7

Reciprocal Illumination

A Comparison of Agriculture in Humans and in Fungus-growing Ants

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> I have seen great surprise expressed in horticultural works at the wonderful skill of gardeners, in having produced such splendid results from such poor materials; but the art has been simple, and, as far as the final result is concerned, has been followed almost unconsciously.
>
> Charles Darwin
> *On the Origin of Species*

The fungus-growing ants of the tribe Attini (subfamily Myrmicinae) rely on the cultivation of fungi for food. The cultivated fungi are the sole source of nutrition for the larvae and the principal source of nutrition for the adults. All of the approximately 210 described attine ant species occur exclusively in the New World. Because the Attini are monophyletic and because no other ants are known to cultivate fungi, fungiculture is thought to have arisen a single time in ants. Attine ant fungiculture is perhaps the most unusual example of the more general phenomenon of ant agriculture, which has originated many times. Diverse ant species and clades cultivate mutualistic plants by removing weeds, eliminating pests, planting seeds, and providing soil and manure; other ant species herd, protect, and even breed mutualistic aphids and other homopterans (Hölldobler and Wilson 1990; Schultz and McGlynn 2000). No doubt many general ecological patterns and principles could be elucidated by comparing the full range of ant and human agriculture. This chapter provides the first step in such an exercise by focusing on the much more limited comparison of the agricultural systems of fungus-growing ants and humans.

Most fungus-growing ant species, including the most "primitive," belong to the eight genera collectively known as the lower Attini (fig. 7.1, table 7.1). Lower attines are mostly inconspicuous, cryptic species with relatively small colonies of a dozen to a thousand individuals and small to moderate-sized fungus gardens (Price et al.

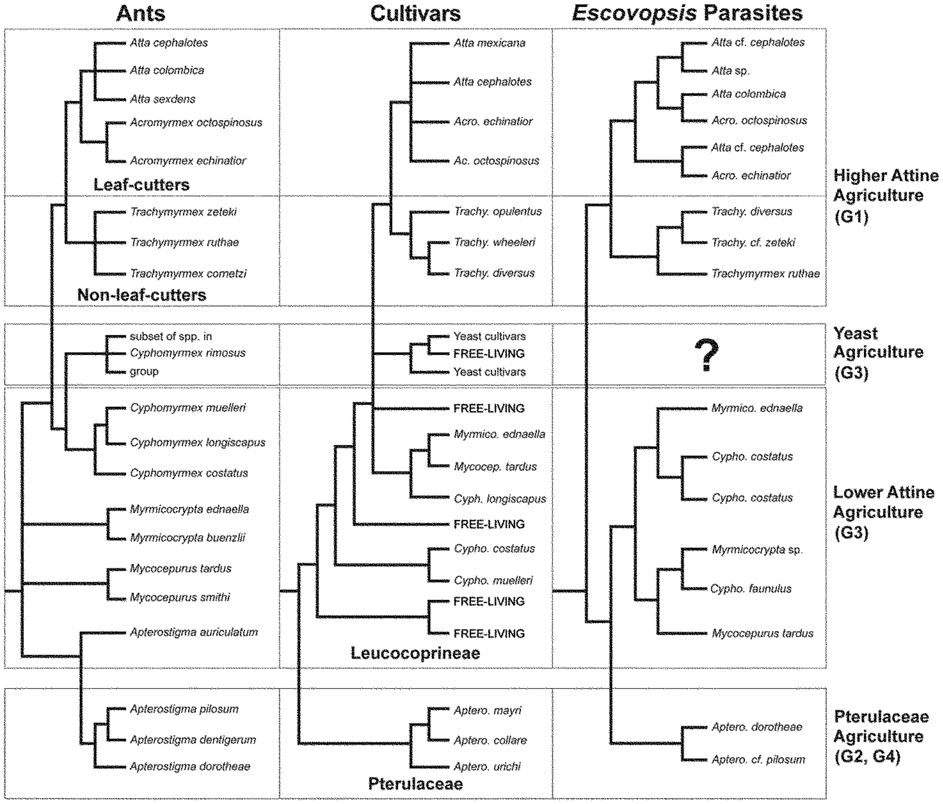

Figure 7.1. The four principal attine agricultural systems, juxtaposing the phylogenies of the attine ants, their domesticated fungi, and their *Escovopsis* garden parasites. The congruence of the topologies at more ancient phylogenetic levels indicates that these organisms have coevolved. G1, G2, G3, and G4 are names used for the respective domesticate groups in some previous publications.

2003). Attine agriculture reaches its most obvious culmination in the leaf-cutting ants, consisting of 43 species in the genera *Acromyrmex* and *Atta*. Leaf-cutting ants are the dominant herbivores of New World tropical forests and savannahs, and the greatest bane of Neotropical agriculture (Cherrett 1986; Fowler et al. 1986a). Colonies of some *Atta* species may contain up to 7 million individuals and persist for 20 years (Fowler et al. 1986b; Price et al. 2003).

Because leaf-cutting ants impact the environment significantly and because their nests and foraging columns are highly conspicuous, humans have paid special attention to them since prehistoric times. They play a major role, for example, in the ancient Mayan creation myth, the *Popul Vuh* (Wheeler 1907; Tedlock 1985). Although most early observers assumed that the ants directly consumed their cut leaves (Buckley 1860), the nineteenth-century English naturalist Henry Walter Bates disagreed, concluding instead that "the leaves are used to thatch the mounds to keep

Table 7.1. The fungus-growing ant genera and subgroups, with approximate numbers of described ant species and their known associated fungal domesticate groups.

Ant Group	Ant Genus	No. of Species	Fungal Domesticate[a]
Lower Attini	*Myrmicocrypta*	24	Lower attine Leucocoprineae (G3)
	Mycocepurus	5	
	Apterostigma (basal spp.)	13	
	Mycetarotes	4	
	Mycetophylax	6	
	Mycetosoritis	5	
	Cyphomyrmex (basal spp.)	22	
	Apterostigma (derived spp.)	34	Pterulaceae (G2, G4)
	Cyphomyrmex (derived spp.)	38	Yeast Leucocoprineae (G3)
Uncertain placement	*Mycetoagroicus*	3	Unknown
Higher Attini	*Trachymyrmex*	40	Higher attine Leucocoprineae (G1)
	Sericomyrmex	19	
	Acromyrmex	27	
	Pseudoatta (social parasites)	1	
	Atta	16	

G1, G2, G3, and G4 are names used for the respective domesticate groups in some previous publications.

out the deluging rains and protect their broods within" (Bates 1863, p. 12). In a striking example of synchronous scientific discovery, Thomas Belt (1874) and Fritz Müller (1874) independently discovered the true purpose of leaf cutting. In the words of Belt: "I believe the real use [the ants] make of [the leaves] is as a manure, on which grows a minute species of fungus, on which they feed;—that they are, in reality, mushroom growers and eaters" (Belt 1874, p. 79).

In this chapter, we ask whether and to what extent analogous ecological forces have shaped the symbioses between humans and their domesticated plants and animals on the one hand and the symbioses between attine ants and their fungi on the other. We also ask whether knowledge about human agricultural evolution can inform and structure attine biological research and, conversely, whether the study of attine biology can inform human agricultural practice. Hundreds of extant and many more extinct species of attine ants have, after all, successfully practiced a stable and sustainable agricultural strategy for approximately 50 million years (Mueller et al. 2001), whereas various populations of the single human species have practiced agriculture for a maximum of 10,000 years (Smith 1998a).

The Attine Agricultural Symbiosis

The fungi cultivated by the majority of attine species are parasol mushrooms in the monophyletic tribe Leucocoprineae (Agaricaceae) (fig. 7.1, table 7.1; Heim 1957; Hervey et al. 1977; Chapela et al. 1994; Mueller et al. 1998). The Leucocoprineae contains the genera *Leucocoprinus* and *Leucoagaricus*, as well as a few species currently assigned to *Lepiota* (Mueller et al. 1998; Johnson 1999). The salient features of the *Leucocoprinus* life cycle are summarized in figure 7.2. The earliest diverging clades within the attine ant genus *Apterostigma* also cultivate fungi from this group (Villesen et al. in press), but all species in one derived *Apterostigma* clade cultivate species of the distantly related coral fungi (Pterulaceae) (Munkacsi and McLaughlin 2001; Villesen et al. in press). Based on cultural characters (Chapela et al. 1994) and on phylogenetic analyses of ribosomal RNA genes (Chapela et al. 1994; Mueller et al. 1998; Rehner et al. unpublished data), the attine fungi are currently divided into four major groups (table 7.1, fig. 7.1): (1) typical lower attine fungi, thought to be least diverged from the ancestral attine domesticate (figs. 7.3, 7.4; Mueller et al. 1998); (2) yeastlike fungi, a derived, monophyletic subgroup within the lower attine fungi that grow as yeast morphs when associated with ants rather than as typical attine mycelial morphs (figs. 7.5, 7.6; Wheeler 1901, 1907;

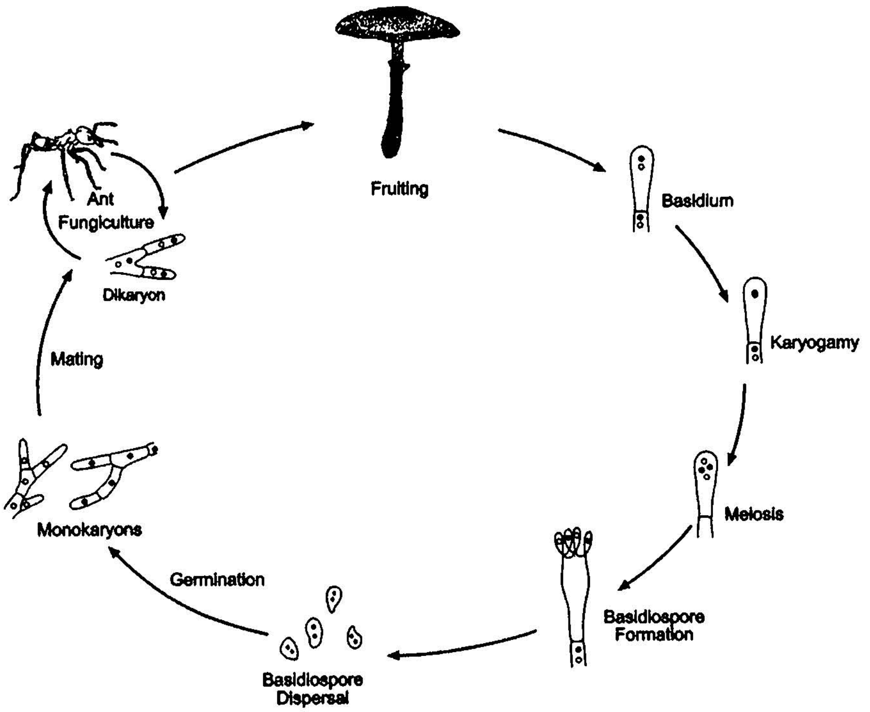

Figure 7.2. The life cycle of *Leucocoprinus*, a typical hymenomycete (true mushroom-forming fungus). The principal cellular and morphological structures produced in the hymenomycete life cycle include: (1) dikaryotic mycelium, containing two physically separate, haploid nuclei, sometimes considered functionally diploid; (2) fruiting bodies (mushrooms) produced from dikaryotic mycelia; (3) basidia, specialized sex cells formed on the gill surfaces and the site of long-delayed nuclear fusion (karyogamy) and meiosis; and (4) basidiospores—haploid meiospores, usually air-dispersed, that germinate to form a monokaryotic and haploid mycelium. Mycelia fuse (plasmogamy or mating) with sexually compatible monokaryons to form a dikaryotic mycelium.

