CECROPIA AND ITS BIOTIC DEFENSES

D. W. DAVIDSON

In all the world, the genus *Cecropia* is unrivaled for the number of myrmecophytes, or true "ant-plants" counted among its species (McKey & Davidson, 1993). Based on the proportion of *Cecropia* species producing Müllerian bodies in at least some parts of their distribution, myrmecophytes comprise the vast majority (ca. 80%) of species in the genus; most nonmyrmecophytes occur at higher elevations and on islands, where their ants are missing (Wheeler, 1942). Geographically, myrmecophytic *Cecropia* occur throughout the latitudinal range of the genus, from southern Mexico to northern Argentina. Given that association with ants is so widespread taxonomically and geographically, it is likely that relationships with ants have been highly influential in the evolutionary diversification of *Cecropia*. Here, I review the benefits which *Cecropia*-ants and their hosts receive from their symbiotic partnerships. I then discuss how interspecific variation in the ant-attractants of *Cecropia* might have evolved and then influenced relationships with particular ant taxa. Finally, I consider factors influencing the diversity of ants, plants, and partnerships in these associations.

BENEFITS TO *CECROPIA*-ANTS

Myrmecophytes are plants with "biotic defenses," or traits which attract ants, mainly as a defense against herbivores and encroaching vines (Davidson & McKey, 1993). By definition, myrmecophytes have evolved not only to provision ants with food resources, but also to grant them residence inside either modified plant parts or preadapted structures. Evolution by plants to attract and house ant colonies can often be in doubt in presumed myrmecophytes with primary domatia, i.e., naturally hollow or hollowed-out stems that are frequently or always occupied by ants, because many of these species have no obvious specializations for housing or feeding associated colonies (Davidson & McKey, 1993). Such is not the case in *Cecropia* species, which accommodate ants by widening their naturally hollow stems at fixed developmental stages, predictable from theories of defensive investment (see below), and temporally correlated with the onset of food body production. Moreover, as described above by Berg, myrmecophytic *Cecropia* also produce prostomata, or weakened sites in the stem walls beneath internodal septa. Prostomata lie at the distal ends of the internodal grooves that occur even in nonmyrmecophytic *Cecropia*, perhaps due to pressure exerted by axillary buds (Bailey, 1922). However, their evolutionary enlargement relative to the internodal groove is thought to be the product of natural selection imposed by mutualistic ants (Schimper, 1888). Both the internodal groove and prostoma are devoid of fibrovascular bundles, collenchyma, and lignified parenchyma (Schimper, 1888). Colonizing queens of obligate *Cecropia*-ants recognize and use prostomata as easily excavated sites where stems can be entered without rupturing stem transport tissues and flooding internodes with mucilage.

The stems of myrmecophytic *Cecropia* are hollow, lacking the pith that often fills stems of nonmyrmecophytic congeners. The thin, spongy medullary lining the hollow stems of myrmecophytes is exploited by queens that found their colonies claustrally, i.e., without foraging, and by using resources from digested wing muscles to produce their first worker broods. Claustrally founding queens scrape this material from the internode walls to seal the prostoma and develop their colonies in seclusion. Foundresses of some *Cecropia*-ants also accumulate and store medullary tissue near their developing broods. Water contained within this succulent material (and lending it the appearance of "bubblepack" under a stereoscope), may nourish developing brood and/or enhance humidity in the vicinity of brood.

In addition, as described above by Berg, *Cecropia* have evolved to supply two types of food rewards for their ants, and at least some ant associates of *Cecropia* appear to reject foods typically taken by ants with more generalized habits. Müllerian bodies, produced at hairy trichilia, located abaxially on the bases of petioles, are harvested by obligate *Cecropia*-ants, but not by opportunistically foraging ants with generalized diets (Davidson & Fisher, 1991). These food rewards contain considerable lipid and at least some protein (Rickson, 1973, 1976) but are approximately 30% glycogen (Rickson, 1971; Marshall & Rickson, 1973), the form of soluble polysaccharide in which animals store excess glucose. Synthesized and stored in plastids, the glycogen component of Müllerian bodies lends credence to the hypothesis that these rewards may be nutritional mimics of herbivorous insects or their larvae and thus may attract ants which typically feed on such prey (Janzen, 1969, 1973).

Worker ants often stand guard at trichilia to await the appearances of Müllerian bodies. In several *Cecropia* species for which the diurnal production schedules of these food bodies have been studied in the greenhouse, the rewards were produced in greatest profusion immediately after dark (Davidson & Fisher, 1991), coincidentally or not, the time of day when many predator-wary herbivores emerge from their diurnal hiding places to settle at feeding sites for the night. The same diurnal schedule of Müllerian body production was demonstrated for two *Cecropia* species in a project from an Organization for Tropical Studies field course in Peru, near the junction of the Rio Sucusori with the Rio Napo (pers. obs.), but a field study by Belin-Depoux et al. (1997) in French Guiana showed production peaking three hours before sunset in *C. obtusa*. Additional field studies of food body production schedules in different species should shed greater light on the adaptive significance of these schedules. Interestingly, both the manual removal of previously emerged Müllerian bodies (Folgarait et al., 1994) and slight downward pressure on petioles (pers. obs.) can induce preemergent bodies to be released early. The significance of pressure changes in these premature emergences is the suggestion that changes in turgor pressure, coincident with shutdown of photosynthesis and transpiration, could trigger their natural release. Fast-growing plants like *Cecropia* move back toward water balance relatively quickly after dark, and the period immediately after dark may represent the start of the least expensive time (nighttime) to produce these rewards.

Cecropia also produce tiny, lipid-rich and protein-containing pearl bodies ("pearl glands" to botanists) on abaxial leaf surfaces (Rickson, 1976). These bodies are not usually apparent in the field, since they are removed rapidly and continuously by obligate ant inhabitants, or in the absence of these, by unspecialized and opportunistic ants. However, pearl bodies are readily found on greenhouse-grown plants and in the field, on plants or plant parts protected from foraging ants. In contrast to trichilia, pearl glands are simple structures. As an alternative or adjunct to extrafloral nectaries, pearl bodies are taxonomically widespread as a biotic defense of myrmecophilic plant species, i.e., those that attract ants with food rewards but not nest sites (e.g., O'Dowd, 1982; Schupp & Feener, 1991). Their occurrence both in nonmyrmecophytic *Cecropia* and in closely related *Musanga* and *Coussapoa* suggests that their presence may be plesiomorphic in the genus.

