



A review of the North American species of the fungus-gardening ant genus *Trachymyrmex* (Hymenoptera: Formicidae)

CHRISTIAN RABELING¹, STEFAN P. COVER², ROBERT A. JOHNSON³ AND ULRICH G. MUELLER¹

¹ Section of Integrative Biology, The University of Texas, 1 University Station C0930, Austin, TX 78712-0253;
email: rabeling@mail.utexas.edu, umueller@mail.utexas.edu

² Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138-2902;
email: cover@oeb.harvard.edu

³ School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501; email: atraj@imap1.asu.edu

TABLE OF CONTENTS

ABSTRACT	1
INTRODUCTION	2
MATERIAL AND METHODS	2
Specimens examined	2
Morphometric measurements	3
Molecular analyses and phylogenetic inference	3
RESULTS	4
Key to workers & queens of <i>Trachymyrmex</i> species occurring in the United States	4
Key to the males of <i>Trachymyrmex</i> species occurring in the United States	6
SPECIES ACCOUNTS	6
<i>T. arizonensis</i> (Wheeler)	6
<i>T. carinatus</i> Mackay & Mackay	8
<i>T. desertorum</i> (Wheeler)	10
<i>T. jamaicensis</i> (André)	11
<i>T. nogalensis</i> Byars	13
<i>T. pomonae</i> Rabeling & Cover, NEW SPECIES	14
<i>T. septentrionalis</i> (McCook)	16
<i>T. smithi</i> Buren	20
<i>T. turrifex</i> (Wheeler)	22
GENERAL DISCUSSION	25
ACKNOWLEDGEMENTS	27
REFERENCES	27
FIGURES	30
Species photographs	30
Molecular phylogeny	50
Distribution maps	51

ABSTRACT

We revise and key *Trachymyrmex* ants occurring in North America north of Mexico. We recognize nine species, including one new species from southern Arizona: *T. arizonensis* (Wheeler), *T. carinatus* Mackay & Mackay, *T. desertorum* (Wheeler), *T. jamaicensis* (André), *T. nogalensis* Byars, *T. pomonae* Rabeling & Cover **sp. nov.**, *T. septentrionalis* (McCook), *T. smithi* Buren, and *T. turrifex* (Wheeler). Two infraspecific taxa are synonymized: *T. smithi neomexicanus* Cole **syn. nov.** (= *T. smithi*) and *T. turrifex caroli* Wheeler **syn. nov.** (= *T. turrifex*). We briefly characterize the previously undescribed queens of *T. desertorum* and *T. nogalensis*, and the males of *T. desertorum* and *T. turrifex*. We include keys for the identification of workers, queens and males, along with distribution maps for all species. A phylogenetic analysis of DNA sequence information for parts of the mitochondrial gene Cytochrome Oxidase I and the first intron of the F1

copy of the nuclear protein-coding gene Elongation Factor 1- α , is used to characterize the intra- versus inter-specific genetic variation of several populations per species. The molecular phylogenetic analysis supports our taxonomic conclusions concerning the North American *Trachymyrmex* species.

Key words: Attini, Formicidae, phylogeny and species boundaries, taxonomy, *Trachymyrmex*, United States

INTRODUCTION

Fungus-gardening ants (tribe Attini) and the leucocoprinaceous fungi they cultivate are a classic example of a mutualism. Attine ants cultivate a monoculture of fungal clones as their major food source, while the fungus receives from the ants nourishment, favorable environmental conditions for growth, and protection from pathogens and fungivores (Mueller *et al.* 2005). All attine ants shelter their gardens, generally by excavating garden chambers in the ground, under logs, or rocks. All attine ants also appear to transmit their fungi vertically from parent to offspring nests. However, different ant lineages cultivate distinct cultivar lineages. For example, the derived higher attines (genera *Trachymyrmex*, *Sericomyrmex*, *Acromyrmex*, and *Atta*) cultivate fungi from a specific cultivar clade in the family Lepiotaceae (Agaricales, Basidiomycota). This clade of higher-attine fungi arose from within a diverse group of fungi that includes the fungi cultivated by the basal attine ant genera, as well as free-living fungi closely related to these ant-symbiotic fungi (Mueller *et al.* 1998; Mueller *et al.* 2005). Within the group of higher Attini, fungi cultivated by leafcutter ants appear to belong to the same fungal species (Mikheyev *et al.* 2006), whereas *Trachymyrmex* and *Sericomyrmex* ants appear to cultivate multiple species of fungi (S.A. Rehner, unpublished; Mikheyev and Mueller unpublished). The evolutionary transition to symbiont specificity in leafcutter ants was apparently accompanied by a simultaneous switch in foraging behavior from debris collecting to the cutting of fresh foliage. Recent molecular phylogenetic analyses indicate that most *Trachymyrmex* species in the US fall within the sister group to the true leafcutter ants, *Atta* and *Acromyrmex* (Brady *et al.* 2006; Schultz *et al.* in prep.). Thus ecological, behavioral, and phylogenetic studies of North American *Trachymyrmex* may provide insights into the evolutionary transition from non-leafcutter to leafcutter ants.

Trachymyrmex is the most species-rich and abundant attine genus in the United States, reaching its highest diversity in the arid Southwest, particularly in Arizona. *Trachymyrmex* is a primarily tropical genus; most species are found in Central and South America. Only a handful of species have radiated north into the temperate zone and these are biologically very interesting. Some North American species are notably cold-tolerant. For example, *T. septentrionalis* reaches the northern limit of its geographic range on Long Island, NY, and at this latitude, has a short active season of only four to five months per year (Beshers & Traniello 1994). During winter, the ants and the fungus garden enter extended dormancy, a phenomenon unique among the Attini (Weber 1956).

The study of North American *Trachymyrmex* began with the description of *T. septentrionalis* by McCook (1881). The first comprehensive account of North American *Trachymyrmex* was in Wheeler's (1907) landmark monograph of the Attini of North America. Wheeler's monograph is still the foundation of our current knowledge because of its detailed ecological and distributional information. Creighton's (1950) "Ants of North America" included the first modern taxonomic treatment of the genus. Since Creighton's revision, four additional taxa have been described, an exotic species, *T. jamaicensis*, reported from Florida, and four infraspecific taxa synonymized. Many new collections, and much new information discovered during the past decade have made a fresh taxonomic treatment of the North American *Trachymyrmex* desirable. Detailed accounts of the biology and natural history of the *Trachymyrmex* species and other fungus-growing ant species in the United States will be published in a forthcoming book (Mueller & Schultz, in preparation).