparasitic relationship with a bird (Wappler et al. 2004). A second study involved bugs (Hemiptera: Heteroptera) from the Early Cretaceous (125 Ma) Yixian Formation of northeastern China (Yao et al. 2014). This study established *Torirostratus pilosus* (Hemiptera: Torirostratidae) as closely related to Cimicidae (bed bugs) and Polyctenidae (bat bugs). An energy-dispersive X-ray spectroscopic examination of the head, antennae, prothorax, metathoracic leg, central abdomen and adjacent mudstone matrix (the latter used as a standard), revealed elevated iron content, and hence the presence of degraded hemoglobin, from an opaque region in the central abdomen (Yao et al. 2014). In a third study, a Mesozoic-aspect female flea with a substantially distended abdomen was examined from the same deposit as the example immediately above. The flea, *Pseudopulex tanlan* (Siphonaptera: Pseudopulicidae), a member of an extinct, mid-Mesozoic lineage related to modern fleas (Huang 2014), had a ballooned abdomen with stretched intersegmental membranes that contained 15 times the volumetric intake of blood as that of modern fleas (Gao et al. 2014). This attribution of blood as the cause of abdominal distension was based on the taxonomic affinity of fleas rather than a chemical analysis. In the last study, a fossil mosquito (Diptera: Culicidae) was discovered in the 44 million-year-old middle Eocene Kishenehn Formation of southwestern Montana, and subsequently analyzed for a large opaque residue in its moderately distended abdomen. Energy-dispersive X-ray spectroscopy and time-of-flight secondary ion mass spectrometry indicated that hemoglobin was present in the mosquito's abdomen (Greenwalt et al. 2013). While these studies can identify with remarkable accuracy the diet of a parasite's last meal—whether keratin flakes from bird feather shafts or vertebrate blood—the precise species identification of the hosts of the last meal remain mostly unknown.

### 11.3.7 Coprolites

Arthropod (Fig. 11.1a) and vertebrate (Fig. 11.1c) coprolites often contain identifiable material assignable to particular insect predators and the hosts of parasites and parasitoids, but are rare as fossils (Labandeira 2002; Robin et al. 2016; Chin 2021). Coprolites of hosts are usually difficult to assign to a producer; nevertheless, they potentially are a significant archive of fossilized trophic relationships that include evidence for parasitism (De Baets and Littlewood 2015; Qvarnström et al. 2016). Such coprolites occasionally reveal prey items consumed by predators such as swallowed insect parasites combed from hair and feathers by vertebrate grooming behavior (Qvarnström et al. 2016). More remotely, parasitoid remains can occur in the coprolites of small terrestrial vertebrates. However, for insects during their 412 million-year-long existence, by far the greatest populations of insect coprolites involve plant cuticle, trichomes and vascular tissue remnants from detritivores and herbivores, and pollen from pollinivores (Labandeira and Phillips 1996; Labandeira 1998). Fluid-feeding parasites and parasitoids would rarely produce a detectible coprolite record.

### 11.3.8 Sedimentary Ichnological Evidence

Sedimentary ichnological evidence provides support for recognizing inquilinism, cleptoparasitism, parasitoidism and scavenging in the fossil record, particularly in the trace fossil record of Pleistocene and Holocene deposits that involve beetle, wasp and bee hosts (Ellis and Ellis-Adam 1993; Bown et al. 1997; Mikulás and Genise 2003; Genise and Cladera 2004). Cleptoparasitism, for example, occurs in the sedimentary ichnological record as fossil traces of *Tombownichnus pepei* that consist of pits in the walls or infillings of *Coprinosphaera*, the brood balls of beetles (Sánchez and Genise 2009). The *Tombownichnus–Coprinosphaera* parasitoid and host relationship has modern equivalents (Halffter and Edmonds 1982; Halffter and Matthews 1999), although the material documented from the middle Eocene–lower Miocene Saramiento Formation of Patagonia, Argentina (Sánchez and Genise 2009) indicates an ancient association. The cleptoparasite culprits remain unknown, although the *Tombownichnus pepei* pit type likely represents pupation chambers excavated by last-instar larvae.

Another example is *T. plenus* from Semnan Province, Iran, that involves curvilinear, narrow burrows up to 8 mm long that invade bee colony cells (Bagheri et al. 2013). These bee nest structures in *Celliforma* nests are attributed to one of the three main groups of bee parasitoids: Meloidae (blister beetles), Bombyliidae (bee flies) or Mutillidae (velvet ants). Similarly, possible parasitoid attack of bee cells are present in ichnofossils of *Celliforma*, attributed to modern Anthophoridae (carpenter bees), from Fuerteventura and Lanzarote of the Canary Islands, Spain. The outer sedimentary linings of individual unopened cells exhibit numerous perforations that suggest considerable pre-imaginal mortality, attributed to predation or fungal attacks (Ellis and Ellis-Adam 1993), but equally could represent parasitoid attack. In another example, direct evidence of a parasitoid entry or an exit hole is provided by a bee cell of Stenotritidae, from the Pleistocene of South Australia (Houston 1987).

Perforations of thickened bee cell walls and small cocoons within the bee cells also have been described from the Paleocene–Eocene Claron Formation of southwestern Utah (Bown et al. 1997). Perforations of these cell walls are rounded, incomplete or complete holes that suggest parasitoid presence, but of unknown taxonomic affiliation. A second instance is the association of *Lazaichnus fistulosus* with beetle pupal chambers, consisting of holes circular to broadly ellipsoidal in outline that penetrate the cell wall and are connected to a single cavity of *Monesichnus ameghinoi* (Mikulás and Genise 2003). This probable parasitoid trace fossil is from the Late Cretaceous to Early Paleogene Ascencio Formation of Uruguay and represents the earliest occurrence of probable parasitoidism in the sedimentary ichnological record (Martin and Varricchio 2011).

## 11.4 Evolutionary and Ecological Biology

Parasitism, in the broadest sense of the term to include parasitoidism, is a very ancient relationship extending into Paleozoic (Leung 2017) and likely even Precambrian (De Baets and Littlewood 2015) time. The varieties of parasitism exist as a continuum (Robin 2021) that ranges from symbiosis where two interacting organisms mutually benefit, to commensalism where one organism benefits and the other has a neutral interaction, and then to predation, parasitism and eventually parasitoidism where one interacting organism benefits and the other is disadvantaged, including death (Araújo et al. 2003). For parasitism, one conservative estimate of the animal kingdom indicates that this life habit has originated at least 223 times in 15 phyla, with the greatest representation occurring overwhelmingly in Arthropoda (Weinstein and Kuris 2016). Within arthropods, it is not necessarily the most diverse clades that exhibit the greatest incidence of parasitism. Clearly, at the family level, originations of parasitism in insects were overwhelmingly concentrated among the holometabolous insects where development included larval and pupal instars (Poulin and Morand 2000). These originations consisted of 84 separate events for holometabolous insects, compared with five originations for hemimetabolous insects, where larval and pupal instars are absent. Hemimetabolous insect occurrences are Dermaptera (one occurrence), Psocoptera (one occurrence), Phthiraptera (one occurrence, included in Psocodea) and Hemiptera (one occurrence) (Fig. 11.2). At the family level of analysis, the distribution of the incidence of originations of parasitism is unrelated to underlying total species diversity (Fig. 11.2). Coleoptera (beetles) are the most diverse clade, yet exhibit only ten occurrences of parasitism. Diptera displays 60 separate occurrences of parasitism (Feener and Brown 1997; Weinstein and Kuris 2016), whereas Hymenoptera (sawflies, wasps, ants and bees), which have a species diversity of 75% that of the Diptera

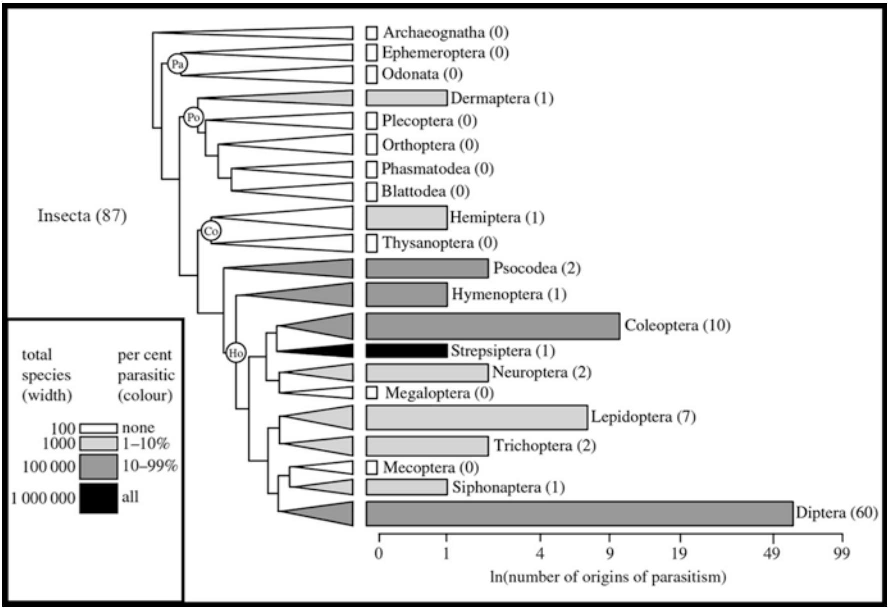


**Fig. 11.2** The origins of parasitism across Insecta. The bar plots are the natural log-transformed number of independent acquisitions of parasitism/parasitoidism within the Insecta, arranged based on taxonomic affiliation (Misof et al. 2014). Bar shading denotes the percent of the group that is parasitic or parasitoidic and bar width is proportional to the log transformed number of species per group. Taxonomic group circled abbreviations: *Pa* Paleoptera, *Po* Polyneoptera, *Co* Condylognatha, *Ho* Holometabola. (Reproduced with permission from the bottom panel of Fig. 1, in Weinstein and Kuris (2016)

(flies), display one or two originations of parasitism (Eggleton and Belshaw 1992; Dowton and Austin 1995b). Nevertheless, it appears that parasitic lineages of insects do not differ from their respective free-living confamilial lineages in the potential for speciation.

In a separate study involving maximum likelihood reconstruction of the major diets of hexapod families, it appears that the hypothesis of larval dietary substrates shaping the major pattern of insect clade richness largely is not borne out (Rainford and Mayhew 2015). An accumulation curve based on dietary originations through geologic time indicated that dietary ecologies of fungivory, phytophagy, predation and ectoparasitism appear early in clade history and display a steady, modest rate of origination (Fig. 11.3). The exceptions were the ecologies of detritivory and especially parasitoidism, whose originations reflect an upward and marked trend during the mid to late Mesozoic; the latter trend is attributable to the radiation of parasitoid Hymenoptera during this interval. The origination data also indicate that the ecology of ectoparasitism behaves very different from that of parasitoidism, with the former originating at a very low rate compared to the latter, indicating that ectoparasitism may not be a viable long-term evolutionary strategy. The evidence for solid phylogenetic conservatism regarding a specialized ecology such as parasitoidism is borne out by the 12 types of parasitoid guilds that ecologically characterize

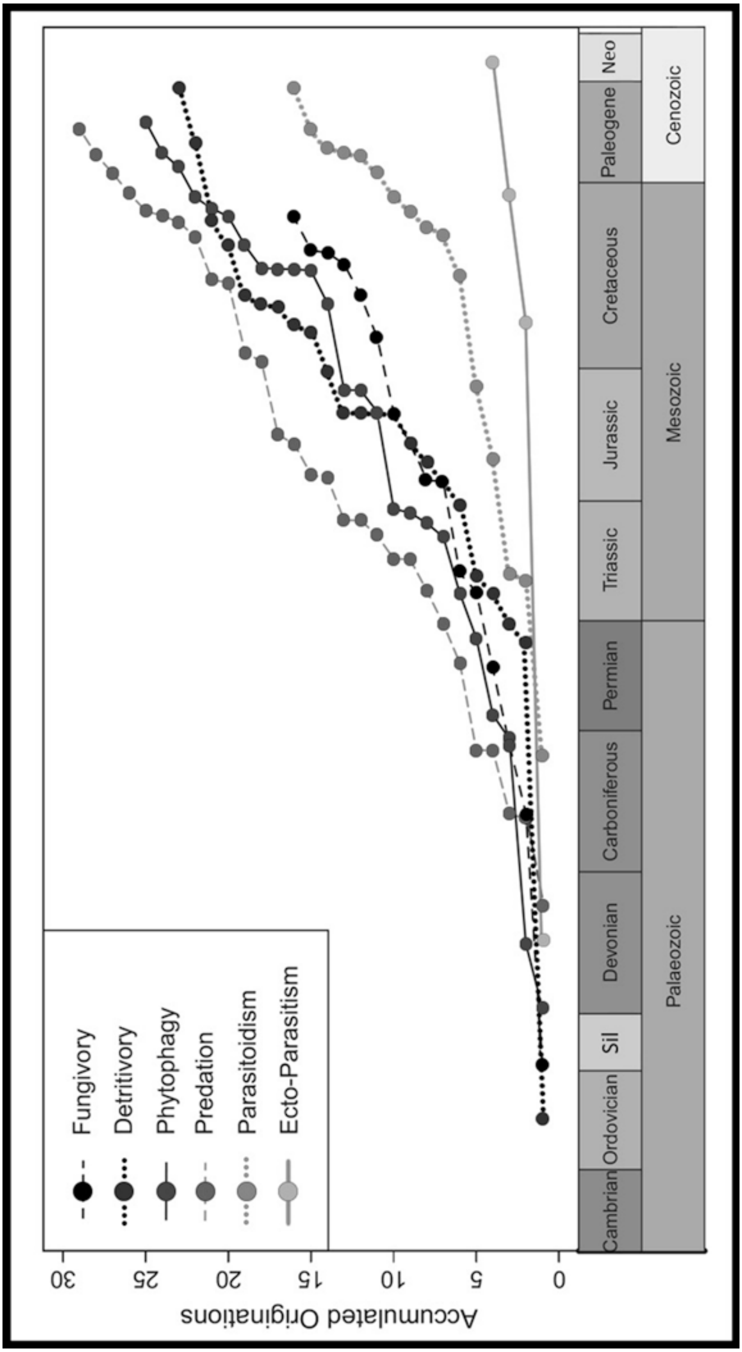


**Fig. 11.3** Accumulation of major dietary-guild originations for the immature stages of insect clades. These data are based on maximum likelihood reconstruction; see Rainford and Mayhew (2015) for details. Abbreviations: *Sil* Silurian, *Neog* Neogene. The thin slice of time next to the recent is the (unlabeled) Pleistocene + Holocene. (Modified for greater clarity and reproduced with permission from Fig. 3 of Rainford and Mayhew 2015)

holometabolous insect communities (Mills 1994). Mills (1994) regarded that parasitoid guilds are defined by three basic features. First, what stage of the host is attacked by the parasitoid? Is it the egg; early, middle or late larval instar; prepupae; pupa; or adult? Second, what is the stage of the host in which it is killed? Third, is the mode of parasitoidism internal (endoparasitoidism) or external (ectoparasitoidism)? The 12 documented combinations of these three features that form modern parasitoid guilds delineate ecological diversity across the seven parasitoid-bearing orders of insects, and provide a phenomenological explanation for Rainford and Mayhew's (2015) conclusion of the evolutionarily dynamic nature of the parasitoid life habit.

The three, major parasitoid harboring groups—Hymenoptera, Diptera and Coleoptera—each display trajectories of particular lineages to and from the parasitoid life habit via particular before-and-after life-habit transitions (Poulin 2011), indicated by arrows in Fig. 11.4a–c. For example, in Coleoptera (Fig. 11.4a), although the thicknesses of the arrows reveal a small number of parasitoid species, the principal movement *toward* parasitoidism has been from mycophagy to cleptoparasitoidism by the families Bothrideridae, Meloidae, Rhipiceridae, Ripiphoridae and Strepsiptera (the latter clade considered a separate order in this report). A second source of movement *toward* parasitoidism has been from specialized egg and clepto-provisioning predation to cleptoparasitoidism by the families Carabidae, Cleridae, Passandridae and Staphylinidae. The principal movement *away from* parasitoidism has been from cleptoparasitoidism to special egg predation by the families Cleridae and Meloidae. The patterns for Diptera (Fig. 11.4b) and Hymenoptera (Fig. 11.4c) display a different pattern and have a greater number of trajectories, higher numbers of transiting species, and a greater number of transiting family-level lineages to and from the parasitoid life habit. These evolutionary shifts are explained in more detail below for each of the three discussed insect orders.

## 11.5 Parasite and Parasitoid Taxa

Insect parasites and parasitoids have evolutionary and ecologically very different life habits. The two life habits have a different set of effects on their hosts and on themselves, based on the particular mode of extracting host resources. These different life habits may be related to the distinctive taxonomic spectra of parasites versus parasitoids. Parasites consist of hemimetabolous lineages—Blattodea, Dermaptera, Psocoptera, Phthiraptera and Hemiptera—that are not represented as parasitoids. Additionally, parasites are represented by a holometabolous lineage, Siphonaptera, which is not represented as parasitoids, and are also represented by another holometabolous lineage, Coleoptera, that is very poorly represented as parasitoids. Only Diptera and Hymenoptera overlap significantly in containing many dominant parasite and parasitoid lineages. In comparison to parasites, the entirely holometabolous character of parasitoids is notable, consisting of Neuroptera, Coleoptera, Strepsiptera, Diptera, Trichoptera, Lepidoptera and Hymenoptera.

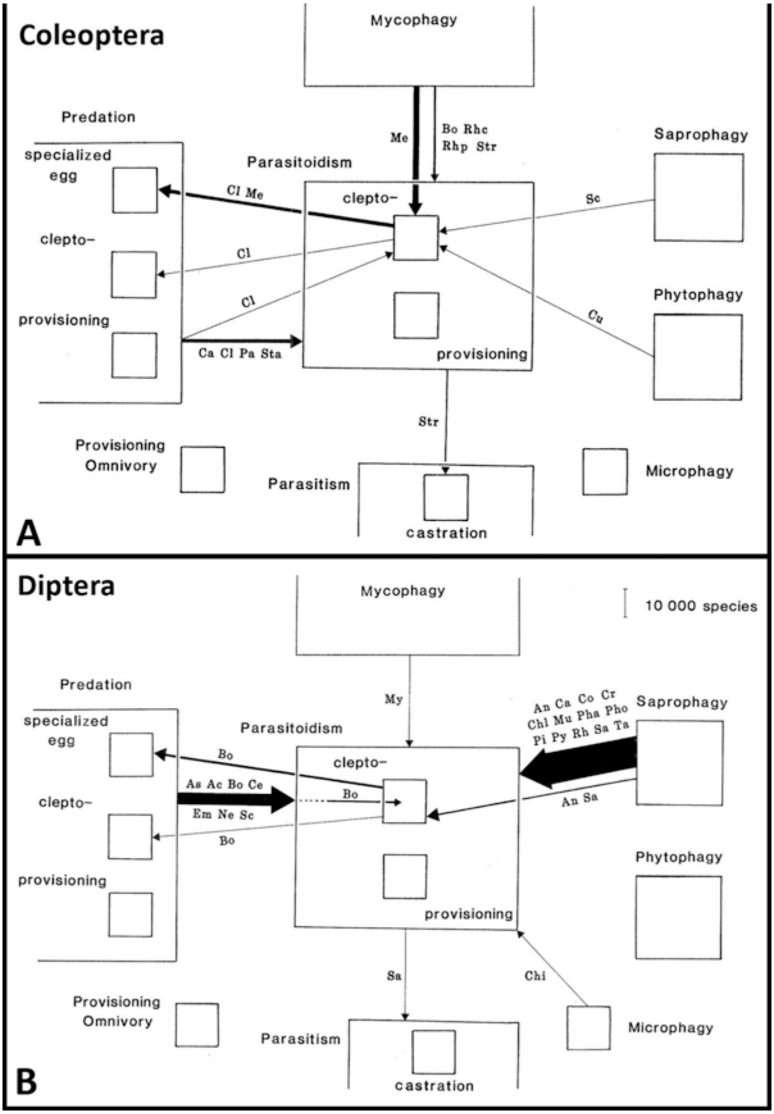


**Fig. 11.4** Evolutionary shifts to and from the parasitoid habit in (**a**) Coleoptera, including Strepsiptera, (**b**) Diptera and (**c**) Hymenoptera. The thickness of the arrow is directly proportional to the number of described parasitoid species in families that are derived from the ancestor making the shift. It does not indicate the number of times the shift has occurred; data compiled as of 1991. Abbreviations of Coleoptera Taxa: *Bo* Bothrideridae, *Ca* Carabidae, *Cl* Cleridae, *Cu* Curculionidae, *Me* Meloidae, *Pa* Passandridae, *Rhc* Rhipiceridae, *Rhp* Ripiphoridae, *Sc* Scarabaeidae, *Sta* Staphylinidae, *Str* Strepsiptera. Abbreviations of Diptera taxa: *Ac* Acroceridae, *An* Anthomyiidae, *As* Asilidae, *Bo* Bombyliidae, *Ca* Calliphoridae, *Ce* Cecidomyiidae, *Chi* Chironomidae, *Chl* Chloropidae, *Co* Conopidae, *Cr* Cryptochaetidae, *Em* Empididae, *Mu* Muscidae, *My* Mycetophilidae, *Ne* Nemestrinidae, *Pho* Phoridae, *Pha* Phaeomyiidae, *Pi* Pipunculidae, *Py* Pyrgotidae, *Rh* Rhinophoridae, *Sa* Sarcophagidae, *Sc* Sciomyzidae, *Ta* Tachinidae. Abbreviations Fig. 11.4 (continued) of Hymenoptera taxa: *Ag* Agaonidae, *Ap* Apidae, *Be* Bethylidae, *Ch* Chrysididae, *Cy* Cynipidae, *Eul* Eulophidae, *Eum* Eumenidae, *Eup* Eupelmidae, *Eur* Eurytomidae, *Ev* Evaniidae, *Fo* Formicidae, *Ga* Gasteruptiidae, *Ic* Ichneumonidae, *Ma* Masaridae, *Po* Pompilidae, *Pt* Pteromalidae, *Sa* Sapygidae, *Sp* Sphecidae, *Ta* Tanaostigmatidae, *To* Torymidae, *Ve* Vespidae. (Reproduced with permission from Figs. 2–4 in Eggleton and Belshaw 1992)

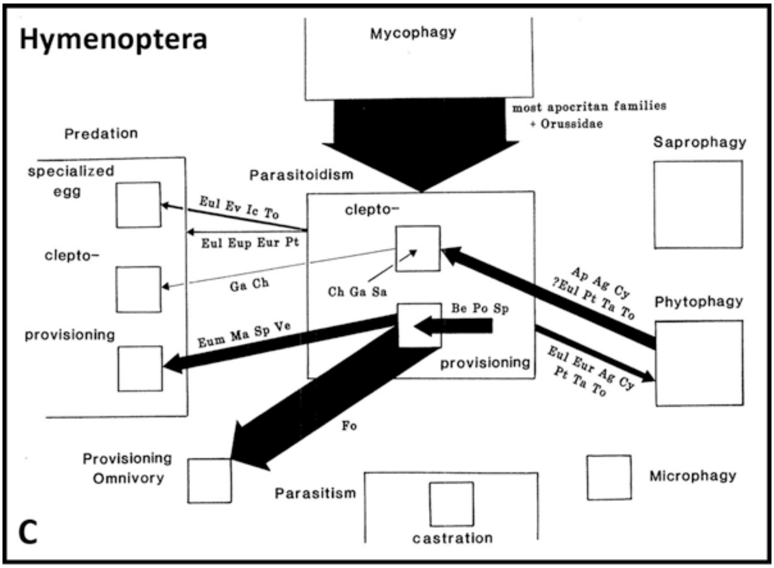


**Fig. 11.4** (continued)

## *11.5.1 Parasite Taxa*

The parasite life style and feeding mode is confined to ten insect orders. The Blattodea, Dermaptera, Psocoptera, Phthiraptera and Hemiptera undergo incomplete metamorphosis, or hemimetabolous development, in which an egg develops into multiple immature developmental stages (instars) that are termed nymphs if terrestrial and naiads if aquatic, ending with a reproductively viable adult insect. The other parasite orders, Coleoptera, Siphonaptera, Diptera, Lepidoptera and Hymenoptera undergo complete metamorphosis, or holometabolous development, in which the egg develops into multiple developmental instars of the distinctive larva stage, followed by another distinctive stage, the pupa, in turn followed by emergence of the adult from the pupa. Whereas parasites occur in insect orders that are hemimetabolous and holometabolous in development, parasitoids occur only in orders with holometabolous development.

### 11.5.1.1 Blattodea (Cockroaches)

Blattodea (Cockroaches) are not considered as having parasitic members; typically, they are considered on the receiving end of any parasitic interaction (Askew 1971). Currently, no cockroach is known to be a parasite or parasitoid of another species (Bell et al. 2007), the probable occurrence of cockroach parasites in the fossil record is noteworthy (Vršanský et al. 2019). From 99 million-year-old Late Cretaceous (Cenomanian) Myanmar Amber, two cockroaches, *Spinka fussa* and *Bimodala ohmkuhnlei* of the Blattidae (American cockroaches) have been described as associated with complex ant nests. These two species occurred in the same, large, amber pieces as the ant nests, and likely were myrmecophiles (Vršanský et al. 2019). (A myrmecophile is a commensal or parasite of the nest of an ant species.) The authors interpret the two cockroach myrmecophile species as engaged in commensalistic and parasitic relationships with their ant hosts, consistent with morphological features in extant ant myrmecophiles. The significance of these extinct, social parasitic cockroaches was their impact on the evolution of complex ant nests in late Mesozoic tropical forests soon after the earliest evidence for ant eusociality in the fossil record.

#### 11.5.1.2 Dermaptera (Earwigs)

Modern Dermaptera (earwigs) consist of 3 suborders, 11 families and 203 genera, and are nocturnal, hemimetabolous insects with distinctively short forewings and terminal abdominal cerci modified into forceps-like pincers (Haas 2018). Two dermapteran lineages, Arixeniidae (bat earwigs) and Hemimeridae (rodent earwigs), often are placed in their own suborders, and live ectoparasitically on mammals (Popham 1984), although recent evidence suggests that the relationships may be more commensalistic than parasitic (Haas 2018). Hemimeridae occur in sub-Saharan Africa on hamster rats and possess a suite of structures, such as dorsoventrally flattened bodies; short, grooved legs to cling to fur; and mouthparts for abrading and feeding on host skin and surface fungi (Rehn and Rehn 1935, 1937; Ashford 1970; Nakata and Maa 1974). Arixeniidae occur with molossid bats in caves in Southeast Asia, and possess a matted pubescent body, long antennae and long legs for rapid movement (Nakata and Maa 1974). A phylogenetic study of Dermaptera (Kocarek et al. 2013) indicates that the Hemimeridae and Arixeniidae each has a sister-group relationship with another dermapteran family, indicating that the parasite lineages are convergently evolved, highly modified earwigs (Fig. 11.5). These relationships indicate the potential for rapid change of parasite external morphology when a new trophic niche becomes available (Kocarek et al. 2013), likely during the Eocene when their rodent and bat hosts initially diversified.

#### 11.5.1.3 Psocoptera (Booklice, Psocids)

The term, Psocoptera (booklice, psocids) currently is not widely used, which is partly attributable to the paraphyletic status that this ancient group of hemimetabolous insects has with respect to the nested clade of Phthiraptera, the parasitic lice (Nagler and Haug 2015; Mockford 2018). Nevertheless, Psocoptera as used in this report is a convenient reference to all intervening, free-living lineages of bark lice that form the broader clade. The Psocoptera includes the variously ranked Trogiomorpha, Amphientometae, Sphaeropsocidae, Psocomorpha (the overwhelming bulk of taxonomic diversity), and the book lice, Liposcelididae (Johnson et al. 2018). Of these, particular attention should be devoted to Liposcelididae. The

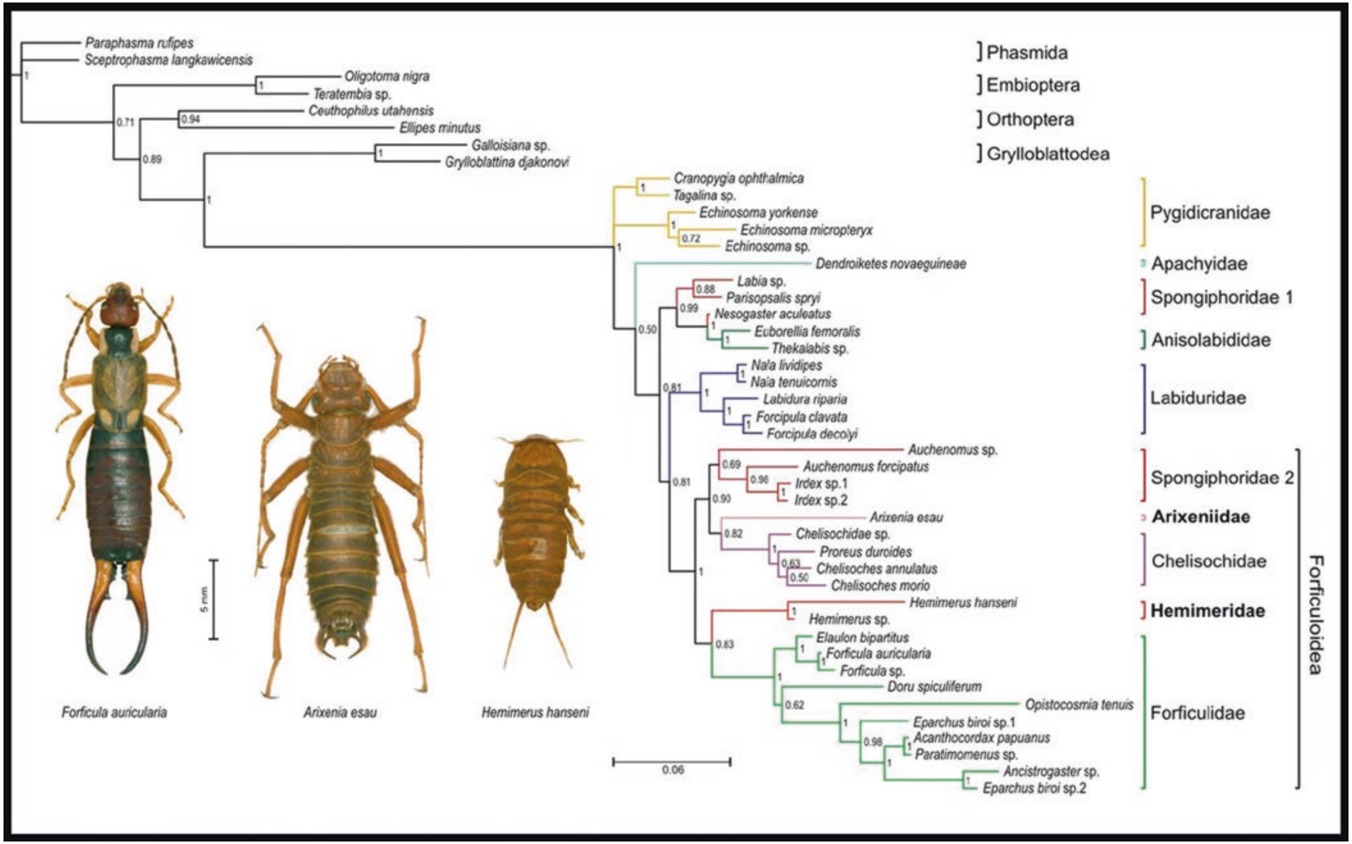


**Fig. 11.5** Bayesian phylogram of Dermaptera (earwig) families based on nuclear sequence data of 18S and 28S ribosomal DNA and histone-3. Numbers above branches indicate posterior probabilities. The Arixenidae and Hemimeridae (bold font) are parasitic clades. (Reproduced with permission from Fig. 2 of Kocarek et al. 2013)

Liposcelididae is the sister-group to the parasitic lice clade of Phthiraptera, consisting of the Amblycera + [Anoplura + (Rhyncophthirina + Ischnocera)] clade, equivalent to the common names of chewing lice 1 + [sucking lice + (chewing lice 2 + elephant/warthog lice)], treated separately below. In particular, the Liposcelididae provides significant clues to the origin of parasitism in the Phthiraptera and provides evidence that demonstrates tendencies toward parasitism in certain psocopteran lineages.

Liposcelididae consist of 9 genera and approximately 200 species of small, pale, dorsoventrally compressed, and often wingless barklice that are inquilines of insect nests (Mockford 1971). In particular, Liposcelididae are morphologically and behaviorally intermediate between free-living Pachytroctidae (thick book lice), from which they originated, and the ectoparasitic Phthiraptera (parasitic lice) clade with which they are sister groups (Johnson et al. 2004, 2018). Notably, the diet of probably the best-studied extant booklouse, synanthropic *Liposcelis bostrychophila*, consists of raw cereal grains treated with yeast (Green and Turner 2005). Other species of the genus evidently consume sloughed off integument such as flakes of skin and covering sheaths of feathers (Lin et al. 2004; Grimaldi and Engel 2005b). Fossils of Liposcelididae are rare, but the lineage has its earliest occurrence in Myanmar Amber (99 Ma), providing a minimal date for the divergence of Liposcelididae and Phthiraptera (Grimaldi and Engel 2005b). Nonetheless, a dated molecular phylogenetic analysis indicates an older separation date at the Triassic–Jurassic boundary (Johnson et al. 2018).

#### 11.5.1.4 Phthiraptera (Parasitic Lice)

Phthiraptera (parasitic lice) consist of 4 suborders, 24 families, 304 genera and 5316 species that are obligate ectoparasites of birds and mammals (Galloway 2018). Phthirapterans are wingless, dorsoventrally flattened, have small eyes or are blind, and possess a variety of sense organs located especially on their antennae and mouthparts for detection of and their positioning on their hosts (Marshall 1981; Clayton et al. 2016). As ectoparasites, they complete all life stages of their development on the bodies of their hosts, requiring their host's moist, warm skin and adjacent humid microenvironment to live and reproduce by attaching their elongate eggs to hair shafts with a cementing substance (Fig. 11.1k). Lice are sensitive to minute temperature gradients across their host's body and die if deprived of their thermally constrained integumental microenvironment for more than several hours to a few days (Tompkins and Clayton 1999).

The major clades of the monophyletic Phthiraptera are the Amblycera and the Ish nocera + (Rhyncophthirina + Anoplura) clades (Johnson et al. 2018). In common parlance these clades are equivalent to, respectively, the chewing lice 1 clade and the chewing lice 2 + (elephant/warthog lice + sucking lice) clade. Phthiraptera were derived from the psocopteran lineage Liposcelididae, with which it shares a sister-group relationship (Grimaldi and Engel 2005b; Johnson et al. 2018). Within Phthiraptera, the basal-most lineage is Amblycera, the chewing lice 1 clade. These lice principally infest birds, but one-eighth of the species represent three nonspeciose, minor families that are on mammals (Galloway 2018). The next derived (and most diverse) clade is Ischnocera, the chewing lice 2 clade, representing 54% of phthirapteran species. Ischnocera primarily parasitize birds, although, as in the Amblycera, about one-eighth is on mammalian hosts. The Amblycera and Ischnocera are characterized by mandibulate mouthparts, broad and flattened heads, and typically consume flaked off skin, integumental exudates such as sebum and sweat, other debris such as fungi associated with feathers and occasionally blood and lymph at the skin surface (Lehane 1991). The major structural differences between these two major types of chewing lice involve their heads and mouthparts. The third clade, Rhyncophthirina, has highly modified chewing mouthparts that have been reduced to tiny pincer-like mandibles at the end of a long tubular extension of the head capsule for imbibing of blood and dermal secretions, akin to piercing and sucking. Rhyncophthirina is a highly specialized, blood-feeding clade that occurs only on mammals and consists of one genus and three species that parasitize the African elephant, wart hog and Red River hog as hosts (Galloway 2018).

Sister-group to the Rhyncophthirina is the Anoplura, the sucking lice, which are the only truly piercing-and-sucking clade with stylate mouthparts within Phthiraptera. Anoplura secure their food by targeting blood vessels and attach their eggs, known as nits, to the hair of their hosts by large, grasping and curved tarsal claws (Fig. 11.1k). Anoplura parasitize most orders of placental mammals by feeding on their blood. About 70% are associated with rodents (Light et al. 2010), but are not found on armadillos, pangolins, elephants, aquatic species except for seals, and are notably absent on bats (Durden and Musser 1994). Based on a phylogenetic analysis of Anoplura (Light et al. 2010), the clade originated during the Late Cretaceous (Campanian Stage) around 77 million years ago, but did not diversify until the early Paleogene, after the ecologic crisis marking the Cretaceous–Paleogene boundary, and presumably coincident with the diversification of many warm-blooded mammal lineages. A notable exception to anopluran and other phthirapteran hosts are bats, which are inferred to be present and diverse during the Paleogene diversification of placental mammals (Teeling et al. 2005). Phthirapteran absence from bat hosts may be attributable to competition from their previously acquired, rich fauna of parasites that included mites, bat bugs, bat flies and fleas, or were limited by the significant drops in bat body temperatures during hibernation (Grimaldi and Engel 2015a). Both limitations would eliminate phthirapterans as hosts (Clayton et al. 2016).

Phthiraptera have a poor, but rather remarkable fossil record. The oldest yet most bizarre specimen is a large, 17 mm long *Saurodectes vrsanskyi* (Fig. 11.1h) of the monotypic Saurodectidae from the Early Cretaceous (130 Ma) Baissa locality in Transbaikalia, Russia (Rasnitsyn and Zherikhin 1999). This specimen bears several anomalous features: a large size of 17 mm in length; well-developed, compound eyes; a pair of peculiar, horn-like appendages extending laterally from each side of the head; long and ambulatory legs; widely separated leg bases; a pair of robust spines behind the forecoxae; and exceptionally small claws. These characters are atypical compared to modern species of Phthiraptera. The initial, reasonable, attribution of the specimen's life style was an ectoparasite of a warm-blooded vertebrate possessing hair, such as a pterosaur, or possibly a mammal of large size (Rasnitsyn and Zherikhin 1999). Nevertheless, the specimen does reveal structures similar to chewing lice of the Ishnocera such as a highly flattened body, a single clawed tarsus and robust truck tracheae and spiracles, but its' very large size would be inconsistent with parasitization of any host except a large vertebrate. However, contrary interpretations regarding the affinities of the fossil suggest that this specimen is not a phthirapteran (Wappler et al. 2004; Dalgleish et al. 2006). Major features indicating that the specimen is not a phthirapteran is the absence or lack of preservation of mandibles and the presence of large lateral head processes (Dalgleish et al. 2006).

