

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

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

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

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

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

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

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

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

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

Leafcutter agriculture

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

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

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