Ants and the Fossil Record

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Abstract

The dominance of ants in the terrestrial biosphere has few equals among animals today, but this was not always the case. The oldest ants appear in the fossil record 100 million years ago, but given the scarcity of their fossils, it is presumed they were relatively minor components of Mesozoic insect life. The ant fossil record consists of two primary types of fossils, each with inherent biases: as imprints in rock and as inclusions in fossilized resins (amber). New imaging technology allows ancient ant fossils to be examined in ways never before possible. This is particularly helpful because it can be difficult to distinguish true ants from non-ants in Mesozoic fossils. Fossil discoveries continue to inform our understanding of ancient ant morphological diversity, as well as provide insights into their paleobiology.

INTRODUCTION

Ants are among the most successful, some would argue *the* most successful, groups of insects to ever live. In terms of both sheer species diversity (7, 81) and ecological impacts on terrestrial systems, the importance of ants cannot be overstated. Ant colonies are often called superorganisms (53) because of the collective functioning of a colony. In tropical forests, ants can comprise upward of 15%–20% of the animal biomass (52). Owing to their eusociality, the impact of ants on their surroundings far exceeds that expected from the relatively small size of individual workers. However, despite their presence on Earth for over 100 million years and despite their current ubiquity, it was apparently not until approximately 50 million years ago that ants achieved the ecological dominance we observe today (9, 28, 76) (**Figure 1**). From beautiful pieces of amber, sometimes with spectacularly preserved specimens entombed within showing the finest details of cuticular sculpturing, to the often shadowy outlines hinting at a structure that seems just out of view provided by an imprint fossil, the ant fossil record offers a tantalizing glimpse of ant diversity at various points in the past.

HISTORY OF PALEOMYRMECOLOGY

The study of fossil ants began primarily with inclusions in Eocene Baltic amber, with the first fossils illustrated as early as 1742 by Sendel (101) in his magnificent folio volume "*Historia Succinorum.*" Following this pioneering work, the first series of papers to discuss this fossiliferous deposit, which were published during 1819–1840 (e.g., 39, 98), were of rather poorly described species of uncertain generic placement. Heer (49) described in 1850 the first fossil ants from Radoboj (Croatia) and Oeningen (Germany), which Mayr (69) later revised. In 1868, Mayr (70) published the first large treatment of Baltic amber ants. It was this publication that stimulated other myrmecologists to study amber ants as well as imprint fossils. In 1915, Wheeler (111) produced his now classic monograph on the ants of the Baltic amber.

Following Wheeler's comprehensive monograph, several studies between 1915 and 1937 investigated ant imprint fossils. The most interesting faunas were described from the Late Eocene–Early Oligocene deposits of Florissant and Bembridge Marls and from the Oligocene deposits of Kleinkems and some localities in eastern France. Cockerell (15) first studied the ant fossils of the Bembridge Marls, followed later by the work of Donisthorpe (32). In 1930, Carpenter (13) reviewed fossil ants described from North American deposits. In the 1930s, Théobald (106) described a diverse Oligocene ant fauna from Aix-en-Provence, France, and Kleinkems, Germany, and also revised several species described by Förster (37) from Brunstatt, France. For the next 30 years, however, fossil ant work basically came to halt, probably due in part to the fact that the deposits known at the time were no older than the Late Eocene and most of the species in these deposits belonged to extant genera. In fact, some species in these deposits do not appear much different from extant species. As a result, the fossil record from that time period told us little about the early evolution of ants, and interest in fossil ants waned.

This changed in 1967 with the discovery of *Sphecomyrma freyi* from Cretaceous (Turonian, ca. 92 mya) New Jersey amber. Wilson et al. (115) described an intriguing combination of morphological features that did start to tell us something about how early ants evolved. It also sparked renewed interest in fossil ants. Since then, a diversity of Cretaceous ants have been discovered. These include species described by Dlussky from Taimyr (18–20) and Canadian ambers (23), discoveries from New Jersey amber (35, 41), and surveys of the ancient ants of Burmese and French ambers (22, 35, 43, 77, 84, 118). More recently the oldest definitive crown-group ant was discovered
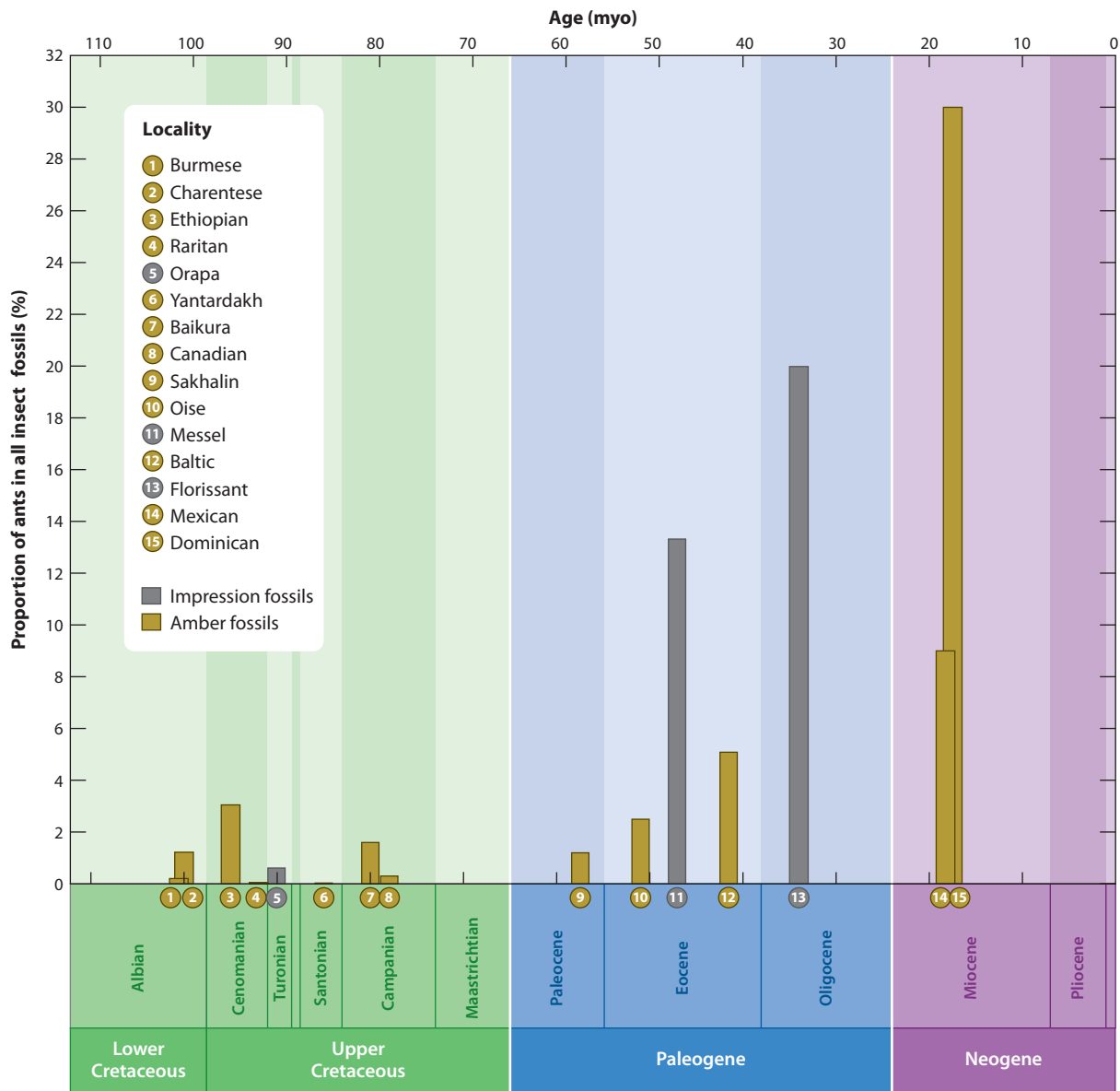
Figure 1

Percentage of ants as a total of all insect fossils from various fossil deposits. Note that the Dominican amber deposit is the average of two different estimates of the proportion of ants as a total of insect fossils (see References 28 and 42).

▶ Erratum

in Late Cenomanian amber of Ethiopia (96). These Cretaceous age fossils have increased our understanding of early ant evolution while raising a series of new questions. At present, there are 52 fossil deposits known to contain at least one fossil ant specimen (**Table 1**) (**Supplemental Figure 1, Supplemental Figure 2**; follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**).
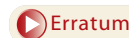
▶ Supplemental Material

PRESERVATION AND METHODOLOGY

Amber Ant Fossils

Fossilized ant bodies come in two forms: as inclusions entombed in amber (the polymerized form of fossil tree resin) (**Supplemental Figure 3**) or as imprints in rock (**Supplemental Figure 4**). Burial conditions differ between the two kinds of fossils, and both have inherent biases as to what

