Fossil ants (Hymenoptera: Formicidae): ancient diversity and the rise of modern lineages

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Abstract

The ant fossil record is summarized with special reference to the earliest ants, first occurrences of modern lineages, and the utility of paleontological data in reconstructing evolutionary history. During the Cretaceous, from approximately 100 to 78 million years ago, only two species are definitively assignable to extant subfamilies – all putative crown group ants from this period are discussed. Among the earliest ants known are unexpectedly diverse and highly social stem-group lineages, however these stem ants do not persist into the Cenozoic. Following the Cretaceous-Paleogene boundary, all well preserved ants are assignable to crown Formicidae; the appearance of crown ants in the fossil record is summarized at the subfamilial and generic level. Generally, the taxonomic composition of Cenozoic ant fossil communities mirrors Recent ecosystems with the "big four" subfamilies Dolichoderinae, Formicinae, Myrmicinae, and Ponerinae comprising most faunal abundance. As reviewed by other authors, ants increase in abundance dramatically from the Eocene through the Miocene. Proximate drivers relating to the "rise of the ants" are discussed, as the majority of this increase is due to a handful of highly dominant species. In addition, instances of congruence and conflict with molecular-based divergence estimates are noted, and distinct "ghost" lineages are interpreted. The ant fossil record is a valuable resource comparable to other groups with extensive fossil species: There are approximately as many described fossil ant species as there are fossil dinosaurs. The incorporation of paleontological data into neontological inquiries can only seek to improve the accuracy and scale of generated hypotheses.

Key words: Fossil record, paleontology, amber, stem group ants, ghost lineages, review.

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"While an ant was wandering under the shade of the tree of Phaeton, a drop of amber enveloped the tiny insect; thus she who in life was disregarded, became precious in death."   Martial, Epigrams Book VI

Introduction

Marcus Valerius Martialis' lines above were written nearly two millennia ago in the first century CE (BOHN 1859). The tree of Phaeton refers to a story from Greek mythology: Phaeton was said to be the son of Helios, the Sun god who drove the chariot that hauled the celestial body through the sky. Phaeton pleaded with his father to pilot the chariot until Helios relented and Phaeton took control. In his inexperience, Phaeton scorched the Earth, creating the vast African deserts. Zeus, having spotted the destruction, killed Phaeton with a bolt of lightning in an effort to lessen the catastrophe. Distraught, Phaeton's sisters gathered and wept at the sight in perpetuity, eventually they transformed into poplar trees, their tears into golden amber. Martial was no doubt referring to the aesthetic beauty of amber fossils; however, the value of amber is now recognized as a direct window into the very distant past. It may not be common for lithified rock fossils to be incorporated into necklaces or bracelets, however these are of course also precious portholes that enrich our understanding and inspire wonder.

With approximately 730 described species from 67 deposits worldwide, the ant fossil record is extensive. While paleomyrmecology dates to the 18th century, the field has advanced rapidly over the last several years. Even as reviews effectively summarize important aspects of paleomyrmecology (LAPOLLA & al. 2013) and synthetic analyses of fossil data yield novel conclusions relating to ant evolution (e.g., ARCHIBALD & al. 2011, GUÉNARD & al. 2015), it remains necessary to reevaluate the field after recent critical discoveries. To be sure, the distillation of 100 million years of morphological, paleoethological, and ecological information will be a perpetual objective. While there are obvious gaps and biases in the fossil record, specimens trapped in amber or impressed in rock have played an important role in detailing the history of one of nature's greatest success stories.

The earliest ants

The earliest definitive ants are from the Cretaceous. Taxa that are confidently assigned to the Formicidae appear first in the fossil record during the Albian (Tab. 1), in Charentese amber from France aged 100 Ma (mega-annum) (NEL & al. 2004, PERRICHOT & al. 2008, PERRICHOT 2015) along with approximately contemporaneous Burmese amber

Tab. 1: A summary of all known ants from the Mesozoic. Taxa denoted with a ◆ are of dubious placement, the phylogenetic position of these genera, along with *Baikuris*, *Cretomyrma*, *Cretopone*, *Dlusskyidris*, and *Petropone*, has never been tested. * Indicates uncertain age. Ages are in millions of years before present. * Indicates uncertain age of locality.

Taxa	Deposit	Age (Ma)	References
Subfamily Brownimeciinae BOLTON			
Tribe **Brownimeciini** BOLTON			
Genus ***Brownimecia*** GRIMALDI, AGOSTI & CARPENTER			
Brownimecia clavata GRIMALDI, AGOSTI & CARPENTER	New Jersey Amber	92.0 [94.3 - 89.3]	GRIMALDI & al. (1997)
Subfamily Sphecomyrminae WILSON & BROWN			
Genus ***Baikuris*** DLUSSKY			
Baikuris casei GRIMALDI, AGOSTI & CARPENTER	New Jersey Amber	92.0 [94.3 - 89.3]	GRIMALDI & al. (1997)
Baikuris mandibularis DLUSSKY	Taimyr Amber*	87.1 [89.3 - 84.9]	DLUSSKY (1987)
Baikuris mirabilis DLUSSKY	Taimyr Amber*	87.1 [89.3 - 84.9]	DLUSSKY (1987)
Baikuris maximus PERRICHOT	Charentese Amber	100 [105.3 - 99.7]	PERRICHOT (2015)
Genus ***Cretomyrma*** DLUSSKY			
Cretomyrma arnoldii DLUSSKY	Taimyr Amber*	87.1 [89.3 - 84.9]	DLUSSKY (1975)
Cretomyrma unicornis DLUSSKY	Taimyr Amber*	87.1 [89.3 - 84.9]	DLUSSKY (1975)
Genus ***Dlusskyidris*** BOLTON			
Dlusskyidris zherichini DLUSSKY	Taimyr Amber*	87.1 [89.3 - 84.9]	DLUSSKY (1975)
Genus ***Sphecomyrma*** WILSON & BROWN			
Sphecomyrma canadensis WILSON	Medicine Hat Amber	78.5 [84.9 - 70.6]	WILSON (1985a)
Sphecomyrma freyi WILSON & BROWN	New Jersey Amber	92.0 [94.3 - 89.3]	WILSON & al. (1967)
Sphecomyrma mesaki ENGEL & GRIMALDI	New Jersey Amber	92.0 [94.3 - 89.3]	ENGEL & GRIMALDI (2005)
Genus ***Zigrasimecia*** BARDEN & GRIMALDI			
Zigrasimecia ferox PERRICHOT	Burmese Amber	98.8 [99.7 - 94.3]	PERRICHOT (2014a)
Zigrasimecia tonsora BARDEN & GRIMALDI	Burmese Amber	98.8 [99.7 - 94.3]	BARDEN & GRIMALDI (2013)
Tribe **Haidomyrmecini** BOLTON			
Genus ***Ceratomyrmex*** PERRICHOT, WANG & ENGEL			
Ceratomyrmex ellenbergeri PERRICHOT, WANG & ENGEL	Burmese Amber	98.8 [99.7 - 94.3]	PERRICHOT & al. (2016b)
Genus ***Haidoterminus*** MCKELLAR, GLASIER & ENGEL			
Haidoterminus cippus MCKELLAR, GLASIER & ENGEL	Medicine Hat Amber	78.5 [84.9 - 70.6]	MCKELLAR & al. (2013a)
Genus ***Haidomyrmodes*** PERRICHOT, NEL, NÉRAUDEAU, LACAU & GUYOT			
Haidomyrmodes mammuthus PERRICHOT, NEL, NÉRAUDEAU, LACAU & GUYOT	Charentese Amber	100 [105.3 - 99.7]	PERRICHOT & al. (2008)
Genus ***Haidomyrmex*** DLUSSKY			
Haidomyrmex cerberus DLUSSKY	Burmese Amber	98.8 [99.7 - 94.3]	DLUSSKY (1996)
Haidomyrmex scimitarus BARDEN & GRIMALDI	Burmese Amber	98.8 [99.7 - 94.3]	BARDEN & GRIMALDI (2012)
Haidomyrmex zigrasi BARDEN & GRIMALDI	Burmese Amber	98.8 [99.7 - 94.3]	BARDEN & GRIMALDI (2012)
Subfamily incertae sedis			
Genus ***Camelomecia*** BARDEN & GRIMALDI			
Camelomecia janovitzi BARDEN & GRIMALDI	Burmese Amber	98.8 [99.7 - 94.3]	BARDEN & GRIMALDI (2016)
Genus ***Cretopone*** DLUSSKY			
Cretopone magna DLUSSKY	Kzyl-Zhar, Kazakstan	91.8 [94.3 - 89.3]	DLUSSKY (1975)
Genus ***Gerontoformica*** NEL & PERRAULT			
Gerontoformica contegus BARDEN & GRIMALDI	Burmese Amber	98.8 [99.7 - 94.3]	BARDEN & GRIMALDI (2014)
Gerontoformica cretacica NEL & PERRAULT	Charentese Amber	100 [105.3 - 99.7]	NEL & al. (2004)

Gerontoformica gracilis BARDEN & GRIMALDI	Burmese Amber	98.8 [99.7 - 94.3]	BARDEN & GRIMALDI (2014)
Gerontoformica magnus BARDEN & GRIMALDI	Burmese Amber	98.8 [99.7 - 94.3]	BARDEN & GRIMALDI (2014)
Gerontoformica maraudera BARDEN & GRIMALDI	Burmese Amber	98.8 [99.7 - 94.3]	BARDEN & GRIMALDI (2016)
Gerontoformica occidentalis PERRICHOT, NEL, NÉRAUDEAU, LACAU & GUYOT	Charentese Amber	100 [105.3 - 99.7]	PERRICHOT & al. (2008)
Gerontoformica orientalis ENGEL & GRIMALDI	Burmese Amber	98.8 [99.7 - 94.3]	ENGEL & GRIMALDI (2005)
Gerontoformica pilosus BARDEN & GRIMALDI	Burmese Amber	98.8 [99.7 - 94.3]	BARDEN & GRIMALDI (2014)
Gerontoformica rubustus BARDEN & GRIMALDI	Burmese Amber	98.8 [99.7 - 94.3]	BARDEN & GRIMALDI (2014)
Gerontoformica rugosus BARDEN & GRIMALDI	Burmese Amber	98.8 [99.7 - 94.3]	BARDEN & GRIMALDI (2014)
Gerontoformica spiralis BARDEN & GRIMALDI	Burmese Amber	98.8 [99.7 - 94.3]	BARDEN & GRIMALDI (2014)
Gerontoformica subcuspis BARDEN & GRIMALDI	Burmese Amber	98.8 [99.7 - 94.3]	BARDEN & GRIMALDI (2014)
Gerontoformica tendir BARDEN & GRIMALDI	Burmese Amber	98.8 [99.7 - 94.3]	BARDEN & GRIMALDI (2014)
Genus *Myanmyrma* ENGEL & GRIMALDI			
Myanmyrma gracilis ENGEL & GRIMALDI	Burmese Amber	98.8 [99.7 - 94.3]	ENGEL & GRIMALDI (2005)
Genus *Petropone* DLUSSKY			
Petropone petiolata DLUSSKY	Kzyl-Zhar, Kazakstan	91.8 [94.3 - 89.3]	DLUSSKY (1975)
Subfamily Aneuretinae EMERY			
◆ Genus *Cananeuretus* ENGEL & GRIMALDI			
◆ *Cananeuretus occidentalis* ENGEL & GRIMALDI	Medicine Hat Amber	78.5 [84.9 - 70.6]	ENGEL & GRIMALDI (2005)
◆ Genus *Burmomyrma* DLUSSKY			
◆ *Burmomyrma rossi* DLUSSKY	Burmese Amber	98.8 [99.7 - 94.3]	DLUSSKY (1996)
Subfamily Dolichoderinae FOREL			
◆ Genus *Eotapinoma* DLUSSKY			
◆ *Eotapinoma macalpini* DLUSSKY	Medicine Hat Amber	78.5 [84.9 - 70.6]	DLUSSKY (1999)
Tribe **Leptomyrmecini** EMERY			
Genus *Chronomyrmex* MCKELLAR, GLASIER & ENGEL			
Chronomyrmex medicinehatensis MCKELLAR, GLASIER & ENGEL	Medicine Hat Amber	78.5 [84.9 - 70.6]	MCKELLAR & al. (2013a)
Subfamily Ectatomminae EMERY			
Tribe **Ectatommini** EMERY			
◆ Genus *Canapone* DLUSSKY			
◆ *Canapone dentata* DLUSSKY	Medicine Hat Amber	78.5 [84.9 - 70.6]	DLUSSKY (1999)
Subfamily Formicinae Latreille			
Genus *Kyromyrma* GRIMALDI & AGOSTI			
Kyromyrma neffi GRIMALDI & AGOSTI	New Jersey Amber	92.0 [94.3 - 89.3]	GRIMALDI & AGOSTI (2000)
Subfamily Myrmicinae LEPELETIER DE SAINT-FARGEAU			
◆ Genus *Afromyrma* DLUSSKY, BROTHERS & RASNITSYN			
◆ *Afromyrma petrosa* DLUSSKY, BROTHERS & RASNITSYN	Orapa, Botswana	91.8 [94.3 - 89.3]	DLUSSKY & al. (2004)
Subfamily Ponerinae LEPELETIER DE SAINT-FARGEAU			
◆ Genus *Afropone* DLUSSKY, BROTHERS & RASNITSYN			
◆ *Afropone oculata* DLUSSKY, BROTHERS & RASNITSYN	Orapa, Botswana	91.8 [94.3 - 89.3]	DLUSSKY & al. (2004)
◆ *Afropone orapa* DLUSSKY, BROTHERS & RASNITSYN	Orapa, Botswana	91.8 [94.3 - 89.3]	DLUSSKY & al. (2004)

from Myanmar dated to 99 Ma (DLUSSKY 1996, ENGEL & GRIMALDI 2005, BARDEN & GRIMALDI 2014).

A definitional question: No retrospective relating to fossil ants would be complete without a discussion of synapomorphies and the challenges inherent in applying a taxonomy based largely on extant taxa to the earliest putative ant ancestors. There is an extensive body of literature relating to what exactly constitutes an ant (e.g., WILSON & al. 1967, DLUSSKY 1983, WILSON 1987, GRIMALDI & al. 1997, BOLTON 2003, GRIMALDI & ENGEL 2005, WARD
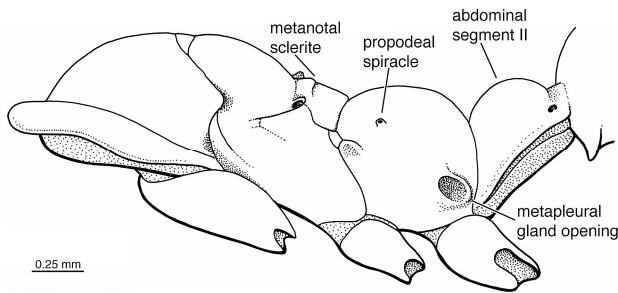
Fig. 1: The mesosoma of a Cretaceous ant, *Gerontoformica robustus* (BARDEN & GRIMALDI, 2014) in lateral view. The metapleural gland opening, visible posteroventrally on the propodeum, has traditionally been a key feature for assigning fossils to Formicidae. Note also the presence of a distinct metanotal sclerite, with clear sutures on all margins – present in many workers of early ant lineages, contrasted with almost all extant species where this segment is lost or reduced to a groove. Redrawn from BARDEN & GRIMALDI (2014).

