

Natural history and phylogeny of the fungus-farming ants (Hymenoptera: Formicidae: Myrmicinae: Attini)

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Abstract

Ants of the tribe Attini comprise a monophyletic group of approximately 230 described and many more undescribed species that obligately depend on the cultivation of fungus for food. In return, the ants nourish, protect, and disperse their fungal cultivars. Although all members of this tribe cultivate fungi, attine ants are surprisingly heterogeneous with regard to symbiont associations and agricultural system, colony size and social structure, nesting behavior, and mating system. This variation is a key reason that the Attini have become a model system for understanding the evolution of complex symbioses. Here, we review the natural-history traits of fungus-growing ants in the context of a recently published phylogeny, collating patterns of evolution and symbiotic coadaptation in a variety of colony and fungus-gardening traits in a number of major lineages. We discuss the implications of these patterns and suggest future research directions.

Key words: Hymenoptera, Formicidae, fungus-growing ants, leafcutter ants, colony life, natural history, evolution, mating, agriculture, review.

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The origin and evolution of the Attini

Attine ants and their fungal cultivars represent a classic example of mutualism. The ants obligately depend on the cultivation of fungus for food and in return provide the fungus with nourishment, protection from pathogens and competitors, and dispersal (WEBER 1972, MARTIN 1987, HÖLLDOBLER & WILSON 1990, CURRIE & al. 1999, MUELLER 2002, MUELLER & al. 2005, SCHULTZ & al. 2005). Many theories have been proposed for how ant fungiculture may have arisen from earlier, facultative associations between the ancestors of the two mutualists (FOREL 1891, VON IHERING 1894, 1898, EMERY 1899, FOREL 1902, WHEELER 1907, SANTSCHI 1910, FARQUHARSON 1914, BAILEY 1920, MAIDL 1934, WEBER 1958, 1972, GARLING 1979, MOFFETT 1986, MUELLER & al. 2001), including a scenario in which a fungal proto-domesticated attracted ants with food rewards and in return had its spores and / or mycelia dispersed by the ants (BAILEY 1920, MUELLER & al. 2001, SCHULTZ & al. 2005). Whatever its origin, the obligate association between attine ants and their cultivated fungi arose approximately 50 million years ago in the forests of the Neotropics, producing over 230 described and many more undescribed extant attine ant species, all of which occur exclusively in the New World and each of which, as far as is known, practices one of five distinct agricultural systems (SCHULTZ & MEIER 1995, MAYHÉ-NUNES & JAFFÉ 1998, BRANDÃO & MAYHÉ-NUNES 2001, MUELLER & al. 2001, SCHULTZ & BRADY 2008) (Fig. 1).

The five attine agricultural systems

Each of the five known attine agricultural systems is characterized by strongly correlated patterns across ant, fungal cultivar, and *Escovopsis* fungal pathogen phylogenies (Fig. 2), and each represents a major evolutionary transition in ant agriculture: (1) **Lower agriculture**, the ancestral condition in the Attini, is practiced by 80 described ant species in 10 genera. (2) **Coral-fungus agriculture** is practiced by 34 described species in the "*Apterostigma pilosum* group," a derived clade within the attine genus *Apterostigma*. Ants practicing this form of agriculture are the only group to utilize fungal cultivars that do not belong to the tribe Leucocoprineae. (3) **Yeast agriculture** is practiced by 18 described species in the "*Cyphomyrmex rimosus* group," a subset of species in the attine genus *Cyphomyrmex*. Members of this group grow cultivars as nodules of yeast-like cells in a unicellular phase instead of the multicellular mycelial phase typical for all other attines. (4) **Generalized higher agriculture** is practiced by 63 described species in the two genera of non-leafcutting "higher attine" ants, *Sericomyrmex* and *Trachymyrmex*. (5) **Leafcutter agriculture**, a derived form of higher agriculture, is practiced by 40 described species of ecologically dominant ants in the two genera *Atta* and *Acromyrmex* (SCHULTZ & al. 2005, SCHULTZ & BRADY 2008).

Natural history of attine ants

Despite the diversity of their agricultural systems, all attine ant species share some general habits associated with fun-

gus gardening. Prior to departing from her natal nest to mate and found a new colony, an attine daughter queen stores a nucleus of fungus from the maternal garden in her infrabuccal pocket, a filtering device located at the bottom of her mouth. Following mating, the foundress queen establishes a suitable nesting location (usually by herself, i.e., by haplometrosis, the condition in most but not all attines and, indeed, in most ants, RISSING & POLLOCK 1988), where she expels the fungal pellet and uses it to start her own garden (HUBER 1905). Cultivars are propagated vegetatively, i.e., as asexual clones, from parent to offspring nests and within nests. It has been noted that, under a scenario of within-garden genetic variability of mycelial strains, this generational subsampling and subculturing of gardens provides the opportunity for the ant-mediated equivalent of "artificial selection" of fungal-cultivar clones (MUELLER 2002). In all attines, the foundress queen cares for the garden and raises the first brood and, in most attines, the foundress forages for garden substrate (i.e., semi-claustral nest foundation). The primary chamber where the foundress will spend her time as she rears her first brood tends to be small and shallow in all attines, likely minimizing energetic costs to the queen. A typical attine worker takes approximately 40 - 60 days to develop from egg to adult (WEBER 1972, TORRE-GROSSA & al. 1982). Upon emergence, the first brood begins foraging, brood care, and excavation duties, and when a sufficient work force is achieved, the queen permanently relinquishes all but egg-laying duties to her workers.

Brood care, one of the most important tasks performed by the workers, is somewhat different in the attines relative to other ants. The eggs and larvae of fungus-growing ants are typically embedded in the garden and covered with mycelium (WEBER 1972, SCHULTZ & MEIER 1995, LOPES & al. 2005). Attine larvae feed exclusively on cultured fungal hyphae (WEBER 1955, MURAKAMI & HIGASHI 1997). In fact, oral trophallaxis of liquid between workers and larvae, which is common in most myrmicines (WILSON 1971, HÖLLDOBLER & WILSON 1990), is extremely rare in the Attini (WEBER 1972, LITLEDYKE & CHERRETT 1976, QUINLAN & CHERRETT 1979, BESHES & TRANIELLO 1996, MURAKAMI & HIGASHI 1997, LOPES & al. 2005). Unlike other ant larvae, attine larvae are densely covered with spinules on the labrum, mandibles, and labium; these spinules undoubtedly function in the mastication of fungal hyphae (WHEELER & WHEELER 1976). (Interestingly, the larvae of the non-attine social parasites and agro-predators in the genus *Megalomyrmex*, which are known to feed on attine fungi, do not have such mouthparts, ADAMS & al. 2000.) In addition, attine larvae, with only a few exceptions (*Myocepurus*, *Sericomyrmex*, and some *Acromyrmex* species), lack hairs on the dorsal and lateral surfaces of their bodies. The near-universality of this condition in attine larvae, in contrast to the nearly universal presence of hairs in all other ant larvae, suggests an unknown biological function likely connected with fungal cultivation. Hairs do consistently occur in the region of the attine larval mouthparts, where they clearly function as "baskets" for anchoring fungal hyphae fed to them by workers. Likewise, a distinctive ring of hairs surrounds the anal region of all attine larvae (SCHULTZ & MEIER 1995). These hairs hold droplets of anal secretions that are imbibed by workers for unknown reasons, suggesting that larvae may play an important but

entirely unexplored role in nutrient flow through attine colonies (BESHES & TRANIELLO 1996, SCHNEIDER 2000, LOPES & al. 2005).

Unlike attine larvae, adult attine ants are not obviously modified for fungus cultivation except for: (I) the presence in some attine species of cuticular crypts hypothesized to support the growth of bacteria that suppress the growth of garden pathogens (CURRIE & al. 2006) and (II) the enlarged heads and thickened mandibles of the larger worker subcastes in the leafcutting genera *Acromyrmex* and *Atta*, which are obviously modified for leaf- and grasscutting (as well as, in the case of *Atta* soldiers, for defense).

Natural history of attine fungal cultivars and *Escovopsis* pathogens

To understand the attine agricultural symbiosis, we must understand the natural history of the attine fungi. All attine fungal cultivars are members of the order Agaricales (Basidiomycota), a large and diverse clade characterized by the production of spore-bearing "mushroom" fruiting bodies. Mushrooms rarely occur in attine nests, however, because the ants suppress fruiting by constantly cropping the mycelium and disrupting hyphal connections, and perhaps through other, as-yet unknown mechanisms. Because traditional mycological taxonomy largely depends on characters of fruiting bodies, their absence in the attine system impeded progress for many years (but see MÖLLER 1893, HEIM 1957, WEBER 1957, HERVEY & al. 1977). We now know that the vast majority of attine ants cultivate fungi in the tribe Leucocoprineae, which consists of two genera, *Leucoagaricus* and *Leucocoprinus*, in the family Lepiotaceae (MUELLER & al. 1998, JOHNSON 1999). In a striking and unique exception to this rule, members of the *Apterostigma pilosum* group, derived within the genus *Apterostigma*, cultivate a distantly related basidiomycete fungus belonging to the coral-mushroom family Pterulaceae (VILLESEN & al. 2004, MUNKACSI & al. 2004, DENTINGER & al. 2009).