Figure 7.3. A free-living (feral) lower-attine mushroom (Leucocoprineae) growing in th leaf litter in Panama. (Photograph by U. G. Mueller.)

Figure 7.4. Lower attine agriculture: the fungus garden of *Cyphomyrmex faunulus* constructed on the underside of a rotten log in São Gabriel, Amazonas, Brazil. (Photograph by T. R. Schultz.)

Figure 7.5. A free-living (feral) attine yeast agriculture mushroom (Leucocoprineae) growing in the leaf litter in Panama. (Photograph by U. G. Mueller.)

Figure 7.6. Attine yeast agriculture: the yeast fungus garden of *Cyphomyrmex salvini* taken from a cavity in a rotten log at La Selva, Costa Rica. (Photograph by T. R. Schultz.)

Weber 1972. 1982; Mueller et al. 1998); (3) the highly derived, monophyletic higher-attine fungi cultivated by the higher Attini, including the leaf-cutting ants, originating from a lower-attine–like leucocoprineaceous ancestor (figs. 7.7–7.9; Rehner et al. unpublished data); and (4) the attine pterulaceous fungi, divided into two monophyletic sister groups: the nonveiled pterulaceous fungi, cultivated by an apparently paraphyletic group of ants in the genus *Apterostigma*, and the veiled pterulaceous fungi, cultivated by a monophyletic group of ants in the genus *Apterostigma* that weave the aerial hyphae into a characteristic tentlike veil that surrounds the garden (figs. 7.10, 7.11; Villesen et al. in press).

Upon leaving the maternal nest, an attine daughter queen carries within her infrabuccal pocket a pellet of natal-nest cultivar, which serves as the nucleus for her new garden (von Ihering 1898; Huber 1905a,b). This behavior leads to the clonal propagation of garden fungi from parent to daughter nests, at least over short evolutionary time periods. The pattern of strict ant–fungus co-cladogenesis expected from this garden-founding behavior is disrupted over longer evolutionary time periods, however, because lower attine colonies occasionally replace their domesticates with free-living fungi and because both lower and higher attine ants replace their domesticates with fungi obtained from other attine ant colonies (Mueller et al. 1998; Bot et al. 2001; Green et al. 2002; Rehner et al., unpublished data).

The majority of attine leucocoprineaceous and pterulaceous gardens are infected by a highly specialized "crop disease" caused by species of the ascomycete fungal genus *Escovopsis* that so far are known only from attine fungus gardens (Currie et al. 1999a, 2003a; Currie 2001a,b). Low-level, chronic *Escovopsis* infections diminish garden and colony growth rates. At times, *Escovopsis* can also overrun and decimate

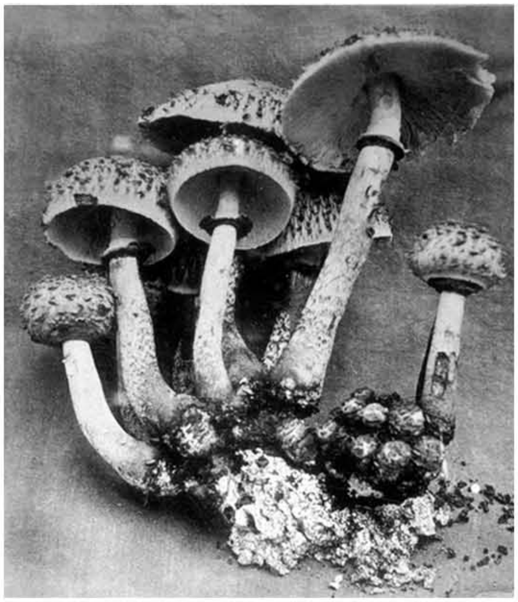

Figure 7.7. A higher attine mushroom (Leucocoprineae), growing from the surface of a nest of the leaf-cutting ant *Acromyrmex disciger*. (Reprinted from Möller 1893.)

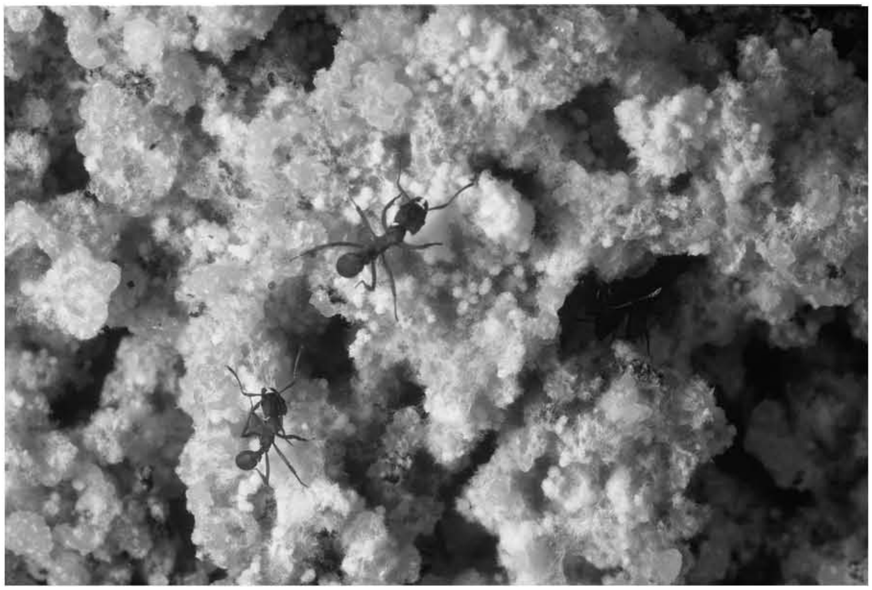

Figure 7.8. Higher-attine agriculture: the fungus garden of *Trachymyrmex septentrionalis*, collected from a subterranean nest in Long Island, New York, USA. Clusters of gongylidia are visible on the garden surface. (Photograph by T. R. Schultz.)

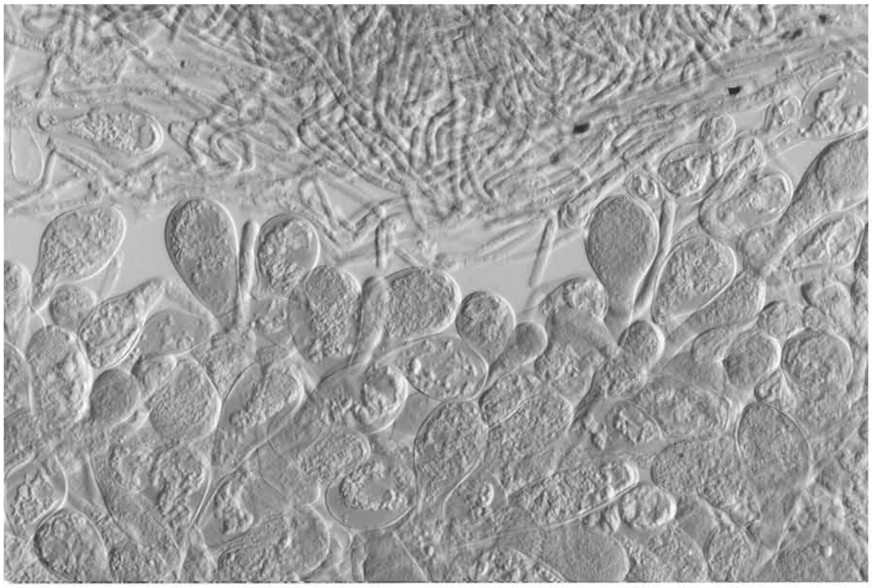

Figure 7.9. Lower half: gongylidia, the nutritious swollen hyphal tips produced by higher attine domesticated fungi and harvested by the ants for food; from the fungus garden of *Atta cephalotes*. Upper half: typical mycelium from the same garden. (Photograph by U. G. Mueller.)

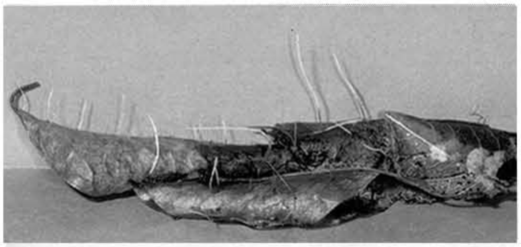

Figure 7.10. Basidiocarps of *Pterula typhuloides*, a free-living species in the Pterulaceae (coral fungi), the family closely related to the domesticates of the pterulaceous-cultivating *Apterostigma* attine ant species, growing on decaying leaves of an unidentified dicot tree on Bordeaux Mountain, St. John, U.S. Virgin Islands. (Photograph by T. J. Baroni.)

gardens, usually resulting in the deaths of both ant and fungal cultivar symbionts (Currie 2001a,b). Ants are able to detect *Escovopsis* spores and hyphae and to remove them by "weeding" (Currie and Stuart 2001); in the leaf-cutting ants, specialized "garbage caste" workers handle garden refuse and have minimal contact with other castes, presumably to prevent the spread of *Escovopsis* within ant colonies (Hart and Ratnieks 2002). In the myrmecological equivalent of biological pest control, attine ants culture actinomycete bacteria of the family Pseudonocardiaceae in specialized locations on their exoskeletons (Currie et al. 1999b, 2003b). The actinomycetes

Figure 7.11. Attine pterulaceous agriculture: the fungus garden of *Apterostigma* collare, constructed in a tree in La Selva, Costa Rica, and surrounded by a mycelial veil constructed by the ants. The veil is characteristic of one of the two subgroups of pterulaceous attine fungal domesticates. (Photograph by T. R. Schultz.)

produce an antibiotic with specific action against *Escovopsis* (Currie et al. 1999b, 2003b). Because the study of attine crop diseases is an entirely new area of research, it is likely that additional fungus-garden pathogens await discovery.

The relationship between attine ants and their associated fungi has been variously regarded as either parasitism, in which the ants benefit at the expense of the fungi, or as mutualism, in which both partners benefit. In either case, the benefit to the ants is clear enough: the colony cannot survive without a fungus garden. The benefit to the fungus is less obvious, however, leading to the widespread assumption, also made about human domesticates, that attine garden fungi are essentially enslaved by the ants (Mueller 2002). This enslavement scenario implies a significant conflict of interest in which the garden fungus is continuously trying to escape from the symbiosis, especially through fruiting (i.e., forming mushrooms), and in which the ants actively suppress the formation of fruiting bodies through constant policing and pruning of mycelium (Autuori 1940; Muchovej et al. 1991; Fisher et al. 1994a,b; Mueller 2002). Evidence in support of this scenario includes the observation that fruiting bodies are absent from well-populated nests but that fruiting may occur in nests in which ant populations are diminished or absent (Mueller 2002). The mutualistic scenario, in contrast, argues that the association significantly increases the fitness of the attine fungus, relative to its fitness in the free-living state, in at least three ways: (1) by increasing its representation in the next generation, (2) by increasing its geographic distribution due to dispersal by foundress queens, and (3) by providing protection from parasites and pathogens (e.g., *Escovopsis*) due to various activities of the ants. Even under a mutualistic scenario, however, some subset of the separate evolutionary interests of ants and fungi are likely to be in conflict (see Mueller 2002). For example, because fungi are dispersed only by queens, a biased sex ratio favoring females serves the interests of the fungi, but not necessarily the interests of the ants. Conflicts of interest are related to issues of control and enslavement, which are discussed below.

