Fungus-Farming Ants (Attini in Part)

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The fungus-farming or attine ants (subfamily Myrmicinae, tribe Attini, subtribe Attina) are a monophyletic group of 245 described species (including five fossil species) in 19 genera, as well as many additional species awaiting discovery and description. With the exception of a recent invasive record from Reunion Island in the Indian Ocean, fungus-farming ants are exclusively New World and primarily Neotropical in distribution. The fungus-farming ants and their closest non-fungus-farming relatives in the subtribe Dacetina, a clade of specialized predators, share a most-recent common ancestor that was likely a generalized hunter-gatherer that lived around 60–65 million years ago, shortly after the end-of-Cretaceous extinction event when conditions favored predaceous and detritivorous life-history strategies. Early in their evolution, fungus-farming ants diverged into two main lineages, the Paleoattina (77 species in 3 genera) and the Neoattina (168 species in 16 genera), the latter including the well-known leaf-cutting ants [5] (Fig. 1).

All attine ants obligately depend upon the cultivation of fungus gardens for food. Upon leaving the maternal nest, a daughter queen carries within her mouth a nucleus of fungus from her mother's garden that serves as a starting culture. After establishing a nesting site, most commonly by excavating a chamber in the soil, the foundress queen isolates her incipient garden from direct contact with the soil by placing it on a rock platform or by suspending it from rootlets or the chamber ceiling. Paleoattine queens start their incipient gardens on platforms that additionally consist of one or both of the queen's detached forewings. Only in the leaf-cutting genus *Atta* are queens known to place their gardens directly on the chamber floor. In all attine ants other than *Atta* species, the queen must forage for substrate on which to grow her incipient garden until her first brood of workers emerges 40–60 days after nest founding [6, 8–10].

Leaf-Cutting Ants

Attine-ant agriculture achieves its most conspicuous evolutionary apex in the leaf-cutting ants in the genera *Acromyrmex* and *Atta,* the dominant herbivores in most Neotropical ecosystems. Unlike the majority of attine ants that forage for and cultivate their fungus gardens on insect frass and other organic detritus, leaf-cutting ants, which originated around 20 million years ago, have acquired the ability to cut and process fresh vegetation (grasses, leaves, and flowers) as nutritional

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Fungus-Farming Ants (Attini in Part), Fig. 1 The leaf-cutting ant *Acromyrmex niger.* (Photo by Alex Wild)

substrates for their fungal cultivars. This key evolutionary innovation renders a mature *Atta* colony the ecological equivalent of a vertebrate herbivore in terms of collective biomass, lifespan, and plant material consumed [10, 30, 31].

A newly mated *Atta* queen, unlike other fungus-farming ants, founds her nest claustrally, excavating a small chamber, sealing herself inside, and nourishing her first brood and her fungus garden by catabolizing stored fat and wing muscle tissue. Prior to nest founding, leaf-cutter queens, unlike all other attine ants for which we have data, mate with multiple males, storing the sperm for life and producing a genetically diverse worker population with multiple patrilines, which may increase overall colony resistance to disease and which, in the case of *Acromyrmex echinatior,* are correlated with physical worker castes. Certainly, sperm from multiple males is necessary for fertilizing the hundreds of millions of worker and daughter-queen eggs (male eggs are unfertilized) laid by an *Atta* queen during the 8- to 15-year lifespan of her colony, which upon maturity may support a standing population of more than five million individuals [10, 11, 15, 31] (Figs. 2, 3).

Unlike other fungus-farming ant species, leaf-cutter ant workers are highly polymorphic, facilitating finely scaled division of labor and rendering *Atta* species among the most highly eusocial of all social organisms. As a result of their proclivity for rapidly denuding fresh vegetation, primarily non-native vegetation that has not coevolved chemical and/or mechanical defenses against them and/or their fungi, leaf-cutter ants are among the most economically important pests of human agriculture in Central and South America [7, 10, 15].

Fungus-Farming Ants (Attini in Part), Fig. 2 A leaf-cutting *Atta* queen and her daughter workers and brood on their fungus garden. (Photo by Karolyn Darrow)

Ant-Cultivated Fungi

The great majority of fungus-farming ants cultivate multiple species of closely related fungi in the tribe Leucocoprineae (division Basidiomycota, order Agaricales, family Agaricaceae) that are most closely related to non-ant-associated species currently assigned to the genera *Leucocoprinus, Leucoagaricus,* and *Lepiota*. The only known exceptions are ants in the *Apterostigma pilosum* species group, a monophyletic subset of the paleoattine genus *Apterostigma,* which cultivate coral fungi in the genus *Pterula* (division Basidiomycota, order Agaricales, family Pterulaceae) [17, 30].

