

Fossil Social Insects



Phillip Barden^{1,2} and Michael S. Engel^{2,3}

¹Department of Biological Sciences, New Jersey Institute of Technology, Newark, NJ, USA

²Division of Invertebrate Zoology, American Museum of Natural History, New York, NY, USA

³Division of Entomology, Natural History Museum, and Department of Ecology & Evolutionary Biology, University of Kansas, Lawrence, KS, USA

The paleontological history of social insects extends into the Early Cretaceous over 130 million years ago. Insects entombed in amber and rock act as historical portholes revealing origins, extinctions, diversification, and in some cases even behavior [18]. Owing in part to their abundance and ubiquity in some terrestrial environments, ants and termites in particular exhibit a rich fossil record spanning hundreds of described species. (There are more known species of fossil social insect than of dinosaurs.) Fossil specimens also capture ecological interactions that remain hallmarks of some social lineages: instances of predation, mutualistic relationships, parasitism, and insight into the origins of social behavior itself. Taken in aggregate, the rock and amber record illustrates the striking ascent of social lineages over deep time, from fledgling newcomers to numerically dominant ecosystem engineers.

Preservation and the Utility of Fossils

Any neontologist – one tasked with studying extant organisms – must confront a sampling problem. It is believed that more than 99% of all species that ever lived on Earth are now extinct. Fossils, therefore, provide key insight into the history of life. Even as molecular phylogenetics allow for increasingly accurate estimates of diversification events, estimates rely on fossils to act as temporal calibrations between rates of genetic evolution and geological time. Beyond calibration, certain extinctions and biogeographic patterns remain unknowable outside of paleontological evidence. Consider attempting to predict the sprawling history of non-avian dinosaurs from their living bird relatives alone. Still, fossilization is an extraordinarily rare event. The probability of any one animal or plant encountering the sequence of events necessary for long-term preservation is remote. A would-be fossil must evade consumption, decomposition, and abiotic degradation before coming to rest in an initial precise set of environmental circumstances only to later undergo a subsequent set of distinct conditions. These long-shot events do not occur equally. Taphonomic biases, which relate to the fossilization process, result in a rock record that is rich in some taxa and entirely lacking in some others. Despite the inherent patchiness of the fossil record, there remain hundreds of thousands of insect fossils, each a datapoint and some with the potential to rewrite portions of evolutionary history.

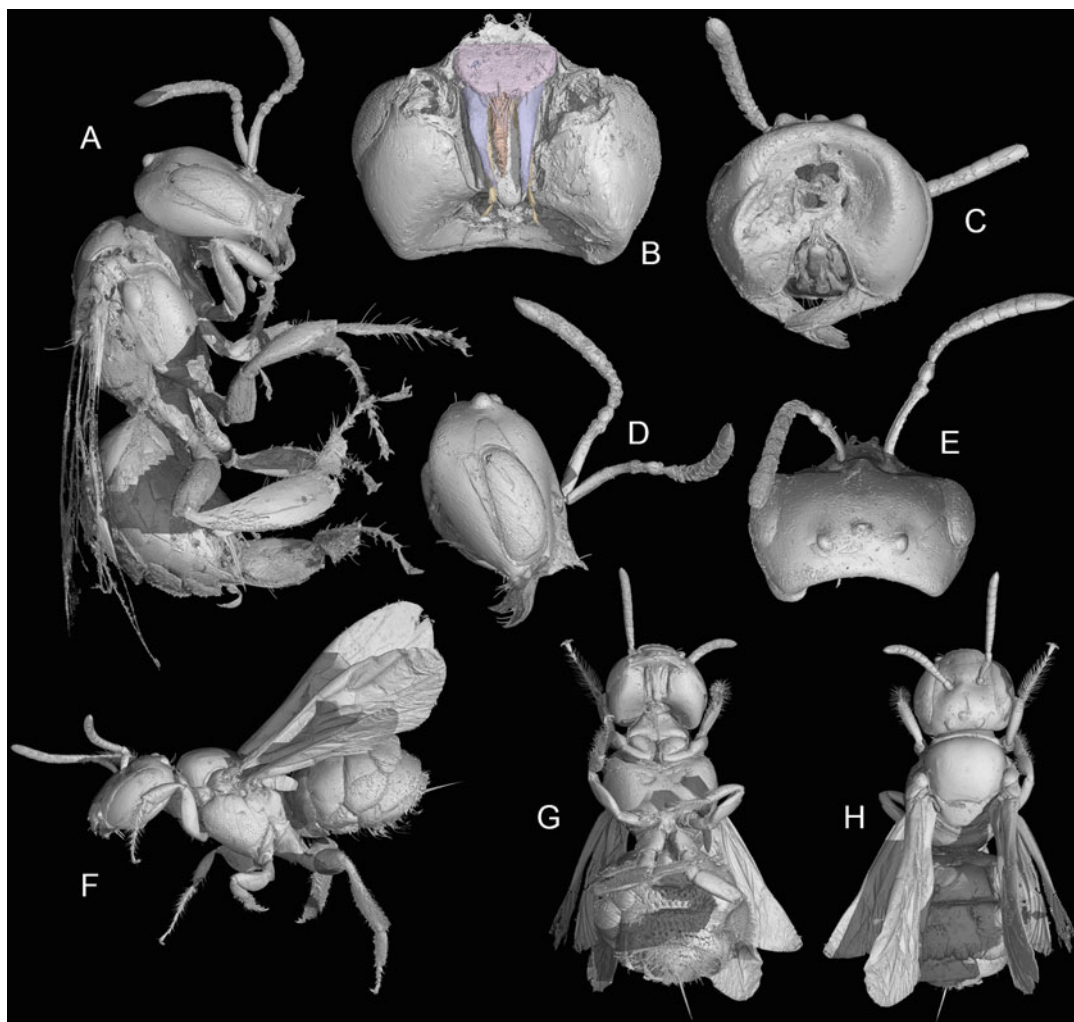
Unlike vertebrate fossils, which typically comprise mineralized replacements of bone, arthropods often preserve in their entirety and in a wide variety of forms. Two broad categories encompass the great majority of fossil insects: remains compressed and impressed in rock and those sealed in amber [18]. Compression and impression localities yield elements of insect cuticle as well as casts and molds with occasional three-dimensional relief. Such fossils typically form after an insect is rapidly buried in lake or marine sediment. A significant portion of the geological record of social insects is preserved in amber, which often preserves fine three-dimensional structure with high fidelity. This preservation can include genitalic structures and internal soft tissue. Amber derives from plant resins that are polymerized over time through heat and pressure. Insects that become trapped in the sticky resin are sealed as *inclusions* within an amber matrix. In general, both amber and rock fossilization require initial burying in lake or marine sediments. The preservation requirements of insect fossils underscore the ecological biases inherent in paleoentomology. Amber only forms where there was once flowing resin. Therefore resin collecting bees or arboreal species living in coastal forests may be especially prone to amber fossilization, while subterranean and desert-dwelling taxa are exceedingly rare. Trace fossils, or ichnofossils, preserve a sparse record of extended phenotypes. While taxonomic identification is challenging, there are a number of fossil ant, termite, and wasp nests [17].

Imaging technologies such as X-ray-based CT scanning and laser confocal microscopy amplify the data richness of fossil samples and now allow for 3D reconstructions of long extinct organisms. These new techniques allow for digital dissections, essentially eliminating typical hindrances such as obscured views and pesky exoskeleton (Fig. 1).

Ecological and Evolutionary Significance of Sociality

Eusociality has had a profound impact on terrestrial environments. A key metric of ecological significance is the abundance of social insects, primarily ants and termites, relative to other organismal groups. In a study of biomass in the Amazon rainforest, ants and termites were estimated to outweigh all vertebrates combined, and recent estimates suggest that termite mass may be equivalent to that of humans globally. Similarly, one paleontological proxy for ecological impact is the numerical abundance of social insects relative to other arthropods in fossil deposits. Fossil deposits may be thought of as sampling events analogous to an ancient array of malaise or pitfall traps. While there are taphonomic biases toward certain arthropods, the ecological ascent of social insects remains clear across well-sampled localities. During the Cretaceous, from 130 Mya (million years ago) until 65 Mya, neither ants or termites comprise more than 1% of all insect specimens across major fossil deposits. This changes markedly during the Cenozoic. Following the Cretaceous-Paleogene (K-Pg) extinction event 66 Mya, ant and termite abundance increases by an order of magnitude. During the Miocene, ant prevalence reaches as high as 35% of all insects in Dominican amber, while termites reach just over 10% (Fig. 2).