Table 1 List of major ant fossil deposits from the Mesozoic and Cenozoic

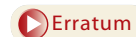| Major Mesozoic ant deposits					
Deposit name	Location	Brief geological details	Age	Percentage of insect fossils that are ants	Ant taxa known
Burmese amber	Northern Myanmar	Inclusions in coniferous fossil resin (Burmite)	Early Cenomanian (98.79 ± 0.62 mya) (93, 102)	0.2% (44)	*Haidomyrmex*, *Sphecomyrmodes* (Sphecomyrminae), *Myanmyrma* (uncertain subfamily), *Burmomyrma* (possibly Aneuretinae) (22, 118)
Charentese amber	Charente-Maritime, France	Inclusions in coniferous fossil resin	Late Albian to Early Cenomanian (99–100 mya) (77)	1.2% (85)	*Gerontoformica* (uncertain subfamily), *Haidomyrmodes*, *Sphecomyrmodes* (Sphecomyrminae) (77, 84)
Ethiopian amber	Wenchit River, central Ethiopia	Inclusions in coniferous fossil resin	Late Cenomanian (93–95 mya) (96)	3% (96)	A fossil taxon yet undescribed in Dolichoderinae
Raritan (New Jersey) amber	Several localities in the Atlantic Coastal Plain	Inclusions in coniferous fossil resin	Turonian (92 mya) (46)	0.05% (46)	*Sphecomyrma, Baikuris* (Sphecomyrminae), *Brownimecia* (Brownimeciinae), *Kyromyrma* (Formicinae) (40, 41, 45, 46)
Orapa	Orapa, Botswana	Imprints in mudstone	Turonian (91 mya) (28)	0.6% (28)	*Afropone* (Ponerinae, but see text), *Afromyrma* (Myrmicinae, but see text) (26)
Kzyl-Zhar	Kzyl-Orda Region, Kazakhstan	Imprints in mudstone lenses in fluvial deposits	Turonian (90 mya) (28)	N/A	*Cretopone, Petropone* (poneromorphs, incertae sedis) (18) ▶ Erratum
Yantardakh	East Taimyr Peninsula, North Siberia, Russia	Inclusions in coniferous fossil resin (retinite)	Santonian (85 mya) (36)	0.001% (18)	*Cretomyrma, Dlusskyidris* (Sphecomyrminae) (18)

(Continued)

Table 1 (*Continued*)

Major Mesozoic ant deposits					
Deposit name	Location	Brief geological details	Age	Percentage of insect fossils that are ants	Ant taxa known
Baikura	Taimyr Peninsula, North Siberia, Russia	Inclusions in coniferous fossil resin (retinite)	Unclear position within Late Cretaceous, provisionally Campanian-Maastrichtian (ca. 80 mya) (28)	1.6% (90)	*Baikuris* (Sphecomyrminae) (20)
Canadian amber	Grassy Lake, northern Alberta, Canada	Inclusions in coniferous fossil resin (chemavinite)	Campanian (78–79 mya) (72)	0.3% (72)	*Sphecomyrma* (Sphecomyrminae), *Canapone* (Ectatomminae), *Eotapinoma* (Dolichoderinae), *Cananeuretus* (Aneuretinae) (24, 35)

Major Cenozoic ant deposits					
Deposit name	Location	Brief geological details	Age	Percentage of insect fossils that are ants	Ant taxa known
Sakhalin amber	Sakhalin Island near Starodubskoye, Russia	Inclusions in fossil resin (rumanite-type)	Paleocene (56–59 mya) (36)	1.2% (28)	*Aneuretellus* (Aneuretinae), *Protopone* (Ponerinae), *Eotapinoma*, *Zherichinius* (Dolichoderinae), *Chimaeromyrma* (Formicinae) (21)
Oise amber	Oise Department, France	Inclusions in angiospermous fossil resin	Early Eocene, Ypresian (52–55 mya) (4)	2.5% (4)	*Platythyrea* (Ponerinae), *Gesomyrmex* (Formicinae), *Tetraponera* (Pseudomyrmecinae), and 37 other morphotypes (4)
Mo-Clay	Denmark (Jutland)	Imprints in marine diatomites	Early Ypresian (52–55 mya) (94)	N/A	*Ypresiomyrma* (Myrmeciinae) (1, 94)
Cambay amber	Gujarat State, western India	Inclusions in angiospermous fossil resin	Early Eocene, Ypresian (50-52 mya) (95)	N/A	Several taxa yet undescribed in Dolichoderinae, Formicinae, Ponerinae, Pseudomyrmecinae (95)
Fushun amber	Fushun City, Liaoning Province, China	Inclusions in fossil resin	Early Eocene, Ypresian (50–52 mya) (52)	N/A	Many taxa listed (54), but see text

(*Continued*)

Table 1 (*Continued*)

			Major Cenozoic ant deposits		
Deposit name	**Location**	**Brief geological details**	**Age**	**Percentage of insect fossils that are ants**	**Ant taxa known**
Green River	Widespread across western United States (northeastern Utah, northwestern Colorado, and southwestern Wyoming). Best collected are deposits from the Piceance Creek Basin	Imprints in lacustrine oil shales and calcareous mudstone	Early Eocene (49–54 mya) (103)	6.9% (28)	Species from Aneuretinae, Dolichoderinae, Myrmeciinae, Myrmicinae, Ponerinae, uncertain subfamily (27), Formiciinae (3)
McAbee	British Columbia, Canada	Imprints in lacustrine shale	Early Eocene, Ypresian (51 mya) (1)	N/A	*Ypresiomyrma* (Myrmeciinae) (1)
Messel	Grube Messel, near Darmstadt, Hesse, Germany	Imprints in bituminous claystone	Middle Eocene (47 mya) (74)	13.1% (67)	*Titanomyrma* (Formiciinae), *Gesomyrmex*, *Oecophylla* (Formicinae) (29, 30, 66)
Eckfeld	Eckfeld Maar	Imprints in lacustrine deposits	Middle Eocene (44 mya) (74)	3.9% (28)	*Gesomyrmex* and *Oecophylla* (30, 31). Also present are Formiciinae, Ponerinae, Formicinae, Dolichoderinae and Myrmicinae
Baltic amber	South coast of Baltic Sea from Poland to Estonia	Inclusions in fossil coniferous resin (succinite)	Middle to Late Eocene (37–42 mya) (109)	5% (28)	Many taxa (29)
Bembridge	Several sites along the coast of Isle of Wight	3D impressions in limestone	Late Eocene (34 mya) (55)	N/A	Many taxa (15, 32)
Florissant	Florissant, Colorado	Imprints in lacustrine shale (diatomite)	Eocene/Oligocene boundary (34 mya) (75)	20% (75)	Species from Aneuretinae, Dolichoderinae, Formicinae, Myrmicinae, Ponerinae, and Pseudomyrmecinae (12)
Bitterfeld amber	Bitterfeld, Lower Saxony, Germany	Inclusions in coniferous fossil resin	Late Oligocene (23 mya) (33)	N/A	Many taxa (26)

▶ Erratum

(*Continued*)

Table 1 (*Continued*)

<table>
<tr><th colspan="6">Major Cenozoic ant deposits</th></tr>
<tr>
<th>Deposit name</th>
<th>Location</th>
<th>Brief geological details</th>
<th>Age</th>
<th>Percentage of insect fossils that are ants</th>
<th>Ant taxa known</th>
</tr>
<tr>
<td>Aix-en-Provence</td>
<td>Bouches-du-Rhône, France</td>
<td>Imprints in gypsum-bearing marls</td>
<td>Late Oligocene (29 mya)</td>
<td>N/A</td>
<td>Many taxa (106), but in need of revision</td>
</tr>
<tr>
<td>Dominican amber</td>
<td>Several sites in Dominican Republic</td>
<td>Inclusions in angiospermous fossil resin</td>
<td>Early Miocene (16–19 mya) (40)</td>
<td>24% (42) or 36% (28)</td>
<td>Many taxa</td>
</tr>
<tr>
<td>Mexican amber</td>
<td>Simojovel, Chiapas, Mexico</td>
<td>Inclusions in angiospermous fossil resin</td>
<td>Early Miocene (15–20 mya) (104)</td>
<td>9% (104)</td>
<td>Many taxa (104)</td>
</tr>
<tr>
<td>Radoboj</td>
<td>Radoboj, Croatia</td>
<td>Imprints in freshwater limestones</td>
<td>Early Miocene (19 mya) (49, 68)</td>
<td>N/A</td>
<td>Many taxa (49), but see text</td>
</tr>
<tr>
<td>Sicilian amber</td>
<td>Sicily, Italy</td>
<td>Inclusions in angiospermous fossil resin (simetite)</td>
<td>Unclear position within Oligocene-Miocene, likely Early Miocene (16–23 mya)</td>
<td>N/A</td>
<td>14 species from 13 genera (11, 34)</td>
</tr>
</table>

kinds of ants tend to become fossilized. Ants in amber tend to be species that foraged on trees or on the ground near trees. They are as a general rule smaller species (10 mm or less in length) presumably because small species were less able to free themselves from the viscous resin. Rare exceptions include *Paraponera dieteri* in Miocene Dominican amber (ca. 20 mm), *Prionomyrmex* species in Eocene Baltic amber (up to 15 mm), and an undescribed myrmeciine worker in Eocene Oise amber (ca. 20 mm). Subterranean ant species that lived in the leaf litter or soil are also rare as amber fossils. When we do find these species in amber, they are almost always winged reproductives that were captured in the resin during their mating flights. An exception is the Early Cretaceous (Late Albian, ca. 100 mya) Charentese amber, which uniquely preserved a high proportion of the litter biota (82). Because there are many similarities between the ant fauna of Burmese and Charentese ambers, it is also possible that the Burmese amber ants were foraging on the soil rather than along the tree trunks.

Imprint Fossils

Imprints in rocks were formed mostly in lake deposits, where the preservation of microscopic features requires the presence of fine-grained sediment such as diatomites, micritic muds, or volcanic tuffs. Such imprints mainly preserve winged reproductives that fell into the water during their mating flights. Although complete bodies may be found, imprint fossils generally fall into two categories: detached wings or body fragments lacking wings and other appendages. Mating behavior affects the likelihood of fossil preservation. Species that fly high and far from their birth

Mating flight: reproductive phase of some ant colonies, which typically involves the mass emergence of winged, virgin queens and males

Ant queen: the
egg-laying caste of an
ant colony; also called
a gyne

Paleosol: fossilized
soil

nests have the greatest chance of burial in lake deposits. Species that spend most of their time
searching and mating on the ground are far less commonly encountered as imprint fossils. In
contrast to amber fossils, imprint fossils generally preserve larger ant species. Imprint fossils are
found by splitting stones, and as a consequence, small specimens are easily overlooked. It is perhaps
not surprising then that most ant imprints are dominated by species with large queens, such as
Oecophylla in Bembridge deposits and the giant *Titanomyrma* in Messel and Green River deposits
(up to 60 mm long!).

