

# Fossil evidence for the early ant evolution

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**Abstract** Ants are one of the most studied insects in the world; and the literature devoted to their origin and evolution, systematics, ecology, or interactions with plants, fungi and other organisms is prolific. However, no consensus yet exists on the age estimate of the first Formicidae or on the origin of their eusociality. We review the fossil and biogeographical record of all known Cretaceous ants. We discuss the possible origin of the Formicidae with emphasis on the most primitive subfamily Sphecomyrminae according to its distribution and the Early Cretaceous palaeogeography. And we review the evidence of true castes and eusociality of the early ants regarding their morphological features and their manner of preservation in amber. The mid-Cretaceous amber forest from south-western France where some of the oldest known ants lived, corresponded to a

moist tropical forest close to the shore with a dominance of gymnosperm trees but where angiosperms (flowering plants) were already diversified. This palaeoenvironmental reconstruction supports an initial radiation of ants in forest ground litter coincident with the rise of angiosperms, as recently proposed as an ecological explanation for their origin and successful evolution.

**Keywords** Formicidae · Evolution · Sociobiology · Palaeobiogeography · Palaeoecology

## Introduction

Our knowledge of the primitive ants has greatly increased in the last decade with the discoveries, mainly in amber, of several Cretaceous fossils belonging to Dolichoderinae, Formicinae, Myrmicinae, Ponerinae, Sphecomyrminae, and specimens bearing numerous plesiomorphies and thus of uncertain subfamily (Fig. 1). Further primitive fossils assigned to the extinct Armaniidae/-inae, only found as compressions in Cretaceous sediments, still have a controversial status in the crown group of ants (Bolton 2003; Dlussky et al. 2004; Engel and Grimaldi 2005). Indeed, it is still not possible to decide whether they are the sister group of the Formicidae or a paraphyletic stem group of the formicoids, given the apparent absence of a metapleural gland (synapomorphy of the Formicidae according to Grimaldi et al. 1997) and the enigmatic structure of their ‘petiole’ looking like that of a compressed, two-dimensional Cenozoic Formicinae (Nel, personal observation). In the discussion below, we follow other authors in excluding them from the Formicidae.

The oldest known definitive ants are currently reported from contemporaneous Albian–Cenomanian ambers of

