

are mutualisms, in which both partners benefit, or whether they are beneficial only to the ants was formerly a matter of argument among both myrmecologists and botanists (e.g., Belt 1874; Schimper 1888, 1898; von Ihering 1891; Rettig 1904; Wheeler 1913, 1942; Skwarra 1934; Brown 1960). Largely because of recent experimental work (e.g., Janzen 1966, 1967; Davidson et al. 1988), the majority of ant-plant symbioses are currently regarded as true mutualisms, in which ants obtain shelter, nourishment, or both and plants obtain protection against both arthropod and vertebrate herbivores. In some cases, plants may also obtain nutrients from ant waste materials and soil, gain protection from competing plants (which are removed by the ants), have their seeds dispersed, and, in rare cases, even get pollinated.

Cases of commensalism, in which ant colonies gain shelter but neither harm nor benefit the host, certainly exist. For instance, many ants occupy hollow stems (e.g., *Camponotus* and *Crematogaster* species), abandoned insect galls (e.g., *Leptothorax* species), and the tangled roots of epiphytes (e.g., *Anochetus* and *Strumigenys* species). Such associations presumably served as evolutionary precursors for mutualisms in which plants receive protection from herbivory in exchange for supplying cavities favoring ant occupation, including hollow branches, stems, and thorns; hollow pseudobulbs; or pouchlike domatia on leaves and petioles. In many cases, plants provide food as well as shelter, including carbohydrate-laden extrafloral nectaries and fatty or proteinaceous pearl bodies. According to O'Dowd (1982), the latter are produced by American, Asian, and African plants in over 50 genera in 19 families. Alternatively, plants may provide food but not shelter, encouraging frequent visitations by a variety of ant species and, presumably, many of the herbivore-repelling benefits that such visitations afford. Schupp and Feener (1991) showed

that more than a third of the plants in a Panamanian forest may practice such a strategy.

The classic case of ant-plant mutualism is that of the New World members of the genus *Acacia* (Leguminosae), which produce both extrafloral nectaries and proteinaceous Beltian bodies. Known for their painful stings, ants in the genus *Pseudomyrmex* occupy the hollow thorns, repelling arthropods (Coleoptera, Hemiptera, Homoptera, Lepidoptera) as well as large browsing mammals. The ants also kill other plants growing within a certain radius around the occupied *Acacia* (Janzen 1966, 1967). Another relatively well-studied case of mutualism is that of *Cecropia* (Moraceae), in which ants (primarily *Azteca* species, including six obligate *Cecropia*-dwellers, but also species of *Camponotus*, *Crematogaster*, *Pachycondyla*, and other genera) occupy the plants' hollow stems, excavating entrance holes in preformed, weakened areas present in the walls of internodes. *Cecropia*-dwelling *Azteca* species are particularly well known for their ferocity, reacting aggressively to any disturbance to their host plant. The plant provides nourishment to the ants in the form of glycogen-rich Müllerian bodies growing on a pad (trichilium) at the base of the leaf petiole (Bailey 1922a; Rickson 1971; Longino 1991). A third example is that of the hollow pseudobulbs of *Hydnophytum*, *Myrmecodia*, and other species of the Hydnophytinae (Rubiaceae) of the Far Eastern tropics. These plants possess swollen tubers with preformed, often complex chambers that in some species are nearly always occupied by ants (usually *Iridomyrmex* species). The plants obtain nutrition from ant excrement and debris absorbed by "warted" surfaces found in some of the chambers (Miehe 1911a, 1911b; Bequaert 1922; Huxley 1978; Jebb 1991).

Some ants cultivate and occupy "ant gardens," clusters of epiphytes planted in the branches of trees on soil and carton provided by the ants (Ule 1902; Kleinfeldt 1978, 1986;