From the Eckfeld maar crater beds in Germany, of middle Eocene (44 Ma) age, is *Megamenopon rasnitsyni* (Amblycera: Menoponidae), a member of primitive chewing lice (Wappler et al. 2004). This specimen exhibits similarities to amblyceran feather lice that parasitize Anseriformes (ducks, geese and swans) and Charadiformes (shorebirds). The presence of feather chaff in gut contests of the specimen confirms its life habit as an ectoparasite (Wappler et al. 2004). From nearby Baltic Amber, a deposit of approximately the same age as Eckfeld, Voigt (1952) described phthirapteran eggs cemented to mammalian hair, likely belonging to an unknown sucking louse of Anoplura.

### 11.5.1.5 Hemiptera (Bugs)

Within the Hemiptera, it is only the suborder Heteroptera (true bugs) and its constituent infraorder, Cimicomorpha, which contains parasitic lineages engaged in hematophagy. Four cimicomorph lineages, Cimicidae (bed bugs), Polyctenidae (bat bugs), Reduviidae (assassin bugs), and extinct Torirostratidae, contain the hematophagous genera within Hemiptera. Given established phylogenies within the Cimicomorpha (Schuh et al. 2009; Weirauch and Munro 2009; also see Yao et al. 2014), hematophagous parasitism originated in the Hemiptera three times: once in Reduviidae, once in the Polyctenidae + Cimicidae clade, and once in the extinct Torirostratidae.

Cimicidae consists of 6 subfamilies and 21 genera, including the common bed bug *Cimex lectularis*, which are obligate parasites of warm-blooded vertebrates, including humans. As a group, cimicids are frequently narrow host specialists, and rarely are vectors for disease-causing viruses and other pathogens (Reinhardt and Siva-Jothy 2007). Cimicids are attracted to hosts by several cues, including temperature, carbon dioxide gradients and animal kairomones, and feed once every 3–7 days (Reinhardt and Siva-Jothy 2007).

Polyctenidae are a family of rare subtropical bugs, the probable sister-group of Cimicidae, that consist of two subfamilies and five genera that are ectoparasites of bats and exhibit substantial host specialization. The family derives its name from the presence of prominent combs that cover several regions of the body, including the antennal bases, gena of the head, and pronotum, prosternum, mesonotum, ventral surfaces of the abdominal segments and tarsi (Askew 1971). Members of

Polyctenidae have hairy bodies, lack ocelli and compound eyes, display wings that are featureless flaps, and have abbreviated fore legs (Maa 1964).

Among predatory Reduviidae (assassin bugs), one subfamily, Triatominae (kissing bugs, conenose bugs), consists of 6 tribes and 18 genera that are responsible for feeding on vertebrate blood and vectoring trypanosomes that cause Chagas disease in humans, a debilitating disorder of the Americas. *Rhodnius prolixus* (common kissing bug) and *Triatoma infestans* (winchuka) are major vectors of Chagas disease and frequently are associated with triggering anaphylaxis (Klotz et al. 2010). The Triatominae is a monophyletic subfamily within the Reduviidae (Weirauch and Munro 2009), although the Reduviidae is phylogenetically very distant from the Cimicidae + Polyctenidae clade within Heteroptera (Schuh et al. 2009).

Presently the only extinct, family-level lineage of hematophagous Hemiptera is Torirostratidae, from 125 million-year-old Early Cretaceous Yixian Formation of northeastern China (Yao et al. 2014). Two well-preserved genera are placed in the Torirostratidae but remain unplaced within the Cimicomorpha. The fossil record of other hematophagous Heteroptera is represented by two occurrences. One is a fossil of Cimicidae from mid-Cretaceous Myanmar Amber, *Quasicimex eilapinastes*. *Quasicimex* exhibits many characters of Cimicidae sensu lato by possessing several apomorphies while concurrently retaining some primitive characters not found in the crown-group (Engel 2008a). The Polyctenidae, however, lack a fossil record. The other occurrence is the infamous reduviid *Triatoma* (kissing bugs), a major vector for blood-borne diseases, which has a fossil record, as *T. dominicana*, that extends to Dominican Amber approximately 21 million-years ago (Poinar Jr 2005). A second specimen reveals that a triatomine–trypanosomid vector association existed through the presence of *Trypanosoma antiquus* individuals in a fecal droplet of *T. dominicana* adjacent to mammalian hairs (Poinar Jr 2005, 2021). This association suggests a vertebrate host was a precursor to Chagas Disease that currently affects millions of humans in Central and South America (Lent and Wygodzinsky 1979).

#### 11.5.1.6 Coleoptera (Beetles)

Within Coleoptera, the representation of parasites is scattered across the taxonomically vast order. Often, descriptions of the life habits of taxa are unclear as to whether a particular species is a parasite or a parasitoid, particularly since the term “parasite” occasionally meant “parasitoid” in the older literature. However, parasite habits have been established for Leiodidae and Meloidae and probably Rhipiceridae, Passandridae and Bothrideridae, although the latter three lineages are overwhelmingly represented by parasitoids and are reviewed more appropriately in Sect. 11.5.2.2. It is highly likely other beetle lineages will be determined to have obligate parasitic life habits in the near future, as the life histories of individual species become better known.

Leiodidae (round fungus beetles) consist of 6 subfamilies and about 3800 species that are small to very small and typically are saprophagous or feed on a variety of fungi in punky wood, although a broad spectrum of feeding habits are present, including parasitism (Newton 2005). One subfamily, Platypsyllinae, consists of 4 genera and about 20 species that are ectoparasites of semiaquatic and aquatic mammals such as insectivores (Talpidae), beavers (Castoridae), mountain beavers (Aplodontidae) and river otters (Mustelidae), consuming flakes of decorticated skin, dermal exudates and probably surficial blood (Newton 2005; Peck 2006). The highly specialized parasite *Platypsyllus* (beaver beetle) is the best documented platypsylline, and the adult, flea-like in overall appearance, is a flat, wingless and blind form that has thoracic hooks for attachment to the hair of its host. The larvae and adults are parasites of the North American beaver, *Castor canadensis*, and the North American river otter, *Lontra canadensis*, and leave their host only to pupate (Peck 2006).

Meloidae (blister beetles) are a diverse, cosmopolitan family of beetles occurring primarily in warm temperate to arid regions that consist of four subfamilies and about 120 genera (Bologna et al. 2010). The diets of adult Meloidae are variable, with phytophagy dominant and predation subdominant. Most larvae are predaceous, feeding on grasshopper egg pods and immatures of aculeate wasps and bees, with development occurring in the soil or wood (Bologna et al. 2010). However, parasite and parasitoid forms occur throughout the family. The life cycle of Meloidae is complex, with the larva undergoing hypermetamorphosis and consisting of four distinct larval instars prior to entering the pupal stage. The first larval instar is an actively mobile, well sclerotized triungulin, which is the dispersal stage for seeking parasite and parasitoid hosts. The triungulin instar is followed by a first instar grub, a feeding stage of robust proportions; then a coarctate instar, a resting stage in diapause; and finally a second grub instar that is active but nonfeeding prior to pupation (Selander and Mathieu 1964). Parasitic (and parasitoidic) larvae use grasshoppers, ground beetles, aculeate wasps and bees as hosts (Engel 2005a; Bologna et al. 2010). Although meloid consumers of other animals are over-represented by parasitoids, the family does harbor several lineages of ectoparasites (Engel 2005a; Bologna and Di Giulio 2011).

The fossil record of beetle parasites, as would be expected, is poor, particularly for non-diverse families. There is no fossil record of the Platypsyllinae, although the Leiodidae has a decent fossil record of 16 occurrences that extends to the Late Jurassic (Perkovsky 1999). Rhipiceridae apparently has a fossil record extending to the middle Eocene (Ponomarenko 1995). Bothrideridae has a known first occurrence from the middle Eocene (Ponomarenko 1995). The Passandridae has a sparse fossil record of three Cenozoic occurrences; the earliest occurrence is from an approximately 44 million-year-old middle Eocene (Lutetian) deposit in Argentina (Ramírez et al. 2016). The Meloidae is a largely Cenozoic lineage that has a sparse fossil record when compared to its extant diversity. The meloid fossil record, however, includes records of triungulin larvae (Engel 2005a; Bologna et al. 2008) that provide evidence for phoresy and other features consistent with an ectoparasitic mode of life (Engel 2005a). The meloid fossil record includes 12 fossil occurrences; the oldest is from the 35 million-year-old late Eocene. The Ripiphoridae have a fossil record extending to the early Cenomanian (Cai et al. 2018; Batelka et al. 2016, 2019). It is unclear if any of these occurrences demonstrate a specific parasitic relationship with an actual, extinct host.

#### 11.5.1.7 Siphonaptera (Fleas)

Flea-like insects, fleas and basal lineages of flies are closely related to one or more lineages of mid-Mesozoic Mecoptera (scorpionflies) (Huang et al. 2012; Lin et al. 2019; but see Byers 1996). The long-proboscid pollinating scorpionfly lineage Aneuretopsychidae (Ren et al. 2011) is a prime suspect as an ancestor of flea-like insects, fleas and the earliest Diptera (Lin et al. 2019). For mid-Mesozoic flea-like insects, mouthpart structure, body form, other specialized features, and known relationships between specific external adaptations for living on a host in modern fleas (Huang et al. 2012; Gao et al. 2012, 2014) indicate that these taxa were ectoparasites feeding primarily on blood. These ectoparasites likely had intimate associations with endothermic vertebrates during the mid Mesozoic (Leung 2017; Labandeira 2019), ranging from the Middle Jurassic to Early Cretaceous (Huang et al. 2012; Gao et al. 2014). However, lineages of mid Mesozoic, early flea-like lineages (Huang et al. 2012, Huang et al. 2013a), known only from East Asia and Australia, are morphologically different from all modern flea taxa that occur worldwide (Leung 2017, 2021; Rasnitsyn and Strelnikova 2017). Unlike modern fleas (Fig. 11.11), Middle Jurassic to Early Cretaceous flea lineages (Fig. 11.6) possessed cylindrical, dorsoventrally or laterally compressed bodies of large size (Strelnikova and Rasnitsyn 2016; Rasnitsyn and Strelnikova 2017). They also had mouthpart modifications such as overall robustness, stylets with variously positioned serrations, and stylet envelopment by two sutured half-tubes of the labium (Labandeira 2019). These mid Mesozoic forms typically lacked jumping hind legs and stereotypical ctenidial combs (Huang et al. 2013a).

A variety of vertebrate groups have been suggested as hosts for mid-Mesozoic "fleas", particularly those with vestitures of feathers such as nonavian dinosaurs and possibly birds, and pelages of hair such as pterosaurs and large mammals (Ji et al. 2006; Wellnhofer 2008; Godefroit et al. 2014). Nevertheless, these oldest fleas, even

**Fig. 11.6** Habitus of the holotype specimen PIN 3064/189 of *Saurophthirus longipes* (?Siphonaptera: Saurophthiridae) was initially described by Ponomarenko in 1976. This specimen exhibits a distended abdomen interpreted to reflect a blood meal. Body length is 12 mm. (Photograph by D. Grimaldi; reproduced with permission from Fig. 1 in Rasnitsyn and Strelnikova 2017)

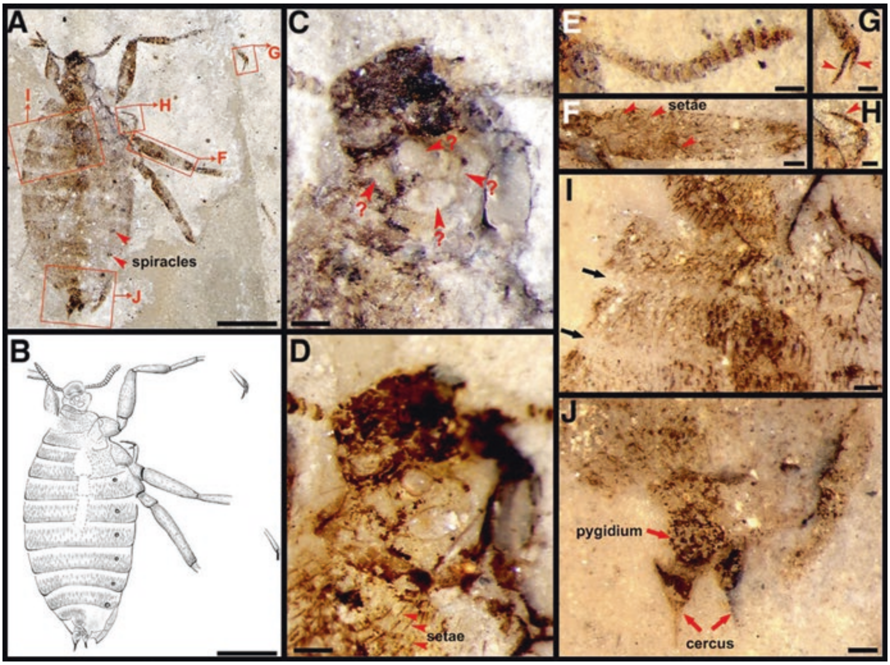


**Fig. 11.7** The holotype female of *Pseudopulex tanlan* (Siphonaptera: Pseudopulicidae) (Gao et al. 2014), from the Early Cretaceous Yixian Formation of northeastern China (CNU-SIP-LL2013002). (**a**, **b**) Photograph and line drawing. Photograph of the head region with (**c**) and without (**d**) alcohol. Red arrows point to four, ovoidal, perhaps membranous structures of unknown function. (**e**) Antenna. (**f**) Mid-leg femur. (**g**, **h**) Tarsal claw. (**i**) Segmental boundary (black arrows) of the abdomen. (**j**) Abdominal terminalia. Scale bars: (**a**, **b**) 2 mm; (**c**–**j**) 0.2 mm. (Reproduced with permission from Fig. 1 of Gao et al. 2014)

with their larger size and massive mouthparts may not have had dinosaurs such as theropods for hosts (Dittmar et al. 2016). Many features described for mid-Mesozoic giant “fleas” (Gao et al. 2012; Huang et al. 2013a) are not found on modern fleas that are known blood-feeding parasites of mammals and birds. The relationship that large parasite size is reflective of large host size has never been tested empirically (Dittmar et al. 2016).

There are three principal lineages of mid-Mesozoic fleas: Pseudopulicidae, Tarwiniidae and Saurophthiridae (Ponomarenko 1976; Huang et al. 2013a). The Pseudopulicidae are latest Middle Jurassic in age and from East Asia. Pseudopulicidae are large bodied, robust, flea-like insects that have a cylindrically shaped body, lack pronotal and genal ctenidial combs as well as saltatorial hind legs, and have an abdomen capable of significant distension (Fig. 11.7a, b, f–j) (Gao et al. 2012, 2014). The head has well developed eyes, moniliform antennae, robust mouthparts with prominent stylets of inwardly directed teeth, and four ovoidal, perhaps membranous structures of unknown function on the dorsal part of the head (Fig. 11.7c–e) (Gao et al. 2012, 2014). A ballooned abdomen evidently had a high volumetric capacity for storing blood (Fig. 11.7a, b). A second, related, group of fleas with some modern, siphonapteran morphology are an Early Cretaceous (Aptian) lineage, Tarwiniidae, from Australia, consisting of laterally compressed and small bodies, slender hind limbs for jumping, pseudoctenidial combs, diminutive eyes, and robust, grasping tarsal claws (Huang 2015; Leung 2017). A third lineage is Saurophthiridae, related to Pseudopulicidae and Tarwiniidae (Huang 2014), or alternatively with Tarwiniidae as sister clade to Strashilidae (Rasnitsyn and Quicke 2002; Nagler and Haug 2015). *Saurophthirus* resembles modern fleas by having a smaller size, more abbreviated mouthparts, and very long legs (Fig. 11.6). However, once considered as pterosaur ectoparasites (Ponomarenko 1976), Saurophthiridae lack ctenidia necessary for their ensconcement during flight on a pterosaur's wing membrane, as proposed by Ponomarenko (1976). By comparison, ichnopsyllid fleas on modern bats possess ctenidia that affix them securely to bat wings in flight (Huang 2014). For Saurophthiridae, life habits were more likely as nest inquilines or cleptoparasites feeding on a variety of dermal fluid substances, rather than as ectoparasites on the body directly feeding on pterosaur blood (Huang 2014). Recent evidence based on reconstruction of massive tracheae required for respiration indicates a larval aquatic existence, while adults might have maintained a parasitic presence on pterosaurs (compare Leung 2021; Shcherbakov 2017; Rasnitsyn and Strelnikova 2017).

These three lineages likely had a similar timing of origin during the mid-Mesozoic. One study indicates that modern fleas originated considerably later, during the Paleogene, and possibly earlier in the Late Cretaceous (Zhu et al. 2015). Such origins and phylogenetic relationships would indicate that mid-Mesozoic lineages of fleas, which evidently became extinct during the mid Cretaceous, constituted a separate clade or group of related clades of flea-like organisms, possibly affiliated with Siphonaptera or originating from a separate scorpionfly ancestor (Huang et al. 2012). Accordingly, mid-Mesozoic "giant" fleas and modern, diminutive fleas were the two, distinctive subclades of a more broadly inclusive Siphonaptera clade (Huang et al. 2012; also see Gao et al. 2014). Both subclades might have evolved independently in parallel with the similarly independent evolution of homoeothermic body temperatures on their respective host clades in a manner similar to blood-feeding Diptera and their major vertebrate host lineages (Lukashevich and Mostovski 2003). The three lineages of Pseudopulicidae, Tarwiniidae and Saurophthiridae evidently are closely related, share several features in common typical of ectoparasites, and likely fed on the blood, lymph, sebum and other dermal secretions of haired early mammals, birds or feathered dinosaurs (Huang 2014).

Modern aspect fleas, typical of all modern Siphonaptera lineages, are found in major amber deposits of the Cenozoic (Leung 2017). The flea lineages fed on the blood of birds and monotreme, metatherian and eutherian mammals (Zhu et al. 2015), through stylate mouthparts that were more gracile in almost every structural aspect than those of the mid Mesozoic (Gao et al. 2014). An extensive list of characters, including mouthpart features, differentiate and link the five, major, mid-Mesozoic flea-like lineages that are related by a *Tarwinia* + [(*Pseudopulex* + *Hadropsylla*) + *Tyrannopsylla*] + [*Saurophthirus* + modern fleas] phylogeny (Huang et al. 2012; Gao et al. 2014). Characters defining the six lineages include those of the head, eyes, antennae, pronotum, coxae, tarsi, genitalia and cerci, but mouthpart traits are important. For example, the labial palps form a short, segmented, robust structure in *Saurophthirus* and modern fleas, whereas they form a long, non-segmented, streamlined, more gracile structure enveloping the mouthpart stylets in all other mid-Mesozoic flea-like lineages except *Tarwinia* (Gao et al. 2014). This indicates that the *Saurophthirus* + modern fleas constitute an expanded Siphonaptera clade that is distantly related to all other mid-Mesozoic fleas.

The earliest hosts for these early true flea lineages were mammals (Perrichot et al. 2012), although four, separate, parasite shifts apparently colonized birds most likely through introductions from ground nesting flea taxa (Whiting et al. 2008; Zhu et al. 2015). During the Cenozoic, several lineages of fleas are documented in ambers, although the most commonly encountered are common fleas (Pulicidae), particularly in Baltic and Dominican ambers (Lewis and Grimaldi 1997; Perrichot et al. 2012; Poinar Jr 2015). Rodent fleas of Ctenophthalmidae and Hystrichopsyllidae (Fig. 11.11) were described from Baltic Amber (Dampf 1910; Pielowska et al. 2018). Marsupial fleas of Rhopalopsyllidae are known from Dominican Amber (Grimaldi and Engel 2005a).

#### 11.5.1.8 Diptera (Flies)

Diptera constitute the greatest variety of parasitism, principally through blood-feeding (hematophagy), of any insect group, and are responsible for the widespread vectoring of parasites that often produce blood diseases principally to vertebrates, including humans. Eight major clades encompass 15 families that collectively are responsible for almost all of the documented parasitic relationships between Diptera and their vertebrate and other hosts (Lehane 1991; Lukashevich and Mostovski 2003). At the family level, hematophagy originated minimally 12 times (Wiegmann et al. 2011), although at lower taxonomic levels of origination are much greater. Dipteran hematophagous clades often are assembled into a nematocerous group (Culicoidea, Chironomoidea, Psychodiodea), a brachycerous group (Tabanoidea, Rhagionoidea), and a cyclorrhaphous group (Muscoidea, Hippoboscoidea, Oestroidea). Notably, these clades collectively represent the widest variety of mouthpart types in insects (Labandeira 1997, 2019), and house a diversity of feeding styles. Most of these families have members that are vectors of a variety of infectious diseases (Lehane 1991), and apparently opportunities were seized in occupation of new ecological niches for transmission of blood parasites sometime during the Early Cretaceous (Leung 2017). The pathogen fossil record indicates that such disease transmission commenced during the Early Cretaceous and has expanded to the Recent (Labandeira 2014a; Poinar Jr 2018, 2021).

The Culicoidea is a major clade of nematocerous flies (Wiegmann et al. 2011) that evolved lineages parasitic on vertebrates through blood feeding. One of the earliest occurrences of Culicoidea is from Late Triassic (late Carnian) strata of the Solite Quarry in southernmost Virginia, U.S.A. (Blagoderov et al. 2007). A particular specimen (Fig. 11.8), unassignable to family, displays the anterior thoracic region, head capsule, eyes, and sufficiently well preserved mouthparts to determine that the proboscis likely has a design consistent with feeding on pollination drops or

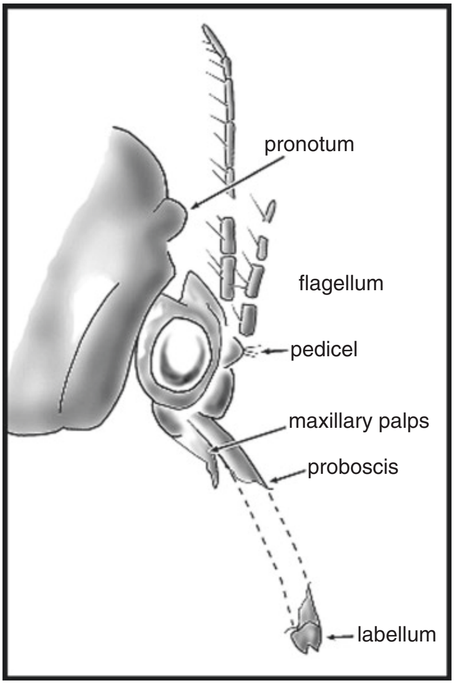


**Fig. 11.8** Detail of head and preserved proboscis of a Culicomorpha specimen from the Solite quarries of southern Virginia, USA. This specimen (VMNH951) shows a long proboscis of a type generally associated with blood feeding, indicating that this form may be the earliest instance of blood feeding with specialized mouthparts in the fossil record. Distance from the top-most part of the head to proboscis tip is 0.5 mm. (Reproduced with permission from Fig. 9 in Blagoderov et al. 2007)

blood (Blagoderov et al. 2007). The specimen lacks the midsection of the proboscis but does reveal its base and terminus with a labellum and an intact maxillary palp. One possibility for the feeding style of this proboscis morphology is that it is a long-proboscid siphonate tube for imbibing pollination drops or related fluids from seed plants (Labandeira 2005). Alternatively, it could represent a stiffened stylate condition consistent with piercing and sucking for blood meals. As the adult diet ground plan of the Culicomorpha is blood feeding (Lukashevich and Mostovski 2003; Labandeira 2005), it is thus more likely that this specimen represents blood feeding. If this is the case, then this specimen represents the earliest documented example parasitic blood feeding in the fossil record.

One of the major families of Culicoidea is Culicidae (mosquitoes), which consist of approximately 40 extant genera that typically attack vertebrate hosts by bending their flexible stylet fascicles through host integument to obtain blood from capillaries, a feeding strategy known as solenophagy (Bouchet and Lavaud 1999). The earliest fossil occurrence of Culicidae is early Cenomanian Myanmar amber on the Early Cretaceous–Late Cretaceous boundary interval at 99 million years ago (Borkent and Grimaldi 2004). This particular specimen also is phylogenetically ancient, a sister-group to all other extant and extinct species of Culicidae. Nevertheless, it is probable that substantially older culicids will be found, extending the blood-feeding habit to the Jurassic (Borkent and Grimaldi 2004). The Cenozoic record of Culicidae is sporadic and specimens are found in several compression and amber deposits (e.g., Szadziewski 1998). Perhaps the most stunning discovery was a 46 million-year-old Eocene mosquito from the Kishenehn Formation of northwestern Montana with blood in its distended abdomen (Greenwalt 2021; Greenwalt et al. 2013). Heme-derived porphyrin molecules of hemoglobin were detected and molecularly characterized by advanced mass spectrometry and other techniques, indicating the presence of blood feeding, although the source of the vertebrate blood remains unknown.

The Chironomoidea include the principal blood-feeding groups of Ceratopogonidae (biting midges, no-see-ums) and Simuliidae (black flies, buffalo gnats). While extant Chironomidae (non-biting midges) are considered as predominately feeding on pollen, nectar, honeydew and other carbohydrate-rich food, extinct forms were hematophagous based on mouthpart structure (Azar and Nel 2012). Chironomidae extend to the Late Triassic–Early Jurassic boundary interval (Grimaldi and Engel 2005a), making them among the earliest hematophagous Diptera. Ceratopogonidae are represented by several, prominent, extant genera that are blood feeders, and the family has a good fossil record (Borkent 2001), extending to the Early Cretaceous (Berriasian Stage) at about 140 Ma. There are several instances of ceratopogonid parasitism in the amber fossil record. One example is a ceratopogonid specimen from Myanmar Amber (99 Ma) that hosted in its gut oocysts of the malarial parasite, *Paleohaemoproteus burmacis*, a pathogen similar to modern species found in reptiles and birds (Poinar Jr and Telford Jr 2005), and likely representing an ancient association. From the same deposit, a second ceratopogonid specimen, *Leptoconops nosopheris*, vectored the trypanosome *Paleotrypanosoma burmanicus* that may have produced trypanosomiasis-like symptoms in an unknown vertebrate host (Poinar 2021).

The fossil record of the Simuliidae begins during the Late Jurassic (Oxfordian Stage) and has a fair record of occurrences up to the recent (Currie and Grimaldi 2000). However, black fly–parasite associations are rare. The earliest fossil Simuliidae has been described from Kazakhstan (Kalugina 1991). From these compression-impression deposits, it appears that the blood-feeding habit in Simuliidae originated early within the clade, and may be the ancestral diet (Kalugina 1991).

The Psychodoidea is a more ancient nematocerous lineage than Chironomoidea that extends to the Late Triassic (Fraser et al. 1996). The only blood-feeding lineage of Psychodoidea is Psychodidae (moth flies), of which the subfamily Phlebotominae (sand flies) represent the only origin of hematophagy within the larger clade (Grimaldi and Engel 2005a, b) and are a major cause globally for transmission of several modern diseases in animals (Lehane 1991). One Cretaceous association involves the phlebotomine *Palaeomyia burmitis* that vectored a trypanosome parasite, *Paleoleishmania proterus*, which presumably developed in reptilian blood cells consumed by the sand fly (Poinar Jr 2004a; Poinar Jr and Poinar 2004a, b). This sand fly–trypanosome–reptile parasitic interaction occurs in mid Cretaceous Myanmar amber (Poinar 2021), and suggests a pathological relationship similar to modern leishmaniasis, a debilitating disease creating ulcers of the skin and viscera in vertebrates.

Tabanoidea consist of two families, Tabanidae (horse flies, deer flies) and Athericidae (watersnipe flies) that are involved in blood feeding. Tabanidae constitute about 32 modern genera of brachycerous flies that bite vertebrates using a slashing and cutting strategy to obtain blood and fluids that pool up within lesions, feeding strategy known as telmophagy (Bouchet and Lavaud 1999). Although the earliest Tabanidae originate from the latest Middle Jurassic of northeastern China (Ren 1998; Labandeira 2010), their original diet has been a mystery as to whether they consumed nectar-like pollination drops or blood (Grimaldi and Engel 2005a). This uncertainty arises because tabanids occur in the fossil record about 40 million years before the appearance of angiosperms, although a broad variety of vertebrates were present at this time. One hypothesis is that pangionine tabanids possessed siphonate mouthparts and were consumers of pollination drops (Labandeira 2010), whereas tabanine tabanids instead bore stylate mouthparts and were consumers of vertebrate blood (Martins-Neto 2003; Lukashevich and Mostovski 2003; Labandeira et al. 2007a, b). A less likely, alternative hypothesis is that for species of mid-Mesozoic tabanids, males consumed plant fluids of ovulate organs in a pollination mutualism. By contrast, conspecific females consumed vertebrate blood necessary for oögenesis and indicative of parasitism, a feeding behavior that occurs in some extant, hematophagous flies (Labandeira 2005).

Tabanids are known from younger earliest Cretaceous deposits of Brazil, the United Kingdom and Russia, some with probable hematophagous habits (Martins-Neto 2003; Lukashevich and Mostovski 2003). One particular specimen from the early Cretaceous of Transbaikalia is of large size with a robust body and gracile legs, a head having an inflated clypeus and elongate proboscis encompassing hardened stylets, and antennae and palps that bear numerous, multiple types of sensillae (Mostovski et al. 2003). These features are consistent with modern blood-feeding tabanids (Lukashevich and Mostovski 2003). In Paleogene deposits, such as Baltic Amber, the diversity of blood-feeding tabanids can be substantial, consisting contemporaneously of four genera and seven species of Chrysopinae and one genus and species of Tabaninae (Pielowska et al. 2018).

Athericidae are a modestly speciose family of 13 genera in which adults feed on nectar or blood and the aquatic larvae are predatory (Stuckenberg 1973). The athericid fossil record is unspectacular, with the exception of its earliest occurrence, the unusual *Qiyia jurassica* from the Jiulongshan Formation of northeastern China (Chen et al. 2014). *Qiya jurassica* possesses the most atypical attachment mechanisms for any ectoparasite: a thoracic sucker (Fig. 11.9). The aquatic fly larva *Q. jurassica* is a stem-group athericid from the latest Middle Jurassic of northwestern China (Chen et al. 2014). The larva is interpreted to have inhabited streams with rapid currents. In addition to this broad, ventral, circular attachment device occupying all three thoracic segments, *Q. jurassica* possesses a diminutive head with distinct piercing-and-sucking mouthparts, and stump-like abdominal prolegs for both attachment and movement. The authors (Chen et al. 2014) suggest that feeding occurred on salamander blood, although recent aquatic insect larvae in rapidly flowing streams with suction attachment discs are frequently predatory rather than parasitic in feeding habits (Leung 2017).

Rhagionoidea consist of one hematophagous family, Rhagionidae (snipe flies), of medium- to large sized flies that contain about 16 genera, several of which are hematophagous and do not transmit disease (Krenn and Aspöck 2012). Nagatomi and Soroida (1985) list only the distantly related *Spaniopsis* and *Symphoromyia* as blood feeders, indicating the hematophagy originated multiple times within the family. Although Rhagionidae enter the fossil record during the Early Jurassic (Lukashevich and Mostovski 2003), the earliest hematophagous forms are of Late Jurassic age, from the Glushkovo Formation of Transbaikalia, Russia (Kovalev and Mostovski 1997). One species with particularly evident hematophagous structures is the female of *Palaeoarthroteles mesozoicus* that houses a robust, hypognathous proboscis, downturned palps and an apparently rigid labium enveloping the stylets (Kovalev and Mostovski 1997; Labandeira 2019). An alternative explanation is that *Palaeoarthroteles* was an insect predator (Lukashevich and Mostovski 2003); however, the absence of spinose legs, stiff bristles surrounding the mouthparts and other features of predatory insects strongly suggests the blood-feeding nature of this insect.

Mormotomyiidae (frightful hairy fly) consists of the monotypic, spiderlike and hirsute *Mormotomyia hirsuta* that occurs on a bat guano substrate below a local cliff face in Kenya (Copeland et al. 2011). Once thought to be a bat parasite because of its habitus and association with guano, recent evidence indicates that it is not a bat parasite (Copeland et al. 2011). Mormotomyiidae evidently are a member of the Ephydroidea, an acalyptrate group basal to the Calyptratae Clade (Kirk-Spriggs et al. 2011).

Within Calyptratae (calyptrate flies), the three superfamilies Muscoidea (often treated as a grade), Hippoboscoidea and Oestroidea (Kutty et al. 2001) collectively bear nine families that contain parasitic taxa. Calyptrate flies are monophyletic and the most derived major clade of flies (Grimaldi and Engel 2005a, b; Kutty et al. 2001), responsible for a considerable amount of pestilence on vertebrates, including humans, particularly as feeders on blood and other fluids in their role as parasites and parasitoids (Oldroyd 1964; Marshall 2012). Many of the blood-feeding forms are found in the ubiquitous family Muscidae (house flies, stable flies), which consist of about 110 genera, including the familiar, synanthropic fly *Musca domestica*. Typically, muscids are predatory or feed on fluid exudates from plants and animals, such as sugar, honeydew, sweat, tears and blood. Blood-feeding muscids principally include *Stomoxys*, *Hydrotaea* and *Haematobia* of the tribe Stomoxyini (Krenn and

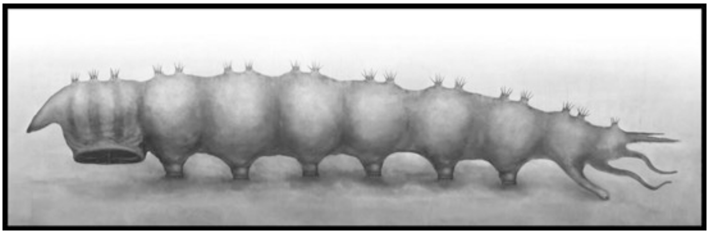


**Fig. 11.9** Reconstruction of the watersnipe fly larva *Qiyia jurassica* (Diptera: Athericidae), from the latest Middle Jurassic of Inner Mongolia, China. The ectoparasitic fly specimen is portrayed in left lateral view displays the ventral thoracic sucker for host attachment and a reduced, partly retractile head. (Reproduced with permission from Fig. 3 of Chen et al. 2014)

Aspöck 2012) that are parasitic on vertebrates, mostly livestock (Cupp et al. 1998; Salem et al. 2012), and represent probably a single origination of hematophagy (Schremmer 1961). Feeding in this tribe is accomplished by sharp, prestomal teeth on the labellum, resulting in surface abrasion of the integument and sponging of blood and other dermal fluids that pool in the lesions. The Tribe Stomoxyini lacks a fossil record, but because the clade is a member of the post-Cretaceous Calyptratae (Grimaldi and Engel 2005a), the lineage likely originated during the Paleogene and acquired parasitic interactions with large mammals at that time.

The Hippoboscoidea, termed Pupipara in the older literature, consists of the four constituent lineages of Glossinidae (tsetse flies), Hippoboscidae (louse flies, keds), Nycteribiidae (bat flies) and Streblidae (bat flies), although the last two lineages are not monophyletic (Griffiths 1972; Kutty et al. 2001). Hippoboscoid flies are united by several, common and distinctive reproductive features. The mature female lays a single mature larva, the puparium, after which the larva immediately pupariates, emerging from the hardened, last-instar larval skin that encloses the pupa (Ferrar 1987). The emergent, hematophagous adult then locates and parasitizes a suitable bird or mammalian host. This unique larval development is probably the most significant K-selection strategy in insects, with females laying only one egg at a time, albeit in succession, and larvae nursed internally in the mother by special uterine “milk” glands (Oldroyd 1964). Hippoboscoidea have considerable mouthpart penetrability and styletal dexterity for puncturing the often-hardened integument of most vertebrate hosts. Perhaps because of thickened and indurated host integument, the adult mouthparts consist of a short, rigid proboscis with prominent, prestomal teeth mounted on a labellum used for abrading and cutting through integumental tissue to feed on upwelling fluids such as lymph and blood (Jobling 1926, 1928, 1929, 1933).

Glossinidae (tsetse flies) are large, hematophagous flies with distinctive mouthparts that are obligately parasitic on vertebrates, including humans (Jobling 1933). From their blood feeding, glossinids are vectors of the trypanosome *Trypanosoma* that cause the debilitating and fatal diseases of rinderpest and nagana in livestock and sleeping sickness in humans throughout modern, sub-Saharan Africa (Lambrecht 2018). Glossinids consist of a single modern and fossil genus, *Glossina*. *Glossina* contains 15 species that is split into three subgenera, each of which occupies a savanna, forest or riverine–lacustrine margin habitat. Two *Glossina* species have been found in the 34 million-year-old, latest Eocene Florissant Formation in Colorado, U.S.A. (Grimaldi 1992), and an additional species is known from a 10 million-year-older occurrence at the Enspel locality in Germany (Wedmann 2000). This biogeographical distribution indicates that *Glossina* had a widespread distribution in the Northern Hemisphere during the Paleogene, and became restricted to sub-Saharan Africa in the Neogene. It remains unknown whether *Glossina* was a vector for diseases similar to sleeping sickness during its earlier, Paleogene existence (Martins-Neto 2003).

Hippoboscidae (louse flies, keds) consist of 3 subfamilies and 21 genera of obligate parasites of birds and mammals. Hippoboscid fossil history is extremely limited and is comprised of two occurrences. One specimen is from Rott, Rhineland, Germany, of late Oligocene age (Chattian Stage) at approximately 25.5 Ma (Statz 1940; Maa 1966). Maa (1966) concluded that the specimen was an early, basal lineage of Hippoboscidae. A more recent find of a Hippoboscid is from the latest Miocene Messinian Stage, approximately 6 million years in age (Bradley and Landini 1984). However, these occurrences say little about the evolutionary biology of hippoboscids (Dittmar et al. 2006). An alternative method is a molecular phylogenetic approach (Dittmar et al. 2006) that places the Hippoboscidae as the sister-group to the Glossinidae, with an origin approximately at the same time as the separation of the Nycteribiidae and Streblidae during the late Eocene (De Moya 2019).