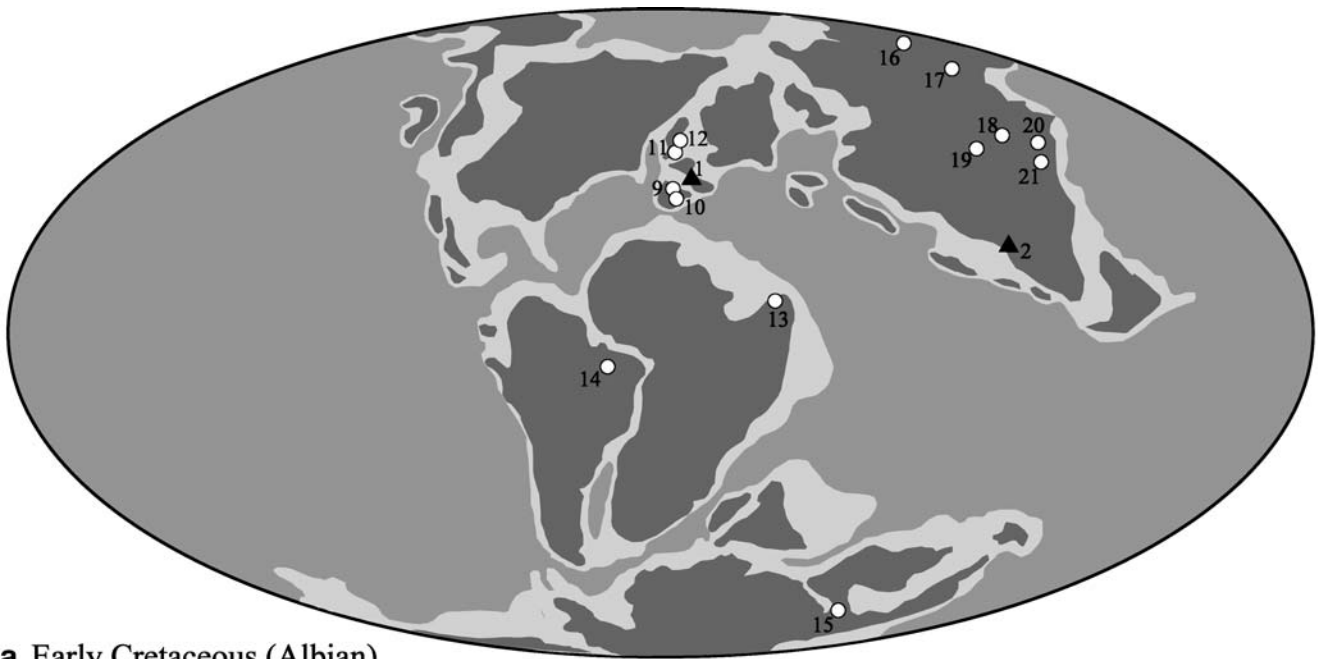
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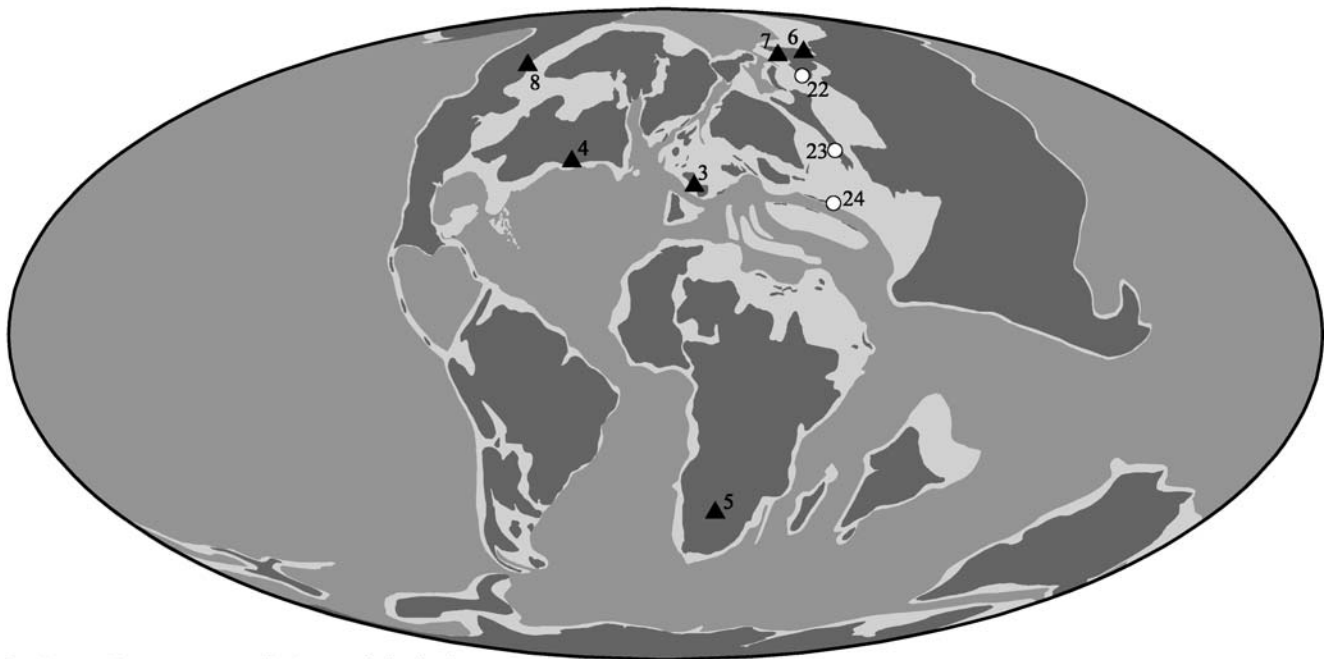
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**a** Early Cretaceous (Albian)