Social insects also make their ecological mark as agents of selection [32]. Today thousands of invertebrate species morphologically mimic social insects, and numerous lineages make their living asinquilines or parasites among insect societies. Ants and termites are rare in Cretaceous deposits; however, there are termitophilous and myrmecophilous beetles described from fossil amber dating to ~99 Ma, indicating that social insects were shaping the evolution of other lineages well before the ecological dominance they exhibit today. Fossil termite inquilines such as varied species of *Termitaradus* (Hemiptera: Termitaphididae) are preserved in Miocene amber deposits, while phoretic triungulins of meloid beetles have been found preserved on bees as early as the middle Eocene. As early as



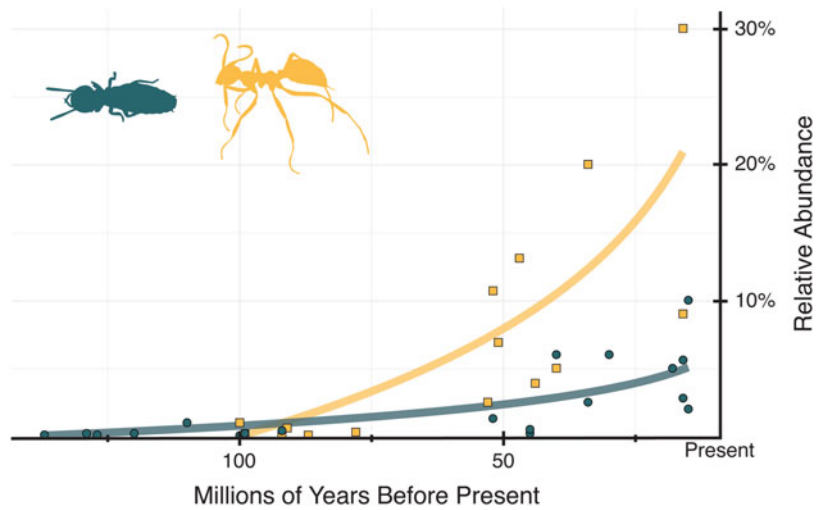
Fossil Social Insects, Fig. 1 Synchrotron-radiation computed tomographic (CT) scans of two bees (Apidae) – *Melikertes clypeatus* (Apinae: Melikertini) and *Boreallodape* sp. (Xylocopinae: Boreallodapini) – in mid-Eocene Baltic amber, along with virtual dissection of the head capsule of the former. (a) Lateral view of worker of *M. clypeatus* (total length ca. 3.2 mm). (b) Head in

ventral view with mandibles removed to reveal labrum (pink), glaeae (purple), and glossal apex (orange). (c) Removed head capsule in posterior view. (d) Head in profile. (e) Head in dorsal view. (f) Lateral view of *Boreallodape* sp. (total length ca. 3.8 mm). (g) Ventral view. (h) Dorsal view

their first appearance in Cretaceous fossil amber, both ants and termites played host to phoretic mites, with parasitic mesostigmatid mites appearing as early as the Eocene in Baltic amber. Incredibly, even the behavior-modifying fungal

infections of ants are documented in the rock record. Bite marks consistent with *Ophiocordyceps* hosts are known in leaf specimens from the Messel formation dating to 48 Mya [20].

Fossil Social Insects, Fig. 2 Abundance of ants and termites relative to other insects in well-sampled fossil deposits. Despite fossil records beginning in the Cretaceous, ants and termites do not comprise more than 1% of all insects in any fossil deposit until the Cenozoic

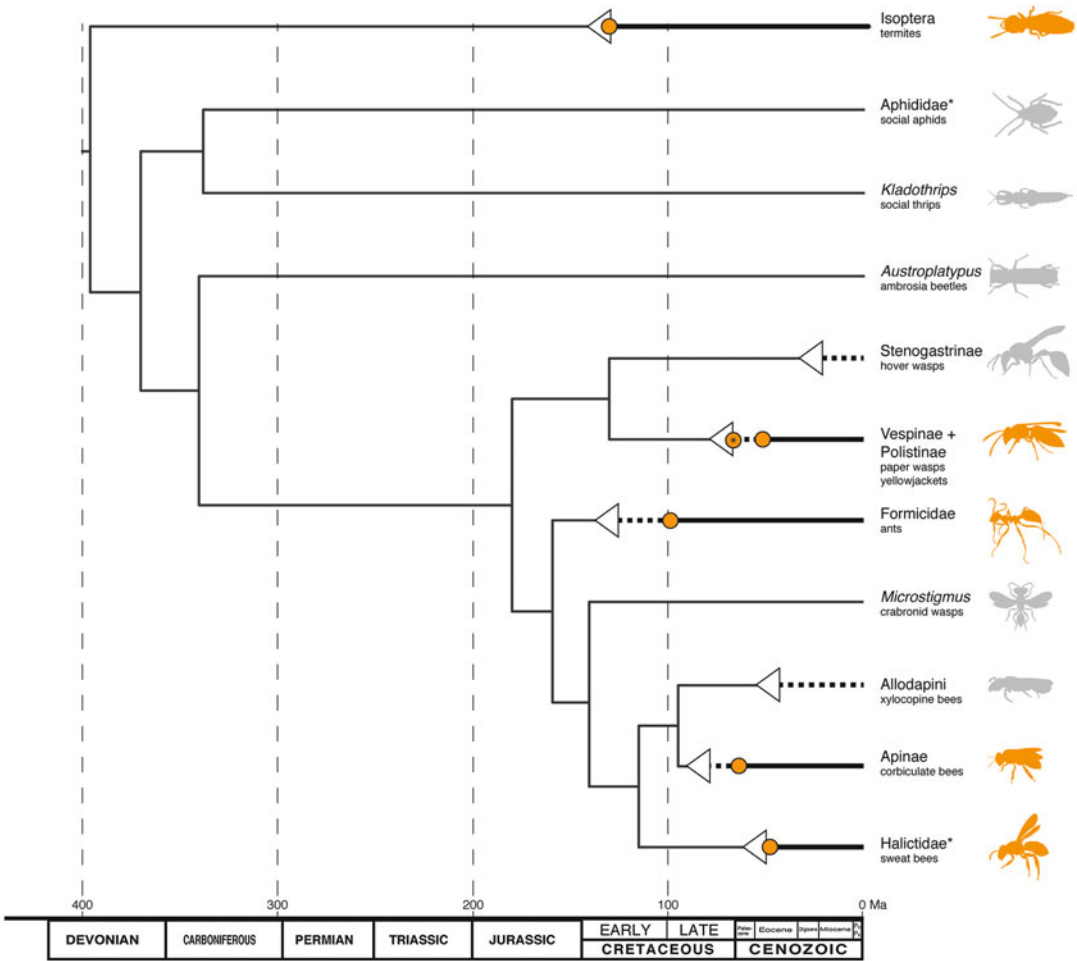


Distribution of Sociality Across the Hexapoda

Advanced sociality is not evenly distributed across insect lineages. There are at least 13 origins of eusociality in insects, of which ten are holometabolous and nine within Hymenoptera (Fig. 3). Hexapods occur in the fossil record as early as the Devonian over 400 Mya ago [18]; however, the first eusocial insect lineage (Isoptera) does not appear until the Jurassic. Social insects may coat landscapes today, but for at least the first 250 million years of insect evolution, there were no insect societies. So far there is no evidence for entirely extinct eusocial lineages. While some stem-groups – early members of living lineages – have gone extinct, every known eusocial origin has persisted to the present. There are six eusocial “ghost lineages” with no known fossils: ► [social aphids](#), ► [thrips](#), ambrosia beetles, crabronid wasps, ► [xylocopine bees](#), and ► [stenogastrine wasps](#). The absence of fossil specimens in these lineages may be a result of ecological sampling bias, or, in the case of aphids, thrips, beetles, and crabronids, a product of their very recent origin.

Presocial Insects

As is true among arthropods today, a multitude of diverse lineages have evolved ► [presocial associations](#), most commonly as gregarious, familial affiliations between parent and offspring but also including examples of aggregative and communal behaviors [9]. Such behaviors are often ephemeral and fail to leave a trace, and yet a record of such ancient ethologies is comparatively widely documented. After more than a century of lucubration, much remains murky regarding the initial stages and conditions necessary for the origin of sociality. Nonetheless, if presociality is a necessary step that, when coupled with a nest, provides the fodder from which more complex social associations may originate, then there has been ample kindling available during the long history of arthropods. At its simplest, parent-offspring associations abound in the fossil record, from marsupial Tanaidacea with preserved marsupia and whipspider mothers bearing their ► [brood](#) on their backs to numerous insects exhibiting either directly or indirectly analogous presocial behaviors. Examples of brood care among hemimetabolous insects have been recorded from Cretaceous