Inside host-plant stems, many obligate *Cecropia*-ants also tend coccids and mealybugs (Hemiptera: Coccidae and Pseudococcidae), and they may excavate pits in external layers of nodal diaphragms to permit coccids to feed on the soft internal layers containing strands of conducting tissues. The numbers and biomasses of Hemiptera are typically low compared with those in plants that almost always house ants but have few or no obviously ant-attractive traits (reviewed in Davidson & McKey, 1993). Becerra & Venable (1989) have argued that myrmecophytes should be selected to reduce ant-tended Hemiptera, which not only consume plant resources but also transmit diseases, alter plant metabolism and development, and are difficult to oppose by chemical defenses. By provisioning symbiotic ants with mainly carbohydrate rewards, myrmecophytes may induce the ants to balance their diets by consuming a greater fraction of their protein-rich associates. Interestingly, in insular *Cecropia* populations lacking ants, at least externally feeding Hemiptera can reach outbreak densities and, combined with overgrowth by vines, may even limit the species' distribution (Janzen, 1973). (See also Fiala et al., 1994, for indications that symbiotic ants may protect myrmecophytic *Macaranga* [Euphorbiaceae], the Asian equivalent of *Cecropia*, from damaging infestations of pseudococcids.)

BENEFITS TO *CECROPIA*

Despite earlier theories postulating no significant effect of ants on plant fitness (Rettig, 1904; von Ihering, 1907; Ule, 1906; Fiebrig, 1909; Wheeler, 1913; Andrade & Carauta, 1982; but see Müller, 1880, and Schimper, 1888), symbiotic ants appear often to benefit myrmecophytic *Cecropia* by protecting their host plants against herbivores (Schupp, 1986; Ferguson et al., 1995; Vasconcelos & Casimiro, 1997; Davidson & Yu, unpubl. data), and/or vines and other vegetation that potentially compete with the hosts for light (Janzen, 1969; Schupp, 1986; Davidson et al., 1988; but see Putz & Holbrook, 1988). The occurrence of ant-occupied trees with foliar damage cannot be taken as evidence against a beneficial role of ants, since alternative ant species may occur and differ in the quality of protection proffered. Moreover, rates of leaf production and investment in biotic defenses may vary across habitats in ways that affect the quality of defense. In a long-term, experimental study in Río Palenque, Ecuador (Schupp, 1986), herbivore densities and herbivory rates were lower on ant-inhabited saplings of *Cecropia* vs. *obtusifolia* than on plants that lacked ants either naturally or after experimental removal. There, *Azteca constructor* was effective in defending its hosts against foliar herbivory by large-bodied, chewing insects, including leaf beetles (e.g., *Coelomera atrocaerulea*, Chrysomelidae). Protection was effective in the dry season but not the wet season, when herbivores were more abundant. During the 15-month investigation, saplings defended by ants against herbivores and encroaching vines grew significantly faster than did those lacking ants. Shorter-term studies concur that obligate *Cecropia*-ants defend against insect herbivores. Thus, Rocha & Bergallo (1992) showed that colony size was positively related to resistance against herbivory.

Leafcutter ants can also pose significant threats to *Cecropia*, especially in habitats not subject to frequent inundations that kill colonies of these ground-nesting species. Vasconcelos & Casimiro (1997) conducted an 18-month, experimental study of such herbivory in central Brazil. Frequency of attack was not related to leaf palatability as assessed in feeding trials, but for three of the four species included in the study, to occupation by colonies of *Azteca* ants. Thus, although the fastest-growing species (*Cecropia distachya*) was most likely to be attacked when ants were absent, and to be favored by leafcutter ants in feeding trials, occupied saplings of this species contained larger worker populations than did stems of a slower-growing species, and their leaves also benefited most from ant attendance. (Likewise, in myrmecophytic Asian *Macaranga*, species suffering most from ant removal are those apparently producing greater quantities of ant rewards, which in turn support larger worker populations [Itioka et al., 2000]). The slower-growing species (*C. ulei*) was least preferred by leafcutters in feeding trials and among plants lacking *Azteca*, but it was also least likely to be colonized by *Azteca* and most likely to lose its *Azteca* colonies. It is possible that slow-growing species invest more in physical and chemical defenses of leaves (see below). Across all four host species, more attacked than unattacked saplings died during the observation period, though the difference was not significant at small sample sizes, and plants attacked more than once grew more slowly than did those attacked just once or not at all.

Most studies of the effects ants on herbivory of myrmecophytic and myrmecophilic plants have focused on worker protection of leaf blades (e.g., Beattie, 1985). However, the location of Müllerian bodies at the bases of petioles in *Cecropia* attracts workers mainly here and to adjacent stems. The principal value of symbiotic ants (as opposed to that of opportunistic, nonresident species that consume just pearl bodies) could therefore be the protection these symbionts afford petioles and stems. (See also Fiala et al., 1994, for a potentially similar situation in *Macaranga* [Euphorbiaceae].) At least some leafcutter ants (*Azteca laevigata*) damage or destroy terminal meristems of *Cecropia* and remove entire leaves by severing their petioles (Vasconcelos & Casimiro, 1997). Moreover, thick-stemmed (pachycaulous) plants are often colonized by stem-boring insects such as the weevils (Coleoptera, Curculionidae) that are extremely common in *Cecropia* stems at higher elevations in the tropics (H. Hespenhide, pers. comm. for Costa Rica; pers. obs., for at least 1500–2000 m in the eastern Andes of southern Peru). At lower elevations, leaf beetles (Chrysomelidae) plague young *Cecropia* throughout their South American distribution (Andrade, 1981, 1984a; Schupp, 1986; Jolivet, 1989; Davidson & Fisher, 1991; Rocha & Bergallo, 1992; Jolivet & Salinas, 1993). Some of these beetles (e.g., in the genus *Coelomera)* lay eggs inside stems, where larvae hatch and emerge to feed on either leaves or their petioles (Andrade, 1981, 1984a; pers. obs.). Where herbivory rates are high, *Cecropia* seedlings are hard-pressed to stay ahead of herbivory by producing new leaves just as the previous ones are either removed entirely or largely consumed, with only skeletons of veins left behind (pers. obs. along rivers of southeastern Peru). The severing or weakening of petioles can be disastrous for plants like *Cecropia*, which invest many resources in very large individual leaves. Like leafcutter ants, stem-inhabiting beetles can also damage terminal meristems, slowing the vertical height growth necessary for *Cecropia* to overtop other fast-growing competitors in light gaps and other disturbed habitats. For seedlings and saplings with one or very few meristems, this type of damage would likely convey substantial material and opportunity costs.

Given the diverse types and high levels of damage attributable to stem-dwelling herbivores, it is possible to conclude that the primary importance of symbiotic ant colonies (vs. opportunists feeding on pearl bodies) is to preclude stem occupancy by herbivorous beetles, perhaps especially in vulnerable young *Cecropia* seedlings and saplings. In accord with this argument, an unusual *Cecropia* species, *C. hispidissima*, illustrates how protection of leaves and stems may be funded by different ant rewards that are monopolized by different ants. Stem-inhabiting colonies of *Pachycondyla* sp. nov. 1 have been found to date only on *Cecropia hispidissima* in Panama, and their workers apparently harvest Müllerian bodies from beneath the stipules and without ever visiting the leaves (T. Kursar, pers. comm.). Nevertheless, atypically large, hard, and purple Müllerian bodies of this host would appear to be adapted for use by the large-bodied *Pachycondyla* rather than by tiny *Azteca* ants. *Pachycondyla* workers do not exclude other ants, such as those of nonresident *Azteca* colonies, from frequent opportunistic foraging on leaves, probably for pearl bodies. In a hypothetical ancestor of myrmecophytic *Cecropia*, opportunistic ants may have harvested pearl bodies and protected leaves without alleviating selection for ways of ridding the plant of stem-dwelling herbivores. Müllerian bodies and prostomata may have evolved under such selection pressures. Moreover, protection of stems from stem-boring insects may start as soon as queens begin to colonize myrmecophytic *Cecropia*; many or most internodes of individual seedlings and saplings are colonized independently by one or more queens, and queens of some species do feed while developing their first worker broods (see below).