Nycteribiidae (bat flies) are 12 genera of dorsoventrally flattened, spider-like flies lacking eyes and wings that are obligate, host specific parasites on bats. Nycteribiids have been implicated in the transmission of bat malaria in Africa (Obame-Nkoghe et al. 2016). They lack a fossil record. Related to Nycteribiidae are Streblidae (bat flies), consisting of 5 subfamilies and approximately 33 genera of blood-feeding flies that are ectoparasitic specialists on a variety of bats (Lehane 1991). Some genera are involved in transmission of bat malaria (Obame-Nkoghe et al. 2016). Although the oldest streblid is early Miocene in age (Poinar Jr and Brown 2012), the clade is thought to have originated during the Eocene, based on the fossil record of the closely related Glossinidae (Dittmar et al. 2006). From the same early Miocene deposit, an unaffiliated streblid harbored *Vetufebrus ovatus* (Haemospororida: Plasmodiidae), a bat malarial parasite (Poinar Jr 2011) that apparently is not vectored by any known extant streblid (Leung 2017). This suggests that this particular parasitic relationship of malaria may be a disease that has become extinct for streblid vectors and their bat hosts (compare van Dijk and De Baets 2021 for other putative examples).

Oestroidea contains four families, Oestridae (bot flies), Calliphoridae (blow flies, carrion flies, greenbottles), Mesembrinellidae (blow flies) and Mystacinobiidae (New Zealand bat fly), which contain significant numbers of parasitic, blood-feeding species. Parasitism likely originated five times in the Oestroidea, based on genus-level phylogenies (Pape 2001; Kutty et al. 2001). As cyclorrhaphan calyptrates, Oestroidea are a recent clade that originated during the late Paleocene to early Eocene epochs of the Cenozoic, about 60–40 million years ago (Cerretti et al. 2017). The most iconic of the oestroid parasitic families, Oestridae consist of about 160 species (Wood 2006) and contain the most conspicuous, diverse and noxious of parasites, as they are internal parasites of mammals and frequently inhabit their host's flesh, occasionally using an intermediate vector such as a dipteran to complete their life cycle (Colwell et al. 2006). A typical life cycle is illustrated by the reindeer warble fly, *Hypoderma tarandi*, documented on reindeer, *Rangifer tarandus*. The fly initially lays eggs during Arctic summer at the base of thin hairs adjacent the skin, followed by hatching and then penetration of the first-instar larva into the skin, soon resulting in development of nodules (warbles) under the skin while the host's proteins from subcutaneous tissue are ingested by the larva (Asbakk et al. 2014). During the following Arctic winter, the larva continues to consume proteins, increasing in size through several instar shifts up to 5 cm long, eventually maturing and leaving the host during early Arctic spring and pupating on the ground, where they emerge as adult flies after several weeks to complete the life cycle (Asbakk et al. 2014). The cumulative load of reindeer warble fly infestation is particularly debilitating on reindeer cows, particularly during calving season in late summer (Ballesteros et al. 2011). Thematically, this life cycle of infestation is similar to bot flies attacking a variety of other large mammals, especially bovids (e.g., Oryan et al. 2009).

Calliphoridae are a diverse, worldwide family consisting of 75 genera, some of which have larvae (screwworms) that cause myiasis and other diseases such as dysentery and paratuberculosis that especially affect livestock (Thomas and Mangan 1989) (Table 11.1). Calliphoridae are of vital importance in carrion communities, assisting the degradation of animal tissues. Several occurrences (puparia) of Calliphoridae are late Neogene in age, the oldest is upper Pliocene, from 3.6 to 2.6 million years ago (Kitching 1980). An earlier record of two puparia in an ironstone nodule attributed to the Calliphoridae, from the late Cretaceous of Canada (Campanian Stage) and described by McAlpine (1970), is erroneous and are attributed to Cyclorrhapha (Grimaldi and Engel 2005a). Since no calyptrate group is known from the Mesozoic (Grimaldi and Engel 2005a), the calyptrate Calliphoridae likely originated during the more recent Paleogene and was parasitic on mammals of medium to large size.

A closely related lineage to the Calliphoridae is the Mesembrinellidae, consisting of three subfamilies and nine genera that occur in humid, primary forests of the Neotropics. Some adults feed on blood and are parasites whereas other species are found on decomposing animal material and fermented substances in fruits (Marinho et al. 2017). The only fossil occurrence is *Mesembrinella caenozoica* from early Miocene amber (Fig. 11.10), from the Dominican Republic (21 Ma). Their origin is placed during the Eocene (Cerretti et al. 2017).

Mystacinobiidae is a closely related family to Calliphoridae, consisting of the enigmatic, monotypic *Mystacinobia zelandica* (New Zealand bat fly) that recently has been discovered (Gleeson et al. 2000). This group is a spider-like, wingless, structurally highly modified fly that feeds on bat guano and is phoretic and possibly parasitic on the New Zealand short-tailed bat (Holloway 1976).

Excluded from the list of parasitic Diptera, Strashilidae is a group of mid-Mesozoic, eastern Eurasian insects exemplified by the morphologically bizarre *Strashila incredibilis* (Fig. 11.1e; Rasnitsyn 1992). They possess features that superficially resemble some ectoparasitic insects. These features include dorsoventral flattening; legs with highly swollen metafemora and grasping terminal claws; prominent lateral, gill-like appendages of the abdomen; and a head with sunken antennae and a ventrally directed, short beak housing reduced piercing-and-sucking mouthparts (Huang et al. 2013b). Males were winged whereas females were wingless. Once thought as terrestrial ectoparasites of pterosaurs and possibly affiliated with Siphonaptera (Rasnitsyn 1992), the group together with Tarwiniidae were considered as sister group to Saurophthiridae (Rasnitsyn and Quicke 2002; Nagler and Haug 2015). Others proposed that Strashilidae as a lineage originating deeper

**Table 11.1** Larval biologies of modern and fossil parasitoid insect taxa

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| NEUROPTERA | | | | | |
| ***Hemerobioformia*** | | | | | |
| Mantispidae | Ectoparasitoid predator | Coleoptera: Scarabaeidae; Lepidoptera: Noctuidae; Hymenoptera: Apidae | Larvae and pupae of soil insects; egg sacs of spiders | Callovian–Recent | Askew (1971), Lambkin (1986), Eggleton and Belshaw (1992), Grimaldi and Engel (2005a), Poinar Jr and Buckley (2010), Haug et al. (2018), Chen et al. (2019) |
| COLEOPTERA | | | | | |
| ***Caraboidea*** | | | | | |
| Carabidae | Ectoparasitoid | Diplopoda; Orthoptera: Stenopelmatidae; Coleoptera: Chrysomelidae; Diptera | Pupae, puparia and eggs of soil arthropods; on plants | Carnian–Recent | Clausen (1940), Erwin (1979), Eggleton and Belshaw (1992), Grimaldi and Engel (2005a) |
| ***Staphylinoidea*** | | | | | |
| Staphylinidae | Ectoparasitoid | Diptera | Puparia in ephemeral habitats | Carnian–Recent | Clausen (1940), Klimaszewski (1984), Eggleton and Belshaw (1992), Fraser et al. (1996), Chatzimanolis et al. (2012) |
| ***Scarabaeoidea*** | | | | | |

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Scarabaeidae | Cleptoparasitoid, predator | Coleoptera: Geotrupidae; other Scarabaeidae | Eggs, larvae and dung brood balls | Tithonian–Recent | Hammond (1976), Eggleton and Belshaw (1992), Krell (2006), Bai et al. (2012) |
| ***Dascilloidea*** | | | | | |
| Rhipiceridae | Endoparasitoid | Hemiptera: Cicadidae | Nymphs | Lutetian–Recent | Elzinga (1977), Eggleton and Belshaw (1992), Ponomarenko (1995), Grimaldi and Engel (2005a) |
| ***Cleroidea*** | | | | | |
| Cleridae | Ectoparasitoid, cleptoparasitoid predator | Hymenoptera: Apidae; Lepidoptera; Orthoptera: Acrididae | Larvae in nests and galls; egg pods | Cenomanian–Recent | Clausen (1940), Foster (1976), Eggleton and Belshaw (1992), Rasnitsyn and Ross (2000), Kolibáč and Huang (2016) |
| ***Cucujoidea*** | | | | | |
| Bothrideridae | Ectoparasitoid | Coleoptera; Hymenoptera: Apidae | Larvae, pupae of dead wood | Lutetian–Recent | Clausen (1940), Roberts (1980), Eggleton and Belshaw (1992), Grimaldi and Engel (2005a) |

(continued)

**Table 11.1** (continued)

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Passandridae | Ectoparasitoid, hyperparasitoid | Coleoptera: Cerambycidae; Hymenoptera: Braconidae | Pupae in dead wood, larvae of parasitoids | Cenomanian–Recent | Clausen (1940), Askew (1971), Eggleton and Belshaw (1992), Grimaldi and Engel (2005a) |
| ***Tenebrionoidea*** | | | | | |
| Meloidae | Ectoparasitoid, cleptoparasitoid | Hymenoptera: Apidae; Orthoptera: Acrididae | Larvae in soil and nests; egg pods and masses | Cenomanian–Recent | Clausen (1940), Pinto and Selander (1970), Askew (1971), Eggleton and Belshaw (1992), Bologna et al. (2008) |
| Ripiphoridae | Ectoparasitoid, endoparasitoid | Blattodea; Coleoptera: Cerambycidae; Hymenoptera: Scoliidae, Tiphiidae, Vespidae | Larvae in wood and nests; mobile adults | Callovian–Recent | Clausen (1940), Linsley et al. (1952), Grimaldi et al. (2005), Batelka et al. (2016, 2019), Cai et al. (2018), Hsiao et al. (2017), Hsiao and Huang (2018) |
| ***Curculionoidea*** | | | | | |
| Anthribidae | Ectoparasitoid, predator | Hemiptera: Coccoidea | Nymphs; egg masses | Hauterivian–Recent | Clausen (1940), Askew (1971), Eggleton and Belshaw (1992), Ülgentürk (2001), Gratshev and Zherikhin (2003) |
| STREPSIPTERA[g] | | | | | |
| “***Protostrepsiptera***”[h] | | | | | |

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Cretostylopidae† | Endoparasitoid[i] | — | Nymphs or larvae[i] | Cenomanian | Grimaldi et al. (2005), Kathirithamby and Engel (2014) |
| Phthanoxenidae† | Endoparasitoid[i] | — | Nymphs or larvae[i] | Cenomanian | Engel and Huang (2016) |
| Protoxenidae† | Endoparastoid[i] | — | Nymphs or larvae[i] | Lutetian | Pohl et al. (2005) |
| ***Eleostrepsiptera***[h] | | | | | |
| Mengeidae† | Endoparasitoid[i] | Zygentoma: Lepismatidae[i] | Nymphs[i] | Lutetian | Clausen (1940), Askew (1971), Kulicka (1979), Godfray (1994), Grimaldi and Engel (2005a), Pohl and Beutel (2008), Kathirithamby (2009), Engel et al. (2016a) |
| ***Neostrepsiptera***[h] | | | | | |
| Bahiaxenidae | Endoparasitoid[i] | — | Nymphs or larvae[i] | Recent | Bravo et al. (2009) |
| Bohartillidae | Endoparasitoid[i] | — | Nymphs or larvae[i] | Aquitanian–Recent | Pohl and Kinzelbach (2001), Kinzelbach and Pohl (1994), Cook (2014) |
| Corioxenidae | Endoparasitoid | Hemiptera: Heteroptera | Nymphs | Lutetian–Recent | Henderickx et al. (2013), Cook (2014) |

(continued)

**Table 11.1** (continued)

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Elenchidae | Endoparasitoid | Hemiptera: Auchenorrhyncha | Nymphs | Aquitanian–Recent | Askew (1971), Kinzelbach and Pohl (1994), Cook (2014) |
| Halictophagidae | Endoparasitoid | Blattodea; Orthoptera: Caelifera; Hemiptera: Auchenorrhyncha; Diptera | Nymphs | Cenomanian–Recent | Kathirithamby (2009), Cook (2014), Engel et al. (2016a) |
| Kinzelbachillidae† | Endoparasitoid[i] | — | Nymphs or larvae[i] | Cenomanian | Pohl and Beutel (2016) |
| Lychnocolacidae | Endoparasitoid[i] | — | Nymphs or larvae[i] | Recent | Engel et al. (2016a) |
| Mengenillidae | Endoparasitoid | Zygentoma: Lepismatidae | Nymphs | Cenomanian–Recent | Pohl and Beutel (2008), Cook (2014), Engel et al. (2016a), Pohl and Beutel (2019), Pohl et al. (2018) |
| Myrmecolacidae | Parasite, then (?) endoparasitoid | Females on Hymenoptera: Formicidae; males on Mantodea and Orthoptera | Larvae or nymphs | Thanetian–Recent | Kinzelbach (1983), Kinzelbach and Pohl (1994), Pohl and Kinzelbach (1995), Cook (2014), Wang et al. (2015) |
| Protelencholacidae† | Endoparasitoid[i] | — | Nymphs or larvae[i] | Aquitanian | Pohl and Beutel (2005), Engel et al. (2016a) |
| Protoxenidae† | Endoparasitoid[i] | — | Nymphs or larvae[i] | Priabonian | Pohl et al. (2005) |

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Stylopidae | Endoparasitoid | Hymenoptera: Vespoidea, Apoidea | Larvae | Lutetian–Recent | Kinzelbach and Lutz (1985), Pohl and Kinzelbach (2001), Kogan and Poinar Jr (2010), Cook (2014) |
| Xenidae | Endoparasitoid | Hymenoptera: Vespoidea, Apoidea | Larvae | Lutetian–Recent | Cook (2014), Engel et al. (2016a) |
| DIPTERA | | | | | |
| ***Culicomorpha*** | | | | | |
| Chironomidae | Ectoparasitoid | Gastropoda: Pulmonata; Ephemeroptera: Rithrogeniidae | Immature; naiad | Norian–Recent | Clausen (1940), Krzeminski and Jarzembowski (1999), Grimaldi and Engel (2005a) |
| ***Bibionomorpha*** | | | | | |
| Cecidomyiidae | Endoparasitoid | Hemiptera: Sternorrhyncha | Nymphs, adults | Albian–Recent | Clausen (1940), Arillo and Nel (2000), Grimaldi and Engel (2005a) |
| Mycetophilidae | Endoparasitoid | Platyhelminthes | Immatures, adults | Cenomanian–Recent | Hickman (1965), Eggleton and Belshaw (1992), Grimaldi and Engel (2005a) |

(continued)

**Table 11.1** (continued)

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| ***Nemestrinimorpha***[j] | | | | | |
| Acroceridae | Endoparasitoid | Araneae: Clubionidae, Lycosidae, Salticidae; Acari | Adults | Kimmeridgian–Recent | Clausen (1940), Askew (1971), Grimaldi and Engel (2005a), Winterton et al. (2007), Kerr and Winterton (2008), Gillung et al. (2018) |
| Nemestrinidae | Endoparasitoid, ectoparasitoid | Orthoptera: Caelifera; Coleoptera: Scarabaeidae, Cerambycidae | Eggs, larvae and nymphs | Toarcian–Recent | Clausen (1940), Greathead (1963), Grimaldi (1995), Mostovski (1998), Ansorge and Mostovski (2002), Grimaldi and Engel (2005a), Wedmann (2007), Zhang et al. (2017) |
| ***Archisargoidea*** | | | | | |
| Eremochaetidae[†] | Endoparasitoid | — | Probably larvae | Tithonian–Cenomanian | Zhang (2017), Grimaldi and Barden (2016) |
| ***Muscomorpha*** | | | | | |
| ***Asiloidea*** | | | | | |
| Asilidae | Ectoparasitoid | Coleoptera: Scarabaeidae, Buprestidae, Cerambycidae, Curculionidae; Hymenoptera: Siricidae | Larvae occurring in dead wood | Kimmeridgian–Recent | Knutson (1972), Eggleton and Belshaw (1992), Grimaldi and Engel (2005a), Haug et al. (2017) |

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Bombyliidae | Ectoparasitoid, endoparasitoid, hyperparasitoid | Orthoptera: Acrididae; Coleoptera: Tenebrionidae; Lepidoptera: Tortricidae, Noctuidae; Diptera: Tachinidae; Hymenoptera: Tenthredinidae, Apidae, Ichneumonidae | Eggs, larvae and pupae variously of free feeders and parasitoids | Callovian–Recent | Clausen (1940), Hull (1973), Rasnitsyn (1985), Eggleton and Belshaw (1992), Yeates and Greathead (1997), Nel and De Ploëg (2004), Grimaldi and Engel (2005a), Wedmann and Yeates (2008) |
| ***Empidoidea*** | | | | | |
| Empididae | Endoparasitoid, ectoparasitoid | Trichoptera: Glossosomatidae, Rhyacophilidae | Pupae | Tithonian–Recent | Knutson and Flint (1979), Vinikour and Anderson (1981), Eggleton and Belshaw (1992), Coram et al. (2000) |
| ***Aschiza***[j] | | | | | |
| Phoridae | Endoparasitoid, cleptoparasitoid | Oligochaeta; Gastropoda: Pulmonata; Opiliones; Araneae; Myriapoda; Hemiptera; Coleoptera; Diptera; Trichoptera; Hymenoptera: Vespoidea, Apoidea | Eggs, nymphs, larvae, other immatures; adults | Albian–Recent | Robinson (1971), Ferrar (1987), Arillo and Mostovski (1999), Eggleton and Belshaw (1992), Brown (1997, 1998), Coupland and Barker (2004), Grimaldi and Engel (2005a) |

(continued)

**Table 11.1** (continued)

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Pipunculidae | Endoparasitoid | Hemiptera: Auchenorrhyncha | Nymphs occurring on plants | Lutetian–Recent | Clausen (1940), Askew (1971), Eggleton and Belshaw (1992), Grimaldi and Engel (2005a) |
| ***Acalyptratae***[j] | | | | | |
| Chamaemyiidae | Endoparasitoid | Hemiptera: Sternorrhyncha | Nymphs | Lutetian–Recent | Hennig (1965), Eggleton and Belshaw (1992) |
| Chloropidae | Endoparasitoid, cleptoparasitoid | Hemiptera: Sternorrhyncha | Nymphs | Lutetian–Recent | Hennig (1965), Narchuk (1972), Ferrar (1987), Grimaldi and Engel (2005a) |
| Conopidae | Endoparasitoid | Blattodea; Orthoptera; Diptera: Calyptratae; Hemiptera: Coccoidea; Hymenoptera: Aculeata | Nymphs, larvae, puparia | Lutetian–Recent | Smith (1966), Hennig (1966), Smith and Cunningham-von Someren (1985), Gibson and Skevington (2013), Rocha et al. (2015) |
| Cryptochaetidae | Endoparasitoid | Hemiptera: Coccoidea: Margarodidae | Nymphs occurring on plants | Lutetian–Recent | Thorpe (1941), Hennig (1965), Eggleton and Belshaw (1992) |
| Pyrgotidae | Endoparasitoid | Coleoptera: Scarabaeidae | Adults | Lutetian–Recent | Hennig (1965), Askew (1971), Eggleton and Belshaw (1992), Grimaldi and Engel (2005a) |

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Sciomyzidae | Endoparasitoid | Oligochaeta; Bivalvia; Gastropoda: Pulmonata; Diplopoda | Immatures and adults in freshwater and terrestrial habitats | Lutetian–Recent | Hennig (1965), Bailey (1989), Vala et al. (1990), Eggleton and Belshaw (1992), Grimaldi and Engel (2005a) |
| ***Schizophora*** | | | | | |
| Anthomyiidae | Endoparasitoid | Orthoptera | Late nymph, adult | Lutetian–Recent | Hennig (1965), Ferrar (1987), Eggleton and Belshaw (1992), Michelson (2000), Grimaldi and Engel (2005a) |
| Calliphoridae | Ectoparasitoid, endoparasitoid, cleptoparasitoid | Oligochaeta; Gastropoda: Pulmonata; Isoptera; Hymenoptera: Formicidae; Mammalia | Adults | Lutetian–Recent | Hennig (1965), Stevens (2003), Stevens et al. (2006), Coupland and Barker (2004), Stevens et al. (2006) |
| Muscidae | Endoparasitoid | Gastropoda: Pulmonata; Diplopoda; Lepidoptera | Immatures and adults of soft-bodied invertebrates | Lutetian–Recent | Hennig (1965), Ferrar (1987), Bailey (1989), Vala et al. (1990), Eggleton and Belshaw (1992), Coupland and Barker (2004) |

(continued)

**Table 11.1** (continued)

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Rhinophoridae | Endoparasitoid | Crustacea: Isopoda | All instars | Lutetian–Recent | Hennig (1965), Bedding (1965), Ferrar (1987), Eggleton and Belshaw (1992), Grimaldi and Engel (2005a) |
| Sarcophagidae | Endoparasitoid, cleptoparasitoid | Oligochaeta; Gastropoda: Pulmonata; Araneae; Orthoptera: Acrididae; Isoptera; Diptera: Tabanidae; Coleoptera: Curculionidae; Lepidoptera: Bombycoidea; Hymenoptera: Bradybaenidae, Aculeata | Eggs, larvae, other immatures; adults | Lutetian–Recent | Hennig (1965), Ferrar (1987), Coupland and Barker (2004), Grimaldi and Engel (2005a), Stevens et al. (2006) |
| Tachinidae | Endoparasitoid | Scorpionida; Araneae; Chilopoda; Isopoda; Embioptera; Orthoptera; Dermaptera; Blattodea; Mantodea; Phasmatodea; Hemiptera: Heteroptera; Coleoptera: Scarabaeidae; Lepidoptera: Ditrysia; Hymenoptera: Symphyta | Nymphs, larvae and adults variously of wood borers and phytophages | Lutetian–Recent | Clausen (1940), Askew (1971), Ferrar (1987), Eggleton and Belshaw (1992), Evenhuis (1994), Lehmann (2003), Stireman III et al. (2006), Cerretti et al. (2014, 2017), Winkler et al. (2015) |
| TRICHOPTERA | | | | | |
| Hydroptilidae | Ectoparasitoid | Trichoptera | Pupae | Santonian–Recent | Labandeira (1994), Wells (1992, 2005), Morris (1998) |
| LEPIDOPTERA | | | | | |
| ***Zygaenoidea*** | | | | | |

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Epipyropidae | Ectoparasitoid | Hemiptera: Auchenorrhyncha; Lepidoptera | Nymphs, larvae on plants | Recent | Askew (1971), Eggleton and Belshaw (1992), Grimaldi and Engel (2005a) |
| ***Pyraloidea*** | | | | | |
| Pyralidae | Ectoparasitoid | Lepidoptera: Saturniidae | Larvae of externally feeding herbivore | Lutetian–Recent | Askew (1971), Eggleton and Belshaw (1992), Sohn et al. (2012), Grimaldi and Engel (2005a) |
| HYMENOPTERA | | | | | |
| **Symphyta** | | | | | |
| ***Orussoidea*** | | | | | |
| Orussidae | Ectoparasitoid | Coleoptera: Buprestidae; Hymenoptera: Siricidae | Larvae of wood borers | Turonian–Recent | Basibuyuk et al. (2000), Whitfield (2003), Grimaldi and Engel (2005a), Vilhelmsen and Zimmermann (2014) |
| **Apocrita** | | | | | |
| ***Stephanoidea*** | | | | | |
| Aptenoperissidae[†] | Ectoparasitoid[i] | — | Larvae of wood borers[i] | Cenomanian | Rasnitsyn et al. (2017), Rasnitsyn and Öhm-Kühnle (2018), Zhang et al. (2018a) |

(continued)

**Table 11.1** (continued)

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Myanmarinidae† | Ectoparasitoid[i] | — | Larvae of wood borers[i] | Cenomanian | Li et al. (2018b), Zhang et al. (2018c) |
| Stephanidae | Ectoparasitoid | Coleoptera: Buprestidae, Cerambycidae; Hymenoptera: Siricidae | Larvae of wood borers | Cenomanian–Recent | Whitfield (2003), Li et al. (2017b), Engel and Huang (2017), Zhang et al. (2018a) |
| ***“Ephialitoidea”*** | | | | | |
| “Ephialtitidae”† | Ectoparasitoid[i] | Coleoptera[i]; Hymenoptera[i] | Larvae of wood borers[i] | Toarcian–Aptian | Zhang et al. (2002a), Rasnitsyn et al. (2003), Grimaldi and Engel (2005a), Peñalver and Engel (2006), Li et al. (2013b, 2015b) |
| ***Megalyroidea*** | | | | | |
| Megalyridae | Ectoparasitoid | Coleoptera: Cerambycidae | Larvae of wood borers | Cenomanian–Recent | Rasnitsyn (1975), Whitfield (2003), Grimaldi and Engel 2005a; Perrichot (2009), Zhang et al. (2018a) |
| ***Trigonalyroidea*** | | | | | |
| Trigonalidae | Endoparasitoid, hyperparasitoid | Symphytan or lepidopteran caterpillar; then Ichneumonoidea or Vespidae larva | Larvae of externally feeding folivores | Aptian–Recent | Weinstein and Austin (1991), Whitfield (2003), Nel et al. (2003), Poinar Jr and Shaw (2007), Grimaldi and Engel (2005a) |

| Taxon$^{a}$ | Parasitoid larval life-habit$^{b}$ | Dominant larval hosts$^{c}$ | Host stage of larval parasitoid attack$^{d}$ | Geochronologic range$^{e}$ | References$^{f}$ |
|---|---|---|---|---|---|
| Maimetshidae$^{\dagger}$ | Endoparasitoid$^{i}$ | — | Externally feeding folivores$^{i}$ | Barremian–Santonian | Rasnitsyn (1975), Rasnitsyn and Brothers (2009), Engel (2016) |
| ***Evanioidea*** | | | | | |
| Andreneliidae$^{\dagger}$ | Ectoparasitoid, predator$^{b}$ | — | Larvae of wood borers$^{i}$ | Barremian | Rasnitsyn and Martínez-Delclòs (2000), Grimaldi and Engel (2005a), Li et al. (2018a, b) |
| Anomopterellidae$^{\dagger}$ | Ectoparasitoid$^{i}$ | Coleoptera$^{i}$; Hymenoptera$^{i}$ | Larvae of wood borers$^{i}$ | Callovian–Tithonian | Li et al. (2013a, 2014b, 2018a) |
| Aulacidae | Ectoparasitoid | Coleoptera: Buprestidae, Cerambycidae; Hymenoptera: Xiphydriidae | Larvae of wood borers | Hauterivian–Recent | Carlson (1979), Rasnitsyn (1980), Jennings et al. (2004), Grimaldi and Engel (2005a), Turrisi and Vilhelmsen (2010), Li et al. (2018a) |
| Baissidae$^{\dagger}$ | Ectoparasitoid$^{i}$ | Coleoptera$^{i}$; Hymenoptera$^{i}$ | Larvae of wood borers$^{i}$ | Berriasian–Turonian | Rasnitsyn (1975, 1991a), Rasnitsyn et al. (1998), Basibuyuk et al. (2002), Nel et al. (2004), Engel (2013), Li et al. (2018a) |

(continued)

**Table 11.1** (continued)

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Evaniidae | Predator, ectoparasitoid | Blattodea | Oothecate eggs | Hauterivian–Recent | Brown (1973), Basibuyuk et al. (2002), Deans et al. (2004), Grimaldi and Engel (2005a), Li et al. (2018a) |
| Gasteruptiidae | Predator–inquiline | Hymenoptera: Apoidea | Eggs and larvae of wasps and solitary bees | Barremian–Recent | Malyshev (1968), Rasnitsyn (1991b), Jennings et al. (2004), Li et al. (2018a) |
| Othniodellithidae[†] | Ectoparasitoid[i], predator[i] | — | Larvae of wood borers[i] | Cenomanian | Engel et al. (2016b) |
| Praeaulacidae[†] | Ectoparasitoid[i] | Coleoptera[i] | Larvae of wood borers[i] | Callovian–Cenomanian | Rasnitsyn (1972), Jell and Duncan (1986), Oberprieler et al. (2012); Li et al. (2014a, c, d, 2015a, 2017c, 2018a) |
| Vectevaniidae[†] | Ectoparasitoid[i] | Coleoptera[i]; Hymenoptera[i] | Larvae of wood borers[i] | Priabonian | Rasnitsyn (2013) |
| ***Proctotrupoidea*** | | | | | |
| Austroniidae | Endoparasitoid[i] | — | Larvae[i] | Cenomanian–Recent | Grimaldi and Engel (2005a), Zhang et al. (2018a) |
| Diapriidae | Endoparasitoid | Diptera: Syrphidae, Sarcophagidae, Tephritidae; Hymenoptera: Formicidae | Fly puparia; brood nest associates of ants | Cenomanian–Recent | Clausen (1940), Whitfield (2003), Engel et al. (2013a), Zhang et al. (2018a), Quevillon and Hughes (2018) |

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Heloridae | Endoparasitoid | Neuroptera: Chrysopidae | Larvae of predators | Callovian–Recent | Shih et al. (2011), Shi et al. (2014), Li et al. (2017c) |
| Maamingidae | Endoparasitoid[i] | — | Larvae[i] | Recent | Early et al. (2001) |
| Mesoserphidae[†] | Endoparasitoid[i] | — | Larvae[i] | Callovian–Barremian | Kozlov (1968), Shih et al. (2011), Shi et al. (2013), Garrouste et al. (2016) |
| Monomachidae | Endoparasitoid[i] | — | Larvae[i] | Kimmeridgian–Recent | Rasnitsyn (1988), Whitfield (2003) |
| Pelecinidae | Endoparasitoid | Coleoptera: Scarabaeidae | Larvae of soil root feeders | Callovian–Recent | Kozlov (1974), Johnson and Musetti (1999), Zhang et al. (2002b), Shih et al. (2009) |
| Peleserphidae[†] | Endoparasitoid[i] | — | — | Cenomanian | Zhang et al. (2018b) |
| Peradeniidae | Endoparasitoid[i] | — | — | Lutetian–Recent | Naumann and Masner (1985), Johnson et al. (2001), Grimaldi and Engel 2005a, 2005b |
| Proctorenyxidae | Endoparasitoid[i] | — | — | Recent | Grimaldi and Engel (2005a) |
| Proctotrupidae | Endoparasitoid | Coleoptera: Staphylinidae, Carabidae, Elateridae | Young larvae of leaf litter | Kimmeridgian–Recent | Askew (1971), Rasnitsyn (1988), Whitfield (2003) |
| Roproniidae | Endoparasitoid | Hymenoptera: Tenthredinidae | Larvae of external feeders | Barremian–Recent | Zhang and Zhang (2001), Whitfield (1998), Garrouste et al. (2016) |

(continued)

Table 11.1 (continued)

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Spathiopterygidae† | Endoparasitoid[i] | — | Insect eggs[i] | Cenomanian | Engel and Ortega-Blanco (2013), Engel et al. (2015), Zhang et al. (2018a) |
| Vanhorniidae | Endoparasitoid | Coleoptera: Eucnemidae | Larvae of wood borers | Santonian–Recent | Clausen (1940), Whitfield (2003) |
| ***Cynipoidea*** | | | | | |
| "Archaeocynipidae"† | Endoparasitoid[i] | — | Larvae[i] | Hauterivian | Rasnitsyn and Kovalev (1988), Grimaldi and Engel (2005a) |
| Austrocynipidae | Endoparasitoid to ectoparasitoid | Lepidoptera: Oecophoridae | Larvae of leaf miners | Recent | Whitfield (2003) |
| Charapidae | Endoparasitoid, hyperparasitoid | Hemiptera: Sternorrhyncha; Hymenoptera: Braconidae | Nymphs, larvae | Recent | Clausen (1940), Askew (1971), Godfray (1994) |
| Eucoilidae | Endoparasitoid | Diptera: Cyclorrhapha | Larvae | Turonian–Recent | Clausen (1940), Askew (1971), Peñalver et al. (2013), Buffington et al. (2014) |
| Figitidae | Endoparasitoid to ectoparasitoid, hyperparasitoid | Diptera: Sarcophagidae, Tephritidae; Neuroptera; Hymenoptera: Cynipidae | Larvae in rotting meat | Turonian–Recent | Clausen (1940), Whitfield (2003), Liu et al. (2007), Buffington et al. (2014) |
| Ibaliidae | Endoparasitoid to ectoparasitoid | Hymenoptera: Siricidae | Eggs and larvae of wood borers | Turonian–Recent | Clausen (1940), Whitfield (2003), Grimaldi and Engel (2005a), Liu and Engel (2010) |

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Liopteridae | Endoparasitoid to ectoparasitoid | Coleoptera: Buprestidae, Cerambycidae, Curculionidae | Larvae of wood borers | Turonian–Recent | Whitfield (2003), Liu et al. (2007) |
| Protimaspidae† | Endoparasitoid[i] | — | Larvae of wood borers[i] | Turonian | Liu et al. (2007) |
| Stolamissidae† | Endoparasitoid[i] | — | Larvae of wood borers[i] | Turonian | Liu et al. (2007) |
| ***Platygastroidea*** | | | | | |
| Platygastridae | Endoparasitoid | Hemiptera: Sternorrhyncha; Diptera: Cecidomyiidae; Lepidoptera; Hymenoptera | Insect eggs, larvae of gallers, scale insects | Hauterivian–Recent | Clausen (1940), Whitfield (1998, 2003), Grimaldi and Engel (2005a) |
| Scelionidae | Endoparasitoid | Orthoptera; Mantodea; Hemiptera; Neuroptera; Coleoptera; Diptera: Tabanidae; Lepidoptera; Araneae | Insect eggs | Aptian–Recent | Brues (1940), Clausen (1940), Grimaldi and Engel (2005a), Nel and Azar (2005), Talamas et al. (2017), Haas et al. (2018) |
| ***Ceraphronoidea*** | | | | | |
| Ceraphronidae | Endoparasitoid, hyperparasitoid | Thysanoptera; Neuroptera; Trichoptera; Diptera: Cecidomyiidae, Cyclorrhapha; Hymenoptera: Sphecoidea | Eggs, larvae, pupae and puparia | Santonian–Recent | Alekseyev and Rasnitsyn (1981), Whitfield (1998, 2003) |

(continued)

**Table 11.1** (continued)

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Megaspilidae | Ectoparasitoid, hyperparasitoid | Hemiptera: Sternorrhyncha; Neuroptera: Hemerobiidae, Coniopterygidae; Mecoptera; Diptera: Cecidomyiidae, Syrphidae, Chloropidae, Chamaemyiidae, Muscidae | Nymphs and larvae of parasitoids and gallers | Cenomanian–Recent | Whitfield (1998, 2003), Grimaldi and Engel (2005a), Zhang et al. (2018a, b) |
| Radiophronidae[†] | Ectoparasitoid[i] | — | Larvae[i] | Albian–Campanian | Ortega-Blanco et al. (2010), Zhang et al. (2018a) |
| Stigmaphronidae[†] | Endoparasitoid[i] | — | Insect eggs and larvae[i] | Hauterivian–Campanian | Rasnitsyn (1991b), Whitfield (1998), Grimaldi and Engel (2005a), Ortega-Blanco et al. (2011b) |
| ***Mymarommatoidea*** | | | | | |
| Gallorommatidae | Endoparasitoid[i] | — | Insect eggs[i] | Barremian–Santonian | Gibson et al. (2007) |
| Mymarommatidae | Endoparasitoid[i] | — | Insect eggs | Cenomanian–Recent | Yoshimoto (1975), Huber (1986), Grimaldi and Engel (2005a), Engel and Grimaldi (2007a), Heraty and Darling (2009), Haas et al. (2018), Zhang et al. (2018c) |

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| ***Serphitoidea*** | | | | | |
| Serphitidae[†] | Endoparasitoid[i] | — | Insect eggs[i] | Hauterivian–Turonian | Brues (1937), Kozlov and Rasnitsyn (1979), Grimaldi and Engel (2005a), Engel et al. (2011), Haas et al. (2018) |
| ***Chalcidoidea***[j] | | | | | |
| Agaonidae | Pollinator, inquiline, galler | Moraceae: *Ficus* | Fig synconia | Priabonian–Recent | Weiblen (2002), Compton et al. (2010), Farache et al. (2016) |
| Aphelinidae | Ectoparasitoid, endoparasitoid, hyperparasitoid | Hemiptera: Sternorrhyncha; Diptera: Cecidomyiidae; Lepidoptera; Hymenoptera: Dryinidae | Nymphs, larvae, eggs | Lutetian–Recent | Clausen (1940), Burks et al. (2015), Peters et al. (2017), Haas et al. (2018) |
| Chalcididae | Ectoparasitoid, endoparasitoid, seed predator, herbivore | Coleoptera; Diptera: Tachinidae; Neuroptera: Myrmeleontidae; Lepidoptera; Hymenoptera: Apoidea; angiosperms | Larvae, pupae, seeds | Ypresian–Recent | Clausen (1940), Askew (1971), Whitfield (2003), Peters et al. (2017), Quevillon and Hughes (2018) |
| Diversinitidae[†] | Endoparasitoid[i] | — | Eggs[i] | Cenomanian | Haas et al. (2018) |
| Encyrtidae | Endoparasitoid, hyperparasitoid predator | Hemiptera: Sternorrhyncha; Coleoptera: Coccinellidae; Lepidoptera; Hymenoptera: Chalcidoidea; Acari | Nymphs, larvae, eggs | Lutetian–Recent | Clausen (1940), Askew (1971), Simutnik (2002), Simutnik and Perkovsky (2006), Heraty and Darling (2009), Peters et al. (2017) |

(continued)

**Table 11.1** (continued)

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Eucharitidae | Ectoparasitoid | Hemiptera: Sternorrhyncha; Hymenoptera: Formicidae | Larvae, prepupae and pupae of ant broods | Lutetian–Recent | Clausen (1940), Askew (1971), Heraty and Darling (2009), Quevillon and Hughes (2018) |
| Eulophidae | Ectoparasitoid, endoparasitoid, hyperparasitoid, predator | Orthoptera: Saltatoria; Hemiptera: Sternorrhyncha; Coleoptera: Chrysomelidae; Lepidoptera; Hymenoptera: Cynipidae; Diptera; Araneae | Larvae, nymphs, pupae and eggs of concealed insects: leaf miners, gallers and case bearers | Lutetian–Recent | Clausen (1940), Askew (1971), Hong (2002), Haas et al. (2018) |
| Eupelmidae | Endoparasitoid, ectoparasitoid, hyperparasitoid, predator | Orthoptera; Hemiptera; Coleoptera: Chrysomelidae; Neuroptera; Hymenoptera: Chalcidoidea, Cynipoidea | Eggs, larvae of leaf miners, fly puparia, and other insects; spider egg sacs | Lutetian–Recent | Clausen (1940), Thorpe (1941), Trjapitsyn (1963), Askew (1971), Whitfield (2003), Gibson (2009) |
| Eurytomidae | Ectoparasitoid, endoparasitoid, seed predator, herbivore | Orthoptera: Grylloidea; Coleoptera; Lepidoptera; Diptera: Tephritidae; Hymenoptera: Formicidae, Cynipoidea | Eggs, larvae in galls, stems and nests; ants | Ypresian–Recent | Clausen (1940), Askew (1971), Hong (2002), Heraty and Darling (2009), Quevillon and Hughes (2018) |
| Leucospidae | Ectoparasitoid | Hymenoptera: Apoidea | Larvae | Aquitanian–Recent | Askew (1971), Engel (2002) |

