

into the attine symbiosis (KOST & al. 2007, MUELLER & al. 2008, SEN & al. 2009). Black yeasts, so far only known from *Apterostigma* ants species, consume the actinomycete bacteria (LITTLE & CURRIE 2007, 2008).

Although the relationships between ants, cultivars, and *Escovopsis* are strongly correlated with phylogeny at the level of the five agricultural systems (Fig. 2) (MUELLER & al. 1998, CURRIE & al. 2003, VILLESSEN & al. 2004, CAFARO & CURRIE 2005, SCHULTZ & al. 2005, GERARDO & al. 2006a, TAERUM & al. 2007, SCHULTZ & BRADY 2008), exceptions are known to occur, e.g., rare instances of *Trachymyrmex* species cultivating lower-attine fungi (MUELLER & al. 1998; U. Mueller, pers. comm.). Within each of the five agricultural systems, the correlation between symbiotic associations and phylogeny generally breaks down altogether (MUELLER & al. 1998, GREEN & al. 2002, GERARDO & al. 2006b, MEHDIABADI & al. 2006, MIKHEYEV & al. 2006, 2007). This pattern is further complicated by the recent discovery that two cultivar clades may be much younger than their ant associates, suggesting that selective sweeps may have replaced earlier cultivar associates (A. Mikheyev, P. Abbott & U. Mueller, pers. comm.). As symbiont phylogenies improve, more violations of the simple coevolutionary pattern will undoubtedly be discovered.

### Natural-history traits of attine ants

In the following sections, we summarize the natural-history traits of ants belonging to each agricultural system (also see Tab. 1). This review is not meant to be exhaustive, nor do the described general patterns necessarily apply to every species in a particular agricultural group. Rather than an exhaustive survey, our goal is to review and collate attine natural-history information in an explicitly phylogenetic context in order to elucidate macroevolutionary patterns and sequences of diversification within and across the major clades of fungus-farming ants.

### Lower agriculture

Phylogenetic analyses indicate that lower agriculture was the system practiced by the first attine ant and the system from which all other forms of attine agriculture arose (SCHULTZ & BRADY 2008). It is perhaps unsurprising, therefore, that the lower-attine agriculturalists include species in the majority of attine ant genera and species, including *Myrmicocrypta*, *Mycocepurus*, some *Apterostigma* (the *A. auriculatum* group), *Kalathomyrmex*, *Paramycetophylax*, *Mycetophylax*, *Mycetarotes*, some *Cyphomyrmex* (the *C. strigatus* and *C. wheeleri* groups), *Mycetosoritis*, and *Mycetagroicus*. Although any given lower attine species is an amalgam of primitive and derived traits, at least some lower-attine species likely retain some traits little changed from those present in the ancestral attine.

**Geographic distribution:** Knowledge of the distributions of most lower-attine species is deplorably poor but, considered as a group, they have a broad geographic distribution, ranging from the US in the north (e.g., *Cyphomyrmex wheeleri* in central California) to Argentina in the south (e.g., *Mycetosoritis asper* in Chubut) (KEMPF 1972, WEBER 1972, BRANDÃO 1991, MAYHÉ-NUNES & JAFFÉ 1998, FERNANDEZ & SENDOYA 2004).

**Colony size and social structure:** The colonies of most lower-attine-ant species tend to be short-lived (a few years) and have small worker-population sizes (tens to hundreds

of workers), although exceptions occur in which colonies may contain more than a thousand workers (e.g., some *Myrmicocrypta*, *Mycocepurus*, and *Cyphomyrmex* species) (WEBER 1972, PRICE & al. 2003, RABELING & al. 2007b, HIMLER & al. 2009). All lower-attine colonies have a monomorphic worker caste and usually one singly-mated queen (HÖLLDOBLER & WILSON 1990, VILLESSEN & al. 2002, FERNÁNDEZ-MARÍN & al. 2004). *Mycocepurus goeldii* may be an exception, however. Based on observation of a mating swarm, KERR (1961) reports that *M. goeldii* queens are inseminated by multiple males.

**Mating and nest-founding behavior:** Mating behavior for most lower attines is poorly known. Some species, particularly wet-forest-dwelling species, have aseasonal and / or unsynchronized mating flights in which reproductives may be produced year-round or over a long period during the rainy season and in which males and females locate one another singly. Other species are seasonal, producing alates that usually fly at the beginning of the rainy season, some in synchronized swarms, documented (KERR 1961, KEMPF 1963) in *Mycocepurus goeldii* and (U. Mueller, pers. comm.) *Cyphomyrmex wheeleri*. *Mycocepurus smithii* is unique within the Attini in that it appears to be entirely parthenogenetic across its range; males of this species are unknown (FERNÁNDEZ-MARÍN & al. 2005, HIMLER & al. 2009, RABELING & al. 2009).

As might be expected of a large, paraphyletic group of multiple, major lineages, including those from which all other attines have arisen, the lower-attine agriculturalists are heterogeneous and difficult to characterize, although the majority retain the putatively primitive states of most nest-founding behaviors. Nest-founding for members of this agricultural group is semi-claustral and mostly haplometrotic (SOLOMON & al. 2004). Multiple queens are occasionally encountered in nests of lower attines, e.g., *Mycetophylax simplex* in southern Brazil (DIEHL-FLEIG & DIEHL 2007) and *Cyphomyrmex faunulus* in the Amazonian Basin (T.R. Schultz, unpubl.), and may be more common than is currently known. Multiple queens occur at fairly high frequencies in *Mycocepurus* species (FERNÁNDEZ-MARÍN & al. 2005, RABELING & al. 2007b, HIMLER & al. 2009; U. Mueller, pers. comm.).

Observations of multiple dealate queens in attine nests do not necessarily indicate pleiometrosis or polygyny, and must be cautiously interpreted for a number of reasons. First, some reports of multiple queens may be erroneous because, in the case of attine species that nest in aggregations (e.g., *Mycocepurus* species, *Kalathomyrmex emeryi*, *Mycetophylax morschi*), the investigator may have accidentally excavated chambers from more than one colony. Second, in most Attini unmated daughter queens sometimes shed their wings, remain in the nest, and behave like workers (e.g., WEBER 1941). When a pair of dealate *Mycocepurus goeldii* queens collected from the same nest chamber were dissected, for example, only one was found to be inseminated and to have developed ovaries (C. Rabeling, pers. comm.). Finally, even when multiple inseminated queens are discovered in the same nest, it remains unclear whether they co-founded the nest (pleiometrosis) or whether one queen joined the other long after nest establishment.

When founding their nests, queens of at least some species of *Myrmicocrypta*, *Mycocepurus*, and *Apterostigma*, and of *Cyphomyrmex longiscapus*, use their detached fore-