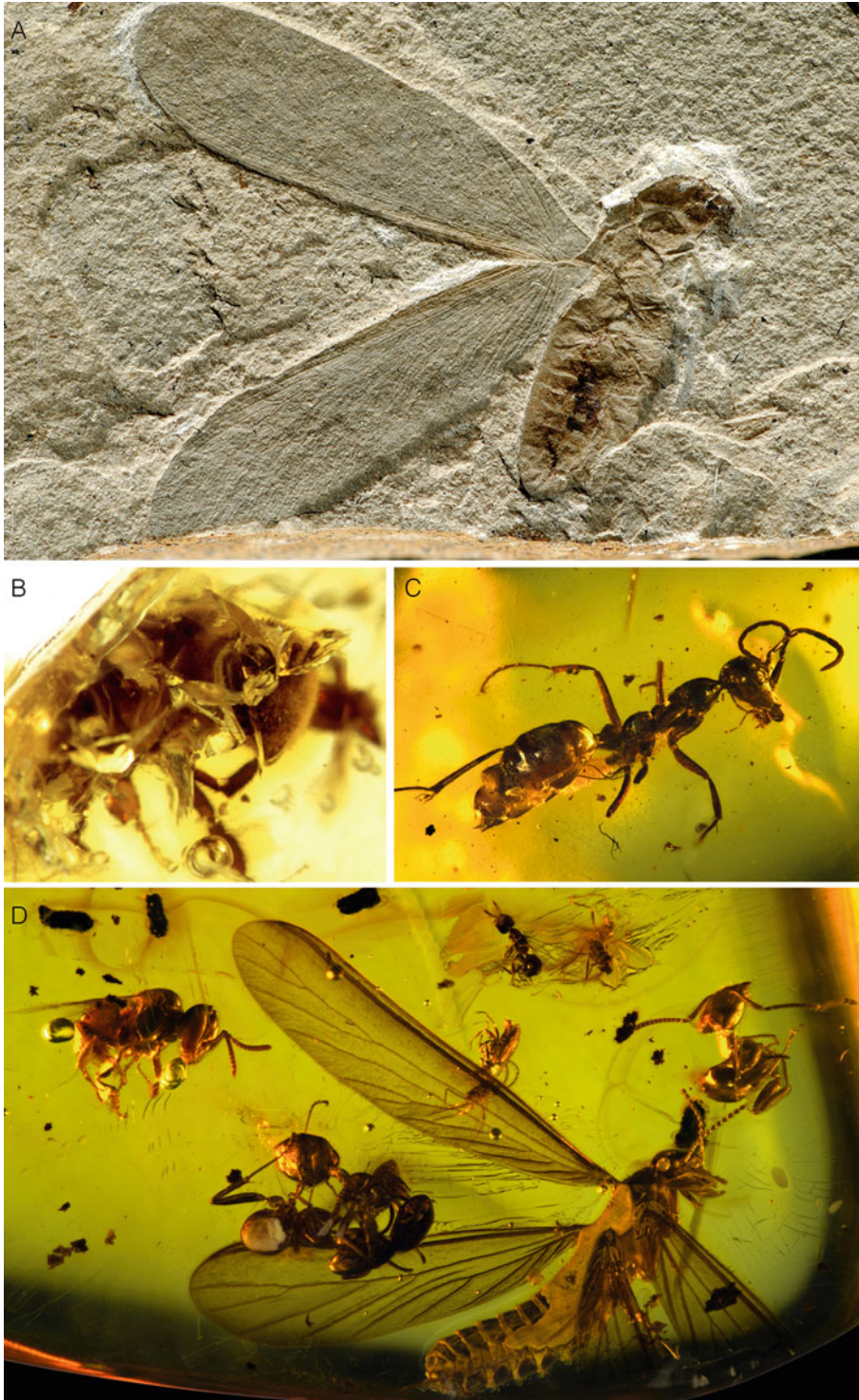


Fossil Social Insects, Fig. 3 The phylogenetic distribution of eusociality among insects. Triangle clade icons indicate estimated clade ages based on molecular divergence dating [8, 28, 30]; circles indicate oldest fossils known for lineages; black lines indicate lineages with

known fossils; dashed lines indicate lineages suspected to exist based on molecular estimates but without known fossils. Ant, aphid, halictid, termite, and *Apis* icons from Phylopic. *Ichnotaxon

earwigs (Dermaptera) and scale insects (Hemiptera), while similar behaviors have been recorded indirectly from Jurassic and Cretaceous carrion beetles (Silphidae). The simple presence of modern families of webspinners (Embiodea) and zorapterans (Zoraptera), all of which are today gregarious, living communally and with considerable brood care, attests to such behaviors as far back as the middle Cretaceous. Fossils revealing considerable maternal investment in their offspring, beyond simple brooding, although rare, are similarly preserved. Cryptocephaline leaf beetles have been recovered from the Miocene

and Eocene with fecal cases preserved, a structure initiated by the mother and later elaborated upon by the offspring for the purpose of protecting the larva from parasites and predators. As the fossil record is by its very nature fragmentary, we are undoubtedly missing ethologies that fail to leave behind a physical mark on the environment, and it is guaranteed that many ancient presocial behaviors have been lost to time. For example, as is increasingly revealed, communication calls of a protective nature, particularly substrate borne calls between mother and offspring, are not captured in the fossil record and yet, by their seeming



Fossil Social Insects, Fig. 4 Fossils of the eusocial trimvirate – termites, bees, and ants. (a) Among the oldest termites known, *Baissatermes lapideus* from the

Cretaceous Zaza Formation (~120 Mya) in Russia PIN 3064/8583; (b) *Cretotrigona prisca* in New Jersey amber (~68 Mya), the oldest eusocial crown-group bee AMNH

ubiquity and phylogenetic distribution, such behaviors must have been prolific among many lineages otherwise preserved as fossils. The study of specific behaviors and paleobiologies among ancient insects remains one of the ripest arenas for future investigation (Fig. 4).

Eusocial Insects

Isoptera: The Original Societies

First, there were ► [termites](#). Termites are the oldest known eusocial organisms by way of fossil record and molecular divergence estimates [6, 22]. Termite alates are known from lithified Cretaceous specimens from southern England, which predate the earliest ants, the next oldest eusocial lineage, by 30 million years (Fig. 3). Although ants and termites act as significant selective agents today, termites apparently had the world largely to themselves throughout the first half of the Cretaceous. A series of termite fossil taxa are known from at least eight Early Cretaceous fossil deposits, although only alate specimens have been recovered, most probably a result of the semi-aquatic landscapes that best preserve impression fossils. Alate termites would have emerged in nuptial flights as they do today, ending up caught in water and ultimately buried in shallow lakebeds, although some became ensnared in amber. From the Early Cretaceous, termites entombed in amber are recorded from Lebanon and Spain.

A remarkable feature of early termite fossils is that they do not belong to the earliest branching isopteran lineages. Instead, the oldest termite fossils diverged after the most recent common ancestor of all living termites [22]. This phylogenetic pattern is driven entirely by the now monotypic family ► [Mastotermitidae](#), a once cosmopolitan

lineage presently restricted to Australia. Fossils attributed to the still-living genus *Mastotermes* are known from Europe, Africa, Asia, and North America, while other genera of mastotermitids have been found in South and North America, Europe, Asia, and Australia (Fig. 5a) [22].

The over 3000 species of living termites are presently classified in nine families [14, 22], most of which belong to the grade of so-called lower termites, i.e., those species with simple guts harboring cellulolytic flagellates responsible for the degradation of lignocellulose to produce nutrients suitable for the termites. The lower termites encompass the extant families Mastotermitidae, Archotermopsidae, Hodotermitidae, Stolotermitidae, ► [Kalotermitidae](#), ► [Stylotermitidae](#), Serritermitidae, and ► [Rhino-termitidae](#). Many analyses consider Rhinotermitidae to be paraphyletic and, in some cases, also encompassing the serritermitids. Termites within these families feed directly on wood or grass and often, but by no means universally, build simpler nests within their food (i.e., single-site nesters living in wood), although harvester termites (Hodotermitidae), a few drywood termites (Kalotermitidae), and more derived rhinotermitids construct subterranean nests. All known Cretaceous termites belong to the lower termites, including a few that are placed in the extinct families Cratomastotermitidae and Archeorhinotermitidae [16, 22]. Most Cretaceous termites, however, belong to a dense grade of termites that intercalate between these lineages and which lack sufficient information as to be placed confidently as to family. These are collectively referred to as the “*Meiatermes* grade” of genera and reflect the remarkable diversity of termites during the period [14, 22].

The earliest-diverging termites, albeit not the earliest of fossils, are those of Cratomastotermitidae, known from alates preserved in the Early Cretaceous Crato deposits of northeastern

←
Fossil Social Insects, Fig. 4 (continued) C88720; (c) *Gerontoformica spiralis*, a stem-group ant preserved in Burmese amber (~99 Mya), among the oldest ants along with those in contemporaneous Charentese French amber; (d) tripartite social menagerie in Miocene-age Dominican

amber (~16 Mya). From left to right: the stingless bee *Proplebeia dominicana*, two *Azteca alpha* ant workers, an *Anoplotermes maboya* termite alate, and a single *Azteca alpha* worker



Fossil Social Insects, Fig. 5 An assortment of fossil termites. (a) *Garmitermes succineus* (Mastotermitidae) in mid-Eocene Baltic amber, with a worker ant of *Liometopum oligogenicum* gripping the tip of its extended leg AMNH BJH118. (b) A Miocene impression of a wing of *Gyatermes styriensis* (Archotermopsidae) from Styria, Austria, LMJ 204.148. (c) A partially preserved soldier of

Krishnatermes yoddha in mid-Cretaceous amber of northern Myanmar (Burma) AMNH JZBu183. (d) *Mastotermes anglicus* (Mastotermitidae) from the Eocene Bembridge Marls, England. (e) An Early Cretaceous alate of *Melqartitermes myrrheus* in Early Cretaceous amber of Lebanon AMNH LISOI

Brazil (113 Mya) [14]. These termites, along with the living and fossil species of Mastotermitidae, show many primitive features relative to all other termites and were characteristically quite large in body size. These two families retained numerous features, including several cockroach-like traits, not found in other termites. For example, cratomastotermitids retained dense crossveins and an archdictyon, while Mastotermitidae lost such features but continued to retain traits such as an anal fan in the hind wing, the lack of a complete basal suture for shedding of the wings, and laying of eggs in a vestigial ootheca-like structure. While Cratomastotermitidae are currently known only from a single locality in the Early Cretaceous, Mastotermitidae are known from the Early Cretaceous through to the present [22].

All other termites to the exclusion of Cratomastotermitidae and Mastotermitidae are classified in the Euisoptera [14]. Although there is some disagreement, many recent analyses recognize the families Archotermopsidae, Hodotermitidae, and possibly also the Stolotermitidae as comprising a monophyletic group Teletisoptera at the base of living Euisoptera [6], although the group arises from amidst the *Meiatermes* grade [16, 22]. Numerous taxa found throughout the Cretaceous collectively form a grade of species along the backbone of the euisopteran tree, comprising the aforementioned *Meiatermes* group. These taxa embody numerous plesiomorphies relative to surviving families of termites and, owing to this mosaic of primitive features as well as the absence of information for many critical traits, are not assignable to higher taxonomic groupings. Nonetheless, taxa from among their ranks inform us greatly of termite evolution, including the earliest evidence of the tripartite castes made famous by termites. Soldiers of *Krishnatermes* and *Ginormotermes* from the mid-Cretaceous are remarkably specialized [16], revealing that such novelties of development, physiology, chemistry, and behavior evolved early within termites, giving them not only the first societies but the first specialized defensive caste (Fig. 5c). These soldiers possessed mandibular traits primitively similar to those of modern-day Archotermopsidae. True fossils of

Archotermopsidae, however, are confined to the Cenozoic, where species of the genus *Archotermopsis* are known in Baltic amber, well outside of the distribution of living species for both the genus and family [22]. Fossil species of *Hodotermes* and *Zootermopsis* are described from impressions of alates from Asia and North America, respectively, while extinct genera such as *Ulmeriella*, *Parotermes*, and *Gyatermes* are also recorded from the Eocene through Miocene of Eurasia and North America. Interestingly, *Gyatermes* (Fig. 5b), from the Miocene of central Europe and Japan, includes some of the largest of all termites, rivaling in size those giants of the Neotropical syntermitine genus *Syntermes*. An extinct family, Termopsidae, is also known from this group, including only a single genus from the Eocene, although it was once confused with many living and fossil genera on the basis of primitive phenetic similarities. Stolotermitidae have few fossil occurrences, with extinct species of *Stolotermes* described from impressions from the Miocene of Japan and New Zealand, and the extinct genus *Chilgatermes* from the Oligocene of Ethiopia [22]. Presently, there is no definitive fossil record for Hodotermitidae.

