Sampling the insects of the amber forest

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Amber, which is fossilized tree resin, is full of surprises. The tail of a feathered dinosaur was recently recovered from mid-Cretaceous (~99 Ma) amber from Myanmar (1), and anole lizards in Miocene Dominican amber (2) showed that lizard communities have persisted for at least 16 My. Carnivorous plants of the family Roridulaceae, presently confined to South Africa, have been discovered in Eocene amber from the Baltic (3). The great majority of creatures in amber, however, are insects, and they often preserve the finest 3D details. A fly and a mite were discovered trapped in a spider web in Early Cretaceous amber from Spain (4), and a scale insect in mid-Cretaceous Burmese amber is associated with eggs and freshly hatched nymphs, showing that brood care in insects dates back at least 100 My (5). Some amber insects even retain the cellular structure of internal soft tissues, such as muscle (6, 7). However, amber does not trap all of the animals in the forest, and even the insects are subject to sampling bias. This is an important consideration when we use the evidence of fossils entombed in amber to interpret terrestrial environments and ecosystems of the past. A study in PNAS by Solórzano Kraemer et al. (8) compares the range of insects trapped in modern tree resin in a Madagascar forest with the diversity of insects that live there, which represents a major step in determining the extent to which inclusions in amber represent the diversity and ecology of ancient forest communities.

Many different plants exude resin. Some of them are extinct, and some living resin producers are not found in the fossil record. Resins harden and darken over time through a process that usually involves polymerization. The rate of this transformation varies with resin chemistry and environmental conditions. Hardened resin that is only thousands of years old is usually referred to as copal (Fig. 1), and the point at which copal becomes amber is the subject of debate (9). Identification of the source of amber can be difficult due to not only the chemical alteration associated with fossilization but also because some amber producers are extinct. The oldest amber so far reported is about 320 My old and comes from a Carboniferous gymnosperm from Illinois (10). Such early amber is mainly a product of extinct seed plants and gymnosperms. Amber from flowering plants appeared in the middle to late Cretaceous but did not become abundant until the Eocene. The *Hymenaea* tree is an important source from the Miocene onward. The composition of *Hymenaea* resin varies depending on the species and region of origin (11). Resin functions to heal wounds suffered by plants and to deter herbivorous insects, so production is stimulated by physical damage and insect attack (9).

The oldest amber known to contain arthropod inclusions (a fly and mites) is Triassic in age, about 230 My old, and it comes from the Dolomite Alps of northeastern Italy. This amber was produced by an extinct conifer, and it also contains bacteria, algae, protists, and fungi (12). The famous Eocene amber from the Baltic region was also produced by a conifer. Baltic amber has yielded the greatest described diversity of any amber deposit: more than 3,000 species, most of which are insects (9, 13). Fossils in amber are critical for constraining the age of many insect groups and, combined with molecular data, can be used to determine a time scale for their evolutionary history. Cretaceous ambers from Lebanon and Myanmar are a particularly important source of earliest records (14), although molecular data indicate that many insect groups originated substantially earlier.

Most fossils, in contrast to those in amber, are preserved as a result of burial and compaction in sediment. The marine fossil record is dominated by the decay-resistant remains of shells, bones, and teeth. Approximately 60% of marine animals are entirely soft-bodied and are only preserved in exceptional circumstances: The fossil record is biased. For this reason, much research on the early evolution of the major animal groups is focused on exceptionally preserved fossil assemblages, which are known as conservation deposits (Konservat-Lagerstätten). The nature and number of these Konservat-Lagerstätten (e.g., fossiliferous amber) fluctuate through time (15).

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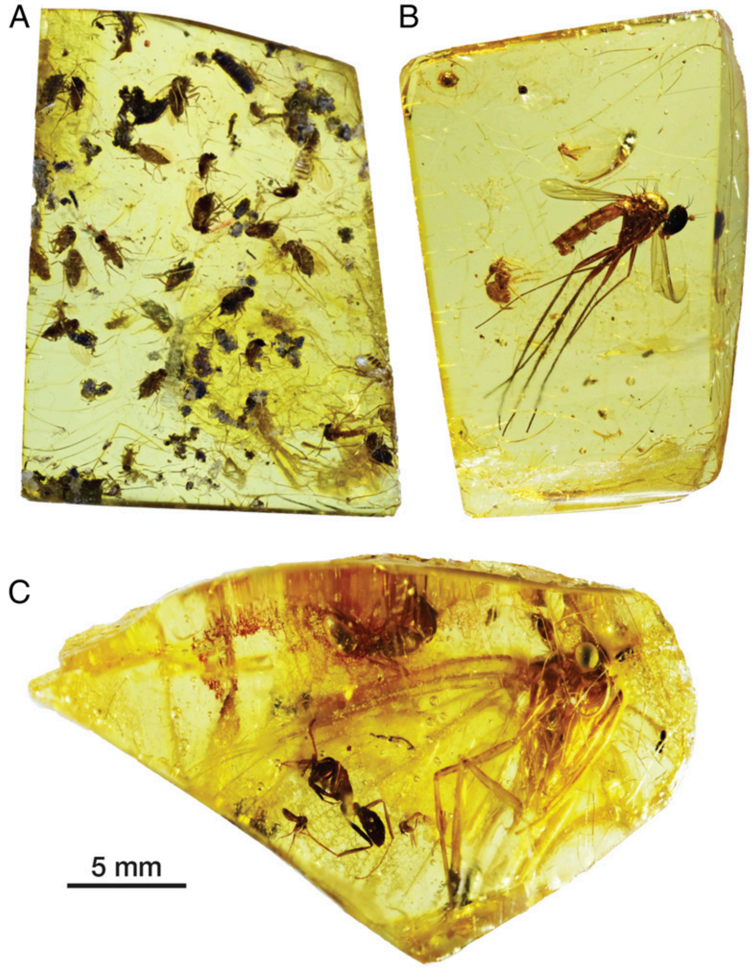