2007, LAPOLLA & al. 2013), and perspectives on the subject are driven largely by fossil material available at the time. Among modern taxa, there are generally four morphological synapomorphies (with some exceptions relating to secondary losses) that define ants:

- Presence of a metapleural gland (in females),
- abdominal segment II differentiated into a distinct petiole segment,
- geniculate (elbowed) antennae, and
- antennal scape elongate (corresponds with above).

Since the discovery of the first Cretaceous ant, the primary synapomorphy for including an early fossil within the family Formicidae has been the presence of the metapleural gland (WILSON & al. 1967). The gland, found only in ants, is fairly complex, exuding a range of antimicrobial and communication-aiding chemicals (HÖLLDOBLER & ENGEL-SIEGEL 1984, YEK & MUELLER 2011). Gland presence is determined by a distinct opening on the mesosoma – while there are spiracles positioned laterally on the propodeum in ants (situated anterodorsally in most Cretaceous taxa), the gland is visible as a separate cavity or slit positioned posteroventrally (Fig. 1). There are no known taxa that exhibit a metapleural gland while lacking a differentiated petiole segment, however, most early ants do not possess the elongate scape characteristic of modern ant workers and queens. Some Cretaceous species also exhibit a distinct metanotal sclerite not present in most extant ant species but known in other aculeates (e.g., *Gerontoformica*, *Sphecomyrma*, some Haidomyrmecines). Beyond these features, only two of forty-five known species from the Cretaceous are unambiguously assignable to modern subfamilies based on other characteristics. So then, if many early fossil taxa fail to meet each criterion for a family-level diagnosis and elude placement within living subfamilies, what exactly a r e they?

The earliest ants known are assemblages of ant synapomorphies and plesiomorphic features exhibited by non-ant relatives. These affinities prompted the erection of two subfamilies known only from Cretaceous fauna: Sphecomyrminae (WILSON & al. 1967) and Brownimeciinae (BOLTON 2003). Sphecomyrmine diagnostic features include the presence of a metapleural gland and a shortened scape that is ~ 25% length of the remaining antennal segments together (full diagnostic features listed in BOLTON 2003). The monotypic subfamily Brownimeciinae – *Brownimecia clavata* GRIMALDI, AGOSTI & CARPENTER, 1997 was initially placed in Ponerinae but has since had its own subfamily erected by BOLTON (2003) – is characterized by a long scape similar to modern taxa, but fits no otherwise described subfamilies, mandible dentition and structure in particular are distinct. Even with these fossil subfamilies, many taxa are regarded as incertae sedis, as they cannot be reliably placed due to preservation quality or yet another unique set of features. Regardless of taxonomic assignment, many of these early taxa are now known to occupy a unique position among the ants.

Paleomyrmecological paradigm shift: The discovery of *Sphecomyrma freyi* WILSON & BROWN, 1967 in Turonian aged amber from New Jersey dated to 92 Ma (GRIMALDI & al. 2000) would shape interpretations on early ant evolution for decades. Prior to any pre-Eocene ant discoveries, it had been suggested that ancestral ant morphology would be similar to modern members of the Tiphiidae (BROWN 1954) with wingless females. Remarkably, the description of *S. freyi* closely matched expectations for this hypothetical ancestor, down to the toothed tarsal claws: a generalized morphology with wasp-like features and some hallmarks of modern ants (WILSON & al. 1967). This example of fossil prediction based on extant fauna is so prevalent it is featured in some introductory textbooks (FUTUYMA 2013). Initial speculation was that *S. freyi* was ancestral to some, but, not all ant lineages, namely: Aneuretinae, Dolichoderinae, Formicinae, Myrmeciinae, and Pseudomyrmecinae (WILSON & al. 1967). It was not until the rediscovery of the myrmeciine *Nothomyrmecia macrops* CLARK, 1934 and subsequent reconsideration that Sphecomyrminae was proposed to be ancestral to all modern ants (TAYLOR 1978). Were these early ants the "ancestral forms" of extant lineages? GRIMALDI & al. (1997) performed a series of phylogenetic analyses that recovered *Sphecomyrma* among a polytomy at the base of the Formicidae, a finding suggestive of, but not entirely confirming, a stem-group relationship with respect to modern ants; Brownimeciinae was at the time recovered with a close relationship to ponerines. Since the first phylogenetic treatment almost twenty years ago, the number of described ants from the Cretaceous has more than doubled (Tab. 1). These discoveries have dramatically expanded known diversity: From apparently highly specialized feeders like *Camelomecia* (BARDEN & GRIMALDI 2016), haidomyrmecines (DLUSSKY 1996, ENGEL & GRIMALDI 2005, PERRICHOT & al. 2008, BARDEN & GRIMALDI 2012, MCKELLAR & al. 2013a, PERRICHOT & al. 2016b), and *Zigrasimecia* (BARDEN & GRIMALDI 2013, PERRICHOT 2014a) to species of *Gerontoformica* with adaptations analogous to those exhibited by living taxa (NEL & al. 2004, PERRICHOT & al. 2008, BARDEN & GRIMALDI 2014), it is now clear that early ants were specialized beyond expectation. With respect to overall head and body shape, Cretaceous ants occupy approximately 10% of the morphospace known from modern taxa (BARDEN & GRIMALDI 2016). Particularly in the case of feeding morphologies, some of these adaptations are not present in any extant species. How might perceptions of early ant evo-
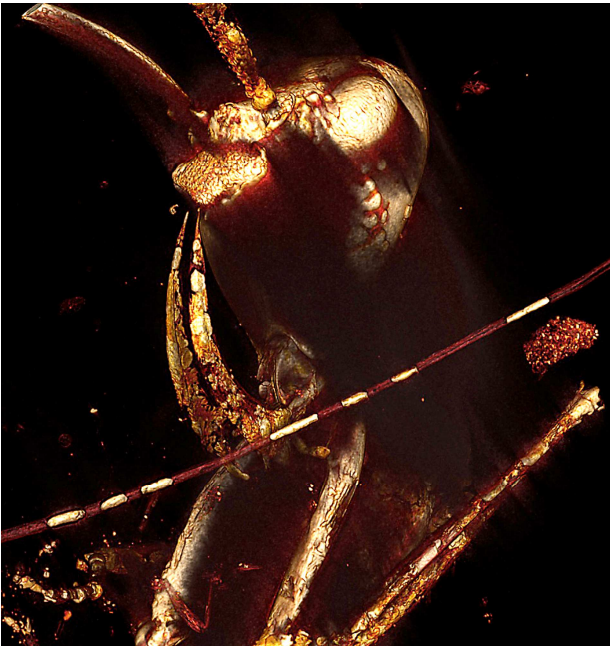
Fig. 2: Micro-CT reconstruction of *Haidomyrmex scimitarus* BARDEN & GRIMALDI, 2012 in Burmese amber. While the red coloration of this image is artificial, any color-scheme applied would be as well as X-ray imaging captures no coloration. Shapes surrounding the specimen are plant and mineral synclusions. Imaging performed at Cornell Biotechnology Resource Center Imaging Facility with help of M. Riccio.

lution developed had Wilson, Carpenter, and Brown first encountered a haidomyrmecine "hell ant" – with its striking scythe-shaped mandibles (Fig. 2) – instead of the generalized *Sphecomyrma freyi* nearly 50 years ago?

Eusocial behavior, manifested in the maintenance of colonies and reproductive division of labor, is itself a defining feature of ants (HÖLLDOBLER & WILSON 1990) and so, if advanced social behavior could be inferred from fossil material, this too would support placement within the Formicidae. A female morphotype without wings may therefore be suggestive of ant affinities and a worker caste, however, there are multiple aculeate groups with wingless females and solitary behavior (Bethylidae, Bradynobaenidae, Mutillidae, Tiphiidae; GOULET & HUBER 1993). Early ants are now known to have exhibited sociality based primarily on two lines of evidence:

1) C a s t e - d i f f e r e n t i a t i o n . It is difficult, if not impossible, to confidently determine that two reproductive castes known from fossil specimens are conspecific. The problem is similar to that of identifying conspecific ontological stages or sexually dimorphic individuals. However, it is possible to infer that castes may belong to the same taxonomic unit at a higher scale based on morphological similarity; such taxa may be considered so-called sciotaxa (BENGTSON 1985). There are congeneric queen and worker castes known from four genera: *Haidomyrmex* (BARDEN & GRIMALDI 2012), *Haidomyrmodes* (determined conspecific; PERRICHOT & al. 2008), *Gerontoformica* (queen described but not named; BARDEN & GRIMALDI 2016), and *Zigrasimecia* (BARDEN & GRIMALDI 2013, PERRICHOT 2014a).

2) C o - o c c u r r e n c e s . Ants are rare in early fossil deposits; material recovered to date suggests that ants were a minor part of ecosystems during the Mesozoic – they comprise less than 2% of all insects in Cretaceous amber (reviewed in GRIMALDI & AGOSTI 2000, DLUSSKY & RASNITSYN 2002, LAPOLLA & al. 2013). It is therefore highly unlikely that multiple conspecific workers will be present in the same fossil specimen. Two workers of *Sphecomyrma freyi* (see GRIMALDI & AGOSTI 2000), three complete and two partial workers of *Zigrasimecia* (PERRICHOT 2014a), as well as between two and eleven conspecific workers of *Gerontoformica* (PERRICHOT & al. 2008, BARDEN & GRIMALDI 2016) have been reported or described as synclusions. These later aggregations appear to suggest fairly advanced social behavior, as colonies would have to be large enough to field at least 11 foraging workers at one time (assuming these individuals are from the same colony).

Recent phylogenetic analyses appear to confirm that most Cretaceous ants correspond to lineages distinct from living, crown group ants, consistent with a stem-group assignment (Fig. 3; BARDEN & GRIMALDI 2016). A crown-group is a monophyletic group comprising the last common ancestor of all extant group members and all descendants of that common ancestor, living or extinct. Except in cases of derived losses, crown-group members possess all synapomorphes, or, defining features, that characterize the group. A stem-group refers to non-crown taxa that are more closely related to the crown group than they are to the nearest extant sister group; a stem-group is paraphyletic with respect to the crown group (JEFFERIES 1979, SMITH 1994). In other words, any taxon more closely related to extant ants than to extant wasps without falling into crown Formicidae, is a stem group ant. Even if the taxon possesses some, but not all of the features that define crown-group ants, it would be positioned within stem-group Formicidae. While some authors (e.g., MAGALLÓN 2004, WARD 2007) have used the term stem group to describe the crown group a n d stem lineages, this usage is not adopted here. Stem group designation should not be informed by existing divergence estimates because estimates themselves are malleable hypotheses that cannot be treated as fixed temporal frameworks. Instead, newly discovered fossils should be appended to datasets utilized to inform divergence estimates. This action prevents chronology of research from acting as a factor in fossil placement. Stem or crown group designation should be based on observable features and ideally from phylogenetic analysis.

Molecular divergence estimates suggest that crown-group ants originated between approximately 115 and 170 million years ago (BRADY & al. 2006, MOREAU & al. 2006, MOREAU & BELL 2013); estimates vary largely according to dataset and analytical assumptions. Broadly, younger molecular estimates are in stronger agreement with the fossil record, in particular because Jurassic estimates conflict heavily with the fossil record, as they exceed the age of the oldest aculeate fossils (RASNITSYN & QUICKE 2002, BRADY & al. 2009; also see "Where the ants are not"). Although there are no ant fossils older than 100 Ma, these estimates suggest that stem-group lineages and the early ancestors of modern ants co-occurred for a substantial period of time. Despite unexpected diversity and
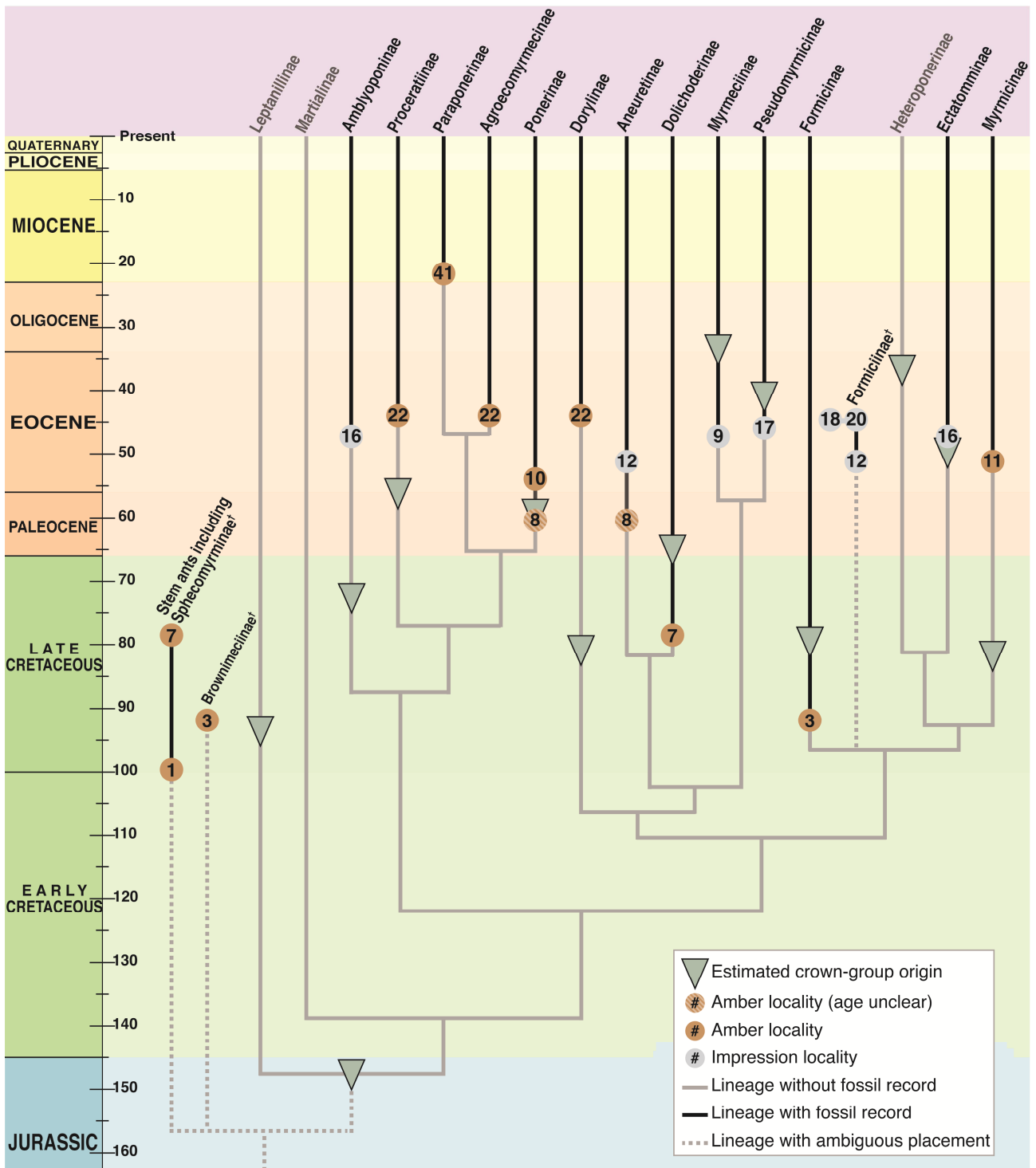
Fig. 3: A dated subfamily-level phylogeny with first confident fossil occurrences for each lineage, last occurrences indicated for extinct lineages. Fossil deposit numbers correspond with Table 2, Figure 4, and Figure 5. Tree topology as well as crown and divergence dates from Moreau & Bell (2013), which is so far the largest Formicidae-wide analysis with respect to taxon sampling. No crown age included for Aneuretinae, *Martialis*, and Paraponerinae as these are monotypic. Agroecomyrmecinae includes no crown age due to insufficient terminal sampling. Lineages with dotted lines were not placed directly through analyses, but rather added to the molecule-derived topology of Moreau & Bell, which did not include fossils. Stem ants and *Brownimecia* were placed according to conservative results of Barden & Grimaldi (2016) – Note that while Sphecomyrminae and stem group ants are depicted on a single lineage, this group is not necessarily monophyletic. Formiciinae placement is based on Ward (2007), although this position was not recovered in the only two phylogenetic treatments of the subfamily (Baroni Urbani & al. 1992, Grimaldi & al. 1997), it seems plausible to this author.