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Mymaridae | Endoparasitoid | Orthoptera; Coleoptera: Hydrophilidae, Dytiscidae | Eggs | Cenomanian–Recent | Kaddumi (2005), Huber (1986, 2005), Heraty and Darling (2009), Heraty et al. (2013), Engel et al. (2013b), Zhang et al. (2018c) |
| Ormyidae | Ectoparasitoid | Gall-forming insects | Larvae of gallers | | Hanson (1992), Peters et al. (2017) |
| Perilampidae | Hyperparasitoid, ectoparasitoid, galler | Neuroptera: Chrysopidae; Diptera: Tachinidae; Coleoptera: Anobiidae, Curculionidae; Hymenoptera: Diprionidae, Ichneumonidae, Cynipidae, Halictidae | Larvae, pupae of wood borers, gallers and parasitoids | Ypresian–Recent | Clausen (1940), Askew (1971), Peñalver and Engel (2006), Heraty and Darling (2009) |
| Pteromalidae | Endoparasitoid, ectoparasitoid, hyperparasitoid | Hemiptera: Sternorrhyncha; Coleoptera: Curculionidae, (including Scolytinae), Anobiidae; Hymenoptera: Xiphydriidae, Cynipidae, Braconidae; Lepidoptera; Diptera: Pupipara; Siphonaptera | Larvae, pupae and adults of wood borers, gallers, seed predators and other parasitoids | Aptian–Recent | Askew (1971), Godfray (1994), Whitfield (2003), Barling et al. (2013), Krogman (2013) |
| Rotoitidae | Endoparasitoid[i] | — | — | Campanian–Recent | Bouček and Noyes (1987), Gumovsky et al. (2018) |
| Signiphoridae | Ectoparasitoid, hyperparasitoid | Hemiptera: Sternorrhyncha | Nymphs, “pupae” | Lutetian–Recent | Clausen (1940), Perkovsky et al. (2010) |

(continued)

**Table 11.1** (continued)

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Tanaostigmatidae | Galler, parasitoid | Various plant lineages | Larvae of gallers | Lutetian–Recent | Grimaldi and Engel (2005a), Weitschat and Wichard (2010) |
| Tetracampidae | Parasitoid, herbivore | Coleoptera: Chrysomelidae; Hymenoptera: Diprionidae; Diptera: Agromyzidae | Eggs, larvae | Campanian–Recent | Yoshimoto (1975), Gumovsky and Perkovsky (2005) |
| Torymidae | Ectoparasitoid, herbivore | Hymenoptera: Cynipidae | Larvae of gallers | ?Campanian–Recent | Askew (1971), Grissell (1980), Heraty and Darling (2009), McKellar and Engel (2012) |
| Trichogrammatidae | Endoparasitoid | Hemiptera; Megaloptera; Neuroptera; Coleoptera; Diptera; Lepidoptera; Hymenoptera | Eggs | Lutetian–Recent | Clausen (1940), Schmidt et al. (2010), Burks et al. (2015), Coty et al. (2016), Peters et al. (2017), Haas et al. (2018) |
| ***Ichneumonoidea*** | | | | | |
| Braconidae | Ectoparasitoid, some endoparasitoids | Psocoptera; Hemiptera: Aphididae; Coleoptera; Neuroptera; Hymenoptera; Orthoptera | Eggs, larvae and adults of wood borers | Hauterivian–Recent | Rasnitsyn (1983), Rasnitsyn and Sharkey (1988), Whitfield (2003), Shaw (2004), Ortega-Blanco et al. (2011c), Perrichot et al. (2008) |

| Taxon$^{a}$ | Parasitoid larval life-habit$^{b}$ | Dominant larval hosts$^{c}$ | Host stage of larval parasitoid attack$^{d}$ | Geochronologic range$^{e}$ | References$^{f}$ |
|---|---|---|---|---|---|
| Ichneumonidae | Ectoparasitoid, some endoparasitoids | Coleoptera; Neuroptera; Diptera; Trichoptera; Lepidoptera; Hymenoptera: Xiphydriidae; Araneae | Aphid nymphs, larvae and pupae of wood borers; ants | Berriasian–Recent | Brues (1937), Rasnitsyn (1983), Whitfield (2003), Perrichot et al. (2008), Li et al. (2017a), Spasojevic et al. (2017), Quevillon and Hughes (2018) |
| **Aculeata** | | | | | |
| ***Chrysidoidea*** | | | | | |
| Bethylidae | Ectoparasitoid | Coleoptera: Curculionidae, Cerambycidae; Lepidoptera | Larvae | Cenomanian–Recent | Clausen (1940), Evans (1969), Grimaldi and Engel (2005a), Perrichot and Nel (2008), Zhang et al. (2018a) |
| "Bethylonymidae"$^{\dagger}$ | Ectoparasitoid$^{i}$ | — | Larvae$^{i}$ | Tithonian–Hauterivian | Rasnitsyn (1975, 1988), Grimaldi and Engel (2005a) |
| Chrysididae | Ectoparasitoid, endoparasitoid, cleptoparasitoid | Phasmatodea; Hymenoptera: Tenthredinidae, Diprionidae, Vespidae, Apoidea; Lepidoptera | Eggs, larvae, pupae | Cenomanian–Recent | Cockerell (1917), Clausen (1940), Kimsey and Bohart (1990), Whitfield (1998), Grimaldi and Engel (2005a), Zhang et al. (2018a) |

(continued)

**Table 11.1** (continued)

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Dryinidae | Ectoparasitoid→endoparasitoid | Hemiptera: Auchenorrhyncha | Nymphs, adults | Hauterivian–Recent | Jervis (1980), Whitfield (1998), Engel (2003), Grimaldi and Engel (2005a) |
| Embolemidae | Ectoparasitoid→endoparasitoid | Phasmatodea; Hemiptera: Fulgoroidea; Hymenoptera: Formicidae | Nymphs, larvae | Hauterivian–Recent | Rasnitsyn (1996), Whitfield (1998), Olmi (1998), Grimaldi and Engel (2005a), Ortega-Blanco et al. (2011a) |
| Falsiformicidae† | Ectoparasitoid[i] | — | Larvae[i] | Hauterivian–Cenomanian | Rasnitsyn (1975, 2002), Perrichot et al. (2014), Zhang et al. (2018a) |
| Plumariidae | Ectoparasitoid[i] | — | — | ?Turonian–Recent | Roig-Alsina (1994), Grimaldi and Engel (2005a) |
| Sclerogibbidae | Ectoparasitoid | Embioptera | Nymphs, adults | Hauterivian–Recent | Whitfield (1998), Penteado-Dias and van Achterberg (2002), Engel and Grimaldi (2006) |
| Scolebythidae | Ectoparasitoid | Coleoptera: Cerambycidae, Anobiidae | Larvae of wood borers | Hauterivian–Recent | Prentice et al. (1996), Melo (2000), Engel and Grimaldi (2007b), Engel et al. (2013c) |

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| ***Vespoidea*** | | | | | |
| Bradynobaenidae | Ectoparasitoid | Arthropods; Solifugida | Larvae and other immatures | Recent | Brothers (1995), Grimaldi and Engel (2005a) |
| Mutillidae | Ectoparasitoid, predator | Blattodea; Coleoptera; Lepidoptera: Limacodidae; Diptera; Hymenoptera: Formicidae, Apoidea | Nymphs, larvae | Lutetian–Recent | Clausen (1940), Lelej (1996), O'Neill (2001), Quevillon and Hughes (2018) |
| Pompilidae | Ectoparasitoid, predator | Araneae | Adults | Cenomanian–Recent | O'Neill (2001), Grimaldi et al. (2002) |
| Rhopalosomatidae | Ectoparasitoid | Orthoptera: Grylloidea | Nymphs?, adults | Cenomanian–Recent | Gurney (1953), Townes (1977), Darling and Sharkey (1990), Lohrmann and Engel (2017), Zhang et al. (2018a) |
| Sapygidae | Ectoparasitoid, cleptoparasitoid, predator | Apoidea: Eumenidae, Megachilidae, Apidae | Eggs and larvae of social insects | Cenomanian–Recent | Torchio (1972), Spahr (1987), Grimaldi and Engel (2005a), Bennett and Engel (2005) |
| Scoliidae | Ectoparasitoid, predator | Coleoptera: Scarabaeidae; Hymenoptera: Sphecidae | Larvae | Barrremian–Recent | Clausen (1940), Lai (1988), Rasnitsyn and Martínez-Delclòs (1999, 2000), Zhang et al. (2002c) |

(continued)

**Table 11.1** (continued)

| Taxon[a] | Parasitoid larval life-habit[b] | Dominant larval hosts[c] | Host stage of larval parasitoid attack[d] | Geochronologic range[e] | References[f] |
|---|---|---|---|---|---|
| Sierolomorphidae | Ectoparasitoid[i], predator[i] | — | — | Turonian–Recent | Evans (1961), Rasnitsyn (2000), Grimaldi and Engel (2005a) |
| Tiphiidae | Ectoparasitoid, predator | Orthoptera: Stenopelmatidae; Coleoptera: Carabidae, Cincidellidae, Scarabaeidae, perhaps Curculionidae | Nymphs, last instar larvae | Aptian–Recent | Clausen (1940), Knisley et al. (1989), Darling and Sharkey (1990), Grimaldi and Engel (2005a) |
| ***Apoidea*** | | | | | |
| Ampulicidae | Ectoparasitoid to endoparasitoid, predator | Blattodea | Nymphs, adults | ?Albian–Recent | Clausen (1940), Bohart and Menke (1976), Brandão et al. (1989), Antropov (2000), Rasnitsyn (2002), Engel and Grimaldi 2005a |
| Crabronidae | Ectoparasitoid to endoparasitoid, predator | Ephemeroptera; Hemiptera: Sternorrhyncha; Coleoptera; Diptera: Syrphidae; Lepidoptera; Hymenoptera; Acari | Larvae, adults, nymphs | Cenomanian–Recent | Clausen (1940), Bohart and Menke (1976), Antropov (2000) |
| Heterogynaidae | Ectoparasitoid to endoparasitoid, predator[i] | — | — | Recent | Bohart and Menke (1976), Grimaldi and Engel (2005a) |
| Sphecidae | Ectoparasitoid to endoparasitoid predator | Orthoptera: Acrididae, Gryllidae, Stenopelmatidae; Blattodea; Lepidoptera: Noctuidae | Nymphs, adults, larvae | Cenomanian–Recent | Clausen (1940), Bohart and Menke (1976), Darling and Sharkey (1990), Antropov (2000) |

[a] Subclades lacking parasitoid behaviors are not included. A dagger (†) indicates an extinct lineage

[b] Only those family-level taxa with parasitoid or related life habits are listed under their respective, encompassing clades. Obligate or facultative parasitic groups that do not kill their hosts are excluded from this list. Parasitoid types—ectoparasitoid, endoparasitoid, hyperparasitoid, cleptoparasitoid—are listed in approximate order of abundance

[c] Major host clades are listed, occasionally with family-level examples to flesh out taxonomic details. This is not an exhaustive list and new parasitoid clades are discovered each year. The extended dash (—) indicates that the taxonomic identities of the hosts remain unknown or would have been based on inadequate data

[d] The major developmental stage of hosts undergoing parasitoid attack is provided. The North American rather European system of naming larval stages is used. A larva designates a developmental stage intercalated between the egg and pupal stages in holometabolous insects. Accordingly, a naiad is the developmental stage of a nonholometabolous insect in the aquatic realm whereas a nymph is the analogous developmental stage in the terrestrial realm. The extended dash (—) indicates that the life habits of the hosts remain unknown or would have been based on inadequate data

[e] The geologic time scale of Walker et al. (2013) is used, one that represents advances in several fields that have contributed to greater precision of age estimates. Range-through data is assumed. Geochronologic ranges are for the broader clade encompassing the parasitoid taxa, and not for individual parasitoid lineages

[f] References include primary sources of original studies as well as reviews of original sources. The sources are not meant to be complete, but rather indicative of the more important life-habit studies and fossil occurrences

[g] All strepsipteran lineages are considered parasitoids, rather than their attribution to parasites mentioned by Eggleton and Belshaw (1992). The parasitoid life habit of Strepsiptera is based on Kathirithamby's (2009) criterion that after strepsipteran hosts are parasitized, they "…develop and obtain nutrients from a single host, thereby castrating and eventually killing it" (page 234)

[h] Major taxonomic subdivisions of the Strepsiptera are after Engel et al. (2016a)

[i] Attribution to a particular parasitoid larval life habit for these fossil and poorly known groups are inferred from one or more of the following four criteria. First is the phylogenetic position of the parasitoid lineage within a broader phylogeny. Second are the known biologies of closely related lineages. Third is the availability of particular host lineages for parasitoidism within the local, contemporaneous biota. Fourth are the limitations of small size for host choice

[j] A probable paraphyletic group

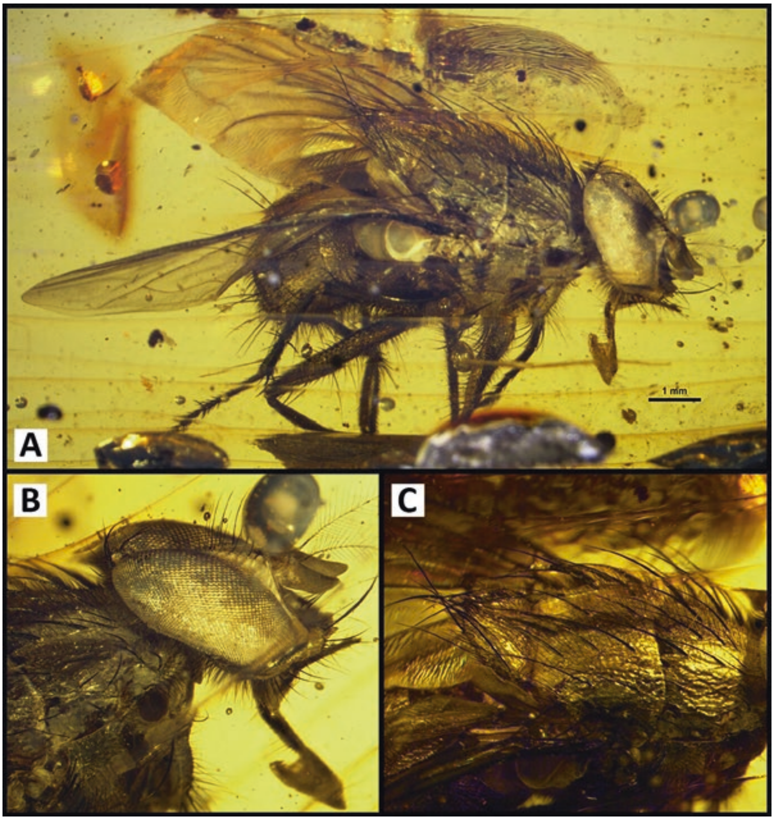


**Fig. 11.10** Holotype of the adult bot fly *Mesembrinella caenozoica* (Diptera: Mesembrinellidae), from early Miocene amber of the Dominican Republic. (**a**) Habitus in dorsolateral view. (**b**) Head and the anterior thorax in right dorsolateral view. (**c**) Thorax in right dorsolateral view. (Reproduced with permission from Fig. 1 in Cerretti et al. 2017)

within Mecoptera (Vršanský et al. 2010). Current evidence suggests, however, a nonparasitic existence. Several features, especially genitalia, are structurally linked to nematocerous Diptera (Huang et al. 2013b), particularly Nymphomyiidae (nymphomyiid crane flies), which presently are a specialized, relict group of neotenic amphibious insects with adults lacking functional mouthparts.

#### 11.5.1.9 Lepidoptera (Moths)

In Southeastern Asia a clade of erebid moths recently have developed a unique modification of the lepidopteran siphon that is adapted to piercing the often-thick integument of large mammals for the imbibition of blood (Bänziger 1968, 1971). The clade consists of ten species of *Calyptra*, formerly assigned to Noctuidae (owlet moths) that now is placed in the Erebidae (vampire moths), and affiliated with the

Tribe Calpini of the Subfamily Calpinae (Zaspel et al. 2012). The clade of *Calyptra* consist of ten species of hematophagous vampire moths in which evidently only males imbibe blood from large mammals that include cattle, zebu, tapirs and occasionally elephants and humans, centered in Southeast Asia but with a geographic range extending to India and southeastern Russia (Bänziger 1971; Zaspel et al. 2007). Related species and genera within Calpini frequent the more delicate membranes of the eyes, rectum and genitalia for feeding on tears, sebum, sweat and other dermal secretions (Bänziger 1968, 1996). A more distantly related clade of fruit piercing and surface scarifying moths are known from the tropics of Africa and South America (Zenker et al. 2010). The mouthpart siphons of these fruit feeding, and blood- and lymph feeding species, are rigid, lack internal stylets, and contain external, spine-like structures at the proboscis tip that are hydraulically stiffened for penetration into skin. The siphonal stylet is powered by a cibarial food pump for ingestion of fluid host tissue (Bänziger 1996; Labandeira 2019). The clade that bears these distinctive mouthparts lacks a fossil record.

#### 11.5.1.10 Hymenoptera (Wasps)

Social parasitism frequently is found in Hymenoptera and is particularly prevalent among bees. A recurring feature of social parasitism is embodied in Emery's Rule, which is narrowly defined as social parasites are the closest relatives of their hosts, frequently at the sister-species level (Wilson 1971). A broader version of this rule states that a clade or related group of social parasites is solely related to their hosts (Smith et al. 2007). An illustration of this phenomenon occurs in allodapine carpenter bees (Apidae: Xylocopinae) (Smith et al. 2007), which exhibit a looser version of relationships between a host clade and its sister social parasite clade (Fig. 11.11), providing evidence for sympatric speciation. As seen in the lack of rigorous correlation of sympatry in Fig. 11.11, there may be inherent flaws in the notion of Emery's Rule, at least in some instances. Confounding processes such as extinction or speciation within one or both of the clades, host-switching, and incomplete sampling (Smith et al. 2007) could derail the observed patterns. Notably, older host–social parasite relationships tend to support sympatric speciation whereas younger such relationships do not. This discontinuity likely is because extinctions may result in a pruning of the older clades such that they appear retrospectively to have originated sympatrically (Smith et al. 2007).

A second type of common parasitic relationship among bees is cleptoparasitism. Cleptoparasitism, the theft of resources by one animal from another animal, is rarely found in the fossil record. However, based on a distinctive forewing shape and other morphometrically-gleaned features, it was possible to assign a cleptoparasite identity to a wing of a bee from the middle Paleocene, at the 60.5 million-year-old Menat locality in central France (Dehon et al. 2017). The presence of cleptoparasite taxa is significant, as it establishes that before the midpoint of the geochronologic history of bees, cleptoparasites were present.

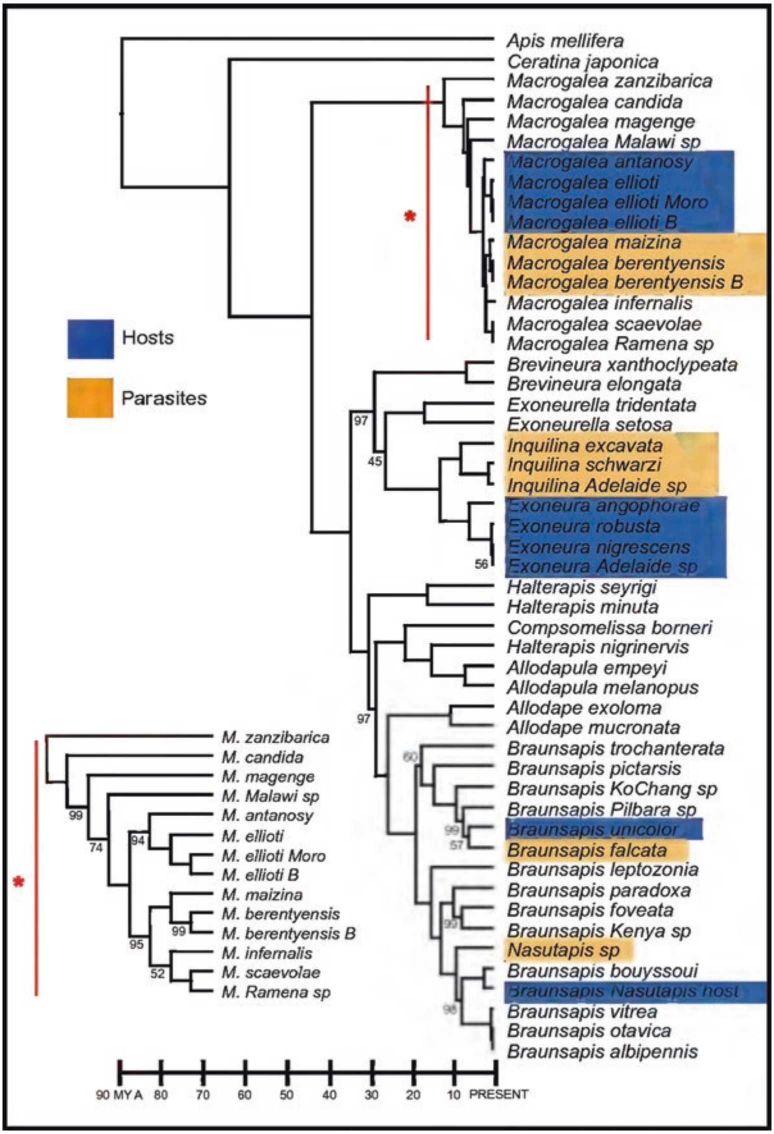


**Fig. 11.11** Chronogram of allodapine bee species based on a penalized likelihood transformed Bayesian consensus phylogram (Smith et al. 2007). The insert shows an enlarged view of the chronogram for the *Macrogalea* species, whose divergences are very recent. The divergence ages are indicated by the geologic time scale at bottom, and posterior probability support values less than 100 are shown. These values ae indicated on the enlarged inset of the chronogram for *Macrogalea*. Host species are indicated within a blue rectangle whereas corresponding parasite species are shown in an adjacent orange rectangle. (Reproduced with permission from Fig. 2 of Smith et al. 2007)

### *11.5.2 Parasitoid Taxa*

The parasitoid life style and feeding mode is confined to seven insect orders, all of which have holometabolous development (Table 11.1). Parasitoids occur in Coleoptera (beetles), Strepsiptera (twisted-wing parasites), Diptera (flies) and Hymenoptera (wasps), and with small numbers in Neuroptera (mantidflies), Trichoptera (caddisflies) and Lepidoptera (moths). There are 146 extant and extinct families of insect parasitoids, in decreasing rank order of familial diversity: Hymenoptera, Diptera, Strepsiptera, Coleoptera, Lepidoptera, Trichoptera and Neuroptera (Tables 11.1 and 11.2). Of these families, 116 (79.5%) are extant and 30 (20.5%) are extinct (Table 11.2).

Morris (1998) cites five criteria that characterize insect parasitoids. However, Morris also states that occasional exceptions occur. The general criteria for an arthropod to be deemed a parasitoid are the following:

1. The larval stage assumes the parasitoid strategy.
2. The adult stage is free living and serves as the agent of dispersal.
3. Host death is obligatory and often is coordinated with the emergence of the adult parasitoid.
4. Host pathology, including death, is generally not dependent on the intensity of parasitoid activity.
5. Only one host is killed in an interaction with a parasitoid.

Criteria 1 and 2 apply to all insects and mites, although some exceptions occur in mites. For criterion 3, some insects fail to kill their hosts, such as some anthomyiid and tachinid fly species, in which their hosts survive a bout with parasitoids and subsequently complete their development (Clausen 1940; English-Loeb et al. 1990). Because of the rarity of these examples, such species are included as viable parasitoids. Criterion 4 is a way of expressing the relationship that parasitoids, such as

**Table 11.2** The fossil record of insect parasitoid families

| Order | Number of families | Percentage representation |
|---|---|---|
| Breakdown by order | | |
| Neuroptera | 1 | 0.7 |
| Coleoptera | 10 | 6.8 |
| Strepsiptera | 17 | 11.6 |
| Hymenoptera | 92 | 63.0 |
| Diptera | 23 | 15.8 |
| Trichoptera | 1 | 0.7 |
| Lepidoptera | 2 | 1.4 |
| *Totals* | ***146*** | ***100.0%*** |
| Breakdown by extant vs extinct | | |
| Extinct | 30 | 20.5 |
| Extant | 116 | 79.5 |
| *Totals* | ***146*** | ***100.0%*** |

braconid larvae on a caterpillar, at maturity are often within an order of magnitude the size of their host, whereas parasites (e.g. a mosquito on a human) are typically multiple orders of magnitude smaller than their host (Morris 1998). These relationships admit of rare exceptions where the ability of a parasitoid to kill its host is dependent on an elevated number of conspecific parasitoids on the same host (Blumberg and Luck 1990). Nevertheless, such density dependency is rare and these arrangements would remain as parasitoid interactions. The close relationship between predation and parasitism is illustrated in criterion 5, whereby if more than one host succumbs to the same parasitoid individual, then the relationship becomes predation (Morris 1998). A related but frequently unstated factor is the size of the host relative to the size of the parasitoid. If host size is large to very large, such as a vertebrate, compared to the size of its insect parasitoid, then successful development of the attacker is not contingent upon death of the host. Such a result would invalidate an essential, obligate feature of the host–parasitoid relationship.

#### 11.5.2.1 Neuroptera (Mantidflies)

Although almost all neuropteran larvae are predators on arthropods, Mantispidae (mantidflies) are the sole family that is a parasitoid of arthropods (Table 11.1) (Morris 1998). One subfamily, the diverse Mantispinae, have larvae that are egg predators of spiders. By contrast, Subfamily Symphrasinae, consisting of about 60 species, are ectoparasitoids of scarab beetle larvae, the pupal cocoons of owlet moths (Noctuidae), and larvae and pupae of aculeate Hymenoptera, particularly vespoid and sphecoid wasps and solitary bees (Parfin 1958; Eggleton and Belshaw 1992). Host-seeking parasitoid larvae of Symphrasinae find their host larvae in the soil or in subterranean cells. Similar to many Coleoptera, larval Symphrasinae undergo hypermetamorphosis with a mobile triungulin stage for detection of an appropriate host, and represent a behavior that originated once (Eggleton and Belshaw 1993). (A triungulin larva is the first larval instar of hypermetamorphic insects, such as blister beetles, which is mobile, active, sclerified and host seeking that becomes legless, grub-like and parasitoid in subsequent instars.)

The Mantispinae and Symphrasinae have earliest occurrences in 99 million-year-old mid-Cretaceous Myanmar Amber (Haug et al. 2018; Shi, pers. comm. 2018); earlier occurrences of Mantispidae extending to the Jurassic lack subfamily placement (Jepson 2015). In Neuroptera, parasitoidism arose once in Symphrasinae, likely from a life habit of soil predation (Haug et al. 2018). The parasitoid life habit evolved into egg predation on spider egg sacs associated with a host seeking, first instar larva that is phoretic on the adult female spider (Gilbert and Rayor 1983; Eggleton and Belshaw 1992). This larval life habit has been documented for an undescribed mantispid, attributed to Mantispinae, for a first instar phoretic larva that is an egg parasitoid on a female disc-web spider (Oecobiidae) in Myanmar Amber (Haug et al. 2018). The other modern subfamily, Symphrasinae, has a fossil record (Jepson 2015) and is known from the same deposit (C. Shi, pers. comm. 2018), although nothing is known of its Cretaceous larval life habits.

#### 11.5.2.2 Coleoptera (Beetles)

The parasitoid habit in Coleoptera is expressed in ten families that occur sporadically across the order, variously as ectoparasitoids, endoparasitoids and cleptoparasitoids that extend to the Middle Jurassic and conceivably as early as the Late Triassic (Table 11.1). For Coleoptera, host-searching behavior occurs typically in first-instar larvae.

Carabidae (ground beetles) consist of approximately 1500 genera and 40,000 species that are allocated into approximately 80 tribes (Arndt et al. 2005). Of these tribes, 7 have parasitoid life histories, including termite symbionts, ant symbionts and ectoparasitoids on various invertebrates (Erwin 1979). When other suspected tribes that house parasitoids are included (Erwin 1979), about a fourth of all carabid tribes have one or more parasitoid species. In general, two major ectoparasitoid groups of carabids are present. The first group attacks hosts in soils that include beetle pupae and millipedes, whereas a second group parasitoidizes leaf beetles on above-ground organs of plants (Erwin 1979). The earliest fossil Carabidae is Late Triassic (Grimaldi and Engel 2005a, b), occurring approximately 230 million years ago, although the parasitoid taxa are undoubtedly more recent than that, given their phylogenetic placement (Maddison et al. 1999).

Staphylinidae (rove beetles) include the subfamily Aleocharinae that consist of many ectoparasitoid genera on cyclorrhaphan, typically Pupipara, flies (Maus et al. 1998). Staphylinidae constitute about 48,000 species of which about one quarter are in the Subfamily Aleocharinae (Thayer 2005). Of the Aleocharinae, only the genus *Aleochara* are parasitoids, consisting of 400 described species and constituting about one-third of the species-level diversity of the subfamily (Maus et al. 1998) and about 0.08% of Staphylinidae. Typical microhabitats for parasitoid aleocharines are moist, fleeting habitats such as carrion, dung, polypore fungi, kelp-laden beach wrack, and decaying plant material in the nests of vertebrates and ants (Eggleton and Belshaw 1992). Aleocharine parasitoid eggs, upon hatching, produce a mobile triungulin stage analogous to the planidium of most dipteran parasitoids (Lawrence et al. 1991; Arnett Jr and Thomas 2001). The triungulin first-instar larva actively searches for potential hosts, attacks the appropriate host and either becomes attached or enters the host, initiating the process of parasitoidization, seen in a variety of hypermetamorphic parasitoids (Falin 2002; Engel 2005a; Haug et al. 2018). Subsequent instars are typically sessile, grub-like and continue the process of parasitoidization to its consummation through starvation of social insect colonies (Askew 1971; Godfray 1994). The earliest fossil Staphylinidae are Late Triassic in age, occurring approximately 230 million years ago and, like Carabidae, are significantly older than their descendant parasitoid taxa that originate during the Early Cretaceous (Chatzimanolis et al. 2012).

Scarabaeidae constitute approximately 27,000 species, of which approximately 5% or less in our estimation are cleptoparasitoids associated with deprivation of food and other resources from social insects (Scholtz and Grebennikov 2005). Five subfamilies of Scarabaeidae contain cleptoparasitoid taxa. Aphodiinae adults have specialized associations, evidenced by distinctive morphological adaptations, with termites and ants (Tangelder and Krikken 1982; Howden and Storey 1992; Stebnicka 1999). Scarabaeinae larvae, some known as "kleptocoprids", breed in dung that consume food resources provisioned by other, larger dung beetles (Halffter and Edmonds 1982; Halffter and Matthews 1999). Dynastinae include larvae that feed on brood and stored honey reserves in beehives (Glaser 1976; Evans and Nel 1989). Cetoniinae consist of Cremastocheilini adults that abscond the food stores in termites, ant and bee nests (Deloya 1988; Alpert 1994). Valginae adults and larvae are associated with termite mounds (Krikken 1978). Some Scarabaeidae (scarab beetles) are cleptoparasitoids that consume provisions of other scarab and closely related geotrupid beetles (Hammond 1976; Halffter and Matthews 1999; Scholtz and Grebennikov 2005). In the most common cleptoparasitoid group, the adult lays eggs into dung balls or analogous brood structures that hatch, followed by the first-instar larvae immediately burrowing and eventually consuming the host egg and all provisions in a dung ball or analogous brood structure (Halffter and Edmonds 1982; Paulian 1988). Some taxa of the scarabaeid subfamilies Valginae and Cetoniinae (Cremastocheilini) that are associates of social insect nests probably are cleptoparasitoids (Krikken 1978; Alpert 1994; Scholtz and Chown 1995). The earliest documented Scarabaeidae is latest Middle Jurassic in age (Bai et al. 2012), although parasitoid forms more likely are no older than mid Cretaceous in age based on their position within Scarabaeoidea phylogeny (Krell 2006).

Rhipiceridae (cedar beetles, cicada parasite beetles), constitute 7 genera and 100 species that are globally distributed, all of which are ectoparasitoids on cicadas (Lawrence 2005). Female rhipicerids such as *Sandalus* oviposit eggs in the cracks and interstices of elm tree bark, where cicadas also have oviposited (Elzinga 1977). Later, triungulin-like larvae and nymphs are flushed by rain and redeposited on the ground, where, after some time, a rhipicerid late-instar ectoparasitoid larva becomes attached to the cicada nymph host (Evans and Steury 2012). In eastern North America, there appears to be annual tracking by the rhipicerid parasite of its cicada host based on fluctuating population levels. The earliest occurrence of rhipicerid beetles in the fossil record is considerably recent, the Lutetian Stage of the middle Eocene (Ponomarenko 1995).

Cleridae (checkered beetles) consist of approximately 3400 species, are mostly predaceous (Kolibác 2010), but have two major parasitoid strategies. Their first is a role as cleptoparasitoids of apid bees, depriving larvae of nest provisions in soil cells and decaying plant material. The first instar larva is host searching or phoretic and feeds only a short time on the host's provisions (Eggleton and Belshaw 1992). Clerids have a second role as parasitoids of lepidopteran caterpillars occurring in galls that occur on plant shoots, although the host locating process is poorly understood (Eggleton and Belshaw 1992). The origin of the parasitoid life habit in Cleridae likely was derived from predation of insects in dead wood habitats. By contrast, the parasitoid habit evolved into predation on bees in soil and plant litter habitats and possibly on grasshopper egg pod predation. The oldest fossils of Cleridae are from the latest Middle Jurassic of China (Kolibáč and Huang 2016).

Bothrideridae (dry bark beetles) consists of 38 genera, 400 species and 4 subfamilies, where one subfamily, Bothriderinae, has ectoparasitoid life habits (Philips and Ivie 2002). Bothrideridae are highly elongate beetles whose adults occur under tree bark or in composted soil. Their nonparasitic larvae feed on fungi whereas their hypermetamorphic, host-seeking, first-instar larvae is a spinose triungulin that attacks and becomes an ectoparasitoid on wood-boring larvae of metallic wood-boring beetles, ambrosia beetles, bark beetles, deathwatch beetles, augur beetles, longhorn beetles, and wood wasps (Horion 1961; Ślipiński et al. 2010). Subsequent larval instars are grub-like and complete an ectoparasitoid existence on their host (Philips and Ivie 2002; Lawrence and Ślipiński 2013). The ectoparasite habit likely originated from mycophagy in an ancestral bothriderid lineage (Crowson 1981), and subsequently evolved into ectoparasitoidism. Ectoparasitoidism currently is confined to the diverse Subfamily Bothriderinae, where adults of several genera bear lightly sclerotized, swollen abdomens probably involved in very fecund levels of egg production. The oldest Bothrideridae are from the middle Eocene (Ponomarenko 1995).

Passandridae (flat bark beetles) consist of 9 genera and 109 species that are ectoparasitoids of the larvae or pupae of wood boring insects such as weevils, longhorned beetles, ambrosia beetles, bark beetles or wood wasps that live in dead wood or under bark (Crowson 1981; Thomas 2002; Burkhardt and Ślipiński 2010). Passandrids also assume a second major parasitoid strategy as hyperparasitoids on braconid wasps (Burkhardt and Ślipiński 2010). The larval body is highly modified for ectoparasitoid habits and display changes in larval morphology from instar to instar (Burkhardt and Ślipiński 2003), similar to hypermetamorphic larvae. Passandrid larval morphology externally is variously sclerotized, flattened and spiny, with an enlarged abdomen and reduced mouthparts. Evidently, parasitoid larvae of Passandridae display limited host specificity. Adults are considerably flat dorsoventrally and occupy subcortical bark habitats. The oldest fossils of Passandridae evidently are Cenomanian in age (Ponomarenko 1995).

Meloidae (blister beetles) are mostly parasitoids of grasshoppers and non-domesticated bees (Lawrence et al. 1991; Arnett Jr et al. 2002). Meloid first-instar triungulin larvae frequently are encountered on flowers, are acquired by foraging male bees, and then are transported to female bees during mating (Lawrence et al. 1991; Arnett Jr et al. 2002). At the bee nest site, the triungulin larvae invade bee cells where eggs reside and successively consume either the egg or the developing larva. Meloid larvae undergo hypermetamorphosis and initially are ambulatory, host-seeking triungulins, followed by sessile, grub-like larval instars that emerge from their host insect nest as adult blister beetles.

About 120 genera and 2500 species of Meloidae have larvae that are predaceous or more frequently parasitoids (Bologna et al. 2010). Larval hypermetamorphosis is common and involves host-searching behavior, and after attack of the host, the larva transforms into a fat, fleshy grub that in turn results in an adult beetle (Bologna et al. 2010). The fossil history of Meloidae extends to the earliest Cenomanian at 99 million years ago, in Myanmar Amber (Poinar Jr and Brown 2014), and consists of a distinctive, miniscule, triungulin larva attached to a jumping ground bug (Hemiptera: Schizopteridae) in a seeming parasitoid association (Poinar Jr and Brown 2014). This suggests that blister beetles and their parasitoid life cycle extend to the Early Cretaceous.