Accounts of other myrmecophytes also suggest that ants may protect against stem-boring insects. Thus, *Pheidole* ants of myrmecophytic *Piper* in Central America have been shown to protect hosts against stem-boring weevils (Letourneau, 1998). Replacement of stem-boring plant parasites by ants is thought to have been an early stage in the evolution of myrmecophytism in other plant taxa with primary domatia (e.g., Ward, 1991). Although ants probably often tended Hemiptera within these domatia, the net effects of ants and Hemiptera on plants may have been positive, especially in habitats where abundant light allowed rapid carbon gain to offset losses to Hemiptera (Davidson & McKey, 1993). Herbivore pressures may also have been more intense in comparatively productive, sunny environments (Davidson & Fisher, 1991; Davidson & McKey, 1993; Davidson & Yu, unpubl. data), reinforcing selection for ant attraction.

Finally, for *Cecropia* species inhabited by more than one species of ant, the quality of defense may vary with the identity of the partner. Obligate symbionts of *Cecropia* differ in their diurnal foraging schedules, the extent of their activity and aggression, the numbers and sizes of workers, and whether or not workers prune vines and other vegetation (Davidson et al., 1991; Davidson & Fisher, 1991; Longino, 1989b, 1991). Evolution on the part of the plant may produce adaptations that favor one ant species over another, but to some extent, the predominant inhabitant may be determined by the outcome of ant–ant competition and be beyond the plant's control (Davidson & McKey, 1993; Yu & Davidson, 1997). Poorly defending ants may sometimes gain possession of their hosts by virtue of rapid colony development, or pleometrosis, i.e., colony founding by two or more queens, whose combined first worker broods should produce larger and more competitive incipient colonies (e.g., Davidson et al., 1991).

INTERSPECIFIC VARIATION IN DEFENSIVE INVESTMENT

Early ecological studies of *Cecropia* were undertaken mainly in the Central America lowlands, where species diversity of both the host plants and their ants is relatively low. It is not surprising, then, that relationships between *Cecropia* and its ants were initially considered rather uniform. That is, all myrmecophytic *Cecropia* produced Müllerian (and perhaps pearl) bodies, and despite very early reports to the contrary (Wheeler, 1942), all *Cecropia* were implied to house *Azteca* ants (Janzen, 1969, 1973; Rickson, 1976, 1977). Not until the early 1990s did research begin to focus on interspecific variation in the ant-attractants of *Cecropia* and the significance of this variation to ant associates (Longino, 1989a; Davidson et al., 1991; Davidson & Fisher, 1991; Yu & Davidson, 1997). It now appears that there is important and interesting interspecific variation in the ontogeny, quantity, and composition of biotic defenses, and that some of this variation both accords well with general theories of plant defensive investment and is important to ants.

Plant defense theory begins by postulating that defenses are costly and are manufactured and used only when benefits, calculated in reduced herbivory, exceed costs. The costliness of biotic defenses in *Cecropia* is perhaps most apparent when ant-attractive traits are lost in the absence of selection imposed by the typical ant associates. It is interesting, then, that populations of *C. peltata* on Jamaica both occur in the absence of their ants and are polymorphic in their expression of trichilia (see treatment of *C. peltata* in Berg, above).

Several other observations also provide evidence for a cost of biotic defenses in *Cecropia*. First, food bodies are produced mainly at stages of leaf development and whole-plant development when they are apt to do the most good, including when chemical and physical defenses are poorly developed. In the species surveyed to date, production of either Müllerian bodies, pearl bodies, or both occurs within days of leaves first beginning to emerge from their stipules, and peaks relatively early in leaf lifetimes (week 1 for a pioneer species, and week 5–6 for a small gap species: Folgarait & Davidson, 1995). Young leaves are especially vulnerable to herbivores (Davidson & Fisher, 1991), probably due to their high foliar nitrogen levels and poorly developed physical and chemical defenses (Folgarait & Davidson, 1995). In addition, the value of a leaf to the plant is greatest at this stage, since most of its productive life span lies ahead (Harper,

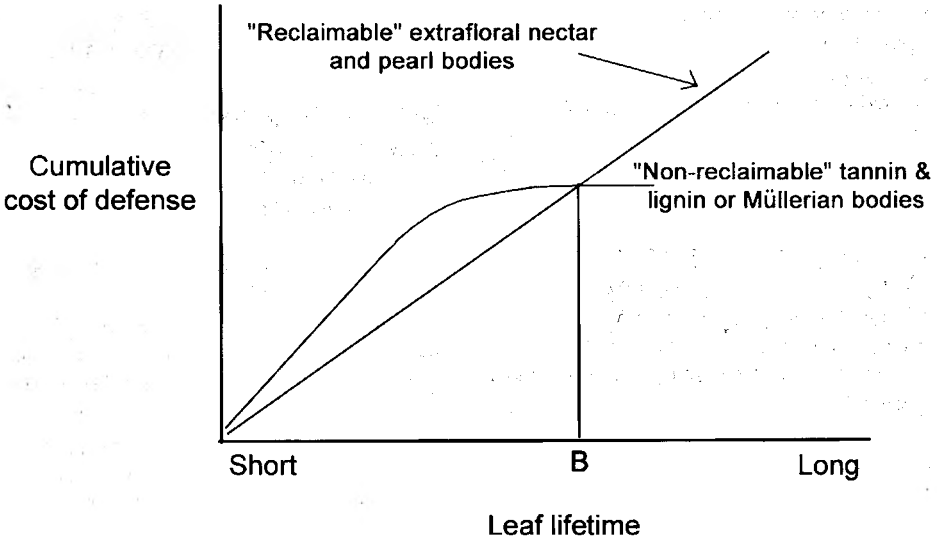

FIG. 1. The McKey (1984) model of plant defenses, modified to accommodate the biotic defenses of *Cecropia*. Cumulative costs of "reclaimable" biotic defenses (e.g., pearl bodies of *Cecropia*) are lower than those of "non-reclaimable" defenses (e.g., tannins and lignins, or trichilia and Müllerian bodies), for relatively short-lived leaves and other plant parts. However, they are higher in species for which "non-reclaimable" defenses can be amortized over the life spans of long-lived leaves.

1989). In relation to whole-plant development, tests of leaf palatability to herbivores suggest that *Cecropia* seedlings are better protected by chemical and physical defenses before than after the plants acquire their ants (Martinelli et al., 1993).