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Tab. 2: All fossil deposits with described ant taxa. Location data from The Paleontology Database (https://paleobiodb.org). * Indicates some controversy surrounding age of the locality. Ages are in millions of years before present. While DLUSSKY & RASNITSYN (2009) consider so-called "Scandinavian amber" distinct from Baltic amber, I do not adopt this distinction here as it is controversial and based largely on faunal composition which appears to have significant overlap. Bitterfeld amber, once considered to be a redeposition of Baltic amber, is in fact a distinct deposit of unique origin based on chemical analyses (WOLFE & al. 2016), and therefore considered here as a separate locality.

No. and deposit name	Location	Age and range	Age reference	Genera
1 Charentese Amber	45.9°N, 0.7°W	100 [105.3 - 99.7]	PERRICHOT & al. (2010)	Table 1
2 Burmese Amber	26.4°N, 96.7°E	98.8 [99.7 - 94.3]	SHI & al. (2012)	Table 1
3 New Jersey Amber	40.4°N, 74.3°W	92 [94.3 - 89.3]	GRIMALDI & al. (2000)	Table 1
4 Kzyl-Zhar, Kazakstan	44.4°N, 67.3°E	91.8 [94.3 - 89.3]	RASNITSYN & QUICKE (2002)	Table 1
5 Orapa, Botswana	22.3°S, 26.4°E	91.8 [94.3 - 89.3]	RAYNER & al. (1997)	Table 1
6 Taimyr Amber*	73.8°N, 101.4°E	87.1 [89.3 - 84.9]	RASNITSYN & QUICKE (2002)	Table 1
7 Medicine Hat Amber	49.8°N, 111.7°W	78.5 [84.9 - 70.6]	MCKELLAR & al. (2013a)	Table 1
8 Fur Formation, Denmark	56.9°N, 8.8°E	55 [55.8 - 54.1]	ARCHIBALD & al. (2006)	*Ypresiomyrma* (ARCHIBALD & al. 2006)
9 Oise Amber	49.3°N, 2.7°E	53.5 [55.0 - 52.0]	ARIA & al. (2011)	*Platythyrea* (ARIA & al. 2011)
10 Fushun Amber	41.8°N, 123.9°E	52.2 [55.8 - 48.6]	WANG & al. (2011)	*Brachytarsites* (HONG 2002), *Camponotus* (NAORA 1933), *Clavipetiola, Curticorna, Curtipalpulus, Eoaenictites, Eogorgites, Eoleptocerites* (HONG 2002), *Eomyrmex* (HONG & al. 1974), *Eoponerites, Eurytarsites, Furcisutura, Fushuniformica, Fushunomyrmex, Huaxiaformica, Leptogasteritus, Liaoformica, Longicapitia, Longiformica, Magnogasterites, Orbicapitia, Orbigastrula, Ovalicapito, Ovaligastrula, Quadrulicapito, Quineangulicapito, Sinoformica, Sinomyrmex, Sinotenuicapito, Sphaerogasterites, Wilsonia, Wumyrmex* (HONG 2002)
11 Green River, USA	43.3°N, 94.5°W	51 [53.5 - 48.5]	SMITH & al. (2008)	*Archimyrmex* (COCKERELL 1923b), *Camponotus* (SCUDDER 1877a), *Dolichoderus, Eoformica, Kohlsimyrma, Mianeuretus, Myrmecites, Pachycondyla, Ponerites, Proiridomyrmex, Solenopsites* (DLUSSKY & RASNITSYN 2002), *Titanomyrma* (ARCHIBALD & al. 2011)
12 McAbee, Canada	50.8°N, 121.1°W	51 [55.8 - 48.6]	EWING (1981)	*Avitomyrmex, Macabeemyrma, Myrmeciites, Ypresiomyrma* (ARCHIBALD & al. 2006)
13 Klondike Mountain, USA	48.7°N, 118.7°W	49 [55.8 - 48.6]	ARCHIBALD (2009)	*Camponotites* (DLUSSKY & RASNITSYN 1999), *Klondikia* (DLUSSKY & RASNITSYN 2002)
14 Ventana Formation, Argentina	41.1°S, 70.8°W	47.7 [48.6 - 40.4]	WILF (2012)	*Archimyrmex* (VIANA & HAEDO ROSSI 1957, ROSSI DE GARCIA 1983)
15 Messel Formation, Germany	49.9°N, 8.8°E	47 [48.6 - 40.4]	MERTZ & RENNE (2005)	*Archimyrmex* (DLUSSKY 2012), *Casaleia, Cephalopone, Cyrtopone* (DLUSSKY & WEDMANN 2012), *Gesomyrmex* (DLUSSKY & al. 2009), *Messelepone* (DLUSSKY & WEDMANN 2012), *Oecophylla* (DLUSSKY & al. 2008), *Pachycondyla* (DLUSSKY & WEDMANN 2012, DLUSSKY & al. 2015), *Protopone, Pseudectatomma* (DLUSSKY & WEDMANN 2012), *Titanomyrma* (ARCHIBALD & al. 2011)
16 Kishenehn Formation, USA	48.4°N, 113.7°W	46 [48.4 - 38.6]	CONSTENIUS (1996)	*Crematogaster, Dolichoderus, Eoformica, Formica, Ktunaxia, Lasius, Ponerites, Proiridomyrmex, Protazteca, Pseudomyrmex, Solenopsites* (LAPOLLA & GREENWALT 2015)
17 Bagshot Beds, UK	50.7°N, 2.1°W	44.6 [47.8 - 41.3]	JARZEMBOWSKI (1996)	*Formica* (COCKERELL 1920), *Formicium* (WESTWOOD 1854, ARCHIBALD & al. 2011), *Oecophylla* (COCKERELL 1920)
18 Sakhalin Amber*	47.4°N, 142.8°E	44.6 [47.8 - 41.3]	BARANOV & al. (2014)	*Aneuretellus, Chimaeromyrma, Eotapinoma, Protopone, Zherichinius* (DLUSSKY 1988)
19 Claiborne amber*	34.4°N, 92.8°W	44.5 [48.6 - 40.4]	SAUNDERS & al. (1974)	*Eocenidris, Iridomyrmex, Protrechina* (WILSON 1985a)

20 Claiborne Formation*	36.4°N, 88.3°W	44.5 [48.6 - 40.4]	SAUNDERS & al. (1974)	*Formicium* (CARPENTER 1929, ARCHIBALD & al. 2011)
21 Eckfeld Formation, Germany	50.1°N, 6.8°E	44.3 [49.0 - 44.0]	MERTZ & al. (2000)	*Gesomyrmex* (DLUSSKY & al. 2009), *Oecophylla* (DLUSSKY & al. 2008)
22 Baltic Amber*	54.9°N, 19.9°E	44.1 [47.8 - 41.3]	WEITSCHAT & WICHARD (2010)	*Agroecomyrmex* (WHEELER 1915), *Aphaenogaster* (MAYR 1868, WHEELER 1915), *Asymphylomyrmex* (WHEELER 1915), *Bilobomyrma* (RADCHENKO & DLUSSKY 2013), *Bradoponera* (MAYR 1868, DE ANDRADE & BARONI URBANI 2003), *Camponotus*, *Carebara* (MAYR 1868), *Cataglyphoides* (DLUSSKY 2008a), *Ctenobethylus* (Box 1), *Dolichoderus* (WHEELER 1915, DLUSSKY 2002a, 2008b), *Drymomyrmex* (WHEELER 1915), *Eldermyrmex* (HETERICK & SHATTUCK 2011), *Electromyrmex*, *Electroponera* (WHEELER 1915), *Enneamerus* (MAYR 1868), *Eocenomyrma* (DLUSSKY & RADCHENKO 2006a), *Fallomyrma* (DLUSSKY & RADCHENKO 2006b), *Formica* (PRESL & PRESL 1822, HOLL 1829, BERENDT 1830, GIEBEL 1856, MAYR 1868, WHEELER 1915, DLUSSKY 2002b, 2008a), *Gesomyrmex* (DLUSSKY & al. 2008), *Glaphyromyrmex* (WHEELER 1915), *Gnamptogenys*, *Hypoponera* (DLUSSKY 2009), *Lasius* (MAYR 1868, WHEELER 1915), *Liometopum* (WHEELER 1915), *Monomorium* (MAYR 1868, WHEELER 1915), *Myrmica* (MAYR 1868, RADCHENKO & al. 2007, RADCHENKO & ELMES 2010), *Nylanderia* (LAPOLLA & DLUSSKY 2010), *Oecophylla* (MAYR 1868, WHEELER & al. 1922), *Pachycondyla* (BOLTON 1995, DLUSSKY 2002b, 2009), *Parameranoplus*, *Paraneuretus* (WHEELER 1915), *Pheidole* (HOLL 1829, MAYR 1868), *Pityomyrmex* (WHEELER 1915), *Plagiolepis* (MAYR 1868, DLUSSKY 2010), *Platythyrea* (WHEELER 1915), *Ponera* (DLUSSKY 2009), *Prenolepis* (MAYR 1868), *Prionomyrmex* (MAYR 1868, BARONI URBANI 2000), *Pristomyrmex* (DLUSSKY & RADCHENKO 2011), *Procerapachys* (WHEELER 1915, DLUSSKY 2009), *Proceratium* (DLUSSKY 2009), *Prodimorphomyrmex* (WHEELER 1915), *Protaneuretus* (WHEELER 1915), *Protoformica* (DLUSSKY 1967), *Protomyrmica* (DLUSSKY & RADCHENKO 2009), *Pseudolasius* (WHEELER 1915), *Stenamma* (DUBOIS 1998), *Stigmatomma* (DLUSSKY 2009, YOSHIMURA & FISHER 2012), *Stigmomyrmex* (MAYR 1868), *Stiphromyrmex* (WHEELER 1915), *Temnothorax* (MAYR 1868, WHEELER 1915, BOLTON 2003, DLUSSKY & RADCHENKO 2006a), *Tetramorium* (RADCHENKO & DLUSSKY 2015), *Tetraponera* (DLUSSKY 2009), *Usomyrma* (DLUSSKY & al. 2014), *Vollenhovia* (WHEELER 1915), *Yantaromyrmex* (DLUSSKY & DUBOVIKOFF 2013)
23 Belarus Amber*	52.1°N, 24.2°E	44.1 [47.8 - 41.3]	ENGEL (2001)	*Liometopum* (NAZARAW & al. 1994, HETERICK & SHATTUCK 2011)
24 Elko Formation, USA	41.1°N, 115.5°W	42.5 [46.3 - 38.6]	HENRY (2008)	*Pseudocamponotus* (CARPENTER 1930)
25 Bol'shaya Svetlovodnaya, Russia*	46.6°N, 138.1°E	35.6 [37.2 - 33.9]	DLUSSKY & al. (2015)	*Agastomyrma, Biamomyrma, Casaleia, Dolichoderus, Emplastus, Formica, Gesomyrmex, Liometopum, Myrmecites, Pachycondyla, Paraneuretus, Proceratium, Ypresiomyrma* (DLUSSKY & al. 2015)
26 Brunstatt, France	47.7°N, 7.3°E	35.6 [37.2 - 33.9]	FIKÁČEK & al. (2011)	*Camponotus, Oecophylla* (FÖRSTER 1891)*, Solenopsis* (THÉOBALD 1937)
27 Célas Gard, France*	44.1°N, 4.2°E	35.6 [37.2 - 33.9]	NEL & al. (2008)	*Tetraponera* (WARD 1990)
28 Kleinkems, Germany	47.7°N, 7.5°E	35.6 [37.2 - 33.9]	FIKÁČEK & al. (2011)	*Aphaenogaster, Dolichoderus* (THÉOBALD 1937), *Eoformica* (DLUSSKY & al. 2009), *Formica, Gesomyrmex, Iridomyrmex, Oecophylla* (THÉOBALD 1937), *Pachycondyla* (THÉOBALD 1937, BOLTON 1995), *Solenopsis* (THÉOBALD 1937, ÖZDIKMEN 2010)