Based on more or less consistent associations between ants and fungi, attine-ant agriculture has been divided into five "agricultural systems." In lower-attine agriculture (Fig. 4), the ancestral system practiced by 84 ant species in 11 genera, ants cultivate multiple, apparently unspecialized leucocoprineaceous fungal species that are facultative symbionts capable of living freely outside

Fungus-Farming Ants (Attini in Part), Fig. 3 An excavation of the subterranean nest of the leaf-cutting ant *Atta laevigata*. (Photo © W. Moffett, Minden Pictures)

Fungus-Farming Ants (Attini in Part), Fig. 4 Workers of the lower fungus-farming ant species *Mycocepurus smithii* on their garden. (Photo by Alex Wild)

of the symbiosis, although this assumption is based on only two collections of fruiting bodies of free-living conspecifics. In the previously mentioned coral fungus agriculture (Fig. 5), 29 *Apterostigma pilosum*-group species cultivate two distinct clades of *Pterula* species of unknown facultative/obligate status closely related to the free-living *Pterula moniliformis*. In a third system, yeast agriculture (Fig. 6), 17 described species in the genus *Cyphomyrmex* cultivate a clade of one or a few leucocoprineaceous species that, when associated with ants, grow in a unicellular phase otherwise unknown in the order Agaricales. Based on two collections of fruiting bodies of free-living conspecifics, the yeast cultivars are thought to be facultative symbionts [5, 17].

A fourth attine agricultural system, higher agriculture, practiced by 110 ant species, is clearly the product of a major evolutionary transition in which a formerly free-living leucocoprineaceous fungal cultivar became "domesticated." Higher-attine cultivars have never been found living apart from ants and are thus considered obligate symbionts. Unlike lower, coral, and yeast fungal cultivars, which are diploid, the multiple species in the clade of higher-agriculture cultivars are polyploid and consistently produce gongylidia, nutritious swollen hyphal tips that are utilized both for food and as a source of enzymes essential for garden growth. Leaf-cutter agriculture (Fig. 2), a derived form of higher agriculture, is practiced by the 50 species of the aforementioned leaf-cutting ants in the genera *Atta* and *Acromyrmex,* which actively cut and prepare fresh plant material as their fungal substrates. Although the majority of leaf-cutting ants are associated with what is thought to be a single higher-attine fungal species, *Leucoagaricus gongylophorus,* some leaf-cutters grow other higher-agriculture fungal species, and some non-leaf-cutting higher-attine ants cultivate *L. gongylophorus*. A few non-leaf-cutting higher attine ant species are also known to cultivate lower-attine fungi, but, with the notable exception of *Apterostigma megacephala*, no lower-attine

Fungus-Farming Ants (Attini in Part), Fig. 5 The "veiled" garden of the coral-fungus-farming ant *Apterostigma collare* on the trunk of a tree

Fungus-Farming Ants (Attini in Part), Fig. 6 A *Cyphomyrmex rimosus* species-group ant tending its yeast garden. (Photo by Alex Wild)

ants are known to cultivate higher-attine fungi [13, 18, 21, 27, 32].

Other Microbial Symbionts

Fungal species in the genus *Escovopsis* (division Ascomycota, order Hypocreales, family Hypocreaceae) are known only from attine fungus gardens, where they constitute a parasitic crop disease, competing with the ants for their fungal cultivars. Bacterial species in *Pseudonocardia, Streptomyces,* and possibly other actinomycete genera grow in specialized crypts on the integuments of many attine-ant species (Fig. 7). The bacteria, nourished by glands lining the crypts, produce antibiotics that serve to control pathogens, most notably the aforementioned crop disease *Escovopsis*. Other microbes that are consistently associated with at least some attine species include black yeasts (order Chaetothyriales, family Cyphellophoraceae; on ant integuments); nitrogen-fixing bacteria in the genera *Klebsiella* and *Azospirillum*; bacteria in the class Mollicutes, which may convert excess dietary arginine into NH_3 for the fungus garden; and *Wolbachia* species. A metagenomic study found that species in three bacterial genera, *Enterobacter, Rahnella,* and *Pseudomonas,* are consistently present not only in the gardens of fungus-farming ants but also in the gardens of fungus-farming pine beetles, ambrosia beetles, and termites [4, 10, 14, 24, 32].