Three final patterns are indicative of a cost to the production of food rewards for ants. First, both Müllerian and pearl bodies are responsive to supplies of key resources (Folgarait & Davidson, 1994, 1995). Fertilization (N-P-K) and high light intensity increase Müllerian body production per unit time and per active lifetime of trichilia. In contrast, pearl body production is enhanced by nutrients but not by higher light intensities, perhaps because these rewards have higher nitrogen content than do Müllerian bodies, and because an increase in carbon fixation under high light draws nitrogen away from pearl body production and into growth as the first priority. Second, across species, there appears to be a trade-off between investment in biotic vs. chemical and physical defenses (Vasconcelos & Casimiro, 1997). Third, both the rate of Müllerian body production, and the total production per lifetime of a trichilium, increase in response to their manual removal, simulating harvesting in the presence of ants (Folgarait et al., 1994).

Granting then that defense can be costly, two important theories have related defensive investment either to resource availability (Coley et al., 1985) or to leaf life spans (McKey, 1984). The resource availability theory starts with the premise that plant growth rates vary in response to the availability of limiting resources, typically light in tropical forests. Plant species characteristic of relatively light-rich environments have evolved rapid growth and low levels of defense, since costly defensive investment would exact opportunity costs in the form of reduced growth that could lead to overtopping by fast-growing competitors. In contrast, slow-growing species of resource-poor (shaded) habitats would have little to lose by defending (i.e., low opportunity costs) and perhaps much to gain, since low resource availability prevents rapid replacement of lost tissues.

In contrast, McKey's leaf lifetime hypothesis suggests that plants should use different kinds of defenses depending on whether leaf lifetimes are short or long (Fig. 1). Relatively fast-growing plants with short-lived leaves should invest mainly in "reclaimable defenses," equated by McKey to biotic defenses (extrafloral nectar and, presumably also, pearl bodies). These defenses have low initial construction costs but significant maintenance costs, so cumulative costs increase linearly through time. As leaves age and acquire other defenses such as toughness, the resources invested in biotic defenses can be routed to new leaves at little expense. Therefore, biotic defenses are often produced on the newest, most valuable, and most vulnerable foliage. In contrast, McKey postulated that comparatively slow-growing plants with long-lived leaves could afford to invest in "non-reclaimable" defenses, such as tannins, lignin, fiber, etc. Once laid down, these defenses were (theoretically) permanent and could not be broken down and remobilized to new tissues. Only in plants with long-lived leaves could the high initial construction costs of non-reclaimable defenses be amortized over a sufficiently long period so that their cumulative costs would be exceeded by the cumulative costs of "reclaimable" defenses.

Interspecific differences in investment in the biotic defenses of *Cecropia* are well explained by these theories if a distinction is made between "reclaimable" pearl bodies and less reclaimable Müllerian bodies and trichilia, with the latter having higher initial construction costs (Folgarait & Davidson, 1994, 1995). The more light-demanding "pioneer" *Cecropia* species, typical of very open (often riparian) habitats, have the relatively rapid growth rates and short-lived leaves characteristic of other tropical rain forest pioneers. In accord with McKey's theory, such species tend to invest proportionately more heavily in pearl bodies and less heavily in Müllerian bodies (evaluated as dry weight of reward per unit of leaf area) than do related but more shade-tolerant species with slower intrinsic growth rates and longer leaf life spans (Folgarait & Davidson, 1994, 1995). Greater investment in Müllerian bodies is also consistent with the resource availability theory of plant defensive investment, because leaf lifetimes tend to be highly correlated with (and lower in) light-rich habitats (Mooney & Gulmon, 1982).

Using the McKey (1984) model as originally formulated to compare myrmecophytes and myrmecophiles with plants lacking biotic defenses altogether may also help to explain the distribution of nonmyrmecophytes within the genus *Cecropia*. Investment in non-reclaimable tannins, fiber, and lignin would be predicted to replace partially or mainly reclaimable biotic defenses in plants with comparatively long leaf life spans. It is interesting in this context to note that nonmyrmecophytic *Cecropia sciadophylla*, a relatively slow-growing *Cecropia* species of infertile soils on higher terraces in Amazonia, produced longer-lived leaves than did any of eight myrmecophytic *Cecropia* species with which it was grown simultaneously, or which were grown in other experiments in temperate greenhouses (D. Davidson et al., unpubl. data). Because of the correlation between intrinsic plant growth rates and mean leaf life spans (Folgarait & Davidson, 1994, 1995), a decline in myrmecophytism with decreasing intrinsic growth rates at high elevation might also be anticipated, but a lack of appropriate ant species could also play a role (Wheeler, 1942). Finally, plant defense theories based on either leaf life spans or resource availability, and developed explicitly for foliar defenses, should also apply to defenses of other plant parts, such as stems benefiting from ant occupation; this is particularly true considering that new stems of *Cecropia* tend to be photosynthetic.

Interspecific differences in *Cecropia* reveal another pattern that was not previously predicted, but was readily apparent because biotic defenses are easily observable externally (Davidson & Fisher, 1991; Folgarait & Davidson, 1994, 1995). The onset of (biotic) defense occurs earlier in seedling development for relatively slow-growing, shade-tolerant *Cecropia* than for their faster-growing, light-demanding relatives—a pattern that could prove typical in other (e.g., chemically defended) genera of tropical trees but is currently poorly explored. Early in seedling ontogeny, leaves are produced without trichilia, and stems both lack prostomata and are too narrow to accommodate ant colonies. In common garden experiments, the production of active trichilia and the swelling of stems concurrent with the appearance of prostomata, occur earlier in time and earlier in development in relatively slow-growing, shade-tolerant *Cecropia* species than in their faster-growing relatives.

Some of the most distinctive myrmecophytic *Cecropia* occur in small light gaps, uncharacteristically shaded habitats for this largely "pioneer" genus. Low light slows growth, increasing the probability that *Azteca* colonies will fail (Vasconcelos & Casimiro, 1997), yet it also prolongs rates of replacement of leaves lost to herbivores. In this context, some species have evolved very early developmental switches to myrmecophytism. For example, in western Amazonia, trichilia first appear on median leaf number six in "*Cecropia pungara*," though at leaf number 13 in the apparently closely related *Cecropia membranacea* (Davidson et al., 1991). (Based on gene sequence data [S. Cook and D. Davidson, unpubl. data], "*C. pungara*" appears to be a distinct species but is treated as a "form" by Berg & Franco [this volume, see discussion under *C. membranacea*].) Remarkably, in "*Cecropia herrerensis*" of northeastern Peru, trichilia are produced on the first set of leaves after cotyledons. From the perspective of the ants that colonize their seedling hosts as soon as swollen stems with prostomata appear, tiny, slow-growing juveniles of small-gap *Cecropia* are a far different resource than are tall, rapidly growing pioneer *Cecropia* of light-rich habitats. Although small-gap species may supply more resources to their colonies per area of leaf surface (Folgarait & Davidson, 1994, 1995), rates of resource supply per plant are the more important factor to developing colonies, and those rates are greater in comparatively fast-growing pioneer relatives of the small gap species. Therefore, it is not surprising that the early-defending, shade-tolerant *Cecropia* can have unusual ant associates (Davidson & Fisher, 1991). For example, "*C. pungara*" is inhabited, not by any of the *Azteca* species (subfamily Dolichoderinae) so widespread on Central and South American *Cecropia*, but by *Pachycondyla luteola* (Ponerinae) and *Camponotus balzani* (Formicinae), and the typical associate of "*Cecropia herrerensis*" in northeastern Peru is *Crematogaster* aff. *curvispinosa* (Myrmicinae).