Because attine fungal cultivars are vertically transmitted from parent to daughter nests by foundress queens, and because the closest free-living relatives of the cultivars remained unknown, for many years it was assumed that attine fungi were ancient clonal lineages that were obligately associated with their ant hosts (WEBER 1972). This assumption was challenged by the first molecular-phylogenetic studies of attine fungi in which it was discovered that the attine cultivars do not form a clade exclusive of free-living forms (CHAPELA & al. 1994, HINKLE & al. 1994). It was challenged again with the discovery that the lower attine cultivars are polyphyletic, representing a minimum of three separate lineages within the Leucocoprineae (MUELLER & al. 1998). Perhaps the best evidence against ancient clonality was the discovery of the same fungal species and strains living both within the attine symbiosis and freely outside of it, occupying the typical lepiotoid niche of growing in the leaf litter (MUELLER & al. 1998, VO & al. 2009). Other studies within genera and species of attine ants and their associated fungi have further demonstrated incongruence between fungal and ant lineages that can only be explained by frequent switching in ant-fungal associations over evolutionary time periods, either due to recruitment of free-living fungi into the symbiosis, trading of cultivars between nests, or both (MUELLER & al. 1998, MUELLER & al. 2001, GREEN & al. 2002). This pattern, in which some lower-attine and yeast-

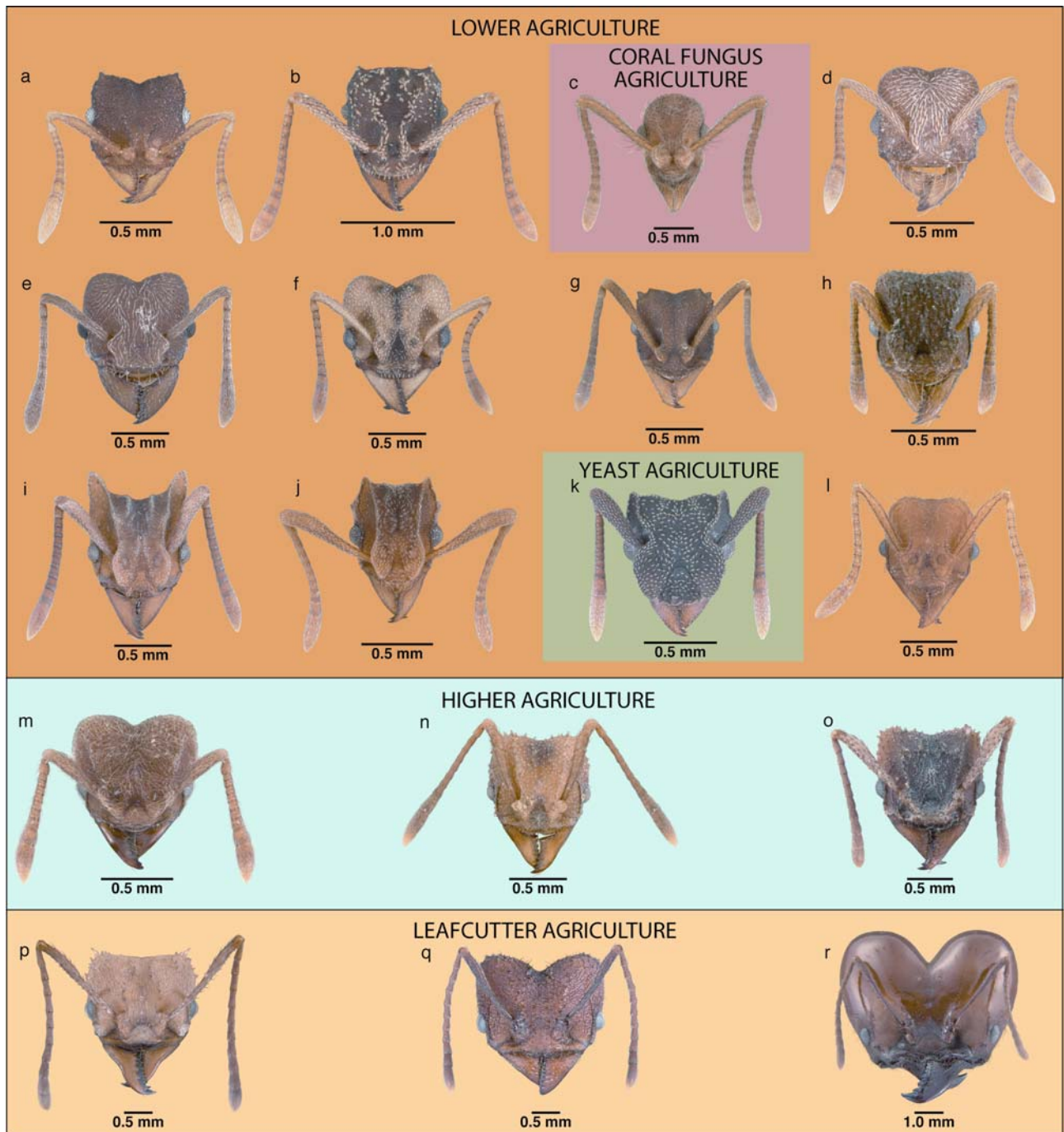


Fig. 1: Representatives of workers of fungus-farming ant genera and major clades, with the five agricultural systems indicated. (a) *Mycocepurus tardus*, (b) *Myrmicocrypta infuscata*, (c) *Apterostigma collare*, (d) *Kalathomyrmex emeryi*, (e) *Paramycoptophylax bruchi*, (f) *Mycetophylax simplex*, (g) *Mycetarotes parallelus*, (h) *Mycetosoritis hartmanni*, (i) *Cyphomyrmex auritus*, (j) *Cyphomyrmex longiscapus*, (k) *Cyphomyrmex rimosus*, (l) *Mycetagroicus triangularis*, (m) *Sericomyrmex parvulus*, (n) *Trachymyrmex cornetzi*, (o) *Trachymyrmex septentrionalis*, (p) *Acromyrmex octospinosus*, (q) *Acromyrmex versicolor*, and (r) *Atta laevigata*.

agriculture fungi are found both inside and outside the attine symbiosis, is consistent with a number of scenarios. One such scenario is that, as are some human crops, the attine cultivars are simply enslaved by the ants, i.e., the lower-attine symbiosis may be a parasitism (MUELLER 2002, SCHULTZ & al. 2005). Another scenario is that the lower-attine cultivars may have a bimodal life-history strategy, expressing separate suites of adaptations depending upon

environmental context (free-living or ant-associated). The latter scenario is supported by the apparent benefits that accrue to fungi when they are associated with ants (relative to fungi living in the leaf litter), including: (1) protection from the considerable competition from other microbes present in the leaf litter, with a corresponding increase in representation (in terms of biomass) in the next generation; (2) protection from parasites, pathogens, and fungivores;