Ichnofossils

In addition to body fossils, the presence of ants can be recorded through ichnofossils (or trace
fossils), i.e., the traces of their activity in paleosols such as burrows and nests. In the case of recent
taxa, the nest architecture can be very distinctive (107), but such architectures are not found in
Mesozoic ichnofossils. The identification of ant nests from the Mesozoic is particularly important
because they potentially predate the earliest occurrence of body fossils. Unless body fossils are
found associated within such nests, however, it remains virtually impossible to identify the kind
of ant that built the nest and even to determine whether the tracemaker was an ant, because
different groups of animals may have evolved similar burrowing techniques (100). For instance,
distinguishing between traces of social insects such as ants and termites can be particularly difficult
(38). The oldest trace fossils that have been suggested to be ant ichnofossils are from the Late
Jurassic of Colorado (47, 48), but this remains highly controversial and was later dismissed by
other authors (10, 38). The oldest nest that seems attributable to ants is from the Late Cretaceous
of Utah (92).

New Imaging Techniques

Traditional light microscopy has long been the only technique available to study fossil insects pre-
served as imprints or amber inclusions. It is still largely in use because it allows for the observation
of most external characters. But critical structures can be inaccessible owing to the position of
the specimen or, in the case of amber, they can be hidden by turbidity, debris, bubbles, or other
inclusions between the amber surface and the insect. Imaging techniques such as X-ray computed
tomography (CT) or microtomography (μ-CT) are now increasingly used in amber studies, which
provide a three-dimensional virtual reconstruction of the fossils (17, 45, 51). Propagation phase-
contrast X-ray synchrotron imaging (PPC-SRμCT), which has been developed specifically for
amber inclusions (60, 105), allows for high-resolution reconstructions as well as virtual dissections
(**Supplemental Figure 5**), thus providing access to all external and internal features (80). The
increasing use of PPC-SRμCT might help reduce the gap between fossils, especially controversial
Cretaceous fossils, and extant species of ants.

▶ Supplemental Material

THE PROBLEM OF RECOGNIZING TRUE ANTS IN THE EARLY FOSSIL RECORD

A critical discussion of ant fossils first needs to establish what synapomorphies are used to define
the family Formicidae. For examination of fossils these are largely going to be morphological,
although, as seen below, behavioral synapomorphies can be inferred from fossils as well. There
are generally four widely accepted morphological synapomorphies that define modern ants
(considered here as ants from the Tertiary to recent periods). These are an elongated scape,
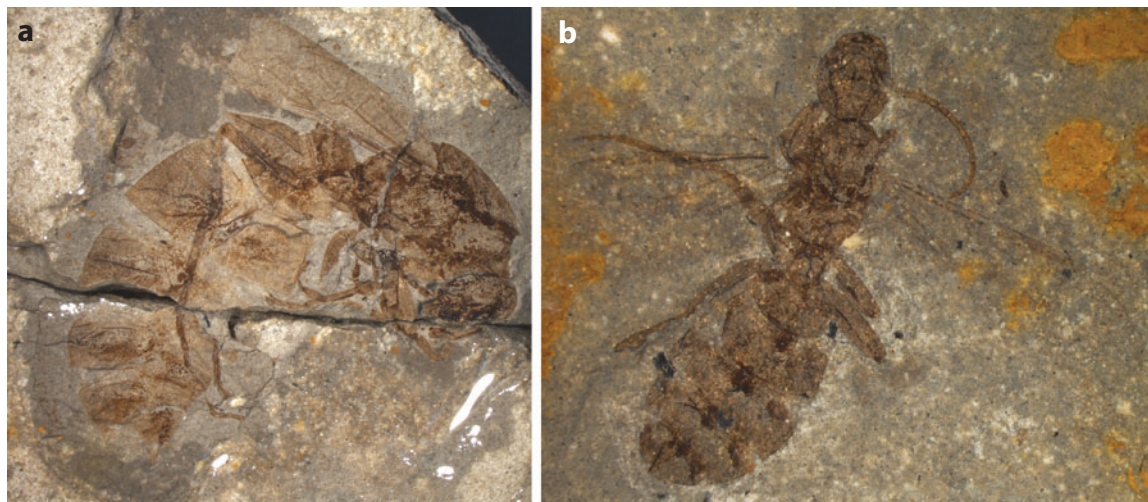geniculate antennae, petiole, and metapleural gland. The elbowed (geniculate) shape of the ant

Figure 2

Armaniidae imprint fossils from Cretaceous of Siberia, Russia. (*a*) *Armania robusta*. (*b*) *Pseudarmania rasnitsyni*. Both fossils are from 95 myo mudstone of Obeschayuschiy. (Images courtesy of G. Dlussky)

antenna is formed by the elongation of the first segment (the scape) and the distinct bend that separates it from the remainder of the antenna (the segmented funiculus). The petiole is the modification of abdominal segment II and in some ant groups segment III is further developed into a postpetiole. The metapleural gland is often considered the major feature used to define the Formicidae (52) because it is unique to ants and nothing even closely equivalent exists in any other group of hymenopterans. The gland appears to secrete antimicrobial and, in some cases, alarm substances (117). It has been secondarily lost in some, largely arboreal or socially parasitic, groups, particularly in the subfamilies Formicinae and Myrmicinae (6). The metapleural gland is usually absent in male ants. A nonmorphological synapomorphy for ants is eusocial behavior, which is expressed morphologically in females by the differentiation of the queen and worker castes (although in some socially parasitic taxa, the worker caste has been secondarily lost).

The Cretaceous specimens have elicited the most debate because with these fossils we can ask, When do the first "true" ants appear? In other words, what among bizarre Cretaceous ant-like hymenopterans is a true ant? Dlussky (19) first described the Armaniidae as an intermediate link between ants and scoliid wasps. There has been considerable discussion of whether this group should be given family rank (1, 6, 19, 26, 41, 42, 83, 89, 108, 114), but the most recent action by Bolton (6) classified them as a subfamily. Here we do not follow this recommendation and consider them at the family rank for the remainder of our discussion (see reasons below). Armaniids are known exclusively as imprint fossils that are poorly preserved (**Figure 2**), making the critical areas of the body difficult or impossible to observe (e.g., seeing whether a metapleural gland is present or not). Still, what we know of them is that armaniids possessed a broadly attached, but poorly developed, petiole, very short scapes, and females do appear queen-like (19). Although Dlussky (19) reported the presence of a metapleural gland in some armaniids, others have questioned this interpretation (41, 77). It is this lack of a definitive metapleural gland that has led some authors to consider the armaniids at the family rank and therefore not true ants (35, 84, 116). In addition to only being known from fragmentary imprint fossils, another major complicating factor in determining whether armaniids are true ants is that no specimens have been found with individuals

that could be construed as workers. Armaniids possess vespoid-like mandibles that either are bidentate (19) or have only an apical tooth present (however, this may be a result of preservation).

The debate about whether armaniids are true ants hinges mainly on just how many synapomorphies of modern ants need to be present in order for the group to be considered an ant. A striking example is a bizarre family of Cretaceous wasps described by Rasnitsyn (88) as the Falsiformicidae, or "false ants." Like Armaniidae, these wasps possessed geniculate antennae with a short scape, a broadly attached petiole, and females with a roughly queen-like appearance (**Supplemental Figure 6**). But no workers have been found, and most importantly, they distinctly lack the metapleural gland and share numerous features with Chrysidoidea. In his description, Rasnitsyn (88) noted that, as indicated by his name for the family, the falsiformicids were distinct from ants despite the presence of a petiole and geniculate antennae. He suggested that the family might be the sister group to the Formicidae s.l. (= Formicidae s.s. + Armaniidae), but additional falsiformicid species recently discovered by Vincent Perrichot from various Cretaceous ambers demonstrate that the family actually belongs in the Chrysidoidea. Therefore, the only definitive synapomorphies that can be used to define true ants seem to be the presence of the metapleural gland, a distinct petiole weakly attached posteriorly, and the differentiation of females into queen and worker castes. As such, and unless the presence of the metapleural gland can be clearly observed, Armaniidae should not be considered true ants.

Another less controversial example in the Cretaceous is the Sphecomyrminae. When Wilson et al. (115) first described *Sphecomyrma freyi* from 92 myo New Jersey amber, it created a sensation in myrmecological circles. Why? Here was an ancient fossilized ant-like organism that possessed a metapleural gland and a distinct petiole weakly attached posteriorly, two synapomorphies that define modern, crown-group ants. Much later, eusociality was inferred on the basis of the discovery of additional sphecomyrmine fossils. Both Grimaldi & Engel (42) and Perrichot et al. (84) used the presence of two wingless female individuals (inferred to be workers) preserved together in the same piece of amber to conclude sphecomyrmines were eusocial, on the basis of the inference that because Cretaceous ant specimens are so rarely encountered, it would be unlikely for two of them to be trapped together unless they were foraging nestmates. The sphecomyrmine *Haidomyrmodes mammuthus* is the first Cretaceous species known in which both queen and worker castes are described (84), perhaps settling the debate of whether sphecomyrmines were eusocial. Of the definitive morphological ant synapomorphies, sphecomyrmines lack only the elongated scapes, and it is the lack of this morphological trait that led Poinar et al. (87) to consider sphecomyrmines not ants, i.e., Sphecomyrmidae. Almost all other authors, however, have considered sphecomyrmines ants (9, 22, 41, 84, 116), and when looking at a *Sphecomyrma* or *Sphecomyrmodes* worker (**Figure 3**), one can easily appreciate most of the general traits of an ant that cannot be confounded with any other insect group. This is somewhat less convincing when observing *Haidomyrmex* or *Haidomyrmodes*, given their very peculiar head morphology (**Figure 4**); however, they clearly possess a metapleural gland and a distinct petiole, and at least *Haidomyrmodes* has females differentiated into castes. Therefore, Sphecomyrminae can readily be considered true ants, and the elongated scape remains a debatable synapomorphy related to how someone classifies crown-group versus stem-group ants (108).