The Isoisoptera comprise Kalotermitidae and Neoisoptera, the latter encompassing Stylotermitidae, Rhinotermitidae, and the extinct family Archeorhinotermitidae. The group extends to at least the mid-Cretaceous. Fossils of both Kalotermitidae and Archeorhinotermitidae are known from Burmese amber inclusions dating to the beginning of the Late Cretaceous. Kalotermitids, commonly referred to as drywood termites, are a family of modest diversity today and although there are several species described from the Cretaceous, the majority of fossils are recorded from Baltic, Dominican, and Mexican ambers, as well as impressions from North America, Eurasia, and New Zealand [22].

Neoisoptera are perhaps the most unequivocally monophyletic suprafamilial lineage of all termites, most easily recognized by the fontanelle, a distinctive opening of the frontal gland on the upper frons of the head capsule. The earliest evidence of neoisopterans comes from *Archeorhinotermes* in mid-Cretaceous amber from

northern Myanmar (Burma), while all other occurrences are confined to the Cenozoic [22]. Intuitively, Archeorhinotermitidae are sister to all other Neoisoptera [14]. Stylotermitidae, although today representing a single genus and 45 species, is recorded from at least as far back as the Early Eocene. Two extinct genera are currently recognized: *Parastylotermes* from the Early Eocene of northwestern India, the middle Eocene of Europe, and from the Eocene-Oligocene boundary to the Miocene of western North America, although the younger species are doubtfully placed, and *Prostylotermes* from the Early Eocene of India [22]. It seems *Prostylotermes* could be sister to *Parastylotermes* + *Stylotermes*. Occurrences of Rhinotermitidae, like stylotermitids, are confined to the Cenozoic, with an abundance of individuals and species preserved in Baltic, Dominican, and Mexican amber, as well as impressions from the Eocene through Miocene [22].

The vast majority of termite species today belong to the “higher termites,” all of which are placed in the family Termitidae. Unlike the lower termites, these include those groups with more diversified diets, complex guts, and more elaborate nesting. Termitids have also lost the intestinal cellulolytic flagellates, replacing them with a diversified flora of prokaryotes who assume a similar biotic function [5]. What drove this shift in gut microbiota and the flourishing of Termitidae relative to all prior termite lineages remains uncertain, but may have been driven by an early adoption of edaphophagous habits (consuming rich organic soils) during the Paleocene-Eocene [6]. Unfortunately, while fossil termitids abound in Miocene ambers, all of these are of derived subfamilies and belong to modern genera, such as the divers ► *Apicotermitinae* and ► *Nasutitermitinae* [22]. Estimates based on both morphological/paleontological and molecular data set an Eocene or Late Paleocene origin for Termitidae [6, 14], and it is from these epochs where our termitid fossil record amounts to just a single termitid. *Nanotermes issacae* is preserved in Early Eocene amber from northwestern India and, while definitively a termitid, it retains numerous generalized features. The only available

material is an alate and does not preserve sufficient details to place it within a given subfamily. It may very well represent a stem termitid. Regardless, *Nanotermes* presents a critical calibration point for understanding the early phases of the termitid origin and diversification, events unfolding in the context of the Paleocene-Eocene thermal maximum and dramatic climatic and floristic changes.

Hymenoptera

The order Hymenoptera is fertile ground for sociality. Most independent origins and the majority of eusocial species are here. But *within* Hymenoptera sociality is uncommon and fairly recent. The number of solitary parasitic wasp species is at least an order of magnitude greater than all social wasps, bees, and ants. The oldest fossil Hymenoptera are two contemporaneous symphytans from the Triassic Madygen Formation in Kyrgyzstan. By contrast, ants – the oldest social hymenopterans – appear in the fossil record in the Cretaceous about 130 million years later. All social Hymenoptera are within the ► *Aculeata*, a lineage defined by the modification of the ovipositor into a ► *stinger*. Aculeates appear in the fossil record during the Middle to Late Jurassic, beginning with the extinct family Bethyloynymidae.

Wasps

Virtually all social wasps are within the family Vespidae. The exception is the genus *Microstigmus* among the ► *spheciform* Crabronidae [24], which lacks a fossil record. Present evidence indicates two separate origins of vespid eusociality, in which case there are two monophyletic groups composed entirely of social taxa. One group, the Stenogastrinae, or hover wasps, contains approximately 60 species distributed throughout India and Southeast Asia. Because hover wasp castes are not fixed – all females retain the ability to reproduce – and colonies are very small, sociality is sometimes referred to as facultative. Other social vespids are distributed worldwide and encompass over a thousand species within the sister subfamilies ► *Vespiniae* (including yellow jackets, hornets) and Polistinae (including paper wasps, ► *Polistes*). Wasps

within Vespinae + Polistinae exhibit a wide variety of social structures, including taxa with fixed and morphologically differentiated reproductive castes.

The oldest vespid fossils date to the Early Cretaceous over 120 Mya with *Curiosivespa* and *Priorvespa* compression fossils from Russia. However, these and other early vespids belong to the Euparagiinae, Eumeninae, and extinct subfamilies, which lay outside of either Stenogastrinae or Vespinae + Polistinae [29]. In fact, there are no stenogastrine fossils, and the earliest fossil member of Vespinae + Polistinae does not occur until the Late Cretaceous. It is an ichnotaxon, *Brownichnus favosites* from the Cretaceous of Utah. *B. favosites* is described entirely from a single fossilized nest and, while originally contested as a social nest, it is now widely recognized as the earliest vespine and the earliest evidence for social behavior in vespids [31] (Fig. 3*). The age of the *B. favosites* is unclear, with estimates ranging between 86 and 66 Mya. Thus, vespid sociality likely began in the Late Cretaceous, after ants but perhaps approximately contemporaneous with social bees.

One of the most conspicuous hymenopteran groups today, *Polistes* paper wasps are known as early as ~55 Mya beginning with *P. vergnei* from the Menat Formation in France. Including this first occurrence, there are a total of six Cenozoic fossil *Polistes* species from compression formations in present day Austria (Miocene), France (Paleocene, Oligocene), and Germany (Oligocene, Miocene). Further cementing the preponderance of polistine fossils in Europe are three extinct monotypic genera: *Palaeopolistes*, *Palaeopolybia*, and *Protopolistes* from England and France. Despite the subfamily's present worldwide distribution, all but one of the ten known fossil polistine species are found in Europe. The exception is *Agelaia electra* – the only fossil member of the tribe Epiponini – from Miocene Dominican amber (Fig. 6a). Today *Agelaia* is locally extinct on Hispaniola and the other oceanic Caribbean islands, but is widespread in Central and South America.

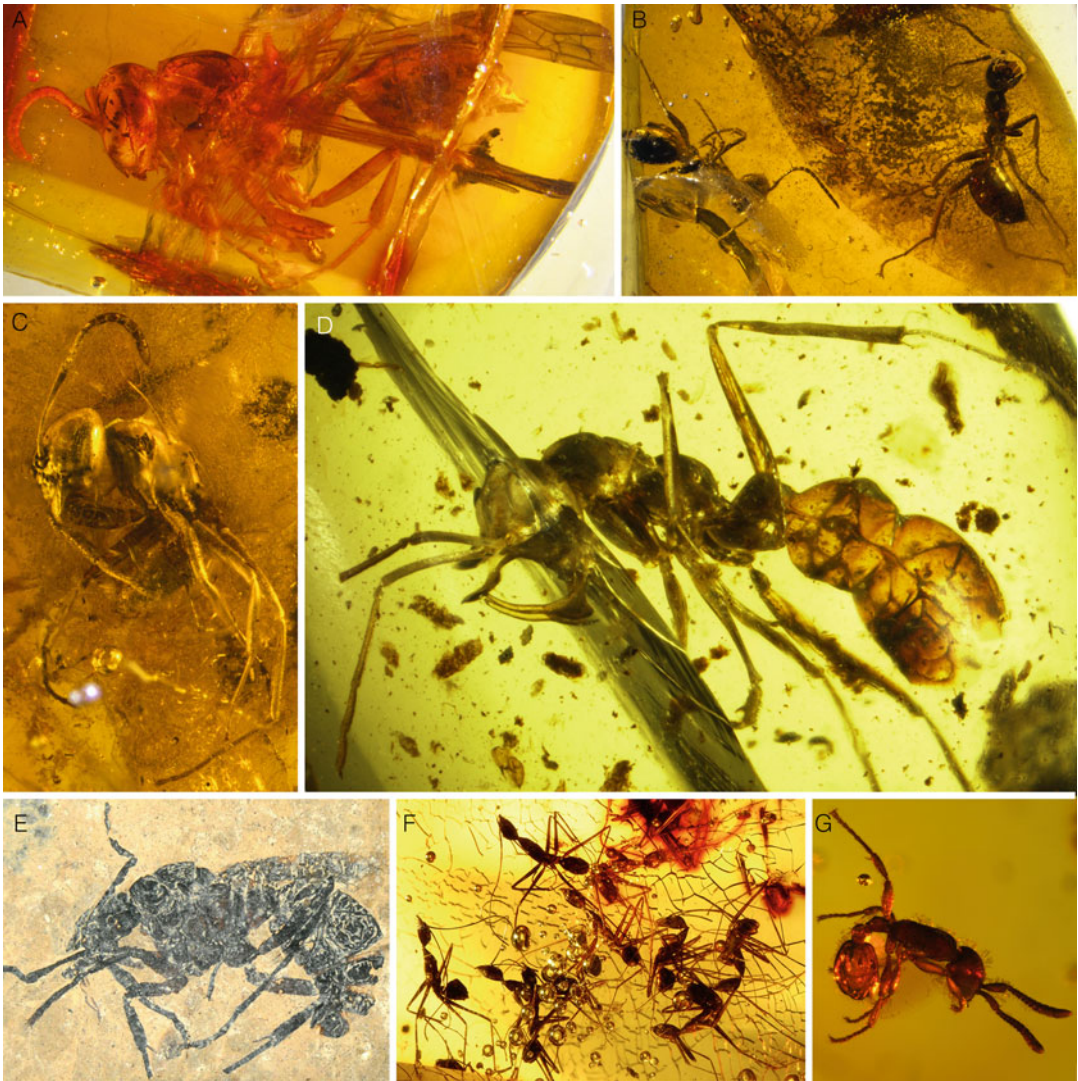
The record of the Vespinae also begins with the Menat Formation. *Paleovespa menatensis* co-occurs with *Polistes vergnei*, and although the

