

The Evolutionary Ecology of Symbiotic Ant - Plant Relationships

DIANE W. DAVIDSON AND DOYLE McKEY

(DWD) Department of Biology, University of Utah, Salt Lake City, Utah 84112;

(DM) Department of Biology, University of Miami, Coral Gables, Florida 33124

Abstract.—A tabular survey of ant-plant symbioses worldwide summarizes aspects of the evolutionary ecology of these associations. Remarkable similarities between ant-plant symbioses in disjunct tropical regions result from convergent and parallel evolution of similarly preadapted ants and plants. Competition among ants has driven evolutionary specialization in plant-ants and is the principal factor accounting for parallelism and convergence. As habitat specialization accompanied the evolutionary radiation of many myrmecophytes, frequent host shifts and de novo colonizations by habitat-specific ants both inhibited species-specific coevolution and co-cladogenesis, and magnified the diversity of mutualistic partners.

The comparatively high species diversity of neotropical plant-ants and myrmecophytes probably results from two historical factors. Most importantly, influenced by Andean orogeny, greater habitat disturbance by fluvial systems has created a mosaic of habitat types unparalleled in other tropical regions; both myrmecophytes and plant-ants have diversified across habitat boundaries. Second, the arrival of a new wave of dominant ants (especially *Crematogaster*) may have condensed the diversity of relatively timid plant-ants to a greater degree in Africa and Asia than in the more isolated Neotropics. Regular trajectories in the evolutionary histories of plant-ants appear to be driven principally by competition, in a manner analogous to the taxon cycles or pulses proposed for other groups.

"In all the plants I have seen bearing sacs on the leaves, to whatever order they belong, it is remarkable that the pubescence consists of long hairs having a tubercular base; and although I do not see what connection that peculiarity can have with the ants' choice of a habitation, it is probable they find some advantage in it." "Ants' nests in swellings of the branches are found chiefly in soft-wooded trees of humble growth, which have verticillate or quasi-verticillate branches and leaves, and especially where the branches put forth at the extremity a whorl or fascicle of three or more ramuli; then, either at each leaf-node or at least at the apex of the penultimate (and sometimes of the ultimate) branches, will probably be found an ant-house, in the shape of a hollow swelling of the branch..." (Spruce 1908).

INTRODUCTION

A synthetic overview of the evolutionary ecology of mutualism has been disappointingly slow to develop (Bronstein 1991). In large part, this shortcoming may reflect the composite nature of mutualisms, which often arise as parasitisms (Thompson 1982), and frequently convey benefits contingent on physical environments, population densities, and third or multi-species interactions (reviewed in Howe 1984, Addicott 1985, Law and Koptur 1986, Schemske and Horvitz 1988, Thompson 1988, Cushman and Addicott 1991). The lack of a conceptual organization for such complex and variable associations inhibits a search for patterns

in historical and ecological factors shaping the evolution of mutualism. Complicating this endeavor still further is that most studies of mutualism focus on pollination and dispersal systems, which account for 80 % of the articles on mutualism in Bronstein's (1991) survey. Despite excellent treatments available for taxonomically and/or geographically restricted suites of such interactions (e.g., Heithaus et al. 1975, Feinsinger and Colwell 1978, Janson 1983, Herrera 1984, Gautier-Hion et al. 1985, Moermond and Denslow 1985, Gottsberger 1990, Bronstein 1992), both the overwhelming numbers and the taxonomic and ecological diversity of these interactions magnify the difficulty of

identifying single or few organizing processes or principles.

Symbiotic associations between ants and myrmecophytic plants offer a useful counterpoint. Sufficiently small in number to be summarized in a single table (Appendix 1), they nevertheless occur in numbers adequate to provide fertile substrate for hypothesis testing. Their presence in tropical regions throughout the world facilitates comparisons among taxonomic and ecological equivalents evolved in isolation on different continents (McKey and Davidson, in press). Despite their considerable diversity and widespread distribution, these relationships are relatively uniform in structure. Thus all myrmecophytic plants provide permanent housing and food to ants which are known or (more often) presumed to protect their hosts from herbivory or competition, or to provision them with nutrients (reviewed recently in Beattie 1985, Huxley 1986, Jolivet 1986, Hölldobler and Wilson 1990).

Here we provide an overview of the symbiotic ant-plant relationships, focusing principally on trees, shrubs and hemiepiphytes of the American and African tropics. (The epiphytic ant-plants have been reviewed recently elsewhere by Davidson and Epstein 1989.) This geographic specialization reflects our comparatively poor understanding of ant-plant relationships in the Oriental and Australian tropics where, with the exception of ant-epiphytes (Jebb 1985, Huxley and Jebb 1991), investigations are fewer in number and less detailed (but see the recent proliferation of work by Fiala and Maschwitz 1990 and 1991, Fiala et al. 1989 and 1991, Maschwitz et al. 1989 and 1991). For myrmecophytes overall, existing evidence is often too meagre for a convincing assessment of the fitness consequences of particular associations. We therefore avoid using the terms "mutualism" and "facilitation" in favor of less restrictive words like "association", "interaction", or "relationship". For similar reasons, the terms "myrmecophyte", "myrmecophytic" and "ant-plant" are used here only to describe plants regularly inhabited by ants, without implying that plants either benefit from the ants or possess traits evolved principally as ant attractants. On occasion, we also refer to "myrmecophilic" plants, those which are not symbiotic with ants but produce obvious ant attractants

such as extrafloral nectaries (EFN's) and/or pearl bodies.

Our principal themes here are the factors which have predisposed particular ants and plants toward symbiotic association, and the ecological forces which have driven evolutionary specialization in each of these taxa. We also summarize the processes generating and maintaining diversity within each of these groups, as well as the factors limiting species specificity and co-cladogenesis. Finally, we speculate about particular evolutionary trajectories which appear to have occurred regularly across independent lineages of plant-ants and ant-plants. As a prelude to all the above, we briefly review the way in which historical context appears to have influenced the evolution of ant-plant symbioses in the American and African tropics.

DIVERSITY, BIOGEOGRAPHY AND HISTORY

Both plant-ants and myrmecophytes achieve their greatest richness in the American tropics (McKey and Davidson, in press). Among ants, the proportion of neotropical and African genera containing specialized plant-ants is approximately the same, whether calculated by biogeographic region (respectively, 10 % and 12 % of genera) or for mesic tropical environments (12.8 % and 14.5 %, respectively). Although the mesic Neotropics hold approximately 1.3 times as many ant genera as does mesic tropical Africa (Brown 1973), the latter land mass has slightly more genera which contain at least one plant-ant. Nevertheless, two of these genera are monotypic and, based on present knowledge, the species richness of plant-ants appears to be about 3.5-fold greater in the Neotropics than in Africa (current estimates of 85 species versus 24, including one species in Madagascar). Differences in diversity occur principally due to the proliferation of plant-ant species within endemic neotropical genera. In the New World, significant radiations of plant-ants occur in endemic *Pseudomyrmex* (N = 32 species), *Azteca* (N probably > 20), *Myrmelachista* (N > 6), and *Allomerus* (N 8), as well as in cosmopolitan *Pheidole* (N 6) and *Pachycondyla* (N 4). In contrast, significant radiations of African plant-ants are limited to *Tetraponera* (N 5) and *Technomyrmex* (N 6),

both widely distributed in the Old World tropics, and even these radiations are comparatively small.

Relative to the ant faunas of both the American and African tropics, those of the Oriental and Australian regions appear to be poor in plant-ant genera (McKey and Davidson, in press); respectively, only 5.6% and 7.3% of regional ant genera, and 7.3% and 9.1% of mesic tropical genera, contain plant-ants. Moderate to large radiations of plant-ants in the Oriental region include only cosmopolitan *Crematogaster* (N 8 species) and *Camponotus* (N 7), as well as endemic *Cladomyrma* (N 5), and current estimates of plant-ants are only 24 species overall. In the Australian region, encompassing northern Australia, New Guinea and associated islands, such radiations are limited to endemic *Anonychomyrma* (probably > 3 species), and the species richness of plant-ants presently stands now at only about 12 species. Although the numbers of plant-ants may increase slightly in these regions due to increased sampling effort (cf. Dorow and Maschwitz 1990, Maschwitz et al. 1991) and taxonomic revision (e.g., S. Shattuck, 1991, 1992b), the relative poverty of plant-ants at the generic level is likely real.

Myrmecophytes probably constitute a similar fraction of all plant genera in the American and African tropics, but their species richness is distinctly greater in the Neotropics (McKey and Davidson, in press). Again unmatched in Africa, major radiations of ant-plants within (mainly) endemic, neotropical genera largely account for this difference. Neotropical plant genera with significant radiations of myrmecophytes include endemic *Cecropia* (N 50-60 ant-plant species), *Tachigali* (N 20), *Triplaris* (N = 17), *Tococa* (N = 40-45), *Clidemia* (N = 15-20) and *Maieta* (N 15), as well as non-endemic *Acacia* (N 12 species), *Ocotea* (N 6) and *Hirtella* (N = 6). In contrast, in Africa only *Acacia* (N 15) and, to a lesser extent, *Cuviera* (N = 8+), *Canthium* (N = 3-6) and *Clerodendrum* (N 3) contain moderate to large numbers of ant-plants, and of these genera only *Cuviera* is restricted to the Ethiopian region. Estimates of myrmecophyte species richness are about three-fold greater in the American than the African tropics, and maximum local (alpha) diversity may be twice as high. Although it is not yet possible to

estimate the frequency of myrmecophytes in the tropical floras of Oriental and Australian regions, substantial radiations of myrmecophytes within genera are comparatively limited (references in McKey and Davidson [in press]). These probably include only *Macaranga* (N 23), *Korthalsia* (N = 7+) and *Neonauclea* (N = 4+) in the Oriental tropics, and *Chisocheton* (N = 6), *Kibara*, *Stegantnera*, and *Semecarpus* (each with N = 4) in the Australian tropics. Altogether, the Oriental and Australian tropics likely hold slightly more than 100 myrmecophyte species.

At the generic level, the determinants of ant-plant and plant-ant diversity in the American and African tropics are probably similar to those regulating species richness of the floras and ant faunas overall (McKey and Davidson, in press). Radiations of myrmecophytes and plant-ants in both areas appear to have been strongly affected by both the climatic and geologic histories of the continents and to have been correlated with diversification in habitat use. As may be common for neotropical plants in general (Gentry 1986, 1989 and in press, but see Simpson and Todzia [1990] for the high Andean flora), generic radiations of ant-plants may often be comprised of neoendemisms with comparatively recent origins. Frequently geographically or edaphically restricted, such species may be products of a "species pump", postulated to have generated new species through habitat specialization during range reexpansions within interglacial intervals of the Pleistocene (Colinvaux, in press). Although the diversity of tropical ant species has not previously been related explicitly to any similar mechanism, a possible link between speciation and habitat specialization is evidenced by the observation that many plant-ants show greater specificity to habitats than to host species (Benson 1985, Davidson et al. 1989 and 1991; Longino 1989a and 1991a).

Given historical and contemporary differences in geological activity, and in correlated rates of habitat disturbance on the two continents, the American tropics should have provided greater opportunity than did tropical Africa for habitat specialization and speciation (McKey and Davidson, in press). Topographically, the mesic African tropics occupy a comparatively flat and featureless plain, much

more homogeneous than mesic tropical America. In the Neotropics, orogenic activity in the Andes has not only influenced the montane and submontane areas directly, but has given rise to the fluvial disturbances that helped to create a spectacular mosaic of landscapes over the vast Amazonian region. No less than 26 % of modern lowland forests of Western Amazonia give evidence of recent erosional and depositional activity, and approximately 12 % of these lands are currently in some stage of succession (Salo et al. 1986, Räsänen et al. 1987). In addition to their role in creating and maintaining a landscape mosaic conducive to rapid speciation, the Andes also appear to have protected the mesic Neotropics from the severe and frequent droughts which could have magnified species extinctions in Africa, as mesic forests were repeatedly reduced and fragmented during Pleistocene times (Raven and Axelrod 1974, Axelrod and Raven 1978).

Finally, neotropical species should also have received greater protection than their African counterparts from Pleistocene temperature variation. Lowland Africa is approximately 500m higher in elevation than is lowland Amazonia, and would have provided fewer refugia for plants and animals during glacial periods. Current evidence (e.g., Bengo and Maley [1991]) indicates that montane forest, including elements now restricted to the cool, moist conditions of the Afromontane zone, extended to low elevations (600 m or perhaps lower) in Central Africa during several periods over the last 135,000 years. Judging from the dramatic drop in ant diversity and abundance with elevation on humid tropical mountains (Janzen 1973), the conditions suggested for these periods would not have been conducive to the success of much of the contemporary ant fauna of lowland African forests. To the extent that climatic fluctuations in Africa exceeded those in the American tropics, these could have led to the dissolution of mutualisms, even without species extinctions, as the fitness consequences of association shifted (e.g., to parasitism) with fluctuations in the abiotic and biotic environments.

SIMILARITIES BETWEEN ANT-PLANT RELATIONSHIPS OF DIFFERENT TROPICAL REGIONS

In the context of the aforementioned differences in species richness, and in the climatic and geologic histories of ant-plants on different tropical land masses, certain similarities in the form and ecology of ant-plant relationships of different continents appear all the more striking. For example, across tropical land masses, large colonies of active and aggressive ants occupy fast-growing and light-demanding pioneer trees (neotropical *Cecropia* and Old World *Macaranga*). In contrast, timid ants inhabit small, slow-growing understorey shrubs or treelets with hairy domatia (e.g., American *Hirtella*, *Duroia*, and many melastomes, and African *Magnistipula*, *Delpydora*, *Cola*, and *Scaphopetalum*). Finally, myrmecophytic trees of secondary forests and forest light gaps (neotropical *Triplaris* and African *Barteria*) grow in circular clearings made by pseudomyrmecine ants, which attack vegetation in the neighborhood of their hosts. McKey and Davidson (in press) have amassed evidence against common ancestry as a general explanation for these remarkable commonalities. While some comparisons between Africa and Asia suggest common descent of ant-plants, plant-ants or both, myrmecophytes and specialized plant-ants appear to have evolved largely independently in America and Africa. No ant-plants of Africa and the Neotropics have apparently shared a myrmecophytic common ancestor. In contrast, the plant-ant habit may be ancient in the sub-family Pseudomyrmecinae and in tribes Myrmelachistini and Tapinomini, and might possibly have preceded the splitting of South America and Africa. However, with these possible exceptions, resemblances between symbiotic associations in the American and African tropics are not due to common descent of one or both partners from an association that predated continental separation or other vicariance events, or which migrated intact from one continent to the other (McKey and Davidson, in press).

The remarkable correspondences between ant-plant associations in the American and African tropics must therefore be due to some combination of: (1) parallel evolution of ants and/or plants from

similar starting material, (2) evolutionary convergence, and (3) the matching of symbiotic partners according to a set of shared rules. The task then is to identify the preadaptations which have been pressed into service and evolutionarily modified in symbiotic ants and plants, and to recognize the selection pressures which have led repeatedly to the correspondences noted above.

PREADAPTATIONS OF PLANTS AND ANTS

Parallel and convergent evolution are usually regarded as evidence that selection pressures have acted in similar ways on organisms of different lineages. Selection, however, is only part of the explanation for these phenomena. Different lineages may follow similar evolutionary trajectories because they share similar developmental constraints which channel the action of selection along a limited number of paths.

Preadaptations for Myrmecophytism

The evolutionary antecedents of specialized myrmecophytic traits are poorly explored. However, comparative studies of myrmecophytes and their less specialized relatives are beginning to suggest plausible and testable hypotheses about the origins of these traits (Benson 1985, McKey 1989 and 1991, O'Dowd and Willson 1989, Fiala and Maschwitz 1991, Schupp and Feener 1991). For example, in various plant taxa, a few similar structures have repeatedly provided the raw materials transformed by selection into myrmecophytic structures. An understanding of the origins of these traits may help to identify constraints which have pressed ant-plants of diverse lineages and biogeographic regions into a limited number of molds. It may also indicate developmental patterns which have facilitated the evolution of myrmecophytism, and suggest why myrmecophytes have evolved repeatedly in some lineages, but rarely or never in others.

Provision of Food for Plants.—Discussion of the evolutionary background of myrmecophytes has tended to emphasize the provision of food for ants. Indeed, there is evidence from many lineages that the ancestors of ant-plants possessed extrafloral

nectaries, pearl bodies, or other traits, which provided food for ants in loose non-symbiotic interactions. The large, complex nectary glands of some ant-plants (e.g., *Acacia*, *Endospermum*, and some *Macaranga*), and the elaborate food bodies of others (e.g., Müllerian bodies of *Cecropia*, and Beccarian bodies of Asian *Macaranga*) are readily accounted for as outgrowths of these traits. As ant-plant interactions intensified into symbiosis, such attributes should have been easily modified by selection acting on the composition and rate of supply of food for ants. The Beltian bodies of Central American ant-acacias may be the only case in which a specialized food-producing structure of a myrmecophyte lacks an obvious antecedent among unspecialized but related plants.

Provision of food ensures that ants are a regular component of the plant's biotic environment, and doubtless facilitates the evolution of more intense interactions. However, myrmecophytes have evolved in only a small subset of the numerous plant lineages whose members are engaged in opportunistic myrmecophilic interactions; other plant traits must also play a role in facilitating or constraining the evolution of symbiotic interactions. Furthermore, in many cases, neither the myrmecophytes nor their close relatives provide food directly to ants. In many cases, EFN's and food bodies are lacking, and scale insects (Coccoidea, Homoptera) are a major source of colony nutrition (Appendix 1). Following Ward (1991), we suggest that many myrmecophytic relationships evolved not from pre-existing myrmecophilic relations, but from parasitisms in which stem-nesting ants began to inhabit live plant cavities and to tend Coccoidea.

Structures for Housing Ants.—We must thus explore plant traits that facilitated the production of cavities that could be modified by selection into specialized structures for housing ants. The evolutionary antecedents of myrmecodomatia, the defining feature of specialized myrmecophytes, have received little attention. Preadaptations and developmental constraints in the evolution of myrmecodomatia will be discussed in detail elsewhere (McKey, in preparation) and are summarized only briefly here.

Table 1 Taxa in which at least some myrmecophytes have long, dense hairs which inhibit insect movements on stems, domatia or both.

Region	Family	Genus	
ETHIOPIAN	Chrysobalanaceae	<i>Magnistipula</i>	
	Dichapetalaceae	<i>Dichapetalum</i>	
	Ebenaceae	<i>Diospyros</i>	
	Rubiaceae	<i>Canthium</i>	
		<i>Cuviera</i>	
	Sapotaceae	<i>Delpydera</i>	
	Sterculiaceae	<i>Cola</i>	
		<i>Scaphopetalum</i>	
	NEOTROPICAL	Boraginaceae	<i>Cordia</i>
		Chrysobalanaceae	<i>Hirtella</i>
Fabaceae		<i>Platymiscium</i>	
		<i>Tachigali</i> ¹	
Gesneriaceae		<i>Besleria</i>	
Melastomataceae		<i>Allomaieta</i> ²	
		<i>Blakea</i> ³	
		<i>Clidemia</i> ⁴	
		<i>Conostegia</i>	
		<i>Henriettea</i> ⁵	
		<i>Maieta</i>	
		<i>Sagraea</i> ⁶	
		<i>Tococa</i> ⁷	
		<i>Pouroima</i>	
	<i>Triplaris</i>		
	<i>Duroia</i> ⁸		
	<i>Hoffmannia</i>		
	<i>Remijia</i>		
ORIENTAL	Melastomataceae	<i>Medinilla</i>	
	Verbenaceae	<i>Callicarpa</i>	
	Piperaceae	<i>Piper</i>	
AUSTRALIAN	Monimiaceae	<i>Stegathera</i>	

¹ At least one species, collected from a hillside over the junction of the Rio Sotileja and the Rio Manu, in southeastern Peru (D. Davidson, unpublished).

² Closely related to *Maieta* (A. Gentry, personal communication)

³ Benson (1985) considers the leaf pouches of *B. formicaria* to be in transition from acarodomatia to ant-domatia. Among the melastomes listed here, *Blakea* is unique in not belonging to the Miconieae.

⁴ At least three independent origins of domatia in *Clidemia* sensu strictu; includes *Myrmidone* (Judd and Skean 1991)

⁵ Includes *Henriettea* (Judd 1989)

⁶ Includes *Ossaea* p.p. (Judd 1989)

⁷ Includes *Microphysca* (Judd and Skean 1991)

⁸ Two independent origins of domatia (foliar domatia and swollen internodes)



Fig. 1. Paired leaf-pouch domatia, covered with dense, erect trichomes, at the base of a leaf of *Delpydera macrophylla* Pierre (Sapotaceae) in southern Cameroon. These pouches are formed by downward folding and rolling of the expanded base of the blade on either side of the midrib. The domatia are usually occupied by timid *Technomyrmex* species.

Stipules have been modified into ant-domatia in a few myrmecophytes; known examples are all from the Old World tropics (Appendix 1). (The only apparent exception is *Acacia*, in which thorns, themselves highly specialized stipules, have been modified into domatia in both neotropical and Old-World representatives.) In many tropical plants, large stipules function as mechanical protection for the growing bud. In some cases, stipules possess ant-attractive structures which provide biotic defense as well. Where stipules are persistent, rather than being shed soon after maturation of associated nodes, ants may find suitable shelter for tending homopterans, nesting, or both. Although ants and their associated debris are observed frequently beneath large stipules, only rarely have these stipules become evolutionarily modified to house ants. Specializations include recurving or inflating of the

stipule to form a more enclosed structure (as in New Guinea *Psychotria* and perhaps African *Dactyloadenia*), location of specialized food bodies on the lower surface of the stipule (Asian *Macaranga*), and possibly the evolution of persistent stipules. In an analogous case, African *Diospyros conocarpa* Gürke & K. Schumann has specialized, hairy domatia formed from persistent cataphylls (Letouzey and White 1970). These structures are leaf-like appendages, usually rapidly deciduous, and formed on the first few nodes of young expanding twigs in many tropical trees with rhythmic growth patterns (Hallé et al. 1978). They are functionally analogous to stipules. In *D. conocarpa*, the cataphylls are folded to form a structure completely enclosed, except for a small opening near the base of the blade, and they are persistent, rather than deciduous, as in related species. These structures

are occupied by *Techomyrmex kohliti* (Forel), which also inhabits several leaf-pouch ant-plants in the same forests.

In Asia, Africa, and the Neotropics, leaf-pouch domatia of strikingly similar form have evolved in numerous myrmecophyte lineages (Appendix 1). Formed near the leaf base, and typically paired on either side of the midrib (but single in some species), they are usually covered with long, dense trichomes (Table 1). Restricted to understory treelets and shrubs, these ant-plants typically are occupied by small, timid ants. Leaf-pouches seem to be formed in one of two ways. In some taxa (e.g., neotropical Melastomataceae, and African Sterculiaceae), invagination occurs in the internal portion of the leaf blade, in a region flanking the base of the midrib. This invagination produces single or paired inflated pouches, each with an entrance on the abaxial leaf surface. In at least four plant families, including most frequently and variably in the Rubiaceae, paired leaf pouches form in a different manner. At the bases of leaf blades, (revolute) leaf margins curl downward, as in African *Delpyodora* (Fig. 1), *Magnistipula*, *Dichapetalum gassitae* Bret., and *Ixora hippoporifera* Bremek., neotropical *Hirtella* and *Remijia*, and Asian *Callicarpa saccata* Steen. Less frequently, (involute) leaf margins curl upward, as in neotropical *Duroia saccifera* Benth. and Hook. Pouches may be bubble-like invaginations (*Gardenia imperialis* L. Pauwels) or, more often, scroll-like hollow tubes.

It has long been postulated that the leaf-pouch domatia of ant-plants evolved from acarodomatia (Schnell 1966, Schnell et al. 1968), presumably by intermediate stages in which domatia could be occupied either by mites or by small ants. Selection led to increased size of domatia with progressive transference of protective function from mites to ants (O'Dowd and Willson 1989). Benson (1985) also argues that leaf-pouch domatia evolved in myrmecophytes from small depressions in leaf surfaces. The original function of these depressions was to shelter ant-tended homopterans. The two hypotheses are not mutually exclusive, as ants may also have used acarodomatia to shelter homopterans (Benson 1985). Hypotheses implicating acarodomatia in the origin of leaf-pouch ant-domatia receive strong support from cases like

Cola marsupium K. Schumann, in which a single leaf presents a graded series of domatia increasing in size from typical acarodomatia at the leaf apex to large inflated pouches at the leaf base (Schnell and Beaufort 1966).

Why have leaf-pouch domatia evolved repeatedly in certain groups, for example, at least nine times in the tribe Miconieae in the Melastomataceae (Table 1)? Leaves of many Miconieae have strongly arcuate venation with sections of the leaf blade vaulted and curved upward between major veins. Even before selection intervened to enlarge these structures, this waffle-like leaf organization may have fortuitously provided invaginations large enough to shelter ant nests. In African Sterculiaceae, where similar domatia have evolved twice, venation is also palmate, with three large veins converging at the leaf base.

The largest group of myrmecophytes is that in which domatia are located in stems, or in stem-like structures such as petioles or inflorescence stalks (Appendix 1). Increasing evidence supports the hypothesis that ants originally colonized cavities created in twigs and petioles by wood-boring insects (Ward 1991, also Appendix 1). Together with cavities formed by spontaneous drying of pith canals, these cavities provided ants with shelter and substrate for brood and symbiotic Coccoidea. When the presence of ants conferred net benefit (e.g., by protection against phytophagous insects, including wood-borers, and any diseases transmitted by these insects), selection acted on the plant to evolve features facilitating its occupancy by ants (Ward 1991). Such traits include specialized swollen twigs and a prostoma, or relatively unligified spot through which ants gain easy access to the domatia.

What traits may have predisposed plants to evolve symbiotic association with ants via this mechanism? Wood-boring insects usually attack soft, pithy portions of stems. The larger the primary diameter of a stem, the thicker its pithy central section. Thus thick-twiggged plants offer greater opportunities than do thin-twiggged taxa for wood-boring insects, and for ants which nest secondarily or primarily in the cavities of living plants. Although much poorly understood interspecific variation in stem structure affects the relationship be-

tween the primary diameters and pith diameters of twigs, myrmecophytes are most likely to evolve in plants with thick twigs.

This observation gains importance when we consider the plant-architectural correlates of stem primary diameter. The best known of "Corner's rules," and one confirmed by quantitative studies (White 1983), states that there is a positive correlation between the primary diameter of a stem axis and the size of appendages (e.g., leaves) borne by it (Hallé et al. 1978). This correlation means that selection acting on leaf size (Givnish 1987) also drives evolutionary change in stem diameter (McKey 1991). Thus, the evolution of stem domatia may be facilitated by an evolutionary increase in leaf size, driven for example, by climatic change, by range extension into more mesic environments (Givnish 1987), or by selection to minimize metabolic cost of woody leaf-support tissues (White 1983). If disparities in leaf size were related to habitat, myrmecophyte frequencies could be correlated with habitat, independently of and perhaps even despite any habitat-related differences in selection imposed by symbiotic ants (McKey, unpublished).

Corner's Rule may help account for several groups of ant-plants with domatia in thickened support structures (Appendix 1). First, myrmecophytism has evolved often in genera whose moist, shaded, understory environments have favored comparatively large, broad leaves and thick stems (e.g., African *Leonardoxa*, and Oriental or Australian *Tapeinosperma*, *Stegauthera*, *Kibara*, and *Myristica*). Ants also live symbiotically with members of the Meliaceae, Sapindaceae, and Anacardiaceae, whose leaves are not only large, but compound. In the Meliaceae, myrmecophytes appear to have evolved independently in four genera, including three Asian taxa (*Aphanamixis*, *Chisocheton* and *Aglaia*) with massive stems supporting large compound leaves. Even within *Aphanamixis*, myrmecophily characterizes forms with relatively large leaves and twigs (Mabberley 1985). Second, thick support structures for large leaves may also have facilitated the frequent evolution of ant-plants in fast-growing pioneer trees, whose large leaves and sparse branching allow them to support a considerable leaf surface area

with minimum investment in woody framework (White 1983). Examples are neotropical *Cecropia*, Asian *Macaranga* and Australian *Eudospermum*, which almost surely converged due to selection on leaf size and tree architecture prior to the evolution of myrmecophytism. Other myrmecophytic pioneers of riverine and forest light gaps include neotropical *Triplaris*, Australian *Nauclea* and African *Barteria* and *Vitex grandifolia* Gürke. In all of the plants in these two categories, ant protection might be especially advantageous, because the large and parenchyma-rich meristems are especially susceptible to damage by wood-boring insects. Since most of these plants produce one-to-few large meristems at any one time, the material and opportunity costs of losing even one meristem could be very high.

Finally, two smaller groups of ant-plants house ants in either false nodes, thickened to support multiple leaves (e.g., two *Cordia* species and *Duroia hirsuta* Poepp. and Endl.), or in stout petioles (*Piper*, *Pourouma* and *Tachigali*). Although petioles might often be too short-lived to function as domatia, they are likely to be comparatively long-lived for both the compound leaves of *Tachigali* and the simple leaves of myrmecophytic understory *Piper* species (in which ant cavities also extend into the stem itself).

Preadaptations and Pathways to Specialization in Ants

Specialized plant-ants are represented disproportionately in particular taxonomic categories of ants, and shared characteristics of these taxa provide evidence of factors predisposing ants to evolve symbiotic relationships with plants. Worldwide, plant-ants have evolved in five of 12 subfamilies in the Formicidae (Appendix 1). They are absent only from subfamilies of specialized legionary and other predatory ants (Cera-pachyinae, Dorylinae, Ectoninae, Leptanillinae, and Myrmeciinae), and from the monotypic Aneuretinae and Nothomyrmeciinae. Until recently, they were also deemed absent from the Ponerinae, the most predatory of five subfamilies containing at least some species that depend directly and substantially on plant resources. However, at least four species of



Fig. 2. Leaves bound together with carton to form the ephemeral nests of *Dolichoderus* (= *Hypoclinea*) *bidens* (L.) in southeastern Peru.

Pachycondyla now appear to be specialized symbionts of *Cecropia* (Davidson et al. 1991, Davidson and Fisher 1991, J. Longino, personal communication). Still, plant-ants are poorly represented in the Ponerinae and among predatory ants in general.