CRETACEOUS ANT FOSSILS

The earliest known ants or ant-like fossils come from the Albian period (100–112 mya) of the Cretaceous. Cretaceous age specimens include a mixture of stem-group and crown-group ants (**Table 1**). Sphecomyrminae appear to be the closest known relatives to extant ants (41, 108, 116). They were present for at least 20 million years in the Cretaceous, with 8 genera and 15 species

Stem group:
a paraphyletic
assemblage composed
of taxa more closely
related to the crown
group than to any
other extant taxon

Supplemental Material

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by University of Barcelona on 09/10/13. For personal use only.

Figure 3

Sphecomyrmodes occidentalis, a worker in mid-Cretaceous (99 myo) Charentese amber, southwestern France (lateral view). (Image courtesy of V. Perrichot)

known exclusively in amber (**Table 1**). They had a wide distribution although apparently restricted to Laurasia, with records in the mid-Cretaceous ambers of Burmese and French ambers, and the Late Cretaceous ambers of New Jersey, Siberia, and Canada (18, 20, 22, 23, 37, 41, 84, 116, 118). Among these, the Sphecomyrmini, comprising *Baikuris*, *Cretomyrma*, *Dlusskyidris*, *Sphecomyrma*, and *Sphecomyrmodes*, had a general morphology very similar to that of living ants, except for their relatively short scapes (**Figure 3**). The Burmese and French Haidomyrmecini, comprising *Haidomyrmex* and *Haidomyrmodes*, had the most peculiar head morphology of perhaps any ant, extinct or extant. The face exhibits a high, unusually concave surface surmounted posteriorly by a small lobe covered by a brush of stiff setae (**Figure 4**), and it is yet unclear if the clypeus is composed of both the concave surface and the brushy lobe or if it is only the lobe. The elbowed, sickle-shaped mandibles give Haidomyrmecini a fierce appearance (**Figure 4**) and were assumed to act as trap-jaws uniquely moving in a plane oblique to the dorsoventral and horizontal axes of the body, so they might have been highly specialized predators (22, 35, 84, 118). More generally, sphecomyrmines were likely foragers on the coniferous trees that produced the resin and on the soil surface of the amber forests. These were tropical to warm temperate forests in a coastal marine setting subject to tidal influences, dominated by gymnosperms but with an understory of ferns, cycads, and sparse, although relatively diversified, angiosperms (44, 72, 85). Sphecomyrmines had already developed eusocial traits, as evidenced by the differentiation of the worker caste and the trapping of several workers in the same amber piece, thus suggesting they were foraging together (84).

Laurasia: large northern continent that existed until the Paleocene consisting of Asia (minus India), Europe, Greenland, and North America
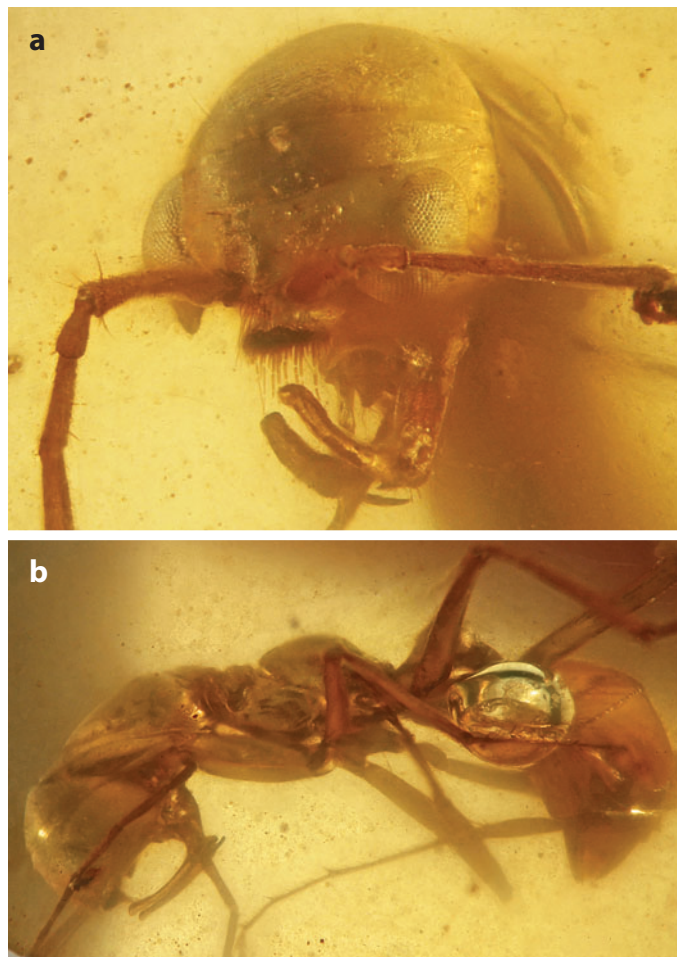
Figure 4

Haidomyrmex sp., a wingless female in mid-Cretaceous (99 myo) Burmese amber. (*a*) Head in frontal view. (*b*) Body in lateral view. (Images courtesy of V. Perrichot)

Kyromyrma neffi, from 92 myo New Jersey amber, is clearly a member of the crown-group ants (Formicinae) (40). The formicines have an easily identifiable synapomorphy that instantly separates them from other ant subfamilies: the acidopore. The acidopore is typically a circular, nozzle-like structure found on the terminal gastral segment of formicine ants (56) that is used to spray formic acid. The single known specimen of *K. neffi* clearly displays an acidopore. In many respects, its overall morphology is that of a fairly generalized formicine, possessing the plesiomorphic states for many characters. The Formicinae are the second most species-rich group of extant ants (6), and they include many examples of trophobiotic ants, those species that gather the exudate from groups of Sternorrhyncha hemipterans such as aphids and scale insects. The presence of formicines in the Cretaceous leaves open the possibility of an early origin of trophobiotic relationships involving ants.

When originally described from the same New Jersey amber, *Brownimecia clavata* was placed incertae sedis within the Ponerinae owing to the presence of a gastral constriction (41). At that time, the ponerines were still broadly defined and, as we now know, also paraphyletic (6, 58, 59).

Following the splitting of the old Ponerinae, Bolton (6) placed *B. clavata* in its own monotypic subfamily (Brownimeciinae), observing that the species did not easily fit into any recognized subfamilies. *B. clavata* has falcate, edentate mandibles, unusual for ants and often associated with dulotic behavior (6). Unlike the armaniids and sphecomyrmines, and more like crown-group ants, *B. clavata* possesses a relatively elongate scape (41). Another interesting morphological feature of *B. clavata* is the presence of clubbed antennae, which, although not uncommon among modern ants, is the only known instance among Cretaceous ants (6).

Two other Cretaceous amber deposits (Burmese and Canadian) are of particular recent interest because they contain, in addition to sphecomyrmines, several fossils that very likely belong to the ant crown group. A possible aneuretine, *Burmomyrma rossi* (22), and a possible myrmeciine (although considered incertae sedis), *Myanmyrma gracilis* (35), from 99 myo Burmese amber have been described. The single known specimen of *B. rossi* is a headless alate. Dlussky (22) considered its general morphology and wing venation to be consistent with the crown-group subfamily Aneuretinae. Another fossil from younger Cretaceous Canadian amber (Campanian, ca. 78 myo), *Cananeuretus occidentalis*, has also been tentatively placed within the Aneuretinae (35). The subfamily Aneuretinae is represented today by a single, presumably relict species, *Aneuretus simoni*, found only on the island of Sri Lanka. Engel & Grimaldi (35) considered *Myanmyrma gracilis* either to be within the poneroid grade or to belong to the Myrmeciinae. The species possesses a gastral constriction, which places it within the poneroid grade, but it shares several other morphological features with the myrmeciines (35). Archibald et al. (1) thought that given the lack of character support and poor specimen preservation, *M. gracilis* was likely not a myrmeciine. They also observed that the short scapes are known only in stem-group ants; however, the strong constriction between abdominal segments III and IV is not known from any stem-group ant.

Discovered in Charentese amber (ca. 100 myo), *Gerontoformica cretacica* is of uncertain taxonomic placement due to the high distortion of the specimen (77), although it is likely a crown-group ant. Nel et al. (77) suggested it is reminiscent of either the Dolichoderinae or the Formicinae on the basis of general habitus. The specimen does have a relatively long scape and the antenna is not clubbed, which suggests it is not a sphecomyrmine or a brownimeciine.

Two other fossils have been assigned to the crown-group ants, *Afropone* to the Ponerinae and *Afromyrma* to the Myrmicinae, on the basis of imprints from Orapa, Botswana (26). The specimens are in poor condition and their assignment to an ant crown group has been questioned (1, 116).

