

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

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

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

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

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

## **Generalized higher agriculture: *Trachymyrmex* and *Sericomyrmex***

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

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

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