Fungus-Farming Ants (Attini in Part), Fig. 7 A worker of *Acromyrmex echinatior* with white patches of actinomycete bacteria on its propleural plates (its "chest"). (Photo by Alex Wild)

Animal Symbionts

In addition to bacteria and fungi, attine-ant agriculture hosts numerous animal symbionts. The nests of leaf-cutting ants in particular represent a rich and reliable ecosystem that is home to hundreds of species of mostly invertebrate commensals and parasites, including many obligate symbionts. For example, in the refuse chamber of a single nest of *Atta sexdens rubripilosa*, the Brazilian entomologist M. Autuori recorded adult forms of 1,491 Coleoptera, 56 Hemiptera, 40 Mollusca, 15 Diptera, 4 Reptilia, and 1 Pseudoscorpion. In excavating a nest of *Atta texana,* D. Waller and J. Moser encountered 90 species of Annelida, Nematoda, Pseudoscorpiones, Arachnida, Myriapoda, Isopoda, Acarina, Collembola, Thysanura, Dictyoptera, Orthoptera, Hemiptera, Coleoptera, Lepidoptera, Diptera, and Hymenoptera. J. L. Navarette-Heredia lists 411 beetle species belonging to 25 families that are associated with species of the leaf-cutting ants *Atta* and *Acromyrmex*. Adams and Longino observed annelids, beetle larvae, nematodes, isopods, and silverfish, as well as ten ant species, associated with nests of the yeast agriculturalist *Cyphomyrmex cornutus*. Even some snake and lizard species live in leaf-cutter ant nests, in some cases obligately, and are able to follow ant pheromone trails [1, 3, 22, 29, 30].

Fungus-growing ant species are also parasitized by other ants. Six species of the ant genus *Megalomyrmex,* which is only distantly related to the fungus-farming ants and otherwise not known to be fungivorous, participate in varying levels of social parasitism/predation of multiple species of fungus-farming ants in the genera *Mycocepurus, Trachymyrmex, Sericomyrmex,* and *Cyphomyrmex*. At the predatory end of the spectrum, “agro-predatory” *Megalomyrmex wettereri* marauders attack and kill or drive out adult fungus-farming ant workers and take over the nest, consuming the garden and brood and then moving on. At the semi-mutualistic end of the spectrum, *M. symmetochus* coexists for years as a social parasite in nests of *Sericomyrmex* fungus-farming ant species, but when the colony is attacked by the agro-predatory ant *Gnamptogenys hartmanni, M. symmetochus* becomes a mutualist, defending the colony with its alkaloid sting venom [2, 10].

Socially parasitic attine-ant species, one in the lower Attina and five in the leaf-cutting higher Attina, have so far been discovered, in all cases closely related to their host ant species, lending support to the hypothesis that social parasites most commonly originate as a within-species alternative life-history strategy, followed by speciation in sympatry [25].

Behavior

All fungus-farming ants share a complex suite of behaviors associated with fungus cultivation. Workers forage for the appropriate substrates, in most species insect frass, seeds, wood chips, and other organic detritus but in leaf-cutting ants freshly cut vegetation. They process the substrate, which in leaf-cutting ants involves masticating the leaf fragments to produce a finely divided paste, which makes the contents available to the fungus. They add the substrate to the garden and inoculate it with mycelium taken from elsewhere in the garden. They harvest the fungus for food and feed it to their larvae. They constantly patrol the garden, recognizing and mechanically weeding out and/or applying antibiotics to unwanted fungi and bacteria. They remove the spent garden and deposit it outside the nest or in specialized dump chambers. Finally, as previously mentioned, a daughter queen carries a nucleus of mycelium from her mother’s garden in order to start her own garden [10, 17, 30, 31].

Like all ants, fungus-farming ants communicate with their nestmates. They mostly do so chemically, via pheromones. Unlike other ants, however, fungus-farming ants must also “communicate” with their fungal cultivars. When attacked by leaf-cutting ants, many Neotropical plants express toxins. In a feedback loop that remains poorly understood, leaf-cutting ants are able to recognize when such a toxin is adversely affecting their symbiotic fungus and will cease to forage for that particular substrate, remembering and avoiding it for multiple weeks afterward. The brains of fungus-farming ants have highly developed olfactory lobes made up of many hundreds of glomeruli, spherical structures in which sensory neurons interface with neurons connected to higher-brain centers. Sophisticated olfaction presumably enables fungus-farming ants to distinguish between substrates while foraging, to distinguish between their resident fungal cultivar and other fungi, and to distinguish between diverse pheromones produced by their nestmates. Interestingly, all leaf-cutting ant species so far studied possess a single uniquely enlarged "macroglomerulus" that may function in the detection of trail pheromone [10, 31].