Agricultural Evolution

Human agriculture arose independently at least nine times during the past 10,000 years (table 7.2). The resulting agricultural systems differ in many ways, most notably in the particular species of domesticated plants and animals. In spite of these differences, some researchers have proposed features shared by all systems. Some have also proposed general conditions that may have propelled some societies to make the transition from the ancestral strategy of hunting-gathering, in which humans obtain all of their nutrition from wild plant and animal sources, to the derived strategy of agriculture, in which humans obtain a significant proportion of their nutrition from domesticated plants and animals (e.g., Sauer 1952; Flannery 1973; Rindos 1984; MacNeish 1991; Harlan 1992; Diamond 1997; Smith 1998a).

Generalizations about human agricultural evolution are complicated by the observation that hunting-gathering and agriculture are two extremes in a complex continuum of food acquisition strategies (Smith 1998a,b, 2001a,b; Pringle 1998). In fact, many stable human societies have employed (and, in some cases, continue

Table 7.2. Nine independent origins of human agriculture, with dates of origin and primary domesticates.

Region	Date	Plant Domesticates	Animal Domesticates
Near East (Fertile Crescent)	10,000 BP	Wheat, barley, lentils	Sheep, goat, pig, cattle
New Guinea	10,000 BP	Banana, taro	Pig
Mesoamerica	9000 BP	Maize, beans, squash	Turkey
Southern China (Yangtze River)	8500 BP	Rice	Pig, water buffalo, chicken, silkworm
Northern China (Yellow River)	8000 BP	Millet	Pig, water buffalo, chicken, silkworm
South Central Andes	7000 BP	Quinua, potato, beans	Llama, guinea pig
Lowland Neotropics	7000 BP	Yams, manioc, arrowroot, beans, peanuts, peach palm	None
Eastern United States	5000 BP	Sunflower, goosefoot, squash	None
Sub-Saharan Africa	5000 BP	Millet, sorghum, African rice	Cattle, guinea fowl

From Diamond (1997), Piperno and Pearsall (1998), Smith (1998a), Denham et al. (2003), and Neumann (2003).

to employ) successful strategies that include various combinations of hunting and gathering, management of local environments, and management of domesticated plants and/or animals. In some cases these domesticates were regularly imported from the wild and thus remained unmodified relative to wild populations (e.g., goats in the ancient Near East; Zeder and Hesse 2000); in others, the domesticates were modified due to human-mediated (artificial) selection (e.g., squash in Mesoamerica; Smith 1997).

Unlike most human agricultural systems (table 7.2), which incorporate multiple, distantly related domesticates, ant colonies are dependent on a single crop. A given attine ant species is remarkably faithful to a particular subclade of closely related fungi within the four groups indicated in table 7.1. Although different colonies of an attine ant species may cultivate different variants (whether these are species or subspecific strains is unknown) within its associated fungal subclade, as far as is known, an ant colony cultivates a single clonal monoculture at any given time. Thus, whereas human agriculturalists rely on multiple domesticates, and no single human domesticate provides a complete diet (table 7.2), attine ant colonies obtain their nutrition from a single fungal clone; the adult diet may be supplemented, however, with leaf sap, nectar, fruit juices, and possibly other food sources (see below) encountered by the foraging adults (Littledyke and Cherrett 1976; Quinlan and Cherrett 1979; Bass and Cherrett 1995; Oliveira et al. 1995; Murakami and Higashi 1997; Leal and Oliveira 2000).

The two most frequently cited advantages of human agriculture are, first, the energy savings compared to hunting and gathering and, second, the relative reliability and predictability of the agricultural food resource (Hayden 1995; Diamond 1997; Piperno and Pearsall 1998). These advantages do not necessarily lead to a state of complete reliance on agriculture, as is demonstrated by the many historical and extant stable-state human societies that practice mixed food-acquisition strategies. Some studies suggest that in resource-rich environments, mixed strategies and perhaps even pure hunting-gathering may require less effort than a strategy of complete reliance on agriculture (Boserup 1965; Lee 1968; Lee and DeVore 1968; Sahlins 1968; Pimentel and Hall 1989; Harlan 1992). However, the issue of the relative labor costs versus nutritional returns of hunting-gathering, mixed strategies, and agriculture is unresolved and remains the subject of continuing research and debate (Piperno in press).

As human populations have increased and wild resources have become limited, agriculture has, as a matter of historical record, replaced hunting-gathering in most human societies (Smith 2001a,b). In contrast, foraging has remained a necessary component of the attine ant food-acquisition strategy because attine fungal domesticates are saprophytic biomass consumers (unlike the plant domesticates of humans, but more like human animal domesticates), and ants must forage to obtain that biomass for their fungi. Various studies (e.g., Turner 1974; Quinlan and Cherrett 1979; Bass and Cherrett 1995) suggest that attine ants expend as much foraging energy and import more biomass than do equivalently sized colonies of predatory/omnivorous hunter-gatherer ants, and that the net yield in ant biomass per unit foraging effort may be similar to that of the hunter-gatherers, at least for the lower Attini. If so, then, of the two cited advantages accruing to human agriculturalists, the second, reliability, must be more important for attine agriculture. Growing fungi allows attine ants to occupy a niche unoccupied by other ants, thereby releasing them from direct competition for protein sources such as live prey and dead arthropods. Unlike humans, who have always relied on animals and plants as sources of food, initially consuming and later cultivating fungal intermediates allowed the ancestors of the Attini to access a food source previously inaccessible to ants, that of living and dead plant tissue. In collecting insect frass and small plant parts for garden substrate, lower attine ants in fact compete for food with fungal and bacterial detritivores rather than with predators and scavengers; they must locate and use these resources before they have been colonized and degraded by microbes. In collecting large volumes of living plant material for garden substrate, leaf-cutting higher attine ants have shifted from competing with detritivores for dead vegetable material to competing with vertebrate and invertebrate herbivores for living plant tissue.

Associating with attine ants also represents a major shift in food acquisition strategy for the leucocoprineaceous fungi: instead of relying on passive dispersal, they use an agent that actively locates, concentrates, and prepares suitable substrates before they are degraded by competitor microbes. In the case of the higher attine fungi, the symbiosis has provided access to an entirely new, previously unavailable resource: living vegetation. Living leaves and other plant parts are normally protected from fungal invasion by a variety of defenses, including waxy coats and other physical barriers; higher attine ants remove those barriers by extensively preparing substrates for consumption by their fungal domesticates (Cherrett et al. 1989). Similar strategies of using animal vectors for directed dispersal to suitable resources have evolved many times among fungi (e.g., pollinator-dispersed rusts; Webber and Gibbs 1989), and it is not implausible that many fungal groups, including the Leucocoprineae, use ants as vectors for dispersal to competitor-free resources.

Agricultural Evolution: Origins

Like humans, the ancestral food-acquisition strategy of ants is that of omnivorous hunter-gatherer. In contrast to human agriculture, attine ant agriculture had a single origin sometime around 45–65 million years ago, and all extant attine ants are descended from a single agricultural pioneer (Schultz and Meier 1995; Meier and Schultz 1996; Wetterer et al. 1998; Mueller et al. 2001). Although an intermediate state probably once existed, in which proto-Attini were facultative associates of symbiotic fungi, no such extant species are known. Detailed ecological investigation may eventually identify a nonattine guild of facultative ant fungivores, as hypothesized by Mueller et al. (2001). Alternatively, ant lineages loosely associated with fungi may have gone extinct during attine evolution because they were outcompeted by early attine ant lineages with tighter coevolutionary associations. A similar competitive sweep has occurred in humans, so that today most human mid-range, low-level food-production economies have been supplanted by agriculture (Smith 2001a,b).

Agriculture was absent during the first 90,000 years of human (*H. sapiens*) history. Yet it has arisen multiple times during the past 10,000 years. This dramatic change in human food-acquisition behavior is sometimes attributed to the global shift toward increasingly benign and stable climatic conditions following the Pleistocene glaciation, which tended to favor agriculture, as well as changes in regional climatic conditions in the major agricultural centers of origin (Piperno and Pearsall, 1998; Smith 1998a). Climate change of a different and more drastic sort also has been suggested as a condition predicating ant agriculture. Citing Janzen (1995), Mueller et al. (2001) speculated that the "nuclear winter" following the Cretaceous-Tertiary extinction event of 65 million years ago may have favored detritivores and precipitated the curious, possibly simultaneous origins of attine fungiculture, restricted to the New World, and termite fungiculture, restricted to the Old World (Mueller et al. 2001). In the words of Janzen (1995, p. 785):

> What animals are most likely to survive a serious nuclear winter? Those whose food in some form does not directly depend on immediate photosynthesis. That is to say, those that eat dormant seeds and insects, those that eat decaying organic matter (especially nongreen plant parts), and those that eat these eaters. And especially those that are very good at finding small particulate bits of these resources, scattered and dwindling until sunlight again can penetrate the clouds in amounts sufficient for serious vegetation growth. That is to say, seed- and detritus-eating invertebrates and the invertebrates and small vertebrates that eat them and each other.

One obvious requirement for the origin of agriculture is that humans must have lived for extended periods of time in the vicinity of, and regularly encountered while foraging, suitable domesticates, such as plants and animals that were potentially useful to humans and that possessed traits that, in aggregate, preadapted them for domestication (Diamond 1997; Smith 1998a). This requirement would appear to have been met by the ancestral attine ant as well, which, like the majority of tropical rainforest ants, foraged in the leaf litter, where it frequently encountered both the vegetative mycelium and fruiting bodies (mushrooms) of leucocoprineaeceous fungi.

In their original forms, proto-domesticates may or may not have been useful to humans. In either case, according to the "camp follower" scenario of agricultural origins (see below), they were likely to have been preadapted to thrive in human-disturbed habitats (Flannery 1973; Bye 1981; Rindos 1984; Harlan 1992; Diamond 1997; Smith 1998a). In the case of immediately useful plants, human hunter-gatherers could have incidentally broadcast the seeds (or other propagules) into disturbed areas around their villages, thrown them away with uneaten refuse into garbage piles, or consumed and subsequently deposited them as human waste. Plants that thrived in such microenvironments would become "camp followers," growing in relatively greater abundances in the vicinity of humans. Alternatively, nonuseful, camp-following weeds preadapted for disturbed habitats could have invaded human settlements on their own, without the aid of humans. In either case, the camp-follower scenario has two requirements: (1) Proto-domesticates must have thrived in one or more microenvironments associated with human-disturbed habitats, and (2) they must have been immediately or potentially useful to humans. Camp-following plants that were not immediately useful may initially have been ignored, tolerated, or even removed by humans. Due to their continuing proximity to humans over time, however, any even minimally useful variants were (consciously or unconsciously) favored, marking the beginning of domestication and human-mediated selection (de Tapia 1992, citing Bye 1981). Even if, as suggested by some researchers (D. Piperno, pers. comm.), camp-following proto-domesticates were not the same species that were subsequently domesticated by humans, it is possible that humans acquired the knowledge and skills that eventually led to agriculture through such early interactions.

