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

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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

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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).

MATERIAL AND METHODS

Specimens examined

Specimens from the insect collections listed below were examined for this study:

AMNH	American Museum of Natural History, New York, NY, U.S.A.
CASC	California Academy of Sciences Collection, San Francisco, CA, U.S.A.
CRC	C. Rabeling Collection, Austin, TX, U.S.A.
LACM	Los Angeles County Museum of Natural History, Los Angeles, CA, U.S.A.
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A.
RAJC	R.A. Johnson Collection, Tempe, AZ, U.S.A.
UCDC	Bohart Museum of Entomology, University of California at Davis, CA, U.S.A.
UGMC	U.G. Mueller Collection, Austin, TX, U.S.A.
USNM	National Museum of Natural History, Washington, DC, U.S.A.
WPMC	W.P. Mackay Collection, El Paso, TX, U.S.A.

Collection localities of all examined specimens are listed under "ADDITIONAL MATERIAL EXAMINED" in the species account section. The examined material plus additional distribution records from the literature were used to create the distribution maps. A more detailed list of all studied US *Trachymyrmex* specimens, including locality and habitat information, collection date and GPS coordinates, will be presented in a web-based database (http://www.antweb.org/).

Morphometric measurements

Specimens were examined and measured using a Wild M-5A microscope fitted with a stage micrometer. Measurement conventions and indices follow Bolton (1987), with the exception of AL (alitrunk length), which we record as ML (mesosoma length).

HL	Head Length	Length of the head in full face view, excluding mandibles, measured in a straight line from the midpoint of the anterior clypeal margin to the midpoint of the posterior margin of the head. In species where the preoccipital margin or the clypeal margin (or both) is concave, the measurement is taken from the midpoint of a transverse line spanning the anteriormost or posteriormost projecting points respectively.
HW	Head Width	Maximum width of head, not including the eye
CI	Cephalic Index	HW*100/HL
SL	Scape Length	Maximum straight line length of the antennal scape excluding the basal constriction or neck close to the condylar bulb
SI	Scape Index	SL*100/HW
ML	Mesosoma Length	Diagonal length of the alitrunk in profile from the point at which the pronotum meets the cervical shield to the posterior base of the metapleuron.

Molecular analyses and phylogenetic inference

DNA was extracted from workers that had been preserved in 95% ethanol. Each individual was removed from the ethanol, dried at room temperature for approximately 30 min, then frozen in liquid nitrogen and ground with a pestle in a 1.5ml Eppendorf tube. DNA was extracted using the Qiagen DNA Micro Kit following the manufacturer's instructions for isolation of genomic DNA from tissues, then suspended in 30–40μl of H_2O.

Parts of the mitochondrial gene cytochrome oxidase 1 (COI) and intron 1 of the F1 copy of the nuclear gene elongation factor 1-α (EF1-α) were amplified using, respectively, the primer pairs Ben & Jerry (Simon *et al*. 1994) and U52.1 & L53 (Ted Schultz, unpublished data). A 10μl PCR reaction contained 0.4–1μl of DNA extract, 1 unit reaction buffer, 1mM dNTPs, 0.5mM primers, and 2.5mM $MgCl_2$ with 0.1 units of Promega AmpliTaq Gold DNA polymerase. COI fragments were amplified under the following conditions: initial denaturation at 95° C for 3min; 35 cycles of denaturation at 95° C for 10sec, annealing at 45° C for 20sec, and 1min ramping to extension temperature at 68° C for 10sec. EF1-α fragments were amplified under: initial denaturation at 94° C for 2min, 35 cycles of denaturation at 94° C for 30sec, annealing at 51° C for 45sec, extension at 72° C for 90sec, and a final extension of 72° C for 10min. Three microliters of the PCR reaction were run on a 1.5% agarose gel and visualized with ethidium bromide. The remaining 7μl were cleaned with a Bioneer PCR purification kit and 1μl of the rediluted product cycle-sequenced with the ABI BigDye Terminator Kit (version 3.1). Forward and reverse sequences were sequenced on an ABI PRISM 3100 automated sequencer.

