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EVOLUTION OF MYRMECOPHYTISM IN WESTERN MALESIAN *MACARANGA* (EUPHORBIACEAE)

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Abstract.—Plants inhabited by ants (myrmecophytes) have evolved in a diversity of tropical plant lineages. *Macaranga* includes approximately 300 paleotropical tree species; in western Malesia there are 26 myrmecophytic species that vary in morphological specializations for ant association. The origin and diversification of myrmecophytism in *Macaranga* was investigated using phylogenetic analyses of morphological and nuclear ITS DNA characters and studies of character evolution. Despite low ITS variation, the combined analysis resulted in a well-supported hypothesis of relationships. Mapping myrmecophytism on all most parsimonious trees resulting from the combined analysis indicated that the trait evolved independently between two and four times and was lost between one and three times (five changes). This hypothesis was robust when tested against trees constrained to have three or fewer evolutionary transformations, although increased taxon sampling for the ITS analysis is required to confirm this. Mapping morphological traits on the phylogeny indicated that myrmecophytism was not homologous among lineages; each independent origin involved a suite of different specializations for ant-plant association. There was no evidence that myrmecophytic traits underwent sequential change through evolution; self-hollowing domatia evolved independently from ant-excavated domatia, and different food-body production types evolved in different lineages. The multiple origins of myrmecophytism in *Macaranga* were restricted to one small, exclusively western Malesian lineage of an otherwise large and nonmyrmecophytic genus. Although the evolution of aggregated food-body production and the formation of domatia coincided with the evolution of myrmecophytism in all cases, several morphological, ecological, and biogeographic factors appear to have facilitated and constrained this radiation of ant-plants.

Key words.—Ant-plant, character evolution, *Crematogaster*, Euphorbiaceae, *Macaranga*, mutualism, myrmecophyte.

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Plant species that are regularly inhabited by ants (myrmecophytes) have evolved in a diversity of tropical plant lineages (Huxley 1991; Davidson and McKey 1993a). In the most specialized of these associations, plants provide a living space (domatium) and nourish their resident ants with lipid- or carbohydrate-rich food bodies (Janzen 1966; Longino 1991; Fiala and Maschwitz 1992a), and the ants protect their host plants from herbivory, competition from vines, and possibly from fungal infection (Fiala et al. 1989; Agrawal 1998; Letourneau 1998; Gaume and McKey 1999). Although myrmecophytism has been the focus of much research on the evolution of mutualisms (Thompson 1994), phylogenetic analyses rarely have been conducted to investigate the origin and diversification of myrmecophytes (but see Chenuil and McKey 1996; Michelangeli 2000; Brouat et al. 2001).

Extensive radiations of myrmecophytic species occur in numerous tropical plant genera, for example, *Cecropia* (Cecropiaceae) and *Tococa* (Melastomataceae), with about 40 species each, and *Macaranga* (Euphorbiaceae) with 26 species (Davidson and McKey 1993b; Michelangeli 2000). In myrmecophytic lineages in general, species differ in a range of traits associated with ant occupation (Huxley and Cutler 1991; Davidson and McKey 1993b; Chenuil and McKey 1996). For example, the nature and development of the domatium (Jebb 1991), the location and composition of the food provision (Rickson 1980; Heil et al. 1998), and the strength and identity of association with the colonizing ant species (Yu and Davidson 1997; Fiala et al. 1999) all differ among closely related myrmecophytes. Phylogenetic studies are required to assess whether this morphological variation is the result of independent origins of myrmecophytic traits or the result of transformation and specialization of traits following a single origin of myrmecophytism (Davidson and McKey 1993b).

Myrmecophytism has evolved repeatedly in plants that share particular ecological and life-history characteristics (Davidson and McKey 1993a). For example, fast-growing trees that colonize early successional microsites in tropical rain forests have independently evolved obligate associations with ants in the Neotropics (e.g., *Cecropia*) and in Asia (e.g., *Macaranga*). Several morphological and ecological traits may have facilitated these parallel origins of myrmecophytism in different early successional lineages (Davidson and McKey 1993b). Pioneer species live in resource-rich environments with vigorous competition from vines, where ant defense may be especially advantageous (Schupp and Feener 1991). Many pioneer species have large leaves on thick, soft-wooded stems (Swaine and Whitmore 1988), which may provide opportunities for stem-boring insects and subsequent ant nesting (Davidson and McKey 1993b; Brouat and McKey 2000). Furthermore, the leaves of many early successional species bear extrafloral nectaries, or food bodies, that are visited by generalist ant species (Whalen and Mackay 1988; Fiala and Maschwitz 1991, 1992b; Schupp and Feener 1991), and se-