Examples of camp-following mutualisms occur in primates, including humans. *Cebus* monkeys feed on the fruit and distribute the seeds of *Gustavia* trees and, by also feeding on the buds, influence the fruiting pattern of the trees to their advantage (Oppenheimer and Lang 1969). Stands of baobab trees (*Adansonia* spp.) in Africa are closely associated with occupied or deserted human villages. Humans eat the fruit and use the leaves as potherbs, the bark as a source of fiber, and the large hollow boles as reservoirs for the storage of water (Harlan 1992). Fruit trees occur in corridors that line the paths used by Congo Pygmies, presumably due to casual discarding of fruit pits and defecation while traveling (Laden 1992, cited in Hayden 1995).

The camp-follower hypothesis shares similarities with a number of hypotheses proposed for the origin of the attine ant–fungus mutualism (reviewed by Mueller et al. 2001). Ant-disturbed microenvironments in which the leucocoprineaceous proto-domesticate most likely thrived include both the nest refuse pile and leaf litter or other substrates adjacent to the nest. The infrabuccal pellet hypothesis proposed by Bailey (1920) and further developed by Mueller et al. (2001) suggests that the proto-domesticate was useful to the ants early in the association, and this hypothesis thus provides a mechanism for active transport of the proto-domesticate by the ants into the vicinity of the nest. The infrabuccal pellet hypothesis is based on the observation that all ants accumulate food particles and detritus in their infrabuccal pockets, a specialized pouch in the bottom of the mouth that filters out and accumulates solid particles picked up during grooming or strained out from liquid food. These infrabuccal pellets have been shown to contain a significant proportion of fungal spores and hyphae (Bailey 1920; Letourneau 1998). Infrabuccal pellets are expelled by individual ants at a rate of about one per day in colony refuse piles inside or outside the nest or, by foragers, at random locations in the vicinity of the nest (Quinlan and Cherrett 1978a; Febvay and Kermarrec 1981; Mueller et al. 2001; Little et al. 2004).

Because spores and hyphae in the pellets are viable, infrabuccal pellets provide a plausible mechanism for the vegetative dispersal of fungi (Wheeler and Bailey 1920), and it is possible that some fungi have capitalized on this mechanism by making their hyphae attractive to ant foragers (Mueller et al. 2001). Although their function remains to be demonstrated, the mycelium of at least some lower-attine fungi possess hyphal swellings (Möller 1893; Urich 1895; Weber 1972; Mueller 2002) that may be homologous with the gongylidia of higher attine fungi (fig. 7.9). The latter are preferentially harvested and eaten by higher attine ants (Quinlan and Cherrett 1978b, 1979; Angeli-Papa and Eymé 1985). If leucocoprineaceous proto-gongylidia function as ant attractants, they are evolutionarily convergent, vegetative analogs of elaiosomes, nutritious seed appendages that serve as an inducement for ant dispersal of the seeds of a variety of unrelated herbaceous plants (Serenander 1906; Handel et al. 1981; Beattie 1985; Handel and Beattie 1990a,b).

Aside from the refuse pile, a leucocoprineaceous proto-domesticate could have thrived in the substrate associated with the nest of the ancestral attine ant. It is plausible that the ancestral attine ant nested between leaves in the leaf litter, the typical substrate of leucocoprineaceous fungi. Nests of various species in the lower attine genera *Apterostigma*, *Cyphomyrmex*, and possibly *Myrmicocrypta* occupy this habitat, as do the nests of many species in the putative sister group of the Attini, the Blepharidattini (*Wasmannia* and *Blepharidatta*) (Schultz and Meier 1995; Diniz et al. 1998; R.C.F. Brandao and J. Delabie, pers. comm.). Like all ants, leaf-litter–nesting ants clean nest substrate surfaces in the vicinity of their brood, removing fungi, bacteria, and other debris and applying antibiotic secretions. Any leucocoprineaceous fungus capable of exploiting this competitor-free microhabitat, whether imported as infrabuccal pellets or invading independently, could become a protected camp follower. Such exploitation might require avoiding ant sensory, mechanical, and biochemical antifungal defenses, whether or not the fungus had an initially neutral effect on ant colony fitness. This would place a camp-following fungus in the same ecological guild as the many arthropod commensals that have successfully overcome the same obstacles to facultatively or obligately inhabit the protected and ecologically predictable microenvironments provided by ant nests (Schultz and McGlynn 2000). Obviously, by evolving ant-attractant properties, a fungus dispersed by ants via infrabuccal pellets would already possess a number of requisite preadaptations for moving into the nest environment and, eventually, becoming domesticated. A single observation of an extant (hence, obligately fungivorous) attine nest is at least consistent with one feature of this camp-follower scenario, that of continuity between adjacent litter-inhabiting and ant-associated fungal individuals: A veiled pterulaceous garden of a litter-nesting *Apterostigma* colony was observed connected to an extensive mycelial mat occupying the leaf litter beyond the nest (Mueller 2002).

Agricultural Evolution: Domestication

Archaeologists have dated domestication events by studying the remains of ancient human-associated plants and animals and identifying morphological traits that are clearly modified relative to the corresponding traits in wild populations. In some cases, the archaeological record preserves domestication sequences spanning thousands of years. Examples of sequential modifications include increasing seed size and decreasing seed coat thickness in a variety of domesticates, and increasingly apical position of seeds on stalks, reduced stalk branching, and seed indehiscence in domesticated grains and maize. If domestication is defined as the management of captive plants and animals, regardless of whether those plants and animals are modified due to domestication by humans, then the earliest detectable changes in the archaeological record provide only minimum dates of origin. In other words, the historical origin of a particular human-domesticate symbiosis is necessarily older than the earliest detectable morphological markers encountered in the archaeological record.

Modifications in domesticates are the result of selective forces exerted by humans, both unconsciously (especially during the earlier stages of association) and intentionally (especially during the later stages). This human-mediated selection is commonly referred to as "artificial selection" in order to distinguish it from "natural selection." Three features of attine fungiculture provide opportunities for the operation of the ant analogue of artificial selection (Mueller 2002). The first is garden founding. Foundress queens depart from their parent nests carrying pellets of garden mycelium that serve as the starting seeds for their new gardens (Weber 1972; Mueller 2002). If genetic variants coexist in the mycelium of the parent garden (e.g., due to somatic mutation), and if foundress queens discriminate between variants when incorporating mycelium into their infrabuccal pockets, then they exert selection on the domesticate population. The second feature is garden propagation. Garden-tending workers select hyphae of growing mycelium from healthy parts of the garden and plant them on newly added substrate (Weber 1972). Again, if domesticate variants coexist in attine gardens, and if workers preferentially propagate one of these variants while ignoring others, then garden-tending workers exert selection on the domesticate population. The third feature is garden reacquisition. Although attine fungi are usually transmitted clonally from parent to daughter nests, genetic evidence indicates that new garden strains are acquired occasionally from the wild and from the gardens of other ants (Mueller et al. 1998; Adams et al. 2000). If foragers are able to distinguish between candidate strains, then they can choose which strains to import into the nest and thus exert selection on the extended fungal population.

In support of the ant-imposed artificial selection hypothesis, Mueller et al. (2004) recently documented that the lower attine ant *Cyphomyrmex muelleri* has an acute ability to discriminate between domesticate strains. When presented with a range of domesticate choices, workers of *C. muelleri* invariably preferred their native garden domesticate, discriminating against even very close relatives of the native domesticate. A similar ability to differentiate between closely related cultivar strains has been described in leaf-cutting *Acromyrmex* species by Bot et al. (2001) and Viana et al. (2001). These observations suggest that attine ants may impose artificial selection against unwanted, presumably inferior domesticates or, alternatively, selectively favor desirable domesticate types that are more nutritious, more resistant to disease, easier to cultivate, or otherwise beneficial. It remains to be determined, however, whether attine ants have the ability to detect and artificially select for ant-benefiting traits in domesticate genotypes or, alternatively, whether naturally arising domesticate mutants spread to fixation in a garden due to competitive superiority over other strains independent of ant-subculturing biases.

Under the assumption that selection regimes on domesticates differ between human-mediated and wild-type environments, fixation of desirable traits in domesticates (favorable gene combinations and mutations) requires reduced gene flow between domesticate populations and their ancestral free-living populations. In the absence of such a reduction, genetic variants favorable for domestication can only become fixed in the domesticate population if selection within the symbiosis is adequately strong and/or gene flow between domesticate and free-living populations is asymmetrical, such that gene flow from the symbiosis into the free-living population adequately outweighs the reverse gene flow, and genes favorable for life within the symbiosis introgress into the population as a whole and are reimported into the symbiosis in subsequent domestication events.

Barriers to gene flow between domesticated and wild populations, both intentional and incidental, have obviously played an important role in the histories of a significant number of human domesticates. These barriers have included the isolation of domesticates in discrete garden plots and livestock pens, asexual propagation (e.g., with cuttings and tubers), the domestication of self-fertilizing plants (e.g., barley, wheat, oats, rice, and sorghum), and the domestication of reproductively isolated polyploid and translocation races (e.g., some potato strains). Domesticated Mesoamerican beans (*Phaseolus vulgaris*), for example, appear to have arisen from a single small population; a second, separate domestication occurred in the southern Andes (Gepts et al. 1986; Gepts and Debouck 1991). Barriers to gene flow also have included the human dispersal of domesticates to areas well outside of their natural ranges, including cross-continental dispersal (e.g., North American and European strains of potatoes and tomatoes are descended from only a few individuals; Rick 1976; Quiros 2003). While under domestication by ants, attine fungi have been similarly isolated from wild populations; however, genetic evidence indicates that these periods of isolation through clonal propagation have been relatively brief when measured on evolutionary time scales (Mueller et al. 1998; Rehner et al., unpublished data). Judging by the distribution of the Attini, it is also likely that, while under domestication, attine fungi have been carried into regions relatively inhospitable to leucocoprineaceous fungi, including deserts and seasonally dry habitats, and it is possible, though by no means proven, that such habitats, removed from natural free-living populations, have served as crucibles for the morphological modifications encountered in some of the attine domesticates (Fowler 1982).