Fig. 1. Inclusions in specimens of East African copal from Moa, Tanzania. (*A*) Phorid flies (Diptera: Phoridae, YPM IP 321405-426). These flies were one of the most abundant dipteran families in the Madagascar resin and sticky traps, particularly those at ground level. (*B*) Arboreal spider (Araneae: Theridiidae, YPM IP 323257), tiny psychodid fly (Diptera: Psychodidae, YPM IP 323258), and long-legged fly (Diptera: Dolichopodidae, YPM IP 323259). Theridiids were one of the most abundant spider families in the Madagascar resin and sticky traps, and dolichopodid flies also occur in both. (*C*) Wasp (Hymenoptera: Chalcidoidea, YPM IP 321552), moth (Lepidoptera: Pyraloidea, YPM IP 238406), and other insects. Lepidoptera are rare in the Madagascar resin. Specimens courtesy of the Peabody Museum of Natural History, Division of Invertebrate Paleontology, Yale University (peabody.yale.edu). Image courtesy of D. E. G. Briggs, J. Utrup, and E. Martin (Yale Peabody Museum of Natural History, New Haven, CT).

They are abundant through the Cambrian, where soft-bodied animals are well represented in deposits such as the famous Burgess Shale in British Columbia; it appears that exceptional preservation was favored by ocean conditions at this time (16). In younger marine rocks, soft-bodied fossils are often confined to more restricted settings, where conditions such as low oxygen or elevated salinity favored their preservation. Such unusual conditions may exceed the tolerance of many animals, however, so that the preserved assemblage is not typical of normal marine life. Insects are preserved as 2D compressions in lake and even some marine sediments (17), but these assemblages are often dominated by forms that lived adjacent to the water. Trapping insects in the sticky resin exuded from trees, in contrast, might appear to provide a solution to the problem of bias; presumably, all of the insects of the forest are vulnerable to capture in this way.

There are probably close to 200 different amber deposits known, which cover more than 200 My of earth history and provide a unique source of information on the evolution of terrestrial life (9, 17). How do we determine how closely the fossils preserved in amber approach the diversity of insects that inhabited the ancient forest? One obvious way is to compare the insects that accumulate in modern resin with those living in the same forest environment as the resin producer. Henwood (18) tried this 25 y ago with field work in Panama on the *Hymenaea courbaril* tree, a living relative of the one that produced the famous Miocene amber from the Dominican Republic and Mexico, but the Panama trees produced insufficient resin. Instead, she compared the insect fauna of Dominican amber (19), which includes more than 1,000 species (13), with lists of insects recovered in a variety of traps in different habitats around the world. Samples recorded from emergence and pitfall traps showed the greatest similarity to the Dominican assemblage, suggesting that the amber sample represented the fauna of the litter and lower levels of the forest. The fossil assemblage is most similar to modern insect faunas from low-altitude rain forests near a river. Solórzano Kraemer et al. (20) embarked on a new investigation of the nature of insect assemblages in amber a few years ago, seeking to refine such comparisons and the inferences drawn from them. They too focused on the *H. courbaril* tree, but in the Chiapas region of Mexico. Once again the number of inclusions in the modern resin was inadequate for comparison with the Miocene amber from the same region. The team set seven different types of trap in a range of habitats in the area and obtained samples during the rainy and dry seasons. The samples most similar to those in the local amber were obtained from sticky traps set on trees and Malaise traps (tent-like structures erected on the ground). This suggested that the abundance of different insects preserved in the Mexican amber depends on their ecology and behavior, and may not reflect their importance in the Chiapas amber forest.

Understanding the nature of amber assemblages requires a direct comparison of insects trapped in modern resin and those that live in the same environment today. Amber collections, in contrast, are often selective: They depend on how the amber fossils from a locality were acquired, and they often favor more showy specimens. The report in PNAS by Solórzano Kraemer et al. (8) documents the results of field work in Madagascar, where they analyzed insects collected from the resin of living *Hymenaea verrucosa*, which exudes it in copious quantities. They compared this assemblage with insects that accumulated on sticky traps on the same trees and in adjacent Malaise traps. The sticky trap counts were closer to those in the resin, although the diversity on the sticky traps was slightly higher, probably because they did not repel herbivores. Further insights could be obtained in the future by comparing the assemblage collected from the *H. verrucosa* resin with examples from East African copal (Fig. 1), which was generated by the same plant 50,000–700,000 y ago (9). It is clear, however, that the sample obtained from sticky traps provides a guide to the likely bias in amber and copal assemblages. The insect assemblages in Mexican Chiapas amber showed greater similarity to those captured in Malaise traps, perhaps reflecting a greater abundance of some families of Diptera in that setting during the Miocene (8, 20). Clearly, the habitats represented in amber assemblages are likely to vary in detail.

Amber is an unparalleled source of information on ancient insects. It contributes to our knowledge of extinct forms, the significance of fossils for phylogenetic studies, the geographic distribution and diversity of insects in the past, and the age of different insect groups (9, 17). This new study (8) provides a benchmark for the study of the ecology of amber communities. Amber inclusions are dominated by insects associated with resiniferous trees, whereas taxa from other habitats, such as lepidopterans, are captured less frequently (Fig. 1). Certain insects and spiders are unlikely to be represented because they do not venture near trees. Amber from other sources and of different ages may provide different samples; however, understanding which part of the forest community is captured by resin/amber provides a long-awaited platform for comparisons between different amber deposits.

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