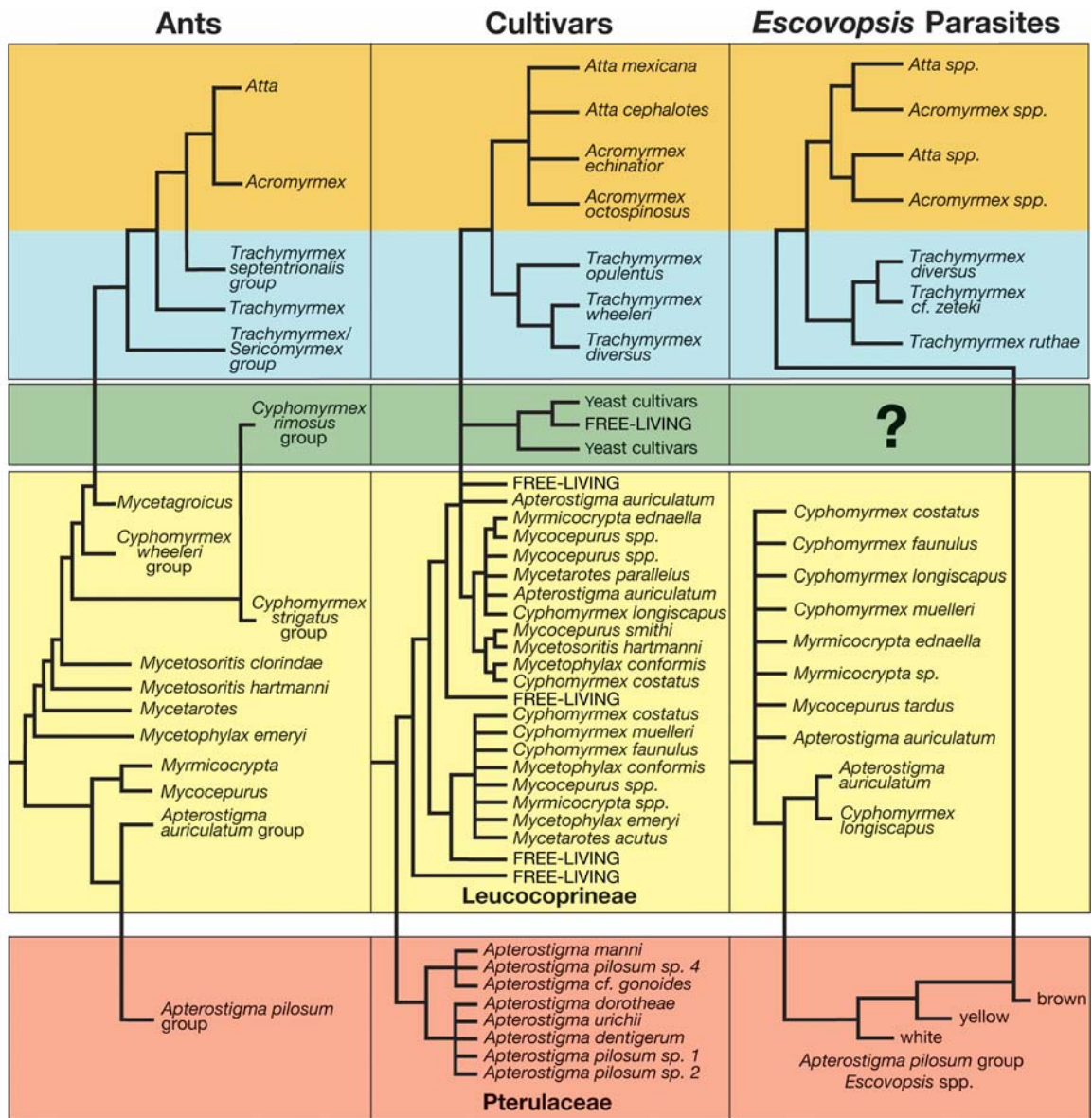


Fig. 2: A summary of current knowledge about the coevolutionary histories of three attine-agricultural symbionts: the ants, their fungal cultivars, and the fungal parasite *Escovopsis*. For each symbiont lineage, the ancestor arises within lower agriculture, in which a paraphyletic grade of ants cultivates a corresponding paraphyletic grade of cultivars that are infected by a corresponding paraphyletic grade of parasites. Broad phylogenetic groups of symbionts are associated with each of the agricultural systems, indicating ancient coevolution, but patterns of origin of these groups differ across symbionts. Parasites of yeast agriculture are unknown. Summarized from MUELLER & al. (1998), CURRIE & al. (2003), VILLENSEN & al. (2004), SCHULTZ & al. (2005), GERARDO & al. (2006b), TAERUM & al. (2007), and SCHULTZ & BRADY (2008).

and (3) geographic dispersal by foundress queens (WEBER 1972, MARTIN 1987, HÖLLDOBLER & WILSON 1990, CURRIE & al. 1999, MUELLER 2002, MUELLER & al. 2005, SCHULTZ & al. 2005). These hypothetical benefits, while plausible, have yet to be demonstrated and quantified.

Attine fungal cultivars are infected by ascomycete fungi in the genus *Escovopsis*, which so far are unknown from any habitat other than attine fungus gardens (CURRIE & al. 1999, CURRIE 2001a, b, CURRIE & al. 2003). Current knowledge indicates that the *Escovopsis* phylogeny conforms to the five agricultural systems, i.e., phylogenetically cohesive groups of *Escovopsis* (clades and grades) infect corresponding phylogenetically cohesive groups of attine culti-

vars (Fig. 2). The ancestral condition in *Escovopsis*, not surprisingly, is to infect lower-attine cultivars. Attine coral fungi are infected by a paraphyletic grade of *Escovopsis* that arose from the lower-attine *Escovopsis*. This grade of coral-fungus *Escovopsis*, surprisingly, gave rise to the clade that infects the higher-attine cultivars (Fig. 2). *Escovopsis* has not been detected or isolated from attine yeast cultivars. A fourth symbiont, a filamentous bacterium (Actinomycetes: *Pseudonocardia*), grows on the integuments of attine ants and produces antibiotics that may help to control the *Escovopsis* pathogen. The attine-actinomycete phylogeny appears to be far less correlated with the five agricultural groups, suggesting the possibility of frequent recruitment

into the attine symbiosis (KOST & al. 2007, MUELLER & al. 2008, SEN & al. 2009). Black yeasts, so far only known from *Apterostigma* ants species, consume the actinomycete bacteria (LITTLE & CURRIE 2007, 2008).

Although the relationships between ants, cultivars, and *Escovopsis* are strongly correlated with phylogeny at the level of the five agricultural systems (Fig. 2) (MUELLER & al. 1998, CURRIE & al. 2003, VILLESSEN & al. 2004, CAFARO & CURRIE 2005, SCHULTZ & al. 2005, GERARDO & al. 2006a, TAERUM & al. 2007, SCHULTZ & BRADY 2008), exceptions are known to occur, e.g., rare instances of *Trachymyrmex* species cultivating lower-attine fungi (MUELLER & al. 1998; U. Mueller, pers. comm.). Within each of the five agricultural systems, the correlation between symbiotic associations and phylogeny generally breaks down altogether (MUELLER & al. 1998, GREEN & al. 2002, GERARDO & al. 2006b, MEHDIABADI & al. 2006, MIKHEYEV & al. 2006, 2007). This pattern is further complicated by the recent discovery that two cultivar clades may be much younger than their ant associates, suggesting that selective sweeps may have replaced earlier cultivar associates (A. Mikheyev, P. Abbott & U. Mueller, pers. comm.). As symbiont phylogenies improve, more violations of the simple coevolutionary pattern will undoubtedly be discovered.

Natural-history traits of attine ants

In the following sections, we summarize the natural-history traits of ants belonging to each agricultural system (also see Tab. 1). This review is not meant to be exhaustive, nor do the described general patterns necessarily apply to every species in a particular agricultural group. Rather than an exhaustive survey, our goal is to review and collate attine natural-history information in an explicitly phylogenetic context in order to elucidate macroevolutionary patterns and sequences of diversification within and across the major clades of fungus-farming ants.

Lower agriculture

Phylogenetic analyses indicate that lower agriculture was the system practiced by the first attine ant and the system from which all other forms of attine agriculture arose (SCHULTZ & BRADY 2008). It is perhaps unsurprising, therefore, that the lower-attine agriculturalists include species in the majority of attine ant genera and species, including *Myrmicocrypta*, *Mycocepurus*, some *Apterostigma* (the *A. auriculatum* group), *Kalathomyrmex*, *Paramycetophylax*, *Mycetophylax*, *Mycetarotes*, some *Cyphomyrmex* (the *C. strigatus* and *C. wheeleri* groups), *Mycetosoritis*, and *Mycetagroicus*. Although any given lower attine species is an amalgam of primitive and derived traits, at least some lower-attine species likely retain some traits little changed from those present in the ancestral attine.

Geographic distribution: Knowledge of the distributions of most lower-attine species is deplorably poor but, considered as a group, they have a broad geographic distribution, ranging from the US in the north (e.g., *Cyphomyrmex wheeleri* in central California) to Argentina in the south (e.g., *Mycetosoritis asper* in Chubut) (KEMPF 1972, WEBER 1972, BRANDÃO 1991, MAYHÉ-NUNES & JAFFÉ 1998, FERNANDEZ & SENDOYA 2004).

Colony size and social structure: The colonies of most lower-attine-ant species tend to be short-lived (a few years) and have small worker-population sizes (tens to hundreds

of workers), although exceptions occur in which colonies may contain more than a thousand workers (e.g., some *Myrmicocrypta*, *Mycocepurus*, and *Cyphomyrmex* species) (WEBER 1972, PRICE & al. 2003, RABELING & al. 2007b, HIMLER & al. 2009). All lower-attine colonies have a monomorphic worker caste and usually one singly-mated queen (HÖLLDOBLER & WILSON 1990, VILLESSEN & al. 2002, FERNÁNDEZ-MARÍN & al. 2004). *Mycocepurus goeldii* may be an exception, however. Based on observation of a mating swarm, KERR (1961) reports that *M. goeldii* queens are inseminated by multiple males.

Mating and nest-founding behavior: Mating behavior for most lower attines is poorly known. Some species, particularly wet-forest-dwelling species, have aseasonal and / or unsynchronized mating flights in which reproductives may be produced year-round or over a long period during the rainy season and in which males and females locate one another singly. Other species are seasonal, producing alates that usually fly at the beginning of the rainy season, some in synchronized swarms, documented (KERR 1961, KEMPF 1963) in *Mycocepurus goeldii* and (U. Mueller, pers. comm.) *Cyphomyrmex wheeleri*. *Mycocepurus smithii* is unique within the Attini in that it appears to be entirely parthenogenetic across its range; males of this species are unknown (FERNÁNDEZ-MARÍN & al. 2005, HIMLER & al. 2009, RABELING & al. 2009).

As might be expected of a large, paraphyletic group of multiple, major lineages, including those from which all other attines have arisen, the lower-attine agriculturalists are heterogeneous and difficult to characterize, although the majority retain the putatively primitive states of most nest-founding behaviors. Nest-founding for members of this agricultural group is semi-claustral and mostly haplometrotic (SOLOMON & al. 2004). Multiple queens are occasionally encountered in nests of lower attines, e.g., *Mycetophylax simplex* in southern Brazil (DIEHL-FLEIG & DIEHL 2007) and *Cyphomyrmex faunulus* in the Amazonian Basin (T.R. Schultz, unpubl.), and may be more common than is currently known. Multiple queens occur at fairly high frequencies in *Mycocepurus* species (FERNÁNDEZ-MARÍN & al. 2005, RABELING & al. 2007b, HIMLER & al. 2009; U. Mueller, pers. comm.).