Ripiphoridae (wedge-shaped beetles) are closely related to Meloidae and currently are all parasites or parasitoids. Ripiphorids are endoparasitoids of cockroach adults; ectoparasites of the wood-boring larvae of longhorn beetles; and endoparasitoids, rarely ectoparasites, of aculeate hymenoptera larvae, especially bees (Eggleton and Belshaw 1992). The eggs of ripiphorid adults typically are laid in the host environment, with the triungulin larvae becoming phoretic, eventually finding and immediately attacking their hosts (Askew 1971). A relevant, postulated fossil interaction, from the Middle Jurassic Yanliao Biota of northeastern China (Fig. 11.12), involves parasitization of wood-boring beetles (Hsiao et al. 2017). In a younger deposit, Ripiphorids are associated with Early Cretaceous parasitism on insects such as cockroaches, based on plesiomorphic taxa discovered from 99 million-year-old Myanmar Amber (Beutel et al. 2016; Batelka et al. 2016, 2019). Certain features of one of these Myanmar Amber taxa, such as a miniaturized ripiphorid, indicate that parasitism rather than parasitoidism (Batelka et al. 2019), was present, suggesting an initial phase of parasitism (Hsiao et al. 2017; Fig. 11.12) that subsequently became replaced by parasitoidism in descendant clades of the Late Cretaceous and Cenozoic.

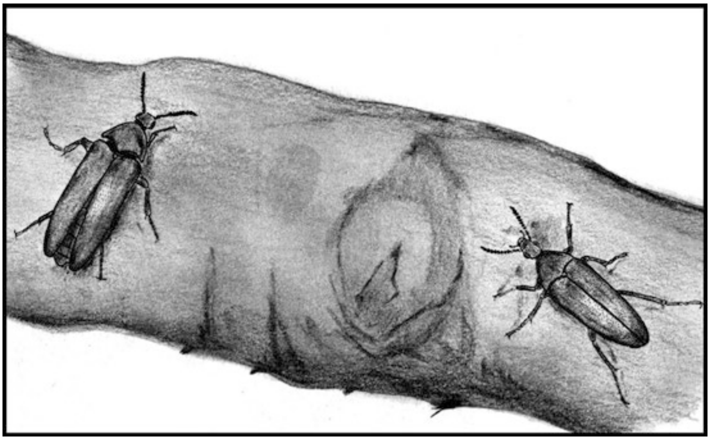


**Fig. 11.12** A reconstruction of the parasitoid wedge-shaped beetle *Archaeoripiphorus nuwa* (Coleoptera: Ripiphoridae) from the Middle Jurassic Yanliao Biota of northeastern China. This setting illustrates a hypothesized behavior whereby ovipositing females search for damaged xylem cells that are caused by xylophagous larvae of beetles. (Reproduced with permission from Fig. 6 in Hsiao et al. 2017)

Anthribidae (fungus weevils) consist of about 360 genera and 4000 species, a few of which, particularly species of *Araecerus* and *Anthribus*, are cleptoparasitoids of soft scales such as *Lecanium* (Ülgentürk 2001; Ülgentürk and Toros 1996; Valentine 2002). The female weevil oviposits her eggs under a soft scale insect and the weevil larvae develop at the expense of the host's eggs (Valentine 2002; Mermudes and Leschen 2014). The earliest fossil record of Anthribidae is mid Early Cretaceous, about 132 million years ago (Gratshev and Zherikhin 2003), although it remains unknown when the cleptoparasitoid habit commenced in this lineage.

Coleoptera parasitoids, compared to the two other major parasitoid offenders, Diptera and Hymenoptera, have a relatively narrow range of hosts, attacking eight orders within the single phylum Arthropoda (Eggleton and Belshaw 1992). Host searching is overwhelmingly accomplished by the larva in Coleoptera, as in Diptera, but unlike Hymenoptera in which the host-searching stage is an adult. Among the ten families of Coleoptera, the parasitoid condition originated at least 14 times (Eggleton and Belshaw 1992), and likely several more times once a reliable phylogeny of Scarabaeidae has been established. These originations have arisen from two major ancestral strategies (Eggleton and Belshaw 1992; Morris 1998), although the transitions to parasitoidism involve mycophagy, nest provisioning, saprophagy and phytophagy (Fig. 11.4a). The first strategy is from mycophagy, often associated with nest provisioning, typical of Bothrideridae, Meloidae, Rhipiceridae and Ripiphoridae. In this pathway, the candidate parasitoid larva is transported via phoresy. It then first feeds on fungi in bark-beetle wood borings, followed by parasitism, or parasitoidizing or killing the existing beetle occupant (Morris 1998). Cleptoparasitoidism originated in blister beetles that feed on pollen in bee nests, and among weevils that feed in the wood borings of bark and ambrosia beetles. A modification of this strategy is found in scarabaeid parasitoids that may have originated ancestrally as saprophages or mycophages associated with nest provisioning (Eggleton and Belshaw 1992). The second strategy is exemplified by aleocharine parasitoids that originated from predaceous precursors. Both strategies have resulted in a greater number of cleptoparasitoids than ectoparasitoids plus endoparasitoids, amounting to a majority of all beetle parasitoids. This cleptoparasitoid to ectoparasitoid and endoparasitoid ratios are unlike analogous proportions in all other parasitoid containing insect orders. Shifts away from the parasitoid life habit have been rare among Coleoptera, involving egg predation and cleptoparasitic provisioning.

#### 11.5.2.3 Strepsiptera (Twisted-Wing Parasites)

Strepsiptera are (controversially) internal parasites or parasitoids; they consist of two suborders, 17 extinct and extant families and about 610 species (Table 11.1). Males resemble normal, adult, winged insects, but have vestigial mandibulate mouthparts, distinctive compound eyes and halteres as forewings (Cook 2014). Female strepsipterans are larviform, live in the host wedged within the intersegmental membrane between abdominal sclerites but have a projecting orifice, the brood canal that is used for mating. Strepsipteran triungulin larvae are structurally convergent on larvae of Ripiphoridae and Meloidae (Kathirithamby 2009) and frequently are confused with each other in the fossil record because of the structural similarity (Beutel et al. 2016). As the triungulin larvae emerge from the female's body, they then consume her. The strepsipteran hypermetamorphic larva is a mobile, hexapodous, host-seeking triungulin instar (Pohl and Beutel 2019), which immediately after burrowing through their host's exocuticle molts into a second instar, a featureless, vermiform individual. This vermiform larva induces the host to produce a gall-like structure from which the larva feeds as it undergoes four more molts, during which the host is castrated. Larval hosts of Strepsiptera include silverfish (Thysanura), cockroaches (Blattodea), mole crickets (Orthoptera), planthoppers and leafhoppers (Hemiptera–Auchenorrhyncha), and bees and wasps (Hymenoptera–Aculeata) (Kathirithamby 2009). For Myrmecolacidae the larval host is different from the host to which the female is embedded (Hayward et al. 2011). The unique life cycle of Strepsiptera likely originated once. Recently, another distinctive hypermetamorphic stage of the strepsipteran life cycle was confirmed by discovery of the first free-living, late-instar larva, probably a female, belonging to a stem-group lineage of Strepsiptera from 44 million-year-old middle Eocene Baltic Amber (Pohl et al. 2019).

Considerable discussion has centered on whether strepsipterans, with the exception of the Mengenillidae, are parasites or parasitoids. Features mitigating against a parasitoid designation are (1) the host does not typically die immediately after adult emergence; (2) multiple females and multiple males can live within a single host; and (3) the adults are parasitic and not the larvae (Kathirithamby 2009). Nevertheless, Strepsiptera castrate their hosts, which renders them genetically dead, closely resembling the standard parasitoid life habit. Additionally, the basal-most extant lineage of Strepsiptera are the Mengeidae, which are considered true parasitoids, indicating that the life habits of the other extant, likely derived families evolved some morphological and behavioral features inconsistent with the ancestral parasitoid condition. Because of castration of their hosts and other nominal parasitoid features, Strepsiptera are here considered as parasitoids. However, if a traditional definition of parasitism in the Strepsiptera is accepted, in which host death is not imminent upon emergence of the parasitoid, then the transition from Mengeidae to other strepsipteran lineages could be construed as a shift from the parasitoid to a parasite life habit.

Although mengeid strepsipterans are endoparasitoids of soil-dwelling silverfish, Strepsiptera probably evolved from a Permian lineage of beetle taxa involved in mycophagy and wood boring (Eggleton and Belshaw 1992). This is particularly relevant since Strepsiptera likely are closely related to or the sister clade to Coleoptera (Misof et al. 2014), and early beetles are associated with wood, such as fungi-consuming polyphagan beetles in conifer host trees from the late Permian of northern China (Feng et al. 2017). After an approximate 190 million-year-long interval of a presumed divergence event from Coleoptera during the Early Permian, early Strepsiptera consisted of three extinct clades. First is extinct "Protostrepsiptera", possessing plesiomorphic features and appearing in 99 million-year-old Myanmar Amber (Grimaldi et al. 2005; Pohl et al. 2005; Kathirithamby and Engel 2014;

Engel et al. 2016a). Second is the oldest known strepsipteran attributable to a modern family, the mobile, primary larva of Mengenellidae, also from earliest Late Cretaceous Myanmar amber (Fig. 11.13). This specimen likely was associated with a wood-boring host larva (Pohl et al. 2018). Third is extinct Mengeidae, occurring in Baltic amber, a true parasitoid. Notably, the current host spectrum of Strepsiptera does not reflect this Late Cretaceous to Paleogene pattern (Poinar Jr 2004b;

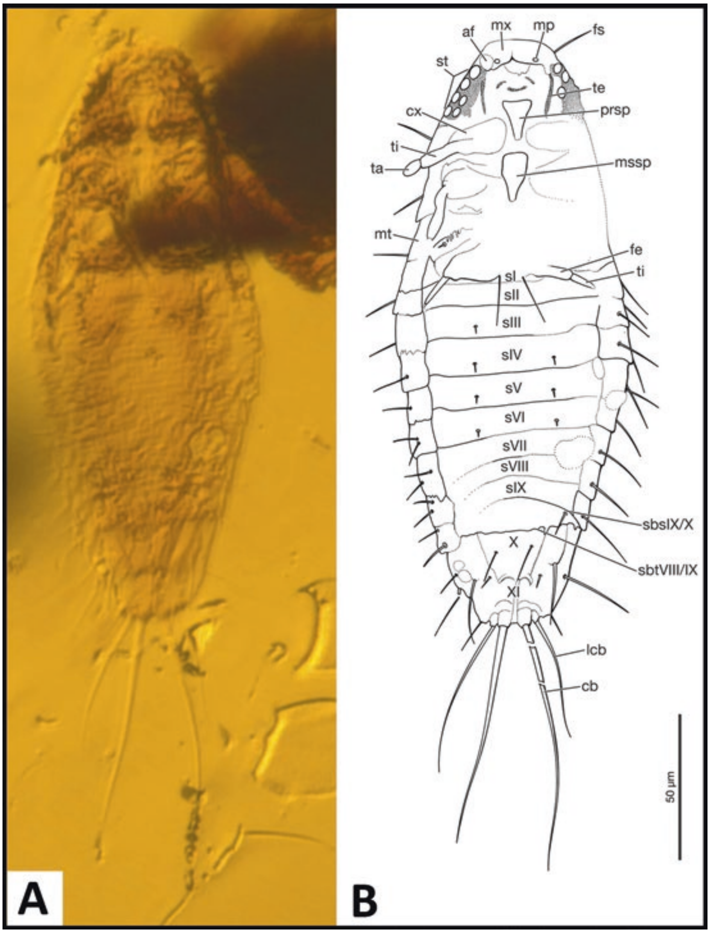


**Fig. 11.13** A ventral view of an unnamed primary larva of a twisted-wing parasite (Strepsiptera: Mengenillidae) in Myanmar amber. (**a**) Photomicrograph of larva. (**b**) Drawing base on photomicrographs with a fluorescence microscope. Details of microscopy from Pohl et al. (2018). Abbreviations: *af* antennal field, *cb* caudal seta, *cx* coxa, *fe* femur, *fs* frontal seta, *lcb* lateral caudal seta, *mp* maxillary palp, *mssp* mesosternal plate, *mt* metanotum, *mx* maxilla, *prsp* prosternal plat, *sbsIX/X* segmented border between abdominal sternites IX/S, *sbtVIII/IX* segmental border between abdominal tergites VIII/IX, *sI–IX* abdominal sternites I–XI, *st* stemmata, *Ta* tarsus, *te* tentorium, *ti* tibia, *X* abdominal segment X, *XI* abdominal segment XI. (Reproduced with permission from Fig. 1 of Pohl et al. 2018)

Kathirithamby 2009). It appears that the early hosts of Strepsiptera may have been more peripheral to their current host distribution, such as wood frequenting cockroaches.

#### 11.5.2.4 Diptera (Flies)

Dipteran parasitoids represent a much wider spectrum of hosts than does their other major parasitoid competitor, Hymenoptera. Dipteran parasitoids attack 22 orders of organisms within the five phyla of Platyhelminthes (flatworms), Mollusca (aquatic and terrestrial gastropods), Annelida (oligochaetes), Arthropoda (including millipedes, crustaceans and arachnids) and Chordata (amphibians) (Table 11.1) (Morris 1998). This host spectrum represents the dominant terrestrial animal phyla, except for Nematoda. Diptera have acquired the parasitoid habit minimally 21 times (Eggleton and Belshaw 1992), representing about 16,000 species or 20% of all dipteran species (Feener and Brown 1997), although Weinstein and Kuris (2016) list 60 times after an exhaustive literature search. The actual number of instances of dipteran parasitoidism will be shown to be about 100 times, once the life habits and phylogenetic relationships of more obscure lineages, particularly the diverse Asilidae, Phoridae and Sarcophagidae, are known (Eggleton and Belshaw 1992). Notably, in three of the four most diverse families—Bombyliidae, Conopidae and Tachinidae—parasitoidism has evolved only once (Feener and Brown 1997; Yeates and Greathead 1997).

Nine major dipteran lineages at the superfamily level harbor parasitoids. Culicomorpha consists of Chironomidae, some of which are ectoparasitoids of pulmonate gastropod immatures and mayfly naiads. Other minor origins of parasitoidism in Diptera include a single origin from microphagy in Chironomidae (nonbiting midges), and another single origin from mycophagy in Mycetophilidae (fungus gnats). Although Chironomidae extends to the Late Triassic, it is unlikely that these associations are as old. Bibionomorpha (e.g., Poinar Jr 2010) include endoparasitoids of flatworms and the nymphs and adults of sternorrhynchan hemipterans, whose associations most likely are relatively recent and Neogene in origin (Eggleton and Belshaw 1992). Nemestrinimorpha are obligate endoparasitoids of spiders and mites, as well as grasshoppers and beetles, and collectively attack all host life stages. Host associations of Nemestrinimorpha likely extend to the Late Triassic for tanglevein flies (Nemestrinidae). The spider flies (Acroceridae) are a more recently evolved lineage that range from the Late Jurassic to the recent (Mostovski 1998). They are endoparasitoids of spiders and mites and are particularly associated with the parasitoidization of several major clades of araneomorph spiders (Gillung et al. 2018; Fig. 11.14). This lineage originated during the Middle Jurassic and diversified during the Late Cretaceous to Paleogene. The Archisargoidea is the only extinct dipteran superfamily that contains a parasitoid lineage (Fig. 11.15), the highly probable endoparasitoid clade Eremochaetidae, known from the Late Jurassic to earliest Late Cretaceous (Grimaldi and Barden 2016). Although considered typically predaceous (Fig. 11.1f), Asilomorpha also are ectoparasitoids or endoparasitoids,

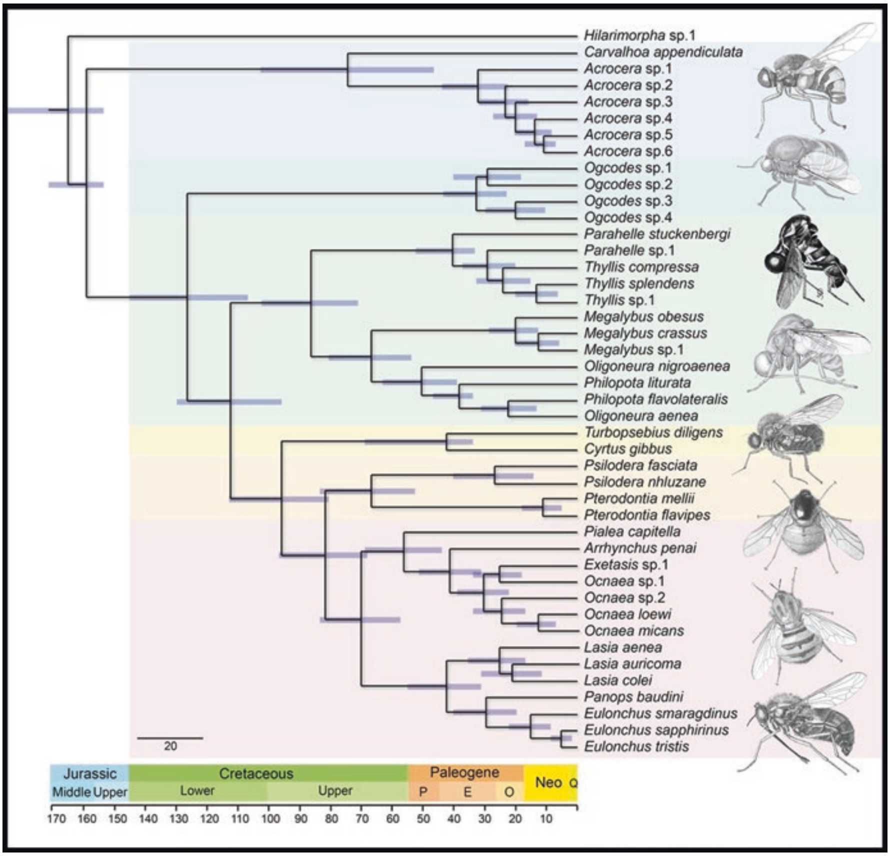


**Fig. 11.14** Estimated divergence times among lineages of the spider fly lineage Acroceridae under the fossilized birth-death process. Bars depict the 95% higher posterior probability density of each estimate. Mean ages, their ranges and other details are provided in Gillung et al. (2018). (Reproduced with permission from Fig. 4 in Gillung et al. 2018)

occasionally hyperparasitoids, of beetle and sawfly larval hosts. These hosts are associated with dead wood, or alternatively the eggs, larvae and pupae of grasshoppers, beetles, externally feeding moth larvae, and other parasitoid groups such as Tachinidae and Ichneumonidae (Yeates and Greathead 1997). Some of these associations likely extend to the Middle to Late Jurassic. Empidoidea are ecto- or endoparasitoids of caddisfly pupae, an association that probably originated during the Late Jurassic (Eggleton and Belshaw 1992).

Cyclorrhaphan flies, consisting of the Aschiza and Schizophora sister groups, underwent a Late Cretaceous and Paleogene wave of diversification, with several lineages acquiring parasitoid life habits (Grimaldi and Engel 2005a). Aschiza are endoparasitoids and cleptoparasitoids of the immatures and adults of pulmonate gastropods, oligochaetes, opilionids, spiders and myriapods, as well as all

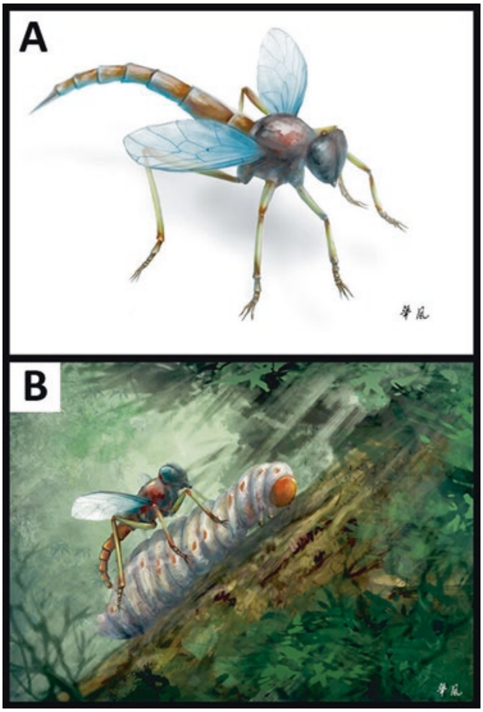


**Fig. 11.15** (**a**) Reconstruction of the short-horned fly adult *Zhenia xiai* (Diptera: Eremochaetidae) from Myanmar amber of the Early Cretaceous–Late Cretaceous boundary interval. (**b**) This endoparasitoid fly is depicted in the act of egg laying into its larval host with a hypodermic ovipositor. (Reproduced with permission from Fig. 4 in Zhang et al. 2016)

developmental stages of hemipteran, beetle, fly caddisfly and wasp hosts (Eggleton and Belshaw 1992). Aschizan associations with this varied repertoire of hosts likely originated in the Late Cretaceous and continued throughout the Cenozoic. Schizophora, constituting the Acalyptratae and Calyptratae clades, are endoparasitoids, rarely ectoparasitoids or cleptoparasitoids, of the immature and adult stages of eight, major, non-insectan lineages of invertebrates and vertebrates. These lineages are pulmonate gastropods, freshwater bivalves, oligochaetes, centipedes and millipedes, scorpions, isopod crustaceans, nymphs of cockroaches, termites, orthopterans, mantids, webspinners, earwigs, sternorrhynchan hemipterans, bugs, beetles, moths, sawflies, larvae of aculeate wasps, puparia of calyptrate flies, and mammalian vertebrates (Feener and Brown 1997). The Acalyptratae in particular developed interactions with the most diverse host spectrum of any insect parasitoid clade, and represent relatively recent Cenozoic events compared to phylogenetically more basal, dipteran parasitoid groups. Schizophora parasitoid interactions originated during the Cenozoic initially from a pattern of generalized parasitoid lineages, but continually gave rise to specialized lineages (Stireman III et al. 2006).

The origins of parasitoidism in Diptera have been the most diverse of any order of insects (Eggleton and Belshaw 1992, 1993; Fig. 11.4b). The most common route to parasitoidism in Diptera is from saprophagy, which evolved 13 times at the family level, often in association with social insects. Parasitoidism via saprophagy has been inferred to occur in Phoridae (scuttle flies), Pipunculidae (bigheaded flies), Conopidae (thickheaded flies), Pyrgotidae (light flies), Cryptochaetidae (scale parasite flies), Chloropidae (frit flies), Anthomyiidae (root maggots), Muscidae (house flies), Calliphoridae (carrion flies), Rhinophoridae (woodlouse flies), Sarcophagidae (flesh flies) and Tachinidae (tachina flies). The second most common route to parasitoidism in Diptera is through predation, which has been documented seven times and frequently has been associated with prey items occurring in or on top of the soil. This route has been inferred for Cecidomyiidae (gall midges), the common ancestor of Nemestrinidae + Acroceridae (tanglevein flies and spider flies), Bombyliidae (bee flies) that are also associated with cleptoparasitoidism, Asilidae (robber flies), Empididae (dance flies), Sciomyzidae (snail-killing flies) and Phacomyiidae (marsh flies). For dipteran parasitoids, it appears that ants are the most common host group (Quevillon and Hughes 2018).

A family-level phylogenetic tree of Diptera indicates that ectoparasitoidism originated 10 times, occurring sporadically throughout the phylogeny, whereas endoparasitoidism originated 17 times, largely confined to the Eremoneura (Wiegmann et al. 2011). This asymmetry in distribution of the two major parasitoid types is attributable to two major morphological features, the piercing ovipositor of some Eremoneura (Yeates and Wiegmann 1999), and compensatory behavioral changes for host seeking in other Eremoneura that lack a penetrative ovipositor (Feener and Brown 1997). Behavioral features promoting parasitoidization that substitute for a rigid, puncturing ovipositor include host consumption of parasitoid eggs that hatch in the gut and invade internal organs (Stireman III et al. 2006), and larvae that aggressively penetrate the host integument (Feener and Brown 1997; Stireman III et al. 2006). These features allow Eremoneura to attack and penetrate hosts that normally would be available only to apocritan Hymenoptera with extensive ovipositor modifications such as lengthening (Eggleton and Belshaw 1992; Feener and Brown 1997). Most Diptera lack a prolonged, robust ovipositor for penetrating long distances through indurated tissues as in Hymenoptera, and instead have a flexible, telescopic ovipositor that is extended by intersegmental membranes, rendering it inefficient for placing parasitoid eggs deep into host tissue (Feener and Brown 1997). Such ovipositor design restricts many dipteran parasitoid-bearing lineages to exposed hosts and a preference for ectoparasitoidism over endoparasitoidism, the latter of which only occasionally occurs across Diptera phylogeny (Eggleton and Belshaw 1993; Wiegmann et al. 2011). Several derived eremoneuran clades—particularly well developed in Tachinidae (tachina flies), Conopidae, Pipunculidae and Phoridae (scuttle flies)—have re-evolved stiffened, piercing, albeit undirected, ovipositors with a sclerotized terminus capable of penetrating their hosts (Feener and Brown 1997; Poinar Jr 2013), allowing for endoparasitoidism. For this reason, there is the dominance of endoparasitoidism over ectoparasoidism particularly among Eremoneura (Table 11.1) (Wiegmann et al. 2011). Nevertheless, dipteran parasitoids have never developed capabilities for attacking wood-boring larvae separated from a bark surface by several centimeters of wood; nor have they been engaged in penetration of thick, hardened tissues such as galls (Eggleton and Belshaw 1993; Quicke 1997). However, a substitute for reaching larvae via an ovipositor is hearing convergence in cricket hosts and their tachina fly parasitoids (Robert et al. 1992).

The second morphological feature is the development of a host-seeking first-instar larva, the planidium, which occur in at least seven dipteran families (Askew 1971) and typically results in endoparasitoidism. Functionally analogous to the triungulin larva of some Neuroptera and Coleoptera and all Strepsiptera, the planidium larva is an active, more or less sclerotized, mobile and host seeking larva that represents a departure from the common practice of the adult female dipteran depositing her eggs directly on, in or adjacent the host (Clausen 1940; Askew 1971). The planidium larva has evolved among Culicomorpha (Chironomidae), Bibionomorpha (Mycetophilidae), Nemestrinimorpha (Acroceridae, Nemestrinidae), Asiloidea (Asilidae), Acalyptratae (Sciomyzidae) and Schizophora (Rhinophoridae) (van Jutting 1938; Greathead 1963; Ferrar 1987; Eggleton and Belshaw 1992), representing a broad swath of Diptera phylogeny and independent originations minimally five or six times.

The trophic origins of the 23 parasitoid families of Diptera are highly diverse but evolved overwhelmingly from saprophagy and predation. For most families it is difficult to ascertain whether parasitoid flies evolved into other trophic modes (Fig. 11.4b). Only two such transitions are known (Eggleton and Belshaw 1992). First, parasitoidism in some Bombyliidae evolved into predation on grasshopper egg pods (Yeates and Greathead 1997). Second, some Sarcophagidae evolved into internal parasites in bees that consume the host only when it dies, a trophic transition that also is suspected in adult scarab beetle and bumble bee hosts. In general, the origin of parasitoidism from predation occurred once in nematocerous clades and several times in brachycerous (non-cyclorrhaphan) clades, whereas parasitoidism via saprophagy is confined to more derived clades among cyclorrhaphan flies. These occurrences are consistent with the predominant detritivore to saprophage diets of cyclorrhaphan flies.

#### 11.5.2.5 Trichoptera (Caddisflies)

Wells (1992) described the life history of *Orthotrichia muscari* a member of Hydroptilidae (purse-case caddisflies) from the Northern Territory of Australia (Table 11.1). This microcaddisfly, in addition to nine other members of the *Orthotrichia aberrans* species group, apparently are parasitoids of similarly aquatic Philopotamidae (fingernet caddisflies) as well as other Hydroptilidae (Wells 2005). This is the only known example of parasitoidism in Trichoptera, and represents the only aquatic mode of parasitoidism that is unique to Insecta.

#### 11.5.2.6 Lepidoptera (Moths)

Members of two families of Lepidoptera are known as ectoparasitoids (Table 11.1). Epipyropidae (planthopper parasite moths) consist of 32 pantropical species that attack fulgoroid planthoppers (Hemiptera: Auchenorrhyncha) and a few lepidopteran larvae (Jeon et al. 2002). The fossil record of planthopper parasite moths is known only for one specimen attached to a leafhopper (Auchenorrhyncha: Cicadellidae) from the early Miocene of the Dominican Republic (Poinar Jr and Poinar 1999). Analogously, Pyralidae (snout moths) contain a single species, *Sthenauge parasitus*, which is an ectoparasitoid on the larvae of the saturniid moth *Aplomerus* (Lepidoptera: Saturniidae), initially feeding on the host's dermal spines but eventually consuming it. Known parasitoidism arose at least twice in Lepidoptera, separately in Epipyropidae and Pyralidae, but likely arose many more times, particularly within lineages of Epipyropidae, given the poor understanding of the life-habits and phylogeny of these moths (Jeon et al. 2002). Parasitoidism in Epipyropidae plausibly evolved from ectoparasitic behavior occurring on the hemipteran host surface, followed by entering the host by piercing its cuticle and then eventually killing it with the exit of the parasite larva (Eggleton and Belshaw 1992). The evolutionary source of parasitoidism in Epipyropidae and Pyralidae is unclear, and there is no fossil record for parasitoid members of either lineage.

#### 11.5.2.7 Hymenoptera (Wasps)

Hymenoptera constitute about 75% of all modern parasitoid species and have the most diverse taxonomic spectrum of parasitoid lineages of any order of insects (Santos and Quicke 2011). The 17 hymenopteran superfamilies of parasitoids are approximately split between ectoparasitoid and endoparasitoid dominated superfamilies; they include 4 superfamilies that contain hyperparasitoids, 4 superfamilies that have predators, and 2 superfamilies with cleptoparasitoids (Gauld and Bolton 1988) (Table 11.1). One superfamily, Chalcidoidea, while overwhelmingly dominated by parasitoid taxa, contains two families, Agaonidae and Chalcididae, which are dominantly represented by taxa such as pollinators, gallers, seed predators and herbivores as well as cleptoparasitoids in plant galls (Eggleton and Belshaw 1992). Family-level diversity per superfamily ranges from 1 to 20. There are 92 families of extant and extinct hymenopteran parasitoids, representing 63% of all insect families with parasitoid life habits (Table 11.2). Of these families, 22 (23.9%) are extinct, some of which represent stem-group lineages. Even though there are 3.75 times more hymenopteran than dipteran parasitoid species, hymenopteran hosts are restricted to one phylum, Arthropoda, and within that phylum only Insecta are attacked (Morris 1998). One possibility for this vast disparity in host utilization is that, whereas parasitoidism arose once or twice in Hymenoptera (Dowton and Austin 1995b). It probably arose at least 10 to 100 times in Diptera (Eggleton and Belshaw 1992). Evidently, competition for the variety of targeted hosts was much less constrained in Diptera.

Sawflies (Tenthredinoidea, Siricoidea) are the sister-group to the parasitoid clades Orussidae and Apocrita, which represent the single (Gauld and Bolton 1988) or dual (Dowton and Austin 1995b) origins of parasitoidism within Hymenoptera. It appears that the parasitoid condition in Hymenoptera is associated with a founder effect of considerably higher content of adenine and thymine, as opposed to cytosine and guanine, in the mitochondrial DNA of Apocrita wasps, when compared to the AT content of non-parasitoid sawflies of Symphyta, including Orussidae (Dowton and Austin 1995a). This extreme codon bias likely occurred during the Early Jurassic, attributable to a founder event reflective of the parasitoid lifestyle (Dowton and Austin 1995b). Because of this causal link between sequence divergence of mitochondrial DNA and parasitoid life habits (Dowton and Austin 1995a), larval sawflies of Symphyta, the basal-most group, would have gone through a predaceous life habit prior to parasitoidism (Morris 1998). Such a life habit could have been present in enclosed feeders such as gallers (Tenthredinidae) or wood borers (Siricidae), in which a feeding strategy included consumption of arthropod cohabitants, including cannibalism, as a trophic prelude to the parasitoid life habit. Facilitating this nutritional transition to the parasitoid condition would be modification of the rigid, cutting ovipositor of a sawfly into a much longer, flexible, piercing or drilling ovipositor of basal Apocrita (Fig. 11.1f), allowing access to larvae through a few centimeters of hard substrates such as wood (Gauld and Bolton 1988). Hymenoptera transformed their sawfly ovipositor into a singular structure that allowed boring and drilling into considerable depths of plant tissue for inserting eggs on or in target larvae. In the process of ovipositor piercing and drilling into plants, chemicals were injected to soften wood, sclerenchyma and other indurated tissues that allowed attack of larval insects within enclosed plant tissues (Gauld and Bolton 1988; Morris 1998). This structural transformation of the ovipositor is considerably different that the condition in Diptera, the other major clade of parasitoid insects, and accounts for the exceptional reach of hymenopteran parasitoids in targeting host larvae.

Orussoidea are a superfamily of sawflies that either have a sister-clade relationship or are paraphyletic to Apocrita. They are ectoparasitoids of wood wasps such as Siricidae or wood-boring beetles such as Buprestidae in dead wood (Gauld and Bolton 1988; Vilhelmsen and Turrisi 2011). A series of basal Apocrita superfamilies of Stephanoidea, “Ephialtitoidea” (Fig. 11.1f), Megalyroidea and Evanioidea are almost all ectoparasitoids of wood-boring larvae that have an overall geochronologic distribution ranging from Early Cretaceous to Recent (Whitfield 2003; Moghaddam and Turrisi 2018; Li et al. 2018a). Within these superfamilies, several extinct, family-level lineages range from late Early Jurassic to mid Cretaceous and are presumed to have similar biologies based on their phylogenetic position within modern lineages of known biologies. One exception to the exclusive ectoparasitoid habits of Stephanoidea, Megalyroidea, Evanioidea and probably “Ephialtitoidea” is the superfamily Trigonalyroidea in which Trigonalidae is an endoparasitoid on external-foliage-feeding, folivorous larvae (Weinstein and Austin 1991; Engel 2016).

The Proctotrupomorpha, the most diverse, monophyletic clade (*sensu* Castro and Dowton 2006) of parasitoid insects, consists of the apocritan superfamilies Proctotrupoidea, Cynipoidea, Platygastroidea, Chalcidoidea, Mymarommatoidea and Serphitoidea (Table 11.1). In many analyses, Proctotrupomorpha also includes the Ceraphronoidea and Ichneumonoidea (Castro and Dowton 2006); by contrast, in other studies these superfamilies are excluded (Dowton et al. 1997; Sharanowski et al. 2010). (The more encompassing view is taken here.) The next three superfamilies are endoparasitoids, the first two of which, Proctotrupoidea and Cynipoidea, attack a variety of larvae occupying principally soil or wood microhabitats, although some families occasionally occur on rotting meat or attack leaf mining larvae (Askew 1971). The third superfamily, Platygastroidea, attack insect eggs, inhabitants of plant galls and scale insects (Whitfield 2003). The next series of superfamilies—Ceraphronoidea, Mymarommatoidea and Serphitoidea—are ectoparasitoids and endoparasitoids on insect eggs, nymphs, larvae, pupae and puparia of hemimetabolous and holometabolous insects (Clausen 1940; Askew 1971). The Ceraphronoidea and Mymarommatoidea have an Early Cretaceous–Holocene fossil record whereas the extinct Serphitoidea, the only extinct superfamily of hymenopteran parasitoids, ranges from Early Cretaceous to mid Cretaceous. The Ceraphronoidea consists of five families, one of which is the Cretaceous Radiophronidae (Fig. 11.16), an inferred ectoparasitoid on larval insects (Ortega-Blanco et al. 2010).

Chalcidoidea and Ichneumonoidea contain a mix of ecto- and endoparasitoids that include hyperparasitoid and predator taxa. At 20 families, Chalcidoidea represents the greatest family-level diversity of any hymenopteran parasitoid superfamily, known for targeting eggs, nymphs, larvae and pupae, especially of concealed insects in cases, galls, leaf mines, seeds, wood borings and insect nests (Clausen 1940; Askew 1971). When compared to other superfamilies, Chalcidoidea display a

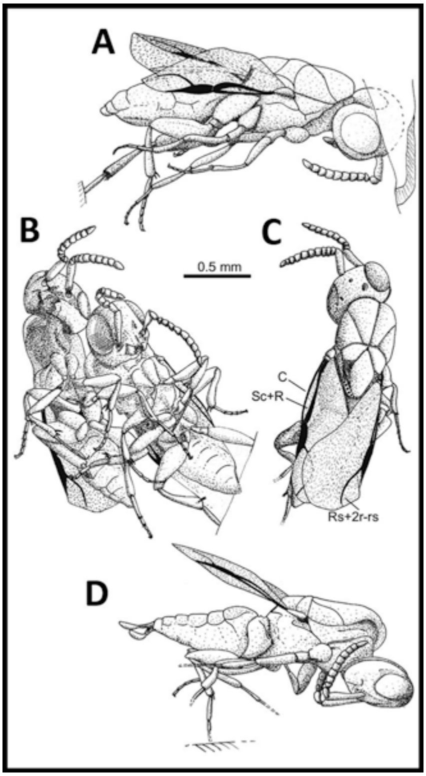


**Fig. 11.16** Camera lucida drawings of the ceraphronoid wasps *Radiophron ibericus* and *R*. aff. *ibericus* (Hymenoptera: Radiophronidae) from the Early Cretaceous Peñacerrada 1 locality of northern Spain (Ortega-Blanco et al. 2010). (**a**) Lateral view of holotype MCNA-8754. (**b**) Ventral view of paratypes MCNA-13030.1 and 13030.2. (**c**) Dorsal view of paratype MCNA-13030.1. (**d**) Lateral view of a male of *Radiophron* aff. *ibericus* gen. et sp. nov. (MCNA-8760). (Reproduced with permission from Fig. 3 in Ortega-Blanco et al. 2010)

more recent geochronologic range, from Cenomanian to the present, mostly represented by Cenozoic first occurrences. One interesting clade, Eucharitidae (eucharitid wasps), are the only insect family to exclusively parasitoidize ants (Lachaud and Pérez-Lachaud 2009), a relationship that represents a conserved association extending to the early Paleogene based on a patterns of ancient colonization of novel hosts and later host tracking (Murray et al. 2013). Ichneumonoidea consist of two families that attack eggs, larvae, pupae and adults of wood borers, but occasionally aphid nymphs and ants; their range is Early Cretaceous to Recent (Poinar Jr 1987). A mid-Mesozoic to Recent member of one of these families, Braconidae, is known to have attacked a weevil of Ithyceridae (Poinar Jr and Shaw 2016), as evidenced by a spent cocoon and an exit hole on its host (Fig. 11.17). Braconidae display a diversification pattern accompanied by numerous host shifts among several insect orders (Shaw 1988).