Alternatively, the histories of many human domesticates suggest that barriers to gene flow may have been relatively permeable and that modifications of domesticates nonetheless occurred due to strong, human-mediated selection. In a prolonged domestication process that may have lasted for hundreds of years, maize (*Zea mays* ssp. *mays*) arose, probably in southern Mexico, from *Zea mays* ssp. *parviglumis* (Wang et al. 1999; Matsuoka et al. 2002). In spite of its extreme morphological modifications, domesticated maize retains the majority of the variability present in its progenitor subspecies, as well as variability acquired through subsequent introgression from another free-living subspecies, *Zea mays* ssp. *mexicana* (Eyre-Walker et al. 1998; Matsuoka et al. 2002; Vigouroux et al. 2002). Similar genetic variability due to persistent outbreeding with wild populations has been demonstrated for rice (Morishima and Oka 1979; Second 1982), barley (Brown and Munday 1982), dogs (Vilà et al. 1997, 1999; Leonard et al. 2002), horses (Vilà et al. 2001), and potatoes (discussed below). So common is this pattern of genetic continuity between human domesticates and free-living ("weed") populations that interactive crop–companion weed reciprocal evolution has been hypothesized as the prevailing norm in human agriculture (Harlan 1965; Wilson 1990), and such reciprocal systems have been demonstrated for pairs of domesticated and free-living populations in *Cucurbita* (Wilson 1989, 1990) and *Chenopodium* (Wilson 1981, 1990).

A relatively unexplored area of inquiry is modifications of humans due to selection pressures exerted by their domesticates and serving the domesticates' evolutionary interests. Whether they serve the evolutionary interests of the domesticates, however, domesticate-related modifications of humans are well documented and include the varying frequencies, in some human populations relative to others, of such traits as lactose intolerance, wheat allergies, resistance to livestock-borne diseases, susceptibility to morning sickness as a function of diet, and ability to detect and/or tolerate a variety of toxic plant secondary compounds (Johns 1990; Jackson 1991; Haig 1993; Diamond 1997). Aside from such population-level genetic adaptations, humans as a species have remained genetically unmodified by their associations with domesticated plants and animals. This paucity of genetic change in humans contrasts sharply with the major changes that have occurred in their domesticates and tends to support the widely held, rather common-sense view that human plant and animal husbandry are symbioses of asymmetrical control, in which one symbiont, humans, has effectively enslaved the other symbionts and adapted them to human needs (discussed in detail below).

Unlike humans, attine ants are extensively modified for their agricultural symbiosis, and all such modifications are obviously the result of genetic (rather than cultural) evolution. Known modifications are largely behavioral and include the detection and removal ("weeding") of *Escovopsis* and other garden parasites (Currie 2001a,b); the cultivation of antibiotic-producing actinomycete bacteria on their exoskeletons (Currie et al. 1999b, 2003b); specialized foraging behaviors to select substrates suitable for their garden fungi; the transport of cultivar by virgin queens from parent to daughter nests (von Ihering 1898; Huber 1905a,b); the weaving of aerial hyphae by Pterulaceae-cultivating *Apterostigma* species into the protective tentlike veils that surround their gardens; and, in *Atta*, the division of workers into ethological and morphological castes specialized for garden tending, foraging, and refuse disposal. In addition, there are a series of suspected, but so far unstudied, nonbehavioral modifications that include physiological adaptations for fungivory; biochemical adaptations that enable attine ant species to specialize on narrowly defined domesticate groups; sensory adaptations for distinguishing between symbiont strains and between suitable and unsuitable fungi (e.g., parasitic fungi like *Escovopsis*); sensory adaptations for evaluating the health or growth rate of the garden in order to adjust foraging or weeding activities (Ridley et al. 1996; Currie and Stuart 2001); and, in the yeast-cultivating *Cyphomyrmex* species, the induction of the yeast morph in their garden fungi.

In contrast to the many adaptations present in the attine ants, modifications associated with domestication in the attine fungi are surprisingly difficult to document. One clear example is gongylidia (fig. 7.9), which serve as food for higher attine ants and which are so distinctive that the vegetative dikaryotic hyphae of the leaf-cutter fungus was described by Kreisel (1972) as a separate species, *Attamyces bromatificus*. When higher attine fungi are cultured in the laboratory in the absence of ants, the production of gongylidia frequently declines over time and may cease altogether, suggesting that gongylidia production is in some way linked to life with attine ants. Whether gongylidia are induced by specific nutritional or environmental conditions present within the symbiosis or whether they are the product of continuous positive selection by the ants during garden propagation remains an open question. Stradling (1978) considered the higher attine fungi to constitute a "rich and complete diet" for leaf-cutter ants, and Bass and Cherrett (1995) found that gongylidia prolonged the lives of *Atta* workers compared to an exclusively hyphal diet. Curiously, the scant data available suggest that, judged by crude protein, lipid, and carbohydrate proportions, the nutritional content of both the hyphae and gongylidia of attine fungi (so far analyzed only for the fungi of *Atta colombica* and *Atta sexdens*) are not obviously modified relative to the nutritional content of free-living leucocoprineaceous fungi, except that gongylidia appear to contain less protein and more lipids and carboydrates than do hyphae (Mueller et al. 2001). It remains possible that the higher attine fungi (or, indeed, all attine fungi) are modified in terms of (1) the production of particular amino acids, lipids, and/or carbohydrates; (2) the production of trace nutrients (e.g., vitamins, minerals, or steroids); (3) the loss of toxins present in the ancestral forms; (4) the production of ant-attractant allomones (Mueller et al. 2001); or (5) the sequestering of ant-produced colony-recognition hydrocarbons (Viana et al. 2001).

A second likely modification occurs in the *Cyphomyrmex* yeast fungi, cultivated by a probably monophyletic subset of ant species within the *Cyphomyrmex rimosus* group (Kempf 1966; Snelling and Longino 1992; Schultz and Meier 1995). Compared to conspicuous attine mycelial gardens, yeast gardens (fig. 7.6) are so easily overlooked that some early researchers concluded that *Cyphomyrmex rimosus*-group ants did not practice fungiculture (Forel 1893; Emery 1895; Urich 1895). Once discovered, yeast gardens proved so unusual that these domesticates are among the few attine fungi to have been specifically assigned a formal taxonomic name (*Tyridiomyces formicarium;* Wheeler 1907). Yeast gardens consist of small, irregularly shaped nodules about 0.5 mm in diameter that are composed of a fungus growing in the yeast phase (i.e., as separate, single cells; fig. 7.6) rather than in the typical mycelial phase, in which cells are connected in linear filaments (fig. 7.4). Ants nourish yeast gardens with insect frass and nectar collected while foraging. Nectar is transported to the nest in the crops of workers and regurgitated directly onto the garden; it is also shared with nestmates via trophallaxis (i.e., regurgitative feeding; Murakami and Higashi 1997).

Yeast-phase growth in the order Agaricales is entirely unexpected. Outside of the attine fungi, yeast morphology is known among the Basidiomycota (basidium-forming fungi, including the true mushrooms) only in two distantly related orders: the Tremellales (the jelly fungi), the basal lineage of the hymenomycetes (the true mushrooms), and the even more distantly related Ustilaginales (smut fungi) (Fell et al. 2001). In these two groups, the yeast phase occurs only in the uninucleate haploid state, whereas the attine *Cyphomyrmex* yeasts appear to be dikaryotic. The attine yeasts were derived independently of these other yeast groups. Although yeast-phase growth has a genetic basis, it appears to be induced in mycelium by the presence of *Cyphomyrmex* ants. This hypothesis is supported by four facts: (1) a free-living fruiting body of a feral yeast domesticate has been collected, produced by typical mycelial growth on leaf litter (fig. 7.5; Mueller et al. 1998); (2) phylogenetic analyses reconstruct the attine yeast fungi as a derived, monophyletic group nested within the leucocoprineaceous "clade 1" subclade of the lower attine fungi (fig. 7.1; Mueller et al. 1998); (3) the mycelial morph is also present in gardens, growing on the integuments of ant larvae (Schultz and Meier 1995); and (4) in culture, the yeast morph eventually reverts to mycelial growth (Mueller et al. 1998).

Because the attine yeast fungi all belong to a compact monophyletic group within the lower attine fungi (fig. 7.1), it is possible that, for reasons unknown and unrelated to ant fungiculture, they share a derived tendency to convert to yeast-phase growth under certain conditions. Under this hypothesis, the ants take advantage of this preexisting tendency to induce the yeast morph (perhaps by unusual gardening behaviors), and the lower attine yeast fungi are not necessarily modified for life with ants. The data, however, favor an alternative hypothesis. The independent origin of the attine yeasts, the complete absence of the yeast phase in other Homobasidiomycetidae (mushroom fungi), and the tight association of the yeast fungi with a probably monophyletic group of *Cyphomyrmex* species (Schultz 1995) all suggest that yeast growth is a derived modification for life with *Cyphomyrmex* ants. The adaptive function of the yeast morph is unknown, but at least two explanations are plausible. First, yeast nodules are easily transportable, allowing for a seminomadic existence and/or rapid escape from predators like army ants (LaPolla et al. 2002) and *Megalomyrmex* "agropredators" (Adams et al. 2000). Second, yeast gardens may be less susceptible to *Escovopsis* infection. So far, *Escovopsis* has not been isolated from yeast gardens (Currie, unpublished data), but this remains a largely uninvestigated question. It is interesting to note that dimorphic ascomycetes in several distinct clades have yeastlike growth phases in association with insects such as ambrosia and bark beetles. The derived yeastlike state occurs in mycangia, and hyphal conversion occurs in the beetle galleries.

Agricultural Pathogens

Human-domesticated plants and animals are infected by a range of pathogens, including fungi, bacteria, viruses, arthropods, and nematodes (Maloy 1993; Agrios 1997). Pathogens have devastated human agricultural societies throughout recorded history. Agricultural diseases are listed in the Old Testament, along with human diseases and war, as one of the great scourges of mankind. The study of crop diseases dates back to the Greek philosopher Theophrastus (c. 370–286 BC). More recently, the Irish potato famine of the 1840s, caused by the late blight of potato agent (*Phytophthora infestans*), resulted in the deaths of more than 2 million people (Lang 2001). This disaster demonstrates the potential of agricultural diseases to devastate human populations.

The gardens of attine ants are also devastated by pathogens. Although other garden pathogens and pests probably await discovery, the only currently known attine garden disease is caused by microfungi in the genus *Escovopsis* (Ascomycota: Hypocreales) (Currie et al. 1999a, 2003a; Currie 2001a), necrotrophic parasites that grow in contact with and extract nutrients from the attine fungal domesticates (Reynolds and Currie, in press). *Escovopsis* infections of fungus gardens are typically chronic, resulting in significantly decreased rates of garden growth and substantially depressed rates of worker production (Currie 2001b). Less typically, *Escovopsis* can rapidly overwhelm gardens, completely overgrowing them and leading ants to abandon the infected gardens, sometimes resulting in colony death (Currie et al. 1999a; Currie 2001a). *Escovopsis* is specialized on the attine symbiosis and has been found only in the nest habitats of both leucocoprineaceous and pterulaceous fungus-growing ants (Currie et al. 1999a; Bot et al. 2001; Currie 2001a,b). Molecular phylogenetic analyses indicate that *Escovopsis* was an early participant in the attine ant–microbe symbiosis and that it shares a long history of coevolution with the ants and their fungal domesticates (both leucocoprineaceous and pterulaceous; Currie et al. 2003a). Thus, like human agriculture, ant agriculture has a long history of crop disease.