29 Kučlín Czech Republic	50.5°N, 13.8°E	35.6 [39.1 - 32.0]	KVAČEK (2002)	*Dolichoderus* (DALLA TORRE 1893)
30 Mossy Creek, USA	30.5°N, 96.3°W	35.6 [37.2 - 33.9]	PaleoBio Database	*Formica* (COCKERELL 1923a)
31 Rovno Amber*	50.6°N, 26.3°E	35.6 [37.2 - 33.9]	PERKOVSKY & al. (2007)	*Aphaenogaster* (DLUSSKY & PERKOVSKY 2002), *Bilobomyrma* (RADCHENKO & DLUSSKY 2013a), *Boltonidris* (RADCHENKO & DLUSSKY 2012), *Carebara* (DLUSSKY & PERKOVSKY 2002), *Dolichoderus* (DLUSSKY & PERKOVSKY 2002, DLUSSKY 2002a, 2008b), *Formica* (DLUSSKY 2008a), *Monomorium* (RADCHENKO & PERKOVSKY 2010), *Pachycondyla* (DLUSSKY 2009), *Plagiolepis, Tapinoma* (DLUSSKY & PERKOVSKY 2002), *Tetraponera* (DLUSSKY 2009), *Vollenhovia* (RADCHENKO & DLUSSKY 2013b)
32 Florissant, USA	38.9°N, 105.3°W	34.1 [37.2 - 33.9]	EVANOFF & GREGORY-WODZICK (2001)	*Aphaenogaster, Archiponera* (CARPENTER 1930), *Camponotus* (CARPENTER 1930, ÖZDIKMEN 2010), *Cephalomyrmex, Dolichoderus, Elaeomyrmex* (CARPENTER 1930), *Eulithomyrmex* (CARPENTER 1930, 1935), *Formica, Iridomyrmex* (CARPENTER 1930), *Lasius* (COCKERELL 1927, WILSON 1955), *Liometopum, Messor, Mianeuretus, Miomyrmex, Petraeomyrmex, Pheidole, Pogonomyrmex, Protaztteca* (CARPENTER 1930), *Pseudomyrmex* (CARPENTER 1930, WARD 1990)
33 Bouldnor Formation, UK	50.7°N, 1.4°W	33.9 [37.2 - 33.9]	HOOKER & al. (2009)	*Britaneuretus, Camponotus* (ANTROPOV & al. 2014), *Colobopsis, Dolichoderus* (DONISTHORPE 1920, ANTROPOV & al. 2014), *Emplastus* (COCKERELL 1915, DONISTHORPE 1920, ANTROPOV & al. 2014), *Leucotaphus* (COCKERELL 1915, ANTROPOV & al. 2014), *Oecophylla* (COCKERELL 1915), *Paraphaenogaster* (ANTROPOV & al. 2014), *Ponerites* (DONISTHORPE 1920, ANTROPOV & al. 2014, SCHMIDT & SHATTUCK 2014), *Solenopsites, Taphopone* (ANTROPOV & al. 2014)
34 Sicilian amber*	37.4°N, 15.1°E	31 [33.9 - 28.1]	RASNITSYN & QUICKE (2002)	*Carebara* (EMERY 1891, FERNÁNDEZ 2004), *Cataulacus, Crematogaster, Ectatomma* (EMERY 1891), *Hypopomyrmex* (EMERY 1891, BROWN & CARPENTER 1979), *Leptomyrmula* (EMERY 1913), *Oecophylla, Plagiolepis, Podomyrma, Ponera* (EMERY 1891), *Sicilomyrmex* (EMERY 1891, WHEELER 1915, BROWN & CARPENTER 1979), *Tapinoma, Technomyrmex* (EMERY 1891)
35 Fonseca Formation, Brazil	20.2°S, 43.3°W	30.1 [37.2 - 23.0]	LARA & al. (2012)	*Fonsecahymen* (MARTINS NETO & MENDES 2002)
36 Quesnel, Canada	53.0°N, 122.5°W	28.5 [33.9 - 23.0]	PaleoBio Database	*Aphaenogaster, Calyptites* (SCUDDER 1877a), *Dolichoderus* (SCUDDER 1877a, SHATTUCK 1994), *Formica* (SCUDDER 1877a)
37 Aix-en-Provence, France	43.5°N, 5.5°E	25.7 [28.4 - 23.0]	RASNITSYN & QUICKE (2002)	*Aphaenogaster, Camponotus* (THÉOBALD 1937), *Carebara* (THÉOBALD 1937, FERNÁNDEZ 2004), *Dolichoderus, Formica, Lasius* (THÉOBALD 1937)
38 Bitterfeld Amber*	51.6°N, 12.4°E	24.6 [25.3 - 23.8]	DUNLOP (2010)	*Bradoponera* (DLUSSKY 2009), *Conoformica* (DLUSSKY 2008a), *Dolichoderus* (DLUSSKY 2008b), *Formica* (DLUSSKY 2008a), *Myrmica* (RADCHENKO & al. 2007), *Pachycondyla* (DLUSSKY 2009), *Plagiolepis* (DLUSSKY 2010), *Plesiomyrmex* (DLUSSKY & RADCHENKO 2009), *Ponera* (DLUSSKY 2009), *Yantaromyrmex* (DLUSSKY & DUBOVIKOFF 2013)
39 Rott, Germany	50.7°N, 7.3°E	24 [23.8 - 24.2]	BÖHME (2003)	*Aphaenogaster* (MEUNIER 1915, RADCHENKO & al. 2007), *Camponotus* (GERMAR 1837, MAYR 1867), *Formica* (MEUNIER 1915), *Liometopum* (MEUNIER 1917, DLUSSKY & PUTYATINA 2014), *Ponera* (MEUNIER 1923), *Prionomyrmex* (DLUSSKY 2012)
40 Foulden Maar, New Zealand	45.5°S, 170.2°E	23.2 [23.3 - 19.0]	LINDQVIST & LEE (2009)	*Austroponera, Myrmecorhynchus, Rhytidoponera* (KAULFUSS & DLUSSKY 2015)
41 Dominican Amber*	19.6°N, 70.8°W	20.5 [26.0 - 15.0]	BRODY & al. (2001)	*Acanthognathus* (BARONI URBANI & DE ANDRADE 1994), *Acanthostichus* (DE ANDRADE 1998a), *Acropyga* (LAPOLLA 2005), *Anochetus*

				(BARONI URBANI 1980a, MACKAY 1991, DE ANDRADE 1994), *Aphaenogaster* (DE ANDRADE 1995), *Apterostigma* (SCHULTZ 2007), *Azteca* (WILSON 1985d), *Cephalotes* (DE ANDRADE & BARONI URBANI 1999, DE ANDRADE 2001), *Cylindromyrmex* (DE ANDRADE 1998c, 2001), *Cyphomyrmex* (DE ANDRADE 2003), *Discothyrea* (DE ANDRADE 1998b), *Dolichoderus* (WILSON 1985d, SHATTUCK 1992, MACKAY 1993), *Gnamptogenys* (BARONI URBANI 1980c, LATTKE 2002), *Gracilidris* (WILSON 1985d, WILD & CUEZZO 2006), *Ilemomyrmex* (WILSON 1985b), *Leptomyrmex* (BARONI URBANI 1980d), *Neivamyrmex* (WILSON 1985c), *Nesomyrmex* (DE ANDRADE & al. 1999, BOLTON 2003), *Nylanderia* (LAPOLLA & DLUSSKY 2010), *Odontomachus* (DE ANDRADE 1994), *Oxyidris* (WILSON 1985b), *Paraponera* (BARONI URBANI 1994), *Pheidole* (WILSON 1985b, BARONI URBANI 1995), *Platythyrea* (LATTKE 2003, DE ANDRADE 2004), *Proceratium* (LATTKE 1991, BARONI URBANI & DE ANDRADE 2003), *Pseudomyrmex* (WARD 1992), *Strumigenys* (BARONI URBANI & DE ANDRADE 1994, 2007), *Tapinoma* (WILSON 1985d), *Technomyrmex* (WILSON 1985d, BRANDÃO & al. 1999), *Temnothorax* (DE ANDRADE 1992), *Trachymyrmex* (BARONI URBANI 1980b), *Zatania* (LAPOLLA & al. 2012)
42 Chiapas Amber*	16.3°N, 92.4°W	19.5 [23.0 - 16.0]	SOLÓRZANO KRAEMER (2007)	*Aphaenogaster* (DE ANDRADE 1995), *Cephalotes* (DE ANDRADE & BARONI URBANI 1999), *Cyphomyrmex* (DE ANDRADE 2003), *Discothyrea* (DE ANDRADE 1998a)
43 Decín, Czech Republic	50.8°N, 14.2°E	19.5 [23.0 - 16.0]	SAMŠIŇÁK (1967)	*Camponotus* (SAMŠIŇÁK 1967)
44 Radoboj, Croatia	46.2°N, 15.9°E	18.2 [20.4 - 16.0]	RASNITSYN & QUICKE (2002)	*Attopsis* (HEER 1849, MAYR 1867), *Camponotus* (HEER 1849, MAYR 1867, DLUSSKY & PUTYATINA 2014), *Casaleia* (HEER 1849, DLUSSKY & PUTYATINA 2014), *Dolichoderus* (DLUSSKY & PUTYATINA 2014), *Emplastus* (HEER 1849, MAYR 1867, DLUSSKY & PUTYATINA 2014), *Formica* (HEER 1849, 1867, DLUSSKY & PUTYATINA 2014), *Gesomyrmex* (HEER 1849, DLUSSKY & PUTYATINA 2014), *Heeridris* (DLUSSKY & PUTYATINA 2014), *Lasius* (HEER 1849, 1867, DLUSSKY & PUTYATINA, 2014), *Liometopum* (HEER 1849, 1867, DLUSSKY & PUTYATINA 2014), *Lonchomyrmex* (HEER 1867, DLUSSKY & PUTYATINA 2014), *Myrmecites, Oecophylla, Paraphaenogaster* (HEER 1849, DLUSSKY & PUTYATINA 2014), *Ponerites* (HEER 1849, 1867, DLUSSKY & PUTYATINA 2014)
45 Bílina, Czech Republic	50.6°N, 13.7°E	18 [20.0 - 16.0]	PROKOP & al. (2010)	*Odontomachus* (WAPPLER & al. 2014)
46 Mfangano Island, Kenya	0.5°S, 34.0°E	17.8 [20.4 - 16.0]	DRAKE & al. (1988)	*Oecophylla* (WILSON & TAYLOR 1964)
47 Borneo Amber	2.7°N, 113.8°E	17 [17.0 - 16.0]	BRODY & al. (2001)	*Cataulacus* (DE ANDRADE & BARONI URBANI 2004)
48 Mokřina, Czech Republic	50.1°N, 12.5°E	16.5 [16.9 - 16.0]	PaleoBio Database	*Carebara* (NOVÁK 1877, FERNÁNDEZ 2004), *Formica* (NOVÁK 1877), *Myrmica* (NOVÁK 1877, RADCHENKO & al. 2007)
49 Shanwang Formation, China	36.6°N, 118.7°E	15.5 [16.0 - 11.6]	ZHANG (1989)	*Alloiomma, Aphaenogaster* (ZHANG 1989, ZHANG & al. 1994), *Camponotites* (HONG 1984, DLUSSKY & al. 2008), *Camponotus* (HONG 1984, ZHANG 1989, ZHANG & al. 1994, HONG & WU 2000), *Dolichoderus* (ZHANG 1989, ZHANG & al. 1994), *Elaphrodites* (ZHANG 1989), *Eurymyrmex* (ZHANG & al. 1994), *Formica* (ZHANG 1989, ZHANG & al. 1994), *Iridomyrmex* (ZHANG 1989), *Lasius* (HONG & al. 2001, ZHANG 1989), *Leptogenys* (ZHANG 1989), *Liometopum* (ZHANG 1989, ZHANG & al. 1994), *Miosolenopsis, Myopopone, Pachycondyla, Tapinoma, Technomyrmex* (ZHANG 1989), *Zhangidris* (ZHANG 1989, BOLTON 2003)

50 Chojabaru Formation, Japan	33.8°N, 129.8°E	15.3 [16.0 - 13.7]	YABUMOTO & UYENO (2009)	*Aphaenogaster* (FUJIYAMA 1970)
51 Kerch, Ukraine	45.4°N, 36.5°E	14.9 [16.0 - 13.7]	PaleoBio Database	*Dolichoderus* (DLUSSKY 1981)
52 Chon-Tuz, Kyrgyzstan	42.2°N, 75.5°E	13.8 [16 - 11.6]	PROKOFIEV (2007)	*Casaleia* (DLUSSKY 1981, BOLTON 1995), *Kotshkorkia, Rhytidoponera* (DLUSSKY 1981)
53 Kuban, Russia	44.9°N, 40.6°E	13.8 [16.0 - 11.6]	PaleoBio Database	*Ponerites* (POPOV 1933, DLUSSKY 1981)
54 Vishnevaya Balka Creek, Russia	45.1°N, 42.3°E	13.8 [16.0 - 11.6]	PaleoBio Database	*Camponotites, Lasius* (DLUSSKY 1981), *Paraphaenogaster, Taphopone* (DLUSSKY 1981, ANTROPOV 2014)
55 Parschlug, Austria	47.5°N, 15.3°E	13.2 [13.7 - 12.7]	PaleoBio Database	*Liometopum* (HEER 1849, DLUSSKY & PUTYATINA 2014), *Myrmica* (HEER 1849, RADCHENKO & ELMES 2010)
56 Berezovsky massif, Ukraine*	48.3°N, 23.5°E	12.2 [12.7 - 11.6]	ZALESSKY (1949)	*Lasius* (ZALESSKY 1949)
57 Oeningen, Germany, Switzerland	47.7°N, 8.9°E	12.2 [12.7 - 11.6]	RASNITSYN & QUICKE (2002)	*Camponotus* (HEER 1849, COCKERELL 1915), *Carebara* (HEER 1849, FISCHER & al. 2014), *Formica* (HEER 1849), *Imhoffia* (HEER 1849, 1867), *Liometopum* (HEER 1849,1867, DLUSSKY & PUTYATINA 2014), *Myrmica* (HEER 1849, RADCHENKO & al. 2007, RADCHENKO & ELMES 2010)
58 Ormety, Georgia	42.0°N, 41.9°E	12.2 [12.7 - 11.6]	PaleoBio Database	*Formica* (POPOV 1933, DLUSSKY 1981)
59 Joursac, France	45.1°N, 3.0°E	8.5 [11.6 - 7.2]	PaleoBio Database	*Camponotus, Formica, Lasius* (PITON & THÉOBALD 1935)
60 Schossnitz, Poland	51.0°N, 16.8°E	8.5 [11.6 - 5.3]	PaleoBio Database	*Carebara* (ASSMANN 1870, FISCHER & al. 2014), *Lasius, Lonchomyrmex* (ASSMANN 1870)
61 Cerro Azul Formation, Argentina	36.7°S, 64.3°W	7.9 [9.0 - 6.8]	FLYNN & SWISHER (1995)	*Attaichnus* (LAZA 1982)
62 Montagne d'Andance, France	44.7°N, 4.7°E	7 [8.7 - 5.3]	PaleoBio Database	*Camponotus, Oecophylla* (RIOU 1999)
63 Apomarma, Greece	35.1°N, 24.9°E	6.3 [7.2 - 5.3]	PaleoBio Database	*Polyrhachis* (WAPPLER & al. 2009)
64 Brunn-Vösendorf, Austria	48.1°N, 16.3°E	6.3 [7.2 - 5.3]	PaleoBio Database	*Aphaenogaster, Camponotus* (BACHMAYER 1960)
65 Auxillac, France	45.1°N, 2.9°E	6.3 [7.2 - 5.3]	PaleoBio Database	*Formica* (PITON & THÉOBALD 1935)
66 Lake Chambon, France	45.6°N, 2.9°E	4.5 [5.3 - 3.6]	PaleoBio Database	*Formica, Lasius* (PITON & THÉOBALD 1935)
67 Willershausen Clay, Germany	51.8°N, 10.1°E	3.1 [3.6 - 2.6]	SOHN & al. (2012)	*Camponotites* (STEINBACH 1967, DLUSSKY & al. 2011)

apparent social behavior, stem-group lineages do not appear to have persisted beyond the Cretaceous-Paleogene (K-Pg) boundary. There is some ambiguity here, as there is an approximately 20 million year blind spot between Canadian Medicine Hat amber (78 Ma; MCKELLAR & al. 2013a), where the last stem-ant groups are known, and the Fur Formation in Denmark (55 Ma; ARCHIBALD & al. 2006), the next confidently-dated ant-yielding locality. It should be noted that Sphecomyrminae was not recovered as monophyletic in recent phylogenetic analyses (BARDEN & GRIMALDI 2016), and therefore additional taxonomic work will be necessary as more specimens are discovered and subsequent phylogenetic hypotheses are generated. Some stem-lineages are presently left as incertae sedis to prevent taxonomic confusion until phylogenetic stability is achieved.