Observations of multiple dealate queens in attine nests do not necessarily indicate pleiometrosis or polygyny, and must be cautiously interpreted for a number of reasons. First, some reports of multiple queens may be erroneous because, in the case of attine species that nest in aggregations (e.g., *Mycocepurus* species, *Kalathomyrmex emeryi*, *Mycetophylax morschi*), the investigator may have accidentally excavated chambers from more than one colony. Second, in most Attini unmated daughter queens sometimes shed their wings, remain in the nest, and behave like workers (e.g., WEBER 1941). When a pair of dealate *Mycocepurus goeldii* queens collected from the same nest chamber were dissected, for example, only one was found to be inseminated and to have developed ovaries (C. Rabeling, pers. comm.). Finally, even when multiple inseminated queens are discovered in the same nest, it remains unclear whether they co-founded the nest (pleiometrosis) or whether one queen joined the other long after nest establishment.

When founding their nests, queens of at least some species of *Myrmicocrypta*, *Mycocepurus*, and *Apterostigma*, and of *Cyphomyrmex longiscapus*, use their detached fore-

Tab. 1: General summary of various attine natural-history traits for the five distinct agricultural groups (cont. p. 43).

	Lower agriculture		Generalized higher agriculture		
	Most species	<i>Mycocepurus</i> spp.	<i>Sericomyrmex</i> clade	<i>T. intermedius</i> clade	<i>T. septentrionalis</i> clade
Geographic distribution	widespread (US to Argentina)	widespread (Mexico to Argentina; Caribbean)	widespread (US to Argentina; Caribbean)	widespread (Central America to Argentina)	US and Mexico
Habitat	diverse	forests, savannahs, cerrados	diverse	diverse	open woodlands, grasslands, mid-elevation deserts
Colony size	small (10 - 500 workers)	intermediate (50 - 1350 workers)	intermediate (< 100 - 3000 workers)	intermediate (< 100 - 3000 workers)	intermediate (< 100 - 1000 workers)
Worker size	monomorphic	monomorphic	monomorphic / weakly polymorphic	monomorphic / weakly polymorphic	monomorphic / weakly polymorphic
Queen mating frequency	monandry	polyandry (<i>M. goeldii</i>); parthenogenesis (<i>M. smithii</i>)	monandry	monandry	monandry?
Nest-founding behavior	haplometrosis, occasional multiple queens; semi-claustral	haplometrosis, multiple queens common; semi-claustral	haplometrosis, occasional pleiometrosis; semi-claustral	haplometrosis, occasional multiple queens; semi-claustral	haplometrosis, occasional multiple queens; semi-claustral
Substrate use	insect frass, seeds, flower parts, fruit, wood particles, arthropod parts?	insect frass, seeds, flower parts, fruit	insect frass, seeds, flower parts, fruit; some species cut fresh vegetation	insect frass, seeds, flower parts, fruit; some species cut fresh vegetation	insect frass, seeds, flower parts, fruit; some species cut fresh vegetation

wings as platforms, presumably to protect the incipient fungal garden from pathogens in the soil (FERNÁNDEZ-MARÍN 2000, FERNÁNDEZ-MARÍN & al. 2004).

Nest architecture: Depending on the species, lower-attine nests and gardens can occur in chambers excavated in the soil, in cavities in rotten logs, between layers of the leaf litter, and superficially in the soil under rotten logs, stones, or other objects. Perhaps the most common – and possibly ancestral – nesting behavior is the excavation of chambers in the soil (as distinct from nesting superficially in the soil), found in all *Mycocepurus*, some *Myrmicocrypta*, a few *Apterostigma*, all *Kalathomyrmex*, *Paramycetophylax*, *Mycetophylax*, *Mycetarotes*, *Mycetosoritis*, and *Mycetagroicus* species, and some *Cyphomyrmex* (mainly in the *C. wheeleri* group) species. Some *Myrmicocrypta*, some *Apterostigma*, and some *Cyphomyrmex* species (especially those in the *C. strigatus* group) construct their nests in rotten wood. For those lower attines that excavate nests in the soil, nest entrances generally consist of a single hole in the ground, in some cases entirely inconspicuous and in other cases surrounded by a crater of excavated soil pellets, the color of which can serve to indicate excavation depth. The nest entrances of *Cyphomyrmex longiscapus* and *C. muelleri* take the form of elaborate "auricles" constructed in embankments, steep forests, and along human-made trails (MUELLER & WCISLO 1998, SCHULTZ & al. 2002; R. Adams, pers. comm.).

Some lower attine nests, e.g., those of some species of *Myrmicocrypta* and *Mycetarotes*, and of *C. longiscapus* and

C. muelleri, consist of a single chamber in the soil (MUELLER & WCISLO 1998, SCHULTZ & al. 2002; J. Sosa-Calvo, pers. comm.; T.R. Schultz, unpubl.). Nests of *Mycetarotes parallelus* may occasionally include a second garden-containing chamber (SOLOMON & al. 2004). Most nests of *Mycetophylax simplex* contain two garden chambers, but one-chambered and three-chambered nests also occur (DIEHL-FLEIG & DIEHL 2007). A nest of *Mycetagroicus cerradensis* had two garden chambers (S. Solomon, pers. comm.). *Mycetophylax morschi* has one to two garden chambers, *Mycetophylax conformis* has one to three garden chambers (KLINGENBERG & al. 2007), *Mycetosoritis hartmanni* and *Cyphomyrmex wheeleri* have two to four chambers, and a nest of *M. clorindae* had two chambers (U. Mueller, pers. comm.). Mature nests of *Mycocepurus goeldii* and *M. smithii* excavated by RABELING & al. (2007b) contained as many as 21 and 15 chambers respectively; in multiple-chambered nests, about half of the chambers contained fungus gardens. *Mycocepurus smithii* nests can have as many as 20 chambers (U. Mueller, pers. comm.). In addition to garden-containing chambers, lower-attine nests may contain multiple empty chambers because, as nests mature, new garden chambers may be constructed at deeper levels. In ground-nesting lower attines, the garden chamber typically occurs at depths of ~ 5 - 40 cm below the surface; however, in *Mycocepurus goeldii* and *M. smithii*, garden chambers may occur at depths of 50 - 150 cm (FERNÁNDEZ-MARÍN & al. 2004, 2005, RABELING & al. 2007b; U. Mueller, pers. comm.; T.R. Schultz, unpubl.). The first nests of the genus

Coral-fungus agriculture	Yeast agriculture	Leafcutter agriculture		
<i>Apterostigma pilosum</i> group	<i>Cyphomyrmex rimosus</i> group	<i>Acromyrmex</i>	<i>Atta</i>	
widespread (Mexico to Argentina)	widespread (Mexico to Argentina; Caribbean)	widespread (US to Argentina; Caribbean)	widespread (US to Argentina; Caribbean)	Geographic distribution
mostly wet forests; 2 cerrado spp.	diverse	diverse	diverse	Habitat
small (10 - 100 workers)	small (25 - 500 workers); <i>C. cornutus</i> : intermediate (> 4000 workers)	large (17,000 - 270,000 workers)	very large (up to 8,000,000 workers)	Colony size
monomorphic	monomorphic	polymorphic	polymorphic	Worker size
monandry	monandry	polyandry	polyandry	Queen mating frequency
haplometrosis, multiple queens may be common; semi-claustral	haplometrosis, occasional multiple queens; semi-claustral	haplometrosis, occasional pleiometrosis; semi-claustral	haplometrosis, occasional pleiometrosis; claustral	Nest-founding behavior
insect frass, seeds, flower parts, fruit, wood particles, arthropod parts?	arthropod frass, plant sap, nectar, arthropod parts?	workers cut fresh vegetation; also fruit, seeds, insect frass	workers cut fresh vegetation; also fruit, seeds	Substrate use

Mycetagroicus (*M. cerradensis*) were recently located and excavated in the Brazilian cerrado; in one nest, two adjacent garden chambers were located at a depth of nearly 4 meters (S. Solomon & U. Mueller, pers. comm.).

Foraging and defense: Lower-attine agriculturalists forage opportunistically for substrate items relatively near to their nests (LEAL & OLIVEIRA 2000). The group contains diurnal- as well as nocturnal-foraging species (WEBER 1972) and the same species may alternate between diurnal and nocturnal foraging depending on seasonal conditions. Garden substrates include a variety of organic material encountered in the leaf litter, including insect frass, seeds, flower stamens, the flesh of fruits, grass stalks and pieces, and wood particles (WEBER 1972, OLIVEIRA & al. 1995, MURAKAMI & HIGASHI 1997, LEAL & OLIVEIRA 2000, DIEHL-FLEIG & DIEHL 2007). By foraging for organic detritus as garden substrate, lower-attine ants have escaped direct competition with other ants for protein sources such as living and dead arthropods (TOBIN 1994). The competitors of these attine-ant foragers are, instead, fungal and bacterial detritivores and the challenge for lower-attine-ant foragers is therefore to locate fresh substrate before it has been invaded and degraded by competing microbes (MURAKAMI & HIGASHI 1997, SCHULTZ & al. 2005).