**b** Late Cretaceous (Maastrichtian)

France and Myanmar and are either considered as *incertae sedis* within the formicid subfamilies or belong to the extinct Sphecomyrminae (Dlussky 1996; Nel et al. 2004; Engel and Grimaldi 2005; Perrichot et al. 2007a). However, this Cretaceous subfamily is largely based on plesiomorphic characters and needs substantial additional fossils before being more accurately defined and its monophyly confidently stated.

In this paper, we discuss the possible geographical and ecological origin of the first Formicidae with an emphasis on the Sphecomyrminae, based on the biogeographical record of all known Cretaceous ants and their supposed habitat as reconstructed for the Cretaceous amber forest from southwestern France. We also discuss the eusociality of these primitive ants as evidenced by their morphological features and their manner of preservation within the fossil record.

◀ **Fig. 1** Palaeogeographical distribution of Early (a) and Late (b) Cretaceous ants (indicated by triangles) and major insect fossil sites (indicated by circles, >100 insects, after Eskov 2002; Rasnitsyn and Zherikhin 2002; maps modified from Scotese 2001 and Ziegler and Rowley 1998). 1 *Gerontoformica cretacica*, subfamily uncertain; *Haidomyrmodes mammothus*, Sphecomyrminae; Late Albian, Charente-Maritime, France (Nel et al. 2004; Perrichot et al. 2007a). 2 *Burmomyrma rossi*, *Myanmyrma gracilis*, subfamilies uncertain; *Haidomyrmex cerberus*, *Sphecomyrmodes orientalis*, *Sphecomyrma* sp., Sphecomyrminae; Late Albian, Myanmar (Dlussky 1996; Grimaldi et al. 2002; Grimaldi and Engel 2005). 3 *Haidomyrmodes mammothus*, *Sphecomyrmodes occidentalis*, Sphecomyrminae; Early Cenomanian, Charente-Maritime, France (Perrichot et al. 2007a). 4 *Sphecomyrma freyi*, *Sphecomyrma mesaki*, *Sphecomyrma* sp., *Baikuris casei*, Sphecomyrminae; *Brownimecia clavata*, Ponerinae; *Kyromyrma neffi*, Formicinae; Turonian, New Jersey (Wilson et al. 1967; Grimaldi et al. 1997; Grimaldi and Agosti 2000; Engel and Grimaldi 2005). 5 *Afropone oculata*, *A. orapa*, *Afromyrma petrosa*, subfamilies uncertain; Turonian, Orapa, Botswana (Dlussky et al. 2004; Archibald et al. 2006). 6 *Cretomyrma arnoldi*, *C. unicornis*, *Dlusskyidris zherichini*, Sphecomyrminae; Santonian, Yantardakh, Taimyr peninsula, Siberia (Dlussky 1975). 7 *Baikuris mandibularis*, *B. mirabilis*, Sphecomyrminae; Santonian? Taimyr Lake, Siberia (Dlussky 1987); 8 *Sphecomyrma canadensis*, Sphecomyrminae; *Canapone dentata*, Ponerinae; *Eotapinoma macalpini*, Dolichoderinae?; *Cananeuretus occidentalis*, Aneuretinae?; Campanian, Alberta, Canada (Wilson 1985; Dlussky 1999; Engel and Grimaldi 2005). 9 Álava amber, Spain, Late Aptian–Early Albian; 10 Montsec, Spain, Berriasian–Valanginian; 11 Purbeck Group, England, Berriasian; 12 Wealden Supergroup, England, Hauterivian–Barremian; 13 Lebanese amber, Hauterivian–Aptian; 14 Santana Fm, Brazil, Aptian; 15 Koonwarra beds, Australia, Aptian; 16 Khetana, East Siberia, Middle Albian; 17 Baissa, Central Siberia, Neocomian; 18 Khutel-Khara, Mongolia, Early Cretaceous; 19 Bon-Tsagan, Mongolia, Barremian–Aptian; 20 Yixian Fm, China, Barremian; 21 Laiyang Fm, China, Early Neocomian; 22 Agapa, Siberia, Late Cenomanian; 23 Kzyl-Zhar, Kazakhstan, Turonian; 24 Agdzakend, Azerbaijan, Cenomanian