The enigmatic armaniids, considered a subfamily by BOLTON (2003), are here considered to lie outside of the Formicidae, following GRIMALDI & ENGEL (2005) and LAPOLLA & al. (2013). DLUSSKY (1983) first described the Armaniidae – then comprising six genera and nine species – following the discovery of impression fossils from a Cenomanian aged deposit in Russia. He also speculated

that the incertae sedis genera *Cretopone* and *Petropone* (Tab. 1) may belong to the family, but could not be reliably placed due to poor preservation. Some taxa now considered armaniids were initially placed in extant subfamilies (DLUSSKY 1975). A thorough review of the "armaniid controversy" can be found in LAPOLLA & al. (2013), but the fundamental problem with these initially described taxa, along with the subsequent five species that would be described (DLUSSKY 1999, DLUSSKY & al. 2004), remains the quality of preservation. Armaniids possess wing venation and a general habitus similar to that of modern ants; however, the presence of a metalpleural gland has not been confirmed in any specimen to date. WILSON (1987) suggested that armaniids, which are known only from winged female and male morphotypes, might represent the reproductive caste of sphecomyrmine workers. With the subsequent discovery of workers and queens in four distinct stem-group genera, this hypothesis can be reasonably refuted. If armaniids do in fact represent the reproductive caste of an early ant lineage, the workers are yet to be found. The true position of armaniids either as a family distinct from the Formicidae, or as an early ant branch similar to other known stem-group lineages, would

be best resolved through combined phylogenetic analysis of worker, queen, and male morphology simultaneously. Other proposed early ants known from imprint fossils have been disputed based on subsequent reevaluation. Following initial placement in the Formicidae, *Cretacoformica explicata* JELL & DUNCAN, 1986 from Aptian-aged (113 - 125 Ma) impression fossils of Victoria, Australia (JELL & DUNCAN 1986) has since been placed as incertae sedis within Hymenoptera as a whole (NAUMANN 1993). BRANDÃO & al. (1990) described *Cariridris bipetiolata* BRANDÃO & MARTINS-NETO, 1990 from a wingless specimen of the Santana Formation of Brazil (110 - 112 Ma) as a myrmeciine worker, however this too has been disputed (discussed below).

Early crown-group ants

The vast majority of the earliest ant taxa are distinct from their modern relatives. Out of a total 45 species described from Cretaceous deposits, nine species have been attributed to modern subfamilies, however, only two are without significant controversy (dubious crown-group ants denoted below with ◆):

Burmomyrma rossi◆ DLUSSKY, 1996 – from Burmese amber dated to the Late Cretaceous ~ 99 Ma (SHI & al. 2012). Along with the type specimen of *Haidomyrmex* from the same locality, the type of *B. rossi* was deposited in the Natural History Museum, London (NHM) where it would await description for nearly 80 years (BARDEN & GRIMALDI 2012). Because the sole specimen (an alate female) is missing the entire head and portions of the mesosoma, DLUSSKY (1996) was initially equivocal in his assignment of *Burmomyrma* to Aneuretinae, stating the "systematic position could not be determined reliably due to poor preservation of the only specimen known". Tentative aneuretine placement was based on highly reduced forewing venation, curved sting, a single segmented petiole, and a gaster without constrictions. This particular assortment of characters cannot be used to assign *Burmomyrma rossi* to any subfamily with confidence, particularly as the wing venation described is not shared by other known aneuretines (BOUDINOT 2015). This taxon is best treated as incertae sedis, particularly when considering fossil calibrations for molecular divergence estimation. Despite the fragmentary nature of the specimen and cautious taxonomic treatment, *Burmomyrma rossi* has been utilized as the oldest minimum age calibration in many Formicidae-wide dating estimates (e.g., BRADY & al. 2006, MOREAU & al. 2006, MOREAU & BELL 2013).

Kyromyrma neffi GRIMALDI & AGOSTI, 2000 – New Jersey "Raritan" amber from the Turonian ~ 92 Ma (GRIMALDI & al. 2000). The single known worker specimen of *Kyromyrma neffi* clearly exhibits an acidopore, a defining feature of the Formicinae (GRIMALDI & AGOSTI 2000). Considered incertae sedis within the subfamily (BOLTON 2003), however, tribal placement within Formicini can be excluded.

Afromyrma petrosa◆◆ DLUSSKY, BROTHERS & RASNITSYN, 2004 – known from Turonian aged mudstone deposits in Orapa, Botswana dated to ~ 92 Ma (RAYNER & al. 1997). Simultaneously described with two other formicid and armaniid species by DLUSSKY & al. (2004), *Afromyrma petrosa* is the earliest putative member of the subfamily Myrmicinae based on the presence of a postpetiole and triangulate mandibles. ARCHIBALD & al. (2006) iden-

tify affinities with both Myrmicinae and Pseudomyrmecinae based on postpetiole presence, however, this particular feature has been misleading in similarly preserved fossils. *Cariridris bipetiolata* (see BRANDÃO & al. 1990) from Aptian aged limestone impressions of the Santana Formation in Brazil was initially placed within the Formicidae based on the supposed presence of a postpetiole. Subsequent authors (GRIMALDI & al. 1997, OHL 2004) have challenged this placement, suggesting that the postpetiole is likely the result of preservational anomalies.

Afropone oculata◆, *Afropone orapa*◆ DLUSSKY, BROTHERS & RASNITSYN, 2004 – Co-occurring with *Afromyrma*, from ~ 92 million year old Botswanan mudstone. While *A. oculata* is known from two winged females and is the type species for the genus, *A. orapa* is described from a putative male specimen and placed tentatively in the genus – all three *Afropone* specimens are poorly preserved. DLUSSKY & al. (2004) assigned *Afropone* to Ponerinae, however also highlighted affinities with numerous subfamilies including a petiole structure similar to Myrmeciinae, general habitus as in modern Pseudomyrmecinae, and a well-separated abdominal segment III seen in Dorylinae, Myrmicinae, and others. ARCHIBALD & al. (2006) note that *Afropone* does not currently fit into Ponerinae or indeed any other currently defined subfamily, suggesting that it may not in fact represent a crown-group ant.

Cananeuretus occidentalis◆◆ ENGEL & GRIMALDI, 2005 – Canadian Medicine Hat amber dated to ~78 Ma in the Campanian (MCKELLAR & al. 2013a). ENGEL & GRIMALDI (2005) placed *Cananeuretus* tentatively into Aneuretinae noting the worker type specimen bears a striking resemblance to *Eotapinoma*, a putatively dolichoderine genus from the same locality. The authors also speculated that *Cananeuretus* might be a stem taxon of (Aneuretinae + Dolichoderinae), a hypothesis that has not been tested.

Canapone dentata◆ DLUSSKY, 1999 – recovered in Canadian Medicine Hat amber. Based on a single wingless female specimen, DLUSSKY (1999) initially placed *Canapone* in Ponerinae though noting the palp count and presence of ocelli might suggest a myrmeciine relative. BOLTON (2003) inferred that the monotypic genus represents an incertae sedis member of Ectatomminae, noting that *C. dentata* exhibits plesiomorphies not found in any modern species. As with other ambiguous taxa, *Canapone* would benefit from a phylogenetic assessment and more thorough examination, however, the type specimen has been lost (MCKELLAR & al. 2013b).

Eotapinoma macalpini◆ DLUSSKY, 1999 – Canadian Medicine Hat amber. There are a total of three described species within the dolichoderine genus *Eotapinoma* with two others known from Sakhalin amber (DLUSSKY 1988), material that was originally thought to be Paleocene in age, but now considered Eocene (BARANOV & al. 2014). The type specimen of *E. macalpini* is a small wingless female, most probably a worker. DLUSSKY (1999) noted similar features between *E. macalpini* and the type species *E. gracilis* from Sakhalin amber, however, assignment was based largely on lacking attributes and some doubt has been raised regarding placement within Dolichoderinae (GRIMALDI & AGOSTI, 2000). The species description and accompanying figures are not sufficient to resolve the position of this taxon and, as with *Canapone dentata*, the type specimen appears to be lost.

Chronomyrmex medicinehatensis MᴄKᴇʟʟᴀʀ, Gʟᴀsɪᴇʀ & Eɴɢᴇʟ, 2013 – From Canadian Medicine Hat amber. Initially figured and reported but not described (MᴄKᴇʟʟᴀʀ & Eɴɢᴇʟ 2012), *C. medicinehatensis* is known from two worker specimens although these are not synclusions: the complete but partially obscured holotype along with a second partial individual. *Chronomyrmex* is readily placed within Dolichoderinae based on the position of petiole-gaster attachment, an apical gastral slit, as well the presence of denticles along the basal mandibular margin. Interestingly, the fossil exhibits most diagnostic features consistent with a placement within the tribe Leptomyrmecini. With respect to earliest subfamilial fossil and for purposes of molecular dating, *Chronomyrmex medicinehatensis*, an undisputed dolichoderine, has functionally replaced *E. macalpini*.

Although they are not yet described, there are probable dolichoderine, formicine, and ponerine specimens in Burmese amber (V. Perrichot, pers. comm.; Pᴇʀʀɪᴄʜᴏᴛ 2014b), which would extend the known fossil record for these subfamilies, in particular Dolichoderinae and Ponerinae, considerably.

Where the ants are not

There are reports of a dolichoderine ant from Ethiopian amber dated to the Cretaceous (Sᴄʜᴍɪᴅᴛ & al. 2010, LᴀPᴏʟʟᴀ & al. 2013), however, it seems the age of this deposit was reported in error. Ethiopian amber is in fact considerably younger, likely Miocene (P. Nascimbene, pers. comm.; Pᴇʀʀɪᴄʜᴏᴛ & al. 2016). Thus, while molecular divergence dating estimates suggest an origin for most modern subfamilies during the Cretaceous (Mᴏʀᴇᴀᴜ & Bᴇʟʟ 2013) very few well-preserved species from this time period are assignable to lineages present today. A lack of crown group ant fossils does not necessarily indicate that divergence estimations are in error. It is well within the realm of possibility that early members of modern subfamilies were present in the mid-Cretaceous along with stem-group ants and were merely less likely to be captured in amber, perhaps due to a hypogeic lifestyle (Lᴜᴄᴋʏ & al. 2013) or localized diversification on landmasses with sparse fossil records such as South America (Mᴏʀᴇᴀᴜ & Bᴇʟʟ 2013) (see Ghost Lineages below). The latter is particularly likely, as all Cretaceous fossil deposits known to yield definitive ant taxa are Laurasian.

Ants, either stem or crown, are conspicuously absent from a number of deposits where we might expect them. From a Laurasian standpoint, there are no known ants from the biologically diverse Yixian Formation in China (120 - 125 Ma; Zʜᴏɴɢʜᴇ 2006), Albian-aged (100 - 113 Ma) Spanish amber with well over 3,000 known bioinclusions (Dᴇʟᴄʟòs & al. 2007, Pᴇʀɪs & al. 2014), or Aptian-aged (113 - 125 Ma) Lebanese amber with several thousand inclusions reported from many outcrops (Azᴀʀ & al. 2010). While Yixian fossils are considerably older than ant-yielding Cretaceous amber from France and Myanmar, the lack of ants in Lebanese and Spanish amber is puzzling. In South America, despite the highly productive Crato Formation in Northeastern Brazil (Aptian age), from which over 350 species spanning 18 orders have been named (Gʀɪᴍᴀʟᴅɪ & Mᴀɪsᴇʏ 1990, Bᴀʀʟɪɴɢ & al. 2015), no ants are known. If molecular-based divergence estimations are correct, it is likely that new and important windows into ant

evolution will reveal themselves as these and other fossil deposits are sampled.

Rise of the ants

Changing of the guard: During the Cenozoic, after a 20 million year gap spanning from the Maastrichtian to the Paleocene (noted above), there is a marked change in the composition and number of ants in fossil deposits. Beginning with the earliest known Cenozoic fossils recovered from the Fur Formation of Denmark (~ 56 Ma; Aʀᴄʜɪʙᴀʟᴅ & al. 2006), all ants are attributable to crown Formicidae. A single species is described from the Fur Formation, *Ypresiomyrma rebekkae* (Rᴜsᴛ & Aɴᴅᴇʀsᴇɴ, 1999), a myrmeciine initially thought to belong to the extant genus *Pachycondyla* (Rᴜsᴛ & Aɴᴅᴇʀsᴏɴ 1999, Aʀᴄʜɪʙᴀʟᴅ & al. 2006). It is difficult to make a meaningful comparison relating to ant abundance or ecology for the Fur Formation with only one species known from many partial individuals after what was apparently an overwater mating swarm (Rᴜsᴛ & Aɴᴅᴇʀsᴏɴ 1999).

