## Research article

## Cryptic speciation in the fungus-growing ants *Cyphomyrmex longiscapus* Weber and *Cyphomyrmex muelleri* Schultz and Solomon, new species (Formicidae, Attini)

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Received 17 December 2001; revised 28 May 2002; accepted 30 May 2002.

**Summary.** Nesting in abundance on stream embankments in the wet forests of Panama, the fungus-growing ant Cyphomyrmex longiscapus sensu lato has become a model organism for the study of behavior, ecology, mating frequency, cultivar specificity, pathogenesis, and social parasitism in the attine agricultural symbiosis. Allozyme markers, morphology, and other evidence indicate that C. longiscapus s.l. is in fact a complex of two species, one of which is new to science and described here as Cyphomyrmex muelleri Schultz and Solomon, new species. Although both species occur sympatrically in the same microhabitats and are ecologically, behaviorally, and morphologically quite similar, they consistently cultivate two distantly related fungal symbionts. Thus, each of the two sibling ant species is specialized on a distinct cultivar species, contradicting the conclusions of a previous study. Information is provided for reliably separating the two ant species; morphometrics, ecology, behavior, biogeography, and natural history are summarized. Possible evolutionary mechanisms underlying cryptic speciation in C. longiscapus s.l. are discussed.

Key words: Cyphomyrmex, Attini, fungus-growing ants, cryptic speciation.

## Introduction

The ant genus *Cyphomyrmex* is of special interest for understanding the evolution of agriculture in fungus-growing ants (subfamily Myrmicinae, tribe Attini) for two primary reasons:

(1) Cyphomyrmex occupies an intermediate phylogenetic position between the "lower" and "higher" (including the leafcutting) attine ants, and is possibly the sister group of the higher attine ants (Schultz and Meier, 1995; Schultz, 1998; Schultz, 2000; TRS, unpubl.); and (2) within Cyphomyrmex there are two distinct forms of fungus cultivation, typical mycelium cultivation and "yeast" cultivation (Wheeler, 1907; Weber, 1972; Mueller et al., 2001); in the latter, the cultivar is maintained in a single-celled growth phase and the garden consists of modular, easily transportable nodules. Based on morphological characters, the genus is divided into two informal subgeneric groups, the "strigatus" and "rimosus" groups (Kempf, 1966). Preliminary data indicate that the strigatus group contains only mycelium cultivators and is probably plesiomorphic and paraphyletic with respect to the rimosus group. In contrast, the rimosus group contains both mycelium and yeast cultivators, is morphologically and behaviorally derived, and is likely monophyletic (Kempf, 1966; Schultz and Meier, 1995; Meier and Schultz, 1996; TRS, unpubl.).

C. longiscapus is one of three species (along with C. costatus and C. wheeleri) that violate Kempf's (1966) otherwise tidy bipartite division of Cyphomyrmex because these species combine morphological features of both subdivisions. Although the fungal cultivars of most Cyphomyrmex species are unknown, Kempf (1966) points out an intriguing preliminary pattern: The three species that combine the features of both groups are also the only species in the rimosus group that are known to cultivate mycelium gardens, whereas, so far as is known, all other rimosus group species cultivate yeast gardens. This pattern suggests that C. longiscapus and related