CENOZOIC ANT FOSSILS

The end of the Mesozoic 65 mya, marked by a well-known mass extinction event, also may have brought about the end of both the armaniids and sphecomyrmines—although the times of their extinctions remain unclear. The last armaniids occur about 91 mya in the Turonian of Botswana; however, insect-rich rock deposits are desperately lacking between 55 and 90 mya. Similarly, the last occurrence of sphecomyrmines is from the Campanian Canadian amber, but insect amber deposits are lacking in the Maastrichtian and Paleocene, so the possibility that sphecomyrmines survived until the Paleocene cannot be excluded. This is unlikely, however, given that the only known early Cenozoic deposit contains clearly identifiable and diverse crown-group ant fossils, and no sphecomyrmines. Dlussky (21) studied Sakhalin amber and found that, as in Cretaceous deposits, ants are rare (just 9 specimens), composing only 1.2% of all insect fossils, and belong to extinct genera from modern subfamilies (Dolichoderinae, Aneuretinae, Formicinae, and Ponerinae). Sakhalin amber finds do, however, demonstrate that Paleocene ants occupied various levels in the ecosystem, perhaps the beginnings of the various niches occupied by modern ants (28). For example, based on their morphology, *Aneuretellus* and *Protopone* likely lived in soil or leaf litter

(21). They had small eyes displaced forward and thickening terminal segments of the funiculus. *Zherichinius* had an elongated body and long legs and antennae, and was perhaps arboreal (21).

From the Ypresian stage (50–55 mya) of the Early Eocene, three amber deposits are known (**Table 1**) that contain diverse ants. From French amber of Oise, two ponerines have been described, one in the extant genus *Platythyrea* (with the oldest report of a possible ergatoid condition), and one a close relative of *Pachycondyla*, and 38 other morphotypes are mentioned in Formicinae, Dolichoderinae, Pseudomyrmecinae, Myrmeciinae, and Myrmicinae (4). In Indian amber of Cambay, a preliminary investigation revealed Formicinae, Dolichoderinae, Pseudomyrmecinae, and Myrmicinae (95). These two deposits apparently contain a mixture of extinct and extant genera (4, 95), which contrasts with the Chinese amber from Fushun in which the 35 known taxa were described exclusively from extinct genera (54). However, the identifications are disputable, the descriptions are in Chinese, and the illustrations are low quality; this material clearly needs additional study. All three deposits are of major significance because they provide the only clues for the transitional composition in ant diversity following the Paleocene-Eocene thermal maximum (PETM) 56 mya. With an estimated increase of 5°C–8°C globally, the PETM was a key period of drastic changes in the terrestrial biosphere (14, 71), and it is likely that many modern ant genera evolved during or shortly after this time (4).

It is during the Eocene and beyond that the number of ant fossils increased significantly, with ants in several deposits composing more than 20% of the insect species present. Mo-Clay (Fur and Ølst Formations in Denmark) is one of the earliest Eocene deposits (55 myo), and a myrmeciine, *Ypresiomyrma rebekkae*, is known from this locality. Rust & Andersen (94) discovered 101 body specimens or isolated body parts of ant queen and male *Y. rebekkae* [originally placed in *Pachycondyla* but later moved to the Myrmeciinae by Archibald et al. (1)]. No other ants have been found in this deposit. It is assumed that insect layers from Mo-Clay were formed in a marine environment and at a distance of about 100 km from the nearest coast (94). This is the earliest evidence we have of mating swarm behavior in ants.

Several important Middle Eocene deposits are known: Green River (27) and Okanagan Highlands (1) in North America, and Messel and Eckfeld (30, 31, 66) in Europe. Compared with earlier deposits, the percentage of insects that are ants rises substantially: at Green River 6.9% and at Messel 13.1%. Middle Eocene deposits are dominated by genera that are extinct, but we do see several extant ant genera appear during this period. Among those are *Dolichoderus* in Green River, *Oecophylla* and *Gesomyrmex* in Messel and Eckfeld, and *Pachycondyla* in Green River and Messel (27, 30, 31). Another interesting feature is that several species are represented by numerous specimens, in stark contrast to earlier deposits. Imprints of *Eoformica pinguis* and *Dolichoderus kohlsi* constitute 40% and 25%, respectively, of all ants in Green River (27); *Titanomyrma gigantea* and *T. simillima* constitute nearly 50% of ants in Messel (45). Four subfamilies dominate these fossil deposits: Aneuretinae, Dolichoderinae, Formicinae, and Formiciinae at Green River (85.6% of all ants) and Messel (90.3% of all ants). Interestingly, the Myrmicinae are quite rare in these deposits, composing just 1.9% of ants in Green River and 1.6% of ants in Messel.

▶ Supplemental Material

One subfamily of ants, the Formiciinae (not to be confused with the Formicinae), appears in the Early Eocene and disappears in the Middle Eocene (**Supplemental Figure 7**). They were originally known only from forewing fossils (12, 110) and initially were not even placed in the Formicidae (110); Lutz (66) later revised the group. A number of remarkable formiciine fossils have been discovered. Formiciine queens were very large; in fact they are the largest ants to have ever lived, with individuals reaching body lengths of 6 cm and possessing wingspans of up to 13 cm (66). In one species, *Titanomyrma lubei*, the body of the queen is larger than the rufous hummingbird (*Selasphorus rufus*) common to North America (3). Unfortunately, workers of these ants remain unknown. Formiciines are known from both European and North American deposits.

One of the best-studied ant fossil deposits dates from the Middle to Late Eocene period (34–42 myo): the Baltic amber. Mayr (70) and Wheeler (111) produced the first taxonomic treatments, but a host of more recent studies have followed. This deposit is important from a number of perspectives, such as its high species diversity (with 118 species; 29), and a significant portion of its identified genera (9%; 29) known today only from the tropics, including *Oecophylla*, *Gesomyrmex*, *Pristomyrmex*, and *Tetraponera*, among others. Wheeler (112) first noted that the Baltic amber was unusual in part because it contains a mixture of both thermophilic and temperate genera. Archibald & Farrell (2) addressed this observation, considering two possibilities that either the Baltic amber forests were tropical/subtropical or that there was less pronounced seasonality in this area than is observed today (the area had milder winters). They concluded that the latter hypothesis was more likely the explanation for this seemingly strange mixture of ant faunas. This is an interesting observation because it implies that what are considered tropical ant genera today may in fact have been associated originally with a more mild, temperate climate.

The first record of polymorphism among worker ants is noted in specimens from Baltic amber. Dimorphic worker specimens (majors and minors) of *Gesomyrmex hoernesi* and *Pheidologeton* sp. have been discovered (31, 111). Ergatoid conditions have been reported for both a male ant (*Anonychomyrma constricta*; 111) and a gyne (*Plagiolepis klinsmanni*; 25) from Baltic amber fossils. Baltic amber fossils have also given insights into other aspects of ant biology. For instance, several fossil ant species (*Ctenobethylus goepperti*, *Lasius schiefferdeckeri*, *Prenolepis henschei*, and *Monomorium mayrianum*) have been found as syninclusions with aphids (Hemiptera: Aphididae: *Germaraphis*), which may be an indication of trophobiotic interactions between the ants and the aphids (e.g., 79). However, due to the presence of wax-secreting structures on the aphids, some authors have doubted that the ants and aphids were associated (50). Wheeler (112) reported a mite on *L. schiefferdeckeri*.

If we examine the three most-speciose extant ant subfamilies (Dolichoderinae, Formicinae, and Myrmicinae), approximately 50% or more of the species from the Eocene are from genera that are extant (**Supplemental Figure 8**). In fact, some fossil species look remarkably similar to extant species. A classic example involving apparent morphological stasis in worker morphology from the Eocene is observed in the common Baltic amber species *Prenolepis henschei*. Wheeler (112) was the first to note that workers of this species looked morphologically very similar to the extant and widespread Nearctic *Prenolepis imparis* (which is also incidentally morphologically very similar to the extant European *Prenolepis* species, *P. nitens*). LaPolla & Dlussky (64) noted differences between the male genitalic structures of *P. henschei* and *P. imparis*, but the morphological similarities among the workers of these two species broadly links the modern fauna back to the Eocene.

From the Oligocene onward (23–34 myo) the percentage of ants as a total of insects found in fossil deposits rises. In the Florissant shale, 20% of insects are ants (13). Carpenter (13) reports a dominance of two subfamilies in the Florissant: Dolichoderinae (ca. 63%) and Formicinae (ca. 33%). In the French deposit of Aix-en-Provence, the Dolichoderinae and Myrmicinae are among the most common ants, each composing approximately 36% of the ants. The Formicinae are the third most commonly encountered ants (ca. 27%) (106).

The Dominican amber (16–19 myo) found in Hispaniola is arguably the best-studied ant fossil deposit in the world. In fact, ants are the largest single group of arthropods known from Dominican amber, with upward of 24%–36% of all fossil insects being ants. Dominican amber in many respects is essentially a modern ant fauna, but there have been notable extinctions since the amber was formed (113). Although fewer than 10% of the genera known from Dominican amber are globally extinct (113), some groups that existed on Hispaniola in the Miocene are absent today. For instance, there were army ants on Hispaniola in the Miocene, but today army ants are not found in the Greater Antilles (113). An interesting dolichoderine putatively placed in the genus *Leptomyrmex* (*L. neotropicus*) was discovered from Dominican amber (5). Today *Leptomyrmex* is

Trophobiosis:
relationship in which
ants receive honeydew
from sternorrhynchans
or caterpillars, which
in return are protected
by the ants

Supplemental Material

found only in the wet forests of Australia, New Guinea, and New Caledonia, so the presence of
the Dominican amber fossil species has presented a biogeographical puzzle since its discovery.
Lucky (65) suggested that the fossil species is a stem lineage of *Leptomyrmex*, and does not belong
to the crown group of modern *Leptomyrmex* species. This conclusion was based on the dating of
the divergence of *Leptomyrmex* from its extant sister group, which is found in the New World.