The Eocene is characterized by increases in the number of ant-yielding deposits and the relative number of ants recovered from those deposits. At least 375 specimens (Dolichoderinae, Formicinae, Myrmeciinae, Myrmicinae, Ponerinae, and Pseudomyrmecinae reported) are known from French Oise amber (~ 53 Ma; Aʀɪᴀ & al. 2011), comprising 2.5% of insect inclusions (LᴀPᴏʟʟᴀ & al. 2013). A single named species is described from Oise amber, *Platythyrea dlusskyi* Aʀɪᴀ, Pᴇʀʀɪᴄʜᴏᴛ & Nᴇʟ, 2011, which represents the oldest fossil species attributed to an extant genus and the earliest confidently aged ponerine. This taxonomic treatment is contrasted with the Fushun amber ant fauna described from Northeastern China (Wᴀɴɢ & al. 2011). There are 36 species from Fushun amber (52 Ma) belonging to 32 genera, 31 of which are found only in this deposit (Hᴏɴɢ 2002) – the only exception is *Camponotus*, which, incidentally, is the first occurrence of this genus. As discussed in LᴀPᴏʟʟᴀ & al. (2013), these taxa are in need of revision. No species are yet described from Cambay amber of Gujarat, India (~ 50 - 52 Ma; Rᴜsᴛ & al. 2010) but at least 125 specimens are now known (comprising 10.4% of all insects in this amber; P. Barden & D. Grimaldi, unpubl.), belonging to Aneuretinae, Dolichoderinae, Formicinae, Myrmicinae, Ponerinae, and Pseudomyrmecinae. This abundance is the highest yet known for any pre-Miocene amber deposit, perhaps owing to the hot and wet paleoclimate or the 40 million year period of isolation the Indian subcontinent experienced which ended near the formation of these fossils. Following description and revision of specimens from Cambay, Fushun, and Oise amber, it will be of great interest to compare the faunal composition of these approximately contemporaneous deposits, not just as well-dated windows into post-K-Pg boundary ants, but each as a representative of distinct paleoenvironments: Oise and Cambay amber derive from angiosperm forests of differing latitudes, while Fushun amber corresponds to an ancient conifer forest. There are myrmicines reported in Oise and Cambay amber, however, these have not been described. Therefore, because *Afromyrma* cannot be confidently assigned to Myrmicinae, the myrmicines described in Fushun amber are so far the oldest named (Wᴀʀᴅ & al. 2015).
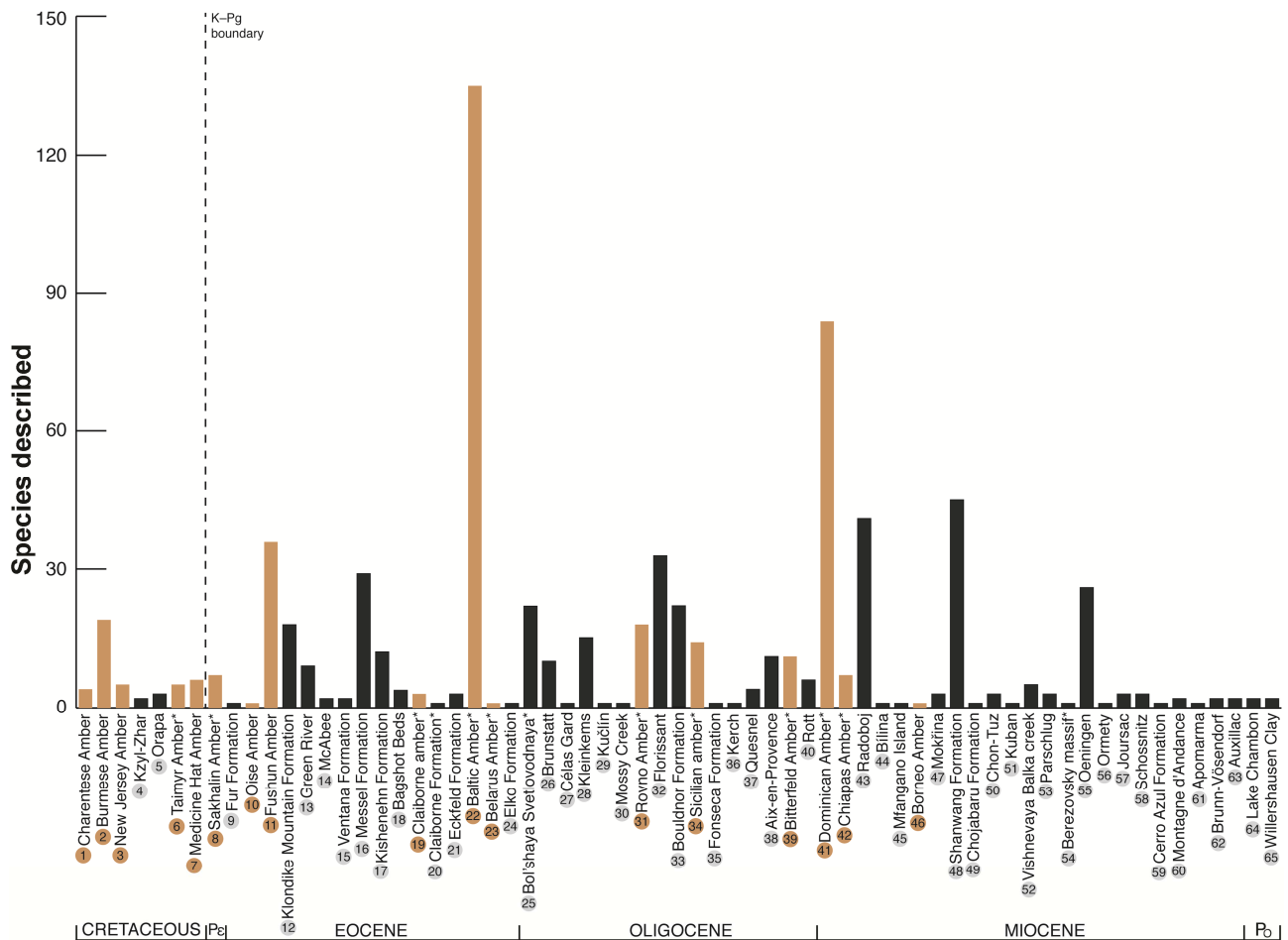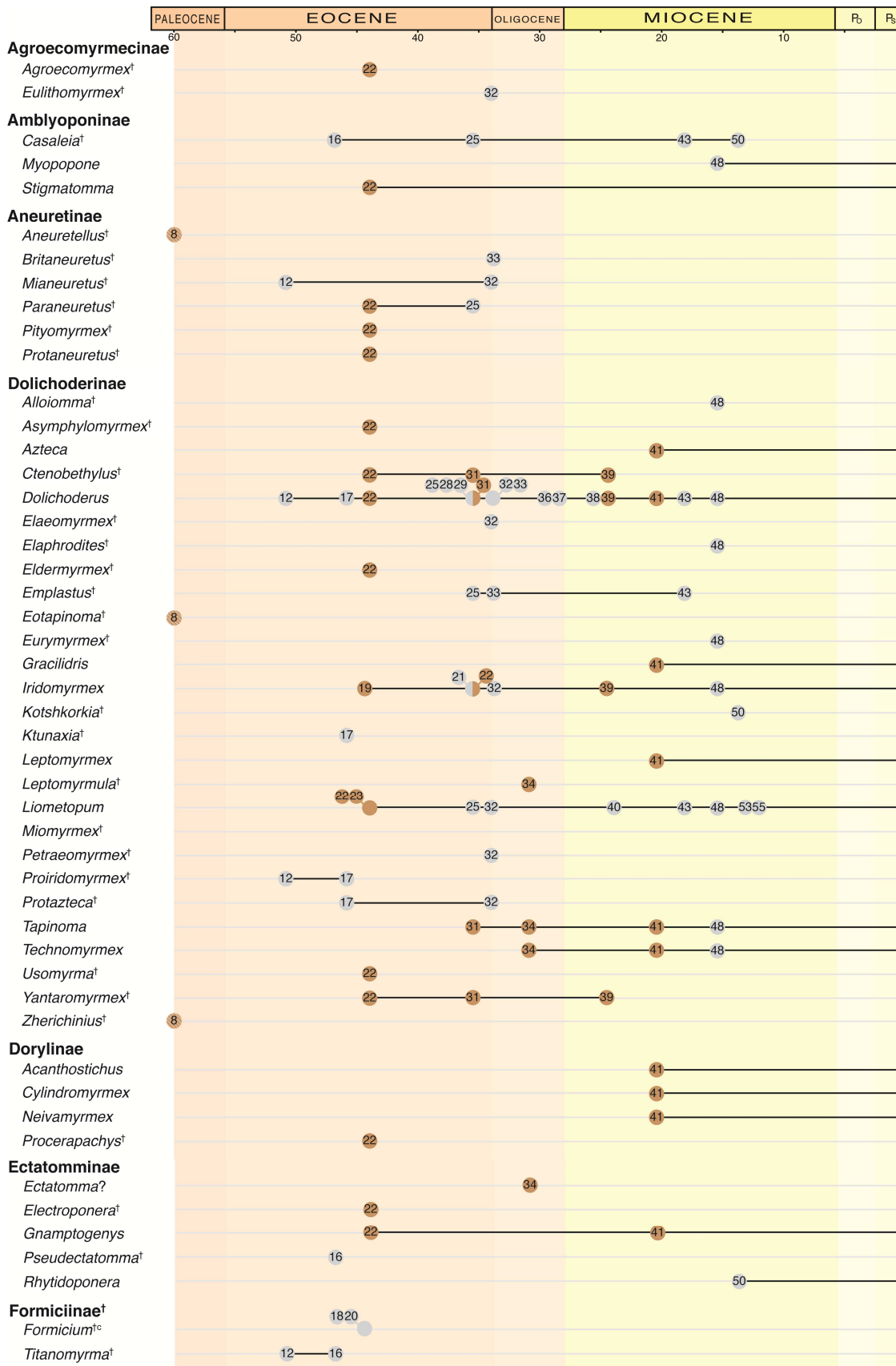
Fig. 4: Number of species described across 67 ant-yielding fossil deposits ordered in chronologically. Numbers correspond to deposits outlined in Table 2. Orange bars correspond to amber deposits while grey bars denote impression localities. *Indicates some uncertainty in age of the deposit.

The temporal midpoint: Following a discussion of early Eocene ambers, we come to an approximate "half-way point" in the 100 million year fossil history of ants. Across all known Cretaceous and early Cenozoic deposits, a total of 83 species have been described. The most recent ~ 50 million years have given rise to a remaining 647 known species, underscoring the sheer volume of material known from younger localities (Fig. 4). There are just a handful of species known from the majority of these fossil deposits, however, many locations shed light on the shape of ancient ant communities. Eocene impression fossil sites also provide the only insight into an intriguing, apparently lost, lineage.

Although all well-preserved Cenozoic ant fossils are attributed to crown Formicidae, there is a peculiar subfamily that is not known to persist beyond the Eocene. WESTWOOD (1854) first described *Formicium brodei* WESTWOOD, 1854 from wing remains obtained in Dorset, England (Bagshot Beds, ~ 44.6 Ma; JARZEMBOWSKI 1996). Westwood said of the fossil: "The most interesting specimen of all the insect-remains yet discovered amongst the [fossil locality]. It is, in fact, the wing of a gigantic ant, which, in its perfect state, must have measured at least 2 inches [~ 5.0 cm] across the expanded wings." Following the discovery of additional material, including whole-body specimens, in Tennessee, USA (Claiborne Forma-

tion, ~ 44.5 Ma; SAUNDERS & al. 1974) (CARPENTER 1929) and Hesse, Germany (Messel Formation, ~ 47.0 Ma; MERTZ & RENNE 2005) (LUTZ 1986), the subfamily Formiciinae was erected (LUTZ 1986). ARCHIBALD & al. (2011) have since revised the subfamily – there are two genera and six species known from four localities in present day North America and Europe (Fig. 5); though *Formicium* is a proposed collective genus, effectively holding all formiciine species with insufficient information to be placed accurately. Archibald and colleagues provided a compelling

Fig. 5: Deposit occurrences for all 211 genera with a fossil record (Cretaceous stem- and crown-group ants are excluded and detailed in Table 1). Grey circles indicate impression fossils while orange circles represent amber inclusions; numbers correspond to deposits outlined in Table 2. Grey lines indicate no fossil record while black lines demonstrate presumed temporal ranges for genera. [‡] Ichnotaxon. [?] Unclear placement. [c] Collective genus sensu ARCHIBALD & al. (2006, 2011). Extant genera under incertae sedis are formally described belonging to a modern genus, but placement remains dubious. For example, *Colobopsis brodiei* DONISTHORPE, 1920 (*Colobopsis* placement following WARD & al. 2016), was recently suggested to be incertae sedis due to poor preservation (ANTROPOV & al. 2014). (pp. 15-18)

PALEOCENE | EOCENE | OLIGOCENE | MIOCENE | Pₒ | Pₛ

60 — 50 — 40 — 30 — 20 — 10

Agroecomyrmecinae
- *Agroecomyrmex*† — 22
- *Eulithomyrmex*† — 32

Amblyoponinae
- *Casaleia*† — 16—25—43—50
- *Myopopone* — 48
- *Stigmatomma* — 22

Aneuretinae
- *Aneuretellus*† — 8
- *Britaneuretus*† — 33
- *Mianeuretus*† — 12—32
- *Paraneuretus*† — 22—25
- *Pityomyrmex*† — 22
- *Protaneuretus*† — 22

Dolichoderinae
- *Alloiomma*† — 48
- *Asymphylomyrmex*† — 22
- *Azteca* — 41
- *Ctenobethylus*† — 22—31—39
- *Dolichoderus* — 12—17—22 25 28 29 31 32 33 36 37 38 39 41—43—48
- *Elaeomyrmex*† — 32
- *Elaphrodites*† — 48
- *Eldermyrmex*† — 22
- *Emplastus*† — 25–33—43
- *Eotapinoma*† — 8
- *Eurymyrmex*† — 48
- *Gracilidis* — 41
- *Iridomyrmex* — 19 21 22–32 39—48
- *Kotshkorkia*† — 50
- *Ktunaxia*† — 17
- *Leptomyrmex* — 41
- *Leptomyrmula*† — 34
- *Liometopum* — 22 23 25-32 40—43—48—53 55
- *Miomyrmex*†
- *Petraeomyrmex*† — 32
- *Proiridomyrmex*† — 12—17
- *Protazteca*† — 17—32
- *Tapinoma* — 31—34 41—48
- *Technomyrmex* — 34 41—48
- *Usomyrma*† — 22
- *Yantaromyrmex*† — 22—31—39
- *Zherichinius*† — 8

Dorylinae
- *Acanthostichus* — 41
- *Cylindromyrmex* — 41
- *Neivamyrmex* — 41
- *Procerapachys*† — 22

Ectatomminae
- *Ectatomma*? — 34
- *Electroponera*† — 22
- *Gnamptogenys* — 22—41
- *Pseudectatomma*† — 16
- *Rhytidoponera* — 50