Aculeate Hymenoptera consist of Chrysidoidea, Vespoidea and Apoidea (Fig. 11.1g) that overwhelmingly are ectoparasitoids, collectively, on all developmental stages of external foliage feeding (Orthoptera, Phasmatodea, Lepidoptera) and piercing-and-sucking (Fulgoroidea, Auchenorrhyncha) insects, as well as beetles, ants and bees (e.g., Fig. 11.1n). A few host specialist lineages parasitoidize atypical hosts of cockroaches, webspinners, solifugids and spiders. An example of a specialist lineage is Sclerogibbidae, a family of Chrysidoidea that are ectoparasitoids (Fig. 11.18) on the nymphs and adults of webspinners (Embioptera), a lineage that extends back to the Early Cretaceous (Engel and Grimaldi 2006).

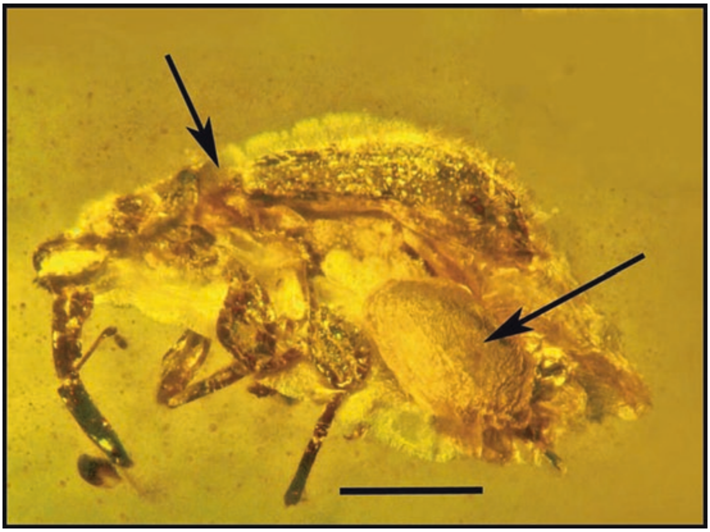


**Fig. 11.17** A New York weevil (Coleoptera: Ithyceridae) attacked by a braconid wasp (Hymenoptera: Braconidae) from Myanmar amber, of transitional Early Cretaceous–Late Cretaceous age (99 Ma). The attached braconid wasp cocoon is indicated by the lower-right arrow, and its larval emergence hole is indicated by the upper-left arrow. Horizontal scale bar is 0.8 mm. (Reproduced with permission from Fig. 1 in Poinar Jr and Shaw 2016)

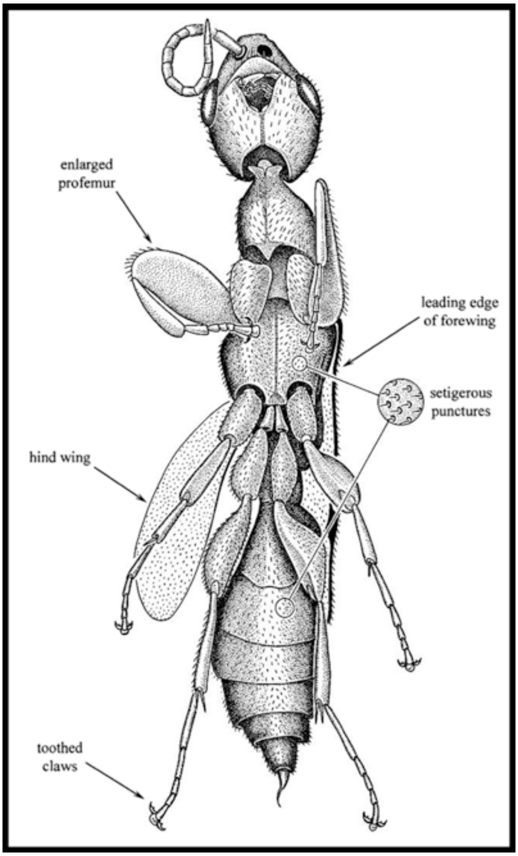


**Fig. 11.18** Ventral view of the habitus of the sclerogibbid wasp *Sclerogibbodes embioleia* (Hymenoptera: Sclerogibbidae), ectoparasitoids of webspinners (Embioptera). (Reproduced with permission from Fig. 2 in Engel and Grimaldi 2006)

The emergence of parasitoidism in aculeates began during the Late Jurassic to Early Cretaceous boundary interval and continued into the Cenozoic. Evolutionary shifts to the parasitoid life habit in Hymenoptera have involved transitions overwhelmingly from mycophagy and to a lesser extent, phytophagy (Fig. 11.4c) (Dowton and Austin 1995a). The origin of parasitoidism from mycophagy involved Orussidae and most Apocrita lineages whereas the shifts from phytophagy or seed predation (Fig. 11.1m) involved principally the chalcidoids Agaonidae, Eulophidae, Pteromalidae, Tanaostigmatidae and Torymidae, in addition to the nutritionally diverse Cynipidae and Apidae (Eggleton and Belshaw 1992). One significant difference between Hymenoptera and Diptera parasitoids involve searching behavior for the target host (Morris 1998). In Hymenoptera, searching behavior is incumbent on the adult wasp, which places its eggs accurately and directly on the host, resulting in minimal movement of the newly hatched larva as it becomes embedded in the host (Askew 1971). A much different mechanism of host searching is found in Strepsiptera and Coleoptera with a host-seeking, active triungulin larva

(Kathirithamby 2009; Beutel et al. 2016). Similarly, in Diptera the eggs are scattered in the general vicinity of the host. Upon hatching, a special, mobile, first-instar larva of the parasitoid, the planidium, searches for the host via various chemical and physical cues (Askew 1971). Three main nutritional regimes are present to which Hymenoptera have shifted from parasitoid ancestors. First, predation was acquired indirectly via larval provisioning of paralyzed hosts by aculeate bees and wasps, or directly from the parasitoid life habit, such as some ichneumonoid wasps (Eggleton and Belshaw 1992). Second, Hymenoptera parasitoid to phytophage transitions occurred in several families that formerly fed on larvae in highly nutritious habitats such as leaf mines and galls, the Cynipidae being the best example (Fergusson 1990). Third, transitions from egg parasitoidism to egg predation are documented in Evaniidae (Askew 1971). Parasitoidism is a widespread life habit in Hymenoptera that is a rich source of secondary predation and phytophagy.

## 11.6 Modern Food Webs and the Mid-Mesozoic Parasitoid Revolution (MMPR)

Much of the ensuing discussion references Fig. 11.19, which documents the diversity of major parasitoid clades and groups from the time of their initial appearance during the late Early Jurassic to their representation in the recent record. The fossil diversity of seven major clades or groups of parasitoids—non-proctotrupomorph Hymenoptera, proctotrupomorph Hymenoptera, aculeate Hymenoptera, non-eremoneuran Diptera, eremoneuran Diptera, Strepsiptera and Coleoptera—record first the establishment of the Mid-Mesozoic Parasitoid Revolution (MMPR) and then the subsequent expansion of parasitoid groups and clades through time. Other clades with rare parasitoid members—Neuroptera, Trichoptera and Lepidoptera—each contain one or two families of parasitoid taxa that are not included because of an insufficient or irrelevant fossil record. The MMPR is a time interval during the late Early Jurassic to late Early Cretaceous (phases 1 and 2) in which bottom-to-top regulation of terrestrial food webs dominated by inefficient clades of predators were replaced by top-to-bottom trophic regulation by considerably more efficient parasitoid clades. After the MMPR, these clades subsequently expanded (phases 3 and 4) as parasitoids became trophically entrenched in terrestrial food webs to the present day. The initial pulse of the MMPR consisted of phases 1 and 2 that represented the earliest occurrences and establishment of most parasitoid lineages in terrestrial habitats from the latest Early Jurassic (Toarcian Stage) to the Early Cretaceous (Albian Stage). Commencing with the Late Cretaceous is the subsequent evolutionary diversification and ecological expansion of parasitoids represented by phases 3 and 4 that continues to the present day.

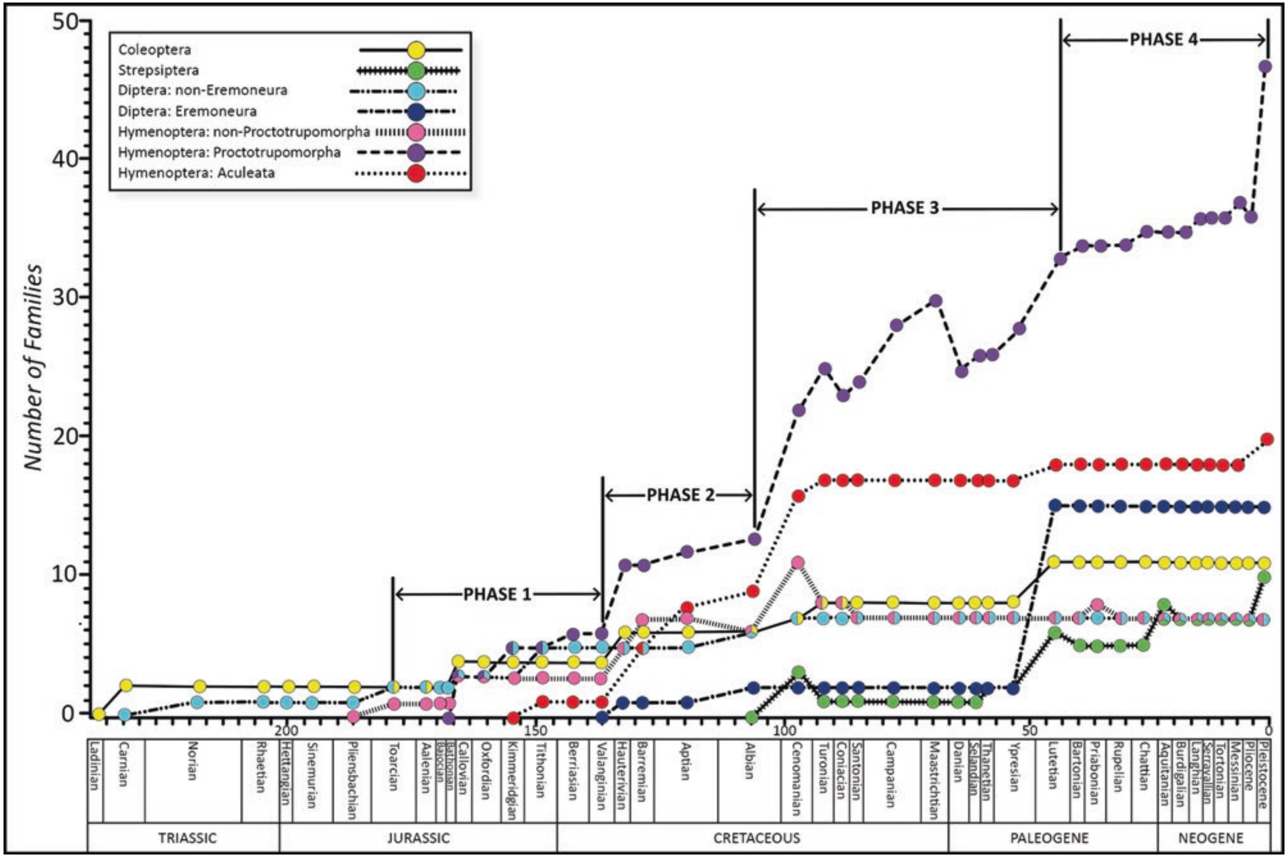


**Fig. 11.19** The Mid Mesozoic Parasitoid Revolution (MMPR) represented by phases 1 and 2, and its subsequent expansion represented by phases 3 and 4. The MMPR is the initial expansion of the parasitoid guild during the mid Mesozoic. Data are taken from Table 11.1. Endpoints for the seven groups of parasitoids at 0 million years indicate modern family-level diversities, equivalent to the Holocene Epoch (not labelled). (Geochronologic scale is taken from Walker et al. 2013)

### *11.6.1 Ovipositors and Host-Seeking First Instar Larvae: Vetting the Parasitoid Taxa*

Among the seven parasitoid clades and groups (Fig. 11.19), evidence for parasitoidism is excellent for non-proctotrupomorph and proctotrupomorph Hymenoptera as well as non-eremoneuran and eremoneuran Diptera. For these four groups, the near certainty of their parasitoid status is attributable to presence of a distinctive female ovipositor or oviscapt whose structure is designed to deposit eggs in or on their arthropod or non-arthropod hosts (Askew 1971). The oviposition of eggs often is accomplished by long ovipositors penetrating through considerable distances or thicknesses of intervening tissue, such as wood in the case of ichneumonid wasps targeting wood-boring larvae through several centimeters of wood (Clausen 1940; Gauld 2008). A second type of evidence is the presence of a highly ambulatory, host-seeking triungulin larva that forms the first larval instar of some Neuroptera, Strepsiptera and Coleoptera, particularly Mantispidae, Ripiphoridae, Meloidae, Bothriderinae of Bothrideridae and all strepsipteran clades, a feature that almost assures a parasitoid designation (Crowson 1981; Evans and Steury 2012). An analogous host-seeking larva, the planidium, exists for many parasitoid Diptera, for example, Mycetophilidae, Nemestrinidae, Acroceridae, Asilidae and Rhinophoridae, that also represents parasitoid status (Eggleton and Belshaw 1992). The confidence level is somewhat lowered for aculeate Hymenoptera, as their ovipositor is modified for stinging and paralyzing prey, rather than necessarily for ovipositing eggs in or on their prey (Gauld and Bolton 1988; Whitfield 2003). However, knowledge of the life histories and biology of modern parasitoid aculeate Hymenoptera provides considerable evidence for assigning an aculeate Hymenoptera fossil species to a predator, parasite or parasitoid. In the case of all fossil Rhipiceridae and all Passandridae (Coleoptera), an assignment to parasitoid status is highly probable, owing to the condition that the modern families are depauperate clades that only possess the single life habit of parasitoidism.

The weakest case for a parasitoid assignment are the remaining, highly speciose families of Carabidae, Staphylinidae and Cleridae in Coleoptera, each of which overall is sparsely represented by extant parasitoid taxa. Depending on the subfamily structure of the fossil occurrences and other parasitoid-relevant information for these three beetle families, a judgement was made regarding whether parasitoids were present for a given lineage occurring in a particular geological stage. For example, nearly all modern parasitoid taxa in Staphylinidae are from Subfamily Aleocharinae (Maus et al. 1998), a subgroup that only extends to the Cenomanian (Cai and Huang 2014; Yamamoto et al. 2016). Parasitoid assignments to Staphylinidae were not made in the absence of Aleocharinae for pre-Cenomanian occurrences and in lieu of evidence for the presence of Aleocharinae only in more recent occurrences. While the full range of parasitoid-bearing families listed in Table 11.1 provides the data for Fig. 11.19, determination of parasitoid presence in the fossil record was more circumspect in the narratives for Sects. 11.6.4–11.6.6 below. It is for this lack of trophic specificity, the lack of evidence from the fossil record, and other reasons of uncertainty that the three beetle lineages did not extend to earlier than the late Early Jurassic (Toarcian Stage), and thus were not considered as parasitoids before the MMPR (Fig. 11.19).

### *11.6.2 The Trophic Cascade and Resource Concentration Hypotheses of Food Webs*

A food web consists of a network of trophic interactions among species that specifically identify the consumers and the consumed within a local community (Loreau 2010; Price et al. 2011). With very few exceptions (e.g., Dunne et al. 2014), well-preserved biotas in the fossil record have not been rigorously analyzed for their food-web structure. For well-preserved biotas, modern or fossil, two competing hypotheses would be important for understanding major changes in food-web trophic structure through geologic time (Matson and Hunter 1992). The first option that describes a food web is the trophic cascade hypothesis (Carpenter et al. 1985; but see Polis and Strong 1996) in which carnivores control herbivores in a local biota, and in so doing regulate plants for consumption by herbivores. The trophic cascade concept often is described as top–down control by higher trophic levels of lower trophic levels. The alternative to the trophic cascade is the resource concentration hypothesis (MacArthur and Levins 1964; Schmitz et al. 2000), in which the trophic structure of plants, herbivores and carnivores is competitively dependent on access of plants to resources that allow for growth. The resource concentration hypothesis frequently is mentioned as bottom–up control by lower trophic levels (autotrophs) of higher trophic levels (Oksanen et al. 1981; Hunter and Price 1992; Power 1992). There is evidence that changes in plant traits, induced by shifts in parasitoid attack, can have major and lasting effects on the food web (Bukovinszky et al. 2008). Both hypotheses have major ecological consequences for the beginnings of parasitoidism during the mid Mesozoic (Fig. 11.19).

The trophic structure of food webs can be affected significantly depending on whether consumption of arthropod prey is conducted by predators or by parasitoids. Compared to predators, parasitoids typically are more speciose, possess greater trophic complexity, have higher host specificities, and their arthropod hosts often remain capable of accommodating additional parasitoid individuals (Lafferty et al. 2006; Price et al. 2011; Dunne et al. 2013). These characteristics indicate that parasitoids are much more efficient, on average, than predators in top–down regulation of the food webs. By contrast, resource limitation to plants often has a negative effect on food-web structure by limiting bottom–up energy available to plants, their herbivores and their consumers (Bukovinszky et al. 2008). A relevant study of this latter phenomenon is the Brussels sprouts (primary producer) to aphid (herbivore) to primary parasitoid (primary consumer) to secondary parasitoid (secondary consumer) food web (Bukovinszky et al. 2008). In this food web (Fig. 11.20), source-plant quality has major, bottom–up, cascading effects across trophic levels that is modulated by the quality and quantity of the resource items for plants, such as nutrients, minerals and sunlight (Bukovinszky et al. 2008). In the study, the particular plant type at the bottom of the food chain was either a wild or a domesticated variety of Brussels sprouts, each variety of which differed considerably in secondary chemistry and morphology. These two varieties of plants affected two species of herbivorous aphids, which were attacked and eventually killed (mummified) by five species of primary parasitoid wasps. These primary parasitoid wasps in turn were attacked and later killed (mummified) by ten species of secondary parasitoid wasps (hyperparasitoids) that belonged to two feeding guilds that differ in how the primary parasitoid host was attacked. The secondary parasitoids also left pupal mummies after emergence from their primary parasitoid host.

The variability in plant quality had major, cascading effects on density-mediated and size-mediated effects of the food web, based on the quality and quantity of resources available to the plant (Fig. 11.20). The wild and the domesticated varieties of the Brussels sprouts plant each had major and different effects on food-web trophic levels. These effects were density (number of individuals), size traits (body size, body architecture, secondary chemistry and leaf thickness), and food-web

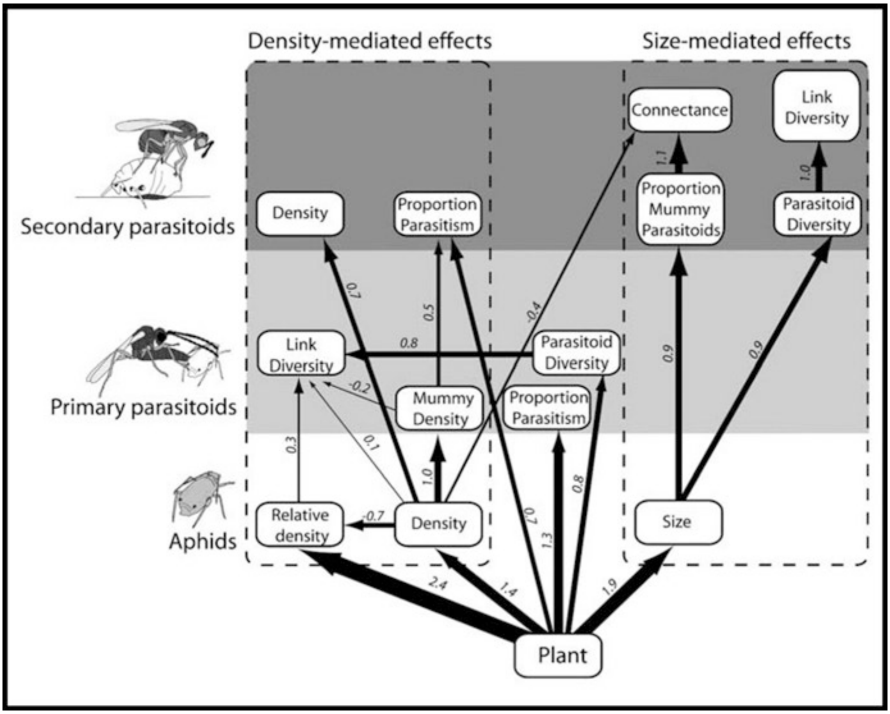


**Fig. 11.20** Summary diagram of direct and indirect effects of plant quality on the structure of aphid-parasitoid communities. Arrow thickness is scaled to standardized coefficients from path analysis to illustrate the relative strength of effects. (Reproduced with permission from Fig. 2 of Bukovinszky et al. 2008)

indices such as connectance (proportion of possible links among all species that are realized) and linkage diversity (feeding links among the species of aphid hosts and the species of their parasitoids) (Bukovinszky et al. 2008). One notable effect was aphid body size on the nonadjacent trophic level of secondary parasitoids. This effect began with larger aphids forming larger mummies that resulted in a greater number and size of mummies in the parasitoid guild, and elevated connectance and linkage diversity, as indicated by arrow widths (Fig. 11.20). This study emphasizes that an increase in plant quality causes bottom-to-up cascades across trophic levels that increase the size and number of herbivores and an abundance of primary and secondary parasitoids. An opposite condition is where a resource limitation, such as scarce availability of plant biomass promotes top-to-bottom regulation of trophic levels within a food web (Hunter and Matson 1992).

### *11.6.3 The Importance of Parasites and Parasitoids in Food Webs*

Rather than examine the trophic structure of food webs as they exist in nature, discussed above, another approach is examination of the effect that the addition of parasites have on food web structure. Whereas insect parasitoids, probably are second only to herbivores as the most common lifestyle frequently included as primary data in food webs, parasites generally are not included (Lafferty et al. 2006). One reason for this is that parasites do not cause the death of their hosts, and their effects would be based on interaction strengths, or measures of the intensity or degree of interactions between two ecologically connected species, which are difficult to assess (Ings et al. 2009). However, within the last decade, parasites increasingly have been included explicitly in food webs (Dunne et al. 2013; Lafferty et al. 2008). Notably, incorporation of parasites in food webs that include predator–parasite and parasite–parasite links approximately doubles the connectance in food webs (Fig. 11.21) and changes other food-web indices. These and other, increased food-web indices include the number of links, nestedness (asymmetry of interactions), chain length (arithmetic average of the lengths of all chains in a food web) and linkage density (Lafferty et al. 2006). These data show that the increase of parasites in food webs may have had a supportive and parallel role in propelling the MMPR that largely was attributable to the evolutionary and ecological diversification of several, related parasitoid clades (Fig. 11.19). Because of the positive effect that parasites (and parasitoids) both have for increased connectance and nestedness in ecosystem stability (Lafferty et al. 2006, 2008), it is quite likely that the MMPR buffered local food-web structure by inserting top–down control of trophic cascades that balanced bottom–up control through resource limitation (Labandeira 2015). One relevant effect of the MMPR shown by the Messel food web study (Fig. 11.22) is that for the Messel lake part of the web, the highest trophic level consumer was a large crocodile. By contrast, the highest trophic level for the Messel forest part of the web was

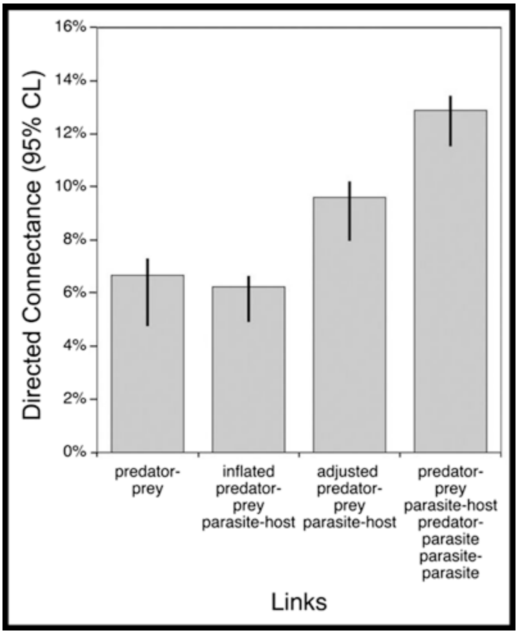


**Fig. 11.21** A comparison of directed connectance (number of potential unidirectional links in a food web that have been realized) with and without parasite links in the Carpinteria Salt Marsh along the California coast. The first bar includes only predator–prey links. The second bar adds observed parasite–host links that may have been incorporated in an inappropriate manner (see Lafferty et al. (2006) for details). The third and fourth bars provide two, different methods for determining how parasites affect directed connectance. The third bar excludes parasite–parasite links. Comparison of the third and fourth bars with the first bar indicates that parasites increase directed connectance in food webs. Error bars represent 95% confidence limits. (Reproduced with permission from Fig. 2 of Lafferty et al. 2006)

a parasitoid fly, which incidentally was one additional trophic level higher than that of the crocodile (Dunne et al. 2014).

### *11.6.4 Top–Down Control of Food Webs by Parasitoids in Modern Ecosystems*

During the past 25 years, an increasing number of studies have demonstrated the consequences that parasitoids have in modern ecosystems (Schowalter 2016). Much of this work has been done with the intricate effects in microcosms of hymenopteran and dipteran parasitoids and their hyperparasitoids on leaf mining and external foliage feeding larvae in tropical food webs (Thompson 1984). One study evaluating host specificity in parasitoids involved a community of 66 parasitoids, 60 predators, 19 herbivores, 5 omnivores, and 3 pathogens associated with broom, *Cytisus*

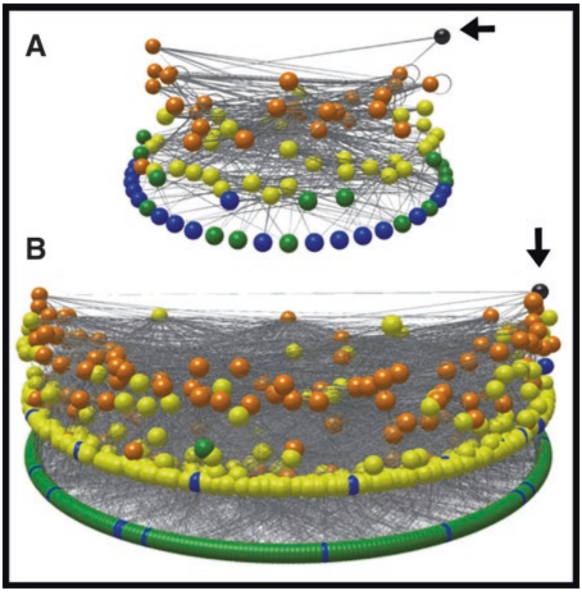


**Fig. 11.22** The Messel lake and forest food webs. (**a**) Lake food web and (**b**) adjacent forest food web. Spheres represent taxa; lines represent feeding links. Links that loop indicate cannibalism. The vertical axis corresponds to short-weighted trophic level (the average of one plus the shortest chain length from a consumer to a basal species and the average of one plus the mean trophic level of all the consumer's trophic resources), with autotrophic taxa and detritus at the bottom level (Williams and Martinez 2004). Images produced with Network3D (Yoon et al. 2004; Williams 2010). Colors of nodes correspond to taxonomic affiliation of species. Green, plants including algae and diatoms; blue, bacteria, fungi and detritus; yellow, invertebrates; orange, vertebrates. The upper arrows refer to the highest trophic level in the lake web, a crocodile (black node); the lower arrow refers to the highest trophic level in the terrestrial web, a hyperparasitoid fly (black node). (Reproduced with permission from Fig. 1 of Dunne et al. 2014)

*scoparius*, at a single site in Berkshire, England (Memmott et al. 2000). This study showed that predators consumed a median of two host species, whereas the median for parasitoids was one host species, indicating greater host specificity for the parasitoids (Memmott et al. 2000). External foliage feeders were more vulnerable than concealed feeders such as leaf miners. The parasitoid sub-webs had considerably lower connectance (higher host specificity) than the predator sub-webs, a feature seen in other studies when parasitoid sub-webs were compared to predator webs (Van Veen et al. 2008). Another measure of parasitoid efficiency concerned a study of a host–parasitoid community in Guanacaste, Costa Rica. In this study (Memmott et al. 1994), leaf-miner host mortality due to parasitoidism varied greatly, but resulted in an overall value of 32.1% of leaf miners succumbing to parasitoids (Memmott et al. 1994).

One important avenue of research has been documenting apparent competition, in which species can interact, or compete, through shared natural enemies such as parasitoids (Holt 1977; Rott and Godfray 2000). In one study of a hyperdiverse community of insects in Belize (Morris et al. 2004), two species of leaf miners, a dipteran and a coleopteran, were removed from a diverse and speciose suite of leaf-mining insects (Fig. 11.23). After the removal of the two species, other species that shared the parasitoids of the removed species experienced lower parasitoid attack rates and increased population densities (Morris et al. 2004), suggesting that apparent competition involving parasitoids is an important feature in structuring tropical insect communities. In another study using a similar ecological context (Bukovinszky et al. 2008), all trophic relationships were examined among a community of aphids, parasitoids and secondary parasitoids in rural England (Müller et al. 1999). The experiment involved 26 species of plants, their 25 species of aphid herbivores, attacked by 18 species of primary parasitoids, and the 28 species of secondary parasitoids—who pursued two different feeding strategies—that attacked them in turn (Müller et al. 1999). The results of this study indicated that, for the 11 webs during the examined period, the ratios of the number of aphid species to number of primary parasitoid species and to the number of secondary parasitoid species were relatively the same across the webs (Fig. 11.24). The ratio of the number of links involving secondary parasitoids and primary aphid parasitoids also was constant across the webs. Quantitative parasitoid overlap graphs for understanding the apparent competition interactions among aphids revealed the robust nature of the indirect links,

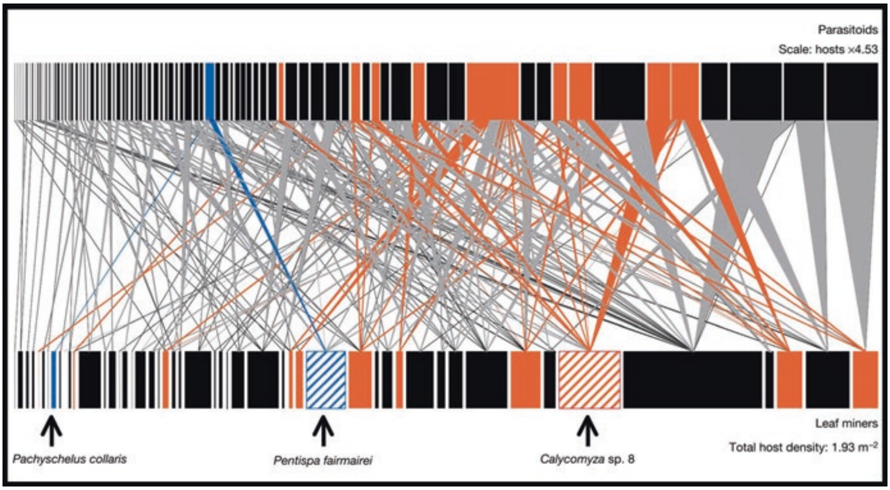


**Fig. 11.23** Quantitative food web (Lewis et al. 2002) showing parasitoid species (top bars), leaf-miner species (bottom bars), trophic links among them, and the species predicted to be affected by a species-removal manipulation. The leafmining fly *Calcomyza* sp. 8 and leaf beetle *Pentispa fairmairei* were herbivore species that were removed. Dipteran leaf-miner species present during the sampling period and predicted to be affected indirectly via parasitoids shared with *Calcomyza* sp. 8 are shown in red. The metallic wood-boring beetle *Pachyschelus collaris* (blue) was also predicted to be affected indirectly by the manipulation through parasitoids that it shares with *P. fairmairei*. Only hosts from which the parasitoids were reared are shown in the web. Bar widths are proportional to species abundance at the study site. (Reproduced with permission from Fig. 1 of Morris et al. 2004)

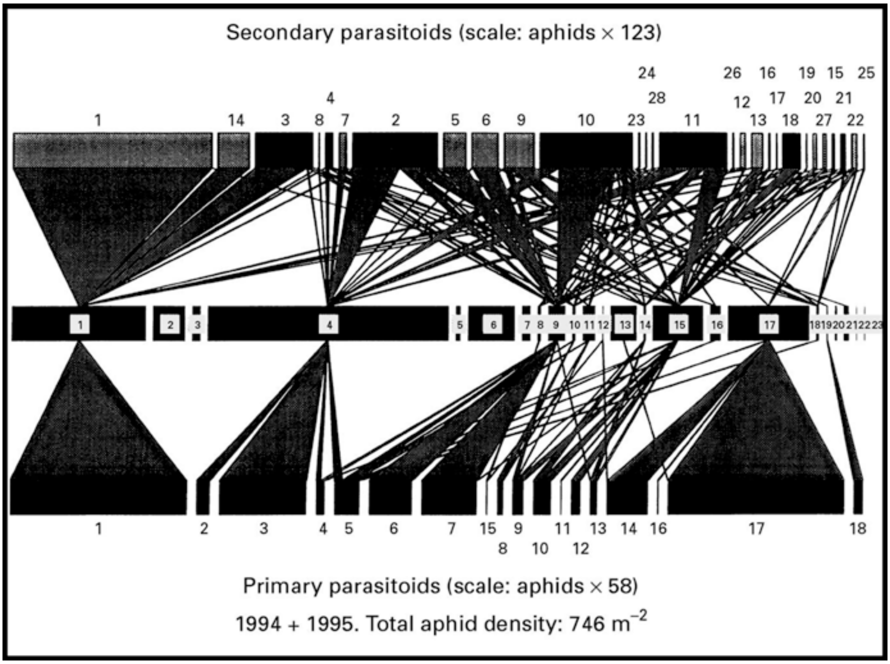


**Fig. 11.24** Summary diagram for describing a complete parasitoid web sampled over 2 years. Relative aphid abundances are shown in the center with primary parasitoids below and secondary parasitoids above. (Hyperparasitoids are in grey and primary parasitoids are in black.) The numbers are the species codes (see Müller et al. 1999). Species densities are shown to scale within each month for aphids and the two categories of parasitoids. See Müller et al. (1999) for a fuller description and interpretation of the web diagrams. (Reproduced with permission from Fig. 4 of Müller et al. 1999)

such that common aphid species shared a few, strong, indirect and mostly asymmetrical links through common primary parasitoids and hyperparasitoids. Both studies (Müller et al. 1999; Morris et al. 2004) and other similar studies (Hirao and Mukrakami 2008; Peralta et al. 2014), indicate that the appearance of parasitoid and hyperparasitoid feeding guilds increases the incidence, extent and efficiency of attack on herbivores, resulting in greater top–down regulation of food webs.

### 11.6.5 *Insect Faunas Before the Mid-Mesozoic Parasitoid Revolution*

Below, four of the most diverse deposits that soon preceded the beginning of the MMPR are discussed, which range from the Middle Triassic–Late Triassic boundary interval (Ladinian–Carnian stages) to the Early Jurassic (Pliensbachian Stage). These deposits originate from disparate locales in Central Asia, South Africa, China and eastern United States. An examination of insect taxa from these deposits reveal the presence of three insect orders—Hymenoptera, Diptera and Coleoptera—that later in the fossil record would contribute the overwhelming bulk of parasitoid taxa (Fig. 11.19). However, it is evident from the taxa in each of the four most diverse deposits of this time interval that parasitoids are absent.

The first deposit is the Madygen Formation, of Ladinian to early Carnian in age, consistent with a date of 237–220 Ma (Walker et al. 2013). Productive sites of the Madygen Formation are located in the Fergana Valley where the frontiers of Tajikistan, Kyrgyzstan and Uzbekistan complexly intersect (Shcherbakov 2008). The principal localities are from the Dzhailyoucho area that consisted of an extensive Triassic lake deposit. No parasitoid insects are known. The relevant taxa are Hymenoptera containing sawflies of the Xyeloidea (Xyelidae), and Diptera that are represented only by the nematocerous taxa of Tipulomorpha (Limoniidae, †Vladipteridae), Psychodomorpha (†Nadipteridae, †Hennigmatidae) and Bibionomorpha (†Protorhyphidae) (Shcherbakov 2008). The second deposit is the Molteno Formation, which is slightly younger and is centered in the early Late Triassic Carnian Stage, approximately 237–228 Ma (Walker et al. 2013), although accurate age dates have not been determined from radioisotopic age dating. All 106 documented Molteno localities (Labandeira et al. 2018) originate from outcrops of the Karoo Basin, mostly in South Africa that surround Lesotho. The major localities are lake deposits such as Aasvoëlberg 411 and Birds River 111 (Anderson and Anderson 2003). No parasitoid taxa are known (Riek 1974). The only Hymenoptera known is a probable sawfly of Xyelidae (Schlüter 2000), and Diptera are absent from the Molteno Formation (Anderson and Anderson 1993; Labandeira et al. 2018).

The second and third localities, from the Late Triassic localities to Triassic–Jurassic boundary interval display no evidence for Hymenoptera, an increased diversity of non-parasitoid Diptera, and the presence of non-parasitoid Coleoptera, all of which indicate that the MMPR was in the future. The third deposit are the related Beishan Formation and Shangtu Formation of Jilin and Hebei provinces, respectively, which are of Late Triassic age (Rhaetian Stage), corresponding to an age date of 209–201 Ma (Walker et al. 2013), although historically the position of these deposits in the latest Triassic to earliest Jurassic continuum have been contentious (Lin 1982, 1986). There are several localities within each of these two formations have produced fossil insects from moderately diverse assemblages (Lin 1982, 1986; Grimaldi and Engel 2005a). Hymenoptera is absent; Diptera is represented by the nematocerous groups of Tipulomorpha (†Eolimnobiidae, Limoniidae) and Bibionomorpha (†Pleciofungivoridae), and Coleoptera consist of taxa that lack known parasitoid members in the later Mesozoic and Cenozoic faunas (Lin 1982, 1986). Parasitoid taxa have not been discovered.