Agricultural Pathogens: Disease Susceptibility and Control

In both human and ant agriculture, domesticates face increased susceptibility to disease for two reasons. First, cultivation involves growing domesticated organisms at greater population densities than those of their free-living counterparts. Higher densities facilitate the spread of pathogens between individuals, contributing to the evolution of increased virulence in the pathogens (Anderson and May 1981, 1982; Ewald 1994). Second, artificial selection, inbreeding, and clonal propagation limit the genetic diversity of agricultural crops compared to their free-living counterparts, and genetic diversity is believed to facilitate the evolution of resistance to pathogens (Jaenike 1978; Hamilton 1980).

The success of agriculture depends on the control of domesticate pathogens. Human agriculture employs dozens of methods to prevent and suppress pathogens. These methods can be assigned to four general categories: exclusion, eradication, protection, and immunization (resistance) (Whetzel 1929; Maloy 1993; Agrios 1997). Exclusion prevents pathogens from entering and establishing themselves in a new area and is typically achieved in human agriculture through quarantines and embargoes. Eradication is accomplished by the removal, elimination, or destruction of pathogens from areas or individuals. Protection requires the separation of infected from uninfected individuals to prevent the spread of pathogens; it is primarily achieved by manipulating the environment, applying protectants, or erecting barriers. Immunization (resistance) uses breeding, medication, vaccination, and nutrition management to modify the domesticates or their growth conditions to make them less susceptible to or more tolerant of pathogens.

Although a full comparison of agricultural disease-control methods used by humans and attine ants is beyond the scope of this review, it is worth considering how the four mechanisms of crop defense in human agriculture parallel those in ant agriculture. First, attine ants practice exclusion by preventing inoculum of potential pathogens from coming into contact with the garden. This is achieved by cleaning nest surfaces and new substrate before it is added to the garden (Stahel and Geijskes 1939; Autuori 1941; Quinlan and Cherrett 1977, 1979) and by excluding the refuse-tending worker caste from physical contact with the fungus garden and with garden-tending castes (Hart and Ratnieks 2002). Second, ants practice eradication by removing pathogen inoculum that comes into contact with the garden before infection can be established. This is primarily accomplished through a behavior called fungus grooming, in which workers use their mouthparts to separate pathogen inoculum from domesticate mycelium (Currie and Stuart 2001). Attine ants also weed out and discard infected garden material (Currie and Stuart 2001). Attine research has so far neglected the category of protection, but relevant features of attine agriculture include: (1) the allocation of colony resources to the production of worker castes dedicated to monitoring gardens and detecting infections; (2) the architectural separation, in the nests of some attine species, of multiple fungus gardens into different chambers, which may prevent infections present in one garden chamber from spreading to other, uninfected fungus gardens; and (3) the permanent quarantine of gardens with advanced *Escovopsis* outbreaks by sealing them off with soil plugs (Currie and Mueller, pers. obs.). The final category of human agricultural disease control is immunization (resistance), and at least one resistance defense mechanism has been established in attine ant agriculture: the use of antibiotics produced by mutualistic filamentous bacteria (Actinomycetes) in the family Pseudonocardiaceae (Currie et al. 1999b, 2003b). Antibiotic compounds are also produced by the ants (Bot et al. 2002) and by the fungal domesticates (Nair and Hervey 1978; Hervey and Nair 1979; Angeli-Papa 1984; Kermarrec et al. 1986; Wang et al. 1999), although the role of the domesticates in disease control remains poorly understood. Resistance is a promising area of future research on the attine agricultural symbiosis, particularly with respect to the selection and spread of domesticate strains that are resistant to *Escovopsis* infection, including, possibly, the *Cyphomyrmex* yeast domesticates mentioned above.

Agricultural Pathogens: Origins

The pathogens that infect human domesticates are typically, but not always, closely related to the pathogens that infect free-living populations of the same or closely related species. Some of these domesticate diseases may have originated subsequent to domestication and then switched hosts from nondomesticated to domesticated plants and animals, whereas other diseases may already have been established before domestication and may have been introduced into human agricultural systems at the same time as, or shortly after, the domestication event. Recent molecular phylogenetic analyses of *Escovopsis* indicate the same pattern in attine agriculture. The sister group to *Escovopsis* is the ascomycete family Hypocreaceae (Currie et al. 2003a,b), which includes a large number of fungi that are pathogens of free-living mushrooms. Thus, it is likely that the ancestor of *Escovopsis* was an established pathogen of the ancestral attine domesticate and that it invaded the attine agricultural symbiosis at the time of its origin.

Alternatively, and perhaps less likely, because the Hypocreales also includes fungi that are parasites of insects, and because some hypocrealean pathogens can even facultatively switch between fungal and arthropod hosts, the ancestor of *Escovopsis* may have been a parasite of attine ants that switched to the fungal domesticates after fungus-growing behavior arose. Under this scenario, *Escovopsis* is analogous to the many diseases that humans have acquired from their domesticated animals, including measles, tuberculosis, smallpox, influenza, pertussis, and malaria (Diamond 1997, 1998).

Agricultural Pathogens: Conclusions

Because the study of natural ecosystems holds great promise for improving both human agriculture (Denison et al. 2003) and medicine (Williams and Nesse 1991), a better understanding of attine disease ecology may generate new ideas for controlling pathogens of human domesticates and perhaps even for controlling the agents of human disease. Attine ants have been using antibiotics derived from mutualistic actinomycete bacteria to suppress *Escovopsis* for millions of years (Currie et al. 1999b, 2003a,b). In addition, attine ants use antibiotics derived from their metapleural and mandibular glands (Bot et al. 2001), and some attine fungal domesticates also produce defensive antibiotics (Nair and Hervey 1978; Hervey and Nair 1979; Wang et al. 1999). Given the long history of this strategy, it is surprising, judging by our short human experience with antibiotics (approximately 60 years) and with agricultural pesticides (approximately 140 years), that *Escovopsis* has not yet evolved a generalized resistance to the actinomycete or other attine antibiotics. The most likely explanation for the continuing effectiveness of anti-*Escovopsis* antibiotics is that *Escovopsis* may be continually coevolving new resistance to particular actinomycete and other attine antibiotics, which are likewise evolving. Under this scenario, attine disease control may have proceeded as an ancient coevolutionary arms race, in which the actinomycete, ant, and domesticated fungal lineages continually evolve new antibiotics, and in which associated *Escovopsis* lineages continually evolve new forms of resistance to those antibiotics. Future research must characterize the antibiotic chemical or chemicals produced by the actinomycetes, ants, and fungi as well as their physiological effects on *Escovopsis*. Future research should also characterize the selection pressures, if any, on the actinomycete symbiont that affect antibiotic evolution.

Attine agricultural disease management incorporates a number of effective features, some of which may be applicable to human agriculture and medicine. First, lower attine domesticates are genetically linked to free-living fungal populations; attine fungi thus retain a large pool of genetic variability that likely serves as a source of pathogen-resistant strains (as well as a source of strains with other desirable features). Second, attine ants use antibiotics produced by evolving populations of bacteria. Again, the genetic variability in these populations probably serves as a source of new antibiotic variants and facilitates rapid response to newly evolved pathogen strains. Third, attine ants police their gardens intensively. Worker castes solely dedicated to gardening constantly patrol gardens, rapidly weeding out and discarding infected mycelium. It is interesting that the leaf-cutting higher attines, which cultivate domesticates that may be inbred and thus less resistant to new pathogen strains, possess physical gardening worker castes of minute ants that appear to be present in greater numbers than the gardening castes of the lower attines and that may generally be better at garden sanitation than are the morphologically unspecialized castes of the lower attines.

The Issue of Control: Enslavement of Domesticates by Agriculturalists versus Manipulation of Agriculturalists by Domesticates

Agricultural evolution—human or ant—is traditionally interpreted from the perspective of the agriculturalist, who appears to act with active intent, rather than from the perspective of the domesticate, which appears to be behaviorally inert and sessile in the case of plants and fungi. Thus, research programs have historically focused on such issues as how the quality of life has improved or worsened for the agriculturalist after the transition from hunting-gathering to agriculture, how the agriculturalist has imposed artificial selection and prevented domesticate escape, or what specific evolutionary modifications have arisen in the domesticate to better serve the agriculturalist (e.g., Sauer 1952; Flannery 1973; MacNeish 1991; Cowan and Watson 1992; Harlan 1992; Diamond 1997; Smith 1998a). These research questions take a one-sided perspective, that of the agriculturalist, and ignore the evolutionary interests of and leverages exerted by the proto-domesticate during the origin and subsequent evolution of the domesticate–agriculturalist association. This biased perspective seems to be intuitively justified because the agriculturalists appear to be in total control: Agriculturalists seem to manipulate critical life-history stages of the domesticate (e.g., timing of growth and reproduction); they dictate the fitnesses of different domesticate types (e.g., through artificial selection, whether intentional or incidental); and they can terminate an existing association either by switching from one domesticate to another or, in the case of humans, even abandon agriculture entirely and return to hunting and gathering. At first glance, then, agriculturalists—humans or ants—seem to direct the fates of domesticates, suggesting that the domesticates are completely enslaved.

An alternative perspective holds that domesticates have partial or even complete control over their evolutionary fates, if not in the present then at least at the origin of domesticate–agriculturalist associations, and that the proto-domesticates were initially acted upon by natural selection in ways that favored increased participation in symbioses with proto-agriculturalists who had yet to evolve the ability to dictate or direct the evolutionary fates of their domesticates (Rindos 1984). Under this perspective, domesticates do not become enslaved, if ever, until the later stages of a coevolutionary process. Precisely when in that process the transition from domesticate participation (complete control) to domesticate enslavement (reduced control) occurs is difficult to discern.

Taking an extremist domesticate-control perspective, one can even postulate that, before the origin of domestication, (1) the proto-domesticates exploited the proto-agriculturalists for their own reproductive purposes; (2) natural selection favored proto-domesticates that associated with proto-agriculturalists in symbiotic relationships that may have decreased the agriculturalists' fitness relative to a domesticate-free (hunting-gathering) strategy; and (3) domesticates ultimately ensnared agriculturalists in relationships that the agriculturalists found difficult to terminate. This radical view of agricultural evolution naturally conflicts with our intuition (and delusion?) that we humans were and are in charge of our past and present agricultural decisions. In contrast to this intuitive agriculturalist-control perspective of human agriculture, a domesticate-control perspective underlies the infrabuccal-pellet dispersal hypothesis proposed for the origin of attine ant fungiculture (Mueller et al. 2001).

Which of these alternative perspectives – the traditional agriculturalist-control perspective, the domesticate-control perspective, or a perspective that recognizes an intermediate tug-of-war–like coevolutionary interplay (Reeve et al. in press)—is the appropriate one depends on the extent to which each participant held control over its evolutionary fate during the initial formation of the domesticate–agriculturalist interaction (evolutionary origin) and retained this control during subsequent evolution to a more derived agricultural state (subsequent evolutionary modification). A thorough comparison of agricultural evolution in humans and ants therefore must consider both origin and subsequent evolution, first comparing human and ant preagricultural states and, in a separate, second analysis, comparing the derived human and ant agricultural systems that arose from those antecedent states.