Formiciinae†
- *Formicium*†ᶜ — 18 20
- *Titanomyrma*† — 12—16

explanation for the massive size of these animals, the largest of which are > 6.0 cm in length. The team showed that giant formiciine ants lived in climates that were hot durin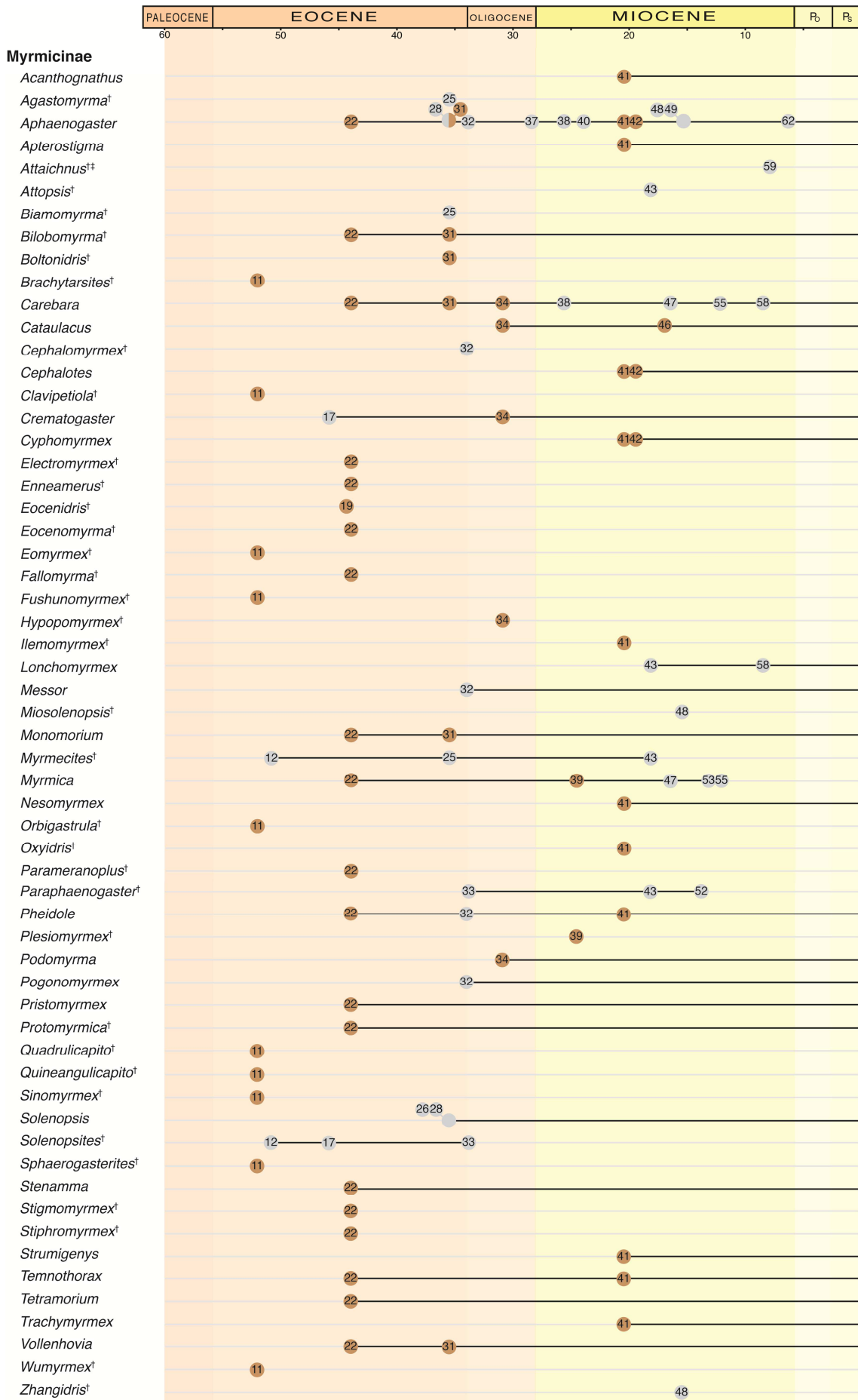g the Eocene, with a mean annual temperature greater than 20.0°C – the same climate constraint that seems to act on large extant species. Formiciine ants were abundant in some deposits, comprising approximately half of the more than 1000 specimens examined by DLUSSKY & WED-
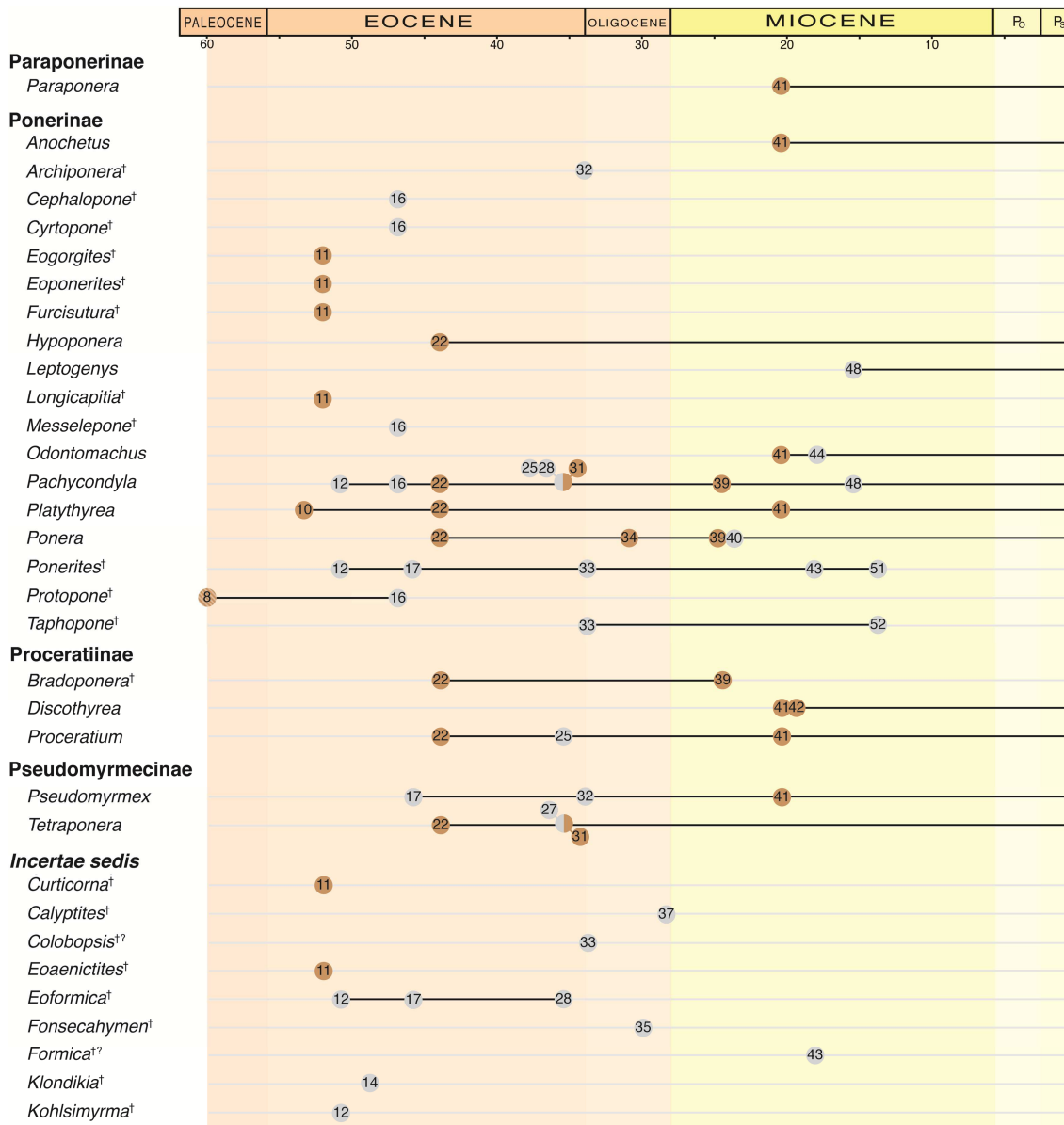
15

Formicinae
- *Acropyga*
- *Camponotites†*
- *Camponotus*
- *Cataglyphoides†*
- *Chimaeromyrma†*
- *Conoformica†*
- *Curtipalpulus†*
- *Drymomyrmex†*
- *Eoleptocerites†*
- *Eurytarsites†*
- *Formica*
- *Fushuniformica†*
- *Gesomyrmex*
- *Glaphyromyrmex†*
- *Heeridris†*
- *Huaxiaformica†*
- *Imhoffia†*
- *Lasius*
- *Leptogasteritus†*
- *Leucotaphus†*
- *Liaoformica†*
- *Longiformica†*
- *Magnogasterites†*
- *Nylanderia*
- *Oecophylla*
- *Orbicapitia†*
- *Ovalicapito†*
- *Ovaligastrula†*
- *Plagiolepis*
- *Polyrhachis*
- *Prenolepis*
- *Prodimorphomyrmex†*
- *Protoformica†*
- *Protrechina†*
- *Pseudocamponotus†*
- *Pseudolasius*
- *Sicilomyrmex†*
- *Sinoformica†*
- *Sinotenuicapito†*
- *Wilsonia†*
- *Zatania*

Myrmeciinae
- *Archimyrmex†*
- *Avitomyrmex†*
- *Macabeemyrma†*
- *Myrmeciites†c*
- *Prionomyrmex†*
- *Ypresiomyrma†*

MANN (2012) from the Messel Formation, an apparent underestimate due to sampling bias. The workers of formiciine ants are not yet known; all known specimens are reproductives, potentially explaining the high abundance of these taxa. Perhaps they gathered in massive nuptial flights similar to the scenario proposed for the Fur Formation species *Ypresiomyrma rebekkae*. The phylogenetic position of Formiciinae has been tested twice. BARONI URBANI & al. (1992) found the subfamily sister to all other ants, a hypothesis recovered by GRIMALDI & al. (1997) in some analyses (other analyses produced a polytomy at the base of Formicidae). In both treatments, the formiciine terminal was represented by a majority of missing characters, which can be problematic in phylogenetic reconstruction if the "wrong" characters are missing and there are few morphological characters overall (WIENS 2003). BOLTON (2003) suggested the subfamily might be sister to the formicomorphs, a scenario that was conser-

16

Myrmicinae

Acanthognathus — 41

Agastomyrma†

Aphaenogaster — 22, 25, 28, 31, 32, 37, 38-40, 4142, 4849, 62

Apterostigma — 41

Attaichnus†‡ — 59

Attopsis† — 43

Biamomyrma† — 25

Bilobomyrma† — 22, 31

Boltonidris† — 31

Brachytarsites† — 11

Carebara — 22, 31, 34, 38, 47, 55, 58

Cataulacus — 34, 46

Cephalomyrmex† — 32

Cephalotes — 4142

Clavipetiola† — 11

Crematogaster — 17, 34

Cyphomyrmex — 4142

Electromyrmex† — 22

Enneamerus† — 22

Eocenidris† — 19

Eocenomyrma† — 22

Eomyrmex† — 11

Fallomyrma† — 22

Fushunomyrmex† — 11

Hypopomyrmex† — 34

Ilemomyrmex† — 41

Lonchomyrmex† — 43, 58

Messor — 32

Miosolenopsis† — 48

Monomorium — 22, 31

Myrmecites† — 12, 25, 43

Myrmica — 22, 39, 47, 5355

Nesomyrmex — 41

Orbigastrula† — 11

*Oxyidris*ˡ — 41

Parameranoplus† — 22

Paraphaenogaster† — 33, 43, 52

Pheidole — 22, 32, 41

Plesiomyrmex† — 39

Podomyrma — 34

Pogonomyrmex — 32

Pristomyrmex — 22

Protomyrmica† — 22

Quadrulicapito† — 11

Quineangulicapito† — 11

Sinomyrmex† — 11

Solenopsis — 2628

Solenopsites† — 12, 17, 33

Sphaerogasterites† — 11

Stenamma — 22

Stigmomyrmex† — 22

Stiphromyrmex† — 22

Strumigenys — 41

Temnothorax — 22, 41

Tetramorium — 22

Trachymyrmex — 41

Vollenhovia — 22, 31

Wumyrmex† — 11

Zhangidris† — 48

EOCENE timeline chart (geological periods: PALEOCENE, EOCENE, OLIGOCENE, MIOCENE, P$_O$, P$_S$; scale 60, 50, 40, 30, 20, 10 Ma)

Paraponerinae
- *Paraponera* — 41
Ponerinae
- *Anochetus* — 41
- *Archiponera*[†] — 32
- *Cephalopone*[†] — 16
- *Cyrtopone*[†] — 16
- *Eogorgites*[†] — 11
- *Eoponerites*[†] — 11
- *Furcisutura*[†] — 11
- *Hypoponera* — 22
- *Leptogenys* — 48
- *Longicapitia*[†] — 11
- *Messelepone*[†] — 16
- *Odontomachus* — 41—44
- *Pachycondyla* — 12—16—22—2528 31—39—48
- *Platythyrea* — 10—22—41
- *Ponera* — 22—34—3940
- *Ponerites*[†] — 12—17—33—43—51
- *Protopone*[†] — 8—16
- *Taphopone*[†] — 33—52
Proceratiinae
- *Bradoponera*[†] — 22—39
- *Discothyrea* — 4142
- *Proceratium* — 22—25—41
Pseudomyrmecinae
- *Pseudomyrmex* — 17—32—41
- *Tetraponera* — 22—27 31
Incertae sedis
- *Curticorna*[†] — 11
- *Calyptites*[†] — 37
- *Colobopsis*[†?] — 33
- *Eoaenictites*[†] — 11
- *Eoformica*[†] — 12—17—28
- *Fonsecahymen*[†] — 35
- *Formica*[†?] — 43
- *Klondikia*[†] — 14
- *Kohlsimyrma*[†] — 12

vatively followed by WARD (2007) and is repeated here (Fig. 3). As with many fossil groups, Formiciinae would benefit from further phylogenetic analysis.

Today, the "big four" subfamilies Dolichoderinae, Formicinae, Myrmicinae, and Ponerinae comprise the vast majority of the biomass and taxonomic diversity in most ecosystems (WILSON & HÖLLDOBLER 2005a). Aside from the Messel Formation where formiciines are highly abundant (DLUSSKY & WEDMANN 2012), dominance of the "big four" is largely consistent into the Eocene. Green River (~ 51 Ma; SMITH & al. 2008), perhaps best known for its wealth of well-preserved fish fossils, has long been a source for ant fossils (SCUDDER 1877b), although they are not as abundant or well preserved as other approximately contemporaneous fossil beds. DLUSSKY & RASNITSYN (2002), in a review and revision of Green River and the Klondike Mountain Formation (~ 49 Ma; ARCHIBALD 2009), report the following composition: Dolichoderinae 61 - 72%, Formicinae 3 - 4%, Myrmeciinae 6 - 13%, Myrmicinae 2 - 4%, Ponerinae 10 - 11%, depending on the placement of

form genera with ambiguous subfamily placement. Following the most recent thorough examination of the Kishenehn Formation (46.0 Ma; CONSTENIUS 1996), LAPOLLA & GREENWALT (2015) summarize the composition of ant subfamilies in well-characterized deposits throughout the Eocene, including Baltic amber (~ 44.1* Ma; WEITSCHAT & WICHARD 2010) and Florissant (34.1 Ma; EVANOFF & GREGORY-WODZICKI 2001). The pattern is similar with dolichoderines comprising the majority (> 50%) of specimens, however, formicines are the next most common in these deposits (~ 26 - 33%), followed by myrmicines and ponerines. Fossil ants from Bol'shaya Svetlovodnaya, Russian Far East (35.6 Ma; KHALAIM 2008, DLUSSKY & al. 2015) exhibit a different pattern, as dolichoderines comprise 18%, formicines 41%, myrmicines 21%, and ponerines 7%. For a complete review of subfamily compositions at major fossil localities, see DLUSSKY & al. (2015).

Increasing in abundance: The "rise of the ants" (WILSON & HÖLLDOBLER 2005b) measured as relative abundance of ants in fossil deposits is now well documented

Box 1: An example of taxonomic uncertainty and revision in fossil ants.

Ctenobethylus goepperti has a particularly storied taxonomic past. Gustav L. MAYR (1868) described *Hypoclinea goepperti* in his monograph on Baltic amber, placing the fossil taxon in the subfamily Dolichoderinae, a group of ants characterized by a slit-like opening present at the anterior end of the abdomen in place of a sting. In the subsequent ~150 years, *H. goepperti* would be transferred to the dolichoderine genera *Bothriomyrmex* (DALLA TORRE 1893), *Iridomyrmex* (WHEELER 1915), and *Liometopum* (SHATTUCK 1992). In the interim, Charles T. BRUES (1939) described ultimately conspecific material as *Ctenobethylus succinalis* within the family Bethylidae, a group of largely parasitoid wasps with apterous females. This incorrect designation was a result of the particular preservation of the holotype: the hind legs of the specimen obscured the "waist", preventing Brues from noting the characteristic petiole segment that would otherwise have prompted placement within Formicidae. This error was recognized and corrected by BROWN (1976), who synonymized *Ctenobethylus succinalis* with *Iridomyrmex goepperti* [the correct formal name at the time]. Most recently, DLUSSKY (1997) transferred *Liometopum goepperti* to *Ctenobethylus*, which is the current valid name. The placement of fossil taxa is often not straightforward, owing to simultaneous description, cryptic preservation, and differing opinion. Although it is not always possible or practical, placement of fossils is best evaluated through phylogenetic analysis.

(GRIMALDI & AGOSTI 2000, DLUSSKY & RASNITSYN 2002, LAPOLLA & al. 2013), although it has been noted that the faunal composition preserved in the fossil record may not accurately reflect that of ancient ecosystems (e.g., SOLÓRZANO KRAEMER & al. 2015). There are some anomalies, but the general trend is as follows: Ants never make up more than 1.5% of insects in fossil localities during the Cretaceous, in the Cenozoic prevalence increases to as high as 13.1% in the Messel Formation during the Eocene (recall that reproductive formiciines are responsible for half of this abundance; DLUSSKY & RASNITSYN 2002, DLUSSKY & WEDMANN 2012) and 20% in the Eocene-aged Florissant Formation (CARPENTER 1930). During the Miocene, in Dominican amber, ant prevalence reaches ~ 27 - 36% (POINAR & POINAR 1999, DLUSSKY & WEDMANN 2012). Today, highly dominant species such as members of *Formica* in parts of Europe and *Iridomyrmex* in some landscapes of Australia (HÖLLDOBLER & WILSON 1990) make up the majority of ant biomass. This fact of modern ecosystems appears to hold true into the past: dominant taxa drive the march to ant abundance in the fossil record.

