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

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

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

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

Supplemental Material

AGE OF ANTS

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

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

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