



Fig. 2: A summary of current knowledge about the coevolutionary histories of three attine-agricultural symbionts: the ants, their fungal cultivars, and the fungal parasite *Escovopsis*. For each symbiont lineage, the ancestor arises within lower agriculture, in which a paraphyletic grade of ants cultivates a corresponding paraphyletic grade of cultivars that are infected by a corresponding paraphyletic grade of parasites. Broad phylogenetic groups of symbionts are associated with each of the agricultural systems, indicating ancient coevolution, but patterns of origin of these groups differ across symbionts. Parasites of yeast agriculture are unknown. Summarized from MUELLER & al. (1998), CURRIE & al. (2003), VILLENSEN & al. (2004), SCHULTZ & al. (2005), GERARDO & al. (2006b), TAERUM & al. (2007), and SCHULTZ & BRADY (2008).

and (3) geographic dispersal by foundress queens (WEBER 1972, MARTIN 1987, HÖLLDOBLER & WILSON 1990, CURRIE & al. 1999, MUELLER 2002, MUELLER & al. 2005, SCHULTZ & al. 2005). These hypothetical benefits, while plausible, have yet to be demonstrated and quantified.

Attine fungal cultivars are infected by ascomycete fungi in the genus *Escovopsis*, which so far are unknown from any habitat other than attine fungus gardens (CURRIE & al. 1999, CURRIE 2001a, b, CURRIE & al. 2003). Current knowledge indicates that the *Escovopsis* phylogeny conforms to the five agricultural systems, i.e., phylogenetically cohesive groups of *Escovopsis* (clades and grades) infect corresponding phylogenetically cohesive groups of attine culti-

vars (Fig. 2). The ancestral condition in *Escovopsis*, not surprisingly, is to infect lower-attine cultivars. Attine coral fungi are infected by a paraphyletic grade of *Escovopsis* that arose from the lower-attine *Escovopsis*. This grade of coral-fungus *Escovopsis*, surprisingly, gave rise to the clade that infects the higher-attine cultivars (Fig. 2). *Escovopsis* has not been detected or isolated from attine yeast cultivars. A fourth symbiont, a filamentous bacterium (Actinomycetes: *Pseudonocardia*), grows on the integuments of attine ants and produces antibiotics that may help to control the *Escovopsis* pathogen. The attine-actinomycete phylogeny appears to be far less correlated with the five agricultural groups, suggesting the possibility of frequent recruitment