



Fig. 6. Mealybug (detail) in amber (Harvard collection piece, AMNH DR-14-403).

earliest documentation of actual homopteran-tending behavior.

## DISCUSSION

Considering the disparate geological records of ants and pertinent groups of homopterans, particularly Sternorrhyncha, the discovery of current symbiotic relationships in Miocene amber has profound implications for understanding ant and homopteran coevolution.

### FOSSIL RECORD OF THE ANTS

Knowledge of Cretaceous ants began merely 30 years ago, with the discovery of two workers (*Sphecomyrma freyi* Wilson and Brown) in a piece of Turonian (90–94 Ma) amber from central New Jersey (Wilson et al., 1967a, 1967b). In the last 15 years, however, many new species and genera of Cretaceous ants have been described, primarily from mid to upper Cretaceous rocks and amber of Russia and Kazakhstan (Dlussky, 1975, 1983, 1987); from Aptian limestone (ca. 110 Ma) of Brazil (Brandão et al., 1990); and from upper Cretaceous amber of Canada (Wilson, 1985a and unpub. data). Wilson (1987) revised the taxonomy of Dlussky's Cretaceous ants, synonymizing several genera. Recently, Grimaldi et al. (1997) reported another worker and a possible male of *Sphe-*

*comyrma* from new collections of New Jersey amber, as well as several other genera of primitive ants based on males, and even a new genus of a very primitive ponerine. Grimaldi et al. (1997) reviewed and evaluated all of the Cretaceous records of ants, and concluded that the specimens in amber are the only definitive Cretaceous Formicidae; the specimens compressed in rock lacked critical features and were deemed ambiguous. Thus far, all ants in Cretaceous amber are among the most primitive morphologically and it is likely the origin of the true ants dates approximately 100–120 Ma.

The fossil record for ants is exceedingly poor in the lowest Tertiary (Paleocene). Only a few taxa are described from the amber of Sakhalin Island, Far East Russia (Dlussky, 1988), apparently Paleocene in age, whereas several taxa are described from Eocene Arkansas amber (Wilson, 1987) and more than 50 genera and hundreds of species are reported from early Eocene Baltic amber (Wheeler, 1915). The lower Tertiary ants indicate a global fauna that was entirely transformed from the Cretaceous fauna, mostly with the emergence of modern subfamilies in the Paleocene (although the Ponerinae actually appear in the Cretaceous) and many modern genera in the early Oligocene (Lutz, 1986).

### FOSSIL RECORD OF THE STERNORRHYNCHA

The evolutionary history of Sternorrhyncha greatly exceeds the evolutionary history of ants. Heie (1987) reviewed the fossil record of aphids (superfamily Aphidoidea), and determined the oldest record thus far to be *Triassoaphis cubitus* Evans from the Triassic of Australia. From the Cretaceous amber of Canada, Richards (1966) reported six genera in three families; from Siberian amber, Konova (1976, 1977) reported eight families, two of them extant. Aphid nymphs are common in both of these ambers and are, in fact, the most abundant inclusions in Canadian amber. This strongly contrasts with the slightly older New Jersey amber, in which aphids are extremely rare (only two specimens out of 1000 insects have been found thus far) and coccoids are the most abundant kind of inclusion (20% of all inclusions) (Grimaldi, 1997). Coccoids are very