The evolution of obligate plant-ants in five subfamilies, approximately 30 genera (Appendix 1), and multiple clades of at least *Pseudomyrmex* (Ward 1991) and *Azteca* (Benson 1985, Longino 1991a and b) confirms the frequency and facility with which plant-ants have evolved, and provides abundant opportunity to find commonalities in lifestyles and traits that may have promoted evolutionary specialization on plants. For example, three of the six principal generic radiations of South American endemics have arisen (one each) in the sub-family Pseudomyrmecinae, and in the tribes Tapinomini (Dolichoderinae) and Myrmelachistini (Formicinae). These ants share the habit of regularly tending homopterans inside (all three taxa) or outside (especially tapinomines) of cavities in live plants. Within each of these groups, common ancestors of contemporary plant-ants likely had additional traits which predisposed them to evolve symbiotic (parasitic as well as mutualistic) associa-

tions with homoptera and plants. Because the relative competitive abilities of ants form an important part of the story, we turn now to consider various ecological differences among ants with different competitive abilities.

Competitive Dominants.—Ecological limitations on populations of arboreal ants in lowland tropical forests add insight into probable origins, correlates and consequences of arboreal nesting habits, including stem-nesting. Colony populations appear to be limited principally by food and nest sites (Wilson 1959b, Carroll 1979, Davidson and Epstein 1989). Because most arboreal ants are generalized foragers of plant and homopteran exudates, and of carrion, interspecific food requirements are strongly overlapping, and competition can be intense. The competitive dominants of each tropical biogeographic region are species which have evolved means of nesting in areas of abundant food. They include Old World *Oecophylla*, *Crematogaster*, *Tetramorium*, *Philidris* and *Polyrachis*, some Australian *Anonychomyrma*, and New World *Crematogaster*, *Camponotus*, *Azteca* and *Dolichoderus* (including *Hypoclinea*, Shattuck, 1992a). These ants either bind leaves together into

temporary nests, or construct potentially more permanent carton homes in the canopy where food is abundant (Fig. 2). Like species which occupy the top of the competitive hierarchy at high temperate latitudes (Vepsäläinen and Pisarski 1982), these species defend not only their nest sites and temporary, localized food patches, but their entire foraging areas, as absolute territories. Although a certain threshold of aggressiveness may have been required before these ants could defend their somewhat exposed nests successfully against vertebrate enemies (e.g., monkeys and woodpeckers; J. Longino, personal communication), an eventual capacity to nest near abundant food almost certainly contributed to the escalation of aggressiveness and dominance.

Most competitive dominants tend populations of Homoptera, whose exudates form a steady and predictable source of colony nutrition and help to fund high worker activity and aggression. These ants lack functional stings, but all possess elaborate chemical weaponry (Blum and Hermann 1978, Attygalle and Morgan 1984, Buschinger and Maschwitz 1984, Merlin et al. 1992). Expended in use, these exocrine products should be characterized by more rapid turnover and greater cost than is associated with longer-lived stings and sturdy exoskeletons. Nevertheless, if chemical defenses are supported by the requisite resource base, they appear to be more effective than stings in contests among ants (Davidson et al. 1988). With their rich sources of homopteran exudates, dominants should often experience an excess of dietary carbon in relation to protein, so that colony expansion is protein-limited. If so, this could explain the "high tempo" lifestyle (sensu Oster and Wilson 1978) characteristic of these ants and help to resolve the enigma of their seeming "inefficiency" in foraging (Oster and Wilson 1978; Hölldobler and Wilson 1990). By spending relatively "cheap" carbon resources on aggression and seemingly extravagant levels of activity, these ants secure dominance over territories whose protein resources fund colony growth.

Chemical weaponry and high activity levels are not the only traits determining dominance in these ants. Abundant food and freedom from nest site limitation appear also to have led to larger colony

sizes and longer life expectancies. If the resource environments of ants have helped to shape the evolution of life history attributes (e.g., rates of egg-laying, worker turnover, etc.), a correlated evolved dependency on rapid rates of resource acquisition may restrict some dominants to the most productive sites in lowland rain forests (Davidson and Epstein 1989). Arboreal dominants are preeminent in monopolizing high quality resources at exposed sites such as EFN's, and Homoptera positioned on flowering and fruiting peduncles, where a plant's phloem resources are frequently most concentrated. As evidence of their competitive impact in one rainforest ant community as a whole, Wilson (1959b) noted that a number of arboreal ant species regularly forage on the ground, whereas only a few exceptional ground nesters forage even in the low arboreal zone, and possibly none of these reaches the upper canopy. (In the Neotropics, terrestrially nesting *Paraponera* and *Ectatomma* are obvious counter-examples, but both genera are exceptional among ponerines for their heavy reliance upon plant exudates, carried as large droplets in the mandibles.) Dominants can restrict the local diversity of other ants, as do the parabiotic associates of neotropical ant-gardens (Davidson 1988). Thus, the diversity of arboreal but not terrestrial ant species is lower inside the territories of *Camponotus femoratus* Fab. and *Crematogaster cf. limata parabiotica* (Forel), than in adjacent areas lacking these ants. Because the species composition and diversity of subordinate species often varies markedly with the identity of dominants, patchiness in the territories of dominants determines a mosaic of ant communities within many tropical forests (Leston 1973, reviewed in Hölldobler and Wilson 1990).

Competitive dominance may be context dependent, e.g., differing in relation to the identities of plant species which form the substrate for ant nesting and foraging (Davidson and Epstein 1989). Thus, host plant associations of *Oecophylla longinoda* (Latr.) (Dejean and Dijcto 1990) and *Tetramorium aculeatum* (Mayr) (Dejean et al. 1992), two widespread dominants in African forests, are correlated with worker preferences for foliage types offered in laboratory experiments.

Weak Competitors.—For competitively subordinate ants, the benefits of combining nesting and foraging locations are conditional on locating nests and resources in sites which are protected from invasion by dominants. Nests in dead or live twigs, stems, and larval insect borings can be defended if the cavity size is not much larger than the head diameters of workers, soldiers, or queens. By sealing a stem nest with her head, a single worker can protect her whole colony or colony fragment from invasion by enemy ants. Thus, along a Pacific Ocean beach at Corcovado National Park in Costa Rica, the many dead twigs of *Coccoloba* (Polygonaceae) trees were occupied by more than nine ant species (six of *Pseudomyrmex* alone), whose head widths were roughly equal and proportional to the internal diameters of their twig cavities (D. Davidson, personal observation). At least some African *Tetraponera* also appear not to nest in stems whose diameter exceeds a threshold value (Terron 1970). For small-bodied ants like the timid *Wasmannia scrobifera* Kempf in Costa Rica, other protected sites may include carton shelters beneath leaves of plants whose dense stem trichomes exclude larger bodied workers (see below).

For comparatively docile and subordinate ants, the advantage of locating their resources inside stem cavities is clear. The evolutionary transition from nesting in dead twigs to nesting in live twigs and other cavities of live plants conveyed the additional opportunity to obtain uncontested resources from phloem-feeding Homoptera (especially Coccoidea), which either invaded such cavities on their own or were brought there by the ants. Moreover, nests in live wood were potentially habitable over much longer time periods than those in dead or decaying twigs and branches, obviating a need for frequent and dangerous nest moves. Longer tenure of living nest sites, which grew rather than decaying with time, may secondarily have allowed the evolution of larger colony sizes and increased opportunities for local monopolization of resources, as well as the selective advantage of aggressive behavior and allelochemicals. Traits conferring a capacity to nest in live plants are not well studied, but they probably involve evolutionary adjustment to an increased threat from nest pathogens. Thus, Ward (1991) points out the tendency for hypertro-

phy of metapleural glands in domatia-inhabiting pseudomyrmecines. Where studied, the function of metapleural secretions has been tied to the suppression of microbial pathogens (e.g., Maschwitz 1974, Hölldobler and Engel-Siegel 1984).

In summary, plant-ants are most frequent in taxa which depend directly or indirectly, but substantially, on plant resources. They are most likely to have evolved in competitively subordinate ants, selected to live in close proximity to food resources, but to nest and feed in comparatively protected and permanent sites which reduce dangerous contact with competitive dominants. Within this subset of ant taxa, selection for evolutionary specialization of plant-ants might have been less likely in groups where potent defensive exocrine compounds (e.g., many *Dolichoderus* species), and worker armor or specialized diets (e.g., cephalotines) diminished the hazards of encounters with dominants.

The transition from more generalized ancestors to specialized plant-ants would not have been difficult. Founding queens should have evolved greater efficiencies in locating hosts that provided superior food or housing or were more easily accessed. By consuming or deterring insect herbivores, ants might then have enhanced their own fitness indirectly by promoting the vigor or prolonging the lifespans of their hosts. However, host specialization by ants, as well as consumption of eggs and larvae of insect herbivores, could have been favored in ants whether the ants and Homoptera had a net positive or negative effect on these hosts. Longino (1987), for example, discusses the case of *Leptothorax obturator* Wheeler, which nests only in cynipid galls of oaks and probably has no fitness effect on the host tree. Selection pressures on ants and plants should often have been asymmetric, leading to the expectation that ant-attractive traits would have evolved in only a subset of the host plants on which obligate plant-ants reside.

Expectations based on this brief review of competitive interactions among arboreal ant species can now be compared with actual patterns in the distribution and ecology of specialized plant-ants.

THE MATCHING OF ANTS AND PLANTS

Appendix 1 is a worldwide summary of all symbiotic ant-plant relationships known to us. To facilitate comparisons among ants of differing lifestyles and competitive abilities (see below), we organize the data by ant genus. Also evident in this summary is the basic asymmetry in the degree to which relationships are obligate for ants versus plants. The vast majority of the ants in the table are thought to be obligate plant-ants (column 7, though these are not necessarily host-specific). However, a substantial fraction of their host genera have no obvious myrmecophytic traits (column 6), despite their regular association with specialized (usually) or unspecialized ants (cf., African *Musanga* and Neotropical *Tetrathylacium*). Few plants with conspicuous myrmecophytic traits (e.g., obvious domatia, or naturally hollow stems with prostomas) lack specialized plant-ants altogether, though some may occur principally with unspecialized ants in marginal habitats, or at the edges of their distributions (see below).

Almost certainly, Appendix 1 includes a mix of relationships in which ants are parasitic, commensalistic, or mutualistic with their hosts, and the net outcome of the interactions might even vary with habitat or ecological context. These outcomes are not wholly predictable from myrmecophytic traits, since even in mutualistic associations, plants need have no obvious specializations to attract ants. Clearly most of the relationships are poorly known, and many of the table entries are incomplete. Yet the table clarifies the types of data which will eventually be essential to describe pattern in these relationships, and we hope it will stimulate the collection of such data in future studies.

Despite limited data, patterns in relationships of ants and host plants correspond roughly to those noted for tropical forest ant faunas as a whole. Across genera, the fastest growing myrmecophytes of disturbed forest edge (i.e., hosts with rapid rates of resource supply to ants) tend to be inhabited by ants from aggressive, dominant, carton-building genera (column 1), e.g., the *Azteca* of neotropical *Cecropia*, and *Crematogaster* of ecologically similar Old World (especially Asian) *Macaranga*. Less aggressive and competitively subordinate ant spe-

cies tend to persist by employing one or more of several strategies likely to reduce interactions with the dominants. We deal with each of these in turn.

Ant Pruning of Host-plant Neighbors

The most common and significant natural enemies of ants are other ants (Haskins 1939). Species with sting defenses, usually inferior to chemical defenses in contests among ants, are disproportionately likely to attack and prune vegetation surrounding their hosts (Davidson et al. 1988, also column 4, Appendix 1). In both Africa and South America, this behavior is most widespread in pseudomyrmecine plant-ants, where pruning has evolved multiple times in independent lineages (Ward 1990). The potent stings of pseudomyrmecines may be an effective deterrent of vertebrates (Janzen 1972), but they are inferior to chemical defenses in repelling colonies of invading ants. Although the *Pseudomyrmex* of *Triplaris* and *Acacia*, and the *Tetraponera* of *Barteria*, do not forage extensively off their host plants, they regularly leave these hosts to sever the petioles of leaves on neighboring plants (Fig. 3). Eventually these neighbors die, leaving the host trees in starkly defined clearings within the forest.

Such clearings have been hypothesized to reward resident colonies by enhancing host-plant vigor or, in drier environments, acting as natural fire breaks (Janzen 1967a). However, experimental evidence suggests that a more immediate selective advantage for attacks on neighboring vegetation is the reduction of threats from more dominant arboreal ants. When permanent wire bridges were made between myrmecophytic *Triplaris* and neighboring trees, the frequency of invasions by dominant *Crematogaster* increased, and whole hosts or portions of these hosts were eventually usurped by *Crematogaster* or *Azteca* species (Davidson et al. 1988). The broad taxonomic distribution of obligate and facultative pruning behavior (the latter occurring only in the presence of enemy ants, Appendix 1, column 4) suggests that dominant competing and predatory ants constitute a major threat to many or most specialized plant-ants. Its prominence in neotropical ants is evidence against the hypothesis that a paucity of dominants charac-

terizes that region (Carroll 1979, see also McKey and Davidson, in press). Presumably, pruning behavior could also serve to defend resident colonies against invasions by leafcutter (Morawetz et al. 1992) and legionary ants, which could devastate the resource base or the colony itself.

Pruning behavior is not strictly limited to ants with functional stings (Appendix 1). Most neotropical *Cecropia* and Old World *Macaranga* and *Endospermum* establish in disturbed second growth vegetation, where vines are particularly abundant and troublesome to both plants and ants, and where weedy dominant ants are a constant threat (Benson 1985). Not surprisingly, the common ant associates of these host genera (*Azteca*, *Crematogaster* and *Camponotus*, respectively) will attack encircling vines (Appendix 1, Janzen 1969, Fiala et al. 1989; Davidson personal observation, Letourneau et al. 1993), though pruning is not typical for these genera as a whole. The comparatively unbranched growth forms of these hosts may also help to limit contact with vines and neighboring plants (Putz and Holbrook 1988) and, therefore, with enemy ants (Benson 1985). In contrast to chemically defended ants, in which pruning is restricted to species inhabiting hosts of secondary forest, species defended principally by strong or weak stings (*Pachycondyla*, *Tetraponera*, *Pseudomyrmex*, and *Allomerus*) also tend to prune around hosts in primary forests, where threats from vines and dominant ants are not so severe. Not all plant-ants in these genera prune, but some species benefit from other forms of protection (see below).

Worldwide, the most dramatic case of allelopathy by ants may be that of *Myrmelachista* (Formicinae) species inhabiting myrmecophytes in the intriguing western Amazonian "Supay chacras" (Quechua for "Gardens of the Devil"). Dominance of lowland forest stands (to > 10,000 m² in size) by multiple species of myrmecophytes, most prominently *Duroia hirsuta* [Poepfig and Endl.] K. Schum., but also *Cordia nodosa* Lam. and *Miconia nervosa* Triana, suggests that the ants kill non-myrmecophytes selectively (Campbell et al. 1989). In a similar phenomenon, at somewhat higher elevations of western Amazonia (700-1200 m), a different *Myrmelachista* species creates monospecific stands of myrmecophytic *Tococa occidentalis*

Naudin (Morawetz et al. 1992). The two congeneric ants share a similar behavioral ecology (D. Davidson, personal observation, for supay chacras, and Morawetz et al. 1992, for *Tococa*). Workers do not appear to forage off their hosts, but do leave their hosts to attack other plants. When seedlings or saplings of plants other than the host species are placed in the vicinities of these hosts, workers gnaw at the vascular bundles of leaves of the introduced plants, and can kill them in a matter of hours to days. Morawetz and colleagues describe the extraordinary capacity of these ants to single out especially vulnerable plant tissues for attack. Thus, workers bite and poison palmate leaves at the base of laminae, where all vascular bundles join, pinnately nerved leaves at nerve bases of the first and second order, and monocots (e.g., palms), nerve by nerve, along the entire leaf. Necrosis originating at the attack sites spreads rapidly over the entire lamina. Within a few hours to a few days, inhabitants of the *Tococa* can successfully kill seedlings and saplings within a radius of 4 m and damage trees up to 10 m in size. Light gaps created by ant activities are subsequently colonized by vegetative propagation of the host.

Although Morawetz and colleagues discount the hypothesis that the killing of host plant neighbors by *Myrmelachista* has evolved principally to exclude enemy ants, several observations suggest that the hypothesis should not be ruled out. First, leaf-cutter ants, an important enemy of the *Tococa*, invade principally by contact with the branches of other plants, not via the main trunk. Second, no generalized arboricolous ants appear to forage within the territories of these specialized *Myrmelachista*. Furthermore, large worker forces may be needed to assure the safety of ants which have left their hosts. Attacks on neighbors of *Tococa* begin when the ant population of one or a few individual hosts is at least 1500 workers in size. Similarly within supay chacras, smaller fragments of the extended colonies show extreme fidelity to their individual hosts, and only workers of the largest trees leave their hosts to swarm over seedlings and other vegetation. Moreover, the latter activities appear to be restricted to hot and sunny conditions (D. Davidson, personal observation), which may allow maximum worker activity and performance levels. To date,



Fig. 3. *Pseudomyrmex dendroicus* Forel on branches of neighboring plants, whose leaves have been pruned by the ants. The long, thin body shape of workers in *Pseudomyrmex* spp. may preclude their use of plants with long, dense trichomes.

there have been no experimental tests of the effects of creating artificial and unseverable bridges between neighboring intact trees and hosts of these *Myrmelachista*. Such experiments would greatly aid in assessing the evolutionary significance of the extraordinary behavior of these ants.

Hiding among Trichomes

The long, dense and erect trichomes on stems and domatia of many myrmecophytic plants form mechanical barriers to the movements of large-bodied ants and create safe havens for colonies of obligate plant-ants with timid and diminutive workers (Davidson et al. 1989; Fig. 4, Appendix 1). Ant-plants with inhibitory hairs on stems, domatia or both, occur in at least 18 neotropical genera (eight within Melastomataceae alone), and eight families, and appear to have evolved independently on at least 21 separate occasions (Table 1). In Africa, such hairy ant-plants occur in at least eight genera and six families, with each generic occurrence representing a single independent origin. Trichome-

myrmecophytes have also evolved in at least four genera in the Oriental and Australian tropics (Table 1), though the symbiotic associates of these plants remain unknown. In many or most genera of hairy ant-plants, long, erect pubescence also occurs in non-myrmecophytic congeners. It therefore seems likely that docile, small-bodied ants initially sought safe nesting and foraging sites on hairy plants prior to the evolution of myrmecophytism in these lineages. A possible contemporary example of such a relationship is that between *Wasmannia scrobifera* and a non-myrmecophytic hairy *Piper* species in Costa Rica (D. Davidson, personal observation). These ants build small fragile carton nests on abaxial leaf surfaces, where they feed on pearl bodies. Nests are not limited to individual host plants, nor are the ants likely to be obligate plant-ants. In some cases, ant dependency on plant trichomes may be restricted to the early stages of colony foundation. Thus, certain *Azteca* species regularly initiate colonies on pubescent ant-plants like *Cordia* and *Tococa* but later prune runways through host-plant trichomes and form carton satellite nests on neighboring trees lacking protective trichomes ("i" in col-



Fig. 4. Tiny *Pheidole minutula* Mayr workers travel easily among the erect trichomes of this myrmecophytic *Clidemia*. Numerous ant species with tiny workers use such "trichome myrmecophytes" as protected feeding and nesting sites, where they are safe from larger-bodied competitors and predators.

umn 4 of Appendix 1; D. Davidson, personal observation, Benson 1985).

Contemporary distributions of ants across myrmecophytes in Africa and the Neotropics illustrate the influence of plant trichomes on the match between ants and plants (Appendix 1). First, in both regions, worker ants of pubescent myrmecophytes are short-bodied (<3 mm), with short turning radii, and do not include longer-bodied pseudomyrmecines. Included here are two neotropical genera with functional stings (*Allomerus* and *Solenopsis*), and docile African dolichoderines in the genus *Technomyrmex* (species formerly placed in *Engramma*, Shattuck, 1992a). All known hosts of *Allomerus* and *Solenopsis* possess long erect pubescence. *Allomerus* is particularly conspicuous in its association with a diversity of pubescent host genera, seven in total. Of the recorded hosts of African *Technomyrmex*, species in five (and possibly six) of eight genera are hairy; only two, *Leonardoxa* and *Ixora hippoporifera*, definitely lack trichomes. To the extent that members of competitively dominant ant genera depend on pu-

bescent ant-plants beyond the incipient colony stage, the particular species represented in these associations are unusually timid for their genera (e.g., the *Crematogaster* cf. *victima* group on melastomes, the tiny *Crematogaster* sp. on *Delpyodora*, and the *Azteca* species inhabiting hairy *Triplaris poeppigiana* Weddell). Second, the body sizes of plant-ants tend to be correlated with trichome spacing (Davidson et al. 1989). This suggests that ancestral ants may have nested preferentially not only on pubescent plants but specifically on those where mean distances between trichomes were no larger than required by their own body sizes. The parallels with nest selection by stem-diameter in generalized stem-nesting ants are obvious (see above).

Third, if ants compete for host plants (see Davidson et al. 1989), and if small, timid species persist only where protected by trichomes from larger dominants (>3 mm, e.g., *Crematogaster* and *Azteca*), then the dominants should prevail on myrmecophytes lacking inhibitory trichomes. This hypothesis is supported not only across ant-plant

genera (Appendix 1), but within several genera which are interspecifically variable in pubescence. In neotropical *Cordia*, for example, glabrous *C. alliodora* (R. and P.) Oken is regularly occupied by aggressive *Azteca*, but smaller and more timid *Allomerus* ants inhabit densely hairy *C. nodosa*. As noted above, a small-bodied and timid *Azteca* species inhabits the hirsute stems of *Triplaris poeppigiana*, though the vast majority of myrmecophytic *Triplaris* species are glabrous and occupied by long and narrow-bodied pseudomyrmecines. Third, dominant *Crematogaster* ants occupy glabrous African *Canthium*, whereas hairy congeneric hosts are associated with timid *Technomyrmex* species (Bequaert 1922, pp. 474-475). The same may perhaps be true in African *Cuviera*, which contains both glabrous and hirsute myrmecophytes. Both *Technomyrmex* and *Crematogaster* are recorded as associates of ant-plants in this genus, but the distribution of different ants in relation to plant pubescence cannot be discerned from existing literature. Finally, as noted above, some ants 3 mm in body length occasionally occupy trichome myrmecophytes but regularly prune trail systems, which facilitate their movements (Davidson et al. 1989).

Association of *Camponotus* ants with spiny palms in the genus *Korthalsia* may also have had its origins in the tendency of ants to feed and nest where the plant's growing tips are protected from the ants' natural enemies. Among the 12 *Korthalsia* species which Dransfield (1984) lists for Sabah, Malaysia, seven have armed ocrea and five do not. Of the species with spiny ocrea, all but *K. ferox* Becc. also show regular associations with ants, whereas this is true for none of the species with unarmed ocrea. Both the long, sharp and comparatively dense spines of species *K. echinometra* Becc., *K. hispida* Becc. and *K. robusta* Blume, and the scattered, short, triangular spines of *K. cheb* Becc., *K. furtadoana* J. Dransf. and *K. rostrata* Blume are more likely to protect the ants from vertebrate predators than from other ants. Dransfield (1981) found greater herbivory by vertebrates (perhaps squirrels) on growing tips of *K. rigida* Blume (with unarmed ocrea and sparsely armed leaf sheaths) than on those of *K. echinometra* and *K. rostrata*. Although he attributed this result to protection that

ants might afford to the latter species, an alternative hypothesis is that both the plants' growing tips and the ant nests benefit from the armature of ocrea and leaf sheaths. This would not rule out some additional benefit to the plant from its ants. Unfortunately, phylogenetic relationships remain undefined for both plants and ants, and it is not yet possible to determine the extent to which the various relationships between ants and armed *Korthalsia* evolved independently. However, Dransfield's (1981) observation that *Calamus* species of New Guinea and the Philippines show parallel evolution of armed ocrea and relationships with ants suggests that myrmecophytism could have evolved more than once within *Korthalsia* as well. Similarly, myrmecophytic rattans in the genera *Calamus* and *Daemonorops* exhibit parallel evolution of ant galleries formed by interlocking combs of spines, forming collars on the leaf sheaths (Dransfield and Manokaran 1978).

Rates of Resource Supply from Plants

The impact of rates of resource supply on the match between ants and plants is best compared within host genera, holding food type approximately constant. Within western Amazonia, for example, the rate of food body production by *Cecropia* varies across both species and habitat types (Davidson et al. 1991, Davidson and Fisher 1991, Folgarait and Davidson 1992). Faced with competition from fast-growing pioneer species of similar stature, more light-demanding species of large riverine disturbances defer costly defense in favor of rapid growth. Because comparatively shade-tolerant species of small forest light gaps experience light competition from much larger neighbors, diversion of limiting carbon from defense to growth might confer little benefit, and even jeopardize the persistence required to take advantage of later canopy openings. Thus, the more shade-tolerant *Cecropia* species produce swollen stems, prostomas, and trichilia much earlier in development than do their light-demanding close relatives (Fig. 5), as well as producing a greater dry weight of Müllerian bodies per unit leaf area. Despite this greater investment (proportional to the plant's resource budget) in biotic defenses by small gap *Cecropia*,

there are at least three reasons why the absolute rates of food provisioning to ants are greater in light-demanding pioneers than in closely related but more shade-tolerant gap species. First, and perhaps foremost, the smaller sizes of forest gap species at the time of colonization by ants are associated with fewer leaves (sources of food rewards) and slower plant growth rates. Second, even with plant size or light environment held constant, small gap *Cecropia* have intrinsically slower growth and leaf production rates than do their more light-demanding counterparts. Finally, comparatively low light intensities in their typical habitats further limit the capacity of the forest gap plants to produce ant rewards.

Ants appear to respond to these quantitative differences in food production rates of *Cecropia* (Davidson et al. 1991, Davidson and Fisher 1991). For example, in southeastern Peru, patterns of ant associations are more closely tied to habitats than to host identities. Although the closest taxonomic relationships appear to be between *Cecropia* in different habitats (C. C. Berg, personal communication), *Azteca ovaticeps* Forel inhabits only intrinsically fast-growing pioneers of riverine and stream-side habitats. In contrast, specialized *Camponotus*, *Pachycondyla* and *Crematogaster* species, and *Azteca australis* Wheeler are the typical residents of relatively slow-growing and congeneric hosts of small light gaps. Although the latter ants frequently colonize riverine *Cecropia*, they seldom establish colonies there, and they may usually be outcompeted by rapidly developing colonies of *A. ovaticeps*. This pattern holds both within and across host species, and it suggests that ant species may coexist locally by virtue of their "included niches". Species with rapidly growing colonies may dominate higher quality hosts, but be unable to tolerate low rates of resource supply. On the other hand, ants with relatively slow-growing colonies tolerate both high and low quality resources, but are usually excluded by competitors from fast-growing hosts.

A similar pattern of niche differentiation is apparent within plant-ant guilds of other myrmecophyte taxa (including epiphytes) of both the New and Old World (Davidson and Epstein 1989, Davidson et al. 1989 and 1991). For example, specialized *Tetraponera* are the typical resi-

dents of *Barteria fistulosa* Masters growing in small forest treefall gaps, but *Crematogaster* dominate in large clearings (D. McKey, personal observation). In *Barteria nigritana* J. D. Hooker, mostly restricted to light-rich coastal shrub vegetation, *Crematogaster* is the only recorded associate. In *Leonardoxa africana* Aubrév., *Petalomyrmex* is the typical associate of adult trees, and of a large proportion of juveniles. However, juveniles growing in deeply shaded sites are usually occupied by *Catantlus* (McKey 1984). The effects of insolation on resource quality can also be apparent within host species, as in the observation that *Polyrachis* species specializing on broad-leaved bamboos build their pavilions only in sunny areas of bamboo clumps (Dorow and Maschwitz 1990).

At present, factors underlying interspecific differences in the resource demands of ants are poorly studied. However, just as the evolutionary diversification of plants has been influenced by tradeoffs in allocation and life history strategies (e.g., Grime 1974), similar tradeoffs are likely to have contributed to a proliferation of divergent ecological tactics in plant-ants (and ants in general, Tschinkel 1991, A. N. Anderson 1991). Included among these life histories may be: 1) opportunistic (ruderal) species with rapid colony growth rates, high worker turnover, high resource demands, small (or moderate) colony sizes with correspondingly weak colony defense, short colony lifespans, and early reproduction; 2) "tolerant" species with slow-growing colonies, low worker turnover, low resource demands, high longevity, deferred reproduction, and effective defense of the nest site, and 3) competitive species with rapid colony expansion, low worker turnover, and large, long-lived, aggressively territorial and well-defended colonies. The evolution of such divergent ecological strategies is likely to have been influenced also by phylogenetic constraints, such as preexisting uses of exocrine glands (Blum and Hermann 1978, Buschinger and Maschwitz 1984), or the form of the proventriculus, which controls the capacity for and efficiency of liquid food storage and transport (Eisner 1957). Such phylogenetic constraints might help to explain why the competitive rankings and strategies of ants are often well-defined (though not perfectly so) at the generic level.



Fig. 5. Tiny seedling of *Cecropia tessmannii*, whose myrmecophytic traits appear approximately with the fifth through seventh leaves past the cotyledon stage, and when plants are < 10 cm tall. Because of its extreme morphological similarity to *C. membranacea*, *C. (prov.) tessmannii* is still technically lumped with that species (C. C. Berg, personal communication). However, *C. membranacea*, a pioneer of large, riverine disturbances, grows more rapidly and acquires its myrmecophytic traits at substantially and significantly later leaf nodes (Davidson and Fisher 1991).

Other Traits of Weakly Competitive Ants

Appendix I reveals numerous exceptions whereby the generic affiliations of ants are imperfect predictors of subordinate or dominant status, as reflected by pruning behavior and association with trichome myrmecophytes or uncontested host plants. Nevertheless, some of these exceptions are consistent with the general principles developed here. For example, despite their chemical defenses, ants in some subgenera of *Camponotus* (especially *Colobopsis* and *Pseudocolobopsis*) can behave as subordinates, living secretive lives inside their hollow stem nests. Yet *Camponotus* of this description occur on a diversity of hosts that lack protective trichomes and, with one exception, they do not prune or attack vegetation around their hosts. At least two factors may explain the capacity of these species to persist on their hosts. First, major workers use their large and often modified heads to seal

stem entrances effectively and to protect nests from invaders. Where ants obtain the majority of their resources from Coccoidea inside stems or domatia (e.g., under ocrea of *Korthalsia*), foraging occurs in seclusion and entails little risk. (A similar explanation may apply to the timid *Pheidole* colonies from myrmecophytic pipers and melastomes, which supply food bodies inside domatia.)