type specimen for *P. menatensis* was discovered in the 1950s, it was not described until 2006. *Paleovespa* is extinct, but eight fossil species are known from Menat, Baltic amber (Eocene), and the Florissant Formation in the United States (Eocene) indicating it was formerly distributed throughout the Northern Hemisphere. The paleontological record of the genus *Vespa* mirrors its present distribution: fossils occur in Baltic amber, as well as Oligocene and Miocene compression deposits in Germany, Croatia, and China. Today, the nocturnal wasp genus *Provespa* comprises three species distributed throughout South Asia. The single fossil species from the Shanwang Formation in Shandong, China (Miocene), indicates that the genus once occurred at a significantly higher latitude, although it is not clear if this has bearing on the origins of the group.

Ants: Dynastic Succession and the Path to Ubiquity

The ant fossil record begins at approximately 99 Mya and comprises approximately 750 species described from over 70 deposits worldwide [2]. The majority of fossil deposits known are present in North America, Europe, and Asia. The Southern Hemisphere, with only nine ant-yielding deposits, remains a major paleomyrmecological gap [23]. At a broad view, the ant fossil record can be effectively cleaved into two temporal “stages” based on the phylogenetic affinities of taxa and the abundance of ants relative to other insects. The first stage spans the Cretaceous (~99–66 Mya) when the majority of ant fossils are distinct from extant lineages and appear to represent a relatively minor component of the insect fauna [3]. The Cenozoic (66 Mya–present) marks a second stage, in which ants rapidly increase in ecological impact (Fig. 2) and all fossil species share derived traits with living lineages.

The oldest definitive ant fossils are recovered from approximately contemporaneous 100–99-million-year-old amber from Myanmar (Burma) and France. In total, there are seven ant-yielding fossil localities of Cretaceous age: Charentese amber from France (~99 Mya); Burmese amber (~99 Mya); Raritan amber from New Jersey (~92 Mya); mudstones from Kzyl-Zhar,



Fossil Social Insects, Fig. 6 (a) *Agelaia electra* (Polistinae) in Miocene Dominican amber (16 Mya) AMNH DR141040. (b) *Sphecomyrma freyi* (Sphecomyrminae) workers preserved in New Jersey amber (92 Mya). *S. freyi* belongs to an extinct stem group and is a morphological mosaic of ant and wasp-like features AMNH NJ943. (c) *Kyromyrma neffi* (Formicinae) in contemporaneous New Jersey amber is the oldest described crown ant – a member of an extant subfamily AMNH NJ1115. (d) A haidomyrmecine “hell ant”

Linguamyrmex vladi in Burmese amber (99 Mya) with scythe-like mandibles and a cranial horn-like appendage AMNH BuPH01. (e) An alate of *Cyrtopone striata* (Ponerinae) from the Eocene Messel Formation of Germany (47 Mya) SMFMEI1392 (from www.AntWeb.com, photographer: Sonja Wedmann). (f) *Leptomyrmex neotropicus* workers (Dolichoderinae) in Dominican amber AMNH DRJVE654. (g) The army ant *Neivamyrmex ectopus* (Dorylinae) in Dominican amber

Kazakhstan, and Orapa, Botswana (~91 Mya); Taimyr amber from Siberian (~87 Mya); and Canadian amber from Alberta (~78 Mya). There are no definitive ant fossils older than 100 million years, despite well sampled Early Cretaceous

fossil insect localities in Brazil, China, and Europe. There are also no ant fossils between 78 Mya and the K–Pg extinction event that ended the Cretaceous 66 Mya. Very few fossil

insect localities are known from this time period and none with significant sampling.

Out of nearly 50 described Cretaceous ant species, the majority are members of extinct stem lineages [3]. A stem lineage possesses some features of what is termed the crown group – in this case, crown-group ants are all living species and their common ancestor. Stem ants possess some, but not all, of the synapomorphies of crown ants and are more closely related to crown ants than any other hymenopteran lineage but do not fall within crown ants. Stem ants therefore diverged from extant ant lineages prior to the most common recent ancestor of extant ants. The most stable synapomorphy among fossil and extant ants is the metapleural gland, an organ not found in any non-ant aculeate and visible as a slit-like or widened opening near the posteroventral margin of the mesosoma in workers and queens. Stem ants possess a metapleural gland but do not possess the distinct elongated first antennal segment or reduced thoracic sculpturing seen in extant workers. A contentious group of winged aculeates, the Armaniidae, is known exclusively from Cretaceous compression fossils and has been proposed as an early ant lineage [23]. So far, no armaniids have been preserved with a clear lateral view of the mesosoma, so the presence of the metapleural gland remains unclear. Here we treat the Armaniidae as *incertae sedis* within Aculeata.

Some stem-ant taxa are generalized morphological intermediates between living ants and their solitary relatives. The first known Cretaceous ant, *Sphecomyrma freyi* from New Jersey amber, was discovered over 50 years ago and cleanly fit early predictions of ancestral ant morphology [33] (Fig. 6b). This initial discovery would set assumptions of ant evolution for decades: that there was a gradual shift in geologic time from solitary wasp ancestors to modern ants, as evidenced by generalized intermediate forms. However, discoveries over the past 10 years reveal that there was a striking diversity among stem-ant taxa as a result of very early adaptive radiations. Examples include haidomyrmecine “hell ants” with dorsally expanded scythe-like mandibles. Some haidomyrmecine taxa, such as *Ceratomyrmex* and *Linguamyrmex*, possessed dramatic horn-

and paddle-like cranial expansions that likely interfaced together with mandibles to capture prey (Fig. 6d). Hell ants are known from French, Burmese, and Canadian amber, indicating that they persisted for at least 20 million years with a significant broad range. With no modern analog, hell ants and other unique Cretaceous taxa exhibit phenotypes outside the bounds of modern ant morphology. Some stem ants, such as species of *Gerontoformica*, mirror diversity seen in modern lineages including wide ranges of cuticular sculpturing, body size, and pilosity (Fig. 1c). These early ants have been placed in the extinct subfamily Sphecomyrminae, although this group may be paraphyletic and is in need of revision. The monotypic subfamily Brownimeciinae from New Jersey amber has been recovered as sister to all extant ants, consistent with the theme of paraphyletic lineages outside of crown ants [3]. Because these early ants belong to stem lineages, they represent significant extinctions. Stem ants do not occur in the fossil record after 78 Mya in Canadian amber and it is not yet clear if these extinctions relate to the K–Pg event.

Only two described Cretaceous ant species are definitely attributable to extant lineages within crown-group ants. *Kyromyrma neffi* from New Jersey amber is the earliest described formicine and clearly exhibits an acidopore (Fig. 6c). *Chronomyrmex medicinehatensis* from Canadian amber is the earliest uncontested dolichoderine and a putative member of the extant tribe Leptomyrmecini. Today, Formicinae and Dolichoderinae are among the “big four” ant subfamilies that contain the majority of species. Seven other Cretaceous species are described within crown ants and extant subfamilies, although these placements must be seen as provisional without additional material [2]. There are reports of formicine, dolichoderine, and ponerine workers from ~99-million-year-old Burmese amber, but these remain undescribed. Molecular-based estimates suggest that crown ants emerged sometime in the Early Cretaceous, perhaps as long as 40 million years before the earliest known ant fossils. These estimates and the presence of crown ants in Burmese amber suggest that crown ants and stem ants overlapped for at least ~20 million

years and as long as 60 million years. During this period of co-occurrence, stem ants appear to have been more abundant and morphologically diverse than crown ants. However, the earliest ant lineages were eventually succeeded by their modern counterparts, who continued to radiate into the Cenozoic.

There is very strong evidence for eusociality in the Cretaceous. The earliest stem ants exhibited reproductive division of labor and maintained morphologically differentiated castes. It is difficult, if not impossible, to assign fossils of morphologically distinct castes to the same species. However, congeneric workers and reproductives are described from the earliest ant-yielding fossil deposits in France and Myanmar (Burma). Multiple stem-ant genera, including haidomyrmecines, are now known from both alate and worker castes [3]. Congeners are united on the basis of synapomorphies, for example, alate (winged), delate (shed wings), and worker (permanently wingless) forms of haidomyrmecines have the same specialized mandibles. Morphological differentiation between stem-ant workers and queens appears to have been slight, and there is yet no evidence of subcaste specialization in these earliest workers. Several stem-ant taxa are described from dealate specimens. The presence of dealates in the Cretaceous is significant. Among insects, wing removal occurs only in termites and ants following a nuptial flight. The resin capture of dealates also indicates that the earliest ant queens would have been foraging and not clastral founders as are many extant formicoid ants. With respect to foraging behavior, there are preserved aggregations of Cretaceous worker ants in the same amber specimen: a single piece of Burmese amber has been described with 11 conspecific worker inclusions [3]. Ants comprise less than 1% of insect inclusions in Burmese amber, strongly suggesting that these aggregations reflect social behavior. Because there appears to have been just one origin for sociality in ants, all crown ants from the Cretaceous are presumed to have been eusocial.