Arthropod corpses are also frequently reported as substrate items (e.g., WEBER 1945, WEBER 1972, LEAL & OLIVEIRA 2000), and, although they may indeed be used for this purpose, there is reason to be cautious about interpreting their function for a number of reasons. First, ob-

servations of arthropod corpses incorporated directly into attine gardens are rare. Second, most reports of attines foraging for arthropod parts are due to the habit of *Cyphomyrmex* species, which transport large quantities of arthropod parts (especially ant heads and beetle elytra) into the nest. Rather than being incorporated into the garden, however, the exoskeleton fragments are usually found adjacent to the garden in mycelium-growing *Cyphomyrmex* species (*C. strigatus* and *C. wheeleri* groups) (U. Mueller, pers. comm.; T.R. Schultz, unpubl.), or serving as platforms for the gardens of yeast-growing *Cyphomyrmex* species (*C. rimosus* group, see below), at least in laboratory colonies (U. Mueller, pers. comm.; T.R. Schultz, unpubl.). It is thus possible that such arthropod parts serve as semi-sterile platforms for the incipient garden (much as the queen's shed forewing does in some other lower attines (FERNÁNDEZ-MARÍN & al. 2004) rather than as garden nutrient substrate, although this hypothesis does not fully explain why workers in mature nests continue to import them in such quantities. Another possibility is that arthropod exoskeletons may serve as substrate for mutualistic actinomycete bacteria, which are known to digest chitin. Whatever the explanation is, the energy expended by *Cyphomyrmex* species to import arthropod parts strongly suggests that they serve an important, as yet unknown, function.

In a comparative study of foraging behavior between lower- (*Cyphomyrmex*, *Mycetarotes*, *Mycocepurus*, and *Myrmicocrypta*) and higher- (*Sericomyrmex* and *Trachymyrmex*) attine genera, LEAL & OLIVEIRA (2000) found

that flowers and fruits were most often collected during the wet season by all attine ant genera; however, during the dry season, lower agriculturalists tended to collect mainly insect feces and corpses and higher agriculturalists relied mainly on plant parts.

Lower attine ants are quite timid, relying on crypsis and death-feigning behavior to avoid attack (WEBER 1972; T.R. Schultz, unpubl.), i.e., they curl up with the head and legs closely tucked against the mesosoma, the antennae tucked against the head, and the gaster reflexed ventrally and tucked against the rear legs and mesosoma. Most lower attines possess morphological features that tend to protect vulnerable body parts when in this defensive posture, including deep scrobes that protect the antennal scapes, expanded frontal lobes that protect the antennal condyles, expanded flanges and in some cases extended ventral grooves on the hind femora that protect the tibiae and tarsi, posterior extensions of the postpetiole that protect the articulation with the gaster, and various tubercles and spines on the thoracic dorsum. Jigging, a conspicuous rhythmic, rocking motion observed in *Myrmicocrypta buenzlii* and *Cyphomyrmex costatus*, is thought to protect the colony from potential predators (WEBER 1957, 1972, KWESKIN 2004).

Symbionts: Because of their smaller sizes and shorter life spans, we might expect lower-attine nests to represent more ephemeral and less predictable resources for potential symbionts than the nests of their higher-attine relatives. Nonetheless, commensals of lower attines include nematodes, mites, millipedes, collembolans, psychodid fly larvae, and nitidulid beetles, and parasites include diapiiid wasps and phorid flies (WEBER 1945, SOLOMON & al. 2004, FERNÁNDEZ-MARÍN & al. 2005, 2006, KLINGENBERG & al. 2007; T.R. Schultz, unpubl.; C. Rabeling, pers. comm.). Agro-predators and social parasites in the *Megalomyrmex silvestrii* species group have been observed to attack and/or parasitize *Cyphomyrmex costatus*, *C. longiscapus*, *C. muelleri*, and an undescribed *Mycocephurus* species in Peru (BRANDÃO 1990, ADAMS & al. 2000; C. Rabeling, pers. comm.). Social parasitism by a congener has so far been observed in only one species of lower attine (C. Rabeling, pers. comm.).

Coral-fungus agriculture

Unlike all other attine ants, which grow litter-decomposing fungi in the gilled-mushroom tribe Leucocoprineae (family Agaricaceae), the 34 known ant species in the *Apterostigma pilosum* group cultivate distantly related fungi belonging to the thread-like coral-mushroom family Pterulaceae (MUNKACSI & al. 2004, DENTINGER & al. 2009). The genus *Apterostigma* is divided by a basal split into two sister clades, one containing all of the coral-fungus-cultivating *A. pilosum* group species, the other containing the lower-attine leucocoprineae-cultivating *A. auriculatum* group species (VILLESEN & al. 2004). The ant phylogeny strongly supports a scenario in which, following that basal divergence, the ancestor of the *A. pilosum* clade switched from a leucocoprineaceous cultivar to a pterulaceous cultivar, a behavior inherited by all of its descendant species. This represents the only known switch to a non-leucocoprineaceous cultivar in all of the Attini, and there are no known cases of any member of this group reverting back to leucocoprineaceous-fungal cultivation (CHAPELA & al. 1994, VILLESEN & al. 2004, SCHULTZ & al. 2005, SCHULTZ & BRADY 2008).

Prior to 1994, what we now call attine pterulaceous fungi were known to differ from other attine cultivars by the presence of abundant clamp connections, considered a plesiomorphic character for basidiomycetes that had been secondarily lost in some lineages, including many Lepiotaaceae (HERVEY & al. 1977). The first phylogeny of attine fungi (CHAPELA & al. 1994) provided additional corroboration that the fungi grown by some *Apterostigma* were distantly related to the rest, although poor taxon sampling precluded any precise placement. Significant progress occurred when MUNKACSI & al. (2004) demonstrated a close relationship to the family Pterulaceae, including the genera *Pterula*, *Deflexula*, and *Pterulicium*, the majority of which are wood- and litter-decomposing forms. Most recently, DENTINGER & al. (2009) have discovered that two free-living species render the pterulaceous cultivars polyphyletic, i.e., the free-living species occupy positions in the cultivar phylogeny between the so-called "veiled" and "unveiled" groups (see below). One of these free-living species is *Pterula moniliformis*, which occurs predominantly or even exclusively as an aberrant asexual form. It is thus possible that a free-living counterpart of the pterulaceous cultivars may now be known and, because it is asexual, that the pterulaceous cultivars may be true clonal domesticates. This clonal hypothesis fails to address the discovery of a *Deflexula*-like fruiting body in an *Apterostigma* nest (MUNKACSI & al. 2004), however, and the natural history of the coral-fungus cultivars remains largely mysterious.

Geographic distribution: The coral-fungus-farming *A. pilosum*-group species occur mostly in forested habitats of the Neotropics from Argentina to Mexico (KEMPF 1972, WEBER 1972, BRANDÃO 1991, MAYHÉ-NUNES & JAFFÉ 1998, FERNÁNDEZ & SENDOYA 2004, VILLESEN & al. 2004). At least two savannah-adapted species occupy the Brazilian cerrados (VASCONCELOS & al. 2008; T.R. Schultz, unpubl.).

Colony size and social structure: With few exceptions, coral-fungus-cultivating ants of the *Apterostigma pilosum* group have relatively small colonies of a dozen to less than one hundred workers, usually consisting of a single queen and monomorphic workers (WEBER 1972, FORSYTH 1981, BLACK 1987, PITTS-SINGER & ESPELIE 2007). Multiple-queen colonies are common in some species, however (U. Mueller, pers. comm.). In a study of 66 nests of *A. collare*, 23 contained no queen, 39 contained one queen, and four contained two queens (PITTS-SINGER & ESPELIE 2007).

Mating and nest-founding behavior: Coral-fungus-cultivating ants share similar mating and nest-founding behaviors with the lower fungus-farming ants. For example, for the few studied species, mating is aseasonal, i.e., reproductives are produced year-round or at least throughout the rainy season, and nest-founding is typically haplometrotic and semi-claustral (FORSYTH 1981, SCHULTZ 1991, FERNÁNDEZ-MARÍN & al. 2004, PITTS-SINGER & ESPELIE 2007). Like some other lower attines, *Apterostigma* queens use their forewings as platforms for the incipient garden (SCHULTZ 1991, FERNÁNDEZ-MARÍN & al. 2004).

Nest architecture: Most of the *Apterostigma pilosum*-group species nest in and under rotten logs, under rocks, and between layers of the leaf litter (LATTKE 1997, MUELLER & al. 2001, VILLESEN & al. 2004; T.R. Schultz, unpubl.). Nests of *Apterostigma collare* in Costa Rica may be found in semi-exposed locations on the trunks of trees or

on the undersides of palm leaves (FORSYTH 1981, BLACK 1987, PITTS-SINGER & ESPELIE 2007; T.R. Schultz, unpubl.). Two Brazilian cerrado species are the only known coral-fungus-growing ants to excavate underground chambers in the soil (VASCONCELOS & al. 2008; T.R. Schultz, unpubl.).

As mentioned above, a phylogeny of the pterulaceous cultivars indicates that these fungi are divided into two sister clades, and that each of those clades is cultivated by a phylogenetically distinct subgroup of *A. pilosum* ants, one monophyletic, the other possibly paraphyletic (VILLESEN & al. 2004). Of these two fungal clades, the so-called "veiled" clade possesses extremely elongate aerial hyphae, which are woven together by the ants to form a tent-like veil over their garden, whereas the "unveiled" clade grows gardens without veils that are superficially similar to lower-attine gardens. In veiled gardens, the veil usually envelops the garden except for one or two entry / exit holes created by the ants, and may function to protect gardens from desiccation, parasites, and / or predators.