## Origin of ants

As shown by the oldest known fossils recently discovered in French and Burmese ambers, the Early/mid-Cretaceous ants appear to be unexpectedly diversified with seven distinct genera within at least two subfamilies recorded from these two ambers: *Haidomyrmodes*, *Haidomyrmex*, *Sphecomyrma* and *Sphecomyrmodes* in the Sphecomyrminae; *Burmomyrma*, *Gerontoformica* and *Myanmyrma* in uncertain subfamilies. Important morphological differences between them represent a strong evolution from the primitive shape of their common ancestor. Furthermore, the contemporaneous occurrence of *Haidomyrmodes*, *Haidomyrmex* and *Sphecomyrmodes* in French and Burmese mid-Cretaceous ambers implies a wide distribution of ants at this time and an earlier origin of the tribes Haidomyrmecini and Sphecomyrmini on a same palaeocontinent. According to palaeogeographical maps (Ziegler 1990; Masse et al. 1993; Scotese 2001 and <http://www.scotese.com> as accessed in April 2007), the western part of Laurasia, including France, was fragmented in insular landmasses and separated from Eastern Laurasia by

epicontinental seas since at least the Early Aptian (ca. 120 Ma) till the Maastrichtian (ca. 70 Ma). Therefore, the Sphecomyrminae would have originated no later than the Early Aptian. These results on the high morphological disparity and wide distribution of early ants well agree with an Earliest Cretaceous age of the Formicidae, as estimated from the fossil record of ants and their vespid relatives (Grimaldi and Engel 2005). Some molecular phylogenetic studies suggested that the first ants arose much earlier in the Earliest Cretaceous or the Jurassic with an estimated minimum/maximum age of 140/168 Ma (Crozier et al. 1997; Moreau et al. 2006). According to Brady et al. (2006), however, a Jurassic origin is highly unlikely. They estimated an age of 115/140 Ma for the crown group ants, based on a wider molecular analysis and incorporation of the fossil record of ants and other aculeate Hymenoptera. So far, fossil ants do not occur before the Albian. Owing to the relative scarcity of Early Cretaceous fossil insect sites, this absence of ant anteriorly to the Albian certainly reflects a bias in the fossil record. However, the fact that they were not collected yet in the very rich fossil deposits of Australia, Brazil, China, England, Lebanon, Russia and Spain (Table 1) likely corresponds to their absence in the corresponding ecosystems and well agrees with the hypothesis that ant subfamilies mainly diverged since the Albian and through the Turonian, coinciding with the rise of angiosperms (Dlussky et al. 2004; Grimaldi and Agosti 2000; Moreau et al. 2006; Ward and Brady 2003; Wilson and Hölldobler 2005a). Because they were already widespread and rather well-diversified at the end of the Albian, it is expected to find fossil ants earlier in the Cretaceous, even if rare and thus with a low probability of being fossilized.

Despite the present and updated data on French and Burmese Albian ants, it is still difficult to estimate the ancestral subfamily. Haidomyrmecini are apparently not basal in ant phylogeny (Bolton 2003), and *Burmomyrma*, *Myanmyrma* and *Gerontoformica* currently remain of uncertain affinities. Given its combination of characters, however, *Gerontoformica* could be close to an “ancestor” of the two subfamilies Formicinae and Dolichoderinae (Nel et al. 2004).

