

Natural history and phylogeny of the fungus-farming ants (Hymenoptera: Formicidae: Myrmicinae: Attini)

Natasha J. MEHDIABADI & Ted R. SCHULTZ



Abstract

Ants of the tribe Attini comprise a monophyletic group of approximately 230 described and many more undescribed species that obligately depend on the cultivation of fungus for food. In return, the ants nourish, protect, and disperse their fungal cultivars. Although all members of this tribe cultivate fungi, attine ants are surprisingly heterogeneous with regard to symbiont associations and agricultural system, colony size and social structure, nesting behavior, and mating system. This variation is a key reason that the Attini have become a model system for understanding the evolution of complex symbioses. Here, we review the natural-history traits of fungus-growing ants in the context of a recently published phylogeny, collating patterns of evolution and symbiotic coadaptation in a variety of colony and fungus-gardening traits in a number of major lineages. We discuss the implications of these patterns and suggest future research directions.

Key words: Hymenoptera, Formicidae, fungus-growing ants, leafcutter ants, colony life, natural history, evolution, mating, agriculture, review.

Myrmecol. News 13: 37-55

ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 12 June 2009; revision received 24 September 2009; accepted 28 September 2009

*Dr. Natasha J. Mehdiabadi** (contact author) & *Dr. Ted R. Schultz** (contact author), Department of Entomology and Laboratories of Analytical Biology, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, NHB, CE518, MRC 188, Washington, DC 20013-7012, USA. E-mail: mehdiabadi@si.edu; schultz@si.edu

* Both authors contributed equally to the work.

The origin and evolution of the Attini

Attine ants and their fungal cultivars represent a classic example of mutualism. The ants obligately depend on the cultivation of fungus for food and in return provide the fungus with nourishment, protection from pathogens and competitors, and dispersal (WEBER 1972, MARTIN 1987, HÖLLDOBLER & WILSON 1990, CURRIE & al. 1999, MUELLER 2002, MUELLER & al. 2005, SCHULTZ & al. 2005). Many theories have been proposed for how ant fungiculture may have arisen from earlier, facultative associations between the ancestors of the two mutualists (FOREL 1891, VON IHERING 1894, 1898, EMERY 1899, FOREL 1902, WHEELER 1907, SANTSCHI 1910, FARQUHARSON 1914, BAILEY 1920, MAIDL 1934, WEBER 1958, 1972, GARLING 1979, MOFFETT 1986, MUELLER & al. 2001), including a scenario in which a fungal proto-domesticated attracted ants with food rewards and in return had its spores and / or mycelia dispersed by the ants (BAILEY 1920, MUELLER & al. 2001, SCHULTZ & al. 2005). Whatever its origin, the obligate association between attine ants and their cultivated fungi arose approximately 50 million years ago in the forests of the Neotropics, producing over 230 described and many more undescribed extant attine ant species, all of which occur exclusively in the New World and each of which, as far as is known, practices one of five distinct agricultural systems (SCHULTZ & MEIER 1995, MAYHÉ-NUNES & JAFFÉ 1998, BRANDÃO & MAYHÉ-NUNES 2001, MUELLER & al. 2001, SCHULTZ & BRADY 2008) (Fig. 1).

The five attine agricultural systems

Each of the five known attine agricultural systems is characterized by strongly correlated patterns across ant, fungal cultivar, and *Escovopsis* fungal pathogen phylogenies (Fig. 2), and each represents a major evolutionary transition in ant agriculture: (1) **Lower agriculture**, the ancestral condition in the Attini, is practiced by 80 described ant species in 10 genera. (2) **Coral-fungus agriculture** is practiced by 34 described species in the "*Apterostigma pilosum* group," a derived clade within the attine genus *Apterostigma*. Ants practicing this form of agriculture are the only group to utilize fungal cultivars that do not belong to the tribe Leucocoprineae. (3) **Yeast agriculture** is practiced by 18 described species in the "*Cyphomyrmex rimosus* group," a subset of species in the attine genus *Cyphomyrmex*. Members of this group grow cultivars as nodules of yeast-like cells in a unicellular phase instead of the multicellular mycelial phase typical for all other attines. (4) **Generalized higher agriculture** is practiced by 63 described species in the two genera of non-leafcutting "higher attine" ants, *Sericomyrmex* and *Trachymyrmex*. (5) **Leafcutter agriculture**, a derived form of higher agriculture, is practiced by 40 described species of ecologically dominant ants in the two genera *Atta* and *Acromyrmex* (SCHULTZ & al. 2005, SCHULTZ & BRADY 2008).

Natural history of attine ants

Despite the diversity of their agricultural systems, all attine ant species share some general habits associated with fun-