Foraging and defense: *Apterostigma* species are very poorly studied. So far as is known, they forage on insect frass, seeds, flower parts, and other organic detritus that rains down from the canopy. Some species also collect wood particles and arthropod parts (VILLESEN & al. 2004). Anecdotal and indirect evidence suggests that some *Apterostigma* species may forage for sources of protein: Captive colonies of an *Apterostigma pilosum*-group species were maintained for an extended period of time on Bhaktar ant diet (a standardized formula consisting of eggs, honey, vitamins, and agarose) (L. Alonso, pers. comm.); a forager of *A. collare* was observed to carry a dead mosquito into its nest (T.R. Schultz, unpubl.); and a study of nitrogen cycling in ants indicates that *Apterostigma* species have nitrogen-isotope ratios more similar to those of predators than to those of leafcutting species (DAVIDSON & al. 2003).

Foragers of coral-fungus-farming ants collect their substrates in a variety of places. In one of the only studied species, *A. collare*, workers move upward to forage, exploring the surfaces of leaves for detritus raining down from the canopy; *Apterostigma* foragers of other species are commonly encountered in the leaf litter and occasionally on low herbaceous plants (FORSYTH 1981, BLACK 1987, SCHULTZ 1991, PITTS-SINGER & ESPELIE 2007; T.R. Schultz, unpubl.).

Symbionts: Commensals of coral-fungus-farming ants are poorly known. An adult chloropid fly emerged from a laboratory nest of an *Apterostigma* species, presumably living in the garden as a larva (T.R. Schultz, unpubl.). Recently, LITTLE & CURRIE (2007) identified black yeasts closely related to the genus *Phialophora* (Ascomycota) growing on the cuticle of *Apterostigma* species ants. The presence of this parasite resulted in twice as much garden loss due to *Escovopsis* than in gardens of black-yeast-free ants (LITTLE & CURRIE 2008), implying that the black yeasts deprive the ants of an important defense against the fungal crop disease *Escovopsis*.

Yeast agriculture

The genus *Cyphomyrmex* is traditionally divided into two species groups, the *C. strigatus* group and the *C. rimosus* group (KEMPF 1964, 1965). The attine ant phylogeny (SCHULTZ & BRADY 2008) indicates that a third group, the *C. wheeleri* group (formerly placed within the *C. rimosus* group, KEMPF 1965), should probably be given sepa-

rate generic status. All species in the *C. strigatus* and *C. wheeleri* groups practice lower-attine agriculture. All species in the *C. rimosus* group for which we have information practice yeast agriculture, in which the fungi are cultivated in yeast gardens consisting of masses of yellowish nodules, each approximately 0.25 - 0.50 mm in diameter. These yeast nodules are clumps of fungal cells in a unicellular phase rather than in the multicellular, mycelial phase typical of all other attine gardens and, indeed, of all known free-living Leucocoprineae.

The attine yeast cultivars are not true yeasts in the phylogenetic sense (i.e., Ascomycetes: Saccharomycetes), but are, rather, "yeast-like" in that they grow in a unicellular phase. In fact, the attine yeast cultivars are members of a highly derived clade of closely related species within the "Clade-1 group" of the Leucocoprineae (MUELLER & al. 1998). Like the lower attine cultivars from which they are derived, the yeast cultivars are capable of a free-living existence and may also have a bimodal life-history strategy (see discussion above) (MUELLER & al. 1998, VO & al. 2009). When in the free-living phase, attine yeast fungi grow as mycelium in the leaf litter and produce typical leucocoprineaceous fruiting bodies (MUELLER & al. 1998, VO & al. 2009). Even in attine nests, they grow as yeasts in the garden but as mycelium on the bodies of the larvae (SCHULTZ & MEIER 1995: figure 12.8). Because yeast-phase growth is otherwise unknown in the order Agaricales, its presence in this attine agricultural system strongly suggests modification for life with ants.

Geographic distribution: The subset of yeast-cultivating ants in the *C. rimosus* group are widespread both geographically and with regard to habitat, with species in the US Gulf states, Mexico, Central and South America to southern Argentina, and the Caribbean (KEMPF 1965, 1972, WEBER 1972, SMITH 1979, BRANDÃO 1991, SNELLING & LONGINO 1992, MAYHÉ-NUNES & JAFFÉ 1998, FERNANDEZ & SENDOYA 2004). *Cyphomyrmex rimosus* may be introduced in the US (SNELLING & LONGINO 1992, DEYRUP 2003). The yeast farmer *C. nesiotus* is endemic to Isabela Island in the Galapagos (SNELLING & LONGINO 1992). Depending on the species, yeast-cultivating ants can be found in wet and seasonally dry forests, savannahs, cerrados, beaches, and human-disturbed habitats such as pastures and clearings (KEMPF 1965, SNELLING & LONGINO 1992; T.R. Schultz, unpubl.). Some species occur at unusually high altitudes (e.g., 2000 m a.s.l. in the Peruvian Andes; T.R. Schultz, unpubl.; S. Solomon, pers. comm.).

Colony size and social structure: *Cyphomyrmex rimosus*-group colonies are typically small with a single queen and monomorphic workers. Multiple queens are occasionally encountered in nests (MURAKAMI & HIGASHI 1997; U. Mueller, pers. comm.). The colonies of most species contain a few dozen to several hundred workers (MURAKAMI & HIGASHI 1997), but in a few species, colonies can be much larger. A typical colony of *C. cornutus* in Costa Rica contained over 4,000 workers (ADAMS & LONGINO 2007).

Mating and nest-founding behavior: There is virtually no information about mating biology in the yeast-farming ants. Based on the presence of reproductives in nests, many species may be aseasonal and may produce reproductives year round or at least for an extended period during the rainy season (FERNÁNDEZ-MARÍN & al. 2004; T.R. Schultz, unpubl.). Species living in seasonally dry habitats may have

seasonally timed mating flights, typically at the start of the rainy season, or they may produce reproductives throughout the rainy season. In a study of sperm counts in ant queens, TSCHINKEL (1987) determined that mating in *Cyphomyrmex rimosus* was consistent with single mating. Nest-founding in yeast-farming ants is haplometrotic and semi-claustral (MURAKAMI & HIGASHI 1997, FERNÁNDEZ-MARÍN & al. 2004, SEAL & TSCHINKEL 2007).

Nest architecture: The nests of *C. rimosus* group species are among the simplest of all attine nests and, depending on the species, may occur on, under, or above the ground. At ground level, they may be found occupying adventitious cavities in the soil, in fissures in rocks, in or under rotting wood, rocks, and other objects, in layers of leaf litter, in hollow twigs, under animal feces, or even in snail shells or other objects such as hollow palm fruits and cacao pods. Above ground, nests may be found in the roots or pseudobulbs of epiphytes, in decaying tree limbs, in moss on tree trunks, and in debris concentrated in tree crotches (KEMPF 1972, WEBER 1972, SNELLING & LONGINO 1992; T.R. Schultz, unpubl.). Field observations suggest that nesting sites of most species are ephemeral and that colonies are highly mobile. Workers respond to disturbance by grabbing brood and yeast nodules and rapidly vacating the nest site. An exception to this rule is *C. cornutus*, which constructs more permanent nests of accreted soil 1 - 2 m above the ground, attached to or hanging from tree trunks, rocks, and epiphytes (ADAMS & LONGINO 2007).

Foraging and defense: The *C. rimosus* group contains both diurnally and nocturnally foraging species. The primary substrate collected by yeast-farming ants is arthropod frass. In one of the few thorough studies of yeast-cultivating ant behavior, MURAKAMI & HIGASHI (1997) found that *C. rimosus* preferentially utilizes millipede frass. They also found that workers actively forage on plant sap and nectar, in some cases regurgitating it onto the yeast garden and in other cases sharing it with nestmates via worker-worker trophallaxis (MURAKAMI & HIGASHI 1997). As mentioned above, both yeast- and mycelium-growing *Cyphomyrmex* species appear to expend significant energy foraging for disarticulated parts of arthropod exoskeletons, which may serve a function other than nourishment for the fungal cultivar.

MURAKAMI & HIGASHI (1997) report age polyethism in *C. rimosus*, in which younger workers more often perform brood care and older workers forage and defend the colony. To ward off predators, *C. rimosus* workers have been observed posturing with their mandibles open and forelegs up and apart so as to grasp potential intruders (WEBER 1972).

Symbionts: Few commensals or parasites are known for the yeast agriculturalists. In a study of *C. cornutus* nests, which the ants construct from accreted soil and which are the largest and most stable nests known for yeast-farming ants, ADAMS & LONGINO (2007) found that they are hosts to the socially parasitic ant *Megalomyrmex mondabora*, as well as to colonies of *Solenopsis*, *Strumigenys*, *Pachycondyla*, *Odontomachus*, *Pheidole*, *Crematogaster*, *Hypoponera*, and *Brachymyrmex* species. Nests of *C. cornutus* are also inhabited by nematodes, thysanurans, and isopods.

Generalized higher agriculture: *Trachymyrmex* and *Sericomyrmex*

The genera *Sericomyrmex* and *Trachymyrmex* include 63 currently known species that form a paraphyletic grade and that practice an agricultural system ("generalized higher agriculture") distinct from the two leafcutting genera *Atta* and *Acromyrmex*, discussed below. Attine ant phylogeny indicates that this paraphyletic grade consists of a succession of three clades, each the sister of the remainder of the grade plus the leafcutters: (1) the "*Sericomyrmex* clade," consisting of *Sericomyrmex*, a morphologically compact, clearly monophyletic group, and *Trachymyrmex* species in the *T. opulentus*, *T. jamaicensis*, *T. urichii*, and *T. iheringi* species groups, (2) the "*T. intermedius* clade," consisting of *T. intermedius*, *T. diversus*, *T. cornetzi*, *T. bugnioni*, and related species, and (3) the "*T. septentrionalis* clade," consisting of *T. septentrionalis* and allied North American species, possibly including *T. saussurei*. All of these groups cultivate members of the genetically diverse "*Trachymyrmex*-cultivar clade" of higher-attine fungi (SCHULTZ & BRADY 2008).