## Palaeobiogeography and palaeoecology

Extant Formicidae are cosmopolitan, but numerous lineages show a continental endemism (Bolton 1995). According to Grimaldi and Agosti (2000), ancestors could have been isolated on different landmasses after the Early Cretaceous fragmentation of Pangaea, and then diversified independently. However, the Early Cretaceous occurrence of ants and ‘formicoids’ on Gondwana is not yet assessed; some fossils found in Australia, Brazil and Lebanon were attributed to

**Table 1** Proportions of Hymenoptera and Formicidae for major fossiliferous Cretaceous deposits

Fossil deposits	A/C	Age	Total insects	Total Hymenoptera	Total ants	References
Lebanon <sup>a</sup>	A	Hauterivian/ Barremian	2,837	250	0	Azar (2000)
Baissa, Siberia	C	Neocomian	>20,000	?	0	Zherikhin et al. (1999); Rasnitsyn and Zherikhin (2002)
Montsec, Spain	C	Berriasian/ Valanginian	900	30	0	Delclòs, personal communication; Rasnitsyn and Martínez-Delclòs (2000)
Las Hoyas, Spain	C	Barremian	1,300	6	0	Delclòs, personal communication
China <sup>b</sup>	C	Neocomian	>580	>72	0	Ren, personal communication
England <sup>c</sup>	C	Neocomian	13,000	48	0	Rasnitsyn et al. (1998)
Australia <sup>d</sup>	C	Aptian	300	10	0	Jell and Duncan (1986)
Ceará, Brazil	C	Aptian	>3,000	26	0	Darling and Sharkey (1990)
Álava, Spain	A	Aptian/Albian	2,300	500	0	Delclòs et al. (2007)
Myanmar	A	Albian	4,210	364	9	Grimaldi et al. (2002)
Charente, France	A	Albian/ Cenomanian	911	135	17	Perrichot et al. (2007b)
Agapa, Siberia	A	Cenomanian	>700	?	0	Eskov (2002)
New Jersey, USA	A	Turonian	>1,100	250	8	Grimaldi et al. (2000)
Orapa, Botswana	C	Turonian	641	108	4	Brothers and Rasnitsyn (2003)
				86	10	Dlussky et al. (2004)
Taimyr, Siberia	A	Santonian	>3,000	?	9	Eskov (2002); Dlussky (1975, 1987)
Alberta, Canada	A	Campanian	>3,000	>300	6	Pike (1994)

A: amber, C: compression

<sup>a</sup> Hammana, Jezzine and Bcharré

<sup>b</sup> Yixian and Laiyang Fms

<sup>c</sup> Purbeck and Wealden groups

<sup>d</sup> Koonwarra beds

Formicidae, but this attribution was later revised and the fossils assigned to other hymenopteran families (Jell and Duncan 1986; Brandão et al. 1989; Darling and Sharkey 1990; Naumann 1993; Dlussky 1999; Poinar and Milki 2001). The oldest accurate record of Gondwanan ants is from the Turonian of Botswana (Fig. 1b) with a rather diverse fauna of Formicidae of uncertain subfamilies (Dlussky et al. 2004; Archibald et al. 2006). If not a bias of the fossil record, and given that ants and Armaniidae are lacking in the three rich Early Cretaceous Gondwanan deposits, this may indicate an earlier diversification of ants on Laurasia. It is interesting to note that the earliest known Armaniidae occur in distinct Barremian/Aptian, Albian and Cenomanian deposits of Russia (Dlussky 1983, 1999), so that there is still no fossil evidence that Armaniidae and Formicidae have co-existed before the Turonian—e.g. in Kazakhstan (Dlussky 1975). Formicidae and Armaniidae (if the later is monophyletic) could have evolved independently on distinct Laurasian insular landmasses, rendering difficult the colonisation of other islands, which could explain their absence in other highly fossiliferous Laurasian outcrops from Spain, England, Russia or China.