Undoubtedly, in part because of their sheer abundance as amber inclusions, which overall
increases the chances of syninclusions, ants in Dominican amber have provided insights into
understanding complex interspecific interactions. This can be illustrated by examining evidence
for trophobiosis among Dominican amber ants. The first definitive cases of trophobiosis have been
observed in Dominican amber (although see Baltic amber, above), one case by inference from the
syninclusions of both trophobiotic partners, and the other example with the ants actually carrying
the trophobionts involved in the trophobiosis (57, 63). In one spectacular fossil, an *Acropyga* winged
queen is still clutching a mealybug between her mandibles, a behavior termed trophophoresy that
is unique to this genus (61–63, 97). Other complex symbiotic relationships have been preserved
in Dominican amber as well. Fungus-growing ants (Myrmicinae: Attini) are unique to the New
World and have been the focus of intense study regarding the nature of the symbiosis between
the ants, the fungus they grow in their gardens, and other associated organisms. We know that
fungus-growing ants were common since at least the early Miocene because five attine species
from three genera have been found in Dominican amber (99).

Mexican amber is of approximately the same age as Dominican amber (**Table 1**) but has
received comparatively less study. It is known that ants compose nearly 10% of insect specimens
from this deposit (104). Several studies have examined the species composition of Mexican amber
(**Table 1**). Given the biogeographic affinities of southern Mexico and Hispaniola in modern
times, a comparison of the amber ant fauna from these two regions could prove illuminating.
There are other fossil deposits of younger age, but generally they are either poorly known or
contain relatively few ants (**Supplemental Figure 1, Supplemental Figure 2**). One exception is
Sicilian amber, the exact age of which remains unclear within the Oligocene-Miocene boundary.
This deposit possesses some unique, extinct genera as the unusual formicine *Sicilomyrmex corniger*
(11, 34). Notably, most inclusions belong to genera not found in other European deposits, which
led Dlussky & Rasnitsyn (28) to conclude this fauna was essentially Afrotropical. Another fossil
deposit of early Miocene age (19 myo) is Radoboj in Croatia, from which many ant species were
described in the nineteenth century by Heer (49), but because it has not been revised in over
100 years, much of the taxonomy of these fossils is woefully out of date.

AGE OF ANTS

Both Wilson & Hölldobler (116) and Moreau et al. (76) correlated the diversification of ants in the
Eocene with the rise of angiosperm-dominated forests and their correspondingly more complex
leaf-litter layers. The diversification of other insect lineages, such as the phytophagous beetles (73),
has been correlated with the rise of the angiosperms as well. However, the role of angiosperms in
the diversification of ants has been challenged (86), and previous attempts to correlate their rise
with ant diversification have been characterized as artifacts of incomplete taxon sampling. Pie &
Tschá (86) found that ants have displayed a constant rate of lineage expansion, rather than a single
burst, which might be expected if correlated with the radiation of angiosperms.

The age of ants has been a focus of several studies. Wilson et al. (115), as discussed above,
discovered the first Mesozoic ant, leading them to speculate that ants originated 100 mya. Crozier
et al. (16) challenged this age using a molecular study that questioned whether ants evolved
concurrently with their first appearance in the fossil record. These authors (16) were the first to

use molecular techniques to infer an age for ants and from their data estimated a Late Jurassic (ca. 185 mya +/− 36 my) origin. The fossil used in the calibration was *Cariridris bipetiolata* (8), at the time considered a myrmeciine. However, subsequently *C. bipetiolata* was found not to be an ant (and was placed in the Ampulicidae), rendering the calibration incorrect. Two large molecular studies undertook the task of estimating the age of ants (9, 76). These two studies, however, came to different age estimates. Moreau et al. (76) inferred an age of 140–168 myo, and Brady et al. (9) inferred an age of 115–135 myo. Brady et al. (9) further inferred an age of 137–143 myo for crown-group ants plus sphecomyrmines. How do we reconcile this range of dates? Differences in how fossil deposits were calibrated, as well as what fossils were utilized in the analysis, may explain the discrepancy. For instance, Brady et al. (9) utilized a much more complete range of aculeate fossils to calibrate a series of multiple outgroup nodes.

The age estimates of both Moreau et al. (76) and Brady et al. (9) are older than what the fossil record reveals, but given the rarity of Mesozoic ants (**Figure 1**) this is perhaps not surprising. What we do know is that since the discovery of *Sphecomyrma freyi*, myriad fossil discoveries have shown that there was a rather diverse sphecomyrmine fauna in the Cretaceous and that definitive crown-group ants (*Kyromyrma neffi* and the Ethiopian dolichoderine) existed concurrently with them. The apparent absence of ants from Early Cretaceous insect-rich deposits such as the Spanish and Lebanese ambers (110 to 125 mya), the Santana Formation of Brazil (120 mya), and the Chinese Yixian Formation (140–145 mya) suggests ants did not originate before 110–120 mya. The question of the age of ants, however, does demonstrate the necessity of combining fossil ants with molecular divergence dating techniques because fossils provide the critical minimum age estimates for the lineages in question. As divergence dating becomes ever more popular, the need for accurately identified and classified fossil specimens will only increase. Investigations for additional Cretaceous fossils, particularly from ancient Gondwanan localities, will help elucidate the timing of the origin and radiation of these highly successful insects.

SUMMARY POINTS

1. Ants have existed on Earth for at least 100 million years and, based on the fossil record, probably evolved somewhere between 110 and 120 mya.

2. The taxonomic placement of the extinct, ant-like Armaniidae, which are likely the closest relatives of the Formicidae, has been controversial, but there are compelling arguments for why they should not be considered formicids.

3. Although the first Mesozoic ant was discovered in 1967, it was not until the past two decades that a number of important Mesozoic ant discoveries have been made, including, most recently, the discovery of a 93–95 myo crown-group ant assignable to the Dolichoderinae from the Cretaceous of Africa.

4. Recent discoveries have shown that the Cretaceous stem group, Sphecomyrminae, although rare as fossils, was surprisingly diverse morphologically, which implies a diverse array of ancient sphecomyrmine behaviors as well.

5. Despite their appearance in the Cretaceous, it was not until the Eocene that ants became common as fossils, and presumably this increase in fossilized remains is correlated with an increase in the general abundance and ecological dominance of ants.

6. Molecular divergence dating techniques are growing in popularity, and the need for accurate fossil ant identification will only become more acute as more studies rely on fossils for calibration of datasets.

DISCLOSURE STATEMENT

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LITERATURE CITED

1. Archibald SB, Cover SP, Moreau CS. 2006. Bulldog ants of the Eocene Okanagan Highlands and history of the subfamily (Hymenoptera: Formicidae: Myrmeciinae). *Ann. Entomol. Soc. Am.* 99:487–523
2. Archibald SB, Farrell BD. 2003. Wheeler's dilemma: Proceedings of the Second Paleoentomological Congress. *Acta Zool. Cracov.* 46(Suppl.-Fossil Insects):17–23
3. Archibald SB, Johnson KR, Mathewes RW, Greenwood DR. 2011. Intercontinental dispersal of giant thermophilic ants across the Arctic during early Eocene hyperthermals. *Proc. R. Soc. B* 278:3679–86
4. Aria C, Perrichot V, Nel A. 2011. Fossil Ponerinae (Hymenoptera: Formicidae) in Early Eocene amber of France. *Zootaxa* 2870:53–62
5. Baroni Urbani C, Wilson EO. 1987. The fossil members of the ant tribe Leptomyrmecini (Hymenoptera: Formicidae). *Psyche* 94:1–8
6. Bolton B. 2003. Synopsis and classification of Formicidae. *Mem. Am. Entomol. Inst.* 71:1–370
7. Bolton B. 2012. *AntCat: An Online Catalog of the Ants of the World.* **http://www.antcat.org**
8. Brandão CR, Martins-Neto R, Vulcano VA. 1989. The earliest known fossil ant (first Southern Hemisphere Mesozoic record) (Hymenoptera: Formicidae: Myrmeciinae). *Psyche* 96:195–208
9. Brady SG, Schultz TR, Fisher BL, Ward PS. 2006. Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proc. Natl. Acad. Sci. USA* 103:18172–77
10. Bromley RG, Buatois LA, Genise JF, Labandeira CC, Mángano MG, et al. 2007. Comments on the paper "Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses" by Stephen T. Hasiotis. *Sediment. Geol.* 200:141–50
11. Brown WL Jr, Carpenter FM. 1978. A restudy of two ants from the Sicilian amber. *Psyche* 85:417–23
12. Carpenter FM. 1929. A fossil ant from the Lower Eocene (Wilcox) of Tennessee. *J. Wash. Acad. Sci.* 19:300–1
13. Carpenter FM. 1930. The fossil ants of North America. *Bull. Mus. Comp. Zool. Harv.* 70:1–66
14. Clementz M, Bajpai S, Ravikant V, Thewissen JGM, Saravanan N, et al. 2011. Early Eocene warming events and the timing of terrestrial faunal exchange between India and Asia. *Geology* 39:15–18
15. Cockerell TDA. 1915. British fossil insects. *Proc. U.S. Natl. Mus.* 49:469–99
16. Crozier RH, Jermiin LS, Chiotis M. 1997. Molecular evidence for a Jurassic origin of ants. *Naturwissenschaften* 84:22–23
17. Dierick M, Cnudde V, Masschaele B, Vlassenbroeck J, Van Hoorebeke L, Jacobs P. 2007. Micro-CT of fossils preserved in amber. *Nucl. Instrum. Methods Phys. Res. A* 580:641–43
18. Dlussky GM. 1975. Superfamily Formicoidea. See Ref. 88, pp. 114–22

19. First description of the Armaniidae.

19. Dlussky GM. 1983. A new family of Upper Cretaceous Hymenoptera: an "intermediate link" between ants and Scolioidea. *Paleontol. J.* 17:63–76
20. Dlussky GM. 1987. New Formicoidea (Hymenoptera) of the Upper Cretaceous. *Paleontol. J.* 20:146–50
21. Dlussky GM. 1988. Ants from (Paleocene?) Sakhalin amber. *Paleontol. J.* 22:50–61

