

vollenweideri, KLEINEIDAM & al. (2001) demonstrated that the primary mechanism is wind. Although some *Atta* species dispose of garden refuse and ant corpses in external dumps (HART & RATNIEKS 2002, WIRTH & al. 2003), most species (e.g., *A. texana*, *A. cephalotes*, *A. laevigata*, *A. sexdens rubropilosa*) construct underground dump chambers (MOSER 1963, JONKMAN 1980). In a system clearly designed to conduct garden pathogens on a one-way route from garden to dump, a specialized refuse-carrying subcaste transports spent garden waste to the refuse pile, where a separate "dump subcaste" (usually older individuals at the ends of their lives) moves around the garbage (HART & RATNIEKS 2002).

Foraging and defense: Leafcutters, which harvest fresh plant material as the primary substrate for their fungus, have been called the dominant herbivores of the Neotropics (WHEELER 1907, HÖLLDOBLER & WILSON 1990). They are major pests of human agriculture (MARICONI 1970, FORTI 1985, CHERRETT 1986, FOWLER & al. 1986a). Both *Atta* and *Acromyrmex* contain separate subsets of species specialized on leaf- and grasscutting (FOWLER & al. 1986a, FOWLER 1988). Substrate preferences may change as leafcutter nests mature, with younger nests concentrating on small herbaceous plants growing closer to the nest (WETTERER 1994). In addition to collecting fresh vegetation as substrate for their fungus, some leafcutter ants (e.g., *Atta cephalotes*) are thought to acquire carbohydrates from plant sap (LITLEDYKE & CHERRETT 1976, QUINLAN & CHERRETT 1979, BASS & CHERRETT 1995). In some *Acromyrmex* species in certain environments, leafcutting may be less important than other kinds of foraging. WETTERER & al. (1998) found that *Acromyrmex octospinosus* in the tropical dry forests of Guanacaste, Costa Rica, is an opportunistic forager, with some nests preferentially taking insect frass and fallen (rather than cut) leaves and flowers. *Acromyrmex coronatus* foragers primarily cut the soft leaves of herbaceous plants (WETTERER 1994, 1995).

Acromyrmex and *Atta* include nocturnal- and diurnal-foraging species; the same species may forage at different times of the day at different times of the year or at different locations depending on temperature, parasite pressure, and other environmental factors (FEENER & MOSS 1990, ORR 1992, WETTERER & al. 1998, WIRTH & al. 2003). Leafcutters form conspicuous foraging columns, and like many other ants, workers follow chemical trails produced by the poison gland and deposited from their modified stings (MOSER & BLUM 1963).

Symbionts: Nests of *Acromyrmex* and especially of *Atta*, including both gardens and refuse dumps, represent large and predictable resources for symbionts. AUTUORI (1942) reports adult individuals of 1,491 Coleoptera, 56 Hemiptera, 40 Mollusca, 15 Diptera, 4 Reptilia, and 1 pseudoscorpion from a single refuse chamber of *Atta sexdens rubropilosa*. NAVARETTE-HEREDIA (2001) lists 411 beetle species belonging to 25 families associated with *Atta* and *Acromyrmex*. Snakes (Colubridae, Elapidae, and Leptotyphlopidae) and lizards (Amphisbaenidae and Teiidae) live in nests of *Atta* and *Acromyrmex* and / or use the nests as oviposition sites. In some cases these associations are obligate. Some of these snakes follow the pheromone trails of their hosts and may feed on the ants and their brood. Snake egg clusters in leafcutter nests may be protected from potential predators and from desiccation (GOELDI 1897,

AUTUORI 1942, GALLARDO 1951, VAZ-FERREIRA & al. 1970, WEBER 1972, VAZ-FERREIRA & al. 1973, BRANDÃO & VANZOLINI 1985). Numerous other studies describe commensals of *Atta*, including those found in *Atta texana* nests (MOSER 1963).

In a survey of non-cultivar microbes in leafcutter-fungal gardens, RODRIGUES & al. (2008) identified a diversity of microfungi, including the ubiquitous *Fusarium oxysporum*, but these microfungi appear to have no specific relationship within the mutualism. In contrast, MUELLER & al. (2008), using various culture media, consistently isolated species in the actinomycete genera *Microbacterium* and *Mycobacterium* from gardens of multiple *Atta* species and from queen infrabuccal pellets of *Atta texana*.

In the Attini, with one exception, social parasites are so far only known from four social parasite / host associations in the genus *Acromyrmex*: *Pseudoatta argentina* (parasite) and *A. lundii* (host) (GALLARDO 1916); an undescribed species (parasite) and *A. rugosus* (host) (SUMNER & al. 2004; J. Delabie, pers. comm.); *A. insinator* (parasite) and *A. echinator* (host) (SCHULTZ & al. 1998); and *A. ameliae* (parasite) and *A. subterraneus* (host) (DESOUZA & al. 2007). In the first two associations, the social parasites are highly modified morphologically and do not produce a worker caste. In the latter two, the social parasites are thought to be very recently evolved because they are morphologically very similar to their hosts and they still produce a minor worker caste.

Conclusions and future directions

Variation in several attine natural-history characters and behaviors is clearly correlated with phylogeny. Consider, as an example, the various evolutionary transitions that led to the genus *Atta*, only one of many extant endpoints in the Attini – albeit one of the most ecologically successful ones. The evolutionary transition that produced the common ancestor of the higher attine ants (*Trachymyrmex*, *Sericomyrmex*, *Acromyrmex*, and *Atta*) was accompanied by a major shift in cultivar type, from a facultative cultivar capable of a free-living existence to an obligate cultivar clearly modified (e.g., in the production of gongylidia food bodies) for life with ants. The evolutionary transition that produced the common ancestor of the leafcutter ants (*Atta* and *Acromyrmex*) was accompanied by a number of transitions in natural-history characters, including shifts from a small-sized queen to a significantly larger-sized queen, from a monomorphic worker caste to a polymorphic worker caste, and from a singly-mated queen to a multiply-mated one. Additional important transitions occurred in the common ancestor of *Atta* species, including shifts to claustral nest founding, to a much larger-sized queen, to a very highly developed worker-caste polymorphism, and to enormous colony sizes of many millions of individuals.

Like *Atta*, every attine clade represents a fascinating evolutionary endpoint that may be retrospectively analyzed, tracing the stepwise evolutionary transitions in natural history characters that occurred on key branches connecting that clade to the ancestral attine. Unlike *Atta*, however, far less is known about the natural histories of most attine genera and species, and, thus, those stepwise evolutionary transitions are far less clear. We look forward to an improved understanding of attine natural history and evolution due to new field and laboratory studies of neglected attine ant