The last glimpse into Mesozoic ants is 78-million-year-old Canadian amber, which bares both stem and crown ants. The subsequent 20 million year long gap in the ant fossil record is

broken by a single anueretine ant, *Napakimyрма paskapooensis*, from the ~58-million-year-old Paskapoo formation in Alberta, Canada. The subfamily ► *Aneuretinae*, represented today by a single species in Sri Lanka, was much more broadly distributed in the past. Fossil aneuretines are described throughout North America, Europe, and Asia, although most of these descriptions are debated. The next oldest Cenozoic taxon, *Ypresiomyrma rebekkae* from the ~55-million-year-old Fur Formation in Denmark, also belongs to a relict subfamily. Today, all ► *myrmeciine* taxa are endemic to Australia and New Caledonia. *Ypresiomyrma* and other fossil myrmeciines from North America, South America, and Europe indicate that this lineage once occupied a much larger distribution and so the product of numerous local extinctions [1]. The remains of *Y. rebekkae* are considered to be the result of an overwater mating flight, providing the earliest fossil evidence of nuptial swarming. ► *Platythyrea dluskyi* is the only ant yet described from ~54-million-year-old Oise amber from France and remains the earliest undisputed described ► *ponerine* [23]. *P. dluskyi* is also the oldest species belonging to an extant genus, which highlights the significant morphological stasis that defines Cenozoic ants, relative to the Cretaceous. Slightly younger Fushun amber preserves the oldest definitive myrmicine as well as the oldest ► *Camponotus* species, *C. tokunagai* [2]. Although there are significant instances of biogeographic shifts evidenced by the fossil record, all Cenozoic taxa are crown ants, and nearly all belong to extant subfamilies. The sole extinct crown-ant subfamily is the Formiciinae (N.B. not Formicinae), a remarkable group of six enormous species known from Eocene alate impression fossils from Great Britain, Germany, Wyoming, and Tennessee. The largest formiciines had a wingspan of 14 cm and so rank among the largest Hymenoptera past or present. Formiciine workers have not been found, and the phylogenetic position of this lineage remains unclear.

The scientific study of fossil ants began with Eocene-age Baltic amber. Gustav Mayr, Ernest André, and William Morton Wheeler each produced significant monographs of ants from Baltic

amber – which is still the most species-rich fossil ant deposit fauna – between the mid-nineteenth and early twentieth century. Highlighting the abundance of this material, Wheeler inspected over 9500 specimens, which at the time were delimited into 92 species within 32 genera. Today there are 134 species and 56 genera. Included among these species are the oldest members of *Agroecomyrmecinae*, ► *Dorylinae*, and *Proceratiinae*.

As Wheeler noted and others have since corroborated, many Baltic amber genera are presently distributed in Southeast Asia and Australasia. The weaver ants constitute a key example. While there are two extant species of ► *Oecophylla* – *O. longinoda* in Sub-Saharan Africa and *O. smaragdina* in South Asia and Australia – the presence of *Oecophylla* in Baltic amber suggests that the group may have originated in Europe. Indeed, other fossil *Oecophylla* species in Great Britain, France, and Germany indicate that the group may have first radiated in the Palearctic. Other presently tropical genera with a presence in Baltic amber include *Gesomyrmex*, *Pristomyrmex*, *Pseudolasius*, *Stigmatomma*, and *Vollenhovia*. *Gesomyrmex* is today endemic to Southeast Asia but also present in Bitterfeld and Rovno ambers as well as impression fossils in Germany, Russia, and Croatia from between 47 and 18 Mya [23]. The Palearctic harbored tropical genera until at least the end of the Miocene. ► *Polyrhachis*, today found only in the Old World tropics, is known from the Late Miocene of Greece (6 Mya) [2].

The Eocene deposits of North America lay in stark contrast to the dynamic faunal shifts of the Palearctic during the last 40 million years. Nearctic fossil deposits such as Green River and Florissant reflect high levels of biogeographic consistency. A recent comparison of biogeographic affinities for fossil and modern ant taxa reveals that all living genera found in Eocene and Miocene Nearctic fossil localities are still present in the Nearctic today [19]. Some members of Nearctic communities appeared long ago. The Kishenehn formation of Montana, USA (46 Mya) preserves the oldest living members of ► *Crematogaster* and ► *Pseudomyrmex* – genera

still found in North America [2]. Approximately 16-million-year-old Dominican amber is the second most fossiliferous ant deposit. While over one-third have gone locally extinct and are no longer found on Hispaniola, almost all Dominican amber genera are extant in the Neotropics. Included in Dominican amber are the earliest ► *fungus-farming ants* and direct evidence of trophophoresis (► *Acropyga* and ► *Azteca*). In the case of *Acropyga*, a remarkable amber fossil preserves an alate queen with a mealybug mutualist in her mandibles. *Azteca* ants are no longer found on the Greater Antilles, but comprise up to half of all Dominican amber ant inclusions. Hyperdominant species such as *Azteca alpha* are largely responsible for driving the pattern of increasing ant abundance throughout the Cenozoic (Fig. 2).

Key paleomyrmecological questions remain unanswered. As evidence of the Cretaceous adaptive radiation of stem ants continues to amass, we still do not know why this multitude of diversity died out while extant ant ancestors marched toward ubiquity. The 20-million-year gap between the last Cretaceous and earliest Cenozoic ant fossils further obfuscates our estimates of how and when these ants went extinct. Fossil deposits in Alaska, India, France, North Carolina, and China that temporally straddle this gap may help to crack these mysteries. The phylogenetic integration of molecular and morphological data will also improve our sense of ant evolution. Most ant fossils belong to living lineages and so provide important clues into the history of the “little things that run the world.”

Bees: Preeminent Pollinators of the Past

Quite unlike the two aforementioned members of the social triumvirate, eusociality is not characteristic of all bees. The bees comprise a diverse monophyletic group of over 20,000 extant species, more than termites and ants combined [25]. Among these, social species are comparatively few and derive from a number of independent origins rather than a single origin each in Isoptera and Formicidae. Social bees amount to less than 7% of the global bee fauna, the most noticeable of which are the three social tribes of corbiculate

bees: the ► **bumble bees** (Bombini), ► **stingless bees** (Meliponini), and ► **honey bees** (Apini).

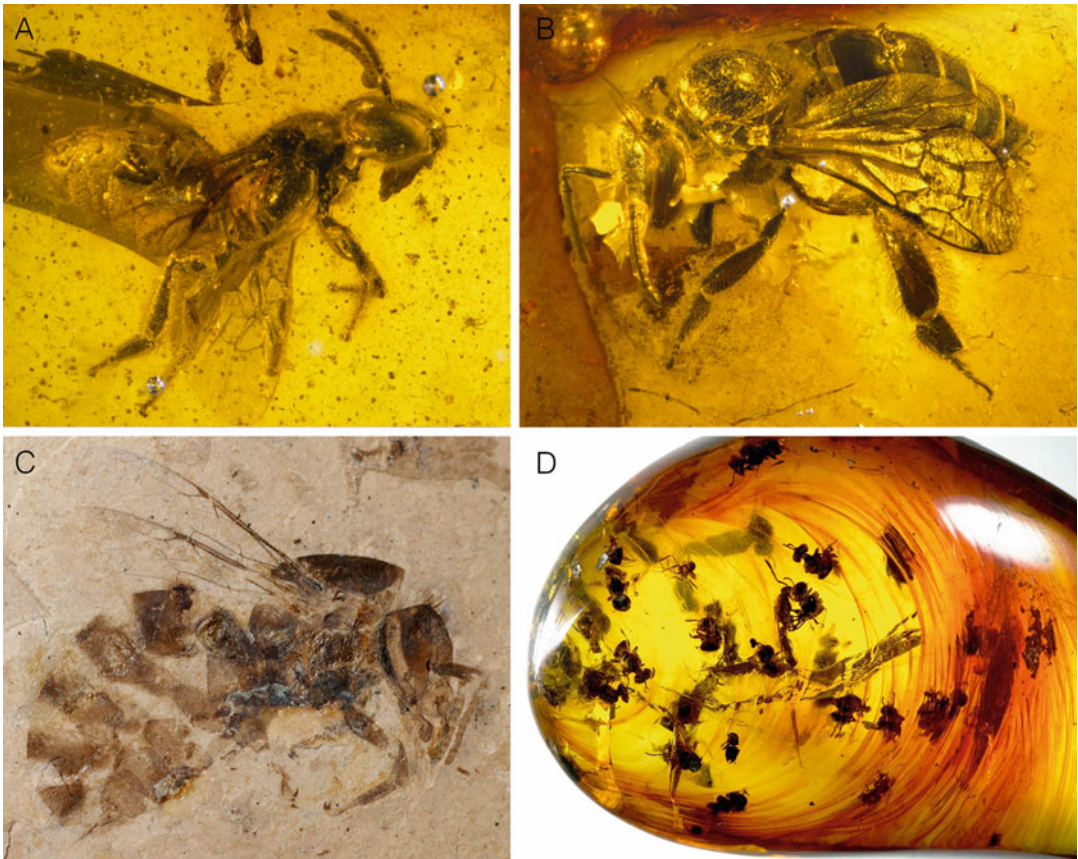
In further contrast to ants, there are comparatively few fossil bees, with fewer than 200 documented extinct species [27]. Many of these do not belong to any of the known social lineages, yet most of the actual specimens are from social taxa, even as they represent few species. That is, most fossil bee *species* are of solitary taxa, yet most *specimens* are of social bees.