On the other hand, the extrafloral nectar of *Endospermum* and the Müllerian bodies of *Cecropia*, are produced on external plant surfaces. Here, the exclusivity of ant resources is protected in part by the temporary nature or temporal pattern of their production. For example, in the northern coastal forests of Papua New Guinea, *Endospermum labios* Schodde produces almost all of its extrafloral nectar in a brief pulse at about 3:00 AM, likely coinciding with the diel maximum in relative humidity there (Fig. 6). In contrast to myrmecophytic *E. labios*, a myrmecophilic congener, *Endospermum medullosum* L.S. Smith produces a greater fraction

of its nectar during other periods of the diel cycle (D. Davidson, unpublished). Although many *Cecropia* species release Müllerian bodies slowly all day long, they also flush large numbers of these bodies just after nightfall (Davidson and Fisher 1991). Moreover, ants with generalized diets are usually not attracted to the bodies (Rickson 1977, D. Davidson, personal observation). *Camponotus* associates of *Endospermum* and *Cecropia* both forage on leaf surfaces principally at night, and workers of *Anoplolepis* (not a plant-ant) can range freely over *Endospermum* during daylight hours (D. Davidson, personal observation). (See also A. N. Anderson's [1991] discussion of nocturnality in Australian *Camponotus*.) *Cladomyrma* of *Neonauclea* are nocturnal as well (D. Davidson, personal observation), though the object of worker foraging on *Neonauclea* has yet to be identified. Finally, some plant-ants in the genera *Myrmelachista* and *Allomerus* are apparently restricted to their hosts diurnally, but make nocturnal forays to the forest floor (J. Longino, personal communication). Together, these observations suggest that competition may be reduced somewhat at night, though the nature of any restrictions on nocturnal activity in dominants is not readily apparent. While activity schedules of temperate and arid zone ants are strongly related to diel variation in temperature and humidity regimes, biotic selection pressures could be equally important or more important determinants of foraging times in ants of moist tropical forests.

ANCESTRAL VERSUS MODERN RELATIONSHIPS

We have argued that the matching of ants and myrmecophytic plants is convergently alike in different tropical regions, and that this convergence arises from the presence of similarly preadapted plants and ants within the respective biotas. In concentrating on the associations as they exist today, we have neglected the pathways by which they may have reached their present form. Ant-plant symbioses have undoubtedly evolved from more casual and opportunistic relationships between plants and ants. In their initial phases, many of these associations would likely have resembled

modern-day relationships in which plants lack obvious specializations for housing ants (Appendix I, "N" in column 6). Like most other forms of mutualism (reviewed in Thompson 1982), many symbiotic ant-plant mutualisms probably began as parasitisms. What factors may have facilitated the transition from parasitism to mutualism, and what character transformations could have accompanied this change?

For plants hosting ants inside primary domatia (live stems and internodes), ancestral relationships probably consisted of ants tending scale insects within natural plant cavities or in insect borings (cf., Ward 1991). From the start, ants must have benefitted from access to exclusive resources in these protected environments. However, to have remained entirely in the sanctity of the host plant, ants would have needed a well-balanced diet. Homopteran exudates contain not only carbohydrates, but some amino acids and lipids (reviewed in Buckley 1987), and ant colonies are known to harvest and eat Homoptera to meet their protein requirements (e.g., Way 1954, Pontin 1978). Furthermore, in both New and Old World tropics, as well as in Australasia, some plant-ants have evolved means of obtaining added protein and fats from elaborated calluses or heteroplasias caused by traumatic injury to either the inside (*Tetraponera* on African *Vitex*, Bequaert 1922) or outside of host plant stems (South American *Pseudomyrmex* on *Triplaris*, and New Guinea *Camponotus* on *Endospermum* [D. Davidson, personal observation], and possibly Central American *Myrmelachista* on *Ocotea* [J. Longino, personal communication]). In large part then, coccoid-tending residents of live stems and cavities could probably have depended on hosts to satisfy most or all of their nutritional needs, even from the earliest stages of their relationships with these plants.

In contrast, the impact of symbiotic ants on their host plants would have depended on the balance struck between resource losses to scale insects and ants, and any anti-herbivore protection the ants may have originally afforded. Although the majority of ants would probably have provided at least some protection against stem and leaf parasites, the Coccoidea would surely have been a liability. Substantial carbohydrate losses sustained by the



Fig. 6. This large drop of extrafloral nectar was produced in a brief pulse at 3:00 AM on the petiolar nectaries of *Endospermum labios*, at the Christensen Research Station near Madang in Papua New Guinea. (Screenhouse plant courtesy of M. Jebb.)

plants should have been most debilitating to carbon-limited (light-limited) plants. Thus, in habitats of low light intensity, natural selection on plants may have acted mainly to exclude both ants and Homoptera. However, where light was abundant, the benefits of ant defense could have outweighed carbohydrate losses (on average). Natural selection on these plants should have favored attraction of ants, rather than resistance to them. In this way, the propensity of ant-parasitized plants to evolve toward myrmecophytism could have been facilitated by high availability of carbon (light) in relation to limiting mineral nutrients, and impeded when such ratios were low. Furthermore, if herbivore pressures are generally more intense in comparatively productive, sunny environments (see Davidson and Fisher [1991] for *Cecropia*), this trend could have reinforced selection for ant attraction in such habitats.

Although our data set lacks the resolution to test this hypothesis, the hypothesis is consistent with the central result of Schupp and Feener's (1991) recent survey of the distribution of ant attractants (EFN's and pearl bodies) within the flora of Barro Colorado Island, Panama. While the occurrence of

such rewards was clearly correlated with phylogeny, it also appeared to depend on the light environment. Plant families characteristic of forest light gaps were overrepresented among ant-defended families. (See also the frequency of superscripts "e" and "g" in column 2 of Appendix 1.) Schupp and Feener hypothesized that the high frequency of ant defenses among forest gap plants may be explained by the comparatively low costs of producing carbohydrate ant rewards in these light-rich habitats, as well as by the tendency for relatively continuous growth and leaf production in gap species. The latter explanation meshes well with McKey's (1989) interpretation of biotic defenses as an alternative to phenological escape from herbivory (i.e., escape from detection, due to variable and unpredictable new leaf production). Phenological escape would be unavailable to plants with continuous leaf production.

There are some indications that the absence of scale insects may be the derived condition in relationships involving pseudomyrmecines (P. Ward, personal communication). Thus, although Coccoidea can be found at the bases of spines on African and Indian *Acacia* housing *Tetraponera*,

Pseudomyrmex-inhabited Central American *Acacia* lack scale insects but supply protein-rich Beltian bodies. Moreover, the gnawing of internal stem walls by *Tetraponera tessmannii* (Stütz) on African *Vitex*, to produce tunnels with terminal nutritional heteroplasias, could have had its origins in the excavation of pits to increase the feeding efficiencies of coccoids, now absent from this system (see Bailey 1922 for *Caviera*).

For plants that continued to be inhabited by ants and scale insects, natural selection would be expected to favor a reduction in the ratio of coccoid to ant biomass. Although many obviously specialized ant-plants still harbor Coccoidea (Appendix 1), there is considerable variation across all the ant-plants in the densities of scale insect populations (D. Davidson, personal observation). At one extreme are the comparatively unspecialized relationships between *Anonychomyrma* (previously *Iridomyrmex* [Shattuck, 1992b]) and *Crematogaster* ants, and a number of pachycaulous understory New Guinea trees. Here, the biomass and density of *Cryptostigma* scales are so great that their populations may well be limited by either plant resources or the availability of feeding sites (D. Davidson, personal observation). In contrast, in its more specialized relationship with *Triplaris americana* L., *Pseudomyrmex dendroicus* Forel maintains only approximately one scale insect per leaf junction, and similarly low coccoid densities are apparent in *Cecropia* stems inhabited by *Azteca ovaticeps* and *A. australis*.

By what proximate mechanisms might plants have responded to selection for reducing losses to Homoptera? For myrmecophilic plants, Becerra and Venable (1989) have argued that EFN production could have arisen as a means of paying ants directly and eliminating parasitic homopteran intermediates. Even if EFN's provided ant rewards comparable to or lower in value than homopteran secretions, reduced resource handling times might have induced ants to feed at nectaries and to abandon their Homoptera. In turn, plants would have benefitted from lower rates of infection with homopteran-mediated diseases and possibly lower resource losses. One difficulty with applying this theory to the evolution of myrmecophytes is that it ignores an important distinction between coccoids

(the usual homopteran associates of plant-ants) and EFN's. While EFN's are relatively promiscuous resources, accessible to many ants, coccoids tended inside cavities can be used exclusively by symbiotic ant associates. If the latter ants are the most effective mutualists of the plant, and provide better protection in the absence of opportunistically foraging competitors, selection may favor loss of EFN's. There is evidence for such a scenario in myrmecophytic Asian *Macaranga*, which, in contrast to their non-myrmecophytic congeners, almost completely lack EFN's (Fiala and Maschwitz 1991).

A second difficulty with the hypothesis of Becerra and Venable (1989) is that it ignores the possibility that colonies might keep pace with the added resources (EFN) through short-term redeployment of workers or long-term growth. If so, ants might continue to tend Homoptera while also feeding from EFN's. A plausible alternative hypothesis is linked to the assumption that growth of ant colonies (like that of plants, Bloom et al. 1985) is limited by the ratio of carbon and nitrogen resources. By rewarding ants with abundant carbohydrate but starving them for protein (Carroll and Janzen 1973), plants might have induced colonies to consume the majority of their Homoptera. In support of this argument, *Oecophylla longinoda* is known to consume more coccoids when given a supplemental sugar source (Way 1954). Moreover, M. Anderson (1991) attributes "switching" between predation and mutualism in ant-homopteran relationships (see also Pontin 1958 and 1978) to changes in the nutritional status of the ant colony. If homopteran populations are regulated in response to ratios of carbon and nitrogen availability to ants, colonies might be expected to maintain their associates at densities which supply these resources at optimal ratios for colony growth. Currently, a lack of data prevents further speculation as to how the relative availability (to ants) of carbohydrate and protein might vary with homopteran densities. Future investigations might profitably focus on natural or experimentally induced variation in the relative biomasses of ants and Homoptera in particular ant-plant systems.

PLANT FITNESS IN RELATION TO ANT SPECIES

In many ecological studies of ant-plant symbioses, investigators have focused principally on the question of whether or not a given ant associate benefits its host species. With recently renewed appreciation for the diversity of ants colonizing individual myrmecophytes comes the realization that ants may differ in the protection afforded their hosts (e.g., Janzen 1975, Oliveira et al. 1987, Rico-Gray and Thien 1989, Davidson et al. 1991, Longino 1991a and b, but see Vasconcelos 1990, for a counterexample), and that associations must be studied in the context of community-wide interactions. While existing data are too meager to correlate protection with specific ant traits, some conjectures are warranted. Rapid colony development, large colony size, and high levels of worker activity should enhance host-plant defense. Large insect herbivores (Coleoptera and Orthoptera) may be best deterred by active, large bodied workers (Davidson and Epstein 1989). In contrast, division of colony biomass among numerous small foragers may promote fine-grained searching and facilitate the detection of small prey, for example, lepidopteran eggs (Letourneau 1983, Vasconcelos 1991). Some authors have suggested that small and timid ants provide little protection against herbivores, but augment the nutrient reserves of their hosts through deposits of feces and refuse (e.g., Janzen 1974b, Beattie 1985). However, at least two studies have confirmed the effectiveness of small, docile *Pheidole* ants in defending against either insect eggs (Letourneau 1983), or herbivorous lepidopteran larvae (Vasconcelos 1991). While nutrient enhancement has been demonstrated convincingly in myrmecophytic epiphytes and palms (Rickson 1979, Rickson and Rickson 1986), tests have disputed the theory for the symbiotic associates of *Macaranga* (Fiala et al. 1989) and *Maieta* (H. Vasconcelos and B. Forsberg, personal communication). On reflection, possibilities for nutrient enhancement are limited by the infrequency of foraging off the host (Appendix 1, column 4) and, consequently, by the inability of ants to concentrate materials from the broader environment.

Two other cases are likely candidates for nutri-

ent augmentation by ants (D. Davidson, personal observation). First, certain *Acteca* species center their carton nests on *Tococa* and *Hirtella* species and contribute to a steady rain of carton and refuse at the base of the host tree trunk. Second, as a rheophyte of stream beds and rocky river beaches, *Myrmecoanuclea strigosa* (Korth.) Merrill grows with its roots anchored in rock crevices. The *Crematogaster* ants, which are its dominant associates in forests west of Lahad Datu, Sabah, pack refuse and feces into domatia at the distal branch tips, from which new swollen internodes arise. The absence of any obvious food reward (including Homoptera) suggests that ants might leave their hosts to forage. If such is the case, workers could concentrate nutrients which enhance fitnesses of hosts growing in extremely nutrient-poor environments.

In some cases, myrmecophytism actually contributes to host-plant damage by destructive vertebrate predators of ant larvae (especially by woodpeckers [Carroll 1983] and monkeys [Freeze 1976, and J. Terborgh, personal communication, for *Cecropia*). Damage by primates may be less common for hosts of ants with powerful stings. First, in Peruvian Amazonia, *Pachycondyla luteola* Roger (the "pungara") is an obligate symbiont of *Cecropia*, and its painful barbed stings reinforce vertebrate learning for a period of seven to ten weeks (D. Davidson, personal observation). Avian preferences for nesting in this (Koeppke 1972) and other myrmecophytes with stinging ants (Young et al., 1990) may be at least partly attributable to the protection which ants afford against primates. Second, the *Tetraponera* of African *Barteria fistulosa* also impressed Janzen (1972) as effective deterrents of vertebrates, and a black colobus monkey avoided ant-occupied *Barteria*, while feeding on an unoccupied individual nearby (McKey 1974). Gray-cheeked mangabey monkeys (*Cercocebus albigena* [Gray]) rip open the branches of this host to prey on *Tetraponera* brood, but only if this can be accomplished by reaching from a perch in a different tree (D. McKey, personal observation). Even large, stinging plant-ants may not affect some vertebrates, however. Gorillas in the Central African Republic feed on *B. fistulosa* leaves and branches apparently undeterred by healthy, active colonies of

Tetraponera (M. Fay, personal communication). Finally, because plant-ants with functional stings also usually prune the vegetation surrounding their hosts, crowns inhabited by such ants are usually sufficiently isolated in forest gaps to avoid the attacks of primates which visit neighboring trees.

TRENDS IN SPECIALIZATION, SPECIFICITY AND COEVOLUTION

Because the evolutionary histories of symbiotic ant-plant systems have been largely independent in biogeographically disjunct tropical regions (McKey and Davidson, in press), intercontinental comparisons may provide general insights into the evolutionary dynamics of such systems. In this section, we discuss evolutionary interactions between ants and plants, focusing on three questions: (1) Has specialization of ants and plants followed similar evolutionary pathways due to parallel and/or convergent evolution in organisms from different continents? (2) Have evolutionary interactions between ants and plants contributed to the generation of diversity in plant-ants and ant-plants? (3) If so, are these interactions a partial cause of intercontinental differences in diversity of ant-plants and plant-ants? Again we focus mainly on the American and African tropics, whose ant-plant associations are best known.

The Nature and Causes of Specificity

Symbiotic ant-plant systems are in general more species-specific than are nonsymbiotic ant-plant interactions (e.g., Schemske 1983). All tropical regions contain examples of ant-plants that are obligately associated with one or a small number of plant-ant species, which in turn have comparably restricted host-plant ranges. In such cases, specificity is doubtless a product of intense evolutionary interaction. However, much of the seeming specificity in ant-plant symbioses may be maintained by ecological processes that require no evolutionary specialization in ant or plant. We have argued that characteristic and repeatedly observed plant-ant matches are the result of species sorting (Jordano 1987) of plants and ants which are mutually pre-adapted in many attributes related to the interaction (Davidson et al. 1989 and 1991, Davidson and

Fisher 1991). Driven by the strong competitive interactions that structure communities of arboricolous ants, the matching of plants and ants is determined by plant and ant traits which modify ant access to plant resources.

In a growing number of ant-plant systems, we now recognize that seemingly specialized plant-ants may be capable of living on any of several hosts, and that many or most myrmecophytes can persist in association with any of several plant-ants. Nevertheless, some relationships are more frequent and/or more durable than others. Understanding the ecological processes which reduce broad potential niches of plant-ants and ant-plants to narrower realized niches is a prerequisite to an evolutionary investigation of such systems (Davidson and Fisher 1991). First, ecological studies suggest simpler alternatives which must be excluded before hypotheses of evolutionary specialization and coevolution can be entertained. Second, if ecological causes of specificity can be defined, these will suggest the likely selective environments in which any evolutionary specialization may have taken place. Third, studies of unusual associations may give clues about the origin of both host-plant specificity and host switches, which seem to have taken place frequently in symbiotic ant-plant systems (Ward 1991).

Evolutionary Specialization of Ants and Plants

If competitive interactions among ants are sufficiently strong and constant, ecological sorting will produce predictable patterns of ant-plant associations and a selective environment conducive to evolutionary specialization (Schemske 1983). Evidence from various tropical regions suggests that evolutionary specialization of ant-plants and plant-ants may have been driven largely by competition among ant species. Even strong pairwise ant-plant mutualisms, it appears, owe many of their traits to an evolutionary background of multispecies antagonistic interactions. Whether these character states were evolved in the context of the symbioses, or merely fine-tuned from pre-existing traits, often cannot be argued confidently from existing data. Nevertheless, many traits of both plant-ants and their hosts may have been elaborated because of

their selective value in the context of symbiotic association.

Ants.—Because ants actively choose their hosts, selection should strongly favor specializations for rapid and efficient host location by queens. In addition to minimizing exposure to predation and other environmental hazards, such adaptations could help to assure priority of access to contested resources. Indeed, competitively inferior ants might even usurp the hosts of more dominant species by evolving rapid means of finding and entering these plants. First, almost nothing is known about the kinds of information that queens employ to locate suitable hosts, but a variety of chemical, visual and other cues may be used at different stages of host identification. Whatever the mechanisms of host identification, the abilities of queens to locate and colonize specific hosts, and their absence from other hosts and habitats (Davidson et al. 1989, Fiala and Maschwitz 1990, Morawetz et al. 1992), provide some of the strongest evidence of evolutionary specialization to the symbiosis. Second, the extreme dorsiventral flattening of the head, thorax and abdomen of *Petalomyrmex* queens could have arisen due to selection for rapid entry of myrmecophytes in the face of intraspecific and interspecific competition for hosts (McKey 1991). Alternatively, however, specialized queen shapes might have evolved first in generalized stem-nesting ants (Longino 1989b), preadapting such ants to become specialized plant-ants. Without additional phylogenetic analysis, adaptations in body shapes remain indistinguishable from preadaptations.

Once foundresses have safely entered a host, their success on plants of different growth rate, maximum size, or lifespan, will likely depend on key energetic, demographic, and life history features of the colony. Intrinsically rapid rates of egg production and development of incipient colonies could be favored on fast-growing plants, and pleometrosis might substitute for this in at least some ant species (Davidson et al. 1991). However, before evolutionary specialization can be inferred from an apparent matching of colony attributes and plant growth rates, careful phylogenetic analysis must exclude the alternative hypothesis that ant traits evolved prior to the origin of the symbiosis. In the case of the *Azteca* and *Cecropia*, this caution is

reinforced by the likelihood that *A. ovaticeps* and its relative *A. alfari*, may have originated from a weedy species which was typical of second growth vegetation (Longino 1991b), and whose life histories could have preadapted it for occupation of relatively fast-growing hosts of riverine succession. In contrast, *A. australis* and its relative *A. xanthochroa* Roger, are probably derived from carton-building ancestors (Longino 1991b), whose comparatively permanent homes may have predisposed them to evolve life history traits typical of modern-day descendants on slower-growing and, in most cases, longer-lived, forest gap *Cecropia*.

Many or most specialized plant-ants appear to have been relatively weak competitors, in which aggressive behavior could well have been maladaptive. Nevertheless, within the limited spheres of their host plants, a number of these ants appear to have evolved greater similarity to dominants, defending absolute territories defined by the boundaries of individual trees. Thus, one scenario apparent in several plant-ant lineages is that of increased colony size and aggression in response to symbiotic association with myrmecophytes (e.g., Janzen 1966). For example, the extended colonies of *Myrmelachista* ants on pure stands of *Tococa occidentalis* (see above) reach an estimated worker population 1-2 million ants (Morawetz et al. 1992). Moreover, on Peruvian *Cecropia*, *Pachycondyla luteola* exhibits the largest and most aggressive colonies achieved by any ponerine ant. Host trees >30 m tall literally seeth with aggressive, stinging workers, and populations almost certainly range into tens or hundreds of thousands of workers (D. Davidson, personal observation). Even if rigorous phylogenetic analysis confirms that closest relatives of these ants have much smaller and less aggressive colonies (as do *Pachycondyla* sp. nov. on Panamanian *Cecropia hispidissima* Cuatrecasas, Davidson and Fisher 1991), ecological studies will be necessary to determine whether the purportedly evolved demographic responses of *P. luteola* are examples of evolutionary accommodation or only plasticity in colony structure. For colonies nesting and feeding in the comparative security of myrmecophytes, increasing worker life spans, and nest sites which grow, rather than decaying (like dead twigs), could lead automatically to larger

worker populations, and greater aggression might follow as a behavioral response to colony size. Similarly, the polygyny and/or pleometrosis noted as typical or occasional in some purportedly highly specialized plant-ants (Janzen 1966 and 1973, McKey 1984, Davidson and Epstein 1989, Longino 1989b, Vasconcelos in press) may be a plastic response to resource availability or competition, since queen number can vary similarly in other ant species (Ward 1989b, Hölldobler and Wilson 1990). Although queens of *Azteca australis* found their colonies individually on isolated hosts in small light gaps, they often cooperate to initiate colonies on the faster growing plants of riverine disturbances, where both rates of food supply and competition from other incipient colonies are greater (Davidson et al. 1991). At present it is unclear whether pleometrosis in the latter environment arises from evolutionary adaptation to competition or merely from greater numbers of alates produced and available in that habitat.

Pruning of vines and other vegetation in the vicinities of hosts is one trait which provides less ambiguous evidence for evolutionary accommodation to competition for hosts. Facultative pruning, requiring the presence of enemy ants, may eventually prove to be widespread among unspecialized close relatives of obligate plant-ants. However, both obligate pruning, and the maintenance of vegetation-free zones at the host-plant base, appear to occur predominantly in ants whose highly specialized diets (Janzen 1966, Davidson et al. 1989, Fiala and Maschwitz 1990, Morawetz et al. 1992) and unitary host genera (but see Ward 1991) provide independent evidence for specialization.

A final category of specialized ant traits may have little or no relevance to competitive ability but nonetheless serve as useful indicators of degree of evolutionary specialization in plant-ants. For example, Ward's (1991) phylogenetic analysis of pseudomyrmecines points to trends for plant-ants to have reduced eye size and palpal segmentation, as well as hypertrophied metapleural glands (except in cacia-ants). Palpal segmentation is also reduced in African *Engramma* (now included in *Technomyrmex*, Shattuck, 1992a), in comparison to other dolichoderines from the Ethiopian region (Hölldobler and Wilson 1990). Reduction in anten-

nal segmentation occurs in some lineages of *Allomerus* (Wheeler 1942), and arboreal stem-nesting *Cladomyrma* have fewer antennal segments than do most other formicines (Hölldobler and Wilson 1990). Although 10-merous antennae are characteristic of more generalized *Myrmelachista* species (subgenus *Hincksidris*) which nest in dead stems, specialized Central American *Myrmelachista* plant-ants have antennae with only 9 segments. Lastly, barbed stings are probably derived in both *Pseudomyrmex* ants (Janzen 1966) and *Pachycondyla luteola* (D. Davidson, personal observation). In general, sting defenses may be more effective against solitary vertebrates than against social insect enemies (Davidson et al. 1988), and barbed stings may have evolved under selection to reinforce learning by vertebrate enemies.

Plants.—In myrmecophytes, domatia and various food rewards offer clear support for evolutionary specialization, all the more so since the production of such structures can entail obvious costs. Ecological costs of myrmecophytic traits may be evident in both the presence of ants, as when ant predators open the nests (see above), and in their absence, e.g., when herbivores invade and inhibit foliar or stem domatia (Jolivet 1991, Vasconcelos 1991). Costs are most evident, however, when myrmecophytic traits are lost in the absence of symbiotic ants. For example, though *Cecropia peltata* L. is myrmecophytic throughout most of its distribution, conspecifics in Caribbean island populations lack Müllerian bodies and have trichilia reduced or absent (Janzen 1973; Rickson 1977). (Non-myrmecophytic *Cecropia schreberiana* Miquel might have been mistaken for *C. peltata* on some of these islands [C. Berg, personal communication].) In more recent history, introduced *Cecropia obtusifolia* Bertoloni of Hawaii, and *C. peltata* imported to both Asia and Africa have either lost their Müllerian bodies or trichilia, or are polymorphic for these characters and exhibit a range of trichilia sizes (D. Davidson, personal observation, Putz and Holbrook 1988). Although it could be argued that such losses are determined environmentally, rather than genetically, African populations of *Cecropia peltata* lacked trichilia even when grown from seed in greenhouses, where progeny of myrmecophytic congeners from their native habi-

tats have never failed to produce trichilia (Davidson, unpublished).

Selection may also act on plant characteristics which influence the outcome of ant-ant competition for the resources offered. In so doing, evolution might enhance traits which favor the most effective mutualists (at levels of defense investment optimal for the plant) over their competitors. Perhaps most remarkable, *Piper* ant-plants apparently produce food bodies only when stimulated to do so by the appropriate *Pheidole* ants (Risch and Rickson 1981), or by specialized parasites of the ant-plant mutualism (Letourneau 1990 and 1991). The persistence of Müllerian bodies on *Cecropia* trees lacking specialized ants (Rickson 1977, D. Davidson, personal observation) provides evidence that these bodies are not recognized by unspecialized ants as suitable food. Moreover, Müllerian bodies of at least *Cecropia* (prov.) "*tessmannii*", *Cecropia hispidissima*, and possibly *Cecropia ficifolia* Snethlage appear to have been modified evolutionarily to favor their usual resident ants (Davidson and Fisher 1991).

In a variety of ways, selection might modify the quality, rate, timing or position of the food reward to encourage either fine-grained or coarse-grained foragers, large or small workers, and aggressive, energy-intensive competitive dominants or timid, energy-conservative subordinates (see above). As an extreme example, plants which provision ants with complete diets may facilitate the persistence of weakly competitive species, whose foraging can then be restricted to the host itself (Appendix 1, column 4). At least some species of *Triplaris* induce fine-grained foraging by ants with highly specialized foraging behaviors. These hosts produce pearl bodies which are unique in their yellow color (perhaps indicative of some distinctive nutritional quality) and are distributed in patches on adaxial leaf surfaces. Perhaps pre-adapted for this behavior by prior dietary specialization on pollen and fungal spores (Wheeler and Bailey 1920), the *Pseudomyrmex* residents of these myrmecophytes accumulate these tiny food bodies on their appendages while constantly traversing leaf surfaces. They groom the material frequently onto their sting sheaths, which serve as storage sites until workers return to their nests (Davidson et al. 1988).

In a number of ant-plant genera, food rewards for ants are often produced in more localized and defensible sites on true myrmecophytes than on myrmecophilic relatives with more promiscuous rewards. Thus, in the *Endospermum* of New Guinea (Airy-Shaw 1980), myrmecophilic *E. medullosum* has moderately sized EFN's scattered across abaxial leaves along primary and secondary veins. Petiolar nectaries are only slightly larger. In comparison, myrmecophytic congeners have greatly enlarged petiolar EFN's and all other EFN's greatly reduced in size and number. Similarly, in the genus *Macaranga*, at least some myrmecophilic species have scattered pearl bodies used by a number of unspecialized ants (D. Davidson, personal observation in New Guinea), whereas the most highly evolved myrmecophytes restrict access to food bodies by hiding them beneath recurved stipules. In incipient myrmecophytes, *M. hosei* King ex Hk. f. and *M. pruinosa* (Miq.) Muell. Arg., whose stems are not naturally hollow and are only partially occupied, accessibility of food bodies appears to be intermediate (Fiala et al. 1991). Thus, although food bodies are locally concentrated on stipules, the stipules are horizontal, leaving them exposed. Experimental studies might focus profitably on the outcome of ant-ant competition in relation to the spatial patterning, accessibility and defensibility of ant rewards. Similar relationships are well accepted for other plant-animal mutualisms (e.g., Feinsinger and Colwell 1978).

Restrictive entrances to domatia (Fig. 7) may render these structures more readily habitable by some ants than others, as well as limiting access to stem-dwelling Coccoidea. Prostomas of myrmecophytic *Leonardoxa* are matched to the shapes and sizes of their associated ants (McKey 1991). Urticating hairs on the prostoma of *Cecropia* (prov.) "*tessmannii*" favor large-bodied queens of *Pachycondyla luteola* over smaller-bodied *Azteca* queens (Davidson and Fisher 1991). In general, neither the selective effects of these traits on different ant associates, nor their consequences for plant fitness are well documented. Nor is it often clear where "preadaptation" stops and adaptation begins. For example, the thin pith cavities of myrmecophytic *Vitex* lianes are easily exploited by the plant's specialist associate, the slender

Tetraoponera tessmannii, but not by stouter ants of similar body length. At present, however, there is no evidence to suppose that either plant or ant has evolved to produce or enhance such a match. Even the long, elliptical prostoma of *Leonardoxa africana*, matched to the flattened queens of *Petalomyrmex* (McKey 1991), might be explained as preadaptation. As in numerous other ant-plants with stem-domatia, this myrmecophyte's prostoma occurs at the node, opposite the leaf insertion, where a reduction in xylem leaves the stem wall relatively thin (Bailey 1922). In future studies, both field experiments and careful phylogenetic analyses of plant and ant lineages will be required to determine how frequently myrmecophytes may have evolved to influence ant-ant competition.

Limits to Specialization

The forces leading to specialization in ant-plant symbioses are both clear and consistent with theoretical arguments predicting greater specialization in mutualistic systems where strong antagonistic interactions occur among competing mutualists (Law and Koptur 1986). What factors then limit species specificity and account for the persistence of systems in which multiple ants coexist on the same host, or a single ant occupies several hosts? What are the limits to specialization? First, the matches produced by ecological sorting do not necessarily result in mutualistic interactions. A plant may be fortuitously 'preadapted' to harbor a persistent parasite, as well as an effective mutualist. Depending on the match, an association might engender strong reciprocal specialization (when most effective mutualists are paired), asymmetrical specialization, or even antagonistic interactions in which specialization in ants and plants proceeds in opposite directions.