Leaf-cutter ant workers are highly polymorphic; an *Atta* soldier weighs 200 times more than her smallest sister. This diversity in worker body size facilitates finely scaled division of labor, with differently sized workers performing different tasks, broadly characterized as, from smallest to largest, gardener-nurses, within-nest generalists, forager-excavators, and defenders. However, because there are more than 30 known tasks to perform, in addition to being polymorphic, leaf-cutter ants are polyethic, i.e., an individual worker is capable of performing multiple tasks. It has been shown experimentally in the laboratory that if the size category of workers most efficient at leaf-cutting is removed, foraging workers in adjacent size categories (i.e., slightly smaller and slightly larger) take over the leaf-cutting task [10].

Molecular Frontiers

As in many biological disciplines, increasingly sophisticated technologies have accelerated exploration of the attine symbiosis at chemical and molecular levels. In the two decades between 1979 and 1999, for example, two antibiotics were isolated from attine fungal cultivars, but in the following single decade, dozens of antibiotics (antibacterial, antifungal, and even antimalarial) were isolated from attine ants, their fungal cultivars, the crop disease *Escovopsis*, and mutualistic *Pseudonocardia* and *Streptomyces* bacterial species [32].

The rate at which genomes and transcriptomes are being generated for attine symbionts continues to accelerate. Currently represented are multiple species of fungus-farming ants, fungal cultivars, *Escovopsis* garden parasites, and *Pseudonocardia* bacteria. Comparative studies indicate that, unlike other ants, all fungus-farming ants lack the genes necessary for synthesizing the amino acid arginine, which the ants instead presumably obtain from their fungal cultivars, and that, relative to non-fungus-farming ants, attine ants have experienced rapid rates of genetic evolution, including high rates of structural gene rearrangement. Genes encoding the enzymes chitinase and beta-hexosaminidase were positively selected for in the ancestor of fungus-farming ants, presumably as an early adaptation to fungivory, and additional such selection occurred at the origin of higher-attine ants, correlated with the more chitinous cell walls of higher-attine fungi [12, 23, 28, 32].

Major genetic changes also occurred in the ancestral higher-attine fungal cultivar, correlated with the loss of an independent, saprotrophic life history. These changes, in aggregate, appear to reflect the increased reliance of higher-attine fungi on their ant mutualists both to preprocess the substrate in order to make it available for fungal digestion and, as was first revealed in pioneering chemical-ecological research by M. Martin in the 1970s, to vector fungal enzymes from the fungus-rich central area of the garden to the upper, most rapidly growing area, where new substrate is incorporated by the ants. Those enzymes are significantly upregulated in gongylidia, the swollen hyphal tips consistently expressed in higher-attine fungi, and include a laccase, six pectinases, and seven proteases. The laccase, which detoxifies phenolic compounds present in the plant material, is expressed in the gongylidia of all higher-attine fungi, but it is expressed in significantly greater concentrations in *L. gongylophorus,* the cultivar utilized by the majority of leaf-cutting ant species [16, 32].

A Model System for Symbiosis

Attine-ant agriculture has become a model system for the study of symbiotic evolution, including the exploration of evolutionary conflicts of interest. Although ant agriculture has been broadly characterized as an arms race between the garden parasite *Escovopsis* and a collective of mutualists, there are also conflicts of interest among the mutualists. There is evidence, for example, that the interests of the fungal cultivars, particularly the lower fungal cultivars, may drive certain aspects of the system at the expense of the interests of the ants and that some aspects of attine agriculture are more parsimoniously explained by the view that the fungi domesticated the ants to feed, protect, and disperse them [10, 19, 26].

Beyond evolutionary theory, attine ants provide a useful nonhuman model for better understanding both human agriculture and medicine. Fungus-farming ants have, after all, practiced agriculture and controlled diseases with antibiotics for 60–65 million years, whereas humans have practiced agriculture for roughly 12,000 years and utilized antibiotics for less than a century. Thus, beyond the obvious benefit of discovering new antibiotics, understanding the evolutionary and ecological dynamics of the multipartite attine agricultural symbiosis is likely to have important and practical implications for the emerging fields of Darwinian agriculture and Darwinian medicine [20, 26].

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