All higher-attine fungal cultivars, including the *Trachymyrmex*-cultivar clade and the leafcutter-cultivar clade, are part of a monophyletic group that arose from the lower-attine fungi (Fig. 2). However, higher-attine fungal cultivars differ from lower-attine and yeast cultivars in two significant ways, both of which suggest significant modification for life with ants. First, higher-attine fungi are not known to have a free-living phase independent of the attine ants, i.e., they appear to be obligate symbionts. Second, only higher-attine fungi produce nutritious swollen hyphal tips ("gongylidia") that are preferentially harvested by the ants for food (SCHULTZ & al. 2005).

Geographic distribution: The distribution of the *Sericomyrmex* clade is broad, from the southern US to Argentina and, in the case of *Trachymyrmex jamaicensis*, to the Caribbean. (*Sericomyrmex* s.str. species range from Mexico to Paraguay.) The precise species composition of the *Trachymyrmex intermedius* clade is not yet fully understood, but the species known to belong to this clade occur in forests and savannahs from Central America to northern South America. *Sericomyrmex* clade species occur in a wide range of habitats, including wet forests, savannahs, cerrados, and mid-elevation deserts (KEMPF 1972, WEBER 1972, BRANDÃO 1991, MAYHÉ-NUNES & JAFFÉ 1998, MAYHÉ-NUNES & BRANDÃO 2002, FERNÁNDEZ & SENDOYA 2004, MAYHÉ-NUNES & BRANDÃO 2005, 2007, RABELING & al. 2007a). Considering its phylogenetic position as the sister group of the leafcutting ants, the geographic distribution of the *T. septentrionalis* group is intriguing: Species known to belong to this clade are restricted to North America (US and Mexico), where they occur in mid-elevation deserts and open oak-juniper-pinyon woodlands (*Trachymyrmex arizonensis*, *T. carinatus*, *T. desertorum*, *T. nogalensis*, *T. pomonae*, *T. smithi*), and, in the case of *Trachymyrmex septentrionalis*, in sandy soils, open grasslands and woodlands, and, in the southern part of its distribution, in shaded clay-soil habitats as well (RABELING & al. 2007a). *Trachymyrmex septentrionalis* has the northern-most distribution of any attine, ranging up the east coast of the U.S. as far north as Long Island and up the Mississippi River as far north as southern Illinois (MIKHEYEV & al. 2008). It is an

important ecological component of pine-sandhill ecosystems in Florida, with more than 1000 nests, 235,000 workers, and 3.5 kg of fungus garden in a single hectare (SEAL & TSCHINKEL 2006).

Colony size and social structure: As might be expected from a large, paraphyletic group of species, colony characteristics vary tremendously across *Trachymyrmex* and *Sericomyrmex* species. Colonies usually consist of a single queen and can range from less than fifty (e.g., *Sericomyrmex parvulus*, *Trachymyrmex bugnioni*) to many thousands of workers (T.R. Schultz, unpubl.). Workers are monomorphic to mildly polymorphic (BESHES & TRANIELLO 1994, 1996).

Mating and nest-founding behavior: Although little is known about mating behavior in most *Trachymyrmex* and *Sericomyrmex* species, the species for which we have information typically have synchronized seasonal mating flights. It remains possible that many species, especially deep-forest species, are aseasonal or produce sexuals for a protracted period during the rainy season. So far as is known, queens mate singly (TSCHINKEL 1987, VILLESSEN & al. 2002). Because the *T. septentrionalis* clade is the sister group of the leafcutting ants (Fig. 2; SCHULTZ & BRADY 2008), which are known to mate multiply (VILLESSEN & al. 2002), mating frequencies need to be further investigated in the *T. septentrionalis* group species.

Nests of *Trachymyrmex* and *Sericomyrmex* species are typically established by a single queen (haplometrosis). Based on studies of newly founded nests in Panama, pleometrosis was found to occur at low frequencies in two *Trachymyrmex* species and one *Sericomyrmex* species (FERNÁNDEZ-MARÍN & al. 2004). So far as is known, foundress queens discard their wings after mating and suspend the incipient garden above the chamber floor on rootlets, a rock, or the chamber ceiling (FERNÁNDEZ-MARÍN & al. 2004). Nest-founding is semi-claustral (FERNÁNDEZ-MARÍN & al. 2004, SEAL & TSCHINKEL 2007).

Nest architecture: Nests of most *Sericomyrmex* and *Trachymyrmex* species consist of one or more underground chambers excavated in the soil, but some species nest in or under rotten logs, under rocks, and in leaf litter on the ground, in tree crotches, and in the aerial roots of palms (MAYHÉ-NUNES & BRANDÃO 2002, 2005, 2007, RABELING & al. 2007a; T.R. Schultz, unpubl.). *Sericomyrmex* species are very poorly studied (URICH 1895a, b, WEBER 1967) but, as far as is known, all *Sericomyrmex* species excavate nests in the soil, some consisting of a single chamber (e.g., *Sericomyrmex parvulus*), others consisting of multiple (up to eight observed), seemingly haphazardly arranged chambers (WEBER 1972; T.R. Schultz, unpubl.). In most *Trachymyrmex* and *Sericomyrmex* species, nest entrances take the typical form of a crater or mound (FERNÁNDEZ-MARÍN & al. 2004, RABELING & al. 2007a). However, nests of *T. opulentus* and *T. ruthae* have distinctive tall and slender chimney-like turret openings that connect, via a roughly vertical tunnel, to a series of vertically arranged subterranean chambers, with newer chambers added at the bottom as the colony matures (T.R. Schultz, unpubl.); some *Sericomyrmex* species may have similar nest openings (URICH 1895a). The nests of *T. bugnioni* may have short turrets, sometimes emerging horizontally from an embankment or from under an overhanging rock or root (T.R. Schultz, unpubl.). *Trachymyrmex zeteki* nest entrances occur in the form of elaborate auricles constructed on

embankments in roadsides and elsewhere (FERNÁNDEZ-MARÍN & al. 2004) that are similar in form to, but much larger than, *C. longiscapus* and *C. muelleri* nest entrances (SCHULTZ & al. 2002). The function of such structures remains poorly understood, but they may serve to deter the entry of parasites and predators.

Foraging and defense: Generalized-higher-attine agriculturalists typically cultivate their gardens on insect frass and plant material encountered in the litter such as flower parts, seeds, grass stalks, and the flesh of fruits (URICH 1895a, b, WEBER 1967, 1972, BESHES & TRANIELLO 1996, FELDMANN & al. 2000). Some species (including *Trachymyrmex diversus*, *T. cornetzi*, and some *Sericomyrmex* species) also cut and carry fresh vegetation, including flower petals, young plant shoots, and tender leaves (URICH 1895a, b, WEBER 1967, 1972, LEAL & OLIVEIRA 2000, VILLESSEN & al. 2002; T.R. Schultz, unpubl.).

Some species of both genera form conspicuous foraging columns of workers carrying cut vegetation, reminiscent of leafcutting ants (WEBER 1972; T.R. Schultz, unpubl.). Like lower attines, most *Sericomyrmex* and most *Trachymyrmex* species react to threat with a death-feigning response. A notable exception is *T. diversus*, which, like the *Acromyrmex* species it resembles, reacts aggressively (T.R. Schultz, unpubl.).

Symbionts: Commensals in *Trachymyrmex* and *Sericomyrmex* nests include mites, millipedes, collembolans, and flies in the genus *Pholeomyia* (Milichiidae) (SABROSKY 1959); parasites include diapiiid wasps (FERNÁNDEZ-MARÍN & al. 2005, 2006) and phorid flies; and predators include army ants (LAPOLLA & al. 2002). *Megalomyrmex silvestrii* species-group ants have been found living in the nests and gardens of generalized higher agriculturalists (WHEELER 1925, BRANDÃO 1990, ADAMS & al. 2000), including *S. amabilis* and *T. opulentus*.

Leafcutter agriculture

A biologically distinct, clearly derived form of higher agriculture, known as leafcutter agriculture, is practiced by the two genera of leafcutter ants, *Acromyrmex* and *Atta*, which grow their fungal cultivars largely on fresh plant material. (A third taxonomically valid genus in this group, *Pseudoatta*, was erected in 1916 for the social parasite species *P. argentina*; it is, however, clearly a derived species of *Acromyrmex*, see SCHULTZ & BRADY 2008.) Because they are highly visible components of the ecosystems in which they occur, and because they have significant impacts on human activity in those ecosystems, the leafcutting ants, especially *Atta* species, are the most well-known and well-studied of the Attini.

As is true for all the higher-agricultural cultivars, the leafcutter cultivars appear to be obligately associated with ants, i.e., they do not appear capable of living outside the symbiosis. However, unlike the genetically diverse fungal cultivars of *Trachymyrmex* and *Sericomyrmex*, the fungi cultivated by most leafcutter species comprise, so far as is known, a single sexually reproducing species, ranging across the southern US to Argentina and Cuba (SILVA-PINHATI & al. 2004, MIKHEYEV & al. 2006; U. Mueller, pers. comm.).