Even when ant-plant associations are fundamentally mutualistic, there may be both genetic and ecological limits to specialization and coevolution (Schemske 1983, Kiester et al. 1984, Howe and Westley 1988). The nature of any genetic constraints is purely a matter for speculation. By and large, we do not know the extent of heritable variation for relevant ant and plant traits, nor whether such variation might limit specialization. Like-

wise, population structure of ant-plants, and especially that of plant-ants, is too poorly understood to support much discussion of how specialization and species origination might take place in these systems. Since sexual selection can drive rapid evolutionary specialization and coevolution in mutualists, added information on ant mating sites and behaviors or data from genetic markers might be especially interesting in helping to determine whether mating could be non-random with respect to the host species where alates originated.

More can be said about potential ecological limits on the intensity of selection for specialization. Most significantly, the outcome of an ant-plant interaction may often depend not only on the specific identities of associates but also on habitat type and plant size. As summarized above, habitat may influence the match between plants and ants through both ecological and evolutionary variation in rates of resource supply to ants. The effects of habitat heterogeneity could also be mediated through other mechanisms that are still poorly understood. For example, on isolated plants, or where nutrient poverty limits productivity and alate production, low frequencies of host plant colonization may reduce the intensity of ant-ant competition for hosts (Vasconcelos, in press, D. Davidson, personal observation). Herbivore pressures on at least some myrmecophytes appear to differ with habitat and plant size (Davidson and Fisher 1991, Janzen 1974a, Letourneau 1983), as does the probability that overgrowing vines will threaten both the host and resident ant colony (Rickson 1977, Davidson and Fisher 1991). Perhaps also varying with habitat are the densities of queen and brood parasitoids, which either kill incipient colonies, or prolong their development (Davidson and Fisher 1991). Finally, the outcome of competition among ants for host plants may be influenced by habitat-correlated physiological effects on colony development. In *Azteca ovaticeps*, queen mortality prior to first worker production is much higher on shaded hosts at the forest edge than on hosts of large, sunny and hot riverine disturbances (Davidson et al. 1991). In both the *Azteca* of South American *Cecropia* and myrmelachistines of African *Leonardoxa*, inter-specific variation in queen color correlates with habitat in a manner consistent with the hypothesis



Fig. 7. Restrictive entrance to domatia of the African myrmecophyte *Leonardoxa africana* (Baill.) Aubrév. (Fabaceae: Caesalpinioideae). The plant's mutualistic ant associate, *Petalomyrmex phylax* Snelling, makes these slit-like entrances at the site of the prostoma, which is of similar shape. The entrance allows access by the specialized dorsoventrally flattened foundresses of *P. phylax*, but not by other ants of similar size. Workers of *P. phylax* are of normal shape, but can easily pass through these entrances because they are much smaller than dealate queens of *Petalomyrmex* or workers of other ant species associated with the plant.

that black queen coloration could be adaptive on fast-growing hosts, possibly because of a positive effect on physiological rates. Queens are black in *A. alfari*, which dominates *Cecropia* of roadsides and pastures in many disturbed regions, and yellowish brown in *A. ovaticeps*, the typical resident of fast-growing riverine *Cecropia* (Longino 1989b). Occurring mainly on *Cecropia* of small forest light gaps, *A. australis* has yellow queens, and may have comparatively slow rates of egg-laying (Davidson et al. 1991). Similarly in *Leonardoxa*, black-bodied queens (and workers) of *Aphomomyrmex* tend to occur in more exposed riverine situations, whereas reddish yellow *Petalomyrmex* are typical of more shaded forest understory.

Within myrmecophyte species, host size-dependent variation in the relative abundances of alternative plant-ants may be determined in some cases by the match between colony resource demands and rates of resource provisioning by the plants. However, other causal mechanisms might also produce correlations between plant sizes and the identities of ant inhabitants. For example, such correlations could occur if ant species differed in the capacity to protect their hosts from herbivory (suggested by Longino 1991a and b, for Central American *Azteca* on *Cecropia*). Additionally, a form of ecological succession may take place, with regular changes in ant inhabitants through individual plant lifespans. Turnover of ant species

through time has been observed on hosts in the genera *Acacia* (Janzen 1975), *Leonardoxa* (McKey 1984), *Tachigali* (Benson 1985), and *Maieta* (Vasconcelos 1990). Just as successional mechanisms may vary across plant communities (Connell and Slatyer 1977), they may also vary across ant-plant systems. One possible explanation for species replacements is that early colonists are eventually replaced by superior competitors (Janzen 1975, McKey 1984, Davidson et al. 1989). In this context, coexistence of multiple ant species on a single host population requires that competitive abilities be inversely proportional to colonizing abilities, with poor competitors making a living as "fugitive species".

Even in the absence of direct interspecific interactions, disparate ant life histories might lead to successional changes among the ants of individual hosts. On Central American *Acacia*, for example, *Pseudomyrmex nigropilosa* Emery is an opportunistic colonist and short-term resident after prior residents have died from fire and other causes (Janzen 1975). A similar mechanism has been proposed by Vasconcelos (1990) to account for the coexistence of *Pheidole minutula* Mayr and *Crematogaster* sp. on *Maieta guianensis* Aublet near Manaus, Brazil. Although the two ant species provide equivalent protection for their hosts, the frequency of *Pheidole* occupancy increases with plant size. Comparatively early death or desertion of hosts by *Crematogaster* (for unknown reasons) leaves plants to be colonized again. Whatever the average relationship between the colonizing abilities of the two ants, larger plants should eventually accumulate *Pheidole* colonies, due to the frequent abandonment of hosts by *Crematogaster*.

To summarize, both the species composition of ant-plant symbioses, and the fitness consequences of particular associations, can vary markedly in space and time. Just as such inconsistencies are postulated to have limited evolutionary specialization in non-symbiotic ant-plant relationships (Schemske 1983, Beattie 1985), they have likely been the predominant obstacles to the evolution of species-specificity in symbiotic associations.

Evolutionary Dynamics of Ant-plant Symbiosis

Given these limitations to species specificity, what are the implications for coevolution? Coevolution has two aspects. The first is co-accommodation, reciprocal evolutionary responses of interacting organisms (Mitter and Brooks 1983). Co-accommodation is most easily recognized when it involves functionally matched characters of associated organisms or coupled character coevolution (Schemske 1983). Several ant-plant systems in both Africa and South America offer examples suggestive of reciprocal specialization of functionally matched characters in plants and associated ants. In this category are matches between the dimensions of ants and the prostomas of their plant associates (McKey 1991, Davidson and Fisher 1991), and between food provisioning by plants and the foraging and pruning behaviors of their ants (Davidson et al. 1988). Though suggestive, the data are not usually sufficient to pass a rigorous test, especially in view of our poor knowledge of phylogenetic relationships (McKey 1991).

The second aspect of coevolution is association by descent (Mitter and Brooks 1983). If ant-plant relationships have persisted and diversified as the associated lineages underwent successive speciation events, their phylogenies should be congruent. If, on the other hand, events such as host-switching and secondary exploitation of preexisting ant-plant mutualisms are frequent, there will be no close correspondence between ant and plant phylogenies. Interspecific hybridization of plants and/or ants will produce yet a third pattern, reticulate evolution. Janzen (1974a) concludes (without rigorous phylogenetic analysis) that the neotropical ant-acacias do not form a tight phyletic group, and postulates that one species may capture ant-adapted traits from another via introgression. Ross (1981) came to similar conclusions regarding African ant-acacias. Aside from the two groups of *Acacia*, there is little information to evaluate the possible role of hybridization in the diversification of ant-plants. Moreover, Janzen's observations might be explained alternatively by genotype-environment interactions. Thus, evolved associations of ants with one acacia lineage could have increased the selection intensity for myrmecophytism in other (possibly preadapted)

lineages, perhaps because ants occasionally colonized these unspecialized hosts.

Of the relatively small number of taxa which have produced modest to extensive radiations of ant-plants or plant-ants, taxonomic uncertainty precludes any examination of the question of association by descent in all but a few cases. And in no case do we have equally robust phylogenies in both ants and plants. By far the best example is Ward's (1991) study of associations between plants and pseudomyrmecine ants, represented by *Pseudomyrmex* and *Myrcidris* (Ward 1990) in the Neotropics, and by *Tetraponera* in Africa, Asia and Australasia. Specialist plant-ants appear to have arisen at least 12 times in this sub-family, on a wide range of hosts. Most of these events have produced only one or a few species of plant-ants, associated with a comparably small number of host species. Such small radiations offer limited opportunity for association by descent. In some cases, apparently secondary pseudomyrmecine colonizations of pre-existing ant-plant mutualisms have given rise to a small number of species on *Cordia*, *Pleurothrium* and possibly *Cecropia* (Ward 1991), all of which are predominantly associated with other ants (*Allomerus*, *Myrmelachista* and *Azteca*, respectively).

The hosts of pseudomyrmecines do include, however, three plant genera with large numbers of ant-plant species. Each of these (neotropical *Aca-cia*, *Tachigali*, and *Triplaris*) is associated with a different monophyletic group of *Pseudomyrmex*. Do these more extensive radiations offer evidence of association by descent? Ward (1991) concludes that at the species level, they do not. First, within each of these groups there is no pairwise specificity of ant and plant species. Not surprisingly, there is no clear pattern of cospeciation. Although in each of these three cases, the plant lineage seems to have evolved in concert with the ant lineage, the pattern of associations suggests host shifts within a taxonomically restricted guild of ants and plants, rather than cospeciation. Furthermore, each of these plant groups also harbors ants from at least one other lineage of *Pseudomyrmex*. Even in these extensive radiations from associated ancestors, coevolution seems to have been diffuse, corresponding to the guild coevolution or ecological replacement hy-

potheses (Howe and Westley 1988), rather than to a hypothesis of pairwise coevolution.

Relationships of various plant-ants to neotropical *Cecropia* paint a somewhat similar picture. Within ponerines of the genus *Pachycondyla*, four probable *Cecropia* specialists represent at least three separate origins of specialization on this host genus. Independent origins include species near both *P. villosa* (Fabricius) and *P. unidentata* Mayr (J. Longino, personal communication) as well as *Pachycondyla* sp. nov. in Panama. Of these, the first two species appear to be stem parasites. Their small, secretive colonies show little activity on host surfaces, though workers of at least the species near *P. villosa* harvest Müllerian bodies and locate entrances at prostomas (J. Longino, personal communication). At present, no data suggest specificity of host range within the genus *Cecropia*. In contrast, *Pachycondyla* sp. nov. appears to have a highly specialized relationship with *C. hispiddissima*, which produces especially large, hard and purple Müllerian bodies (Davidson and Fisher 1991, B. Fisher, personal communication). A close phylogenetic relationship between this ant and the Peruvian *P. luteola* cannot yet be ruled out (W. L. Brown, personal communication). Colonies of the latter ant occur only on *C.* (prov.) "*tessmannii*", whose relationship to *C. hispiddissima* is currently uncharacterized. The affiliations of *Pachycondyla* sp. nov. and *P. luteola* with their respective hosts are the most likely candidates for pairwise coevolution between ants and *Cecropia* trees, and the evidence is still weak. Even if ant and plant phylogenies turn out to be congruent here, and if speciation events are determined to have been synchronous in ant and plant lineages, any postulated cospeciation would appear to have been minimal, based on the small number of *Pachycondyla* specialized to *Cecropia*.

Three other ant genera provide support for multiple independent colonizations of *Cecropia*. The genus *Camponotus* includes at least two host generalists, *C. balzani* Emery in southeastern Peru, and an unnamed species of *Camponotus* sub-genus *Pseudocolobopsis* in northern Peru (Davidson, unpublished; R. Snelling, personal communication). Multiple radiations of specialized *Azteca* (Longino 1989b, 1991a and b) were mentioned above. Although phylogenies are not yet defined within ei-

ther ant genus, the overlapping and generalized host ranges of closely related ant species argue against cospeciation as the major mechanism by which diversity is generated. Finally, at least one *Crematogaster* species (near *C. curvispinosa* Mayr, J. Longino, personal communication) appears to be a specialist on *Cecropia* in northeastern Peru (vic. Genaro Herrera), but inhabits at least several different hosts within the genus (D. Davidson, personal observation). With specialized symbionts representing four of the five sub-families of plant-ants, and multiple origins within at least three ant genera, *Cecropia* presents a strong case for the ease with which taxa of generalized stem-nesting ants have colonized myrmecophytes over evolutionary time.

Like *Pseudomyrmex* and *Tetraponera*, many other plant-ant genera are associated with numerous, unrelated plant hosts (Appendix 1). Of 31 plant-ant genera (including various subgenera of *Camponotus*), only 11 are known from a single host genus, and three of these are records for species whose specialization as plant-ants (column 7) remains in doubt. As in pseudomyrmecines, these broad generic host ranges are probably due both to multiple independent origins of the plant-ant habit within the ant genus, and to secondary colonization of additional hosts by plant-ant species. However, the taxonomic information necessary to distinguish between these possibilities is lacking. *Allomerus* is a particularly intriguing case. All known species are specialist plant-ants. Unless we assume that non-specialist *Allomerus* once existed but are now all extinct (the genus has no fossil record [Hölldobler and Wilson 1990]), then the host range of this genus (seven plant genera in five families) is due to secondary colonizations and host shifts.

Perhaps the clearest evidence against cospeciation is offered by those cases in which a prerequisite for cospeciation, host-specificity, is not fulfilled. Several plant-ant species are associated with two or more quite unrelated hosts. At least three specialist plant-ant species of *Pseudomyrmex* occupy more than one plant genus (Ward 1991), with *P. viduus* F. Smith recorded from 5 genera in as many families. *Aphomyrmex afer* Emery is associated with *Vitex* (Verbenaceae) and *Leonardoxa* (Fabaceae) (R. Snelling, personal communication). *Technomyrmex* (formerly

Engramma) *kohlii* is associated with five genera (*Cola*, *Scaphopetalum*, *Canthium*, *Diospyros* and *Delpydera*) belonging to four families (Bequaert 1922; R. Snelling, personal communication). These appear to be cases in which secondary colonization of ant-plants has occurred several times.

At least one other case, however, does suggest association by descent. African *Leonardoxa* includes two myrmecophytes, which cladistic analysis has shown to be sister species (McKey 1991). They are inhabited by *Aphomyrmex afer* and *Petalomyrmex phylax* Snelling, respectively, the only two African representatives of the formicine tribe Myrmelachistini. Though these two ants are obviously closely related (Agosti 1991), further taxonomic work will be required to determine whether they are sister species or relicts of formerly diverse genera in which all congeners have gone extinct.

Habitat Specialization and the Generation of Diversity in Ant-plant Symbioses

Our analysis indicates that cospeciation in lineages of plants and of host-specific ants has been infrequent at best. Ant-plant pairs may be co-evolved, but associations seem to be shuffled or broken frequently, rather than diversified in concert via cospeciation. Pairwise coevolution thus can account for little of the diversification of these symbioses. How then have symbiotic ant-plant associations diversified? Mounting evidence suggests that evolutionary interactions in these systems, in both Africa and the Neotropics, correspond more closely to two other models of coevolution, not mutually exclusive, the guild coevolution hypothesis and the ecological replacement hypothesis (Howe and Westley 1988). These hypotheses envisage diffuse evolutionary interactions among sympatric guilds of associated organisms. Speciation may be accompanied by shifts in patterns of host associations, producing new mixes and matches. In these guilds, one member may replace another as the predominant associate of a particular member of the other guild. Guilds are also open. New ants may colonize pre-existing ant-plant mutualisms, perhaps displacing or completely re-

placing other ants, and new plants may join a guild of ant-plants.

We postulate that habitat-dependence in the outcome of different ant-plant interactions has been the principal force driving host shifts and ecological replacements within these guilds. Thus, the main obstacle to species-specificity and pairwise coevolution of ants and plants has at the same time facilitated diversification by other mechanisms.

Host plant quality, as recognized by ants, may vary more with habitat than with host species. Thus, Janzen (1966) has called attention to disparities in the habitat associations of *P. nigrocinctus* (Emery) and *P. spinicola* Emery (= *P. ferruginea*), though the two closely related (Ward 1991) species coexist locally. In some parts of their ranges, these two species also coexist with *P. flavicornis* F. Smith (= *P. belti*), which has yet a different pattern of habitat association (Janzen 1983). In another example, distributions of obligate *Cecropia* ants, both within and across genera, are usually more responsive to habitats than to host species (Harada and Benson 1988, Longino 1989b, 1991a and b, Davidson et al. 1991). As is the case for acacia-ants, the consequent mixing and matching of ants and *Cecropia* species may favor diffuse rather than pairwise coevolution. Likewise, effects of different ants on plant fitness may vary with habitat, for example, if the quality of defense against herbivores mattered less under favorable than unfavorable resource regimes.

Thus, genetic differentiation may be associated more frequently with habitat specialization, both in plants (Davidson and Fisher 1991) and in ants, than with specific identities of associates. However, habitat-dependence may still drive a type of cospeciation. For example, a plant and an associated ant may have parallel genetic responses to environmental variation, both of them diverging from conspecifics in a different habitat. Or, genetic differentiation in one symbiont, driven by habitat specialization, may induce divergence in its associate (Thompson 1987). The likelihood of such events, in which both ant and plant remain associated while undergoing habitat-related divergence, may depend on guild diversity. Thus, when an ant-plant colonizes a novel environment, poor success of the usual ant associate certainly provides selec-

tive pressure for adaptation of the ant to the new habitat. But it also provides opportunities for the establishment of other ant species. The richer the local guild of plant-ants, the greater the likelihood that a member of the guild will establish successfully, replacing the usual associate and preventing its specialization for the novel habitat. In depauperate guilds, preadapted ants are fewer, and the usual associate may be more likely to persist and adapt to the novel environment. A possible example is the relationship between *Leonardoxa* spp. and their *Petalomyrmex* and *Aphomyrmex* ants. Plausibly a case of cospeciation, this system involves a small number of ant and plant species (McKey 1991). Neither the two plants nor the two ants ever occur sympatrically, and few other myrmecophytes and domatia-inhabiting ants share their habitats. Perhaps pairwise specificity and cospeciation are more likely to occur in modest and geographically limited radiations such as these, where taxonomic poverty of sympatric guilds of ant-plants and plant-ants offers little scope for host-switching and secondary colonization. The latter processes may dominate in species-rich guilds. If our hypothesis is correct, it would suggest that diversity begets diversity due to genotype-environment interactions in tropical ant-plant symbioses.

EVOLUTIONARY TRENDS IN SPECIES REPLACEMENTS WITHIN PLANT-ANT GUILDS

Host-switching, secondary colonization, and ecological replacement seem to be the predominant modes by which ant-plant associations are modified. Once a new association is forged, it is likely to engender selection on one or both partners, and to give rise to evolutionary diversification. But how do new associations form and spread? What is their effect on preexisting associations? Can we recognize patterns in the radiation of plant-ants and ant-plants? Once again, it may be possible to understand the evolutionary dynamics of ant-plant associations in the context of competitive interactions among ants, and habitat-dependence in the outcome of ant-ant and ant-plant interactions. While many species replacements may have occurred without perceptible trace, contemporary systems in which ant-plants are associated with multiple unre-

Table 2. Earliest fossil records of ants for genera (worldwide) in which specialized plant-ants have evolved (summary excerpted from Hölldobler and Wilson 1990): A = Arkansas amber (USA, middle Eocene); Ba = Baltic amber (northern Europe, early Oligocene); Br = Britain (Oligocene); Do = Dominican amber (Dominican Republic, late Miocene^a); F = Florissant shales, Colorado, USA, Oligocene); Sh = Shanwang shales (China, Miocene); Si = Sicilian amber (Sicily, Miocene).

Sub-family and tribe	Genus	Earliest fossil find
PONERINAE		
Tribe Ponerini	<i>Pachycondyla</i>	Early Oligocene ^{Ba,Br,D}
PSEUDOMYRMECINAE		
	<i>Myrcidris</i>	No fossil record
	<i>Pseudomyrmex</i>	Oligocene ^{D,F}
	<i>Tetraponera</i>	Early Oligocene ^{Ba}
MYRMICINAE		
Tribe Cephalotini	<i>Zacryptocerus</i>	Late Miocene ^D
Tribe Crematogastrini	<i>Crematogaster</i>	Miocene ^{Si}
Tribe Leptothoracini	<i>Leptothorax</i>	Early Oligocene ^{Ba}
Tribe Pheidolini	<i>Pheidole</i>	Oligocene ^{D,F}
Tribe Solenopsidini	<i>Allomerus</i>	No fossil record
	<i>Solenopsis</i>	Late Miocene ^D
Tribe Tetramoriini	<i>Tetramorium</i>	No fossil record
Tribe Dacetini	<i>Strumigenys</i>	No fossil record
Tribe unclassified	<i>Catantlucis</i>	Miocene ^{Si}
	<i>Podomyrma</i>	No fossil record
	<i>Atopomyrmex</i>	No fossil record
DOLICHODERINAE		
Tribe Tapinomini	<i>Anonychomyrma</i>	No fossil record
	<i>Axinidris</i>	No fossil record
	<i>Azteca</i>	Early Miocene ^D
	<i>Tapinoma</i>	Miocene ^{Si}
	<i>Technomyrmex</i>	Miocene ^{Si}
FORMICINAE		
Tribe Plagiolepidini	<i>Plagiolepis</i>	Early Oligocene ^{Ba,Si}
Tribe Myrmelachistini	<i>Aphomyrmex</i>	No fossil record
	<i>Cladomyrma</i>	No fossil record
	<i>Myrmelachista</i>	No fossil record
	<i>Petalomyrmex</i>	No fossil record
Tribe Camponotini	<i>Camponotus</i>	Early Oligocene ^{Ba,Si}

^a Note added in proof. Although Hölldobler and Wilson (1991) date the Baltic amber as late Oligocene, more recent work summarized by Kirshina and Grimaldi (1991) suggests an earlier estimate. We use the latter date because it is conservative in relation to our hypothesis.

lated plant-ants may offer examples of species replacements in progress. The various ant associates of myrmecophytes usually occupy different places in a competitive hierarchy. An understanding of their competitive relationships, and how they coexist today, should provide insights into the ecological mechanisms that have driven their evolutionary histories.

Without more phylogenetic evidence than exists today, we have only a snapshot of a process in motion, and cannot know its direction with certainty. Nevertheless, we attempt a provisional distinction between original associates and secondary colonists of several ant-plant associations. First, we focus on two ant lineages which seem to have played predictable and frequent roles in the ecological replacement of primary associates. We then examine likely causes of such pattern, based on what is known of the biology and competitive relationships of the ants involved. Generalizing from these examples, and referencing the fossil record, we propose a hypothesis of taxonomic progressions within lineages of plant-ants. This hypothesis, combined with information on the geological history of mesic-forest environments in different tropical regions, leads to new interpretations of intercontinental differences among ant-plant symbioses.

Directionality of Species Replacements

The primary and secondary associates of many myrmecophytes can be very difficult to distinguish (Ward 1991). Nevertheless, patterns in the biogeographic and taxonomic distribution of host associations in some ant-plant systems suggest that myrmecophytes have been colonized recently by unspecialized arboreal ants or by host-shifting plant-ants, resulting in partial or complete replacement of a prior ant associate. In none of the examples that follow is the evidence for directionality conclusive. Nevertheless, taken together the evidence is strongly suggestive, and the approach has enabled us to propose testable hypotheses and to define critical points where data required to test these hypotheses are lacking.

Crematogaster as Secondary Associates of Myrmecophytes.—Several ant-plant relationships

provide indications that ants of the genus *Crematogaster* have partially or completely replaced prior ant associates of the host plant. First, the pattern of ant associations with the two African *Barteria* species suggests that ancestral host relationships may have involved *Tetraponera* ants. For *T. aethiops* (F. Smith) and *T. latifrons* (Emery), two host-specific associates of *B. fistulosa* Mast. (Janzen 1972), taxonomic isolation from other sections of the genus suggests comparatively ancient origins for the association (P. Ward, personal communication). *Tetraponera* has not been found to inhabit the other described species of *Barteria*, *B. nigritana* Hook. f., which instead houses an apparently unspecialized *Crematogaster*. The latter association may have arisen via secondary colonization of hosts in the more disturbed, light-rich, coastal scrub sites frequented by this plant species. Interestingly, while *B. fistulosa* is occupied by its specialist *Tetraponera* in forest light gaps, it too occurs with unspecialized *Crematogaster* in large, human-made clearings in coastal forests of Cameroon (D. McKey, personal observation).

Second, although *Crematogaster* spp. are presently the numerically dominant associates of East African ant-acacias, *Tetraponera* ants may have been the original inhabitants. Invasion of East African acacias by *Crematogaster*, which generated two new specialists on *Acacia*, may have largely pushed the weakly competitive pseudomyrmecine into marginal high-elevation sites (Hocking 1970). At lower elevations (ca. 900 m), *T. penzigi* (Mayr) appears to be competitively subordinate to *Crematogaster mimosae* (Santschi) and *C. nigriceps* Emery, and has exclusive possession of only 0.7 % of the trees. At higher elevations, it maintains control of up to 8.5 % of host trees. In sites where it cooccurs with the two *Crematogaster*, the pseudomyrmecine appears to persist mainly in unoccupied parts of *Crematogaster*-occupied trees. There it ensures exclusive occupancy of stipular swellings by boring entrance holes too small to accommodate *Crematogaster*, and by plugging or protecting these entrances with carton baffles.

Asian *Macaranga* may be another case where contemporary numerically dominant *Crematogaster* ants have largely replaced the original inhabitants. Poorly known associations occur between two

Camponotus species [provisionally subgenus *Colobopsis*] and both *Macaranga griffithiana* M.A. and *Macaranga puncticulata* Gage (Fiala et al. 1990). Each of these hosts grows principally in swamplands (Whitmore 1973 and 1975), marginal habitats where rates of plant growth and supply of ant resources are likely to be reduced. Finally, one *Crematogaster* lineage may also have replaced another. Thus, *Macaranga* hosts in some undisturbed primary forests are occupied by a species with black workers and 11-segmented antennae, whereas hosts of forest and riverine edge typically contain any of an unrelated complex of species with yellowish workers and 10-segmented antennae (D. Davidson, personal observation). Despite habitat segregation under natural conditions, a mixture of the two ant lineages occurs in the extensive *Macaranga* forests left after logging. Clearly, in view of the habitat specificity of both myrmecophytes and their ants, the rapid conversion of primary forests can be expected to alter these symbiotic associations greatly in future years.

In the Neotropics, unspecialized *Crematogaster* are recorded as clear newcomers and secondary associates of several older ant-plant relationships, including those between *Pseudomyrmex* and *Triplaris* (Davidson et al. 1988; Oliveira 1987), *Pseudomyrmex* and *Acacia* (Janzen 1983), and *Azteca* and *Zacryptocerus* with *Cordia alliodora* (R. Carroll, personal communication). These Neotropical examples include no obvious case in which colonization by *Crematogaster* has led to complete replacement of a prior associate, and American *Crematogaster* have only rarely evolved into specialist plant-ants. Included in the latter category are only the *Crematogaster* cf. *victima* of many neotropical leaf-pouch myrmecophytes, and a derivative of the opportunistic and widespread *C. curvispinosa* on *Cecropia* in northeastern Peru (D. Davidson, personal observation).

Azteca as Secondary Associates of Neotropical Myrmecophytes.—In species richness, *Azteca* are the preeminent competitive dominants among New World plant-ants (Appendix 1), and play ecological roles analogous to those of *Crematogaster* in many Old-World systems (Carroll 1983). Like *Crematogaster*, they may be displacing subordinate species in many relationships. For example,

both *Crematogaster* and *Azteca* ants displaced *Pseudomyrmex dendroicus* when permanent wire bridges were made between the host trees and neighboring vegetation (Davidson et al. 1988). Moreover, as we also suspect for Old-World *Crematogaster*, some displacements of primary associates by *Azteca* may have been so thorough that distinguishing contemporary from prior associations is fraught with uncertainty. For example, ants of the genus *Azteca* are the numerically predominant associates of myrmecophytic *Cecropia* today, but associations of *Cecropia* with other ants, such as *Camponotus* and *Pachycondyla*, may be older. Each of these latter genera includes species which are *Cecropia* specialists, and in both cases ongoing competition with *Azteca* may exclude them from riverine and other riparian habitats, where *Cecropia* is most abundant and fast-growing (see above, Davidson and Fisher 1991).

Replacements may also be occurring within the genus *Azteca*. In Amazonian Peru, *Azteca ovaticeps* and its relative, *A. alfari* appear to be relative newcomers, dominating contemporary *Cecropia* populations along riverine and forest edge. The two species are closely allied to ants of other early successional ant plants (Longino 1991b). These ants include *A. foreli* Emery, which inhabits live stems of a variety of rainforest trees, and *A. longiceps* Forel, from mid-elevation *Triplaris* of the Costa Rican Pacific coast. Still other representatives of this species-group occur on *Cordia alliodora*. Thus, *A. ovaticeps* and *A. alfari* may have originated during a comparatively recent host switch onto *Cecropia*. In support of this conjecture are rare observations of apparent mistakes in colony founding behavior. Queens of *A. ovaticeps* occasionally attempt to enter *Cecropia membranacea* by burrowing into the trichilia, rather than into prostomas, even though suitable prostomas are available in uncolonized internodes (D. Davidson, personal observation). The arrival of *A. ovaticeps* may have driven *A. australis* out of riverine environments and deeper into the forest, where it persists on a variety of forest light-gap *Cecropia* species (see above; Davidson and Fisher 1991).

Azteca australis could itself be a secondary colonist. A member of the *A. muelleri* species complex, it is likely descended from generalized

carton-building ancestors with well-defended central nest sites (Longino 1991a and b). Members of this group still maintain carton masses inside the boles of their hosts (Longino 1991a). Ants in this species complex may have gotten their first foothold on myrmecophytic *Cecropia* by building external carton nests on hosts whose prior residents (possibly *Camponotus* and *Pachycondyla* species) had died.