ANTS SYMBIOTIC WITH *CECROPIA*

Table 1 presents a list of obligate *Cecropia*-ants as we presently know them. Most impressive is their taxonomic diversity. All ants belong to the same insect family, the Formicidae, and the major systematic categories of ants are the subfamilies. The associates of *Cecropia* represent four ant subfamilies, including all but one of those in which at least some species are known to rely heavily on plant resources. Absent are only the Pseudomyrmecinae, stem-nesters found frequently in narrow twigs, where workers can effectively use their heads to block small entrances against invasions of competing and predatory ants.

The most common and best-known associates of *Cecropia* belong to the dolichoderine genus *Azteca*. This group is endemic to the New World, and its diversity and abundance are greatest in the lowland tropics. Approximately 63 species and numerous named varieties remain in the genus after reconciling Brandão (1991) and Longino (1991) with Kempf (1972), and 13 of these species are specialists on *Cecropia* (Table 1). The genus includes many free-living species as well as specialized plant-ants associated with myrmecophytes in at least 16 genera and 9 families (Davidson & McKey, 1997). *Azteca* ants tend to have populous colonies, finely divided into many small workers that tend Hemiptera (Coccidae and Pseudococcidae), scavenge, and hunt live prey, (usually insects, and sometimes including competing ants; Carroll, 1983; Adams, 1990a). Based on nitrogen isotopic ratios, various *Azteca* species place among the most predatory of arboreal ants (Davidson et al., 2003) and are the most nitrogen-deprived of neotropical ants (Davidson, in press). Abundant carbohydrates from hemipteran honeydew may fuel both the large worker populations, which are maintained principally by carbohydrates rather than by protein resources (Davidson, 1997), and the infamous aggression exhibited by these ants (Carroll, 1983). Monogynous (single-queen) colonies are often polydomous, i.e., occurring as numerous affiliated nests distributed over one or more crowns. The large colony sizes of *Azteca* are correlated with low population densities, perhaps reflecting high mortality of incipient colonies with comparatively few hemipteran associates and thus limited protein resources. Wilson (1985 & pers. comm.) has argued that low population densities may be correlated with high local extinction rates that could account for the extinction of *Azteca* from West Indian islands, despite their presence there in fossil ambers from the late Oligocene or early Miocene.

Interspecific and intraspecific spatial territoriality have been demonstrated for a number of *Azteca* species (Adams, 1990a, 1990b, 1994; see also Leston, 1973, and Carroll, 1979) and may have preadapted members of this genus for defense of myrmecophytic host plants. *Cecropia* and other myrmecophytes provide carbohydrates which fuel large, aggressive, and territorial worker populations (Davidson & McKey, 1993; Davidson, 1997). *Azteca* colonies subdivide labor by physical subcastes, with (mainly) major workers stationed on limbs at key branch intersections, at the bases of plants, and at colony borders (Adams, 1990a, 1990b, 1994). Defending workers frequently exhibit characteristic postures, with mandibles open and gasters upraised, ready to release carbon-based alarm pheromones should enemy ants approach. Relatively long-distance recruitment of nestmates (over meters) is apparently mediated in *Azteca* by trail pheromones from the Pavan's glands. Signaling food finds and breaches in colony defense, short distance recruitment (over several centimeters) occurs in response to alert/alarm products (cyclic ketones) of the pygidial gland, as well as through worker-to-worker contact and tactile displays. Outcomes of territorial interactions appear to be determined by mutual assessment of asymmetries in colony size, mediated in part by recruitment responses that escalate with proximity to nests and nestmate reinforcements. With increased aggressiveness at or near nest sites, resident advantage can blunt advances of numerically superior colonies. Finally, because the traits summarized here occur in free-living *Azteca* species, they almost certainly evolved in the context of territorial defense against other ants. Although many of the same traits undoubtedly preadapted *Azteca* to protect their host plants, arguments that such behaviors of *Azteca* evolved by selection on *Cecropia* for "induced defenses" (Agrawal, 1998) are currently not convincing because they ignore the basic biology of ants in this genus.

TABLE 1

Known or presumed obligate *Cecropia*-ants.[a]

Subfamily & Species	Geographic Distribution	Reference
DOLICHODERINAE		
Azteca spp.		Longino, 1989, 1991
A. alfari[b]	Central America through Amazonia	
A. aragua	Aragua State, Venezuela	
A. australis	W Amazonia (Peru, Bolivia), Amazonas, Brasil	
A. coeruleipennis	S Mexico through NW Costa Rica	
A. constructor	Guatemala through Guyana	
A. isthmica	Panama and Colombia	
A. lattke	Venezuela (coast ranges & Cordillera de Merida)	
A. merida	E slopes, Cordillera de Merida, Venezuela	
A. muelleri	S Brasil	
A. ovaticeps[b]	Lowland tropics of Central and South America	
A. petalocephala	SW of Coroico, (La Paz), Bolivia	
A. salti	Sierra Nevada de Santa Marta, Colombia	
A. xanthochroa	Mexico through Panama	
PONERINAE		
Pachycondyla luteola	W Amazonia	Davidson et al., 1991
P. prov. *dianae*[c]	SE Panama	W. L. Brown, in ms
P. "insignis"[c]	Mid-elevation wet forest, Costa Rica	J. Longino 2000[d]
P. unidentata rugulosa[c]		Emery 1902
FORMICINAE		
Camponotus balzani	Amazonia	Davidson et al. 1989, 1991; Benson 1985
MYRMICINAE		
Crematogaster nr. *curvispina*	Descent from E Andean cordillera in SE Peru	D. W. Davidson, unpubl.
Pheidole sp.		

[a] Other ants may nest opportunistically in *Cecropia* stems without using prostomata or Müllerian bodies (Longino, 1989a; Davidson & Fisher, 1991). This phenomenon is especially common in plants with obligate associates nesting polydomously, only in growing tips. Polydomy, or fragmentation of single colonies over multiple nest sites (here, disjunct stems of a single host plant) is characteristic of *Azteca alfari* and *A. ovaticeps* (Longino, 1989b).

[b] Members of the *Azteca alfari* group thought to have descended from ancestors that nested in live stems (Longino, 1989, 1991). The remaining *Azteca* species are proposed to be descendants of carton-nesting ancestors.

[c] These names are conditional proposals (*sensu* Art. 15 of the 1985 ICZN) by the late W. L. Brown Jr., and thus not made available here. Their appearance here or in any duplication of this article does not constitute publication.

[d] See Longino (2000) for natural history, distribution, etc. The species appears to be a specialist on sapling *Cecropia*, and colonies mature before saplings grow to tree size. Occupation of saplings by this species may lead to the demise of seedlings by precluding colonization by the more typical Azteca ants.