The fossil record of bees as a whole is sparse and largely confined to a few deposits within a restricted subset of epochs and stages. This record is also heavily biased in composition not only toward taxa with numerous and abundant workers, especially those who collect resins such as stingless bees, but to taxa occurring predominantly in forests, with the caveat that even then the preserved fauna is scarcely reflective of melittological diversity. That bees are particularly rich in arid regions naturally means there is a considerable absence of information as such environments, lacking the water to rapidly sediment over remains, are entirely lacking in our record of bee history. In effect, we look through a glass darkly in attempting direct observation of the early stages of bee evolution, and so that to extrapolate from apparent absences would be unwise. That is, absences in the fossil record are often not analogous to present-day ecological absences. Despite the considerable temporal and spatial lacunae in our sampling of bees from the fossil record, those few elements available do provide some clues toward a greater understanding.

Among the seven families of bees generally recognized today [25], eusocial species are found in the ► **Halictidae** and Apidae. Within the Halictidae, social species are mainly found in the genera ► **Lasioglossum** and ► **Halictus** in the Halictini, and *Augochlora* and *Augochlorella* in the Augochlorini, collectively accounting for three independent origins of such societies. There are also instances of facultatively eusocial species within both tribes, such as the facultatively eusocial and nocturnal ► **Megalopta**. Indeed, there is considerable lability to social evolution among the halictids, with reversions from a eusocial ancestry to solitary life histories

in addition to the aforementioned cases in which an individual species may be solitary or social depending on the environmental context. Presently, the earliest definitive fossils of Halictidae date to the Eocene, of which there are species in Baltic amber and as compressions from British Columbia. All of the known fossils belong to the Halictinae, and most of these are known from the Miocene, particularly in Dominican amber. However, none of the species represents a eusocial taxon, and aside from providing important calibration points, the present halictine fossil record does not give direct insights into their social evolution.

Like the various eusocial lineages of halictids, there is no fossil record for the xylocopine tribe Allodapini. In fact, fossil occurrences for the entire subfamily Xylocopinae are scant, and while individuals of the large carpenter bees (*Xylocopa*) are recorded from Miocene and Eocene-Oligocene deposits of China, Europe, and North America, occurrences of other xylocopines are few or lacking. Aside from the handful of fossil *Xylocopa*, there is but a single specimen of the small carpenter bees (*Ceratina*) from the Eocene-Oligocene boundary of Florissant, Colorado, but attribution of this poorly preserved specimen to genus remains uncertain. The only remaining Xylocopinae in the fossil record are three species of an extinct genus, *Boreallodape*, in Baltic amber, which is sometimes found in large numbers within an individual piece of amber [11] (Fig. 7a). *Boreallodape* is distinct from any living tribes of Xylocopinae and has been placed in a tribe of its own, as Boreallodapini, apparently the sister-group of the Allodapini. Although traditional hypotheses considered solitary life to be ancestral in the Allodapini, recent studies suggest that group-living behavior is instead ancestral. Although still speculative, if the occasional abundance of individuals within a single piece of amber is an adumbration of some level of social interaction in these bees, then it could be that sociality, to one degree or another, is ancestral to the combined clade of Boreallodapini + Allodapini. Social behavior in *Boreallodape* must remain a mere hypothesis for now. Until fossil material can provide a more



Fossil Social Insects, Fig. 7 Representative Cenozoic fossil bees. (a) *Boreallodape mollyae* (Boreallodapini) in mid-Eocene Baltic amber AMNH BBS153. (b) A worker of *Thaumastobombus andreniformis* (Electrapini) in Baltic

amber AMNH BJH164. (c) An Oligocene impression fossil of a worker of *Apis henshawi* (Apini) from Rott, Germany. (d) An aggregation of workers of *Proplebeia dominicana* (Meliponini) in Miocene Dominican amber

direct determination, the melittological fossil record is limited in what it can reveal of xylocopine sociality.

In contrast to Halictidae and Allodapini, the corbiculate bees have one of the better-documented records among bees, or at least a preponderance of individuals for a subset of species [27]. The corbiculate bees include the most iconic of bees and of social insects, the bumble bees (tribe Bombini), stingless bees (tribe Meliponini), and honey bees (tribe Apini). Honey bees alone account for a vast literature on the nature and evolution of social interactions and colonial life, and collectively the study of these three lineages dominates the history and current investigation of sociality in bees. A fourth

corbiculate tribe completes the group as we understand them today, with the ► [orchid bees](#) (tribe Euglossini) representing the largely solitary or communal cousins of the other corbiculate tribes, although cases of semisocial or even primitively eusocial behavior have been discussed for some species of *Euglossa*.

The corbiculate bees are a monophyletic group most closely related to the wholly solitary bees of the tribe Centridini. Relationships among the tribes of corbiculate bees remain controversial, although most analyses support a single origin of eusocial behavior within the lineage. Bumble bees occupy the primitively eusocial behavioral grade, while stingless bees and honey bees are both highly eusocial, with the distinct queen and

worker castes so characteristic of such societies. While many analyses consider honey bees and stingless bees to be most closely related, so that highly social behavior evolved once from a primitively eusocial corbiculate ancestor, this hypothesis is not universally accepted. Others contend, with some justification, that the conditions observed in Apini and Meliponini are independent evolutionary novelties. There are at least three groups of extinct corbiculate bees that cannot be placed within any of the modern tribes. Two of these include species with morphologically distinct workers, indicating highly social behavior [11]. The extinct tribes Electrapini and Melikertini – the latter of which recovered as the closest sister to the stingless bees – are known from the Eocene of Europe and Asia, with individuals preserved both as amber inclusions and compressions. The third extinct group resembles the workers of bumble bees and was perhaps of a similar primitively social grade. Integrating these extinct groups into analyses with modern taxa recovers single origins for both general eusociality and highly social behavior among corbiculate bees [12].

The record for the surviving corbiculate tribes is heterogeneous, and by no means are the individual tribes or genera equally represented. Orchid bees have the poorest record, with fewer than ten individuals known as inclusions from the Miocene amber deposits of Chiapas, Mexico, and the Dominican Republic, as well as material in Pleistocene or younger copal from Colombia. These represent species of the three pollen-collecting genera *Euglossa*, *Eufriesea*, and *Eulaema*. While they provide important calibration points and reveal the presence of orchids within their respective paleoenvironments (in lieu of fossil orchids themselves), each is remarkably modern in character. Those in Dominican amber do provide interesting historical biogeographic points, given that euglossines are today absent from the fauna of Hispaniola. A poorly preserved compression of a corbiculate bee from the Eocene Green River shales of Wyoming and Utah, USA, had a wing venation that most closely approximates that of Euglossini. However, other characters of importance for determining anything other than a phenetic placement among

corbiculates are not preserved. The genus, dubbed *Euglossopteryx*, given the similarity of wing venation to Euglossini, could represent a stem-group orchid bee, or could be a stem group to Bombini.

Bumble bees, like the orchid bees, have a piddling fossil record, with only slightly more material available. All are known from compressions of various degrees of completeness, and in a few cases preserved solely as wings. This sampling of fossil bombines has recently been reviewed, applying morphometric tools to determine the phenetic similarity in shape space between each and the breadth of subgeneric clades across *Bombus*. Interestingly, most of the compressions most closely aligned with the subgenera *Cullumanobombus*, *Melanobombus*, and *Mendacibombus*, the last is the earliest diverging of the surviving bumble bee clades. Two groups from the Oligocene appear to represent extinct subgenera along the stem leading to crown-group *Bombus*, but their placement is solely based on the phenetic wing-shape space and so requires cladistic confirmation by integrating further characters from elsewhere on the body. Presently, the record of bumble bees, such as it is, provides few insights into their evolution beyond that what can be observed is consistent with our understanding based on modern diversity.

Meliponini and Apini together account for the majority of fossil bee specimens, and one species alone is known from well over 10,000 workers. The extinct stingless bee *Proplebeia dominicana* from the Miocene amber of the Dominican Republic is one of the most abundant inclusions in these deposits, and individuals are commonly sold in gem and mineral stores (Fig. 7d). Stingless bees also include the oldest definitive record of a crown-group bee, a worker of the meliponine *Cretotrigona prisca* recovered in Maastrichtian-aged amber from New Jersey, USA [10, 26] (Fig. 4b). This attests to the previous presence of stingless bees on the Appalachia landmass of Mesozoic North America, relatively shortly before its joining Laramidia as the Western Interior Seaway closed. *Cretotrigona prisca* also provides an absolute minimum age for highly eusocial behavior among corbiculates at the latest Cretaceous. Where known, stingless bees are preserved solely

in amber and copal, with species in Dominican, Mexican, Sicilian, Ethiopian, and Baltic ambers. Species in amber are of extinct genera, while those in copal are not only of modern genera but almost exclusively still-surviving species. While *Proplebeia* in Dominican and Mexican ambers are abundant, those of the other genera are often rare.

Fossil honey bees are documented from numerous Oligocene and Miocene deposits, mostly across Eurasia. There is a preponderance of extinct species that belong to a grade leading to a crown-group clade comprising the modern subgenera *Micrapis* (the ► [dwarf honey bees](#)), *Megapis* (the ► [giant honey bees](#)), and *Apis s.str.* (the cavity-nesting honey bees) within the genus *Apis*. Interestingly, the diversity of honey bees has declined over time, leaving us fewer species today than what once occurred [21]. This pattern is all the more remarkable when we recall that the fossil record is fragmentary, revealing only a portion of the diversity that was once present. In addition, the record nicely documents changes in traits such as forewing venation, showing a gradual shift in the position of veins through time and ultimately leading to the unique pattern we observe in modern *Apis*. While most available fossils belong to groups other than the modern subgenera, at least one can be assigned to a living subgenus. *Apis lithohermaea* from the Miocene of Japan, represented by a worker preserved in soft diatomite, is a giant honey bee. Most critical of all, the fossil record of *Apis* is vital to understanding the historical biogeography of honey bees. While today all honey bees have a native distribution in the Old World, during at least the Miocene they occurred in western North America [15]. *Apis nearctica* has been recovered from mid-Miocene shales of central Nevada and demonstrates the dangers of basing ancient biogeographic patterns solely on the present-day occurrence of living species. Like horses, ginkgoes, and *Ailanthus*, honey bees were once native to the New World but became extinct and were subsequently reintroduced by humans during the colonial era.