22. Dlussky GM. 1996. Ants (Hymenoptera: Formicidae) from Burmese amber. *Paleontol. J.* 30:449–54

23. Dlussky GM. 1999. New ants (Hymenoptera, Formicidae) from Canadian amber. *Paleontol. J.* 33:409–12

24. Dlussky GM. 1999. The first find of the Formicoidea (Hymenoptera) in the Lower Cretaceous of the Northern Hemisphere. *Paleontol. J.* 33:274–77

25. Dlussky GM. 2010. Ants of the genus *Plagiolepis* Mayr (Hymenoptera, Formicidae) from Late Eocene ambers of Europe. *Paleontol. J.* 44:546–55

26. Dlussky GM, Brothers DJ, Rasnitsyn AP. 2004. The first Late Cretaceous ants (Hymenoptera, Formicidae) from southern Africa, with comments on the origin of the Myrmicinae. *Insect Syst. Evol.* 35:1–13

27. Dlussky GM, Rasnitsyn AP. 2003. Ants (Hymenoptera: Formicidae) of Formation Green River and some other Middle Eocene deposits of North America. *Russ. Entomol. J.* 11:411–36

28. Dlussky GM, Rasnitsyn AP. 2007. Paleontological record and stages of ant evolution. *Uspehi Sovrem. Biol.* 127:118–34

29. Dlussky GM, Rasnitsyn AP. 2009. Ants (Insecta: Vespida: Formicidae) in the Upper Eocene amber of Central and Eastern Europe. *Paleontol. J.* 43:1024–42

30. Dlussky GM, Wappler T, Wedmann S. 2008. New Middle Eocene formicid species from Germany and the evolution of weaver ants. *Acta Palaeontol. Pol.* 53:615–26

31. Dlussky GM, Wappler T, Wedmann S. 2009. Fossil ants of the genus *Gesomyrmex* Mayr (Hymenoptera, Formicidae) from the Eocene of Europe and remarks on the evolution of arboreal ant communities. *Zootaxa* 2031:1–20

32. Donisthorpe H. 1920. British Oligocene ants. *Ann. Mag. Nat. Hist.* 9:81–94

33. Dunlop JA. 2010. Bitterfeld amber. See Ref. 78, pp. 57–68

34. Emery C. 1891. Le formiche dell'ambra Siciliana nel Museo Mineralogico dell'Universita di Bologna. *Mem. R. Accad. Sci. Inst. Bologna* 5:141–65

35. Engel MS, Grimaldi DA. 2005. Primitive new ants in Cretaceous amber from Myanmar, New Jersey and Canada. *Am. Mus. Novit.* 3485:1–23

36. Eskov KY. 2002. Appendix: alphabetic list of selected insect fossil sites. 4.2. Fossil resins. See Ref. 91, pp. 444–46

37. Förster B. 1891. Die Insekten des "Plattigen Steinmergels" von Brunnstatt. *Abh. Geol. Spec. Elsass-Lothr.* 3:333–59

38. Genise JF, Bellosi ES, Melchor RN, Cosarinsky MA. 2005. Comment—advanced Early Jurassic termite (Insecta: Isoptera) nests: evidence from the Clarens Formation in the Tuli Basin, Southern Africa (Bordy et al., 2004). *Palaios* 20:303–8

39. Germar EF. 1837. Fauna insectorum Europae. Fasciculus 19. Insectorum protogaeae specimen sistens insecta carbonum fossilium. Halle, Ger.: Kümmel. 1–25 pp.

40. Grimaldi DA, Agosti D. 2000. A formicine in New Jersey Cretaceous amber and early evolution of ants. *Proc. Natl. Acad. Sci. USA* 97:13678–83

41. Grimaldi DA, Agosti D, Carpenter JM. 1997. New and rediscovered primitive ants in Cretaceous amber from New Jersey, and their phylogenetic relationships. *Am. Mus. Novit.* 3208:1–43

42. Grimaldi DA, Engel MS. 2005. *Evolution of the Insects*. New York: Cambridge Univ. Press. 755 pp.

43. Grimaldi DA, Engel MS, Nascimbene PC. 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *Am. Mus. Novit.* 3361:1–71

44. Grimaldi DA, Nascimbene PC. 2010. Raritan (New Jersey) amber. See Ref. 78, pp. 167–91

45. Grimaldi DA, Nguyen T, Ketcham R. 2000. Ultra-high-resolution X-ray computed tomography (UHR CT) and the study of fossils in amber. In *Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey*, ed. DA Grimaldi, pp. 77–91. Leiden: Backhuys Publ.

46. Grimaldi D, Shedrinsky AM, Wampler TP. 2000. A remarkable deposit of fossiliferous amber from the Upper Cretaceous (Turonian) of New Jersey. In *Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey*, ed. DA Grimaldi, pp. 1–76. Leiden: Backhuys Publ.

47. Halfen AF, Hasiotis ST. 2010. Neoichnological study of the traces and burrowing behaviors of the western harvester ant *Pogonomyrmex occidentalis* (Insecta: Hymenoptera: Formicidae): paleopedogenic and paleoecological implications. *Palaios* 25:703–20

23. First description of species from the morphologically bizarre Haidomyrmecini (Sphecomyrminae).

26. Detailed fossil discoveries from Botswana that challenged the notion of a Laurasian origin for ants.

40. First description of a definitive crown-group ant.

48. Hasiotis ST. 2004. Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses. *Sediment. Geol.* 167:177–268

49. Heer O. 1850. Die Insektenfauna der Tertiargebilde von Oeningen und von Radoboj in Croatien. Zweite Abtheilung: Heuschrecken, Florfliegen, Aderfluger, Schmetterlinge und Fliegen. *Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss.* 11:1–264

50. Heie OE. 1987. Palaeontology and phylogeny. In *Aphids: Their Biology, Natural Enemies, and Control*, ed. AK Minks, P Harrewijn, 2A:367–91. Amsterdam: Elsevier

51. Henderickx H, Cnudde V, Masschaele B, Dierick M, Vlassenbroeck J, Van Hoorebeke L. 2006. Description of a new fossil *Pseudogarypus* (Pseudoscorpiones: Pseudogarypidae) with the use of X-ray micro-CT to penetrate opaque amber. *Zootaxa* 1305:41–50

52. Hölldobler B, Wilson EO. 1990. *The Ants*. Cambridge, MA: Harvard Univ. Press. 732 pp.

53. Hölldobler B, Wilson EO. 2008. *The Superorganism: The Beauty, Elegance, and Strangeness of Insect Societies*. New York: WW Norton & Co. 522 pp.

54. Hong YC. 2002. *Amber Insects of China*. Beijing: Sci. Technic Publ. House. 653 pp.

55. Hooker J, Grimes ST, Mattey DP, Collinson ME, Sheldon ND. 2009. Refined correlation of the UK Late Eocene–Early Oligocene Solent Group and timing of its climate history. *Geol. Soc. Am. Spec. Pap.* 452:179–95

56. Hung ACF, Brown WL. 1966. Structure of gastric apex as a subfamily character of the Formicinae. *J. N.Y. Entomol. Soc.* 74:198–200

57. Johnson C, Agosti D, Delabie JH, Dumpert K, Williams DJ, et al. 2001. *Acropyga* and *Azteca* ants (Hymenoptera: Formicidae) with scale insects (Sternorrhyncha: Coccoidea): 20 million years of intimate symbiosis. *Am. Mus. Novit.* 3335:1–18

58. Keller RA. 2000. Cladistics of the tribe Ectatommini (Hymenoptera: Formicidae): a reappraisal. *Insect Syst. Evol.* 31:59–69

59. Keller RA. 2011. A phylogenetic analysis of ant morphology (Hymenoptera: Formicidae) with special reference to the poneromorph subfamilies. *Bull. Am. Mus. Nat. Hist.* 355:1–90

60. Lak M, Néraudeau D, Nel A, Cloetens P, Perrichot V, Tafforeau P. 2008. Phase contrast X-ray synchrotron imaging: opening access to fossil inclusions in opaque amber. *Microsc. Microanal.* 14:251–59

61. LaPolla JS. 2004. *Acropyga* (Hymenoptera: Formicidae) of the World. *Contrib. Am. Entomol. Inst.* 33:1–130

62. LaPolla JS. 2005. Ancient trophophoresy: a fossil *Acropyga* (Hymenoptera: Formicidae) from Dominican amber. *Trans. Am. Entomol. Soc.* 131:21–28

63. LaPolla JS, Cover SP, Mueller UG. 2002. Natural history and distribution notes on the mealybug-tending ant *Acropyga epedana*, with descriptions of the male and queen castes. *Trans. Am. Entomol. Soc.* 128:367–76

64. LaPolla JS, Dlussky GM. 2010. Review of fossil *Prenolepis* genus-group species. *Proc. Entomol. Soc. Wash.* 112:258–73

65. Lucky A. 2011. Molecular phylogeny and biogeography of the spider ants, genus *Leptomyrmex* Mayr (Hymenoptera: Formicidae). *Mol. Phylogenet. Evol.* 59:281–92

66. Lutz H. 1986. Eine neue Unterfamilie der Formicidae (Insecta: Hymenoptera) aus dem mitteleozänen Ölschiefer der "Grube Messel" bei Darmstadt (Deutschland, S-Hessen). *Senckenberg. Lethaea* 67:177–218

67. Lutz H. 1990. Systematische und palökologische Untersuchungen an Insekten aus dem Mittel-Eozän der Grube Messel bei Darmstadt. *Cour. Forschungsinst. Senckenberg* 124:1–165

68. Lutz H. 1997. Taphozönosen terrestrischer Insekten in aquatischen Sedimenten—ein Beitrag zur Rekonstruktion des Paläoenvironments. *Neues Jahrb. Geol. Palaontol. Abh.* 203:173–210

69. Mayr GL. 1867. Vorläufige Studien über die Radoboj-Formiciden, in der Sammlung der k.k. geologischen Reichsanstalt. *Jahrb. K. K. Geol. Reichs.* 17:47–62

70. Mayr GL. 1868. Die Ameisen des Baltischen Bernstein. *Beitr. Naturk. Preuss. Königsberg* 1:1–102

71. McInerney FA, Wing SL. 2011. The Paleocene-Eocene thermal maximum: a perturbation of carbon cycle, climate, and biosphere with implications for the future. *Annu. Rev. Earth Planet. Sci.* 39:489–516

66. Recognized the giant ants of the Eocene, the Formiciinae, as a distinct lineage.

70. First monograph of a fossil ant fauna and first attempts at reconstruction of incomplete fossil specimens.

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org by University of Barcelona on 09/10/13. For personal use only.