[e] This variant of *P. unidentata* was synonymized with *P. unidentata* in an unpublished manuscript by W. L. Brown Jr., but sentiment remains among myrmecologists for considering it to be a specialist on *Cecropia* saplings.

Among the usually predacious and scavenging Ponerinae, there appear to have been no fewer than three (and perhaps even four) independent evolutionary colonizations of *Cecropia* (Table 1). All of the ponerines specialized to live in *Cecropia* are species in the genus *Pachycondyla*, relatively large-bodied ants occurring in both the New and Old World tropics. Most *Pachycondyla* species are terrestrial, but some species are arboreal, nesting opportunistically in cavities of dead or live stems, or in and around epiphytes and debris, in the upper or lower rainforest canopies. Of the arboreal species, several are known to occupy abandoned internodes of seedling and sapling *Cecropia.* Among the *Pachycondyla* specialized to live in *Cecropia*, *Pachycondyla* "insignis" appears to be related to *P. villosa* and *P. bugabensis,* two generalized arboreal predators (Longino, 2000). *Pachycondyla luteola* and *Pachycondyla* (provisionally) "dianae" (W. L. Brown manuscript), are morphologically distinctive from one another and from *Pachycondyla* species nov. 2, as well as geographically disjunct in their distributions. Host-specific on "*Cecropia pungara*," *Pachycondyla luteola* departs most notably from other ponerines in behavior and colony size, typically just tens to hundreds of workers in the genus as a whole (Peeters, 1997). One might speculate that hemipteran tending may occur in this species and provide carbohydrates to subsidize the large worker populations. However, the fearsome stings of these aggressive ants—painful over weeks to months—have deterred investigators from opening *P. luteola* nests in all but small seedlings and saplings where Hemiptera are least apt to have colonized. Workers both prune encroaching vines and exhibit absolute fidelity to their host-plants, feeding principally on food rewards provided by the plant (Davidson & Fisher, 1991). As is typical of ponerines, queens do not found their colonies claustrally; instead they collect, store and use Müllerian bodies in the early establishment of their colonies. Thus, they must leave the prostoma open in order to reach the trichilia, a practice that makes them susceptible to loss of brood to parasitoid wasps (Perilampidae, Davidson & Fisher, 1991). External foraging by nonclaustral queens (frequently multiple, competing queens per colony) may provide some protection to juvenile plants immediately after colonization and prior to colony establishment.

Formicines and Myrmicines are also represented among the associates of *Cecropia*. *Camponotus balzani* (subfamily Formicinae), a host generalist, is extremely timid and largely nocturnal, and seldom ventures away from stems to patrol leaves (Davidson & Fisher, 1991). Another formicine, a species of *Myrmelachista*, is not listed in Table 1, because rather than collecting and feeding on Müllerian bodies, it appears to feed on the abundant queens of *Azteca* spp. that colonize a variety of *Cecropia* along the eastern escarpment of the Peruvian Andes (pers. obs.). Within the Myrmicinae, *Crematogaster* (Table 1) is a genus of ecologically dominant ants that are most diverse in the Old World tropics, where they are frequently obligate plant-ants (Davidson & McKey, 1993). Their possibly late arrival in the New World tropics (Brown, 1973) might account for why small-bodied, stem-nesting and carton-building ants in the endemic neotropical genus *Azteca* were able to diversify and become codominant with this ecologically similar genus. The species associated with "*Cecropia herrerensis*" is most closely related to *C. curvispinosa*, a generalized cavity nester, widespread in the Neotropics (J. T. Longino, pers. comm.) and found occasionally in *Cecropia* at high elevations (pers. obs.). Although colonizing queens have occasionally been found with incipient colonies on "*C. herrerensis*," sometimes cofounding with conspecific queens, larger colonies are more often resident without their queens, which may either occupy trunks of adjacent *Cecropia* or live off the host altogether. Nevertheless, documentation of queen colonization and the collection, storage, and use of Müllerian bodies suggests that the ants are specialized associates of *Cecropia*.

A third myrmicine, in the cosmopolitan genus *Pheidole*, is listed here on the basis of a single collection in *Cecropia* sp. at relatively high elevation (ca. 1500 m) on the descent from the eastern cordillera of the Andes in southeastern Peru (D. Davidson, unpubl. data). Although the queen was not located, a large colony occupied numerous internodes of a relatively tall plant, and was harvesting and storing Müllerian bodies near its brood. Until more colonies of the *Pheidole* are located, and queens are shown to recognize and colonize these hosts, the lone record must be regarded with suspicion. If the ant is eventually confirmed as an obligate symbiont of *Cecropia*, the finding would be consistent with the pattern of novel associates occurring at the elevational and latitudinal limits of the distributions of myrmecophytes (Davidson & McKey, 1993; McKey & Davidson, 1993).

Even among the predominant associates of *Cecropia* in the genus *Azteca*, there appear to have been multiple evolutionary colonizations of myrmecophytic hosts. Based on both morphological and behavioral evidence (Longino, 1991), and gene sequence data (Ayala et al., 1996), at least two independent lineages of *Cecropia*-ants have been distinguished. One lineage, the *Azteca alfari* group (*A. alfari* and *A. ovaticeps*), is likely derived from ancestors that nested in live stems. The other, the *A. muelleri* group (*A. muelleri* plus *A. aragua*, *A. australis*, *A. isthmica*, *A. petalocephala*, *A. salti*, *A. xanthochroa*, and possibly *A. constructor* and *A. merida*), has probably descended from carton-nesters, and species in this lineage still build carton nests within their hosts. Carton nests consist of masticated plant material, sometimes mixed with ant or vertebrate feces and soil (reviewed in Longino, 1986; Davidson & Epstein, 1989), all building materials that are available practically anywhere. Although the occurrence of stem-nesters may often be limited by the availability of suitable stems, nesting in carton frees ants to locate their nests near abundant food. Thus, the two *Azteca* lineages may have had very different histories of association with *Cecropia*. Carton-nesting ancestors of contemporary *Cecropia*-

ants may have initially sought out *Cecropia* because of its pearl bodies (see above), just as other carton-nesting taxa are sometimes overrepresented on hosts supplying extrafloral nectar (Hölldobler & Wilson, 1990; Davidson & Epstein, 1989). In contrast, stem-nesters would have been restricted to habitats where suitable hollow stems were available; wide stems with weak pith are characteristic of pioneer plants in disturbed habitats.