Conclusion

Between what matters and what seems to matter,
how should the world we know judge wisely?

There may be no satisfactory answer to E.C. Bentley's question, but our few glimpses into ancient life should at least be cautionary, demanding that we temper our extrapolations and ultimate conclusions, especially when based solely on our modern diversity and in the absence of sobering evidence from the fossil record. An ignorance of the past, even the recent past, leads to vanity, flattering ourselves in oversimplified, even foolhardy, interpretations of events.

At its simplest, diversity is shaped by two forces: origination and extinction, the "alpha and omega" of evolution [13]. The former builds diversity and disparity into the phylogenetic branches of life, while the latter prunes the tree. As previously noted, most life that has ever existed is now gone, having fallen prey to a multiplicity of stochastic events in the nearly four-billion-year history of life on our planet. The same is true of social insects. Their modern societies, for all of their glory and wonder, are a mere shadow of the variety that once existed, and each is vastly removed from the paleoecological, paleoclimatological, and sundry abiotic contexts in which sociality originated. The selective pressures we observe acting on modern insect societies may account for their persistence and maintenance in a proximate sense, but may be divergent from the ultimate causative pressures that first brought them forth from presocial progenitors.

Eusociality is a recent development in the context of other major innovations in the history of life, even in the grander history of insects. While sociality has been a principal actor in the ecological success of some insect lineages – Termitidae, higher ants, social wasps, and corbiculate bees – it has been a minor player in the greater triumph of insects, and has not apparently conveyed any

great power to many social groups (e.g., many lower termites, halictine bees). Social insects, with all of their ecological heft, account for the tiniest fraction of insect diversity. Success is best judged as a complex, hyperdimensional space rather than a linear spectrum. If considering biomass, breadth of geographic coverage, and ecological lability, then the triumvirate of social insects – termitids, ants, and corbiculate bees – are unquestionably successful.

Sociality does not promote diversification, nor is it a bulwark against extinction. Termites and ants, for example, were social for tens of millions of years before independent events promoted a radiation of species in select subgroups of their respective ranks. Similarly, many social lineages have experienced declines in diversity, such as the reduction in the number of tribes of corbiculate bees or the gradual reduction in species of honey bees since the Miocene, a pattern that mirrors the loss of species in another highly social genus – *Homo*.

In the nearly half century since the last overview of social insect antiquity, the records of these various lineages have been transformed. When last summarized, there was a single occurrence of termites and ants in the Cretaceous, none for the bees [7]. The diverse Cenozoic faunas of Dominican and Mexican amber had not yet been thoroughly explored, and even the well-trodden trails of Baltic amber – the most intensely studied source of insect inclusions – took us down new and unexpected avenues of illumination of social-insect evolution. New deposits, technologies, and tools brought forth not only a wealth of then unknown diversity, but transformed the manner by which such fossils are routinely evaluated. Just as the last review [7] was revelatory compared to the one that preceded it [4], it is exciting to imagine what discoveries await us in the half century to come.

Cross-References

- [Acropyga](#)
- [Azteca](#)
- [Dwarf Honey Bees](#)
- [Giant Honey Bees](#)

References

1. Archibald, S. B., Cover, S. P., & Moreau, C. S. (2006). Bulldog ants of the Eocene Okanagan Highlands and history of the subfamily (Hymenoptera: Formicidae: Myrmeciinae). *Annals of the Entomological Society of America*, 99(3), 487–523.
2. Barden, P. (2017). Fossil ants (Hymenoptera: Formicidae): Ancient diversity and the rise of modern lineages. *Myrmecological News*, 24, 1–30.
3. Barden, P., & Grimaldi, D. A. (2016). Adaptive radiation in socially advanced stem-group ants from the Cretaceous. *Current Biology*, 26(4), 515–521.
4. Bequaert, J. C., & Carpenter, F. M. (1941). The antiquity of social insects. *Psyche*, 48(1), 50–55.
5. Brune, A., & Dietrich, C. (2015). The gut microbiota of termites: Digesting the diversity in the light of ecology and evolution. *Annual Review of Microbiology*, 69, 145–166.
6. Bucek, A., Šobotník, J., He, S., Shi, M., McMahon, D. P., Holmes, E. C., Roisin, Y., Lo, N., & Bourguignon, T. (2019). Evolution of termite symbiosis informed by transcriptome-based phylogenies. *Current Biology*, 29(21), 3728–3734.
7. Burnham, L. (1978). Survey of social insects in the fossil record. *Psyche*, 85(1), 85–133.
8. Cardinal, S., & Danforth, B. N. (2013). Bees diversified in the age of eudicots. *Proceedings of the Royal Society B: Biological Sciences*, 280(1755), 20122686.
9. Costa, J. T. (2006). *The other insect societies*. Cambridge: Harvard University Press, xiv+[i]+767 pp.
10. Engel, M. S. (2000). A new interpretation of the oldest fossil bee (Hymenoptera: Apidae). *American Museum Novitates*, 3296, 1–11.
11. Engel, M. S. (2001a). A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). *Bulletin of the American Museum of Natural History*, 259, 1–192.
12. Engel, M. S. (2001b). Monophyly and extensive extinction of advanced eusocial bees: Insights from an unexpected Eocene diversity. *Proceedings of the National Academy of Sciences, USA*, 98(4), 1661–1664.
13. Engel, M. S. (2004). Geological history of the bees (Hymenoptera: Apoidea). *Revista de Tecnologia e Ambiente*, 10(2), 9–33.
14. Engel, M. S., Grimaldi, D. A., & Krishna, K. (2009). Termites (Isoptera): Their phylogeny, classification, and rise to ecological dominance. *American Museum Novitates*, 3650, 1–27.
15. Engel, M. S., Hinojosa-Díaz, I. A., & Rasnitsyn, A. P. (2009). A honey bee from the Miocene of Nevada and the biogeography of *Apis* (Hymenoptera: Apidae: Apini). *Proceedings of the California Academy of Sciences, Series 4*, 60(3), 23–38.
16. Engel, M. S., Barden, P., Riccio, M. L., & Grimaldi, D. A. (2016). Morphologically specialized termite castes and advanced sociality in the Early Cretaceous. *Current Biology*, 26(4), 522–530.

17. Genise, J. F. (2017). *Ichnoentomology: Insect traces in soils and paleosols*. Berlin: Springer, xxviii+695 pp.
18. Grimaldi, D., & Engel, M. S. (2005). *Evolution of the insects*. Cambridge: Cambridge University Press, xv +755 pp.
19. Guénard, B., Perrichot, V., & Economo, E. P. (2015). Integration of global fossil and modern biodiversity data reveals dynamism and stasis in ant macro-ecological patterns. *Journal of Biogeography*, 42(12), 2302–2312.
20. Hughes, D. P., Wappler, T., & Labandeira, C. C. (2010). Ancient death-grip leaf scars reveal ant-fungal parasitism. *Biology Letters*, 7, 67–70.
21. Kotthoff, U., Wappler, T., & Engel, M. S. (2013). Greater past disparity and diversity hints at ancient migrations of European honey bee lineages into Africa and Asia. *Journal of Biogeography*, 40, 1832–1838.
22. Krishna, K., Grimaldi, D. A., Krishna, V., & Engel, M. S. (2013). Treatise on the Isoptera of the world. *Bulletin of the American Museum of Natural History*, 377, 1–2704.
23. LaPolla, J. S., Dlussky, G. M., & Perrichot, V. (2013). Ants and the fossil record. *Annual Review of Entomology*, 58, 609–630.
24. Matthews, R. W. (1968). Microstigmus comes: Sociality in a sphecid wasp. *Science*, 160(3829), 787–788.
25. Michener, C. D. (2007). *The bees of the world* (2nd ed., p. 953). Baltimore: Johns Hopkins University Press.
26. Michener, C. D., & Grimaldi, D. A. (1988). The oldest fossil bee: Apoid history, evolutionary stasis, and antiquity of social behavior. *Proceedings of the National Academy of Sciences, USA*, 85(17), 6424–6426.
27. Michez, D., Vanderplanck, M., & Engel, M. S. (2012). Fossil bees and their plant associates. In S. Patiny (Ed.), *Evolution of plant-pollinator relationships* (pp. 103–164). Cambridge: Cambridge University Press.
28. Misof, B., Liu, S., Meusemann, K., Peters, R. S., Donath, A., Mayer, C., Frandsen, P. B., Ware, J., et al. (2014). Phylogenomics resolves the timing and pattern of insect evolution. *Science*, 346(6210), 763–767.
29. Perrard, A., Grimaldi, D., & Carpenter, J. M. (2017). Early lineages of Vespidae (Hymenoptera) in Cretaceous amber. *Systematic Entomology*, 42(2), 379–386.
30. Peters, R. S., Krogmann, L., Mayer, C., Donath, A., Gunkel, S., Meusemann, K., Kozlov, A., Podsiadlowski, L., Petersen, M., Lanfear, R., & Diez, P. A. (2017). Evolutionary history of the Hymenoptera. *Current Biology*, 27(7), 1013–1018.
31. Wenzel, J. W. (1990). A social wasp's nest from the Cretaceous Period, Utah, USA, and its biogeographical significance. *Psyche*, 97(1–2), 21–29.
32. Wilson, E. O. (1971). *The insect societies*. Cambridge: Harvard University Press, x+[i]+548 pp.
33. Wilson, E. O., Carpenter, F. M., & Brown, W. L. (1967). The first Mesozoic ants, with the description of a new subfamily. *Psyche*, 74, 1–19.