Analogously and in contemporary times, *Azteca* may be invading other myrmecophytic associations. In the Manu National Park and Tambopata Reserve of southeastern Peru, at least two carton-building species (probably *A. ulei* Forel var. *cordiae* Forel and *A. traili* [Emery] var. *tococae* Forel) are residents of trichome myrmecophytes *Cordia nodosa* and *Tococa* spp. (Appendix 1). Queens of both ants initiate their colonies inside domatia covered by protective hairs, and their incipient colonies exhibit host-plant fidelity. Nevertheless, larger, established colonies not only leave their hosts regularly to forage, but build satellite nests (often as ant-gardens) on neighboring trees. These ants also prune trail systems through the protective stem trichomes. On *Cordia*, *Azteca* ants occur mainly on hosts in environments of unusually high light intensity, and conspecific trees in the primary forest understory are occupied by *Allomerus*. If we are correct in assuming that plants with long, dense and erect pubescence became myrmecophytes in the context of persistent occupation by tiny and competitively subordinate ants, then larger-bodied, aggressive and dominant *Azteca* appear to have both restricted the distribution of *Allomerus*, and perhaps eliminated the former residents of *Tococa*. Although *Tococa* is colonized occasionally by timid *Crematogaster* cf. *victima* and a species of *Solenopsis*, we have never found established colonies of these ants on the *Tococa* of southeastern Peru.

Identifying and Characterizing Dominants

Crematogaster and *Azteca* are the two genera for which biogeographical and phylogenetic information is most suggestive of a frequent role as secondary colonists in species replacements among plant-ant guilds. They are also the preeminent

competitive dominants in the arboreal ant faunas of Africa and Asia, and New World tropics, respectively. Isolated from these continents, the Australian tropics (including New Guinea and associated islands) contains a unique set of competitive dominants and relative newcomers to ant-plant symbioses. Among these ants (all dolichoderines) are two genera previously classified as *Iridomyrmex* (Shattuck 1992b), but now considered to be distinct taxa and endemics of either the Australian (*Anonychomyrma*) or Oriental and Australian regions (*Philidris*). Also included are pantropical *Technomyrmex* (a single species of which is apparently native to the New World, Shattuck, 1992a).

Several other kinds of evidence substantiate the inferential evidence about the relative competitive abilities of ants involved in ant-plant symbioses. Field experiments have demonstrated that *Crematogaster* and *Azteca* are the principal formicid enemies of New World *Pseudomyrmex* on *Triplaris* (Davidson et al. 1988, see also Oliveira 1987). Furthermore, both host-plant fidelity and pruning of host-plant neighbors are indicative of weak competitive ability (Davidson et al. 1988, 1989) and occur with some frequency in *Pseudomyrmex*, *Tetraponera*, *Pheidole*, *Camponotus*, and in various myrmelachistines. In contrast, these behaviors are atypical of *Crematogaster*, *Anonychomyrma*, *Azteca*, and *Technomyrmex* (Appendix 1, column 4). Rare occurrences are limited to early successional environments where vines and competitors are particularly threatening, as for the *Azteca* of New World *Cecropia*, and *Crematogaster* of Asian *Macaranga*. They can also characterize ants which are unusually timid for their genera, as are the *Azteca* exhibiting host-plant fidelity on pubescent species of *Triplaris*.

Implicit in their capacity to invade myrmecophytes previously dominated by other ants, secondary colonists likely owe their success to evolutionary novelties which have enhanced their colonizing and/or competitive abilities. The genera listed above as competitive dominants are alike in possessing potent exocrine products which help to convey competitive superiority in interactions with other ants (Blum and Hermann 1978, Buschinger and Maschwitz 1984). Structural characteristics of waists and gasters permit workers to elevate gasters

and direct toxins toward enemy ants. The same adaptations can be effective against potential nest raiders, as when *Crematogaster* workers seal hollow stem nests with protruding gasters bearing poison droplets on modified spatulate stings (Forel 1928). Many dominants are also carton-builders, which monopolize resources in the arboreal zone by constructing primary or ancillary nests over Homoptera and other localized food sources such as extrafloral nectaries.

These traits contribute to the capacity of dominant ants to monopolize "promiscuous" plant rewards such as EFN's and surface-feeding Homoptera, which are either totally unprotected or only partly secluded beneath clasping or folded stipules of myrmecophiles. Thus in Borneo, *Crematogaster* species dominate the exposed EFN's of most individuals of myrmecophilic *Endospermum* (Euphorbiaceae), *Ryparosa* (Flacourtiaceae), and *Macaranga aetheadenia* Airy Shaw (D. Davidson, personal observation). *Crematogaster* are also preeminent among visitors to other myrmecophilic Malaysian *Macaranga* spp. (Fiala and Maschwitz 1991). In New Guinea, scale-tending *Crematogaster* are the numerically predominant inhabitants of the stout hollow stems of weedy *Nauclea* (D. Davidson, personal observation). Myrmecophiles with nectaries partly secluded beneath folded or clasping stipules include New Guinea *Archidendron* (Fabaceae) and Oriental *Shorea* (Dipterocarpaceae), both often dominated by *Technomyrmex* ants (D. Davidson, personal observation, Tho, *vide* Maschwitz and Fiala, in press). By sealing off the folded stipules with carton, these ants may restrict their competitors' access to EFN. An ability to monopolize externally located food resources may also confer a competitive advantage to dominants on myrmecophytes which produce such resources. This result would be especially likely if evolutionary interactions of the plants with prior ant associates had led to increased size and/or number of EFN's and food bodies, or otherwise increased the rate of food production to a level at which the plant becomes attractive to competitive dominants requiring high rates of resource supply.

Processes of Species Replacements

How have secondary colonists managed to replace primary associates with highly evolved mechanisms for locating and exploiting hosts? Even very aggressive and dominant ants may have difficulty evicting weakly competitive ants, once the latter have established their colonies. Thus it seems likely that many secondary colonists first achieved access to myrmecophytes by occupying hosts whose usual partners were absent for one reason or another. For example, like the *Azteca* discussed above, some *Crematogaster* could have gained a preliminary foothold on myrmecophytes by building carton nests on plants which had outlived their ant colonies. Early stages of this scenario may be represented in the New World associations of *Crematogaster* with myrmecophytic acacia species in second growth environments (Janzen 1983). Although *Crematogaster* are apparently unable to replace *Pseudomyrmex* on smaller acacias, they can resist colonization by the latter species on larger acacias which have lost their former *Pseudomyrmex* colonies.

The more characteristic ant associates may be absent for other reasons. First, by opening domatia to feed on ant larvae, vertebrate predators of ants may make these domatia unsuitable for continued habitation by weakly competitive species. For example, after swollen internodes of *Cordia alliodora* are opened by woodpeckers, unspecialized *Crematogaster* often move in and employ carton baffles to seal breaks in the domatia (R. Carroll, personal communication). Second, older domatia are frequently abandoned by the usual residents, as colonies move to follow new growth and productivity. In *Cecropia* (Davidson et al. 1991), *Remijia* (Benson 1985), *Leonardoxa* (D. McKey, personal observation), *Endospermum*, *Korthalsia*, and other genera (D. Davidson, unpublished), such abandoned domatia are often occupied by unspecialized ants, which gain at least protected nest sites if not food (Davidson and Fisher 1991, Longino 1991a). A possible case of progressive specialization in such ants may be seen in the unnamed *Crematogaster* species which occupies *Cecropia* near Genaro Herrera in Loreto, Peru (D. Davidson, personal observation). Related to *C. curvispinosa*

(J. Longino, personal communication), it is apparently descended from generalized stem-nesters, rather than from a carton-building lineage. Specialization on *Cecropia* could have been favored by selection sharpening the host-finding abilities of foundresses which occasionally colonized the woody bases of forest-gap plants, and eventually evolved to recognize Müllerian bodies as food.

Third, the typical ant associates may fail to either colonize or to persist on hosts in inappropriate habitats. Small forest light gaps are marginal for western Amazonian *Cecropia*, and comparatively low colonization rates on isolated and inconspicuous gap plants appear to have provided safety for refugees from riverbanks, as well as opportunities for *in situ* colonization of this host genus. All four little-known genera of *Cecropia* ants persist principally in forest light gaps. Both *Camponotus balzani* and *Pachycondyla luteola* colonize riverine plants, but rarely persist there, being excluded by *Azteca*. In contrast, species of *Crematogaster* and *Camponotus* (*Pseudocolobopsis*) occur on several light gap species at Genaro Herrera, but apparently do not even colonize plants of riverine and forest edge. Their relationships with *Cecropia* may have evolved *in situ*. Alternatively, past competition with *Azteca* may have led to a shift in their habitat preferences.

Finally, colonists may also gain a foothold at the latitudinal or elevational limits of ant-plant associations. Latitudinally, the genus *Triplaris* ranges northward into Mexico; in southwestern Chiapas near Mapastepec, it is occupied by a variety of apparently unspecialized species of *Azteca*, *Crematogaster* and *Pseudomyrmex*, rather than by the more typical specialized pseudomyrmecine associates (D. Davidson, personal observation). At least one specialized *Cecropia* ant, dry forest *A. coeruleipennis* Emery, may have evolved *in situ* in Central America (Longino 1989a and b), a peripheral and comparatively species-poor region within the overall distribution of *Cecropia*. These events might well have resulted from independent secondary colonizations of a host which reached Central America from South America in advance of its typical ant symbionts, or which colonized habitats unsuited to the usual associates.

Elevational segregation among plant-ants of particular hosts suggests that new colonizations might occur at the elevational limits of species distributions. In the lowlands of Cameroon, myrmecophytic *Leonardoxa* consistently house one of two closely related myrmelachistine ants, *Petalomyrmex phylax* or *Aphomyrmex afer*, depending on host species (McKey 1991). However, in submontane forests of the Rumpi Hills (500-1700 m), where neither of these ants occurs in association with *Leonardoxa*, the plants are inhabited by a bewildering array of other ants, including at least two species each of *Crematogaster*, *Axinidris* and *Technomyrmex*, and one species each of *Tapinoma* and *Leptothorax* (R. Snelling, personal communication). Some of these ants are known not to be host-specific, and they may be secondary colonists of a preexisting association of *Leonardoxa* with myrmelachistine ants, although firm conclusions on directionality of this shift must await further work. Finally, in the Neotropics, altitudinal replacements should be common at the periphery of the Andes. Although we know of no published data to test this prediction, Longino (1991b) relates that the ranges of some *Azteca* residents of *Cecropia* segregate altitudinally, with some species occurring as high as 2000 m in elevation.

As secondary colonists of myrmecophytes become increasingly specialized for exploiting their new hosts, selection should enhance the host-finding abilities of these species. With their priority-of-colonization eroded, primary associates may eventually be displaced to marginal habitats or replaced altogether.

Taxonomic Progressions Within Plant-Ant Lineages

Since ant-plant symbioses have been shaped by repeated evolutionary colonizations and strong competition among ants, major taxa of plant-ants might be expected to exhibit regular taxonomic progressions in species distributions and characteristics. Similar progressions have been described for adaptive radiations in several well-studied animal groups, including ants (Wilson 1959a and 1961), carabid beetles (Erwin 1985), and birds (Ricklefs and Cox 1972; Diamond 1986). These accounts are related

in their emphasis on competition as the force driving evolutionary trajectories in animal lineages. Wilson's seminal exposition of the "taxon cycle" in Melanesian ants proposes that ants invade new geographic areas principally via marginal habitats where competition from other ants is reduced. From this tenuous foothold, and driven by arrivals of new and more dominant species, they diversify and evolve competitive strategies which eventually enable their invasion of more species-rich forest habitats. In apparent contrast, Erwin's recent account of "taxon pulses" in carabid beetles proposes that young carabid taxa first appear in productive and central moist equatorial habitats. There, they force the specialization and migration of older taxa into less competitive peripheral latitudes and habitats. Apparent disparities in the phrasing of Wilson's and Erwin's theories obscure their common ground. Both ideas have their roots in Darlington's (1957) "centrifugal speciation", whereby intense biotic interactions drive waves of species and higher taxa from tropical to temperate regions. Moreover, whether species originate in new and permissive environments, or as evolutionary novelties in biotically restrictive environments, young species are those with "r-selected" life histories, and generalized and expanding distributions. Older, progressively "K-selected" species are driven by biotic interactions to increasing specialization and more circumscribed distributions. There they persist by either unique strategies for evading natural enemies, or by tolerance of unfavorable conditions. Vermeij (1978) has argued cogently for similar evolutionary trajectories in various marine invertebrate taxa.

The evolutionary history of plant-ants strongly suggests similar taxonomic progressions. Three types of evidence support such an interpretation. First, as discussed above, taxonomic and biogeographic patterns in some ant-plant symbioses suggest directionality in species replacements, and particular taxa occupy predictable roles as victims (e.g., Pseudomyrmecinae) and agents (e.g., *Crematogaster* and *Azteca*) of such replacements. Second, and also discussed above, field experiments and observations strongly support interspecific competition among ants, often habitat-dependent in its outcome, as the principal mechanism of

species replacements. Furthermore, roles of different ants in postulated replacements are consistent with their status (independently determined) in competitive hierarchies. Third, within ant-plant guilds, the postulated replacements of subordinate genera, such as *Pachycondyla*, *Plagiolepis*, *Camponotus*, *Pseudomyrmex*, and *Tetraponera*, by dominant genera such as *Crematogaster*, *Technomyrmex*, and *Azteca*, are consistent with the historical sequence in which these taxa are represented in the fossil record (Table 2, based on Hölldobler and Wilson 1990, and see below).

The diversification of ant taxa began in earnest no later than the beginning of the Tertiary Period (Hölldobler and Wilson 1990), and it eventually made ants the most important natural enemies of one another. At protected nests and feeding sites, timid, twig-inhabiting myrmelachistines and pseudomyrmecines, probably among the earliest plant-ants, sought out pubescent plants or insect borings and other cavities of live plants. But in the background, competition was escalating. Evolutionary advancements in offensive and defensive weaponry intensified the pressures on timid and secretive plant-ants. As discussed above, evolutionary novelties and secondary colonizations appear to have arisen differentially in environments where disturbance favored weedy species with early and high reproductive allocation, superior colonizing ability, and thus priority of access to ant domatia. Here also, high productivity (associated with high light intensities) subsidized rapid colony growth and the evolution of costly chemical weaponry. Individually or in combination, these traits made their bearers formidable enemies of existing plant-ants, driving them into ever more restrictive specialization on one or a few hosts, into marginal habitats, and in some cases into extinction. Eventually, many secondary colonists appear to have partly or completely replaced the primary associates of several myrmecophyte lineages. These secondary associates were often pressured in turn by successive waves of newly evolved dominants.

What examples support such a scenario? Myrmelachistine ants provide perhaps the best illustration of the fate of an old group of competitively subordinate ants, whose members have been driven to suboptimal habitats, to extreme special-

ization, or to extinction, by dominant ants. As circumscribed by Hölldobler and Wilson (1990), following Wheeler (1920), this tribe is pantropical and includes six genera, two of which are endemic to each of the major tropical regions (the New World, tropical Africa and the Oriental tropics). In a recent and still incomplete analysis of generic relationships in Formicinae, Agosti (1991) casts doubt on the monophyly of the tribe, placing *Cladomyrma* in a different informal genus-group from all the others. We follow the usual treatment of the tribe, but acknowledge the need for further work to resolve phylogenetic relationships of these ants.

Myrmelachistine genera have no fossil record (Table 2), possibly because most have long been specialist plant-ants with restricted ecological distributions. However, they are likely to have been widespread prior to Miocene times, since two ant genera from a tribe (Gesomyrmecini), considered by Wheeler (1920) to be closely related (but see Agosti 1991), are represented in early Oligocene Baltic amber (Hölldobler and Wilson 1990). One of these, *Gesomyrmex*, is represented by four extant species of the Oriental region (Wheeler 1929a). They share with the Oriental myrmelachistine *Cladomyrma* certain similarities, such as reduced antennal segmentation (believed to be a derived character) and worker polymorphism with major, media, and minor workers. Furthermore, *G. kalshoveni* Wheeler of Java, is recorded as nesting in twig cavities of *Artocarpus* in primary forest (Wheeler 1929b). These bits of information on an ant genus regarded by Wheeler (1929a) as "living fossils which have undergone no significant modification since the Early Tertiary" suggest that the plant-ant habit may have a long evolutionary history in the Formicinae, currently regarded as having diverged very early from the basal lineage of the Formicidae (Hölldobler and Wilson 1990).

In all parts of their pantropical distribution, myrmelachistines appear to have experienced ecological contraction. Although no phylogeny is available for the New World genus *Myrmelachista*, interspecific patterns in its distribution and ecology reveal the likely imprint of past competition. *Myrmelachista* are often conspicuous leaf foragers in montane forests of Central and South America,

where dominant *Crematogaster* and *Azteca* ants are largely missing (J. Longino, personal communication). In sharp contrast, congeners of tropical lowlands are stem-nesters with a relatively inconspicuous presence on leaf surfaces. Among residents of Costa Rican *Ocotea*, workers of a *Myrmelachista* plant-ant at 500-700 m elevation (at Rara Avis) do not attack vines (B. Fisher, personal communication), though those of a congener at 50 m in nearby La Selva Biological Station do prune (D. Davidson, personal observation). Finally, in western Amazonia, perhaps the center of neotropical ant diversity (Wilson 1987), *Myrmelachista* residents of *Duroia hirsuta* and *Cordia nodosa* appear to protect themselves not only by pruning vegetation other than potential host plants, and by maintaining extensive clearings ("supay chacras"), but by effectively hiding from larger-bodied ants amid the dense stem hairs of these two hosts. (Morawetz et al. [1992] argue that creation of similar clearings by a *Myrmelachista* species on *Tococa* is not a product of past competition. However, this assertion is based strictly on the probably valid assumption that clearings enhance the light environment and productivity of host plants; it did not stem from any direct test for the effects of competition from other ants [see, e.g., Davidson et al. 1988]). Overall, the pattern reveals that increasing specialization for resisting dominant ants may have been required for persistence in highly competitive and diverse lowland rainforest faunas.

The evolutionary fortunes of myrmelachistines also appear to have declined in the Old World tropics. In Africa, they are represented by only two monotypic genera (*Petalomyrmex* and *Aphomyrmex*). The former is restricted to a single host species and confined to a very small area of Lower Guinea coastal forest. Both species are plant-ants, though interestingly, neither prunes nor inhabits pubescent myrmecophytes. *Cladomyrma* is one of two myrmelachistine genera known from Asia (with the status of *Pseudaphomyrmex* remaining uncertain), and all five described species are specialized plant-ants (Agosti 1991). Some of their hosts (e.g., *Saraca*) are shared with *Crematogaster*, suggesting the potential for competitive interactions with this group of dominant ants. Furthermore, patterns of host association indi-

cate that *Crematogaster* may have replaced *Cladomyrma* in some systems. Thus *Cladomyrma* persists on Asian *Neonauclea*, but *Crematogaster* dominates closely related *Myrmeconauclea*. Too little is known of phylogenetic relationships among representatives of any of these lineages to draw firm conclusions.

Pseudomyrmecines appear to be another relatively old group in which the plant-ant habit may be ancient, and in which competitively subordinate plant-ants have been restricted or replaced by more recently evolved, competitive dominants. *Tetraponera* first appears in fossil deposits in the early Oligocene and *Pseudomyrmex* in the Oligocene (Table 2). The monotypic *Myrcidris*, a plant-ant whose specializations indicate a long history of association with plants, may be a relict that is the sister group to all other pseudomyrmecines, though other interpretations are possible (Ward 1990). As discussed above, plant-ants of this relatively old subfamily are among the most frequent apparent victims of the expansion of younger groups such as *Crematogaster* and *Azteca*.

Other groups of competitively subordinate ants for which there is circumstantial evidence of replacement by more recently evolved dominants also occur relatively early in the fossil record. These include *Pachycondyla*, *Camponotus*, and *Plagiolepis*, all of which appear in the early Oligocene. *Cecropia* specialists derived from widely distributed *Pachycondyla villosa* and *P. unidentata* (J. Longino, personal communication) are probably more recent secondary colonists, inhabiting mainly older and woody stems abandoned by other ants. At present, no evidence indicates that these are replacing former inhabitants. *Allomerus*, another genus being pressured by contemporary dominants, has no fossil record, perhaps because all of these ants have been plant-ants with highly restricted distributions.

In contrast to these weakly competitive groups, genera implicated as dominant ants and secondary or tertiary colonists of existing associations appear to be more recent arrivals. The first fossil records of *Crematogaster* and *Technomyrmex* are in the Miocene, and *Azteca* appears in the early Miocene (Table 2).

Taxonomic Progressions and Intercontinental Comparisons of Ant-Plant Symbioses

If taxonomic progressions such as those postulated above play major roles in transforming ant-plant symbioses over evolutionary time, then long-term evolutionary history assumes an added dimension as an important factor shaping intercontinental differences in the nature of ant-plant symbioses. Contemporary patterns will reflect the point to which taxonomic progressions in plant-ants have proceeded in a region. The location of this point should depend on the ages of regional mesic-forest communities (to which most ant-plant symbioses are restricted), the traits of the particular dominant and subordinate ants evolved there during this period, and the degree to which the region is isolated from the products of taxonomic progressions begun elsewhere.

West Gondwanaland, today represented by its derivative continents Africa and South America, has been considered the cradle of the angiosperms (Raven and Axelrod 1974). Mesic tropical forest and its typical constituents, including plant-ants, have had a long history on both these continents. In Africa, for example, despite climatic vicissitudes and shifts in continental position, a large area of lowland tropical rain forest has persisted unbroken since the Late Cretaceous-Paleocene (75-55 my B.P.) up to the present (Axelrod and Raven 1978). That taxonomic progressions in Africa and South America began with similar starting material, and have continued for about the same amount of time, may account for many of the striking similarities in ant-plant symbioses of these two regions (McKey and Davidson, in press). Interestingly, these two continents share old, competitively subordinate ant groups like myrmelachistines and pseudomyrmecines. Although these taxa would respond in analogous ways to the later onslaught of dominants, the dominants are derived from different genera on the two continents. Whereas in the Neotropics, the preeminent competitive dominants consist of endemic *Azteca*, *Crematogaster* dominate in the Old World, where they are much more prevalent than in the American tropics (Appendix 1).

During virtually all the Tertiary, South America was an island continent (Barron et al., 1981, Gentry 1982). Perhaps the later appearing dominants, *Crematogaster* and *Acteca*, evolved long after direct exchange between the two continents (via overland connections or island filter bridges) became impossible. Evidence suggests that *Crematogaster* could be an Old World genus which arrived relatively late in the New World, possibly as part of a widespread tropical Laurasian biota, elements of which could have reached the Neotropics via North America. First recorded in Sicilian amber in the Miocene, the genus is represented in Dominican amber (late Miocene), and might conceivably have invaded South America via Panama, a connection in place since the Pliocene (Keigwin 1978, Barron et al. 1981, Marshall et al. 1982). Moreover, species richness of *Crematogaster* is greater in the African and Oriental tropics than in the Neotropics (Brown 1973), and the genus has evolved numerous specialized plant-ants in the former two regions, but only two such described species in the American tropics. From our summary in Appendix 1, relationships involving *Crematogaster* account for only 7.6 % of all 66 symbiotic ant-plant relationships listed for the Neotropics, but 39.5 % of 43 associations and 27.3 % of 33 relationships in Africa (including Malagasy) and the Oriental tropics, respectively. Based on analyses at the generic level, our calculations fail to take into account the substantial radiations of species within the genus *Crematogaster* on Asian *Macaranga* (Appendix 1), as well as the nine species of *Crematogaster* occurring on African *Musanga* (though probably none is a specialized plant-ant). No parallel radiations occur in the American tropics.

During the Tertiary, while the South American biota was evolving in isolation, there were repeated opportunities for biotic exchange between tropical Africa and tropical Laurasia. The latter region has long harbored mesic tropical forests, though opinions vary on whether these forests are as ancient as those of West Gondwanaland (Raven and Axelrod 1974). At the very least, the Oriental tropics were an area of moist, equable climate relatively removed from the major vicissitudes of Neogene and later climatic change (Raven and Axelrod 1974).

Biotic connections of tropical alliances, at least through the early Tertiary, may account for similarities in taxonomic composition of both subordinate and dominant plant-ants of the African and Oriental regions (e.g., *Tetraponera* as well as *Crematogaster* and *Oecophylla*). They may also help to explain some possible cases of common ancestry among ant-plant associations of the African and Oriental tropics (McKey and Davidson, in press).

Of the major tropical regions, the Australian tropics (northern Australia, New Guinea, and associated islands) are outstanding for the geologic youth of their tropical mesic-forest environments. By the Paleocene, Australia was connected with the rest of the world only by a cool-temperate pathway to South America via Antarctica (Raven and Axelrod 1974). At the start of its northward movement 45-49 my B.P., what is now tropical northern Australia was all well south of the Tropic of Capricorn, and was still 10 degrees south of its present position by the Miocene, when direct migration from the Asian tropics first became possible (Axelrod and Raven 1972). As for New Guinea, neither it nor its principal antecedents existed prior to about 40 my B.P. Only by the Miocene did it lie close enough to the proto-Indonesian arc to begin receiving large numbers of immigrants from tropical Asia. (However, as vertebrate distributions illustrate, such migration was never directly overland [Axelrod and Raven 1982]). Thus tropical northern Australia and mesic-forest portions of New Guinea have been populated to a large degree by taxa derived from the Asian tropics via intervening islands (Wilson 1961; Raven and Axelrod 1974). Nevertheless, the contemporary distributions of at least some plant-ants (e.g., *Anonychomyrma*, see Shattuck, 1992b) reveal an almost certain origin in Australasia.

Tropical forests of northern Australia and New Guinea provide uniquely little evidence for replacement of older and competitively subordinate ant genera by contemporary dominants. The origins of tropical rain forests in the Australian region have apparently been too recent to have allowed significant radiations of specialized plant-ants in more ancient and weakly competitive ant genera prior to the arrival and expansion of the dominants. If so, this could help to explain why the fraction of

ant-plants obviously specialized as myrmecophytes is so low in the Australian region (column 6 in Appendix 1). Compared to 51.2 % of 39 Neotropical ant-plant genera, 59.4 % of 32 African genera, and 41.4 % of 29 Oriental myrmecophyte genera, only 10.7 % of 28 such genera in the Australian region have conspicuous specializations to attract ants. In the last of these areas, only *Endospermum*, *Canthium* and *Calamus* have convincingly ant-attractive traits (Appendix 1). Present day plant-ants of this region consist principally of dominant species of *Anonychomyrma* (formerly included in *Iridomyrmex*, Shattuck 1992b), *Technomyrmex* and *Crematogaster*, as well as *Philidris* on epiphytic myrmecophytes (Shattuck 1992b). These ants occupy only a small number of variously preadapted host genera, where they maintain scale insects at remarkably high biomass, possibly limited by stem volume. Consistent with their status as dominants, they do not exhibit host fidelity in foraging. Neither pruning of host-plant neighbors, nor hiding among dense trichomes is required for persistence of such capable competitors. Two associations with weakly competitive ant genera may also be comparatively recent in origin. The *Camponotus* of *Endospermum* obtain their protein not from specially evolved plant structures, nor from protected sources within the stem (e.g., homoptera or the heteroplasias of, e.g., *Vitex*), but through a form of parasitism of external stem walls, i.e., the induction of heteroplasias from cambium (D. Davidson, personal observation). Moreover, at least one proposed myrmecophyte in this genus often occurs without its ants (Airy-Shaw 1980). Similarly, Ward (1991) notes that the unnamed *Tetraponera* tending coccids in terminal branches of *Cupaniopsis* has a much narrower geographic range than does its host, and that the symbiosis is apparently young.

In attempting to explain intercontinental differences in diversity, it will be extremely difficult to distinguish the relative importances of two major historical factors. These are regional differences in 1) the condensation of diversity through competition; and 2) the magnification of diversity, as affected by habitat diversity and its effects on rates of evolutionary host shifts and *de novo* evolutionary colonizations (see above and McKey and Davidson, in press.).

CONCLUSIONS

Similar selection pressures acting on correspondingly preadapted ants and plants have produced strikingly parallel and convergent evolution in the symbiotic ant-plant relationships of different tropical regions. Although current concepts of ant-plant coevolution focus on the pairwise interaction between ant and host plant, these alone cannot account for the patterns we observe. Even in relationships where pairwise interactions are undoubtedly strong, multispecies interactions appear to have determined many features of present-day symbioses. The most important force driving the evolutionary biology of ant-plant symbioses is interspecific competition among arboreal ants. Plants differ in the kinds of resources which they offer to ants, in the rates at which they supply these resources, and in traits which influence the relative competitive abilities of foraging and nesting ants. As in other communities structured by competition, plant-ants sort out across plants in ways that are predictable from their particular resource requirements and competitive abilities and the spectrum of available resources (see also Bristow 1991). In the American, African and Asian tropics, competitively dominant ants are associated with the most light-demanding and fast-growing hosts, which supply resources at the rates required to fuel rapid colony growth, interspecific aggression and other traits required for dominance. In contrast, competitively subordinate ants are restricted to plants which supply resources at rates too low to support dominant ants, or to those from which dominant ants can be excluded by long, dense plant hairs, pruning of neighboring vegetation, or by other ant and plant traits which favor competitively subordinate species. Competitive interactions among ants determine whether patterns of ant-plant association are sufficiently predictable for strong interactions to shape the evolution of ants and plants. When competitive interactions in plant-ant guilds result in constancy in the pairing of particular ants and plants, reciprocal evolutionary interactions may occasionally give rise to pairwise coevolution.

Parallel and convergent selection pressures acted on similar biological material on different tropical land masses. In American, African, Asian and

Australian regions, the same important preadaptations facilitated evolution of the plant-ant habit in several lineages of arboricolous ants. Foremost among these traits were the habit of tending Coccoidea, and the differential competitive abilities determined by generically typical offensive and defensive weaponry, or by inherent colony growth rates and other life-history attributes. Likewise, similar sets of plant traits facilitated the evolution of myrmecophytes on different continents. Structures evolved independently of ant-related selective pressures were co-opted repeatedly as myrmecophytic traits in plant lineages that eventually produced ant-plants. These traits included both the long, dense hairs typical of many myrmecophyte stems and domatia, and stems strongly thickened as support structures for large leaves, and available as nest sites for opportunistic ants. These similarities in starting material have rendered even more pronounced the striking parallel and convergent evolution of ant-plant symbioses in the New World and Old World tropics.