This scenario is consistent with experimental evidence sorting out the contributions of host specificity and habitat specificity to the determination of pairings between *Cecropia* and its ants. Yu and Davidson (1997) cultivated several *Cecropia* species from seeds in screen tents in Amazonian Peru, until all of the species had expanded their stems and produced prostomata. They then placed them out in two habitats, riverine edge and forest gaps (created or augmented) and monitored colonization over 2–3 months. *Azteca ovaticeps*, a member of the stem-nesting *A. alfari* group, proved to be habitat-specific (to riverine edge) and not host-specific, but the reverse was true of *A. australis* of the carton-nesting *A. muelleri* group. The relatively small thorax and reduced wing musculature of *A. ovaticeps* queens (Davidson et al., 1991) was consistent with its inability to seek out potential hosts in gaps dispersed throughout the forest. In contrast, with its large thorax, presumably correlated with a greater wing muscle mass, *A. australis* queens were successful at locating seedlings in both habitats. However, in behavioral assays, queens preferred to colonize species with high pearl body production; they also were underrepresented among foundresses on hosts with low pearl body production and successfully produced brood during the experimental period only on the preferred hosts (Yu & Davidson, 1997). (The dearth of pearl bodies themselves is not likely to have caused failure of brood production, since the queens found their colonies claustrally.)

A parsimonious interpretation of the history of the relationships between the two ant lineages and their hosts might therefore suggest that the two were differently preadapted to use *Cecropia*, and that aspects of their preadaptations survive to influence their use of these myrmecophytes today. Thus, *Azteca australis* and its allies occur naturally mainly on hosts with high pearl body production (Davidson & Fisher, 1991; Yu & Davidson, 1997; Folgarait & Davidson, 1994, 1995). In contrast, *A. ovaticeps* and its sister species, *A. alfari*, are restricted to large-scale disturbances throughout their ranges (Longino, 1989, 1991; Davidson & Fisher, 1991). Interestingly, in greenhouse experiments, *A. alfari* did not even feed on pearl bodies (Baird 1967).

This overview of *Cecropia*-ants suggests that *Azteca* were likely the original associates of *Cecropia*. Not only are they the most diverse and widespread among the many symbionts of these ant-plants, but species in the *Azteca muelleri* group (including *A. australis*) may have built carton nests on these plants to use pearl bodies, even before Müllerian bodies had evolved. For this and other reasons, the *muelleri* group may have been first among the *Azteca* species to inhabit myrmecophytic *Cecropia*. In seeking out host plants with pearl bodies, queens of carton-nesting *Azteca* might have initially colonized larger plants, not seedlings, and it is difficult to believe that these foundresses could have initiated their colonies on plants with preexisting colonies of stem-nesting species. On the other hand, queens of stem-nesters may very well have gotten their start on *Cecropia* by colonizing seedlings that had not yet acquired other ants. As for the *Cecropia*-ants in other genera, these are almost certainly all derived from stem nesters, and with the exception of *Camponotus balzani* (widespread in the Amazon basin), are all species with limited biogeographic and/or host ranges that suggest relatively recent origins of their relationships with *Cecropia*. A subset of these ant species, in the genera *Pachycondyla* and *Crematogaster*, also coexist with much more widespread and common species that are their likely progenitors (Table 1).

The richness and diversity of the ants symbiotic with *Cecropia* imply that colonization of *Cecropia* by unspecialized ants over evolutionary time has been a relatively easy transition. At least two factors could have facilitated this transition. First, for many ants with generalized diets, long-lived and secure nest sites, such as those afforded by cavities in live plants, may be more limiting than are food resources. Second, pachycaulous stems with weak pith probably evolved in *Cecropia* as a form of minimal support structure for large leaves (Hallé et al., 1978; White, 1983; Davidson & McKey, 1993). Once evolved, these large stems were easily coopted as desirable and accessible nest sites for ants of diverse body sizes and colony sizes. In the context of the susceptibility of stems to exploitation by damaging herbivores (see above), such ants may have provided net benefits to their hosts and exerted selection pressures favoring the evolution of other ant-attractive traits.

COEVOLUTION OF ANTS AND *CECROPIA*

Coevolution consists of coadaptation and cospeciation (Brooks, 1979). Coadaption signifies that each species in the partnership has evolved one or more traits in response to selective pressures exerted by the other. There is little question that this has occurred in *Cecropia* and its ants, but since most *Cecropia*-ants are found on more than one host species, and many *Cecropia* species can be inhabited by more than one ant associate, coadaptation likely was diffuse. In diffuse coadaptation, selection pressures responsible for the evolution of a trait in one partner come from a set of associates, rather than from one species in particular (Janzen, 1980).

What traits are indicative of coadaptation? In *Cecropia*, prostomata and trichilia with Müllerian bodies are surely characteristics that have evolved due to selection pressures exerted by symbiotic ants, and pearl bodies could have evolved in response to selection imposed (originally) by opportunistic, as well as (later) symbiotic associates. Moreover, once these traits had evolved, there is evidence that they may have been modified by selection pressures generated by particular ant species (Davidson et al., 1991; Davidson & Fisher, 1991). Thus, the unusually large and protruding (rather than recessed) prostoma of "*Cecropia pungara*," together with its much larger Müllerian bodies, may be interpreted as adaptative responses to its occupation by relatively large-bodied *Pachycondyla* and *Camponotus* species. *Pachycondyla luteola* is also unique among well-studied *Cecropia*-ants in its nutritional dependency on Müllerian bodies during the earliest stages of colony founding, and despite this dependency, *P. luteola* queens refuse smaller Müllerian bodies transferred from other species of *Cecropia* (D. W. Davidson & P. Hererra, unpubl. data). Although composed of glycogen, as in congeneric species (F. Rickson, pers. comm.), the Müllerian bodies of "*C. pungara*" must be distinctive in some other way; based on superficial examination, they are unusually hard and less apt to degrade during storage. The Müllerian bodies of *C. hispidissima* appear to have evolved with *Pachycondyla* prov. *dianae*, a species even larger-bodied than *P. luteola*, and are larger and harder even than those of "*Cecropia pungara*." Other *Cecropia*, for example "*C. grisita*" (a name used for material not yet matched with any of the recognized *Cecropia* species) in southeastern Peru, have especially small Müllerian bodies (Folgarait & Davidson, 1994, 1995) or bodies to which obligate ants from different habitats react abnormally (Davidson & Fisher, 1991, for an *Azteca ovaticeps* colony placed on *Cecropia ficifolia*). Among the six common species co-occurring in southeastern Peru, "*C. grisita*" is the only one that never houses large-bodied ants, e.g., *Camponotus balzani* (Davidson et al., 1991), perhaps because of the unusually narrow stems at the time when seedlings are being colonized.