The term "control" subsumes a set of factors, all of which help empower a symbiotic partner to elude the domination and exploitation of a coevolving partner. These factors include a partner's ability to (1) facultatively leave or escape from a symbiosis to lead an independent existence; (2) facultatively switch between partner species; (3) choose between genetic variants of the other partner (and thus influence or even dictate selective processes operating on the other partner); and (4) manipulate behavior or life-history parameters (e.g., growth and reproduction) of the other partner to modify it for the manipulator's benefit, sometimes even to the detriment of the manipulated partner. A partner that scores high in all these abilities is least likely to be exploited by the other partner, whereas a partner that scores low in all of these abilities is more likely to be exploited and enslaved (i.e., domesticated). Humans undoubtedly score high in the listed abilities in their recent agricultural systems, but, for understanding agricultural origins, it is necessary both to assess these abilities in the preagricultural states and to consider the perspectives of both the proto-agriculturalist and the proto-domesticate.

Domesticate control is easier to assess for the preagricultural coevolutionary interactions between the attine ants and their fungi than it is for human preagricultural interactions. For example, as discussed above, leucocoprineaceous fungi may use ants for dispersal via infrabuccal pellets, and they may have done so for millions of years preceding the origin of attine agriculture. Once dependent on vectoring by ants, such fungi may have evolved the ability to manipulate ant behavior by presenting ants with food rewards, a process convergent with the evolution of similar ant-reward structures (elaiosomes) that have originated many times in plants (Serenander 1906; Handel et al. 1981; Beattie 1985; Handel and Beattie 1990a,b). If so, then the fungi would have evolved to track the nutritional requirements and sensory preferences of the ant proto-agriculturalists before the advent of fungiculture, and the ants would have been engaged as reactive participants (passive respondents) in a coevolutionary process dictated by the evolutionarily "proactive" fungi.

Did such a stage, in which "reactive" humans coevolved with "proactive" plants, exist before the advent of human agriculture 10,000 years ago? It is possible, although this process is unlikely to have left any archaeological evidence that could conclusively document such a stage. As discussed previously in this chapter, ancestral humans probably dispersed plants in a number of ways, including as seeds (e.g., seeds that remained viable after passing through the human gut), as cuttings that were accidentally discarded at human campsites, or even as living stakes that were thrust into the ground during the building of fences, shelters, and other structures (Flannery 1973; Bye 1981; Rindos 1984; Harlan 1992; Diamond 1997; Smith 1998a). The associations between human-dispersed plants and humans are analogous to the association between infrabuccally dispersed fungi and ants, and it is such incidental associations that are expected to provide the raw material for further evolution. This further evolution includes derived agricultural behavioral repertoires that enhance the interaction for the benefit of the agriculturalist and that may eventually lead to intentional, planned domestications of the same or of other species.

Learning through trial, error, observation, and imitation no doubt played a major role in the development of the agricultural behavioral repertoires of humans, whereas the behavioral repertoires of ants were gradually modified through the prolonged interaction of mutation and selection—the evolutionary analogs of trial and error. This distinction between learning versus mutation-induced behavioral change is critical because learning can greatly accelerate adaptive modification in a species. Through learning, human agriculturalists rapidly modified the behavioral repertoires they used in their coevolutionary interactions with plants. Thus, in the case of a change in the human–domesticate relationship that benefited the human at the expense of the domesticate, the rapid pace of human behavioral change could preclude a corresponding evolutionary response in the domesticate. Through learned behaviors humans could prevent the facultative escape of a domesticate or prevent a domesticate from evolving toxicity or some other defense against human control. This rapid response on the part of humans leads to the rapid loss of control on the part of the domesticate and results in eventual enslavement (see criteria for control above). Learning thus enabled humans to take the role of the proactive partner during preagricultural and agricultural evolution and relegated the domesticate to the role of reactive partner. We can only speculate about the sophisticated agricultural systems the attine ants might have achieved during their 50 million years of evolution if ants were capable of human-scale learning and transmission of cultural information.

We suspect that most readers will resist our suggestion that human agriculturalists were once under the partial control of their proto-domesticates during the early evolutionary process that ultimately led to human agriculture. Human intuition suggests that we are not under the control of the cabbages and tomatoes that we plant in our backyards, that cabbages cannot facultatively escape from our gardens and from their inevitable destinies of death in our kitchens, and that cabbages have not enslaved us to labor on their evolutionary behalf. Human intuition can be misleading, however. We know, for example, that human symbionts can sometimes induce profound behavioral changes in humans that benefit the symbiont. The rabies virus induces drastic aggressive behavior to facilitate its spread to new potential hosts, and coca plants induce in humans a physical addiction and a craving for more coca, which requires the cultivation of more coca plants. Though seemingly far-fetched and in conflict with our intuitions, we cannot at this point rule out similar manipulations during the preagricultural evolution of humans, a stage when humans began to assemble the behavioral repertoires that ultimately led to agricultural systems guided by human planning and intentional experimentation.

A properly unbiased evolutionary analysis of human agriculture (conducted, for example, by a Martian evolutionary biologist), neither anthropocentric nor domesticate-centric, needs to address what the separate, selective advantages were to both humans and their domesticates during the long preagricultural process that eventually led to more derived agricultural systems. Many recent domesticates were clearly imported into the human agricultural symbiosis in a process of instantaneous enslavement guided by human foresight (e.g., grocery-store "button mushrooms" and cherry trees). The domestication of other organisms, however, including those that were domesticated earliest, was preceded by a long coevolutionary process, the dynamics and outcomes of which may well have been determined by an interplay of control exerted by the proto-domesticates and the proto-agriculturalists. It is during this ancient time period, perhaps 50,000–100,000 years ago and occurring well before the recognized origin of true agriculture 10,000 years ago, that the incipient states of human-domesticate coevolutionary associations may be most directly comparable to the coevolutionary ant–fungus associations that led to attine agriculture.

The Issue of Control: Conclusions

Did ants domesticate fungi or did fungi domesticate ants? We have already explained why, before the origin of attine agriculture, the fitness of nondomesticated leucocoprineaceous fungi may have been increased through a symbiotic association in which the fungi used ants as dispersal agents. Once this association evolved into an agricultural symbiosis, the attine fungi could have retained some measure of control, manipulating the relationship in their continuing self-interests. As already pointed out, compared to free-living fungi, attine-cultivated Leucocoprineae are better dispersed and distributed, better protected from parasites and pathogens, and possibly better represented in terms of sheer abundance due to the husbanding activities of their ant hosts. With the possible exception of the higher attine fungi, the attine domesticates retain the ability to leave the symbiosis and to become feral. The same cannot be said for the ants, which are highly modified for and obligately dependent on fungiculture, and which are generally faithful to particular domesticate clades (although not to single domesticate genotypes). This asymmetry in terms of commitment to and modification for the symbiosis might superficially seem to support the notion that the fungi retain more control than do the ants.

A few studies provide weak evidence that attine fungi may exert some measure of control over their ant hosts. Bot et al. (2001) described incompatibility interactions within experimentally created ant–fungus associations involving two sympatric *Acromyrmex* leaf-cutter ant species and their fungal symbionts. The degree to which ants from a particular colony were motivated to remove and destroy an unfamiliar domesticate strain (ant–fungus incompatibility) was uncorrelated with the ant species from which the strain was taken but was correlated with the degree of genetic difference between the unfamiliar strain and the ants' resident domesticate strain; this genetic difference precisely paralleled observed patterns of somatic incompatibility between fungi, characterized by antagonistic interactions between fungal strains. Significantly, ant–fungus incompatibility disappeared when the ants were deprived of their resident domesticate and force-fed an unfamiliar domesticate for at least several days; at that point, the new strain assumed the role of resident strain with regard to ant–fungus incompatibility. Because the ants' incompatibility with unfamiliar fungi was due to recognition cues produced by the resident fungus, one interpretation of the results (not favored by Bot et al. 2001) is that the resident fungus manipulates its ant hosts' behavior as a means to guarantee its monopoly. Alternatively, the ants may simply take advantage of the preexisting fungal incompatibility system to maintain fungal monocultures. In either case, the fungi have retained the ability to interact antagonistically with other conspecific fungi, and Bot et al. (2001) suggest that the fungal domesticates also may have retained the ability to escape from a particular ant association and to move laterally to a new ant nest (e.g., when their current ant hosts are threatened by disease or senescence).

Ridley et al. (1996) and North et al. (1997, 1999) suggested that the cultivated fungus of the leaf-cutter *Atta sexdens rubropilosa* regulates the selection of plant material by foragers by chemically signaling the ants regarding the suitability or toxicity of substrates, and that it uses chemical manipulation to compel a colony of ants to provide it with a healthy diet. Alternatively, the ants may be judging the health of the garden and the suitability of the substrates via indirect cues, communicating these judgments to other ant nestmates and adjusting their behaviors accordingly. Obviously, the issue of fungus versus ant control in the attine agricultural symbiosis is not resolved, but it remains a promising area for future research (Mueller 2002). One obvious line of inquiry is whether there is variability in the ability of fungal domesticate strains to attract new ant hosts or to move in and replace resident domesticates, independent of the strains' ant-beneficial traits.

Ant and Human Agriculture: Synthesis

Links between domesticated fungi and free-living populations are known for two of the four attine agricultural systems (table 7.1), specifically, for the lower attine and yeast domesticates (figs. 7.3, 7.5; Mueller et al. 1998; Vo and Mueller, unpublished data). Links to free-living populations cannot be ruled out for the pterulaceous *Apterostigma* domesticates (Munkacsi and McLaughlin 2001; Villesen et al. in press). The remaining group, the higher attine fungi, represents a highly derived clade descended from a lower-attine–like leucocoprineaceous ancestor. Like some human domesticates, higher attine fungi appear to be inbred and possibly largely self-fertilizing (Rehner, unpublished data), a feature that may preserve gene combinations optimal for the requirements of their ant hosts. Although higher attine fungi are known to produce fruiting bodies, these mushrooms are known only within garden chambers or on the external surfaces of nest mounds, physically connected to and an extension of the garden mycelium (fig. 7.7; Möller 1893; Mueller 2002). Because free-living higher attine mushrooms are unknown, it remains possible that the higher attine fungi are not viable outside the symbiosis.

Attine ants may obtain carbohydrates and proteins from sources other than their fungus gardens. Some authors have asserted that some of the most derived higher attine cultivators, leaf-cutter ants in the genus *Atta*, obtain about 95% of their carbohydrates from foraging outside the nest (Littledyke and Cherrett 1976; Quinlan and Cherrett 1979; Bass and Cherrett 1995). This figure, however, may be a gross overestimate because it depends on largely uninvestigated assumptions about the total caloric requirements of the colony and about the proportion of that requirement furnished by the cultivated fungus (Turner 1974), and it neglects the possible contribution due to larva-worker anal trophallaxis (Schneider 2000). Foraging for nectar and other sugary liquids and the redistribution of these resources by trophallaxis to other adult nestmates (but not larvae) has been observed in the yeast-cultivating ant *Cyphomyrmex rimosus* (Murakami and Higashi 1997) and in the leucocoprineaceous-cultivating lower attine ants *Myrmicocrypta ednaella* (Murakami and Higashi 1997) and *Mycocepurus goeldii* (Oliveira et al. 1995; Leal and Oliveira 2000). Some anecdotal evidence suggests that *Apterostigma* species may forage for sources of protein. For example, captive colonies of *Apterostigma* species have been maintained with an ant diet prepared from a mixture of eggs, honey, vitamins, and agarose (L. Alonso, pers. comm.); a forager of *Apterostigma collare* was observed carrying a dead mosquito into its nest (Schultz, unpublished obs.); and a recent study of nitrogen cycling in ants indicates that *Apterostigma* species are relatively high on the food chain, with nitrogen isotope ratios more similar to those of predators than to those of attine leaf-cutter ant species (Davidson et al. 2003).