Finally, the extreme scarcity of Early Cretaceous ants could also be related to peculiar, confined habitats of the

primitive ants, which would have limited the possibility of fossilisation. Wilson and Hölldobler (2005a) have suggested that the first ants arose and radiated in forest ground litter and soil with the rise of angiosperms. The presence of ants in the arthropod fauna of the Cretaceous French amber strongly supports this scenario, as it probably stems from the unusual preservation of litter-inhabiting species in addition to organisms living on trees (Perrichot 2004, 2005). The corresponding palaeoenvironment is estimated to have been a tropical moist forest growing near the shore in a mosaic of estuarine and mangrove-like context, and thus with a marine influence (Perrichot 2005). The amber-producer (Araucariaceae or the extinct gymnosperm family Cheirolepidiaceae) was likely the dominant tree of this ecosystem but various angiosperms were also present in some confined, limnetic environments (Gomez et al. 2004).

## Conclusion

*Haidomyrmodes mammothus* is the first Cretaceous ant species known by both the gyne and worker (Perrichot et al. 2007a). This provides evidence for the true sociality of



primitive ants based on the differentiation of two morphological castes, which was hitherto suggested by the existence of workers in other Cretaceous genera, but where the gyne remained unknown. Further evidences of eusociality for the early ants are based on morphological characters such as the metapleural gland or the structure and relative length of antennal segments (Grimaldi et al. 1997). Dlussky (1996) suggested semi-sociality for *Haidomyrmex* with its highly specialized craniomandibular system “which has arisen only in a specialized hunter providing its progeny with food”. Engel and Grimaldi (2005) suggested that the type specimen of *Haidomyrmex* could be a kind of “major” worker, unable to feed itself, which implies the presence of “minor” workers with mandibles of different shape. Only workers and gyne (but not males) of the recent genus *Harpegnathos* have rather similar mandibles with distal half curved upward (but distinctly less than in the *Haidomyrmecini*) and a tooth at elbow (Emery 1911, internet site <http://www.antweb.org/world.jsp> from April 2007). *Harpegnathos* species are predaceous and the workers can feed themselves (Hölldobler and Wilson 1990: 569–570). It is also notable that workers have ocelli, which is rare in Ponerinae. *Haidomyrmodes* is represented by workers with ocelli and an alate gyne with distinct antennal scapes, both having mandibles rather similar to those of the type specimen of *Haidomyrmex*. This suggests that these mandibles were likely functional for hunting in all castes. It remains that a social organisation is strongly suggested for the Early Cretaceous ant genus *Haidomyrmodes*.

Primitive ants from Cretaceous amber of France now include an alate gyne in one genus (*Haidomyrmodes*) and workers in three distinct genera (*Haidomyrmodes*, *Sphecomyrmodes* and *Gerontoformica*). Furthermore, the occurrence of two workers of *Sphecomyrmodes* in a single piece of amber suggests that they were foraging socially, as is the case for workers of *Sphecomyrma* in Turonian New Jersey amber (Grimaldi and Engel 2005). In addition, the oldest known spiders of the family Zodariidae are fossilised in the same amber from Archingeay/Les-Nouillers (Perrichot 2005). It is interesting to note that these fossils possess characteristics of modern representatives, which are highly specialized predators feeding exclusively on ants (Pekár and Král 2002). Such a specialization implies that prey were rather abundant and possessed effective methods of defence. If the strict myrmecophagous habit assumed for these Cretaceous zodariids is valid, then their occurrence may indicate a relative abundance of ants in Western Europe as soon as the Late Albian.

Other eusocial insect lineages such as termites, wasps and bees also developed during the Early Cretaceous (Grimaldi and Engel 2005; Poinar and Danforth 2006). Wilson and Hölldobler (2005b) have discussed and proposed a new model for the origin of the insect eusociality, but the fact that this phenomenon apparently occurred in a

relatively short period during the Early Cretaceous in insect clades of different ecologies remains largely unexplained.

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