The fourth deposit is the Cow Branch Formation of the Martinsburg area along the North Carolina–Virginia state border in the eastern United States. The Cow Branch Formation is Late Triassic (Rhaetian Stage) to Early Jurassic (Hettangian Stage) in age, equivalent to 209–199 Ma (Walker et al. 2013). The specific, major locality yielding the fossils is the Solite Quarry, which is one segment of a series of rift basins throughout the east coast of North America that are represented by very fine-grained shales (Grimaldi and Engel 2005a). The Solite Quarry has not yielded Hymenoptera. However, Diptera are diverse compared to other Late Triassic to earliest Jurassic intervals, consisting of the nematocerous Tipulomorpha (†Vladipteridae, Limoniidae), Psychodomorpha (Psychodidae, †Eoptychopteridae, an undetermined family), Culicomorpha (†undetermined family), Bibionomorpha (†Procramptonomyiidae, †Protorhyphidae, †Paraxymyiidae, †Crossaphididae), and stem-group Brachycera (†Prosechamyiidae; Blagoderov et al. 2007). Although the undetermined family of Culicomorpha could have been a parasite as a blood feeder (Fig. 11.8; Blagoderov et al. 2007), all other evidence from subsequent fossil lineages and modern biology would disallow a parasitoid interpretation for this culicomorph. The Solite Coleoptera includes Staphylinidae (Fraser et al. 1996), a rove beetle, which almost certainly did not belong to a subclade such as the Aleocharinae that includes modern parasitoid members (Klimaszewski 1984).

### *11.6.6 Insect Faunas During the Mid-Mesozoic Parasitoid Revolution*

Four of the most informative insect faunas for documenting the initial expansion interval of the MMPR during phases 1 and 2 range from the latest Middle Jurassic (late Callovian Stage) to the mid Early Cretaceous (mid Albian Stage), before the shift from phase 2 to phase 3. The deposits, from oldest to youngest, originate from northeastern China, south-central Kazakhstan, southern England in the United Kingdom, and back to northeastern China. Insect taxa from these four deposits collectively exhibit (1) the first appearances and diversification and ecological expansion of non-proctotrupomorph and proctotrupomorph hymenopteran parasitoids; (2) to a lesser extent, the expansion of non-Eremoneura Diptera and Coleoptera; and (3) the modest beginnings of the Aculeata Hymenoptera and perhaps Strepsiptera diversifications. The oldest Early Cretaceous amber deposits such as Lebanese and Álava amber are undoubtedly extensions of Phase 2 of the MMPR, but their parasitoid faunas remain largely unstudied. By the end of phases 1 and 2 of the parasitoid diversification events, six of the seven major clades of parasitoids were established; the exception was Strepsiptera.

The first two insect faunas are Jurassic in age and they provide documentation for diversification of the earliest lineages of parasitoids. The first fauna is from the Jiulongshan Formation, representing the Yanliao Biota, and located in the Daohugou area where the three provinces of Liaoning, Hebei and Inner Mongolia come together (Ren et al. 2010a; Huang 2016). The age of the Yanliao Biota is 165 Ma, based on secure radioisotopic age dates (Ren et al. 2010b; Huang et al. 2016), and equivalent to the late part of the Callovian Stage (Walker et al. 2013). Yanliao fossils occur mostly in medium to dark hued tuffaceous siltstones that were deposited in fluvial and geographically extensive lacustrine environments (Ren et al. 2010b). By the time the Jiulongshan Formation was deposited, there is evidence for the commencement of a major evolutionary expansion of hymenopteran parasitoid lineages. Probable parasitoids of Neuroptera consisted of one family, Mantispidae, with two genera and two species. Possible parasitoid taxa of Coleoptera may have been present, representing two families, Staphylinidae and Ripiphoridae, four genera and four species (Tan et al. 2010), indicating that beetles were a very minor component of the parasitoid guild. For Staphylinidae, there is no evidence that any subfamilies known to house parasitoid taxa, such as Aleocharinae, were present during the late Middle Jurassic. Dipteran parasitoid taxa were less diverse, consisting of Nemestrinimorpha (Nemestrinidae) and Eremochaetidae representing two families, five genera and eight species (Zhang et al. 2017; Ren et al. 2019), marking the early presence of dipteran parasitoids in the MMPR. Well-represented hymenopteran taxa include a diversity of plant-associated sawflies ("symphytans") that are placed in the superfamilies Xyeloidea (Xyelidae, †Daohugoidae), Tenthredinoidea (†Xyelotomidae), Pamphilioidea (†Xyelydidae), Cephoidea (†Sepulcidae), Siricoidea (Anaxyelidae, Siricidae), and the parasitoid Orussoidea (†Karatavitidae) that shares a sister-group relationship with parasitoid Apocrita. Apocritan parasitoids occur in the three superfamilies Evanioidea (†Anomopterellidae, †Praeaulacidae), Ephialtitoidea (†Ephialtitidae) and Proctotrupoidea (Heloridae, †Mesoserphidae, Pelecinidae, Roproniidae) that collectively account for approximately 15 genera (Rasnitsyn and Zhang 2004, 2010; Gao et al. 2010; Huang and Cai 2016; Li et al. 2018a; Wang et al. 2019; Table 11.1). This distribution of hymenopteran parasitoid families indicates that eight major, family-level lineages of orussoid sawflies and apocritan parasitoid wasps were present, extending into the basal Proctotrupomorpha superclade during Yanliao time (Fig. 11.19). The Jiulongshan Formation probably represents the earliest, most extensive sample of Phase 1 of the MMPR of any biota worldwide.

The second major insect fauna is the Karabastau Formation, representing the Karatau Biota, located along the Karatau Range, near the towns of Aulie (formerly Mikhailovka) and Uspenovka (formerly Galkino) in southern Kazakhstan, and considered Late Jurassic in age. Because of the multiple localities representing multiple stratigraphic horizons at Karatau, the deposits are assigned to a time range that includes the Oxfordian and Kimmeridgian stages (Rasnitsyn and Zherikhin 2002), corresponding to 164–152 Ma (Walker et al. 2013), making the Karatau Biota seven million years younger, on average, than the Yanliao Biota. The insect fossils occur in dark grey shales that preserve detail such as wing eyespots, delicate surface ornamentation and fine hairs on body surfaces (Rohdendorf 1968a; Grimaldi and Engel 2005a). Neuroptera consists of only one genus and species of Mantispidae. Concerning the parasitoid taxa, Coleoptera consisted of 2 families, Staphylinidae and Anthribidae, consisting of 10 genera and 12 species, although Staphylinidae at Karatau have not been assigned to the extant parasitoid subfamily Aleocharinae (Tichomirova 1968; Yu et al. 2019), which contains many modern parasitoid species (Klimaszewski 1984). Parasitoid Diptera include Nemestrinimorpha (Nemestrinidae and Acroceridae) and Archisargoidea (Eremochaetidae), consisting of 3 families, 8 genera and 16 species of potentially parasitoidic flies (Rohdendorf 1968b; Mostovski 1998; Zhang et al. 2016) (Table 11.1) comparable in diversity to that of the Yanliao

Biota. No evidence exists for parasitoid Strepsiptera, Trichoptera or Lepidoptera. Hymenoptera included a similar spectrum of sawflies (Rasnitsyn 1968) and parasitoid lineages that were more diverse than those in the Yanliao Biota. The hymenopteran parasitoid lineages include the parasitoid sawfly Orussoidea (†Karatavitidae), and parasitoid wasps Ephialtitoidea (†Ephialtitidae), Megalyroidea (Megalyridae), Evanioidea (†Anomopterellidae, †Praeaulacidae), Proctotrupoidea (Heloridae, †Mesoserphidae) and the basal aculeate lineage Chrysidoidea (†"Bethylonymidae") (Kozlov 1968; Rasnitsyn 2002) (Table 11.1). The same number of eight, family-level lineages of hymenopteran parasitoids was present in the Karatau Biota as in the Yanliao Biota, but with two family substitutions and a doubling of species to approximately 30, indicating evolutionary stability at the family level but an increased proliferation of species. In general, it appears that parasitoids of the Karatau Biota represent continued stability of major parasitoid lineages when compared with the Yanliao Biota, but increased generation of genera and species at lower taxonomic levels.

The third insect fauna considered during the initial expansion of the MMPR comes from the Lulworth Formation, constituting the lower unit of the Purbeck Limestone Group, and its upper unit, the Durlston Formation, which crop out along the Vale of Wardour area in Dorset, southern England (Rasnitsyn et al. 1998; Coram et al. 2000; Coram and Jepson 2012). The age of the Purbeck strata is earliest Cretaceous (Berriasian Stage), with a corresponding age date of 145–139 Ma (Walker et al. 2013), and is approximately 16 million years younger than the Karatau Biota. The strata of the Purbeck Biota containing the insect fossils consist of fine-grained, mostly thinly bedded limestone occasionally interrupted by algal mat layers (Coram 2003). Parasitoid-containing lineages of Neuroptera, Coleoptera, Strepsiptera, Diptera, Trichoptera, and Lepidoptera are absent. However, as in the preceding two fossil units, a near full complement of sawflies is present, excluding the Orussoidea—the only parasitoid sawfly clade. Apocritan wasps consist of Megalyroidea (Megalyridae), Evanioidea (cf. Aulacidae, †Baissidae, †incertae sedis), Proctotrupoidea (Diapriidae, Proctotrupidae), Ichneumonoidea (Ichneumonidae), the aculeate lineages Chrysidoidea (†"Bethylonymidae") and Apoidea (Sphecidae), and the undetermined apocritan *Apocrites* (Coram and Jepson 2012) (Table 11.1). Including unassigned but distinctive lineages, there are 10 family-level lineages of hymenopteran parasitoids representing about 20 species in the Purbeck Biota.

The Yixian Formation is the fourth insect fauna that highlights Phase 2 of the MMPR (Fig. 11.19). Fossils from the Yixian Formation formed the distinctive Jehol Biota that originate from seven or eight major, fossil-yielding localities, mostly in Liaoning Province of northeastern China, west of Beipiao City and near Liaodong Bay, an arm of the Yellow Sea (Zhang et al. 2010). Although once controversial (Ren et al. 2010b), the date currently is established as mid Early Cretaceous, from 126 to 122 Ma (Swisher III et al. 1999), equivalent to late Barremian to early Aptian in age (Walker et al. 2013), and approximately 18 million years younger than the Purbeck Biota. The fossils occur in broad outcrops of lake deposits with light-colored, highly oxidized, fine-grained mudstone and siltstone strata of buff-colored tuffaceous shales (Ren et al. 2010b). Neuroptera consists of seven genera and nine species of Mantispidae. Potentially parasitoid Coleoptera consisted of 2 families, Staphylinidae and Carabidae, accounting for 21 genera and 37 species (Yu et al. 2019). The overwhelming majority of the beetles were Staphylinidae, although subfamily placement is tricky (Tan et al. 2010). Parasitoid Diptera include Nemestrinimorpha (Nemestrinidae) and Eremochaetidae, consisting of two families, six genera and ten species (Han et al. 2019), generally consistent with the values from the earlier Karatau and Yanliao biotas. For Hymenoptera, the several, major, symphytan lineages detailed in the previous three biotas are repeated in the Jehol Biota. Hymenopteran parasitoid lineages are Ephialtitoidea (†Ephialtitidae), Evanioidea (Aulacidae, †Baissidae, Evaniidae, †Praeaulacidae), Proctotrupoidea (†Mesoserphidae, Heloridae, Pelecinidae, Roproniidae, Serphidae), Ichneumonoidea (Ichneumonidae), and the aculeate Chrysidoidea (†"Bethylonymidae") and Vespoidea (Scoliidae) (Table 11.1). The increase to 13 hymenopteran families of the Jehol Biota from the 8 or 9 occurrences from the previous three biotas is significant. In addition, the presence of approximately 60 Jehol species assigned to the 13 families triples the species from the Purbeck Biota, which consist of about 20 species allocated to 9 families. The Jehol data indicate that there was a quantitative increase in the numbers of parasitoid families and species from Phase 1 to Phase 2 of the MMPR.

### *11.6.7 Insect Faunas After the Mid-Mesozoic Parasitoid Revolution*

After phases 1 and 2 established the MMPR, Phase 3 increased the upward trend by adding a considerable number of families of two lineages: proctotrupomorph Hymenoptera and aculeate Hymenoptera (Fig. 11.19). During Phase 3, the trend lines for all other lineages remained at the same relative levels as they did for Phase 2. In Phase 4, there were increases of families in proctotrupomorph Hymenoptera, eremoneuran Diptera, Coleoptera and the earliest occurrence of valid Strepsiptera; the levels of other lineages essentially held flat. These differences in representation of the seven parasitoid lineages in phases 3 and 4 can be gleaned from four diverse insect faunas that strategically sample every few tens of millions of years the Late Cretaceous and Paleogene.

Some of these trends may be conditioned by taphonomic style, in which the history of the parasitoid fossil record is very asymmetric. Because of the relative hard boundary of no biologically significant amber deposits occurring before approximately 135 million years ago (Labandeira 2014a), deposits before, during and after the MMPR have a differing taphonomic cast, from which the primary data originates. Deposits prior to the MMPR—Madygen (237–220 Ma), Molteno (237–228 Ma), Beishan–Shangtu (209–201 Ma) and Cow Branch biotas (209–199 Ma)—consist only of compression-impression fossils. Deposits during the MMPR—the Yanliao (165 Ma), Karatau (approximately 158–156 Ma), Purbeck

(154–139 Ma) and Jehol (125 Ma) biotas—also contain compression fossils, although during this time the first appearance of major amber deposits such as Lebanese amber (130–120 Ma) (Maksoud et al. 2017) and Spanish Álava Amber (112–104 Ma) occur (Peñalver and Delclòs 2010; Azar et al. 2010). By contrast, insect faunas deposited after the MMPR—Myanmar Amber (99 Ma), Canadian Amber (79–78 Ma), Messel (48 Ma) and Dominican Amber (20.5 Ma) biotas—incorporated more amber material. Consequently, this difference between deposits before and after the MMPR imparted a distinctive preservational trend. Because of this distribution of compression–impression versus amber deposits, there are different taphonomic qualities imparted to each of these 12 deposits. Advantages of compression deposits are: (1) a greater temporal completeness compared to amber deposits that are absent from deposits older than about 135 million years; (2) fossils occurring on rock slabs typically with expansive two-dimensional surfaces; and (3) representation of a range of ecosystems, such as those from fluvial, lacustrine, deltaic and swamp environments (Labandeira 2014a). Advantages of amber deposits are: (1) typically a significantly higher quality or preservation; (2) good availability of trophic data to understand inter-organismic relationships and food webs; and (3) elevated documentation of pathogens, parasites, parasitoids and evidence for disease that rarely are found in compression–impression deposits (Labandeira 2014a; Poinar 2021). Although these two, major modes of preservation are different, they are nevertheless complimentary; for example, amber deposits preserve small to miniscule insects that would rarely be preserved in compression deposits. Compression and amber deposits jointly provide a much more accurate of the fossil record than would their individual representations.

The first major insect fauna of Phase 3 is Myanmar Amber originating in Kachin State, in the Myitkyina and Upper Chindwin Districts along the Hukawng Valley of northern Burma (Cruikshank and Ko 2003). The lithostratigraphic context of Myanmar Amber is still poorly known, although the amber comes from lignite layers interbedded with thin strata of sandstones, siltstones, shale and micritic limestone (Zherikhin and Ross 2000). Source trees of most of Myanmar Amber are the gymnospermous Araucariaceae (*Agathis*) and angiospermous Dipterocarpaceae, which have yielded a lowermost Late Cretaceous radioisotopic date of approximately 99 Ma, equivalent to the early interval of the Cenomanian Stage (Shi et al. 2012) and approximately 23 million years more recent than the Jehol Biota. Myanmar Amber contains a diverse insect biota (Rasnitsyn and Ross 2000; Ross et al. 2010; Ross 2018 and updates). The single neuropteran parasitoid taxon of Myanmar Amber is Hemerobioformia (Mantispidae). Coleopteran parasitoid taxa were Caraboidea (Carabidae), Staphylinoidea (Staphylinidae), Cleroidea (Cleridae), Cucujoidea (Passandridae), Tenebrionoidea (Meloidae, Ripiphoridae) and Curculionoidea (Anthribidae). Strepsipteran parasitoids were Protostrepsiptera (†Phthanoxenidae, †Cretostylopidae), Eleostrepsiptera (†?Mengeidae) and Neostrepsiptera (†Kinzelbachillidae). The single, possible, trichopteran parasitoid taxon is Hydroptilidae. Dipteran parasitoid taxa consisted of Nemestrinimorpha (Acroceridae, Nemestrinidae), Archisargoidea (†Eremochaetidae), Asiloidea (Asilidae, Bombyliidae), Empidoidea (Empididae) and Aschiza (Phoridae, Pipunculidae). Also diverse were hymenopteran parasitoid taxa that consisted of Stephanoidea (†Aptenoperissidae, †Myanmarinidae, Stephanidae), Megalyroidea (Megalyridae), Trigonalyroidea (†Mametshidae), Evanioidea (Aulacidae, Evaniidae, Gasteruptiidae, †Othniodellithidae, †Praeaulacidae), Proctotrupoidea (Austroniidae, Diapriidae, Heloridae, Pelecinidae, †Peleserphidae, †Spathiopterygidae), Platygastroidea (Platygastridae, Scelionidae), Ceraphronoidea (Ceraphronidae, Megaspilidae, †Stigmaphronidae), Mymarommatoidea (†Gallorommatidae, Mymarommatidae), Serphitoidea (†Serphitidae), Chalcidoidea (Chalcidae, indeterminate family, Mymaridae), Ichneumonoidea (Braconidae, Ichneumonidae), and the aculeate Chrysidoidea (Bethylidae, Chrysididae, Dryinidae, Embolemidae, Scolebythidae), Vespoidea (Pompilidae, Rhopalosomatidae, Sapygidae, Sierolomorphidae, Tiphiidae, Vespidae) and Apoidea (Crabronidae, Sphecidae) (Grimaldi et al. 2002; Ross et al. 2010; Engel et al. 2012a; Cai and Huang 2014; Cai et al. 2017, 2018; Li et al. 2017a, b, 2018a, b; Ross 2018 and updates) (Table 11.1). Parasitoid Hymenoptera in the Myanmar Biota numbers 42 families, representing a third more than that of the earlier Jehol Biota. There are approximately 90 hymenopteran species, about an increase of three times that of the Jehol Biota. The Myanmar Biota represents a considerable expansion in the number of parasitoid species, indicating that these deposits record a major parasitoid diversification event following Phase 2 but before deposition of the Myanmar Biota (Fig. 11.19). However, some of this increase in Myanmar parasitoid diversity could be attributable to exceptional preservation and a concerted effort to mine, process and expand tonnages of material sold abroad (Sokol 2019).

The second major deposit of note, also representing Phase 3, is Canadian Amber, originating from Grassy Lake in southern Alberta, but also occurring at Cedar Lake in western Manitoba where it is secondarily deposited (McKellar and Wolfe 2010). The stratigraphic source of the amber at Grassy Lake are six sub-bituminous coal seams of the Foremost Formation (Pike 1995) that have a late Campanian age, approximately equivalent to 78–72 Ma (Walker et al. 2013), about 24 million years after deposition of Myanmar Amber. The source of the amber initially was thought to be araucariaceous, but plant anatomical and spectroscopic analyses indicate a cupressaceous origin, in particular the tree *Parataxodium* (McKellar et al. 2008). Potential parasitoid taxa of Coleoptera are Caraboidea (Carabidae), Staphylinoidea (Staphylinidae), and Cleroidea (Cleridae). One, unidentified, triungulin larva unassignable to family (Skidmore 2018) represents a parasitoid Strepsiptera. Dipteran parasitoid taxa are still relatively modest compared to earlier occurrences, consisting of taxa in Bibionomorpha (Cecidomyiidae, Mycetophilidae), Asiloidea (Bombyliidae), Empidoidea (Empididae) and Aschiza (Phoridae). No parasitoid taxa of Neuroptera, Trichoptera or Lepidoptera are present. For Hymenoptera, the parasitoid lineages are Evanioidea (Aulacidae), Trigonalyroidea (Mametshidae), Proctotrupoidea (Diapriidae, Proctotrupidae), Cynipoidea (Figitidae, Liopteridae), Platygastroidea (Platygastridae, Scelionidae), Ceraphronoidea (Ceraphronidae, Megaspilidae, Stigmaphronidae), Mymarommatoidea (Mymarommatidae), Serphitoidea (†Serphitidae), Chalcidoidea (Eulophidae, Eupelmidae, Mymaridae, Rotoitidae, Tetracampidae, Torymidae, Trichogrammatidae), Ichneumonoidea (Braconidae, Ichneumonidae) and the aculeate Chrysidoidea (Bethylidae, Chrysididae, Dryinidae, Scolebythidae) and Apoidea (Sphecidae) (Carpenter et al. 1937; Evans 1969; Yoshimoto 1975; Poinar Jr and Huber 2011; Perrichot et al. 2011; McKellar and Engel 2011a, b, 2012, 2014; McKellar et al. 2013; Engel et al. 2013c; Skidmore 2018) (Table 11.1). Parasitoid Hymenoptera consists of 27 families and 112 described species in Canadian Amber, representing somewhat fewer families but a greater number of species than that of Myanmar Amber. The parasitoid wasp fauna from Canadian Amber houses very few extinct lineages and the first documented occurrences of some modern parasitoid lineages, reflecting a relatively flat level of diversity during the middle of Phase 3, after the MMPR (Fig. 11.19), but with evident taxonomic turnover.

The third deposit toward the end of Phase 3 is Messel, in Hesse, western Germany, and consists of a maar lake resulting from a deep, explosive eruption of rhyolitic magma that formed a deep depression subsequently infilled by sediment (Lorenz and Kurzlaukis 2007). The resulting small lake trapped microorganisms, plants, insects and vertebrates that were excellently preserved (Dunne et al. 2014). The sediments consist of an oil shale that contain fossils entombing a wealth of micromorphological detail, including leaf cuticle, differential hues representing original color patterns, insect setae and other delicate features (Felder and Harms 2004). The Messel Biota was ecologically characterized in a food-web study, consisting of approximately 700 biological species or trophic groups, and the resulting, highly resolved food web (Fig. 11.22) was constructed for the full ecosystem and the separate lake and terrestrial sub-ecosystems (Wedmann 2005; Dunne et al. 2014). The parasitoid community of the Messel Biota is well established (Dunne et al. 2014; Labandeira and Dunne 2014) from both the primary literature and its ecological context in the associated DRYAD data (Labandeira and Dunne 2014). A single parasitoid species represents Hemerobioformia (Mantispidae), and coleopteran parasitoids consisted of Caraboidea (Carabidae), Staphylinoidea (Staphylinidae), and Scarabaeoidea (Scarabaeidae). The sole Strepsiptera parasitoid is Neostrepsiptera (Myrmecolacidae). The Diptera parasitoids were Culicomorpha (Chironomidae), Bibionomorpha (Cecidomyiidae), Nemestrinimorpha (Nemestrinidae) and Muscomorpha–Asiloidea (Asilidae). The Hymenoptera provided the overwhelming bulk of parasitoid taxa, consisting of Proctotrupoidea (family indeterminate), Chalcidoidea (Chalcididae, Eucharitidae, Eulophidae, Torymidae), Ichneumonoidea (Braconidae, Ichneumonidae), the aculeate Vespoidea (Pompilidae, Scoliidae, Tiphiidae), and Apoidea (Sphecidae) (Dunne et al. 2014). The hymenopteran parasitoids of the Messel Biota consisted of 11 families and 12 species. For such a diverse ecosystem, this is a modest account of parasitoidism for the Messel Biota towards the end of Phase 3 (Fig. 11.19). Nevertheless, in the food web analysis

(Dunne et al. 2014; Labandeira and Dunne 2014), the highest trophic level in the forest web was a parasitoid fly (Wedmann 2007) (Fig. 11.22).

Dominican Amber is the fourth and last deposit after the MMPR to be examined. Dominican Amber originates from the Cordillera Septentrional, the northwest–southeast trending mountain axis along the Cordillera Oriental that parallels the coast of the Dominican Republic (Penney 2010). The amber is associated with lignite seams that are interspersed among sandstone and occasionally siltstone in the La Toca and Yanigua Formations that represent environments close to sea level that subsequently have been uplifted and deformed (Iturralde-Vinent and MacPhee 1996). The age of Dominican Amber has been controversial for the past 35 years. Based on a variety of techniques, the age of Dominican Amber is now usually considered as lower Miocene (Grimaldi 1996; Iturralde-Vinent 2001; Penney 2010), equivalent to 16–23 Ma (Walker et al. 2013). The midpoint of this range is about 21 Ma, which is the often-used age of Dominican Amber. The source of the amber is the extinct species of the tree *Hymenaea protera* (Fabaceae), whose leaves, stipules, buds, flowers and pollen are often found dispersed within the amber. The Dominican Amber Biota constitutes one of the most diverse and abundant amber biotas known, and contains a broad spectrum of insect taxa (Arillo and Ortuño 2005; Penney 2010; Poinar Jr 2010). A parasitoid-bearing lineage of Neuroptera is Hemerobioformia (Mantispidae) and Coleoptera that contributed two parasitoid-bearing groups: Staphylinoidea (Staphylinidae) and Tenebrionoidea (Ripiphoridae). Strepsipteran parasitoids were Neostrepsiptera consisting of Bohartillidae, Elenchidae, Myrmecolacidae and Protelencholacidae. Parasitoid-bearing dipteran lineages are Culicomorpha (Chironomidae), Bibionomorpha (Mycetophilidae), Nemestrinimorpha (Acroceridae), and in Muscomorpha: Asiloidea (Asilidae), Empidoidea (Empididae), Aschiza (Phoridae, Pipunculidae) and Schizophora (Muscidae, Tachinidae). For Trichoptera, the sole parasitoid-bearing lineage, Hydroptilidae, is present. Similarly, the obligately parasitoid lineage of Lepidoptera, Zygaenoidea (Epipyropidae), has been recorded. Hymenopteran parasitoid-bearing lineages were the most abundant compared to the seven preceding biotas and contained many major elements of the MMPR. These elements were Orussoidea (Orussidae), Evanioidea (Evaniidae), Platygastroidea (Platygastridae, Scelionidae), Ceraphronoidea (Ceraphronidae), Chalcidoidea (Encyrtidae, Eulophidae, Eupelmidae, Leucospidae, Mymaridae, Pteromalidae, Torymidae), Ichneumonoidea (Braconidae), and the aculeate Chrysidoidea (Bethylidae, Chrysididae, Dryinidae, Sclerogibbidae, Scolebythidae), Vespoidea (Mutillidae, Pompilidae) and Apoidea (Crabronidae, Sphecidae) (Arillo and Ortuño 2005; Engel 2008b; Penney 2010; Poinar Jr 2010) (Table 11.1). The diversity of parasitoid-associated hymenopteran families in the Dominican Amber Biota is 22 families and 94 species, a considerable increase over the Messel Biota but very roughly comparable to the earlier Canadian and Myanmar amber biotas. It appears that the Dominican Amber Biota is positioned in the middle of a plateau of parasitoid diversity representing the 40 million-year-long interval from the middle Eocene (Lutetian Stage) to the late Miocene (Messinian Stage).The parasitoid guilds have a very modern cast, and notably none of the family-level lineages are extinct.

## 11.7 Parasitoid Clade Diversification in the Early Mid-Mesozoic Parasitoid Revolution

The beginning of the MMPR was mentioned informally as long ago as the mid twentieth century by Carpenter (1954) who recognized the significance of Middle Jurassic wasps with very long ovipositors. The Mid-Mesozoic Parasitoid Revolution (MMPR) is defined as consisting of phases 1 and 2, from the Early Jurassic (Toarcian Stage) to the Early Cretaceous (Albian Stage), which constituted the core of the parasitoid expansion. This period is the MMPR. Phases 3 and 4, from the Cenomanian Stage to the present, is considered the subsequent, post-MMPR expansion, whose diversities for some clades or groups remained flat (Hymenoptera–Aculeata, non-proctotrupomorph Hymenoptera, non-eremoneuran Diptera) whereas for others there were substantial diversity increases (Hymenoptera–Proctotrupomorpha, Diptera–Eremoneura, Coleoptera, Strepsiptera) (Fig. 11.19). This latter period is the post-MMPR expansion. (Another major biological event is the Mesozoic Marine Revolution (Vermeij 1977). This event also had an initial pulse and a subsequent period of expansion.)

Four major insect lineages participated in the MMPR: Hymenoptera, representing 63% of fossil and modern family-level occurrences, Diptera (15.8%), Strepsiptera (11.6%) and Coleoptera (6.8%), and the other lineages of Neuroptera, Trichoptera and Lepidoptera having minor effects (2.8%) (Table 11.2). However, subclades of these lineages played different roles chronologically during the four phases of the ascendancy of parasitoids in continental ecosystems (Table 11.3). For the MMPR, consisting of phases 1 and 2 that range from the late Early Jurassic to the late Early Cretaceous, the overwhelming majority of parasitoid families were members of non-proctotrupomorph Hymenoptera, Proctotrupomorpha–Hymenoptera,

**Table 11.3** The four phases of the Mid-Mesozoic parasitoid revolution[a]

| Phase | Time interval of expansion | Major clades or groups represented[b] |
|---|---|---|
| 1 | (late) Early Jurassic–(early) Early Cretaceous (Toarcian–Valanginian) | Hymenoptera: Proctotrupomorpha; Diptera: Non-Eremoneura; Coleoptera; Hymenoptera: non-Proctotrupomorpha |
| 2 | (early) Early Cretaceous–(late) Early Cretaceous (Hauterivian–Albian) | Hymenoptera: Proctotrupomorpha; Hymenoptera: Aculeata; Hymenoptera; non-Proctotrupomorpha; Coleoptera; Diptera: non-Eremoneura |
| 3 | (early) Late Cretaceous–mid Paleogene (Cenomanian–Ypresian) | Hymenoptera: Proctotrupomorpha; Hymenoptera: Aculeata; Coleoptera; Diptera: non-Eremoneura |
| 4 | mid Paleogene–Neogene (Lutetian–Recent) | Hymenoptera: Proctotrupomorpha; Hymenoptera: Aculeata; Diptera: Eremoneura; Coleoptera; Hymenoptera: non-Proctotrupomorpha; Strepsiptera |

[a] This table is a summary of Fig. 11.19

[b] Listed in order of family-level abundance. This list excludes families of Neuroptera, Trichoptera and Lepidoptera (N = 4) for insufficient numbers to demonstrate a valid pattern

non-Eremoneura–Diptera and Coleoptera (Fig. 11.19). Lineages such as Strepsiptera, Eremoneura–Diptera and Aculeata–Hymenoptera were largely dominant during Phase 3 and especially in Phase 4 that span the earliest Late Cretaceous (Albian Stage) to the Holocene. It is for this reason that there is a focus on two of the most important lineages of the MMPR, the non-proctotrupomorph Stephanoidea and Evanioidea.

### *11.7.1 Stephanoidea (Stephanid Wasps)*

Stephanidae (stephanid wasps) are a relatively nonspeciose family of parasitoid wasps important during phases 1 and 2 of the MMPR in that recent studies have considered Stephanidae as the sister group to all other extant Apocrita, the parasitoid wasps (Sharkey et al. 2012). This enigmatic lineage possesses peculiar characters that distinguish it from all other families of extant and extinct Hymenoptera. Examples of the distinctiveness of Stephanidae include a distinct tuberculate crown that occurs on the head capsule; and a hind femur usually swollen with two or three large, ventral, tooth-like processes and several denticles of lesser size. Additional features are a propodeum (first abdominal segment) with a dorsal profile that is continuously rectilinear throughout, and a metasomal base (the abdomen excluding the propodeum) of the thorax that nearly contacts the metacoxa (Hong et al. 2011; Rasnitsyn and Zhang 2010). Although stephanid wasps are morphologically unusual and rarely encountered in modern habitats, the clade is comprised of ten extant genera with nearly 350 species (van Achterberg and Yang 2004; Aguiar 2004, 2006; Aguiar and Jennings 2005; van Achterberg and Quicke 2006; Aguiar et al. 2010; Hong et al. 2010; Hong and Xu 2011). The geographic distribution of Stephanidae principally is among subtropical and tropical forests worldwide (van Achterberg 2002; Aguiar 2004; Hong et al. 2011). Consistent with their modern, species-poor occurrence, stephanids have a poor fossil record consisting of six genera. Three of these genera are of amber provenance, and are *Archaeostephanus* from the Late Cretaceous of New Jersey, and *Kronostephanus* and *Lagenostephanus* from the Late Cretaceous of Myanmar (Engel and Grimaldi 2004; Engel et al. 2013a, b; Li et al. 2017b). The three Eocene genera are *Protostephanus* from the Florissant Formation of Colorado, USA, and *Electrostephanus* and *Denaeostephanus* from the Baltic Region of northern Europe (Cockerell 1906; Brues 1933; Engel and Grimaldi 2004; Engel 2005b; Engel and Ortega-Blanco 2008). The amber fossil species are widely distributed geographically from Myanmar, the Baltic Region and to New Jersey, USA, while the sole compression fossil comes from Colorado, USA. A second stephanid wasp, *Lagenostephanus lii,* was described from mid-Cretaceous Myanmar Amber (Li et al. 2017b). *Lagenostephanus* is an early apocritan lineage based on overall habitus (Fig. 11.25), particularly head, leg and wing features (Fig. 11.26). It likely resembled morphologically early members of Phase 1 of the MMPR.

A phylogeny of Stephanidae was provided based on character scoring of morphological features from all extinct and extant genera (Li et al. 2017b). Phylogenetic

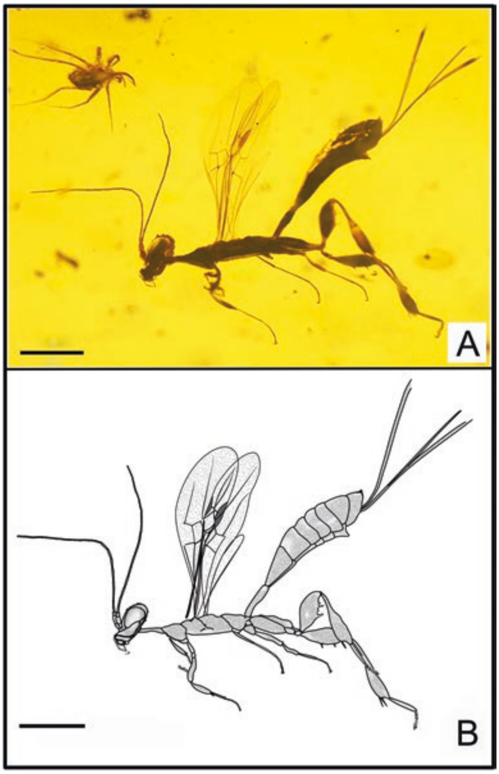


**Fig. 11.25** *Lagenostephanus lii*. Holotype CNU-HYM-MA-2014010. (**a**) Photograph of specimen. (**b**) Line drawing of habitus. Scale bars = 1 mm. (Reproduced with permission from Fig. 2 of Li et al. 2017b)

relationships among genera within Stephanidae were presented in a geochronological context consistent with their localities and paleogeographic distributions plotted along a strict consensus tree (Fig. 11.27a). As the two earliest amber stephanids are represented by *Kronostephanus* in the basal subfamily Schlettereriinae and the more derived *Lagenostephanus* in the subfamily Stephaninae, there has been the suggestion that Stephanidae likely were more diverse during the Late Cretaceous (Li et al. 2017b). The earliest Late Cretaceous occurrences and diversification events imply that the origin of Stephanidae occurred geochronologically earlier, perhaps significantly so, than earliest Late Cretaceous. It is notable that in the more basal subfamily Schlettereriinae, the amber genus *Kronostephanus* belongs to a Eurasian distributed clade, and the other amber genus, *Archaeostephanus* from New Jersey amber, occurs in North America during the Late Cretaceous, a biogeographical pattern exhibiting a cosmopolitan distribution for the earliest occurring lineages. The other amber genus, *Lagenostephanus*, also originates from Myanmar. Two middle Eocene amber genera, *Electrostephanus* and *Denaeostephanus* come from the Baltic Region, while a compression fossil genus of late Eocene age, Protostephanus, is from Florissant, Colorado, and has a North American Eocene provenance. As shown (Fig. 11.27b), extant stephanid genera are biogeographically widely distributed. An extant basal genus, *Schlettererius*, is distributed in the Palearctic and

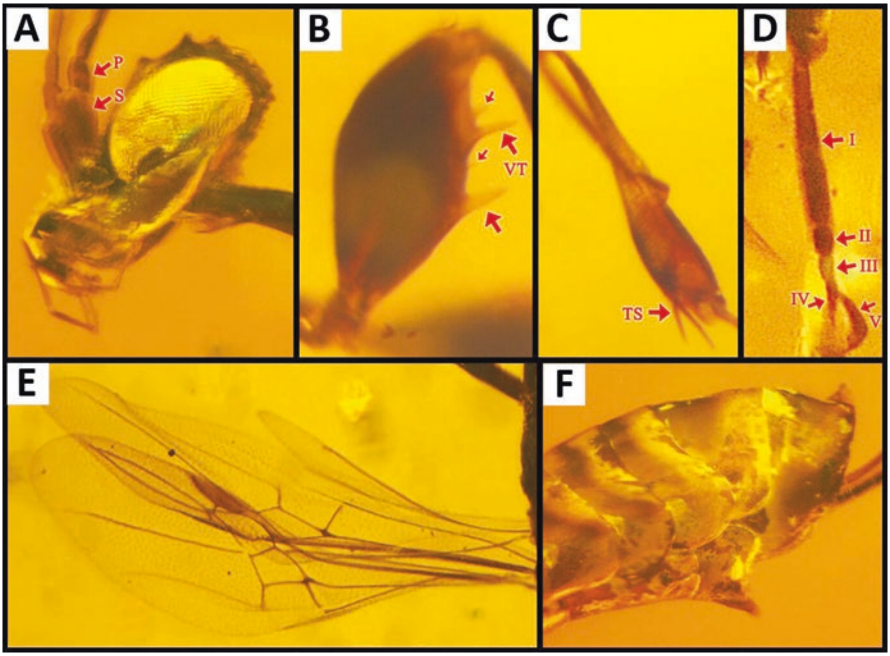


**Fig. 11.26** The holotype (CNU-HYM-MA-2014010) of the stephanid wasp *Lagenostephanus lii* (Hymenoptera: Stephanidae) shown in Fig. 11.25, a probable endoparasitoid of wood-boring larvae (Li et al. 2017a, b, c). (**a**) Head in lateral view. (**b**) Hind femur. (**c**) Hind tibia. (**d**) Hind tarsus. (**e**) Hind tarsus. (**f**) Portion of the metasoma in lateral view. Abbreviations: *P* pedicel, *S* scape, *TS* tibial spurs, *VT* ventral tooth, *I–V* five segments of the tarsus. (Reproduced with permission from Fig. 3 of Li et al. 2017b)

Nearctic regions. In addition, *Stephanus* (Stephaninae) is mainly distributed in Eurasia, inhabiting the Oriental and Palearctic regions. As northeastern Asia and northwestern North America became increasingly interconnected during the middle to Late Cretaceous from 80–100 million years ago (Sanmartin et al. 2001; Shih et al. 2009, 2010), a biogeographical connection might have been present for stephanid taxa to migrate from the Palearctic to the Nearctic. Moreover, the seven genera of *Afromegischus*, *Foenatopus*, *Megischus*, *Pseudomegischus*, *Parastephanellus*, *Stephanus* and *Schlettererius* are distributed in Eurasia, which share three of the five genera of *Afromegischus*, *Foenatopus*, *Madegafoenus*, *Megischus* and *Profoenatopus* that are distributed in the Afrotropical Region. Four other modern biogeographic regions are more depauperate, each harboring less than four extant genera. These deep-time and modern biogeographic data clearly indicate that Stephanidae historically have been most diverse in Eurasia but have been widely distributed biogeographically during the past 100 million years and probably a two or three tens of millions of years earlier.