The ants of Baltic amber are well known. In the first comprehensive study of a fossil ant assemblage, MAYR (1868) produced a landmark volume, recording over 1,400 specimens belonging to 49 species. Incredibly, a single species, *Ctenobethylus goepperti* (MAYR, 1868) (Box 1) was represented by 680 amber inclusions, or, ~ 33% of all Baltic amber ants. WHEELER (1915) would go on to survey the collection Mayr utilized, along with an additional ~ 700 specimens studied by ANDRÉ (1895) and more than 9,500 new fossils. Out of this aggregation of 11,678 specimens, Wheeler found that 46% of all specimens were *C. goepperti*. Said Wheeler: "It is far and away the most abundant and dominant ant in the amber fauna … These various specimens seem to me to show conclusively that *I. goepperti* [*C. goepperti*] was everywhere abundant in the amber forests, that it formed populous colonies, whose workers foraged in files and attended plant-lice on the oak and Pinites trees, much as the species of *Liometopum* of the present day forage on the conifers and oaks in the western United States, and on the oaks in Austria, Italy and the Balkan Peninsula." The next three most abundant species, *Formica flori* MAYR, 1868, *Yantaromyrmex geinitzi* (MAYR, 1868), and *Lasius schiefferdeckeri* MAYR, 1868 comprise ~ 11%, 11%, and

10% of specimens respectively, indicating that the four most abundant species make up almost 80% of all inclusions known in Baltic amber.

This trend applies to several other deposits, and has often been noted by Dlussky (e.g., DLUSSKY & RASNITSYN 2002, 2009, DLUSSKY & al. 2015) and others (LAPOLLA & GREENWALT 2015). Among the Green River ants, the incertae sedis *Eoformica pinguis* (SCUDDER, 1877b) comprises 40% of all impression fossils and the dolichoderine *Dolichoderus kohlsi* DLUSSKY & RASNITSYN, 2002 25% (LAPOLLA & al. 2013). In the Florissant formation, dolichoderines *Protazteca elongata* CARPENTER, 1930 and *Liometopum miocenicum* CARPENTER, 1930 comprise ~ 27% each, with the formicine *Lasius peritulus* (COCKERELL, 1927) representing ~ 25% of ants. Among the 22 named species present in the Bouldnor Formation (~ 34 Ma; HOOKER & al. 2009), two species of *Oecophylla* represent 52% of ants and *Leucotaphus gurnetensis* (COCKERELL, 1915) 25% after preservational bias is taken into account (ANTROPOV & al. 2014). The ant abundance of Radoboj, Croatia (~ 18 Ma; RASNITSYN & QUICKE 2002) is somewhat more equally distributed, with three prevalent formicine species, *Formica ungeri* HEER, 1849, *Lasius occultatus* (HEER, 1849), and *Lasius longaevus* (HEER, 1849) corresponding to ~ 19%, ~ 15%, and ~ 11% of ant impression fossils (DLUSSKY & PUTYATINA 2014). There are two notable exceptions to the dominant species "rule" of well sampled Cenozoic fossil deposits: the Kishenehn Formation where no species holds more than 10% of specimens (LAPOLLA & GREENWALT 2015) and Bol'shaya Svetlovodnaya, which is also apparently devoid of a highly abundant species (DLUSSKY & al. 2015).

In Dominican amber, the dolichoderine *Azteca alpha* WILSON, 1985a makes up approximately 30 - 50% of all ants from this deposit (WILSON 1985d, JOHNSON & al. 2001), perhaps the most extreme example of dominance (Fig. 6). Taken with the ant prevalence estimate of DLUSSKY & WEDMANN (2012), this suggests that *A. alpha* comprises between ~ 11 - 18% of all insects from Dominican amber in total. If this single species of extremely dominant ant was present in any other pre-Miocene deposit, it alone would increase abundance dramatically, irrespective of all other taxa. It is hard to overstate the impact that highly abundant species have had on the increase in ant prevalence over time in fossil deposits.

Fig. 6: An assemblage of the highly abundant ant *Azteca alpha* Wilson, 1985a in Dominican amber. Highly abundant species such as *A. alpha* constitute the majority of fossil specimens recovered in some deposits.

Agents of selection: Increases in ant prevalence undoubtedly acted as a selective force on numerous other organismal groups, and there is evidence for this effect in amber. Parker & Grimaldi (2014) reported the first known myrmecophilous insect from Cambay amber dated to the Early Eocene – a staphylinid beetle belonging to the supertribe Clavigeritae. All of the over 350 extant species of Clavigeritae are obligate myrmecophiles uniquely adapted to living in ant colonies (Parker 2016). In Baltic amber, there is a fascinating report of a parasitic mite belonging to the genus *Myrmozercon* – most species of which appear have species-specific ant hosts today – clinging to the head capsule of a *Ctenobethylus goepperti* worker (Dunlop & al. 2014). The presence of highly specialized myrmecophiles in the Eocene is significant, as it indicates, along with divergence estimations and increases in fossil abundance, that ants were ecologically significant enough to support obligate individual- or colony-level parasites. For a review of evidence for symbiotic relationships between ants and mealybugs in amber, see Johnson & al. (2001) and LaPolla & al. (2013). Along with driving diversification as hosts of parasitic species, ants are thought to have pruned branches of the tree of life. Khramov & al. (2015) offer a fossil-based window into the role of ants in the extinction of an insect lineage. Prior to the K-Pg boundary, nearly all green lacewing fossils are attributable to the subfamily Limaiinae, however, this group does not persist beyond the Eocene. Khramov and colleagues hypothesize that the apparent extinction of Limaiinae was a result of Cenozoic increases in ant abundance. While the larvae of three extant chrysopid subfamilies possess structures to defend against sternorrhyncha-tending ants (these neuropteran larvae feed on sternorrhyncha), such features are presumed absent on limaiines, which would have left them susceptible to extensive predation.

Ghost lineages

There are three subfamilies with absolutely no fossil record (Fig. 3). So-called "ghost" lineages exist when, based on the phylogenetic position of the lineage in question, there is an expectation of fossil occurrences, but this expectation is not met (Norell 1992). The placement of Martialinae and Leptanillinae, which branched earlier than other crown formicids, suggests the ancestors of these two groups should have been present during, and before, the diversification of other crown ants. In addition, the subfamily Heteroponerinae is not currently known in any fossil deposit, though its sister taxon, Ectatomminae, is known from multiple fossils: one dubious occurrence in Canadian Medicine Hat amber and four genera known from four Cenozoic fossil localities (Fig. 5). Why are there no known fossils for these three subfamilies, given their placement among other taxa?

First, it is possible, more so with reference to Martialinae and Leptanillinae, that the positions of these lineages have been recovered in error. There has been substantial discussion regarding the topology of the ant tree and these early branches in particular (Moreau & al. 2006, Brady & al. 2006, Rabeling & al. 2008, Kück & al. 2011, Lucky & al. 2013, Moreau & Bell 2013, Ward 2014). Although it appears that most analyses support the relationship figured here (Fig. 3; Moreau & Bell 2013), this potential source of error is nevertheless included for completeness. Very likely, the paleontological absence of these lineages reflects preservation bias based on the geographical position of fossil deposits or habitat specialization. The majority of ant-yielding fossil localities are in the Northern Hemisphere (Fig. 7), which would seem to preclude the entrapment of heteroponerine and martialine ants (presently distributed almost entirely in the Southern Hemisphere). Members of Martialinae and Leptanillinae are subterranean or leaf litter dwelling, which could render them less likely to be preserved as fossils in tree resin or mud. However, there are ants with similar lifestyles preserved in amber. For example, two species of *Discothyrea* are known from Dominican and Mexican amber (De Andrade 1998a), which presumably occupied similar cryptic niches. Finally, it is possible that the morphological features currently defining these lineages were
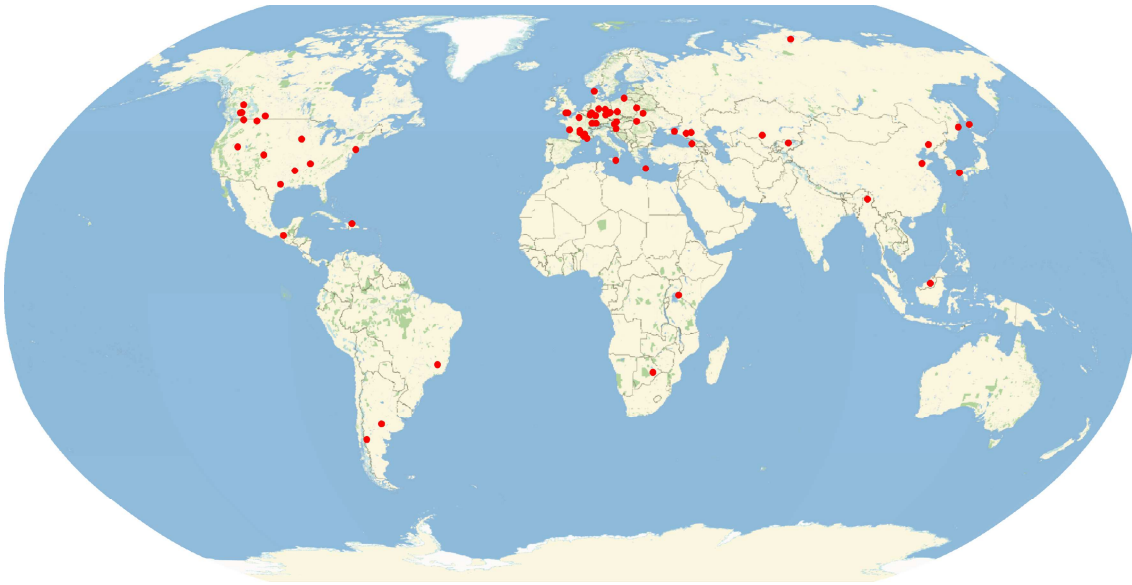
Fig. 7: Map of fossil deposits with described taxa.

recently derived; meaning early fossils would not be attributed to these groups as we know them today.

Improved sampling of known fossil deposits will likely reduce the overall number of ghost lineages both at the subfamily and generic level. Crown ants are reported, but not described, from Canadian Hat Creek amber (50 - 55 Ma) as putative members of *Dolichoderus*, *Leptothorax*, and *Technomyrmex* (POINAR & al. 1999). There are also reported and described members of Amblyoponinae, Formicinae, Ponerinae, Ectatomminae, and Dolichoderinae in the Miocene-aged Foulden Maar fossil site of New Zealand (KAULFUSS & al. 2015,2015b) – interesting not just as a much needed window into the Southern Hemisphere, but as the later two subfamilies are not currently found in New Zealand. In a survey of what is probably the most thoroughly sampled fossil ant locality, PENNEY & PREZIOSI (2013) used species richness curves to suggest that 29% of species from Baltic amber remain undiscovered. Remarkably, despite high prevalence today, the genus *Tetramorium* was only recently discovered from Baltic amber (RADCHENKO & DLUSSKY 2015). If a substantial proportion of species still remain to be discovered from a deposit heavily studied since the mid-19th century, what important taxa do other localities hold?

Lazarus taxa and biogeographic history

While Recent taxa may lead our expectations of fossil occurrences, there are two examples where fossil species have heralded neontological discovery. WILSON (1985d) described *Gracilidris humiloides* (WILSON, 1985a) (initially *Iridomyrmex*) from Dominican amber as part of a fossil assemblage that detailed faunal turnover in the Caribbean (WILSON 1985e). Over twenty years later, WILD & CUEZZO (2006) described a highly similar, putatively congeneric, extant species based on several worker specimens collected in South America. Today, the extant species is known from single localities in both Argentina and Paraguay, as well as throughout southern Brazil (FEITOSA & al. 2015). Foraging workers have only been reported during dusk and night, potentially explaining their previ-

ous evasion. Another fossil lineage "rediscovered" after presumed extinction relates to the genus *Leptomyrmex*, a distinct group of ants with a peculiar modern day distribution. Until very recently extant members of *Leptomyrmex* were known to exhibit an exclusively Australasian distribution (LUCKY 2011), which made the discovery of *Leptomyrmex neotropicus* BARONI URBANI, 1980 in Dominican amber contentious (see WILSON 1985d, BARONI URBANI & WILSON 1987). Incredibly, worker and male specimens of a new *Leptomyrmex* species were collected in Brazil (BOUDINOT & al. 2016), greatly expanding the known range for living members of this group. This surprising discovery highlights the value of fossils in biogeographic reconstruction.

As with divergence estimation informing fossil placement, ancestral area reconstruction based on extant taxa should not be utilized to infer evolutionary relationships. Moreover, biogeographic analyses that do not incorporate fossil ranges known to be discordant with modern distributions should be considered incomplete. Certain relictual distributions are rendered invisible under such sampling protocols. There are clear cases of local extinction driving distributional patterns among living species. Myrmeciine ants, endemic to Australia and New Caledonia today, occupied a much greater range in the past: Fossils are known from South America, North America, Europe, and Asia spanning from the early Eocene to the Miocene (Fig. 5; BARONI URBANI 2000, WARD & BRADY 2003, ARCHIBALD & al. 2006, DLUSSKY 2012, DLUSSKY & al. 2015). The formicine genus *Oecophylla* presently occupies parts of Sub-Saharan Africa, Southern India, Southeast Asia and northern regions of Australasia. Despite this current tropical distribution, several fossils are known throughout Europe, ranging in age from just 7 Ma to ~ 56 Ma, suggesting that the group may have indeed originated in the Palaearctic (DLUSSKY & al. 2008). Ectatommine fossils have been found in present day Europe (DLUSSKY 2009) suggesting their current distribution is a reflection of range loss. The famous "relict ant" *Aneuretus simoni* EMERY, 1893, currently known only from Sri Lanka as the sole ex-

tant member of Aneuretinae, is itself an exemplar of range contraction: Fossil aneuretines have been described throughout Asia, Europe and North America (WHEELER 1915, CARPENTER 1930, DLUSSKY & al. 2015).

Taking a broad approach to exploring faunal composition of large bioregions, GUÉNARD & al. (2015) were able to extract patterns suggesting both fluidity and stasis in community structure over time. By comparing fossil and present-day ant communities at the genus level, Guénard and colleagues demonstrated expected high similarity between fossil and present day faunas in the same geographic area such as the Nearctic, and also fascinating evidence for similarity between fossil communities in the western Palaearctic and present day Indo-Malayan tropics. The later discovery suggests that current tropical fauna were once more widely distributed, a finding supported by the fossil history of taxonomic groups described above.

Conclusions

The paleomyrmecological record is exceedingly rich; in terms of described species, ants are comparable to perhaps the most famous icons of paleontological research. It is surprisingly difficult to estimate the total number of valid dinosaur taxa, but most recent estimates suggest between 675 species (BENTON 2008) and 527 genera, the majority of which are monotypic with 1.12 species per genus (WANG & DODSON 2006, BENTON 2008). A true species count incorporating recent discoveries and synonymization is elusive, however, the comparison stands: There are approximately as many described fossil ant species as there are valid dinosaur species. And yet, fossil ants have only been integrated into a handful of synthetic investigations with extant fauna. For neontologists, the value of this resource reaches far beyond molecular calibration or brief mentions with respect to the suspected age of the clade of interest. While the phylogenetic distribution of other fossil groups may be weighted toward the earliest branches of the clade in question, the ant fossil record spans from these earliest lineages to very recently derived groups; most fossils are woven into the lineages that are present and heavily studied today. Ancient phenotypic variation, temporal information, and accurate biogeographic reconstruction are only accessible through the integration of fossil data. The nature of this integration is changing as methods for direct incorporation of fossil data (combined or "total" evidence analyses) are developed (e.g., WARE & al. 2010, PYRON 2011, RONQUIST & al. 2012) and synthetic approaches outlined (GUÉNARD & al. 2015).

Acknowledgments

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