Thus, judged on the human agriculture-based continuum, the Attini practice a mixed food-acquisition strategy, exemplified in humans by the North American Hopewell civilization (2100–1600 years ago), which combined sophisticated farming with hunting and fishing (Smith 2001a), and by early lowland Neotropical agriculturalists (table 7.2), who combined agriculture with hunting and gathering (Piperno and Pearsall 1998). There are two important differences between the ant and human systems, however. First, nutritionally, attine ants are obligately dependent on agriculture and facultatively dependent on foraging for food; whereas they are obligately dependent on foraging for nutritional substrate for their fungi. Humans have so far retained all nutritional options, including potential reversion to hunting and gathering, and human agriculture is therefore facultative rather than obligate as in the Attini. Agriculture is necessary, however, for the maintenance of current human population levels. Second, in most Attini, foraging apparently provides an additional source of carbohydrates, whereas in many human mixed-strategy systems with an agricultural component, such as the Hopewell example, foraging provides additional protein. Foraging for carbohydrate and cultivating protein may be more common in human agriculture than is generally recognized, however (Bray 2000). Such a system of protein production is exemplified by the environmental management strategy of the pre-Columbian savannah people of the Bolivian Amazon, who, through the construction of earthworks forming large weirs and artificial ponds, harvested fish on a massive scale (Erickson 2000).

Among the most ancient human domesticates, perhaps the closest analogues of the attine fungi are the root crops such as potatoes, yams, arrowroot, taro, and manioc, which, like the attine fungi, are clonally propagated. The simplicity of vegetative cultivation makes tubers ideal proto-domesticates, leading some authors to argue that these and other root crops may be more ancient than seed crops such as wheat, corn, maize, and barley (Sauer 1952; Johns 1990; Harlan 1992; Piperno and Pearsall 1998; Bray 2000; Piperno et al. 2000; Lang 2001). For example, Australian aborigines regularly cut off and replant the stems and tops of gathered wild yams (Gregory 1886, cited by Harlan 1992), and natives of the Ubangui-Chari region of equatorial Africa use some gathered yams immediately and plant the surplus near their camps for future use (Chevalier 1936). Because tubers are propagated clonally, artificial selection is also a straightforward process (Rindos 1984). "Strikingly superior types can be found by screening large natural populations" and, once under cultivation, "if clones are found that are better tasting, less poisonous, more poisonous, more productive, etc., they can be propagated and cultivars are developed immediately" (Harlan 1992, p. 131).

One root crop, the potato (*Solanum* spp.), has become the fourth most intensively cultivated food crop in the world. Potatoes were first domesticated between 7,000 to 10,000 years ago in the Lake Titicaca basin of the central Andes, and this region remains the center of potato genetic diversity (Hawkes 1990). Here farmers make use of eight domesticated potato species, representing 2000 to 3000 known varieties, in a stable, traditional system of subsistence agriculture that has persisted since the origin of this human–plant association (Brush et al. 1981; Hawkes 1990; Lang 2001; Quiros 2003). Human management of this extended multi-species base, which contains both free-living and domesticated populations, provides many striking parallels with attine ant management of their associated leucocoprineaceous and pterulaceous fungi.

Traditional Andean potato farmers propagate their crops clonally by replanting tubers with desirable traits. This allows for the persistence, over many years, of selected clonal lineages, and, paralleling the exchange of fungal strains between ant nests (Mueller et al. 1998; Green et al. 2002), potato farmers share and distribute the most favorable domesticate strains via extensive intervillage "seed" (i.e., vegetative clone) networks. The particular beneficiaries of these networks are farmers living in mostly lowland climates who must frequently replace their domesticates, which, in those climates, are more prone to blight, aphid-borne viruses, and other potato pathogens (Brush et al. 1981). It has likewise been suggested that particular strains of attine fungi may be adapted to particular ecological conditions (Mueller et al. 1998; Green et al. 2002). Even though some subsistence farmers may grow separate plots of commercially improved potato varieties as a cash crop, they continue to grow the more genetically variable native varieties for subsistence because they taste better, they store better, and they remain viable year after year, whereas the commercially improved varieties can only be clonally propagated for 1–3 years before they lose their vigor, possibly due to viral infections (Brush et al. 1981).

Paralleling the ability of both lower and higher attine ants to discriminate between fungal strains (Bot et al. 2001; Viana et al. 2001; Mueller et al. 2004), Andean potato farmers recognize about 100 different phenotypic domesticates with colorful names like "cat's nose" and "eyes of a jungle native" (Quiros 2003), but these phenotypes may be produced by a variety of genotypes. Thus, native phenotype-based classification and selection maintains genetic diversity (Brush et al. 1981; Rindos 1984). Growing inside and around the periphery of Andean potato fields are feral and wild potatoes, which interbreed with domesticates and produce volunteer seedlings that also grow in or near the fields (Brush et al. 1981; Quiros 2003). These are generally tolerated by farmers, and individuals with desirable properties are occasionally recruited into domesticate pools (Brush et al. 1981). Free-living populations of lower attine fungal domesticates are likewise present in the vicinity of attine nests and readily available for domestication (figs. 7.3, 7.5; Mueller et al. 1998; Vo and Mueller, unpublished data).

As noted by Rindos (1984), this diversity base allows potatoes to better respond to the evolution of pathogens and pests, including a variety of viruses, bacteria, fungi, nematodes, and insects. Brush et al. (1981) observed no organized strategies to control pests and pathogens in the cultivated fields of Andean subsistence potato farmers. In contrast, the most intensively cultivated potatoes in Europe and North America are descended from a few individuals purchased in a market in Panama after the Irish potato blight disaster of the 1840s (Quiros 2003). This genetically monotonous domesticate lineage is highly susceptible to disease, including the A1 strain of the late blight disease (*Phytophthora infestans,* the cause of the Irish potato famine) and the recently widespread A2 strain. The predominant disease-management strategy in intensive potato agricultural systems is a cycle of developing new chemical fungicides, leading to selection on the pathogen for resistance against the fungicides, leading to the development of another generation of fungicides, and so on. An alternative strategy, developed by the International Potato Center (CIP), relies on developing resistant strains of potatoes by drawing on the genetic diversity of the potatoes of the Andean highlands. When the CIP developed a potato variety incorporating a single, major gene with highly specific resistance against a single, dominant pathogen strain, they found that, initially, the potato was immune to the pathogen. The pathogen rapidly evolved to overcome that resistance, however, and became virulent. When the CIP developed a variety that incorporated multiple, minor resistance genes, the potato was not entirely immune, but the pathogen persisted under less drastic selection that did not generate the rapid spread of major resistance. This latter, preferred strategy, modeled on the traditional approach, achieves a mutual coexistence in which hosts and pathogens coexist at levels that are acceptable to farmers (Lang 2001).

This successful, long-term strategy of mutual pathogen-domesticate coexistence in traditional human potato agriculture parallels the pattern found in attine fungiculture. Attine fungi are clonally propagated from strains obtained both from free-living sources and from the nests of other fungus-growing ants. Free-living populations of Leucocoprineae are presumably genetically diverse. They may or may not be targeted by *Escovopsis* pathogens (this is an entirely unstudied phenomenon), but if they are, then they represent, like Andean feral and wild potatoes, a diverse source of resistant domesticate strains. Like humans, ants may select new domesticates based on various desirable traits; in any case, if *Escovopsis* is capable of infecting free-living fungi (both leucocoprineaceous and pterulaceous) and if *Escovopsis* is abundant, then the mere presence of a successfully growing mycelium or fruiting body (figs. 7.3, 7.5) within the foraging area of the nest is potential proof of its ability to resist locally dominant pathogens. The modified higher attine (figs. 7.7, 7.8) and yeast (figs. 7.5, 7.6) domesticates may represent the analogues of our more highly domesticated potatoes; the putatively inbred higher attine domesticates (Rehner et al. unpublished data) may even be analogous to the potato varieties cultivated in North America and Europe, which are descended from only a few individuals but which retain sexual competency and are routinely crossed to produce botanical seed and new varieties (C. Quiros, pers. comm.).

Andean subsistence potato agriculture appears to strike a balance between the selection of desirable domesticate strains on the one hand and constant, low-level outcrossing with feral and wild strains on the other. The decisive factor optimizing this balance appears to be pathogen pressure. A similar set of forces may be at work in the attine agricultural symbiosis. If so, then the insights gained from an examination of human potato agriculture may help explain the continuing existence of genetically linked free-living and domesticated populations of lower attine fungi (Mueller et al. 1998; Vo and Mueller, unpublished data) and the persistence of occasional sexual recombination in the apparently inbred and self-fertilizing higher attine fungi (Rehner et al., unpublished data).

Conclusion

There are clearly many differences between ant and human agriculture. Humans are a single species perhaps 100,000 years old. Attine ants represent a clade of more than 210 known extant species that is 50 million years old. Humans mostly domesticate plants and animals. Attine ants domesticate fungi. Humans are omnivorous and are facultative agriculturalists (i.e., they can choose to return to nonagricultural hunting and gathering). The attine ants, at least at the colony level, are obligate fungivores and obligate fungiculturalists, and they perish when deprived of their fungus gardens. Perhaps most important, modern humans act with conscious intent, and they can thus improve their agricultural systems quite rapidly through learning. Ant behavior is largely genetically determined and evolves through the much slower processes of mutation and selection. While the earliest stages of human domestication probably involved unconscious, incidental associations with plants and animals, these associations were later subjected to conscious planning and experimentation. Certainly, learned behaviors and the cultural transmission of information dominate the last 10,000 years of human agriculture and animal breeding. Just as important, human agriculture is a single facet of larger societal systems replete with social hierarchies, traditions, religions, and other factors that are not clearly comparable to anything in ants. Although these features of humans have proven to be an effective short-term evolutionary strategy, it remains to be seen whether they will remain effective over as long a time period as the one characterizing the success of attine ant agriculture.

In spite of these differences, many significant similarities remain between ant and human agriculture. These similarities strongly suggest that both systems represent convergent solutions to similar ecological problems, including the management of coevolving agricultural pests and pathogens. If so, then many seemingly commonsense notions about human agriculture deserve to be reexamined through a comparison with ant agriculture. Ultimately, both systems are biological and are thus subject to the rules of natural selection. By comparing the parallel agricultural systems of ants and humans, perhaps these rules may be brought more sharply into focus.

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