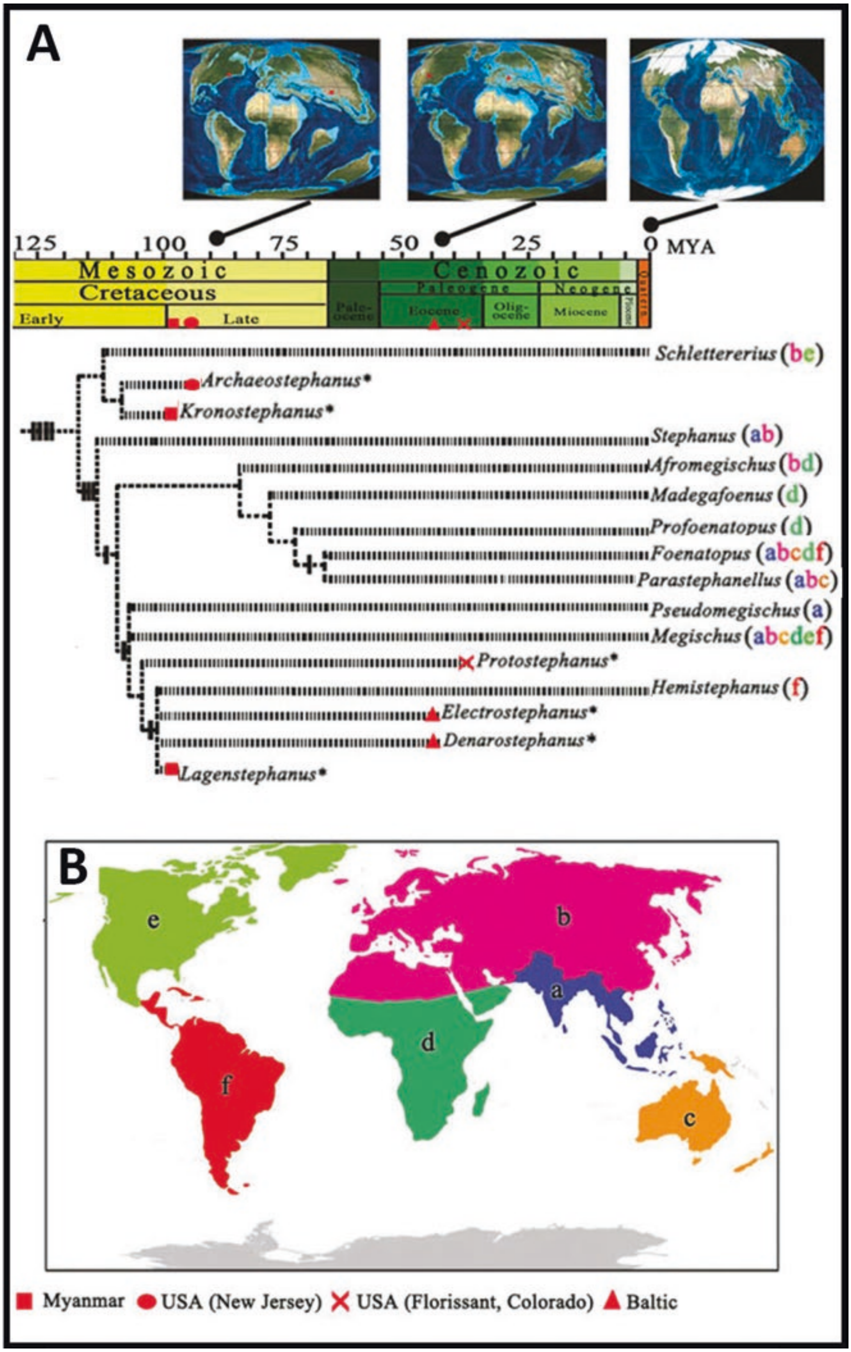


**Fig. 11.27** (**a**) Oriental (including India and Myanmar): *Foenatopus, Megischus, Parastephanellus, Pseudomegischus, Stephanus*. (**b**) Palearctic (including all of China and Japan): *Afromegischus, Foenatopus, Megischus, Parastephanellus, Schlettererius and Stephanus*. (**c**) Australasian and Oceanian (including New Guinea and islands east): *Foenatopus, Megischus and Parastephanellus*. (**d**) Afrotropical: *Afromegischus, Foenatopus, Madegafoenus, Megischus and Profoenatopus* (**e**) Nearctic: *Megischus, and Schlettererius*. (**f**) Neotropical (including all of Mexico and the Caribbean): *Foenatopus, Hemistephanus and Megischus*

### *11.7.2 Evanioidea (Ensign Wasps)*

Evanioidea (ensign wasps) also illustrate the diversification of Hymenoptera during phases 1 and 2 of the MMPR, reaching successive stepwise increases in species richness during phases 1 and 2 of the Middle Jurassic to Early Cretaceous as the major non-proctotrupomorph lineage (Table 11.1; Fig. 11.19, pink dot trajectory). Evanioidea are a moderately diverse superfamily of parasitoid wasps that are characterized by two apomorphies (Li et al. 2018a). First, the metasoma is attached high on the propodeum (Goulet and Huber 1993; Grimaldi and Engel 2005a), hence designation of the group as ensign wasps. Second, all functional metasomal spiracles are lost except on the seventh segment (Goulet and Huber 1993; Grimaldi and Engel 2005a). Historically, the superfamily Evanioidea included the three extant families of Evaniidae, Gasteruptiidae and Aulacidae, and later five extinct families from the Mesozoic were added, the Andreneliidae, Anomopterellidae, Baissidae, Othniodellithidae and Praeaulacidae (Rasnitsyn 1972, 1975; Rasnitsyn and Martínez-Delclòs 2000; Engel et al. 2016b). Subsequently, additional ensign wasps were reported, including *Exilaulacus loculatus* (Li et al. 2018a) from mid-Cretaceous Myanmar amber (Fig. 11.28), which was followed in the same report by a preliminary phylogeny of Evanioidea. This phylogeny resulted from morphology and DNA sequence data of selected fossil and extant genera that employed two phylogenetic analytical methods: maximum parsimony and Bayesian inference (Li et al. 2018a). Several distinctive relationships within Evanioidea resulted from the phylogenetic analyses (Fig. 11.29). First, the extinct family Praeaulacidae is paraphyletic and occurs at the base of Evanioidea in-groups. Second, Anomopterellidae is a monophyletic clade and is the sister clade to the remaining families. Third, Aulacidae, Baissidae and Gasteruptiidae do not form a monophyletic clade. Fourth, Othniodellithidae is a monophyletic clade in a position that is more basal to the Andreneliidae + Evaniidae clade. Fifth, Andreneliidae is the sister clade of Evaniidae, and both lineages are monophyletic clades. These results provided clarity to previous, mostly ambiguous, results regarding Evanioidea phylogeny. The inclusion of all evanioid genera, especially fossil taxa, provided a straightforward perspective of Evanioidea phylogenetic events accompanying phases 1 and 2 of the MMPR.

Based on 59 genera and 171 described fossil species of Evanioidea (Zhang and Rasnitsyn 2008; Li et al. 2013a, 2018a), histograms show the frequency of Evanioidea species, genera and family richness during a 169 million-year-long interval from Middle Jurassic to Miocene (Li et al. 2018a; Fig. 11.30a). From these geochronologic, epoch-level data (Fig. 11.30a), a relatively flat level of genus-level richness existed throughout the Mesozoic from 174 to 5 Ma, followed by a considerable decline in the transition to the Cenozoic, and ending in a flat, low level of richness from the mid Eocene to the mid Miocene spanning approximately 40–14 million years ago. Although species-level richness during this time interval is considerably more variable and accentuated, the general pattern is similar to that of generic richness, with both reaching a peak during the Early Cretaceous, followed by a distinct downturn and low levels of occurrences thereafter during the Cenozoic.

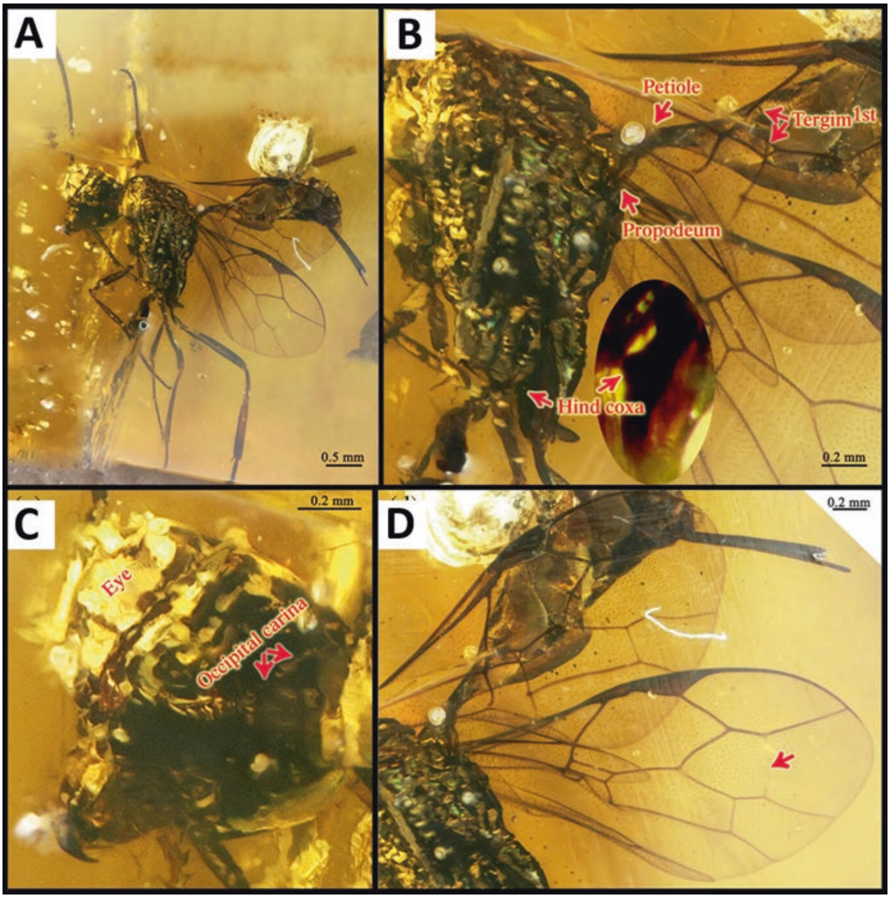


**Fig. 11.28** Holotype (CNU-HYM-MA-2014008) of the ensign wasp *Exilaulacus loculatus* (Li et al. 2018a, b) (Hymenoptera: Evaniidae). (**a**) Photograph of the overall habitus. (**b**) Mesosoma and metasoma. (**c**) Head. (**d**) Wings. (Reproduced with permission from Fig. 16 of Li et al. 2018a)

However, the internal composition of families within Evanioidea does vary substantially and displays distinctive patterns (Fig. 11.30b). The species richness of Anomopterellidae peaked during the Middle Jurassic, decreased in the Late Jurassic, after which the Anomopterellidae record disappears, presumably attributable to extinction. A similar pattern is present for Praeaulacidae, a lineage with high richness during the Middle and Late Jurassic that decreased considerably during the Late Cretaceous, after which the Praeaulacidae record ceases, again attributable to extinction. By contrast, the species richness of Baissidae peaks during the Early Cretaceous, apparently becoming extinct by the Cenozoic. Andreneliidae and Othniodellithidae are present, respectively, solely during the Early Cretaceous and Late Cretaceous. The earliest known fossils of the extant family Evaniidae are from the Early Cretaceous, and the majority of species are recorded during the Cretaceous,

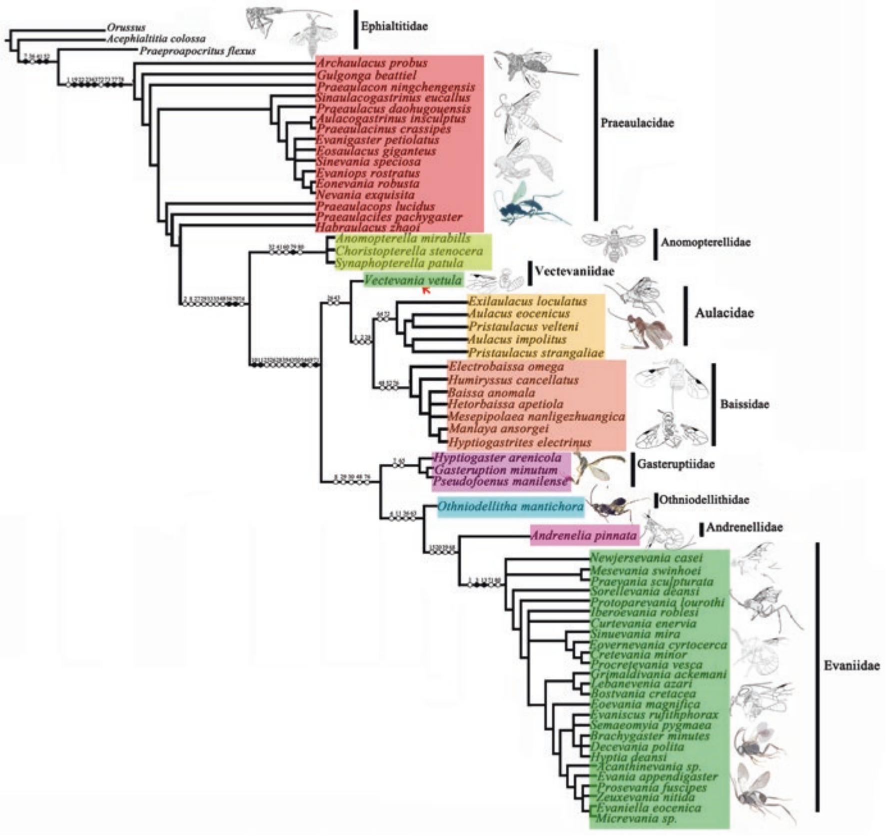
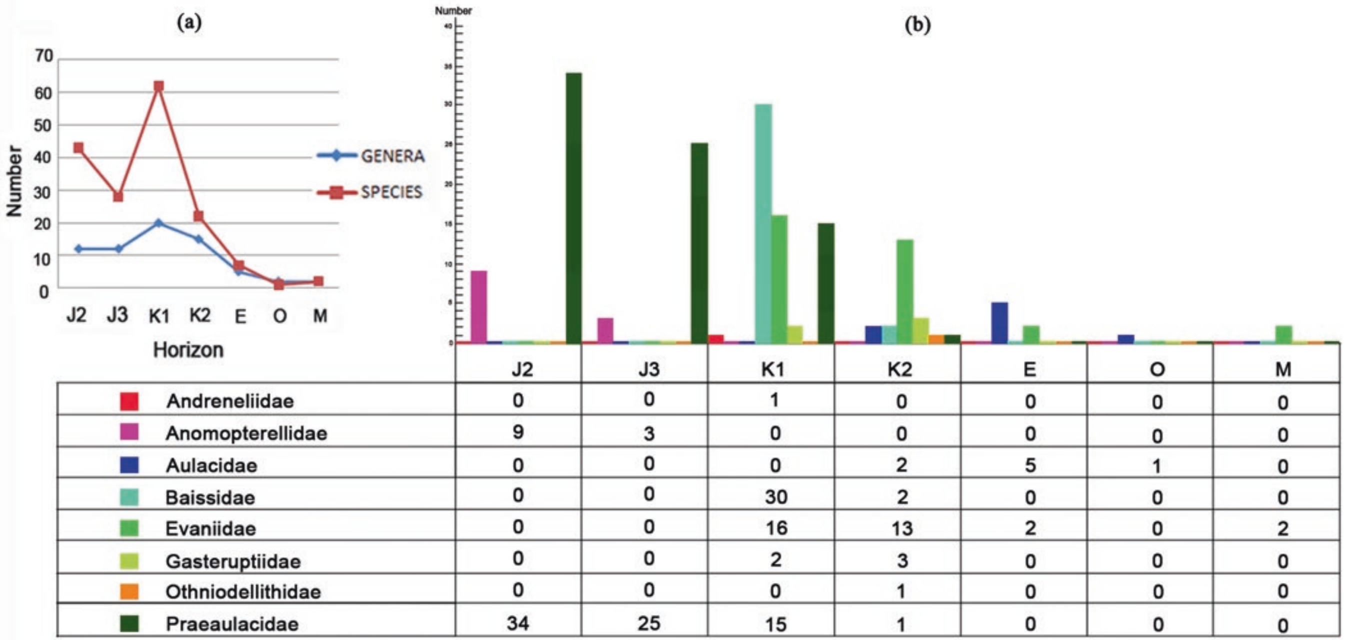


**Fig. 11.29** Phylogeny of extant and extinct Evanioidea, based on a strict consensus tree recovered from parsimony analyses of morphological characters, with 582 steps, a consistency index of 0.21 and a retention index of 0.63. Solid circles indicate nonhomoplastic changes and open circles indicate homoplastic changes. (Reproduced with permission from Fig. 24 of Li et al. 2018a)

but a substantial decrease is documented for the Cenozoic. Evaniidae currently are evolutionary relicts. The two, other extant families of Gasteruptiidae and Aulacidae are first documented, respectively, during the Early Cretaceous and Late Cretaceous, both of which persist to the present also as evolutionary relicts. Based on these patterns of species and genera richness through time, there are four families with more than four species occurrences within an epoch that have a distinct pattern of occurrence during the MMPR (phases 1 and 2) and continuing to the post MMPR (phases 3 and 4). Praeaulacidae and Anomopterellidae dominate phases 1 and 2; Baissidae and Evaniidae have elevated occurrences during phases 2 and 3; and Aulacidae has the greatest number of occurrences in Phase 4 (Fig. 11.19). This suggests that Evanioidea, as non-proctotrupomorph Hymenoptera (Fig. 11.19), was one of the earliest participants in the MMPR, and was the greatest contributor of Hymenoptera



| | J2 | J3 | K1 | K2 | E | O | M |
|---|---|---|---|---|---|---|---|
| 🟥 Andreneliidae | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 🟪 Anomopterellidae | 9 | 3 | 0 | 0 | 0 | 0 | 0 |
| 🟦 Aulacidae | 0 | 0 | 0 | 2 | 5 | 1 | 0 |
| 🟩 Baissidae | 0 | 0 | 30 | 2 | 0 | 0 | 0 |
| 🟩 Evaniidae | 0 | 0 | 16 | 13 | 2 | 0 | 2 |
| 🟨 Gasteruptiidae | 0 | 0 | 2 | 3 | 0 | 0 | 0 |
| 🟧 Othniodellithidae | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 🟩 Praeaulacidae | 34 | 25 | 15 | 1 | 0 | 0 | 0 |

**Fig. 11.30** Taxonomic richness of Evanioidea during the Middle Jurassic to Miocene, showing the contribution of an early parasitoid clade to the Mid-Mesozoic Parasitoid Revolution. (**a**) Total number of Evanioidea species (N = 171) and genera (N = 59) resolved to epoch time intervals during the Middle Jurassic to Miocene. (**b**) The genus and species richness of families (N = 171 occurrences) within the Evanioidea resolved to epoch time intervals during the Middle Jurassic to Miocene. Abbreviations: *J2* Middle Jurassic, *J3* Late Jurassic, *K1* Early Cretaceous, *K2* Late Cretaceous, *E* Eocene, *O* Oligocene, *M* Miocene. Data for the Paleocene, Pliocene and Pleistocene epochs are not reported. (Reproduced with permission from Fig. 25 of Li et al. 2018a)

to Phase 1 and Phase 2, proportionately less so in subsequent phases. This early evolutionary expansion of a major parasitoid group likely was involved in the ecological transformation of terrestrial food webs.

Although divergence-time estimation has played an important role in evolutionary biology (De Baets and Littlewood 2015; Warnock and Engelstädter 2021), it is relevant also in evaluating historical ecological processes such as the MMPR. As a prelude, a study based on total-evidence analysis concluded that the time-of-origin for the order Hymenoptera was at 309 million years ago (Ronquist et al. 2012), or the middle of the Pennsylvanian Period, with node dating providing a very similar result of 311 Ma. Such an age date would be consistent with a major diversification of basal Hymenoptera during the Permian. Nevertheless, the results of that study for both the time of origin and time interval of early diversification of Hymenoptera are considerably older than most previous estimates and the relevant fossil record. A subsequent analysis of the same dataset using the joint and complementary dating of clades (nodes) and terminal lineages (tips) (O'Reilly et al. 2015, O'Reilly and Donoghue 2016) produced a time-calibrated phylogeny of Hymenoptera congruent with the fossil record (Rasnitsyn 1969, 1975, 1988, 2002). These latter estimates acknowledge the origin and early diversification of Hymenoptera as a Middle Triassic to Early Jurassic event (Grimaldi and Engel 2005a), also consistent with the fossil record. However, because of the sparseness of the relevant fossil record it is difficult to evaluate a 74 million-year-long gap. This gap exists between the earliest Late Triassic fossils of Hymenoptera at 235 Ma—*Triassoxyela foveolata* and *Leioxyela antiqua* from the Madygen Biota (Rasnitsyn 1964)—and the presumptive origin of Hymenoptera at 309 Ma (Rasnitsyn 1969; Rasnitsyn and Quicke 2002; Ronquist et al. 2012). A similar pattern exists in Evanioidea (Ronquist et al. 2012), which shows that the earliest divergence time of Evanioidea based on total-evidence dating was the Late Triassic at about 221 Ma (Late Triassic, Norian Stage), 43 million years earlier than a node-dating result of 178 Ma (Early Jurassic, Toarcian Stage) under an internal growth rate model. Currently the earliest record of Evanioidea is several occurrences of Praeaulacidae dated as 165 Ma, of latest Middle Jurassic age (Callovian Stage). These occurrences are *Archaulacus* (Li et al. 2014c), *Aulacogastrinus* (Rasnitsyn 1983), *Eosaulacus* (Zhang and Rasnitsyn 2008), *Nevania* (Zhang and Rasnitsyn 2007), *Praeaulacus* (Rasnitsyn 2008), *Praeaulacon* (Zhang and Rasnitsyn 2008), *Sinaulacogastrinus* (Zhang and Rasnitsyn 2008), the anomopterellid *Anomopterella* (Rasnitsyn 1975) and *Synaphopterella* (Li et al. 2013a). This timing from fossil occurrence data indicates that diversification within Evanioidea would have appeared no later and no earlier than Middle Jurassic. Although combining the divergence time estimation (Ronquist et al. 2012) with the origin age of Evanioidea may push this lineage to the Early Jurassic, or conceivably Late Triassic, currently there is no fossil evidence for such an early origination. A Middle Jurassic origination, indicated by the fossil record, is consistent with the parasitoid habit as a fundamental feature of Evanioidea, and its initial appearance during early Phase 1 of the MMPR, coincident with the Toarcian to Callovian stages of the late Early to Middle Jurassic.

## 11.8 Discussion: Trophic Specialization and the Mid Mesozoic Parasitoid Diversification

Several recent studies have sought to account for the emergence of parasitoids during the mid Mesozoic. One study reconciled the insect fossil record that shows an upward, rather constant increase in family-level diversity with likely times of considerable evolutionary change resulting from key innovations that should result in a spikier trajectory of insect diversity (Condamine et al. 2016). Two distinct types of diversity analyses were used to reconcile both patterns of insect diversity through time. One approach, using the entire fossil record of family-level data, recorded distinct bursts of diversification that occurred early in insect evolution and subsequently declined gradually to a modern level, interrupted only by occasional extinction events. The second approach employed molecular phylogenetic data that contained 82% of extant insect families and identified surges of diversification, but only for the four, hyperdiverse holometabolous orders. Both approaches did not detect any effect from the origin of angiosperms on insect diversity, a consequence that has been borne out previously from several fossil diversity studies (Dmitriev and Zherikhin 1988; Labandeira and Sepkoski Jr 1993; Jarzembowski and Ross 1996; Labandeira 2014b; but see Wilson et al. 2013). The lack of an effect of angiosperm diversity on insects also is borne out from long-term analyses of major mouthpart types through time (Labandeira 1997, 2019; also see Nel et al. 2018). Rather, the authors concluded that clade-specific innovations were responsible for major diversification events that should be captured by the insect fossil record (Condamine et al. 2016). Such innovations would have included the highly elongate, valved ovipositor of Hymenoptera; the extensible, telescoped ovipositor of Diptera; and the host-seeking, mobile, triungulin larva of Coleoptera and planidium larva of Diptera. Specifically, one of these events involved "… shifts within Diptera and Hymenoptera [that] may be consistent with the development of trophically specialized habits (i.e. parasitoid) …" (Condamine et al. 2016, p. 8). A specific example may be the combination of small size, koinobiont, endoparasitoid and superparasitoid life habits that are associated with a high rate of diversification in particular lineages of wasps such as microgastrine Braconidae (Mardulyn and Whitfield 1999). Given that Diptera and Hymenoptera constitute about 79% of all parasitoid taxa in the fossil record (Table 11.2), there is reason to indicate that the high diversification rate was an indirect reference to the MMPR.

In a separate study (Rainford and Mayhew 2015), a recent phylogeny of Hexapoda, with age dates, was used to ascertain whether specific patterns existed between diet and associated patterns of insect diversity such as clade richness. Two indices of phylogenetic clustering, the net relatedness index and the nearest taxon index, provided the total phylogenetic distance of an insect family with a particular diet (for details see Rainford and Mayhew 2015). (The total phylogenetic distance is the number of all pairwise differences in character states between two phylogenies.) The results of the study indicated that for the diets of detritivory, fungivory, phytophagy, predation, parasitoidism and ectoparasitism, there were no associations between particular dietary substrates and clade richness. Moreover, there was no evidence that clade richness promoted the evolution of antagonisms such as ectoparasitism and parasitoidism. A major conclusion of the study was that taxa with specialized feeding ecologies such as ectoparasitism and parasitoidism exhibited significant phylogenetic clustering and thus were closely related to other taxa with the same diet than to other such taxa with different diets. The results of the study are consistent with previous evaluations (Wiegmann et al. 1993) that failed to demonstrate a stable relationship between parasitoidism and clade richness. These conclusions also highlight the strong dietary conservatism for parasitoid insect families that originated during the mid Mesozoic.

The issue of what caused the triggering of the MMPR is a difficult issue to address. Nevertheless, there are several preconditions that are germane to the issue. The MMPR required multiple steps of biological organization that produced a cascade of events beginning in the late Early Jurassic that was entrenched by the late Early Cretaceous. First, an essential prerequisite was the establishment of Holometabola, which already was present during the Late Carboniferous (Haug et al. 2015). Second, was the development of several key innovations, particularly: (1) the specialized drilling ovipositor of apocritan Hymenoptera; (2) the development of the host-seeking triungulin and planidium first-instar stages of Neuroptera, Coleoptera, Strepsiptera and Diptera; and (3) the telescoped ovipositor of Diptera (Feener and Brown 1997; Gauld 2008; Evans and Steury 2012). Third, was the ecological restructuring of terrestrial ecosystems such that bottom–up, resource-driven food-web structure was replaced by top–down regulation with the emergence of the parasitoid guild that more efficiently regulated primary consumers such as herbivores (Labandeira 2015). Whether the accumulation of these phylogenetic, morphological and ecological aspects caused the separation of the early MMPR into phases 1 and 2, and what propelled phases 3 and 4 during the Late Cretaceous through the Cenozoic, remains a question for further analyses of more finely resolved data.

A related, albeit vexing, issue involves the evolution of the parasitoid community and its component guilds (Mills 1994). The particular issue of concern is whether host evolution of parasitoid lineages proceed from generalist to specialist, the traditional view, or alternatively from specialist to generalist, the uncommon perspective. The traditional version of parasitoid host breadth is that the parasitoid penchant for high animal host specificity in resources results from high extinction rates and a low rate of diversification (Stireman III 2005). Such a view would indicate that host-range evolution proceeds from generalist to specialist and thus should preferentially occur at the terminal lineages of clades. A test of this hypothesis used tachina flies (Diptera: Tachinidae) and it was found, surprisingly, that generalist taxa were iteratively derived from specialist taxa (Gauld et al. 1992; Stireman III 2005). This result highlighted problems in ancestral state reconstruction in previous phylogenetic trees and the need for additional evidence in establishing parasitoid host specificities. Although it is unclear if the specialist-to-generalist pattern in Tachinidae is typical of most parasitoid insects (Stireman 2003; Stireman III 2005), other studies, albeit more limited, have displayed an opposite pattern (Eggleton and Gaston 1992;

Feener and Brown 1997). These data may indicate that for parasitoids, host breadth of intermediate selectivity would be favored (Ferns and Jervis 2016), generating specialists and generalists on opposite sides of the host specificity continuum.

## 11.9 Summary and Conclusions

Many extant and extinct insects are predators, parasites or parasitoids. However, explicit recognition of parasitoidism as a distinct ecological process on par with predation and parasitism has been a relatively recent development. Parasitoidism historically was categorized by its location on the host (ectoparasitoidism versus endoparasitoidism), by presence on the same host individual of multiple conspecifics (superparasitoidism) or by multiple non-conspecifics (multiparasitoidism). Other descriptive designations common in the parasitoid literature are hyperparasitoidism, the condition of parasitoids living on other parasitoids, and cleptoparasitoidism, the killing of a host individual resulting from a parasitoid absconding food or other vital resources. Direct and indirect evidence for predation, parasitism and parasitoidism in the fossil record consists of biomolecular data, taxonomic affiliations, morphological and functional attributes, gut contents and coprolites of body fossils, in addition to host-tissue damage, plant–insect interactions and sedimentary structures of trace fossils. Parasite and parasitoid insect clades overwhelmingly have targeted 84 clades of holometabolous insects and minimally targeted 4 clades of hemimetabolous insects. The accumulation curve of originations for parasitoid larval dietary substrates through geologic time records a major upward trend, in contrast to more gently increasing trends for fungivory, phytophagy and predation. Contrary to parasitoid evolutionary trajectories, the larval dietary trajectory for ectoparasites resulted in evolutionary cul-de-sacs that did not lead to major diversification events. Parasitoids from three orders of insects—beetles (Coleoptera), flies (Diptera) and wasps (Hymenoptera)—document the multiple and complex paths that various lineages transit into and out of the parasitoid life habit.

Parasites and parasitoids have fossil records ranging from poor to fair, although their modern diversities can be very elevated. Ten groups of parasites occur among hemimetabolous and holometabolous insects. Hemimetabolous parasites are cockroaches (Blattodea) consisting of an extinct fossil lineage; earwigs (Dermaptera), with two lineages parasitic on bats and rodents; bark lice (Psocoptera) containing a sole lineage inhabiting mammal nests; chewing lice and sucking lice (Phthiraptera), composed of four major clades parasitic on birds and principally mammals; and bugs (Hemiptera), consisting of three blood-feeding lineages. Holometabolous parasites are beetles (Coleoptera), of diverse parasitic life habits; fleas (Siphonaptera), whose modern lineages likely form a clade with older mid-Mesozoic giant fleas; flies (Diptera), with blood feeding possibly originating in the Triassic; erebid moths (Lepidoptera) that convergently evolved stylate mouthparts for blood feeding; and wasps (Hymenoptera), with few parasites but an inordinate proliferation of hyperdiverse apocritan parasitoid lineages. The ten parasite taxa differ from the seven parasitoid taxa in five basic ways that involve life-history features and disposition of their hosts. Of parasitoids, the major groups are mantispids (Neuroptera), with 1 origination; beetles, with 10 originations; twisted-wing parasites (Strepsiptera), with a single origination; flies, with approximately 60 originations; caddisflies (Trichoptera) and moths (Lepidoptera), with 1 and 2 originations respectively; and wasps with either 1 or 2 originations, depending on the authority. The bulk of parasitoid diversity is Hymenoptera, accounting for 75% of all extant parasitoid species, consisting of 92 families in 17 superfamilies, and containing 63% of all extinct and extant families (Tables 11.1 and 11.2). Hymenoptera were the major driver of the Mid Mesozoic Parasitoid Revolution (MMPR), resulting in a dramatic expansion of parasitoidic lineages during the Middle Jurassic to Early Cretaceous.

Modern terrestrial food webs are important for understanding the MMPR. Bottom–up food webs explained by the resource concentration hypothesis, account for the pre-MMPR interval leading up to the latest Early Jurassic. Four biotas typical of pre-MMPR time are the Madygen, Molteno, Beishan–Shangtu and Solite biotas, of Middle to Late Triassic age. Once parasitoids originated during the late Early Jurassic, the body-fossil record indicates that their subsequent family-level diversity is subdivided into four temporal phases, each phase of which is characterized by a stepwise increase from the previous diversity level of particular parasitoid clades or groups (Fig. 11.19). During MMPR Phase 1 (Toarcian to Valanginian stages) and Phase 2 (Hauterivian to Aptian stages), a shift ensued from pre-MMPR bottom–up regulation of food webs to MMPR top–down regulation of food webs. This shift is explained by the trophic cascade hypothesis and the trophic efficiency of parasitoids compared to predators (Slansky 1986; Godfray 1994; Harvey et al. 2009). Four biotas typical of the MMPR time interval are the Yanliao, Karatau, Purbeck and Jehol biotas. Two case studies involving early hymenopteran parasitoid clades, Stephanoidea and Evanioidea, document the initial radiation of MMPR lineages that contain lineages that currently are mostly extinct or relict. The post-MMPR interval consisted of Phase 3 (Cenomanian to Lutetian stages) and Phase 4 (Bartonian Stage to recent), during which there was further consolidation of insect parasitoid taxa in food webs. Four biotas illustrative of the post-MMPR interval are Myanmar Amber, Canadian Amber, Messel and Dominican Amber biotas.

There appears to be no association between the MMPR and angiosperm diversity. Rather, three clade-specific innovations are indicated: (1) notably the host-seeking, triungulin larva in Neuroptera, Coleoptera and Strepsiptera, and planidium larva in Diptera; (2) the extrudable, telescoped ovipositor in Diptera; and (3) the long, valved and flexible ovipositor in Hymenoptera. The likely cause of the MMPR required multiple steps of biological organization that produced a series of events from the late Early Jurassic to the late Early Cretaceous. First, was the necessity of the holometabolous condition. Second, was development of the three key innovations of a drilling ovipositor in apocritan Hymenoptera, the host-seeking triungulin and planidium first-instar stages in several holometabolan lineages, and the telescoped ovipositor of Diptera. Third, was reformatting the ecological structure of terrestrial ecosystems from resource driven to trophic-cascade driven food webs resulting from appearance of the parasitoid guild. One outcome of the MMPR, host specialization, is not necessarily associated with clade diversification among parasitoids, as the evolution of host breadth proceeded from specialist to generalist in Tachinidae, the most diverse clade of dipteran parasitoids.

## 11.10 An Outlook Toward the Future

Hopefully, this contribution will set the stage for further exploration into the paleobiology and evolutionary biology of parasites and parasitoids. Six major questions are posed to spark future work in this fascinating field.

1. What specific feature or features render the parasite life habit an evolutionary cul-de-sac when compared to the evolutionarily more successful parasitoid life habit?
2. Can other evidence be marshalled to understand the vertebrate host identities of the several "giant" flea lineages from the mid Mesozoic?
3. How does the evolutionary transformation from parasitism to parasitoidism occur? Are there modes in which nonparasitic modes of feeding evolve directly into parasitoidic modes of feeding without going through a parasite stage?
4. Are there biological factors determining why some orders undergo one or two originations of the parasitoid life habit (e.g., Strepsiptera, Hymenoptera), whereas other orders undergo many more such originations (e.g., Coleoptera, Diptera)?
5. What accounts for the spectacular increase in taxonomic diversity of parasitoid clades such as Strepsiptera, Eremoneura, Proctotrupomorpha and Aculeata, during the past 170–120 million years? Are such increases explained by innovations such as triungulin or planidium larval stage, a telescopic ovipositor or an elongate drilling ovipositor?
6. Does the postulated transformation of mid-Mesozoic food webs from those initially driven by primary-producers to subsequent ones driven by efficient parasitoid consumers leave other ecological effects on terrestrial ecosystems?

Much of the deep-time history of predation, parasitism and parasitoidism remains unknown. These six questions will be best answered through interdisciplinary collaboration by paleoecologists, entomologists knowledgeable in fossil and modern insect groups, taphonomists, food-web specialists and others that can pool their knowledge in solving issues of common interest.

**Acknowledgements** We are grateful to Kenneth De Baets and John Huntley for the invitation to provide this review. We thank two reviewers for constructive evaluations of this contribution. Jennifer Wood assembled the figures; Jon Eizyk ably secured copyright permissions for reproduction of the figures. The Smithsonian Institution Libraries provided facilities and interlibrary loan articles essential for the completion of this review. Kevin Johnson and Sandra Schachat provided valuable feedback. We thank David Smith and Matthew Buffington for access to Hymenoptera specimens that were examined for the Stephanoidea and Evanioidea studies. The Paleobiology

Data Base was used in inquiries regarding the fossil records of fossil taxa mentioned in this report. This is contribution 374 of the Evolution of Terrestrial Ecosystems Consortium at the National Museum of Natural History, in Washington, D.C.

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