Diversity of both myrmecophytes and their attendant ants appears to accumulate mainly across habitats, rather than biogeographical regions (McKey and Davidson, in press). Among ant-plants, evolutionary diversification across habitat boundaries often appears to reflect the conflicting selection pressures imposed by different plant resource environments. Like other tropical plants (McKey et al. 1978, Coley 1983), myrmecophytes have responded evolutionarily to particular resource regimes by altering their relative investments in defense versus growth and, perhaps, their relative allocation of different kinds of resources to defensive function (Davidson and Fisher 1991, Folgarait and Davidson 1992). In turn, ecological and evolutionary responses of plants to different resource environments determine the quantity and quality of resource supply to ants. On the whole, then, both partners in ant-plant associations may be more sensitive to habitat than to taxonomic differences among symbiotic partners.

Strong competition among mutualists has been proposed as a major factor driving the evolution of specialization in mutualisms (Law and Koptur 1986), and it could help to account for the origins of many specialized ant-plant symbioses. Neverthe-

less, where sufficiently well-studied, phylogenies of plant-ants, together with host distributions of these ants, suggest that pairwise coevolution and cospeciation have been rare. Rather than simple, pairwise ant-plant systems, guilds of interacting ants and plants seem to be the most frequent arena of ant-plant evolutionary interaction. Perhaps as a consequence, plant-switching and secondary colonization (rather than cospeciation or some other form of association by descent) may have been the usual processes by which these mutualisms diversified. Repeated colonization of myrmecophyte taxa has occurred as unspecialized ants have exploited preexisting mutualisms and specialized plant-ants have switched hosts. Habitat-dependence in the effect of associations on fitness of the participants seems to have been the principal force leading to the evolution of new associations. The motor driving such evolutionary opportunities was likely the climatically induced range expansion that placed ants or plants into habitats sufficiently novel to change selection regimes, and to increase encounters with new associates (McKey and Davidson, in press).

Regardless of how species originate, a complex mosaic of habitats should help to maintain higher local diversity, with greater species richness of myrmecophytes and/or specialist plant-ants, and a greater number of ant/plant combinations. Since the potential for evolution of new associations via host shifts and secondary colonization depends in part on the sizes of locally interacting ant and plant guilds, high local diversity may lead to higher rates of species origination. Thus, independently of distributional changes driven by varying climates, beta-diversity is likely to have enhanced alpha-diversity.

As summarized here, the determinants of diversity of plants and ants in these symbiotic mutualisms will likely generalize to other components of tropical floras and faunas. In particular, we expect that diversification of tropical plants has often involved evolutionary adjustments in the amounts and kinds of defenses, in response to habitat differences in absolute and relative availabilities of essential resources. Consequently, habitat mosaics related to edaphic factors and incident solar radiation should often determine mosaics in the primary productiv-

ity available to consumer organisms. Habitat specialization to different productivity regimes has likely been important to both the generation and maintenance of diversity in many tropical consumer guilds whose member species have strongly overlapping resource requirements (cf., Terborgh 1983 for primates, and S. Robinson and J. Terborgh, personal communication, for birds).

Habitat specialization may frequently also represent the intermediate and final stages of a taxon pulse, in which new, opportunistic, abundant, and widespread species are driven to progressively greater specialization, finer niche differentiation, diminished distribution and abundance, and perhaps even eventual extinction (Wilson 1959a and 1961, Ashton 1969, Erwin 1985, Diamond 1986). If taxon cycles or pulses are general features of animal and plant lineages, they might aid in explaining patterns in the relative abundance distributions of taxa within higher taxa. Dial and Marzluff (1989) have discussed the frequency of "hollow curve distributions", or the overdominance of particular minor taxa within major taxa (subunits/unit). Thus, the degree of dominance of most dominant taxa is greater than that predicted by a variety of null models based on Poisson processes, random cladogenesis, and simultaneous or sequential resource subdivision, and it is compounded at lower levels of the taxonomic hierarchy. Taxon pulses might regularly give rise to such patterns if the enumeration of taxa at successively lower levels of the taxonomic hierarchy (where taxa are more numerous) were more likely to pick up comparatively rare groups which had recently acquired evolutionary novelties, and which represented intermediate stages of a taxon pulse.

Our analyses of the evolutionary dynamics of ant-plant symbioses here and elsewhere (McKey and Davidson, in press) lead us to propose new hypotheses to explain differences in the diversity of ant-plants and plant-ants across different tropical regions. Such disparities are quite pronounced between the American and African tropical regions, where ant-plant symbioses are best understood. Previous explanations for differences in the biodiversity of species-rich Neotropical and depauperate African rain forests have emphasized the contrasting climatic histories of these two regions.

Focusing on range contractions during periods of unfavorable climate, these explanations attribute Africa's lower diversity to greater extinction during the Pleistocene, as Africa's climate became drier, and refugia were fewer than in Amazonia (Raven and Axelrod 1974). We propose that differences between the two regions in the rates of species origination may be at least as important as extinction rates. The relatively stable geological history of most of Africa, including the rainforest zone, has created a landscape with relatively little elevational relief (hence few sharp spatial contrasts in temperature and rainfall), comparatively little edaphic variation, and relatively infrequent and spatially limited fluvial disturbance. In contrast, the Andean orogeny, and subandean tectonic activity, have helped to create a landscape of great elevational, climatic, and edaphic complexity, especially in western Amazonia. This has resulted in a complex and dynamic mosaic of habitats. Colinvaux (in press) suggests that species origination usually takes place when ranges are re-expanding during periods of climatic amelioration. If this is so, then in the Neotropics, especially in western Amazonia, range expansion would be much more likely than in the African forest zone to place ants and plants into novel habitats, leading to speciation, the formation of new associations, or both.

Although poorly known by comparison, Asian rain forests occur in regions (especially Borneo) where topography is substantially more variable than that of tropical Africa. Aided by forest fragmentation on numerous island land masses, this topography has contributed to the diversification of several myrmecophyte lineages here. Myrmecophyte diversity in Asia appears to be intermediate between that of the African and American tropics. On the other hand, both regions of the Old World tropics may have had the generic diversity of their plant-ant faunas condensed, relative to that of the New World, by the comparatively early arrival of a new wave of competitively dominant *Crematogaster*. The relatively recent origin of rain forests in the Australian tropics (including New Guinea and associated islands) appears to have limited the diversification of myrmecophytes in all but the epiphytic Hydnophytinae (Jebb 1991, Huxley and Jebb 1991). In addition, the elaboration of

myrmecophytic traits, which have evolved so frequently elsewhere in associations with weakly competitive ants, may have been limited in Australia by the cooccurrence of contemporary dominant and subordinate ants at the time when rain forests were evolving.

ACKNOWLEDGEMENTS

This work was supported by the NSF grants RII-8310359 and BSR-9003079, the Guggenheim Foundation, the Christensen Research Institute and the University of Utah's Faculty Research Committee (to Davidson) and the Swiss Natural History Society, the National Geographic Society, and the University of Miami (to McKey). We thank R. Snelling for numerous ant identifications, graciously fit into an overburdened schedule, and for helpful conversations about ants. J. Longino and P. Ward made invaluable comments on several previous drafts of the manuscript, and they and R. Snelling made available many of their unpublished observations. Any mistakes remaining are our own. We are also very grateful to M. Hossaert for facilitating our extensive E-Mail correspondence. The manuscript benefitted immeasurably from consultations over recent years with myrmecologists and botanists specializing in particular taxa or floras. These include: C. C. Berg, W. L. Brown, Jr., W. Burger, J. Dransfield, A. H. Gentry, W. Judd, J. Longino, J. Miller, T. Musthak Ali, S. Renner, S. O. Shattuck, J. C. Solomon, C. M. Taylor, H. van der Werff, P. S. Ward, and J. L. Zarucchi. Finally, since ant-plant symbioses are being drastically altered by habitat destruction around the world, we are particularly grateful for the natural parks and reserves that have permitted us and others to study these interactions in their pristine form.

LITERATURE CITED

- Addicott, J. 1985. Competition in mutualistic systems, pp. 217-247. In Boucher, D. H., ed., *The Biology of Mutualisms*. Oxford University Press, Oxford.
- Agosti, D. 1991. Revision of the Oriental ant genus *Cladomyrma*, with an outline of the higher classification of the Formicinae (Hymenoptera: Formicidae). *Systematic Entomology* 16: 293-310.
- Airy-Shaw, H. K. 1980. The Euphorbiaceae of New Guinea. *Kew Bulletin*, Additional Series 8: 1-243.
- Anderson, A. N. 1991. Parallels between ants and plants: implications for community ecology, pp. 539-558. In Huxley, C. R. and Cutler, D. F., eds. *Ant - Plant Interactions*. Oxford University Press, Oxford.
- Anderson, M. 1991. An ant-aphid interaction: *Formica fusca* and *Aphthargelia symphoricarpi* on Mount St. Helens. *American Midland Naturalist* 125: 29-36.
- Ashton, P. S. 1969. Speciation among tropical forest trees: some deductions in the light of recent evidence. *Biological Journal of the Linnean Society* 1: 155-196.
- Attygalle, A. B. and E. D. Morgan. 1984. Chemicals from the glands of ants. *Chemical Society Review* 13: 245-278.
- Axelrod, D. I. and P. H. Raven. 1972. Paleobiogeography and origin of the New Guinea flora, pp. 919-941. In Gressitt, J. L., ed., *Biogeography and Ecology of New Guinea*. Dr. W. Junk Publishers, The Hague.
- Axelrod, D. I. and P. H. Raven. 1978. Late Cretaceous and Tertiary vegetation history of Africa, pp. 77-130. In Werger, M. J. A., ed., *Biogeography and Ecology of Southern Africa*, Volume I. Dr. W. Junk Publishers, The Hague.
- Bailey, I. W. 1992. The anatomy of certain plants from the Belgian Congo with special reference to myrmecophytism. *Bulletin of the American Museum of Natural History* 45: 585-621.
- Barron, E. J., C. G. A. Harrison, J. L. Sloan II, and W. W. Hay. 1981. Paleogeography, 180 million years ago to the present. *Eclogae Geologicae Helveticae* 74: 443-470.
- Beattie, A. J. 1985. *The Evolutionary Ecology of Ant-Plant Mutualisms*. Cambridge University Press, Cambridge.
- Beccari, O. 1884. Piante ospitrici, ossia piante formicarie della Malesia e della Papuasias. *Malesia* (Genoa), 2: 1-340.
- Becerra, Judith X. I. and D. L. Venable. 1989. Extrafloral nectarials: a defense against ant-Homoptera mutualisms? *Oikos* 55: 276-279.
- Bengo, M. D. and J. Maley. 1991. Analyses des flux polliniques sur la marge sud du Golfe de Guinée depuis 135 000 ans. *Comptes rendues de l'Academie des Sciences de Paris Série II* 313: 843-849.
- Benson, W. W. 1985. Amazon ant-plants, pp. 239-266. In Prance, G. T. and T. E. Lovejoy, eds., *Amazonia*. Pergamon Press, New York.
- Bequaert, J. 1922. Ants of the American Museum Congo Expedition. A contribution to the myrmecology of Africa. IV. Ants in their diverse relations to the plant world. *Bulletin of the American Museum of Natural History* 45: 333-583.
- Berg, C. C. 1978. *Espécies de Cecropia da Amazônia Brasileira*. *Acta Amazonica* 8: 149-182.

- Berg, C. C., R. W. A. P. Akkermans, and E. C. H. van Heusden. 1990. Cecropiaceae: Coussapoa and Pourouma with an introduction to the family. *Flora Neotropica*, Monograph 51. New York Botanical Garden, New York.
- Bloom, A. J., F. S. Chapin, III, and H. A. Mooney. 1985. Resource limitation in plants—an economic analogy. *Annual Review of Ecology and Systematics* 16: 363-392.
- Blum, M. S. and H. R. Hermann. 1978. Venoms and venom apparatuses of the Formicidae: Myrmeciinae, Ponerinae, Dorylinae, Pseudomyrmecinae, Myrmicinae, and Formicinae, pp. 801-869. In Bettini, S., ed., *Arthropod Venoms*. Springer-Verlag, Berlin.
- Bower, F. 1887. On *Humboldtia laurifolia*, Vahl, as a myrmekophilous plant. *Proceedings of the Philosophical Society of Glasgow* 18: 320-326.
- Brandbyge, J. 1986. A revision of the genus *Triplaris* (Polygonaceae). *Nordic Journal of Botany* 6: 545-570.
- Brandbyge, J. 1990. Woody Polygonaceae from Brazil: new species and a new interpretation. *Nordic Journal of Botany* 10:155-160.
- Breteler, F. J. 1986. The African Dichapetalaceae. A Taxonomic Revision, IX. *Agricultural University of Wageningen Papers* 86-3, 74 pp.
- Bristow, C. M. 1991. Why are so few aphids ant-tended?, pp. 104-119. In Huxley, C. R. and D. F. Cutler, eds. *Ant-Plant Interactions*. Oxford University Press, Oxford.
- Bronstein, J. L. 1991. Mutualism studies and the study of mutualism. *Bulletin of the Ecological Society of America* 72: 6-8.
- Bronstein, J. L. 1992. Seed predators as mutualists: ecology and evolution of the fig / pollinator interaction, pp. 1-44. In Bernays, E. A., ed., *Insect-Plant Interactions*, Volume IV. CRC Press, Boca Raton, Florida.
- Brown, W. L., Jr. 1962. The neotropical species of the ant genus *Strumigenys* Fr. Smith: synopsis and keys to the species. *Psyche* 69: 238-267.
- Brown, W. L., Jr. 1973. A comparison of the Hylean and Congo-West African rain forest ant faunas, pp. 161-186. In Meggers, B. J., E. S. Ayensu and W. D. Duckworth, eds. *Tropical Forest Ecosystems in Africa and South America*. Smithsonian Institution Press, Washington, D. C.
- Buckley, R. C. 1987. Interactions involving plants, homoptera, and ants. *Annual Review of Ecology and Systematics* 18: 111-35.
- Burger, W. C. 1971. Piperaceae. *Fieldiana, Botany* 35: 5-227.
- Burger, W. C. and H. van der Werff. 1990. Flora Costaricensis, Family # 80 Lauraceae. *Fieldiana, Botany* 23: 1-138.
- Buschinger, A. and U. Maschwitz. 1984. Defensive behavior and defensive mechanisms in ants, pp. 95-150. In Hermann, H. R., ed., *Defense Mechanisms in Social Insects*. Praeger Scientific, New York.
- Campbell, D. G., P. M. Richardson and A. Rosas, Jr. 1989. Field screening for allelopathy in tropical forest trees, particularly *Duroia hirsuta*, in the Brazilian Amazon. *Biochemical Systematics and Ecology* 17: 403-407.
- Carroll, C. R. 1979. A comparative study of two ant faunas: the stem-nesting ant communities of Liberia, West Africa and Costa Rica, Central America. *American Naturalist* 113: 551-561.
- Carroll, C. R. 1983. *Azteca* (*Horniga azteca*, *Azteca* ants, *Cecropia* ants), pp. 691-693. In Janzen, D. H. ed., *Costa Rican Natural History* 691-693. University of Chicago Press, Chicago.
- Carroll, C. R. and D. H. Janzen. 1973. The ecology of foraging by ants. *Annual Review of Ecology and Systematics* 4: 231-258.
- Coley, P. D. 1983. Intraspecific variation in herbivory on two tropical tree species. *Ecology* 64: 426-433.
- Colinvaux, P. In press. Pleistocene biogeography and diversity in tropical forest of South America and Africa. In Goldblatt, P., ed., *Biological Relationships between Africa and South America*. Yale University Press, New Haven.
- Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111: 1119-1144.
- Coode, M. J. E. 1981. Elaeocarpaceae, pp. 38-185. In Henty, E.E., ed., *Handbooks of the Flora of Papua New Guinea*, 2. Melbourne Press, Melbourne.
- CSIRO. 1970. *The Insects of Australia*. Melbourne University Press, Melbourne, 1029 pp.
- Cushman, J. H. and J. F. Addicott. 1991. Conditional interactions in ant-plant-herbivore mutualisms, pp. 92-103. In Huxley, C. R. and D. F. Cutler, eds., *Ant-Plant Interactions*. Oxford University Press, Oxford.
- Darlington, P. J., Jr. 1957. *Zoogeography: The Geographical Distribution of Animals*. John Wiley and Sons, New York.
- Davidson, D. W. 1988. Ecological studies of neotropical ant-gardens. *Ecology* 69: 1138-1152.
- Davidson, D. W. and W. W. Epstein. 1989. Epiphytic associations with ants, pp. 200-233. In Lüttge, U. (Ed.), *Vascular Plants as Epiphytes*. Springer-Verlag, Berlin.

- Davidson, D.W. and B. L. Fisher. 1991. Symbiosis of ants with *Cecropia* as a function of the light regime, pp. 289-309. In Huxley, C. R. and D. K. Cutler eds., *Ant - Plant Interactions*. Oxford University Press, Oxford.
- Davidson, D. W., R. B. Foster, R. R. Snelling, and P. W. Lozada. 1991. Variable composition of some tropical ant-plant symbioses, pp. 145-162. In Price, P. W., T. M. Lewinsohn, G. W. Fernandes and W. W. Benson, eds., *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*. John Wiley & Sons, Inc., New York.
- Davidson, D. W., J. T. Longino, and R. R. Snelling. 1988. Pruning of host plant neighbors by ants: an experimental approach. *Ecology* 69: 801-808.
- Davidson, D. W., R. R. Snelling and J. T. Longino. 1989. Competition among ants for myrmecophytes and the significance of plant trichomes. *Biotropica* 21: 64-73.
- de Candolle, C. 1916. Piperaceae Philippinenses novae vel nuper repertae. *Philippine Journal of Science (Botany)* 11: 207-225.
- Dejean, A. and C. Djéto. 1990. The choice of the nesting site by *Oecophylla longinoda*: roles of imprinting and selective attraction to plants, pp. 85-86. In Veeresh, G. K., B. Mallik and C. A. Viraktamath, eds., *Social Insects and the Environment*. Proceedings, 11th International Congress of the International Union for the Study of Social Insects. Oxford University Press, New Delhi.
- Dejean, A., C. Djéto and S. Ngnokam. 1992. Les relations plantes-fourmis: nouvel aperçu. *Mémoires de la Société royale belge d'Entomologie* 35: 563-567.
- Dejean, A., R. Mony, S. Ngnokam and C. Djéto. 1990. Arboreal nesting in various African ants, p. 659. In Veeresh, G. K., B. Mallik and C. A. Viraktamath, eds., *Social Insects and the Environment*. Proceedings, 11th International Congress of the International Union for the Study of Social Insects. Oxford University Press, New Delhi.
- de Wit, H. C. D. 1942. Conspectus of the genus *Archidendron* F. von Mueller (Legum.). *Bulletin of the Botanical Garden of Bütenzorg* 17: 256-272.
- Dial, K. P. and Marzluff, J. M. 1989. Nonrandom diversification within taxonomic assemblages. *Systematic Zoology* 38: 26-37.
- Diamond, J. 1986. Evolution of ecological segregation in the New Guinea montane avifauna, pp. 98-125. In Diamond, J. and T. J. Case, eds., *Community Ecology*. Harper and Row, New York.
- Ding Hou. 1978. Anacardiaceae, pp. 395-548. In van Steenis, C. G. G. J. and W. J. J. O. de Wilde, eds., *Flora Malesiana Series I, Volume 8*. Kluwer, Dordrecht.
- Dorow, W.H.O. and U. Maschwitz. 1990. The Arachne-group of *Polyrachis* (Formicidae, Formicinae): weaver ants cultivating homoptera on bamboo. *Insectes Sociaux* 37: 73-89.
- Dransfield, J. 1978. New records of rattans (Palmae: Lepidocaryoideae) for Peninsular Malaysia. *Malayan Nature Journal* 30: 523-531.
- Dransfield, J. 1981. A synopsis of the genus *Korthalsia* (Palmae: Lepidocaryoideae). *Kew Bulletin* 36: 163-194.
- Dransfield, J. 1984. *The Rattans of Sabah*. Forest Department, Sabah, 182 pp.
- Duviard, D. and P. Segeren. 1974. La colonisation d'un myrmécophyte, le parasolier, par *Crematogaster* spp. (Myrmicinae) en Côte-d'Ivoire forestière. *Insectes Sociaux* 21: 191-212.
- Eisner, T. 1957. A comparative morphological study of the proventriculus of ants (Hymenoptera: Formicidae). *Bulletin of the Museum of Comparative Zoology, Harvard* 116(8): 439-490.
- Erwin, T. L. 1985. The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles, pp. 437-472. In Ball, G. E., ed., *Taxonomy, Phylogeny, and Zoogeography of Beetles and Ants*. Dr. W. Junk, Dordrecht.
- Feinsinger, P. and R. K. Colwell. 1978. Community organization among neotropical nectar-feeding birds. *American Zoologist* 18: 779-795.
- Fiala, B. and U. Maschwitz. 1990. Studies on the South East Asian ant-plant association *Crematogaster borneensis/Macaranga*: adaptations of the ant partner. *Insectes Sociaux* 37: 212-231.
- Fiala, B. and U. Maschwitz. 1991. Extrafloral nectaries in the genus *Macaranga* (Euphorbiaceae) in Malaysia: comparative studies of their possible significance as predispositions for myrmecophytism. *Biological Journal of the Linnean Society* 44: 287-305.
- Fiala, B., U. Maschwitz and Y. P. Tho. 1991. The association between *Macaranga* trees and ants in South-east Asia, pp. 263-270. In Huxley, C. R. and D. F. Cutler, eds., *Ant - Plant Interactions*. Oxford University Press, Oxford.
- Fiala, B., U. Maschwitz, Y. P. Tho, and A. J. Helbig. 1989. Studies of a South East Asian ant-plant association: protection of *Macaranga* trees by *Crematogaster borneensis*. *Oecologia* (Berlin) 79: 463-470.
- Folgarait, P. and D. Davidson. 1992. Interspecific and intraspecific variation in defense investment in *Cecropia*, p. 18. In *Abstracts of the Annual Meeting of*

- The Association for Tropical Biology*, August 9-13, Honolulu, Hawaii.
- Forel, A. 1904. In und mit Pflanzen lebende Ameisen aus dem Amazonas-Gebiet und aus Peru. *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere* 20: 677-707.
- Forel, A. 1928. *The Social World of Ants in Relation with that of Man*, 2 vols, trans. Ogden, C. K. G. P. Putnam's Sons, London, 551 + 445 pp.
- Foreman, D. B. 1978. Myristicaceae (excluding *Horsfieldia*), pp. 175-215. In J. S. Womersley (Ed), *Handbook of the Flora of Papua New Guinea*, Volume 1. Melbourne University Press, Melbourne.
- Freese, C. H. 1976. Predation on swollen-thorn acacia ants by white-faced monkeys. *Cebus capucinus*. *Biotropica* 8: 278-281.
- Gautier-Hion, A., J. M. Duplantier, R. Quris, F. Feer, C. Sourd, J. P. Decoux, G. Dubost, L. Emmons, C. Erard, H. Hecketsweiler, A. Mougazi, C. Roussillon, and J. M. Thiollay. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* (Berlin) 65: 324-337.
- Gentry, A. H. 1986. Endemism in tropical vs. temperate plant communities, pp. 153-181. In Soulé, M. E., ed., *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, Massachusetts.
- Gentry, A. H. 1989. Speciation in tropical forests, pp. 113-134. In Holm-Nielsen, L. B., I. C. Nielsen and H. Balslev, eds., *Tropical Forests*. Academic Press, New York.
- Gentry, A. H. In press. Diversity and floristic composition in lowland tropical forest in Africa and South America. In Goldblatt, P. ed., *Biological Relationships between Africa and South America*. Yale University Press, New Haven.
- Gibbs, P. E. and N. Taroda. 1983. Heterostyly in the *Cordia alliodora* - *C. trichotoma* complex in Brazil. *Revista Brasileira de Botânica* 6: 1-10.
- Givnish, T. J. 1987. Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytologist* 106 (Suppl.): 131-160.
- Gottsberger, G. 1990. Flowers and beetles in the South American tropics. *Botanica Acta* 103: 360-365.
- Grime, J. P. 1974. Vegetation classification by reference to strategies. *Nature* (London) 250: 26-31.
- Hallé, F., R. A. A. Oldeman, and P. B. Tomlinson. 1978. *Tropical Trees and Forests*. Springer-Verlag, Berlin. 441 pp.
- Hallé, N. 1970. Rubiacées (2e partie), pp. 1-335. In Aubréville, A. and J.-F. Leroy, eds., *Flore du Gabon*, Volume 17. Muséum National d'Histoire Naturelle, Paris.
- Harada, A. Y. and W. W. Benson. 1988. Espécies de *Azteca* (Hymenoptera, Formicidae) especializadas em *Cecropia* (Moraceae): distribuição geográfica e considerações ecológicas. *Revista Brasileira de Entomologia* 32: 423-435.
- Hartley, T. G. 1966. A revision of the Malesian species of *Zanthoxylum* (Rutaceae). *Journal of the Arnold Arboretum* 47:171-221.
- Haskins, C. 1939. *Of Ants and Men*. Prentice-Hall, New York, 244 pp.
- Heithaus, E. R., T. H. Fleming, and P. A. Opler. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology* 56: 841-854.
- Herre, E. A., D. M. Windsor, and R. B. Foster. 1986. Nesting associations of wasps and ants on lowland Peruvian ant-plants. *Psyche* 93: 321-330.
- Herrera, C. M. 1984. A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. *Ecological Monographs* 54: 1-23.
- Hocking, B. 1970. Insect associations with the swollen thorn acacias. *Transactions of the Royal Entomological Society of London* 122: 211-255.
- Hölldobler, B. and H. Engel-Siegel. 1984. On the metapleural glands of ants. *Psyche* 91: 201-224.
- Hölldobler, B. and E. O. Wilson. 1990. *The Ants*. Belknap Press, Cambridge, Massachusetts, 732 pp.
- Howe, H. F. 1984. Constraints on the evolution of mutualism. *American Naturalist* 123: 764-777.
- Howe, H. F. and L. C. Westley. 1988. *Ecological Relationships of Plants and Animals*. Oxford University Press, Oxford, 273 pp.
- Huxley, C. R. 1986. Evolution of benevolent ant-plant relationships, pp. 257-282. In Juniper, B. and Sir R. Southwood, eds, *Insects and the Plant Surface*. Edward Arnold, London.
- Huxley, C. R. and M. H. P. Jebb. 1991. The tuberous epiphytes of the Rubiaceae 1: a new subtribe - the Hydnophytinae. *Blumea* 36: 1-20.
- Ibarra-Menríquez, G. and R. Dirzo. 1990. Plantas mirmecófilas arbóreas de la Estación de Biología "Los Tuxtlas", Veracruz, México. *Revista Biológica Tropical* 38:79-82.
- Janson, C. 1983. Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science* 219: 187-189.
- Janzen, D. H. 1966. Coevolution of mutualism between ants and acacias in central America. *Evolution* 20: 249-275.