Geographic distribution: *Atta* and *Acromyrmex* have a broad geographic distribution, from the southern US through Central and South America and Cuba (KEMPF 1972, WEBER 1972, BRANDÃO 1991, MAYHÉ-NUNES &

JAFFÉ 1998, FERNÁNDEZ & SENDOYA 2004); some *Acromyrmex* species occur as far as 44° south latitude (FARJI BRENER & RUGGIERO 1994). A population of *Acromyrmex octospinosus* introduced around 50 years ago occurs on the Caribbean island of Guadeloupe (MIKHEYEV & al. 2006).

Leafcutters can be found in a range of habitat types, including deep wet forests, forest clearings and edges, savannahs, cerrados, and deserts that receive seasonal rains. Some *Acromyrmex* species occur as high as 2500 m in elevation (FARJI BRENER & RUGGIERO 1994).

Colony size and social structure: Among the largest of all ant colonies, mature *Atta* colony sizes are measured in millions of individuals – in *A. sexdens rubropilosa* as many as eight million (FOWLER & al. 1986b) – while mature *Acromyrmex* colonies, depending on the species, may contain 17,500 to 270,000 workers (FOWLER & al. 1986b, WETTERER 1995). Worker-queen polymorphism in *Acromyrmex* is significantly more pronounced than in *Trachymyrmex* species and significantly less pronounced than in *Atta* species, i.e., it is intermediate between the two groups. Some *Acromyrmex* species in some environments may have as few as two discrete physical worker subcastes (WETTERER & al. 1998), whereas *Atta* species typically possess a broad continuous spectrum of worker sizes that perform an estimated fifty or more discrete tasks (OSTER & WILSON 1978). In both *Acromyrmex* and *Atta*, smaller subcastes tend to brood and garden, larger subcastes forage and cut vegetation, and, in *Atta*, a very large soldier subcaste attacks and repels invaders (WEBER 1972, HÖLLDOBLER & WILSON 1990).

Mating and nest-founding behavior: *Acromyrmex* and *Atta* mating flights are seasonally timed, generally occurring after the first substantial rain of the wet season (*Acromyrmex*: e.g., DIEHL-FLEIG 1993, JOHNSON & RISSING 1993; *Atta*: AUTOURI 1956, MOSER 1967, FERNÁNDEZ-MARÍN & al. 2004). Queens of both genera are known to mate with multiple males (KERR 1961, CORSO & SERZEDELLO 1981, TSCHINKEL 1987, JOHNSON & RISSING 1993, BOOMSMA & RATNIEKS 1996, FJERDINGSTAD & BOOMSMA 1997, 1998, FJERDINGSTAD & al. 1998, MURAKAMI & al. 2000, VIL-LESEN & al. 2002) and to store more than 100 million sperm (MOSER 1967). After mating and usually before nest-founding, leafcutter-ant queens shed their wings. Foundresses of most *Acromyrmex* species and of all *Atta* species excavate a chamber in the soil. Typically only one queen establishes a nest (haplometrosis), but pleiometrosis has been observed in *Atta texana* and *Atta mexicana* at very low frequencies (ECHOLS 1966, MINTZER & VINSON 1985, MINTZER 1987) and at high frequencies in some populations of *Acromyrmex versicolor*, in which most co-foundresses are not closely related (RISSING & al. 1986, HAGEN & al. 1988, RISSING & al. 1989). Laboratory experiments and field observations suggest that pleiometrosis may also occur in *Acromyrmex striatus* at low frequencies (DIEHL-FLEIG & DE ARAUJO 1996). It has been hypothesized that pleiometrosis occurs in these species because they occur in environments where suitable nesting sites are limited and / or where risk of predation is high (ECHOLS 1966, RISSING & al. 1986, MINTZER 1987, RISSING & al. 1989, DIEHL-FLEIG & DE ARAUJO 1996).

Foundress *Acromyrmex* and *Atta* queens nourish their incipient fungus gardens with fecal droplets and their first broods with trophic eggs. As is typical for most Attini,

Acromyrmex queens found their nests semi-claustrally, foraging for substrate with which they additionally nourish their gardens (HUBER 1905, WEBER 1972, RISSING & al. 1986, CORDERO 1963, DIEHL-FLEIG & LUCCHESI 1992, WHEELER & BUCK 1995, FERNÁNDEZ-MARÍN & al. 2003). In contrast, *Atta* queens found their nests claustrally, never leaving the nest chamber (HUBER 1905, BRUCH 1919, 1921, AUTOURI 1942, WHEELER 1948, CORDERO 1963, WEBER 1972, MARICONI 1974, WEBER 1982, RISSING & al. 1986, MINTZER 1987, DIEHL-FLEIG & LUCCHESI 1992, FERNÁNDEZ-MARÍN & al. 2003). Thus, until the emergence of the first adult workers 40 - 60 days after nest-founding, the *Atta* queen, garden, and brood must survive and grow using energy and raw materials derived solely from the queen's catabolized flight muscle and fat reserves, accounting for the two- to ten-fold greater weight (400 - 800 mg) of *Atta* queens relative to other attine queens (MINTZER 1987, 1990, FERNÁNDEZ-MARÍN & al. 2004, SEAL & TSCHINKEL 2008).

Garden placement by foundresses differs between the two leafcutter-ant genera. *Acromyrmex* foundresses attach the incipient garden to elevated roots or to the chamber ceiling, presumably to protect it from exposure to soil pathogens (FERNÁNDEZ-MARÍN & al. 2003, 2004; U. Mueller, pers. comm.), whereas *Atta* foundresses place the incipient garden (and their eggs) directly on the soil floor (HUBER 1905, AUTOURI 1942, MARICONI 1974, WEBER 1982, MINTZER 1987, FERNÁNDEZ-MARÍN & al. 2003, 2004).

Nest architecture: Some *Acromyrmex* species locate their single large gardens under rotten logs or other large objects (e.g., some nests of *A. octospinosus*). "Mound-building" *Acromyrmex* species (e.g., *A. heyeri*) locate their similarly large gardens in a single superficial depression in the surface of the soil covered over by an elevated mound of litter and debris (BOLLAZZI & al. 2008). A few species locate their gardens above the ground in tree crotches or on the upper sides of horizontal lianas, likewise covering them over with accumulated litter (e.g., *Acromyrmex hystrix*) (WEBER 1946; T.R. Schultz, unpubl.). Soil-nesting *Acromyrmex* species, in contrast, divide their fungus gardens among a dozen or more excavated subterranean chambers of varying depth (GONCALVES 1961, 1964, FOWLER 1979, VERZA & al. 2007, BOLLAZZI & al. 2008). *Atta* nests are invariably built in the soil and can be extensive, consisting of many hundreds or over a thousand subterranean chambers, each containing a garden about the size of a cabbage (STAHEL & GEIJSKES 1939, WEBER 1946, JACOBY 1950, MOSER 1963, JONKMAN 1980, MOREIRA & al. 2004a, b). Such nests alter the chemical and physical properties of the soil and have significant ecological effects, e.g., on nutrient cycling (COUTINHO 1982, HAINES 1983, MOUTINHO & al. 2003, WIRTH & al. 2003). At the surface, *Atta* nests may occupy great areas of excavated earth containing many entrance and exit holes and surrounded by multiple outward-radiating trunk trails, built and kept free of debris by the ants. In some species, including *Atta laevigata* and *A. vollenweideri*, the nest may be connected by underground tunnels to openings many scores of meters away, possibly to protect foragers from predators or the sun. *Atta* nest architecture incorporates a ventilation system in which air enters through openings at the nest periphery and exits through openings at the center (JACOBY 1939, STAHEL & GEIJSKES 1939). The mechanism driving air flow was long thought to be thermal convection, but, in a study of *Atta*

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

and symbiont species, next-generation whole-genome analyses of attine ants and their symbionts, improved ant and symbiont phylogenies, and robust ancestral-character-state reconstructions and cophylogenetic analyses.

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Zusammenfassung

Ameisen der Tribus Attini sind eine monophyletische Gruppe von etwa 230 beschriebenen und weit mehr unbeschriebenen Arten, die für ihre Ernährung von der Pilzzucht abhängen. Im Gegenzug versorgen sie ihre Pilzcultivare mit Nahrung, beschützen und verbreiten sie. Alle Arten dieser Tribus kultivieren Pilze, und es findet sich eine erstaunliche Heterogenität hinsichtlich der Vergesellschaftung mit Pilzen und des Agrarsystems, der Koloniegröße und der Sozialstruktur, des Nestbauverhaltens und des Verpaarungssystems. Diese Vielfalt ist der Hauptgrund dafür, dass die Attini ein Modellsystem für das Verständnis der Evolution komplexer Symbiosen geworden sind. Hier geben wir einen Überblick über die naturgeschichtlichen Charakteristika von pilzzüchtenden Ameisen im Kontext mit einer kürzlich veröffentlichten Phylogenie, indem wir Muster von Evolution und symbiotischer Koadaptation bei ausgewählten Kolonie- und Pilzzuchtmerkmalen in einer Reihe wichtiger Evolutionslinien herausstellen. Wir diskutieren die Implikationen dieser Muster und zeigen zukünftige Forschungsrichtungen auf.

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