

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

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

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

Coral-fungus agriculture

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

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

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

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

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

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