Other ant-related traits of *Cecropia* might have originated either through coadaptation with associated ants or as preadaptations, arising through alternative selection pressures. For example, among the *Cecropia* species present in southeastern Peru, *C. membranacea* and "*C. pungara*" are distinctive in initiating Müllerian body production prior to the broadening of stems and the production of prostomata. Since the trait occurs in *C. membranacea*, on which *Pachycondyla luteola* queens fail to establish colonies, it is possible that it evolved in a different context and merely preadapted "*Cecropia pungara*" for use by this nonclaustral ant species (Yu & Davidson, 1997). The long, relatively sparse stem hairs of "*C. pungara*" could either be an adaptation to facilitate movements of its relatively large ant species (*Pachycondyla luteola* and *Camponotus balzani)* or have provided a preadapted nest site where urticating hairs deterred potential predators of ant brood. Rates of production of Müllerian and pearl bodies, or leaves bearing both rewards, could either have coevolved with or been preadapted to colony growth rates of particular ant species. Pearl body production may be low in *Cecropia membranacea* (Folgarait & Davidson, 1995) because its most frequent associate, *Azteca ovaticeps*, relies only weakly or not at all on these food rewards (Baird, 1967), or because of low nitrogen levels in the frequently inundated habitats of this species. Glaucous stems, such as those that restrict climbing by all but the most obligate ant associates of some myrmecophytic *Macaranga* (Federle et al., 1997), occur as a developmental stage (D. W. Davidson, unpubl. data) or polymorphism in some *Cecropia* species. While this trait might have evolved to limit access to all but beneficial ants, it could also have originated as a defense against insect herbivores. (Recent evidence [D. W. Davidson et al., unpubl. data] suggests the latter for *Cecropia* vs. *strigosa*.) Finally, selection to enhance the integrity of the internodal septa inside *Cecropia* stems (thicker and harder in myrmecophytes than in nonmyrmecophytes: see Bailey, 1922) could occur either for structural reasons or to allow for competition among multiple foundresses and their incipient colonies. By assuring that multiple colonies of one or more species can develop in isolation from one another, the plant should both increase its chances for successful establishment of at least one colony, and help to magnify selection among competitors for rapid colony development rates.

Among ants, coadapted traits resulting from association with one or more *Cecropia* species would include the recognition and use of both prostomata and Müllerian bodies by queens and workers. In both the introduced (Wetterer, 1997) and native ranges of *Cecropia* (Davidson & Fisher, 1991), ants that are not obligate *Cecropia* associates tend not to recognize Müllerian bodies as food. Those in the introduced ranges have also not been observed to use prostomata to nest in *Cecropia* stems (Putz & Holbrook, 1988; Wetterer, 1997). In contrast, queens of obligate associates in the *Azteca alfari* group appear to have evolved head shapes that facilitate stem entry at prostomata (Longino, 1989b). Facing high risk of predation during colony founding, queens of obligate *Cecropia*-ants should also have evolved to locate their hosts quickly from a distance, by responding to possible chemical cues elaborated by one or more hosts. At closer range, queen transfer experiments have shown that both *Azteca australis* and *Pachycondyla luteola* exhibit strong preferences for host species on which brood production is most successful (Yu & Davidson, 1997, and above). The latter species colonizes just "*Cecropia pungara*," the only species on which this ponerine ant succeeds in establishing colonies, and *C. membranacea*, believed to be a very close relative (Yu & Davidson, 1997).

Finally, many *Cecropia*-ants attack and prune vines and other vegetation that contacts their host plants (Janzen, 1969; Davidson et al., 1988). This behavior, present in the associates of many myrmecophytes, reduces access to the plants by competing and predatory ants (Davidson et al., 1988). Occurring among *Cecropia*-ants in (at least) a number of *Azteca* species (e.g., Janzen, 1969) and in *Pachycondyla luteola* (Davidson et al., 1988), the behavior may be an aspect of territoriality that evolved either before the relationship with *Cecropia*, or as longer colony lifetimes became possible in the long-lived and relatively protective nesting environments provided by myrmecophytes.

Despite abundant evidence for coadaptation, there is little support for cospeciation or cocladogenesis in either *Cecropia* or its ants. Thus, although particular associates may be highly species-specific (e.g., *Pachycondyla luteola* on "*Cecropia pungara*," *Pachycondyla* sp. nov. 1 on *Cecropia hispidissima*, and *Crematogaster* aff. *curvispina* on "*Cecropia herrerensis*"), no substantial radiation of partner lineages appears to have occurred through cocladogenesis. Nevertheless, cospeciation cannot be firmly ruled out, and evidence might yet be found as relationships of *Azteca* and *Cecropia* come under greater scrutiny.

EVOLUTIONARY COLONIZATION, HOST SHIFTS, AND HABITAT SHIFTS

De novo or evolutionary colonization is the alternative to cocladogenesis in magnifying the diversity of *Cecropia* and its ants over evolutionary time. As described above, the transition from free-living ants to symbiotic associates of *Cecropia* has occurred frequently and apparently easily, and accounts for much of the diversity in these symbionts (Table 1). Moreover, after these species were evolutionarily committed to *Cecropia*, the combination of habitat shifts in plants and host switches in ants would have further enhanced the diversity of ant–plant partnerships. In turn, the facility with which *Cecropia* spp. acquired new ant partners may have permitted the genus to attain high species diversity through frequent evolutionary habitat shifts, often correlated with changes in growth rates and defensive investment (Davidson & Fisher, 1991; Folgarait & Davidson, 1994, 1995). Although many lowland rain forest *Cecropia* species require some sort of light gap for establishment, species differ widely in their light requirements, as well as characteristic soil types. As exemplified by species encountered in southeastern Peru, some are tightly bound to riparian edge (e.g., *C. latiloba* and *C. engleriana*), others to frequently inundated soils (*C. membranacea*, "*C. pungara*," and *C. utcubambana*), some to less fertile terra firme (*C. ficifolia*, *C. polystachya*, and "*C. grisita*"), and still others to high-elevation cloud forests along the eastern Andean cordillera (*C. angustifolia* and *C. tacuna*). In their comparison of ant–plant relationships in Africa and the Neotropics, McKey & Davidson (1993) argued that a fine-scale habitat mosaic, created by Andean orogeny and rivers meandering widely and at different elevations over geologic time (Salo et al., 1986), has been profoundly important in magnifying diversity within a number of ant-plant taxa, including *Cecropia*, and in the partnerships of habitat-shifting plant species with novel ant taxa. Thus, compared to Africa, where geomorphology is more monotonous, the Neotropics have 3.5-fold greater species richness of plant-ants, despite just 1.3 times as many total ant species.

Yu & Davidson (1997) have attributed to the independent (horizontal) dispersal of symbionts both the predominance of *de novo* colonization over cospeciation in the *Cecropia*-ant system and the diversity of mechanisms associated with evolutionary colonization and species-specificity. Thus, rather than being codispersed with their partners, as is the case in many symbiotic associations between mutualists, or between parasites and hosts, colonization of *Cecropia* seedlings and saplings occurs anew each generation, allowing much opportunity for evolutionary colonization and host shifts that may, in turn, inhibit pairwise coevolution and cocladogenesis. In this circumstance, historical coincidences such as coordinated or exclusionary dispersal (to the same or different habitats, respectively) may be as important to, or more important than, competition for partners in setting the stage for future coevolution. Moreover, pairings between *Cecropia* and its obligate associates are explained largely by the effects of local propagule pools, queen preferences and host locating abilities, and colony performances on young seedlings and saplings, i.e., by events early in the life histories of these associations (Yu & Davidson, 1997).

Almost certainly, given the species richness of *Cecropia* and the widespread distribution of this important neotropical genus, additional ant associates remain to be discovered. Analysis of these new species, together with continued progress in reconstructing the phylogenies of both *Azteca* and *Cecropia* with molecular and other characters will provide new and informative tests of the ideas developed here.