- Janzen, D. H. 1967a. Fire, vegetation structure and the ant-Acacia interaction in Central America. *Ecology* 48: 26-35.
- Janzen, D. H. 1967b. Why mountain passes are higher in the tropics. *American Naturalist* 101: 233-249.
- Janzen, D. H. 1969. Allelopathy by myrmecophytes: the ant *Azteca* as an allelopathic agent of *Cecropia*. *Ecology* 50: 147-153.
- Janzen, D. H. 1972. Protection of *Barteria* (Passifloraceae) by *Pachysima* ants (Pseudomyrmecinae) in a Nigerian rain forest. *Ecology* 53: 885-892.
- Janzen, D. H. 1973. Dissolution of mutualism between *Cecropia* and its *Azteca* ants. *Biotropica* 5: 15-28.
- Janzen, D. H. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day and insularity. *Ecology* 54: 687-708.
- Janzen, D. H. 1974a. Swollen-thorn acacias of Central America. *Smithsonian Contributions to Botany* 13: 1-131.
- Janzen, D. H. 1974b. Epiphytic myrmecophytes in Sarawak: mutualism through the feeding of plants by ants. *Biotropica* 6: 237-259.
- Janzen, D. H. 1975. *Pseudomyrmex nigropilosa*: a parasite of a mutualism. *Science* 188: 936-37.
- Janzen, D. H. 1983. *Pseudomyrmex ferruginea* (Hormiga del cornizuelo, acacia-ant), pp. 762-764. In Janzen, D. H. ed., *Costa Rican Natural History*. University of Chicago Press, Chicago.
- Jebb, M. H. P. 1991. Cavity structure and function in the tuberous Rubiaceae, pp. 374-389. In Huxley, C. R. and D. F. Cutler, eds., *Ant - Plant Interactions*. Oxford University Press, Oxford.
- Jolivet, P. 1986. *Les Fourmis et les Plantes*. Paris: Boubée, 254 pp.
- Jolivet, P. 1991. Ants, plants, and beetles: a triangular relationship, pp. 397-406. In Huxley, C. R. and D. F. Cutler, eds., *Ant - Plant Interactions*. Oxford University Press, Oxford.
- Jordano, P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *American Naturalist* 129: 657-677.
- Judd, W. S. 1989. Taxonomic studies in the Miconieae (Melastomataceae). III. Cladistic analysis of axillary-flowered taxa. *Annals of the Missouri Botanical Garden* 76: 476-495.
- Judd, W. S. and J. D. Skean, Jr. 1991. Taxonomic studies in the Miconieae (Melastomataceae) IV. Generic realignments among terminal-flowered taxa. *Bulletin of the Florida Museum of Natural History, Biological Sciences* 36: 25-84.
- Keigwin, L. D., Jr. 1978. Pliocene closing of the Isthmus of Panama, based on biostratigraphic evidence from nearby Pacific Ocean and Caribbean Sea cores. *Geology* 6: 630-634.
- Kiester, A. R., R. Lande, and D. W. Schemske. 1984. Models of coevolution and speciation in plants and their pollinators. *American Naturalist* 124: 220-243.
- Koepcke, M. 1972. Ueber die Resistenzformen der Vogelneester in einem begrenzten Gebiet des tropischen Regenwaldes in Peru. *Journal für Ornithologie* 113: 138-160.
- Krishna, K. and D. Grimaldi. 1991. A new fossil species from the Dominican amber of the living Australian termite genus *Mastotermes* (Isoptera: Mastotermitidae). *American Museum Novitates* 3021:1-10.
- Law, R. and S. Koptur. 1986. On the evolution of non-specific mutualism. *Biological Journal of the Linnean Society* 27: 251-267.
- Leenhouts, P. W. and M. Vente. 1982. A taxonomic revision of *Harpullia* (Sapindaceae). *Blumea* 28: 1-51.
- Leston, D. 1973. The ant mosaic - tropical tree crops and the limiting of pests and disease. *Pest Articles and News Summaries* 19: 311-336.
- Letourneau, D. K. 1983. Passive aggression: an alternative hypothesis for the *Piper-Pheidole* association. *Oecologia* (Berlin) 60: 122-126.
- Letourneau, D. K. 1990. Code of ant-plant mutualism broken by parasite. *Science* 248: 215-217.
- Letourneau, D. K. 1991. Parasitism of ant-plant mutualisms and the novel case of *Piper*, pp. 390-396. In Huxley, C. R. and D. K. Cutler, eds., *Ant - Plant Interactions*. Oxford University Press, Oxford.
- Letourneau, D. K., A. G. Feyner, and M. Jebb. 1993. Coping with enemy-filled space: herbivores on Endospermium, in Papua New Guinea. *Biotropica* 25:95-99.
- Letouzey, R. and F. White. 1970. Ébénacées, pp. 3-184. In A. Aubréville and J.-F. Leroy (Eds), *Flore du Cameroun*, Volume 11. Paris: Muséum National d'Histoire Naturelle.
- Letouzey, R. and F. White. 1976. Chrysobalanacées nouvelles du Cameroun et du Gabon. *Adansonia*, ser. 2, 16: 229-243.
- Letouzey, R. and F. White. 1978. Chrysobalanacées, pp. 3-138. In Aubréville, A. and J.-F. Leroy, eds., *Flore du Cameroun*, Volume 20. Muséum National d'Histoire Naturelle, Paris.
- Longino, J. T. 1987. Ants in live oak galls in Texas. *National Geographic Research* 3: 125-127.
- Longino, J. T. 1989a. Geographic variation and community structure in an ant-plant mutualism: *Azteca*

- and *Cecropia* in Costa Rica. *Biotropica* 21: 126-132.
- Longino, J. T. 1989b. Taxonomy of the *Cecropia* - inhabiting ants in the *Azteca alfari* species group (Hymenoptera: Formicidae): evidence for two broadly sympatric species. *Natural History Museum of Los Angeles County, Contribution in Science* 412: 1-16.
- Longino, J. T. 1991a. *Azteca* ants in *Cecropia* trees: taxonomy, colony structure and behavior, pp. 271-288. In Huxley, C. R. and D.K. Cutler, eds., *Ant - Plant Interactions*. Oxford University Press, Oxford.
- Longino, J. T. 1991b. Taxonomy of the *Cecropia*-inhabiting *Azteca* ants. *Journal of Natural History* 25: 1571-1602.
- Mabberley, D. J. 1979. The species of *Chisocheton* (Meliaceae). *Bulletin of the British Museum of Natural History (Botany)* 6: 301-386.
- Mabberley, D. J. 1985. Florae malesianae praecursores LXVII. Meliaceae (divers genera). *Blumea* 31: 129-152.
- Mabberley, D. J. 1987. *The Plant-Book*. Cambridge University Press, Cambridge. 707 pp.
- Maguire, B. and R. E. Weaver, Jr. 1975. The Neotropical genus *Tachia* (Gentianaceae). *Journal of the Arnold Arboretum* 56: 103-125.
- Marshall, L. G., S. D. Webb, J. J. Sepkoski, and D. M. Raup. 1982. Mammalian evolution and the great American interchange. *Science* 215: 1351-1357.
- Maschwitz, U. 1974. Vergleichende Untersuchungen zur Funktion der Ameisenmetathorakaldrüse. *Oecologia* (Berlin) 16: 303-310.
- Maschwitz, U. and B. Fiala. 1992. A new ant-tree from SE Asia: *Zanthoxylum myriacanthum* (Rutaceae), the thorny ivy-rue (Chenkering, Kabu Kabu Utah). *Malayan Nature Journal* 46: 101-109.
- Maschwitz, U., B. Fiala, Y. F. Lee, V. K. Chey, and F. L. Tan. 1989. New and little-known myrmecophytic associations from Bornean rain forests. *Malayan Nature Journal* 43: 106-115.
- Maschwitz, U., B. Fiala, J. Moog and L. G. Saw. 1991. Two new myrmecophytic associations from the Malay Peninsula: ants of the genus *Cladomyrma* (Formicidae, Camponotinae) as partners of *Saraca thaipingensis* (Caesalpinaceae) and *Crypteronia griffithii* (Crypteroniaceae). 1. Colony foundation and acquisition of trophobionts. *Insectes Sociaux* 38: 27-35.
- McKey, D. 1974. Ant-plants: selective eating of an unoccupied *Barteria* by a colobus monkey. *Biotropica* 6: 269-270.
- McKey, D. 1984. Interaction of the ant-plant *Leonardoxa africana* (Caesalpinaceae) with its obligate inhabitants in a rainforest in Cameroon. *Biotropica* 16: 81-99.
- McKey, D. 1988. Promising new directions in the study of ant-plant mutualisms, pp. 335-355. In Greuter, W. and B. Zimmer, eds., *Proceedings of the XIV International Botanical Congress*. Koeltz, Königstein/Taunus, Germany.
- McKey, D. 1989. Interactions between ants and leguminous plants, pp. 673-718. In Stirton, C. H. and J. L. Zarucchi, eds., *Advances in Legume Biology, Monographs in Systematic Botany, No. 29*. Missouri Botanical Garden, St. Louis.
- McKey, D. 1991. Phylogenetic analysis of the evolution of a mutualism: *Leonardoxa* (Leguminosae: Caesalpinioideae), pp. 310-334. In Huxley, C. H. and D. K. Cutler, eds., *Ant - Plant Interactions*. Oxford University Press, Oxford.
- McKey, D. and D. W. Davidson. In press. Ant - plant interactions in Africa and the Neotropics: history, biogeography and diversity. In P. Goldblatt (Ed), *Biological Relationships between Africa and South America*. Yale University Press, New Haven.
- McKey, D., P. G. Waterman, C. N. Mbi, J. S. Gartlan and T. T. Struhsaker. 1978. Phenolic content of vegetation in two African rain forests: ecological implications. *Science* 202: 61-64.
- Merlin, P., J. C. Brackman, D. Daloz, M. Pasteels and A. Dejean. 1992. New C_{26} γ -lactones from the Dufour's gland of the urticating ant *Tetramorium acaule*. *Experientia* 48: 111-113.
- Mitter, C. and D. R. Brooks. 1983. Phylogenetic aspects of coevolution, pp. 65-98. In Futuyma, D. J. and M. Slatkin, eds., *Coevolution*. Sinauer, Sunderland, Massachusetts.
- Moermond, T. C. and J. S. Denslow. 1985. Neotropical avian frugivores: patterns of behavior, morphology, and nutrition with consequences for fruit selection, pp. 865-897. In Buckley, P. A., M. S. Foster, E. S. Morton, R. S. Ridgely, and N. G. Smith, eds., *Neotropical Ornithology*. American Ornithological Society, Washington, D. C.
- Monteith, G. B. 1986. Presidential Address. Some curious insect-plant associations in Queensland. *Queensland Naturalist* 26: 105-114.
- Monteith, G. B. 1987. *Endospermum*, ants and uraniid moths in Australia. *Queensland Naturalist* 28: 35-41.
- Morawetz, W., M. Henzl and B. Wallnöfer. 1992. Tree killing by herbicide producing ants for the establishment of pure *Tococa occidentalis* populations in the Peruvian Amazon. *Biodiversity and Conservation* 1:

- 19-33.
- Nkongmeneck, B.-A. 1985. Le genre *Cola* au Cameroun. *Annales de la Faculté de Sciences, Biologie-Biochimie, Université de Yaounde* 3: 5-27.
- O'Dowd, D. J. and M. F. Willson. 1989. Leaf domatia and mites on Australasian plants: ecological and evolutionary implications. *Biological Journal of the Linnean Society* 37: 191-236.
- Oliveira, P.S., A. T. Oliveira-Filho and R. Cintra. 1987. Ant foraging on ant-inhabited *Triplaris* (Polygonaceae) in western Brazil: a field experiment using live termite-baits. *Journal of Tropical Ecology* 3: 193-200.
- Oster, G. F. and E. O. Wilson. 1978. *Caste and Ecology in the Social Insects*. Princeton University Press, Princeton, New Jersey, 352 pp.
- Pennington, T. D. 1981. *Meliaceae*. Flora Neotropica, Monograph No. 28. New York Botanical Garden, New York, 470 pp.
- Philpson, W. R. 1984. A synopsis of the Malesian species of *Steganotheca* (Monimiaceae). *Blumea* 29: 481-497.
- Philpson, W. R. 1985. A synopsis of the Malesian species of *Kibara* (Monimiaceae). *Blumea* 30: 389-415.
- Pontin, A. J. 1958. A preliminary note on the eating of aphids by ants of the genus *Lasius*. *Entomologist's Monthly Magazine* 94: 9-11.
- Pontin, A. J. 1978. The numbers and distribution of subterranean aphids and their exploitation by the ant *Lasius flavus* (Fabr.). *Ecological Entomology* 3: 203-207.
- Prance, G. T. 1972. *The Chrysobalanaceae*. Flora Neotropica, Monograph No. 9. New York Botanical Garden, New York, 410 pp.
- Prance, G. T. 1989. *Chrysobalanaceae*. Flora Neotropica, Monograph 9S. New York Botanical Garden, New York, 267 pp.
- Putz, F. E. and N. M. Holbrook. 1988. Further observations on the dissolution of mutualism between *Cecropia* and its ants: the Malaysian case. *Oikos* 53: 121-125.
- Räsänen, M. E., J. S. Salo and R. Kalliola. 1987. Fluvial perturbation in the western Amazon basin: regulation by long-term sub-Andean tectonics. *Science* 238: 1398-1401.
- Raven, P. H. and D. I. Axelrod. 1972. Plate tectonics and Australasian paleobiogeography. *Science* 176: 1379-1386.
- Raven, P. H. and D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Garden* 61: 539-673.
- Renner, S. 1986. The neotropical epiphytic Melastomataceae: phytogeographic patterns, fruit types and floral biology. *Selbyana* 9: 104-111.
- Ricklefs, R. E. and G. W. Cox. 1972. Taxon cycles in the West Indian avifauna. *American Naturalist* 106: 195-219.
- Rickson, F. R. 1977. Progressive loss of ant-related traits of *Cecropia peltata* on selected caribbean islands. *American Journal of Botany* 64: 585-592.
- Rickson, F. R. 1979. Absorption of animal tissue breakdown products into a plant stem—the feeding of a plant by ants. *American Journal of Botany* 66: 87-90.
- Rickson, F. R. and M. M. Rickson. 1986. Nutrient acquisition facilitated by litter collection and ant colonies on two Malaysian palms. *Biotropica* 18: 337-343.
- Rico-Gray, V. and L. B. Thien. 1989. Effect of different ant species on reproductive fitness of *Schomburgkia tibicinis* (Orchidaceae). *Oecologia* (Berlin) 81: 487-489.
- Ridley, H. N. 1910. Symbiosis of ants and plants. *Annals of Botany* 24: 457-483.
- Ridsdale, C. E. 1978. A revision of the tribe Naucleaceae s.s. (Rubiaceae). *Blumea* 24: 307-366.
- Risch, S., M. McClure, J. Vandermeer and S. Waltz. 1977. Mutualism between three species of tropical *Piper* (Piperaceae) and their ant inhabitants. *American Midland Naturalist* 98: 433-444.
- Risch, S. J. and F. R. Rickson. 1981. Mutualism in which ants must be present before plants produce food bodies. *Nature* (London) 291: 149-50.
- Robbrecht, E. 1979. The African genus *Tricalysia* A. Rich. (Rubiaceae-Coffeaceae). 1. A revision of the species of subgenus *Empogona*. *Bulletin du Jardin Botanique National de Belgique* 49:239-360.
- Rojo, J. P. 1972. *Pterocarpus* (Leguminosae-Papilionaceae) revised for the world. *Phanerogamartum Monographiae* 5. Verlag von J. Cramer, Leutershausen, Germany, 119 pp.
- Ross, J. H. 1981. An analysis of the African *Acacia* species: their distribution, possible origins, and relationships. *Bothalia* 13: 389-413.
- Salo, J., R. Kalliola, I. Häkkinen, Y. Mäkinen, P. Niemelä, M. Puhakka and P. D. Coley. 1986. River dynamics and the diversity of Amazon lowland forest. *Nature* (London) 322: 254-258.
- Schemske, D. W. 1983. Limits to specialization and coevolution in plant-animal mutualisms. pp. 67-109. In Nitecki, M. H. ed., *Coevolution*. University of Chicago Press, Chicago.

- Schemske, D. W. and C. C. Horvitz 1988. Plant-animal interactions and fruit production in a neotropical herb: a path analysis. *Ecology* 69: 1128-1137.
- Schnell, R. 1966. Remarques morphologiques sur les "myrmécophytes." *Mémoires de la Société Botanique de France* 1966: 121-132.
- Schnell, R. 1967. Contribution à l'étude des genres Guyano-Amazoniens *Tococa* Aubl. et *Maieta* Aubl. (Mélastomacées) et de leurs poches foliaires. *Adansonia* 6: 525-532.
- Schnell, R., G. Cusset, V. Tchinye and N. T. Anh. 1968. Contribution à l'étude des "acarodomaties." La question des aisselles des nervures. *Revue Générale de Botanique* 75: 5-64.
- Schnell, R. and F. Grout de Beaufort. 1966. Contribution à l'étude des plantes à myrmécodomaties de l'Afrique intertropicale. *Mémoires de l'Institut Fondamental d'Afrique Noire*, No. 75: 1-66. Mélanges Botaniques, Dakar.
- Schumann, K. 1890. Einige weitere Ameisenpflanzen. *Verhandlungen des Botanischen Vereins für Brandenburg* 31: 113-123.
- Schumann, K. and K. Lauterbach. 1901. *Die Flora der deutschen Schutzgebiete in der Südsee*. Berlin.
- Schupp, E. and D. H. Feener, Jr. 1991. Phylogeny, lifeform and habitat dependence of ant-defended plants in a Panamanian forest, pp. 175-197. In Huxley, C. R. and D. K. Cutler, eds., *Ant - Plant Interactions*. Oxford University Press, Oxford.
- Shattuck, S. O. 1991. Revision of the dolichoderine ant genus *Axindris* (Hymenoptera: Formicidae). *Systematic Entomology* 16: 105-120.
- Shattuck, S. O. 1992a. A Generic revision of the ant subfamily Dolichoderinae (Hymenoptera: Formicidae). *Sociobiology* 21:1-181.
- Shattuck, S. O. 1992b. Review of the Dolichoderine ant genus *Iridomyrmex* Mayr with descriptions of three new genera (Hymenoptera: Formicidae). *Journal of the Australasian Entomological Society* 31:13-18.
- Simpson, B. B. and C. A. Todzia. 1990. Patterns and processes in the development of the high Andean flora. *American Journal of Botany* 77: 1419-1432.
- Snelling, R. R. 1979a. *Aphomyrmex* and a related new genus of arboreal African ants (Hymenoptera: Formicidae). *Contributions in Science from the Natural History Museum of Los Angeles County* 316: 1-8.
- Snelling, R. R. 1979b. Three new species of the palaeotropical arboreal ant genus *Cataulacus* (Hymenoptera: Formicidae). *Contributions in Science from the Natural History Museum of Los Angeles County* 315: 1-8.
- Snow, D. W. 1981. Tropical frugivorous birds and their food plants: A world survey. *Biotropica* 13:1-14.
- Solereder, H. 1920. Über eine heterophylle philippinische Ameisenpflanze aus der Familie der Melastomataceae, nebst Bemerkungen über das Auftreten von Amylodextrin-Körnern in den sog. Perldrüsen. *Naturwissenschaftliche Wochenschrift* 35: 689-691.
- Spruce, R. 1908. *Notes of a Botanist on the Amazon and Andes*. Vol. II. Johnson Reprint Corporation, New York, 542 pp.
- Steenis, C. G. G. J. van. 1967. Miscellaneous Botanical Notes XVIII. *Blumea* 15: 145-155.
- Steenis, C. G. G. J. van and W. J. J. O. de Wilde, eds. 1950-1989. *Flora Malesiana*. Kluwer, Dordrecht.
- Stevens, P.F. 1978. Meliaceae, pp. 135-174. In Womersley, J. S. ed., *Handbooks of the Flora of Papua New Guinea*. Volume 1. Melbourne University Press, Melbourne.
- Stitz, H. 1910. Westafrikanische Ameisen. I. *Mitteilungen aus dem Zoologischen Museum in Berlin* 5: 127-151.
- Stitz, H. 1913. Ameisen und Pflanzen. *Die Naturwissenschaften*, 1: 1281-1288.
- Stone, B. C., and T. C. Whitmore. 1970. Notes on the systematy of Solomon Islands' plants and some of their New Guinea relatives. XI. *Tapeinosperma* (Myrsinaceae). *Reinwardtia* 8: 3-11.
- Svoma, E. and W. Morawetz. 1992. Drusenhaare, Emergenzen und Blattdomatien bei der Ameisenpflanze *Tococa occidentalis* (Melastomataceae). *Botanische Jahrbucher* 114:185-200.
- Tennant, L. E. 1989. A new ant-plant, *Tetrathylaciun costaricense*, p. 27. Abstracts, *Symposium on Interactions between Ants and Plants*, Oxford, England, July 1989.
- Terborgh, J. 1983. *Five New World Primates*. Princeton University Press, Princeton, New Jersey.
- Terron, G. 1970. Recherches morphologiques et biologiques sur *Tetraponera anthracina* Santschi et sur son parasite social temporaire *Tetraponera ledouxi* Terron. *Thèse, Docteur es Sciences Naturelles, Université de Toulouse*. 313 pp.
- Thompson, J. N. 1982. *Interaction and Coevolution*. Wiley, New York, 179 pp.
- Thompson, J. N. 1987. Symbiont-induced speciation. *Biological Journal of the Linnean Society* 32: 385-393.
- Thompson, J. N. 1988. Variation in interspecific interactions. *Annual Review of Ecology and Systematics* 19: 65-87.
- Thorne, R. F. 1973. Floristic relationships between

- tropical Africa and tropical America, pp. 27-47. In Meggers, B. J., E. S. Ayensu and W. D. Duckworth, eds., *Tropical Forest Ecosystems in Africa and South America*. Smithsonian Institution Press, Washington, D. C.
- Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton University Press, Princeton, New Jersey.
- Tschinkel, W. R. 1991. Insect sociometry, a field in search of data. *Insectes Sociaux* 38:77-82.
- Vasconcelos, H. L. 1990. The relationship between plant size and ant associates in the ant-plant *Maieta guianensis*. *Annual Meeting of the British Ecological Society (poster session)*, Manchester, England.
- Vasconcelos, H. L. 1991. Mutualism between *Maieta guianensis* Aubl., a myrmecophytic melastome, and one of its ant inhabitants: ant protection against insect herbivores. *Oecologia* (Berlin) 87: 295-298.
- Vasconcelos, H. In press. Ant colonization of *Maieta guianensis* seedlings, an Amazon ant-plant. *Oecologia*.
- Vepsäläinen, K. and B. Pisarski. 1982. Assembly of island ant communities. *Annales Zoologici Fennici* 19: 327-335.
- Verdcourt, B. 1979. *A Manual of New Guinea Legumes*. Botany Bulletin, No. 11. Office of Forests, Papua New Guinea, 645 pp.
- Vermeij, G. J. 1978. *Biogeography and Adaptation*. Harvard University Press, Cambridge, Massachusetts, 332 pp.
- Villiers, J.-F. 1984. Le genre *Calpocalyx* (Leguminosae, Mimosoideae) en Afrique. *Adansonia* 6: 297-311.
- Warburg, O. 1894. Ueber Ameisenpflanzen. *Biologisches Centralblatt* 12: 129-142.
- Ward, P. S. 1989a. Systematic studies on pseudomyrmecine ants: revision of the *Pseudomyrmex oculatus* and *P. subtilissimus* species groups, with taxonomic comments on other species. *Quaestiones Entomologicae* 25: 393-468.
- Ward, P. S. 1989b. Genetic and social changes associated with ant speciation, pp. 123-148. In Breed, M. D. and R. E. Page, eds. *The Genetics of Social Evolution*. Westview Press, Boulder, Colorado.
- Ward, P. S. 1990. The ant subfamily Pseudomyrmecinae (Hymenoptera: Formicidae): generic revision and relationship to other formicids. *Systematic Entomology* 15: 449-489.
- Ward, P. S. 1991. Phylogenetic analysis of ant-plant associations involving pseudomyrmecine ants, pp. 335-352. In Huxley, C. R. and D. K. Cutler eds., *Ant - Plant Interactions*. Oxford University Press, Oxford.
- Way, M. J. 1954. Studies on the association of the ant *Oecophylla longinoda* (Latr.) (Formicidae) with the scale insect *Saissetia zanzibarensis* Williams (Coccidae). *Bulletin of Entomological Research* 45: 113-134.
- Wheeler, W. M. 1920. The subfamilies of Formicidae, and other taxonomic notes. *Psyche* 27: 46-55.
- Wheeler, W. M. 1929a. The identity of the ant genera *Gesomyrmex* Mayr and *Dimorphomyrmex* Ernest Andre. *Psyche* 36: 1-12.
- Wheeler, W. M. 1929b. Note on *Gesomyrmex*. *Psyche* 36: 91-92.
- Wheeler, W. M. 1942. Studies of neotropical ant-plants and their ants. *Bulletin of the Museum of Comparative Zoology* 90: 1-262, 57 pls.
- Wheeler, W. M. and I. W. Bailey. 1920. The feeding habits of pseudomyrmecine and other ants. *Transactions of the American Philosophical Society* 22: 235-279.
- Wheeler, W. M. and J. C. Bequaert 1929. Amazonian myrmecophytes and their ants. *Zoologische Anzeiger* 82: 10-39.
- Whiffin, T. 1972. Observations on some upper Amazonian formicarial Melastomataceae. *SIDA* 5: 33-41.
- White, P. S. 1983. Corner's rules in eastern deciduous trees: allometry and its implications for the adaptive architecture of trees. *Bulletin of the Torrey Botanical Club* 110: 203-212.
- Whitmore, T. C. 1973. Euphorbiaceae, pp. 105-113. In Whitmore, T. C. ed., *The Tree Flora of Malaya*, Volume 2. Longman, Kuala Lumpur.
- Whitmore, T. C. 1975. *Macaranga*, pp. 140-159. In Airy Shaw, H. K. ed., *Euphorbiaceae of Borneo*. Kew Bulletin Additional Series 4.
- Wilson, E. O. 1959. Some ecological characteristics of ants in New Guinea rain forests. *Ecology* 40: 437-447.
- Wilson, E. O. 1961. The nature of the taxon cycle in the Melanesian ant fauna. *American Naturalist* 95: 169-193.
- Wilson, E. O. 1985. Invasion and extinction in the West Indian ant fauna: evidence from the Dominican amber. *Science* 229: 265-267.
- Wilson, E. O. 1987. The arboreal ant fauna of Peruvian Amazon forests: a first assessment. *Biotropica* 19: 245-251.
- Young, B. E., M. Kaspari and T. E. Martin. 1990. Species-specific nest site selection by birds in ant-acacia trees. *Biotropica* 22: 310-315.
- Zizka, G., U. Maschwitz and B. Fiala. 1990. Pflanzen und Ameisen: Partnerschaft fürs Überleben. *Palmengarten* 15: 1-126.

Appendix 1. Summary of ants living regularly in symbiotic association with one or more host species. Questionable or missing data are indicated by question marks. Columns:

(1) Ant genera (superscript ^{ct} indicates carton-building typical of the genus, though not necessarily of plant-ant species) in biogeographic regions (**N**) = Neotropical, (**E**) = Ethiopian, (**M**) = Malagasy, (**O**) = Oriental, and (**A**) = Australian regions.

(2) Host taxa have growth forms: **T** = tree; **U** = treelet or understory tree; **S** = shrub; **L** = liana or vine, **R** = rattan, **B** = bamboo and **H** = hemiepiphyte. Habitats include: **b** = mountain brooks; **e** = edge, second growth, riparian environments; **g** = forest light gaps; **l** = littoral scrub; **p** = primary forests; **s** = savannahs or dry forest, and **a** = aguajals or swamps.

(3) Ants nest in domatia comprised of: **L** = leaf pouches; **S** = naturally hollow stems; **Sp** = pithy stems, hollowed by ants; **I** = swollen internodes; **P** = swollen petioles or bases of petioles; **Ps** = petiolar sheath; **R** = swollen rachi and petioles; **St** = persistent stipules (inflated or folded); **Sh** = persistent spathe; **Th** = swollen thorns; **F** = swollen flowering shoots; **G** = gall-like swellings; **C** = carton shelters around domatia, folded leaves, and/or hairs or spines; **Cl** = cavity formed by leaf base clasping stem; **B** = insect borings; **O** = inflated ocrea (proximal extension of leaf sheath beyond the petiole), **A** = erect, narrow auricles on each side of petiole, at the terminus of the sheath; **Ac** = acanthophylls, or basal pinnae reflexed backward to form a secluded cavity at the base of a palm frond; **Ga** = galleries enclosed by interlocking combs of spines, forming collars on leaf sheaths, and **T** = vast chambers excavated inside tree trunks by ants and partitioned by carton. Plant pubescence: **y** = domatia and stems bear long, dense hairs or spines, likely to inhibit movements of larger bodied ants; **n** = such hairs or spines lacking, or **s** = only a subset of plants have these hairs.

(4) Ants prune vines and vegetation around their hosts: **Y** = obligate for plant-ants in this genus; **S** = in at least some ant associates of the host genus; **F** = where known, pruning is facultative, i.e., in the presence of enemy ants; **N** = not yet reported for the ant genus on this host genus. Host fidelity (foraging predominantly or entirely on the host): **y** = yes; **n** = no; **i** = for young (incipient) but not established colonies.

(5) Food types include: **P** = pearl bodies; **B** = other specialized food bodies; **H** = exudates and bodies of homoptera (Coccoidea); **E** = extrafloral nectar; **N** = floral nectar; **G** = uncharacterized exudates of tiny glands; **F** = fungi; **W** = lipid-rich and/or protein-rich plant wounds, or heteroplasias caused by traumatic injury by ants; **O** = pollen; **T** = glandular trichome.

(6) Plants have evolved apparently specialized structures to house ants: **Y** = yes; **N** = no.

(7) Estimated number of congeneric ant species found regularly on the host genus; probability of more (+) or several more (++) indicated parenthetically. Square brackets denote ants known to be unspecialized, or whose specialization is in doubt.

(8) References for data on ants or plants: **Bq** = Bequaert 1922; **W** = Wheeler 1942; **S&B** = Schnell and Beaufort 1966; **B** = Benson 1985; **H** = Huxley 1986; **J** = Jolivet 1986; **H&W** = Hölldobler and Wilson 1990; **D** = Davidson et al. 1989; **IP** = in press; **PC** = personal communication, **DD** and **DM** = respective author's observations.