72. McKellar RC, Engel MS. 2012. Hymenoptera in Canadian Cretaceous amber (Insecta). *Cretac. Res.* 35:258–79

73. McKenna DD, Farrell BD. 2006. Tropical forests are both evolutionary cradles and museums of leaf beetle diversity. *Proc. Natl. Acad. Sci. USA* 103:10947–51

74. Mertz DF, Renne PR. 2005. A numerical age for the Messel fossil deposit (UNESCO World Heritage Site) derived from 40Ar/39Ar dating on a basaltic rock fragment. *Cour. Forschungsinst. Senckenberg* 255:67–75

75. Meyer HW. 2003. *The Fossils of Florissant*. Washington, DC/London: Smithson. Books. 258 pp.

76. Moreau CS, Bell CD, Vila R, Archibald SB, Pierce NE. 2006. Phylogeny of the ants: diversification in the age of angiosperms. *Science* 312:101–4

77. Nel A, Perrault G, Perrichot V, Néraudeau D. 2004. The oldest ant in the Lower Cretaceous amber of Charente-Maritime (SW France) (Insecta: Hymenoptera: Formicidae). *Geol. Acta* 2:23–29

78. Penney D, ed. 2010. *Biodiversity of Fossils in Amber from the Major World Deposits*. Manchester, UK: Siri Sci. Press

79. Perkovski EE. 2007. Syninclusions of ant *Lasius schiefferdeckeri* (Hymenoptera, Formicidae) and aphid *Germaraphis* (Homoptera, Aphidinae) in Rovno and Saxonian ambers. *Vestn. Zool.* 41:181–85

80. Perreau M, Tafforeau P. 2011. Virtual dissection using phase-contrast X-ray synchrotron microtomography: reducing the gap between fossils and extant species. *Syst. Entomol.* 36:573–80

81. Perrichot V. 2012. *AntWeb. Fossil ants.* **http://www.antweb.org/fossil.jsp**

82. Perrichot V, Girard V. 2009. A unique piece of amber and the complexity of ancient forest ecosystems. *Palaios* 24:137–39

83. **Perrichot V, Lacau S, Néraudeau D, Nel A. 2008. Fossil evidence for the early ant evolution. *Naturwissenschaften* 95:85–90**

84. Perrichot V, Nel A, Néraudeau D, Lacau S, Guyot T. 2008. New fossil ants in French Cretaceous amber (Hymenoptera: Formicidae). *Naturwissenschaften* 95:91–97

85. Perrichot V, Néraudeau D, Tafforeau P. 2010. Charentese amber. See Ref. 78, pp. 192–207

86. Pie MR, Tschá MK. 2009. The macroevolutionary dynamics of ant diversification. *Evolution* 63:3023–30

87. Poinar GO Jr, Archibald B, Brown A. 1999. New amber deposit provides evidence of Early Paleogene extinctions, paleoclimates and past distributions. *Can. Entomol.* 131:171–77

88. Rasnitsyn AP. 1975. Hymenoptera Apocrita of Mesozoic. *Trans. Paleontol. Inst. Acad. Sci. USSR* 147:1–134 [in Russian]

89. Rasnitsyn AP. 2002. Superorder Vespidea Laicharting, 1781. Order Hymenoptera Linné, 1758 (=Vespida Laicharting, 1781). See Ref. 91, pp. 242–54

90. Rasnitsyn AP, Kulicka R. 1990. Hymenopteran insects in Baltic amber with respect to the overall history of the order. *Prace Muz. Ziemi* 41:53–64

91. Rasnitsyn AP, Quicke DLJ, eds. 2002. *History of Insects*. Dordrecht, The Neth.: Kluwer Acad. Publ.

92. Roberts EM, Tapanila L. 2006. A new social insect nest from the Upper Cretaceous Kaiparowits Formation of southern Utah. *J. Paleontol.* 80:768–74

93. Ross A, Mellish C, York P, Crighton B. 2010. Burmese amber. See Ref. 78, pp. 208–35

94. Rust J, Andersen NM. 1999. Giant ants from the Paleogene of Denmark with a discussion of the fossil history and early evolution of ants (Hymenoptera: Formicidae). *Zool. J. Linn. Soc.* 125:331–48

95. Rust J, Singh H, Rana RS, McCann T, Singh L, et al. 2010. Biogeographic and evolutionary implications of a diverse paleobiota in amber from the early Eocene of India. *Proc. Natl. Acad. Sci. USA* 107:18360–65

96. Schmidt AR, Perrichot V, Svojtka M, Anderson KB, Belete KH, et al. 2010. Cretaceous African life captured in amber. *Proc. Natl. Acad. Sci. USA* 107:7329–34

97. Schneider SA, LaPolla JS. 2011. Systematics of the mealybug tribe Xenococcini (Hemiptera: Coccoidea: Pseudococcidae) with a discussion of trophobiotic associations with *Acropyga* Roger ants. *Syst. Entomol.* 36:57–82

98. Schweigger AF. 1819. *Beobachtungen auf naturhistorischen Reisen. Anatomisch-physiologische Untersüchungen über Corallen; nebst einem Anhange, Bemerkungen über den Bernstein enthaldend*. Reimer, Berlin. 127 pp.

99. Schultz TR. 2007. The fungus-growing ant genus *Apterostigma* in Dominican amber. In *Advances in Ant Systematics: Homage to E.O. Wilson—50 Years of Contributions*, ed. RR Snelling, BL Fisher, PS Ward. *Mem. Am. Entomol. Inst.* 80:425–36

83. Utilized the emerging diverse Cretaceous age fossil record to discuss the origins and paleobiogeography of ants.

100. Seilacher A. 2007. Arthropod tunnel systems. In *Trace Fossil Analysis*, ed. A Seilacher, pp. 45–60. Berlin/Heidelberg: Springer

101. Sendel N. 1742. *Historia succinorum corpora aliena involventium et naturae opere pictorum et caelatorum ex Augustorum I et II cimeliis Dresdae conditis aeri insculptorum*. Leipzig, Ger.: Gleditsch. 328 pp.

102. Shi G, Grimaldi DA, Harlow GE, Wang Jing, Wang Jun, et al. 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretac. Res.* 37:155–63

103. Smith ME, Singer BS, Carroll AR. 2008 Synoptic reconstruction of a major ancient lake system: Eocene Green River Formation, western United States. *Geol. Soc. Am. Bull.* 120:54–84

104. Solórzano Kraemer MM. 2007. Systematic, palaeoecology, and palaeobiogeography of the insect fauna from the Mexican amber. *Palaeontogr. A* 282:1–133

105. Soriano C, Archer M, Azar D, Creaser P, Delclòs X, et al. 2010. Synchrotron X-ray imaging of inclusions in amber. *C.R. Palevol.* 9:361–68

106. Théobald N. 1937. Les insectes fossiles des terrains oligocènes de France. *Mém. Soc. Sci. Nancy* 2:1–473

107. Tschinkel WR. 2003. Subterranean ant nests: trace fossils past and future? *Palaeogeogr. Palaeoclim. Palaeoecol.* 192:321–33

108. Ward PS. 2007. Phylogeny, classification, and species-level taxonomy of ants (Hymenoptera: Formicidae). *Zootaxa* 1668:549–63

109. Weitschat W, Wichard W. 2010. Baltic amber. See Ref. 78, pp. 50–83

110. Westwood JO. 1854. Contributions to fossil entomology. *Q. J. Geol. Soc. Lond.* 10:378–96

111. Groundbreaking monograph of the Baltic amber ants; for many years the gold standard for fossil ant study.

111. Wheeler WM. 1915. The ants of the Baltic amber. *Schrift. Phys. Ökonom. Ges. Königsberg* 55:1– 142

112. Wheeler WM. 1930. The ant *Prenolepis impars* Say. *Ann. Entomol. Soc. Am.* 23:1–26

113. Wilson EO. 1985. Invasion and extinction in the West Indian ant fauna: evidence from the Dominican amber. *Science* 229:265–67

114. Wilson EO. 1987. The earliest known ants: an analysis of the Cretaceous species and an inference concerning their social organization. *Paleobiology* 13:44–53

115. Discovery of first Mesozoic ant.

115. Wilson EO, Carpenter FM, Brown WL Jr. 1967. The first Mesozoic ants, with the description of a new subfamily. *Psyche* 74:1–19

116. Wilson EO, Hölldobler B. 2005. The rise of the ants: a phylogenetic and ecological explanation. *Proc. Natl. Acad. Sci. USA* 202:7411–14

117. Yek SH, Mueller UG. 2011. The metapleural gland of ants. *Biol. Rev.* 86:774–91

118. Barden P, Grimaldi D. 2012. Rediscovery of the bizarre Cretaceous ant *Haidomyrmex* Dlussky (Hymenoptera: Formicidae), with two new species. *Am. Mus. Novit.* 3755:1–16

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