Appendix 1

(1) Ant Taxa	(2) Host Taxa, Growth Form and Habitat	(3) Nest in	(4) Ant Traits	(5) Food Type	(6) Spec. Myrm.	(7) # Ant Spp.	(8) References
PONERINAE							
Pachycondyla (N)	CECROPIACEAE <i>Cecropia</i> ^{T-se}	S.n	SF,y	BP	Y	3[1]	Davidson & al., 1991; J. Longino PC
PSEUDOMYRMECINAE							
MYRTACEAE							
Myrcidris (N)	<i>Myrcia</i> ^{U,p}	S.n	?;y	H	Y	1	" + Ward 1990
BORAGINACEAE							
Pseudomyrmex (N)	<i>Cordia</i> ^{Te}	l.n	?;y	H	Y	3	" ; W
CECROPIACEAE							
(N)	<i>Coussapoa</i> ^{H,e?g?}	?;?	?;?	?	?	1	"
EUPHORBIACEAE							
(N)	<i>Sapium</i> ^{T-se?g?}	Sp.n	?;y	E?H	N	1	"
FABACEAE							
(N)	<i>Acacia</i> ^{S-sepp}	Th.n	S,y	BE	Y	12	" + Janzen 1966, 1974a; Manniques & Dirzo 1990
(N)	<i>Pithecellobium</i> ^{T-se}	S.n	?;y	E(?)H	Y?	1	" + Ward 1989a
(N)	<i>Platymiscium</i> ^{T,?}	?;?	?;?	H?	N	2(+)	" + W
(N)	<i>Pterocarpus</i> ^{T,ca}	FR,n	?;?	?	Y	[1]	" + Forel 1904; Spruce 1908; Rojo 1972
(N)	<i>Tachigali</i> ^{T,peg}	P.n	S,y	H	Y	9(+)	

	LAURACEAE									
(N)	<i>Ocotea</i> ^{US,p}	Sp.n	?,?	H	N	1	"			
(N)	<i>Pleurothyrant</i> ^{US,p}	Sp.n	?,?	H	N	1	"			
	POLYGONACEAE									
(N)	<i>Ruprechtia</i> ^{US?}	S.n	?,?	H?	Y?	[1]	" + Spruce 1908; B; Brandbyge 1990			
(N)	<i>Triplaris</i> ^{T,egg}	S.n	S.y	HFw	Y	6(+)	" + DD; Davidson & al. 1988;			
							Brandbyge 1986			
	BIGNONIACEAE									
(E)	<i>Stereospermum</i> ^{T,?}	Sp.n	?,?	HE(?)	N	1	" + Bq; J			
(O)	<i>Stereospermum</i> ^{T,e}	Sp.n	?,?	HE	N	[1]	DM			
	FABACEAE									
(E)	<i>Acacia</i> ^{S,s}	G.n	?,?	HE	Y	1	Ward 1991; Hocking 1970			
(O)	<i>Acacia</i> ^{S,s}	Th.n	?,?	HE	Y	[1]	T. Musthak Ali PC; P. Ward PC;			
							DM			
(M)	<i>Mimosa</i> ^{S,s}	Sp.n	N,y	H	N	1	P. Ward PC			
	GRAMINEAE									
(O)	<i>Gigantochloa</i> ^{B,e}	B?.n	?,?	H	N	1	P. Ward PC			
	PASSIFLORACEAE									
(E)	<i>Barteria</i> ^{T,ep}	Sp.n	Y,y	HFOWE ^{b,y}		2	Ward 1991; Janzen 1972			
	SAPINDACEAE									
(A)	<i>Cupatiopsis</i> ^{T,s}	Sp.n	?,y	H	N	1	"			
	VERBENACEAE									
(E)	<i>Vitea</i> ^{T,e}	Sp.n	?,y	FW	N	1	" + Bq; J			
	MYRMICINAE									
	Tribe Cephalotini									
	^c <i>Zacryptocerus</i>									
(N)		I.n	N,y	?	Y	1	Carroll 1983; W; J. Longino PC			
	BORAGINACEAE									
	<i>Cordia</i> ^{T,egg}									

FABACEAE									
(N)	<i>Platymiscium</i> ^{1,2}	?,?	?	N	1	B; W			
Tribe Solenopsidini (provisional)									
<i>Allomeris</i> ^{4c}									
(N)	<i>Cordia</i> ^{U,p}	1,y	F,s	PH	Y	4(+)	W; B; D; D; Yu	PC	
CECROPIACEAE									
(N)	<i>Pourouma</i> ^{U,p}	P,y	?,?	B	Y	1	B; Berg & al.	1990	
CHRYSOBALANACEAE									
(N)	<i>Hirella</i> ^{U,p}	L,y	?,?	E	Y	1(+)	B; Prance	1972, 1989	
MELASTOMATACEAE									
(N)	^d <i>Tococa</i> ^{U,nc}	L,y	?y	H	Y	3(+)	W; B; Herre & al.	1986	
(N)	^e <i>Clidemia</i> s.s. ^{S,se}	L,y	?,?	GH	Y	1(+)	B		
RUBIACEAE									
(N)	<i>Duroia</i> ^{U,e,gg?}	L,y	?,?	?	Y	1(+)	B; Wheeler & Bequaert	1929	
(N)	<i>Remijia</i> ^{U,e}	L,y?	?,?	?	Y	1(+)	B; Schumann	1890	
Solenopsis									
(N)	<i>Gesneria</i> ^{S,p}	L,y	?,?	?	Y	1	B; H		
RUBIACEAE									
(N)	<i>Duroia</i> ^{U,eg}	L,y	?,?	?	Y	1(+)	Wheeler & Bequaert	1929	
(N)	<i>Hoffmannia</i> ^{S,p}	L,y	?,?	?	Y	1	B; H		
<i>Monomorium</i>									
(O)	<i>Myrmeconuclea</i> ^{S,e}	1,n	?,?	?	Y	[1]	Maschwitz & al.,	1989	
Crematogastrini									
<i>Crematogaster</i> ^{4c}									
(N)	<i>Cecropia</i> ^{T,g}	S,n	N,y	BPH	Y	1	DD		
(E)	<i>Musanga</i> ^{T,e}	S,n	N,n	H	N	[9+]	Duviard & Segeren	1974	

	EUPHORBIACEAE						
(E)	<i>Macaranga</i> ^{U,pe}	St.n	N.n	E(P?)	Y?	1	Bq
(O)	<i>Macaranga</i> ^{T,eg}	S.n	Y.y	BH	Y	6(+)	Fiala & al. 1989; Fiala & Maschwitz 1990, 1991; J. Longino PC; DD Tennant 1989
(N)	<i>Tetrahyliacium</i> ^{U,pe}	S.n	??	H	N	[1+]	
	FABACEAE						
(E)	<i>Acacia</i> ^{S,s}	G.n	N.n	HE	Y	4	Hocking 1970
(O)	<i>Acacia</i> ^{S,s}	Th.n	??	HE	Y	[1]	DM
(O)	<i>Acacia</i> ^{S,s}	B.n	??	?	N	[1]	DM
(O)	<i>Humboldtia</i> ^{U,p}	I.n	??	E(H?)	Y	1	DM
(E)	<i>Leonardoxa</i> ^{U,p}	I.n	??	E	Y	2(+)	DM
(O)	<i>Saraca</i> ^{T,e}	I.n	??	E(H?)	Y?	1	Maschwitz & al. 1991
	FLACOURTIACEAE						
(E)	<i>Buchnerodendron</i> ^{U,p}	S.n	??	H?	N	[1]	Bq; J
	LOGANIACEAE						
(E)	<i>Anthocleista</i> ^{T,ea}	St.n	??	E	N	[1+]	DM B; D
	MELASTOMATACEAE						
(N)	<i>Clidemia</i> s.s. ^{S,e}	L.y	N.n?	GH	Y	1(+)	B; Judd & Skee 1991; D
(N)	<i>Mateta</i> ^{S,pe}	L.y	N.n?	GH	Y	1(+)	D; B; Vasconcelos 1990; Schnell 1967
(N)	<i>dTococa</i> ^{U,pe}	L.y	??	H	Y	1(+)	B; Schnell 1967; Whiffin 1972; D; B
	MELIACEAE						
(A)	<i>Aphanamixis</i> ^{U,p}	Sp.n	??	H	N	[1+]	Warburg 1894; Mabberley 1985; DD
(A)	<i>Chisocheton</i> ^{U,p}	Sp.n	??	H	N	[1+]	DD
	PALMAE						
(O)	<i>Korhalsia</i> ^{R,p}	O.s	N.y?	H	Y	3(+)	Zizka & al. 1990; DD
	PASSIFLORACEAE						

(E)	<i>Barteria</i> ^{T,pc}	I,n	?,?	HFOWE ^b Y	[1+]	Bq; S&B; DM
(E)	<i>Barteria</i> ^{T,1}	I,n	N,?	HFOWE ^b Y	[1+]	Bq; S&B; DM
RUBIACEAE						
(E)	<i>Canthium</i> ^{T,c,U,p}	I,s	?,?	H	[1+]	Bq; DM; S&B
(E)	<i>Civiera</i> ^{L,p}	I,s	?,?	H	1(+)	Bq; DM; S&B
(E)	<i>Gardenia</i> ^{T,ae}	L,n	?,?	HE	[1]	DM; S&B
(O)	<i>Myrmeconauclea</i> ^{S,e}	I,n	?,?	?	1	Ridsdale 1978; Maschwitz & al., 1989
(E)	<i>Nauclea</i> ^{T,a}	I,n	?,?	H	[1+]	Bq; S&B
(O)	<i>Neonauclea</i> ^{T,S,?}	I,n	?,?	H	1(+)	Bq; J; Ridsdale 1978
(E)	<i>Psychotria</i> ^{S,e}	St,n	?,?	H	1(+)	S&B
(E)	<i>Rothmannia</i> ^{T,p,?}	I,s	?,?	H	1(+)	Bq; S&B
(E)	<i>Uncaria</i> ^{L,pg,?}	I,n	?,?	H	1(+)	Bq; S&B
RUTACEAE						
(O)	<i>Zanthoxylum</i> ^{U,e}	S,y	?,?	?	[1]	Maschwitz & Fiala 1992
SAPOTACEAE						
(E)	<i>Delpyodora</i> ^{U,p}	L,y	?,?	?	1(+)	DM
VERBENACEAE						
(E)	<i>Clerodendrum</i> ^{U,e}	S,n	?,?	E?	[1+]	J; H; S&B
BORAGINACEAE						
(N)	<i>Cordia</i> ^{U,p,?}	I,y	?,?	P	1(+)	W; B
GESNERIACEAE						
(N)	<i>Bestleria</i> ^{S,p}	L,y	?,?	?	1	B
MELASTOMATACEAE						

Pheidolini

Pheidole^{ca}

(N)	<i>Chlidemia</i> s.s. ^{S,e}	L _y	N _y	G(H?)	Y	1(+)	B; D
(N)	<i>Conostegia</i> ^{S,p}	L _y	? _y	?	Y	1,[1]	B; Judd & Skean 1991; L. Tennant PC
(N)	<i>Maieta</i> ^{S,e}	L _y	N _y	PH	Y	1(+)	B; D; Vasconcelos 1990, 1991; Herre #IP & al. 1986
(N)	<i>Tococa</i> ^{U,pe}	L _y	? _?	T	Y	1(+)	B; D
	MYRSINACEAE						
(A)	<i>Tapinosperma</i> ^{U,p}	S _n	? _?	?	?	1	H&W; Stone & Whitmore 1970
	PIPERACEAE						
(N)	<i>Piper</i> ^{S,p}	Ps _n	S _y	BGP?	Y	2[+]	Burger 1971; Burger & van der Werff 1990; Letourneau 1983; Risch & al. 1977; DD
	Leptothoracini						
	<i>Leptothorax</i>						
(E)	FABACEAE						
	<i>Leonardoxa</i> ^{U,p}	l _n	? _?	E	Y	1	R. Snelling PC; DM
	Dacetini						
	<i>Strumigenys</i>						
(N)	MELASTOMATAACEAE						
	<i>Tococa</i> ^{U,e}	L _y	? _?	?	Y	[1]	Wheeler & Bequaert 1929; Brown
1962							
	Tribe Unspecified						
	<i>Atopomyrmex</i>						
(E)	FABACEAE						
	<i>Calpocalyx</i> ^{U,p}	Sp _n	? _?	HE	N	1	R. Snelling PC; Villiers 1984; DM
	<i>Cataulacus</i>						
(E)	FABACEAE						
	<i>Leonardoxa</i> ^{U,p}	l _n	N _y	E	Y	2(+)	McKey 1984; Snelling 1979b; DM
	RUBIACEAE						
(E)	<i>Canthium</i> ^{U,p}	l _y	? _?	H	Y	1(+)	Bq; DM
(E)	<i>Claviera</i> ^{U,p}	l _s	? _?	H	Y	1(+)	Bq; DM
	MELIACEAE						
	<i>Podomyrma</i>						

(A)	<i>Chisocheton</i> ^{U,p}	B,n	N,n	HW?	N	I(+)	Stevens 1978; Mabberley 1979; DD
	RUBIACEAE						
(A)	<i>Canthium</i> ^{?,?}	Sp,n	N,y	H	Y	I	G.B. Monteith & P. Flower PC
(E)	FABACEAE						
	<i>Leonardoxa</i> ^{U,p}	I,n	?,?	E	Y	I(+)	DM
(E)	RUBIACEAE						
(E)	<i>Civiera</i> ^{U,p}	I,n	?,?	?	Y	I(+)	Bq; DM
(O)	<i>Myrmeconautoclea</i> ^{S,e}	I,n	?,?	H	Y	[I+]	Maschwitz & al., 1989
	MELASTOMATACEAE						
(N)	<i>Contostegia</i> ^{S,e}	L,y ^l	N,n	H	Y	[I]	Tennant PC; DD
	DOLICHODERINAE						
	Tapinomini						
	<i>Anorychomyrma</i>						
(A)	<i>Aphananixis</i> ^{U,p}	Sp,n	N,n	H	N	I	Warburg 1894; M. Jebb PC
(A)	<i>Chisocheton</i> ^{U,p}	B,n	N,n	H	N	I	Stevens 1978; M. Jebb PC
	MONIMIACEAE						
(A)	<i>Stegathera</i> ^{U,p}	I,s	N,n	H	?	I(+)	Bq; J; Philipson 1984
	MYRISTICACEAE						
(A)	<i>Myristica</i> ^{U,p}	I,n	N,n	H	N	I(+)	Bq; Foreman 1978; J; DD
	MYRTACEAE						
(A)	<i>Syzygium</i> ^{T,eg}	T,n	N,n	H	N	I(+)	Monteith 1986 & PC; DD
	PALMAE						
(O)	<i>Daemonorops</i> ^{R,p}	G,a,n	N,?	H	N	I(+)	DD; Ridley 1910
(O)	<i>Korthalsia</i> ^{R,p}	O,s	?,?	?	Y	I	Beccari 1884
	SAPINDACEAE						
(A)	<i>Mischocarpus</i> ^{U,p}	?,?	?,?	H	?	I(+)	M. Jebb, <i>vide</i> H
	FABACEAE						
(E)	<i>Leonardoxa</i> ^{U,p}	I,n	?,?	E	Y	[2+]	R. Snelling PC; Shattuck 1991; DM

<i>Aztecet</i> ^r															
(N)	BORAGINACEAE	I,n	N,?	H	Y	4-5	W; Carroll 1983; Manriquez & Dirzo 1990								
	<i>Cordia</i> ^{T,se}						W; B; D								
(N)	CECROPIACEAE	I,y ⁱ	N,i	HG	Y	2-3+	Bq; W; Davidson & Fisher 1991; Longino 1991b; Manriquez & Dirzo 1990								
(N)	<i>Cecropia</i> ^{T,seg}	S,n	S,y	BPH	Y	13(++)	Forel 1904								
(N)	<i>Coussapoa</i> ^{He,g?}	?,?	?,?	?	?	[1]	B; Prance 1972; DD								
	CHRYSOBALANACEAE	L,y	N,?	E	Y	1(+)	B; H								
(N)	<i>Hirtella</i> ^{U,p}						W; B								
(N)	FABACEAE	S,n	N,?	?	N	1(+)									
(N)	<i>Ormosia</i> ^{T,se}	P,n	?,?	H	Y	1-2									
(N)	<i>Tachigala</i> ^{T,seg}														
(N)	FLACOURTIACEAE	S,n	?,?	H	N	[1+]	Tennant 1989								
	<i>Tetrathylacium</i> ^{U,pe}														
(N)	LAURACEAE	Sp,n	N,n	H	N	1(+)	D; H. van der Werff PC								
	<i>Pleurothyrium</i> ^{U,p}														
	MELASTOMIACEAE	L,y	?,?	H	Y	1(+)	B								
(N)	<i>Clidemia</i> s.s. ^{S,e}	L,y	?,?	?	Y	1(+)	B; W. Judd PC								
(N)	<i>Sagraea</i> ^{S,e}	L,y ⁱ	N,i	H	Y	2(+)	W; B; D								
(N)	<i>Tococa</i> ^{U,pe}	S,y	N,y	G	Y	1, [1]									
(N)	POLYGONACEAE	L,y	?,?	?	Y	1(+)	Wheeler & Bequaert 1929								
	<i>Triplaris</i> ^{T,p}						DD								
(N)	RUBIACEAE	I,y	N,i	G?H	Y	1	B								
(N)	<i>Duroia</i> ^{U,se}	B,n	N,n	?	N	[1]									
(N)	<i>Duroia</i> ^{U,se}														
(N)	<i>Remijida</i> ^{S,p}														

<i>Tapinoma</i> ^d									
FABACEAE									
<i>Leonardoxa</i> ^{U,p}	(E)	I,n	?,?	E	Y	[1]	R. Snelling PC; DM		
<i>Humboldtia</i> ^{U,p}	(O)	I,n	?,?	HE	Y	[1]	DM; T. Musthak Ali PC		
CECROPIACEAE									
<i>Poikilospermum</i> ^{L,e}	(O)	Sp,n	N,?	H	Y?	[1]	D. Samson PC; R. Snelling PC		
EBENACEAE									
<i>Diospyros</i> ^{U,p}	(E)	L,y	?,?	HE	Y	1	R. Snelling PC; Letouzey & White 1970; DM		
FABACEAE									
<i>Archidendron</i> ^{U,g}	(A)	StC,n	N,n	E	Y?	[1]	DD; de Wit 1942; Verdcourt 1979		
<i>Humboldtia</i> ^{U,p}	(O)	I,n	N,?	E	Y	[1]	F. Rickson PC		
<i>Leonardoxa</i> ^{U,p}	(E)	I,n	?,?	E	Y	2(+)	DM		
MYRISTICACEAE									
<i>Myristica</i> ^{U,p}	(A)	I,n	N,n	H	N	1(+)	J; DD; Beccari 1884		
RUBIACEAE									
<i>Canthium</i> ^{L,e}	(E)	I,y	?,?	?	Y?	1(+)	Bq; DM		
<i>Caviera</i> ^{S,p}	(E)	I,n	?,?	H	Y	1	Bq		
<i>Caviera</i> ^{U,p}	(E)	I,s	?,?	?	Y	1(+)	Bq; DM		
<i>Ixora</i> ^{U,p}	(E)	L,n	?,?	?	Y	1	DM; D. Olson PC		
SAPOTACEAE									
<i>Delpyodora</i> ^{U,p}	(E)	L,y	?,?	?	Y	1	R. Snelling PC; DM		
STERCULIACEAE									
<i>Cola</i> ^{St,u,e}	(E)	L,y	?,?	?	Y	1	Bq; Nkongmeneck 1985; DM		
<i>Scaphopetalum</i> ^{St,u,p}	(E)	L,y	?,?	?	Y	1	Bq; Dejean et al. 1990; DM		
FORMICINAE									
Myrmelachistini									
<i>Aphomyrme</i>									
FABACEAE									

(E)	<i>Leonardoxa</i> ^{U,p}	In	N,y	H	Y	1	McKey 1984; 1991
	VERBENACEAE						
(E)	<i>Vitex</i> ^{1,e}	Sp.n	?,?	H	N	1	R. Snelling; DM
	CRYPTERONACEAE						
(O)	<i>Crypteronia</i> ^{1,p}	Sp.n	?,?	HE	Y?	1	U. Maschwitz & al. 1991
	FABACEAE						
(O)	<i>Millettia</i> ^{1,?}	S,?	?,?	H	Y?	1	U. Maschwitz & al. 1989
(O)	<i>Saraca</i> ^{1,e}	In	?,?	HE	Y?	1	U. Maschwitz & al. 1991
	RUBIACEAE						
(O)	<i>Neonauclea</i> ^{U,e}	In	S,y	H	Y	1+	R. Snelling PC; DD
	BORAGINACEAE						
<i>Myrmelachista</i>							
(N)	<i>Cordia</i> ^{1,p,g}	I,y	Y,i ^e	GH	Y	1(+)	Campbell et al. 1989; DD
	LAURACEAE						
(N)	<i>Licaria</i> ^{1,p}	Sp.n	?,?	H	N	3(+)[2]	J. Longino PC
(N)	<i>Ocotea</i> ^{U,p}	Sp.n	S,y	GH	N	6(+)	J. Longino PC; DD; H. van der Werff PC; Manriquez & Dirzo 1990
(N)	<i>Pleurothyrium</i> ^{U,p}	Sp.n	N,y	H	N	1(+)	J. Longino PC; D; H. van der Werff PC
	MELASTOMACEAE						
(N)	<i>Miconia</i> ^{1,?}	?,?	?,?	?	?	[1]	B; Forel 1904
(N)	<i>Tococa</i> ^{S,U,e}	L,y	Y,i	T	Y	1	Campbell et al. 1989 Morawetz et al. 1992; Svoma and Morawetz 1992
	MELIACEAE						
(N)	<i>Guarea</i> ^{1,p}	Sp.n	N,y	H	N	2(+)[1]	J. Longino PC; Pennington 1981
	RUBIACEAE						
(N)	<i>Duroia</i> ^{U,p,e}	I,y	Y,i	(G?)H	Y	1(+)	Campbell et al. 1989; DD
	FABACEAE						
	<i>Petalomyx</i>						

(E)	<i>Leonardoax</i> ^{U,p}	I,n	N,y	E	Y	1	McKey 1984; 1991; Snelling 1979
Plagirolepidini							
<i>Plagirolepis</i>							
(E)	<i>Cold</i> ^{S,U,pe}	L,y	?,?	?	Y	1	Bq
Camponotini							
<i>Camponotus</i> (subgenus <i>Pseudocolobopsis</i>)							
CECROPIACEAE							
(N)	<i>Cecropia</i> ^{TU,pg}	S,n	N,y	BPH	Y	2	DD
<i>Camponotus</i> (Oriental and Australian subgenera often referred to as <i>Colobopsis</i>)							
BIGNONIACEAE							
(O)	<i>Stereospermum</i> ^{T,e}	Sp,N	?,?	HE	N	[1]	DM; T. Musthak Ali PC
FLACOURTIACEAE							
(A)	<i>Ryparosa</i> ^{T,p}	S,n	?,?	?	?	1	H&W
RUBIACEAE							
(O)	<i>Myrmeconauclea</i> ^{S,e}	I,n	?,?	?	Y	[2]	Maschwitz & al. 1989
RUTACEAE							
(O)	<i>Zanthoxylum</i> ^{U,e}	S,y	?,?	?	Y	[1]	Maschwitz & Fiala 1992
VERBENACEAE							
(O)	<i>Clerodendrum</i> ^{U,e}	S,n	?,?	E	Y	1	J; Beccari 1884
<i>Camponotus</i> (other subgenera)							
CECROPIACEAE							
(N)	<i>Cecropia</i> ^{T,seg}	S,n	N,y	BPH	Y	1	B; D
EUPHORBIACEAE							
(A)	<i>Endospermum</i> ^{T,pe}	Sp,n	S,y	EW	Y	1	Bq; J; DD, Monteith 1987; Letourneau et. al. PC
(O)	<i>Macaranga</i> ^{T,es}	S,n	?,?	?	Y	2	Fiala & al. 1990; F. Rickson PC
PALMAE							

(O)	<i>Daemonorops</i> ^{B,p}	Ga.?	?,?	H	N?	4	Ridley 1910; DD; Rickson & Rickson 1986; Dransfield & Manokaran 1978.
(O)	<i>Korthalsia</i> ^{B,p}	O.s	N.?	H	Y	3(+)	B; H&W; DD; Dransfield 1984
(O)	RUBIACEAE						
(O)	<i>Myrmeconuclea</i> ^{S,e}	I.n	?,?	?	Y	[1]	Maschwitz & al., 1989
(N)	<i>Patina</i> ^{E,p}	I.n	?,?	?	Y?	[1]	W
	<i>Polytrachis</i>						
	GRAMINEAE						
(O)	<i>Gigantochloa</i> ^{B,e}	B.n	N.y	H	N	2	Dorow & Maschwitz 1990
(O)	<i>Schizostachyum</i> ^{B,e}	B.n	N.y	H	N	2	Dorow & Maschwitz 1990
	UNDETERMINED ANTS						
	ACTINIDIACEAE						
(O)	<i>Saurauia</i> [?]	L.?	?,?	?	?	?	J
	ANACARDIACEAE						
(A)	<i>Euroschinus</i> ^{T,p}	S.n	?,?	?	?	?	Ding Hou 1978
(O)	<i>Lannea</i> ^{T,p}	S.n	?,?	?	?	?	J
(A or O?)	<i>Semecarpus</i> ^{TU,p}	S.n	?,?	?	?	?	H&W
	CHRYSOBALANACEAE						
(E)	<i>Dactyladenia</i> ^{U?S??}	St.n	?,?	?	?	?	F. J. Bretelet PC
(E)	<i>Magnistipula</i> ^{T?S??}	Li.y	?,?	E	Y	?	Letouzey & White 1976, 1978
	DICHAPETALACEAE						
(E)	<i>Dichapetalum</i> [?]	L.y	?,?	E?	Y	?	Bretelet 1986 & PC
	ELAEOCARPACEAE						
(A)	<i>Elaeocarpus</i> ^{TU,p}	S.?	?,?	?	?	?	J; Coode 1981
	EUPHORBIACEAE						

(A)	<i>Drypetes</i> ^{3,2}	S,?	?,?	?	?	?	?	M. Jebb PC
(A)	<i>Glochidion</i> ^{U,3}	S,?	?,?	?	?	?	?	M. Jebb PC
(A)	<i>Homalanthus</i> ²	S,?	?,?	?	?	?	?	M. Jebb PC
(N)	<i>Mabea</i> ^{2,2}	Sp,?	?,?	?	?	?	?	Spruce 1908
(A)	<i>Pimelodendron</i> ^{2,4}	S,?	?,?	?	?	?	?	M. Jebb PC
	FABACEAE							
(N)	^a <i>Tachigall</i> ^{U,p}	P,y	?,?	?	Y	?	?	DD
	GENTIANACEAE							
(N)	<i>Tachia</i> ^{St,p}	S,n	?,?	E?	Y?	?	?	Bq; B; Spruce 1908; Maguire & Weaver 1975
	LAURACEAE							
(A or O)	<i>Cryptocarya</i> [?]	S,?	?,?	?	?	?	?	H&W
	LOGANIACEAE							
(O)	<i>Fagraea</i> ^{H,p}	P,n	?,?	?	?	?	?	J
	MELASTOMATACEAE							
(N)	^a <i>Allonaieta</i> ^{S,3}	L?,y	?,?	?	?	?	?	A. Gentry PC
(N)	<i>Blaked</i> [?]	L?,y	?,?	?	?	?	?	B
(N)	^a <i>Henriettea</i> ^{2,2}	L,y	?,?	?	Y	?	?	W. Judd PC; S. Renner PC; B; H.
(O)	<i>Medinilla</i> ^{H,b}	L,y	?,?	P,?	Y	?	?	J; Solereder 1920
(N)	<i>Topobea</i> [?]	P,?	?,?	?	Y?	?	?	S. Renner PC
	MELIACEAE							
(A)	<i>Aglaiia</i> ^{U,p}	Sp,n	?,?	?	N	?	?	H&W
	MONIMIACEAE							
(A)	<i>Kibara</i> ^{U,p}	I,n	?,?	H	Y?	?	?	Bq; J; Philipson 1985
	NYCTAGINACEAE							
(O)	<i>Pisonia</i> [?]	S,y	?,?	?	?	?	?	H&W
	PALMAE							

(O)	¹ <i>Calanus</i> ^{R,p?}	Cl,y	?,?	?	N	?	Bq; J. Dransfield PC
(O)	¹ <i>Calanus</i> ^{R,c?}	O,y	?,?	?	Y	?	J. Dransfield 1981
(A)	¹ <i>Calanus</i> ^{R,c?}	O,y	?,?	?	Y	?	J. Dransfield 1981
(O)	¹ <i>Calanus</i> ^{R,c?}	Gal,y	?,?	?	Y	?	Dransfield & Manokaran 1978
(E)	¹ <i>Eremospathid</i> ^{R,c?}	Cl,y	?,?	?	Y	?	J. Dransfield PC
(E)	¹ <i>Laccosperma</i> ^{R,c?}	O,y	?,?	?	Y	?	J. Dransfield PC
(E)	<i>Laccosperma</i> ^{R,c?}	Ac,n	?,?	?	Y	?	J. Dransfield PC; Zizka & al. 1990
(O)	¹ <i>Pogonotium</i> ^{R,c?}	A,y	?,?	?	Y	?	Dransfield 1979 & PC
	PIPERACEAE						
(O)	<i>Piper</i> ^{?,?}	L,y	?,?	?	Y?	?	J; de Candolle 1916
	RUBIACEAE						
(E)	<i>Bertiera</i> ^{St,U,p}	St,n	?,?	?	N	?	S&B
(E)	^p <i>Heimia</i> ^{Sp}	l,n	?,?	H	Y	?	Bq; J
(A)	^q <i>Nauclea</i> ^{U,e}	S,n	?,?	?	N	?	M. Jebb PC
(A)	<i>Psychotria</i> ^{S,c?}	St,?	?,?	H	?	?	Bq; Schumann & Lauterbach 1901
(E)	<i>Triclystia</i> ^{U,p}	Sp,n	?,?	H	N	?	Hallé 1970; Robbrecht 1979
(E)	<i>Vangueriaopsis</i> ^{?,?}	l,?	?,?	?	?	?	S&B; H&W
	RUTACEAE						
(A)	<i>Zanthoxylum</i> ^{U,e}	S,n	??	?	Y?	?	Hartley 1966; Maschwitz & Fiala PC
	SAPINDACEAE						
(A)	<i>Harpullia</i> ^{U,p}	Sp,s	?,?	?	N	?	Leenhouts & Vente; 1982; M. Jebb PC
	SCROPHULARIACEAE						
(O)	<i>Wightia</i> ^{l,?}	Sp,?	?,?	?	?	?	J
	SIMARUBACEAE						
(N)	<i>Picrolemma</i> ^{?,?}	?,?	?,?	?	?	?	B
	SYMPLOCACEAE						
(A)	<i>Symplocos</i> ^{U,p}	?,?	?,?	?	?	?	M. Jebb PC
	THYMELAEACEAE						

- | | | | | | |
|-----|----------------------------------|-----|----|----|---------------------------|
| (O) | <i>Wikstroemia</i> ^{??} | ?? | ? | ? | J |
| | VERBENACEAE | | | | |
| (O) | <i>Callicarpa</i> ^{U,æ} | L,y | ?? | EG | Y ? van Steenis 1967; H&W |
- a Habitats listed for *Tachigali* include forest light gaps. In these semelparous trees, gaps colonized are often those left by dead maternal parents.
- b Extrafloral nectaries well developed only on orthotropic axes (thus most abundant on seedlings and sucker shoots, found also at growing tip of trunk).
- c Includes *Paracryptoceras* (see Hölldobler and Wilson 1990).
- d Includes *Microphysca* (Judd and Skean 1991).
- e Includes *Myrmidone* (Judd and Skean 1991).
- f The indumentum of these rattans is composed of spines of varying size and density; the scattered, triangular spines of some *Korthalsia* species probably do not inhibit ant movements, as in other hairy ant-plants. They may prevent vertebrates from opening domatia to feed on ant brood (see text).
- g Some *Pheidole* spp. use carton to construct nests or shelters, but use of carton is not as elaborate in this genus as in *Crematogaster* or *Azteca*.
- h *Anthobembix hospitans* (Becc.) Perkins, cited by Bequaert (1922) is a synonym of *Stegantthera hospitans* (Becc.) Kan. & Hat., cited by Hölldobler and Wilson (1990) (Philipson 1984).
- i Ants create "trail systems" by cutting trichomes on stems and domatia.
- j Includes *Ossaea* p.p. (Judd 1989; Judd and Skean 1991).
- k Includes *Pterocladon sprucei* Hook. f. ex Cogn. (synonymous with *Miconia bailloniana* Macbr.; S. Renner, personal communication) of Forel 1904.
- l Pattern of host fidelity is complex in this case, which involves supay chacras (see text).
- m *Gerrardia* (*G. amplifolia*) of Bequaert [1922] and Hölldobler and Wilson [1990] is a synonym of *Ryparosa* (Mabberley 1987).
- n A cloud-forest shrub of Colombia. *Allomateta* resembles *Maieta* but has poorly developed or (on occasion) no domatia.
- o Myrmecophytism is included in *Henriettella*, which Judd and Skean (1991) now place in *Henriettea*.
- p "*Sina spininoda* Andr." (= *Tetraponera aethiops* [F. Smith]. Pseudomyrmecinae) was recorded by Stütz (1910, 1913) from "*Epitaberna myrmoecia* K. Schum." (= *Heinastia myrmoecia* [K. Schum.] N. Halle). Herbarium material examined by one of us (DM) indicates that the intermodal swellings of this plant are too small to harbor this large ant, and we suspect this record is an error.
- q All Asian *Nanclaea* listed by Bequaert (1922) and Hölldobler and Wilson (1990) are treated by Ridsdale (1978) as *Neonanclaea* or *Myrmeconanclaea*.

This work is dedicated to the memory of Alwyn Gentry, whose recent passing is a tragic loss to tropical biology.