DNA sequences were inspected manually using the DNA sequence editor SeqMan (DNAStar). Sequences were aligned in MacClade version 4.06 (Maddison & Maddison 2003). Phylogenies were generated using maximum likelihood as an optimality criterion under the General Time Reversible (GTR) model of nucleotide substitution with Garli version 0.951 (Zwickl 2006; freely downloadable: http://www.zo.utexas.edu/faculty/antisense/garli/Garli.html). Initially, we ran six analyses, always resulting in very similar topologies. Finally, a 50% majority rule consensus tree was computed from 560 bootstrap repetitions. DNA sequences are deposited at GenBank (http://www.ncbi.nlm.nih.gov/) as accessions EF539726-EF539829.

RESULTS

Key to workers & queens of *Trachymyrmex* species occuring in the United States

Trachymyrmex workers within a colony often vary slightly in size, thus some of the characters used in this key can vary within colonies. For best results, we recommend checking the characters on several specimens from each collection or nest series when using this key. To increase the usability, we highlight the morphological characters used in this key by pointing arrows to the respective characters in one representative figure per couplet; the highlighted character can be seen in figures marked with bold font, underlining, in square brackets (e.g.: in couplet (1) see figure [**8B**] for shallow antennal scrobe described by preocular and frontal carinae).
The key works for queens also if one substitutes the word "pronotal" for "promesonotal" when referring to mesosomal teeth or spines (except references to "median anterior pronotal tubercles," which are not present in queens).

1 In full-face view, preocular and frontal carinae subparallel, converging gradually towards the posterior corners of the head, forming a long, shallow antennal scrobe (Figures 8 [**8B**]& 19) **2**
- In full-face view, preocular and frontal carinae NOT subparallel, frontal carinae often extending towards

the posterior corners of the head, but preocular carinae always curving mesially towards the frontal carinae, rarely actually touching them (Figures 1, 3, 5 [**5B**], 6, 10, 11, 12, 13, 15, 17) **3**

2 In full-face view, antennal scapes reaching or just slightly surpassing the posterior corners of head. In side view, center of clypeus with several long, conspicuous, coarse, erect hairs, nearly as long as those in the row of long hairs along the anterior clypeal margin that project over the dorsal surface of the mandibles (Figure 19) ..... ***turrifex***

- In full-face view, antennal scape surpassing posterior corner of head by the maximum diameter of the scape or more. In side view, clypeus usually with only a few short, stiff erect hairs present, when present these are much shorter than the row of long hairs along the anterior clypeal margin (Figure 8) ..... ***jamaicensis***

3 Frontal carinae relatively short, not extending towards the posterior corner of the head. Preocular carinae curving strongly to meet the frontal carinae, forming short, distinctive "scrobes", that end slightly behind the level of the eye (Figure [**10B**]). Antennal scape long (SI 117–152), narrowing abruptly as it approaches the antennal insertion, a small but conspicuous lobe is present just distal to the narrowing (Figure [**10C**]) (Figures 10 & 11) ..... ***nogalensis***

- Frontal carinae long, extending well past the eye towards the posterior corners of the head. In side view, preocular carinae not joining the frontal carinae (rarely touching the carinae in *T. carinatus*). Antennal scapes shorter (SI 113). Scape gradually narrowing as it approaches the antennal insertion, lobe as described above absent (Figures 1, 3, 5, 6, 12, 13, 15 & 17) **4**

4 In full-face view, frontal lobes prominent, shaped uniquely as in Figure [**1B**], the posterior margin of the lobe forming a broad notch with the posterior portion of the frontal carinae. Antennal scapes long (worker SI 103–113; queen SI 96–105). First gastric tergite strongly tuberculate (Figure 1) ..... ***arizonensis***

- In full-face view, frontal lobes simple, rounded or triangular (Figure [**3B**]). Antennal scapes shorter (worker SI 105; queen SI 96). Gastric tubercles variously developed, sometimes small or nearly absent (Figures 3, 5, 6, 12, 13, 15 & 17)..... **5**

5 Combining the following: in larger workers head clearly broader than long, slightly broader than long to square in smaller workers (CI 100–111); posterior border notably emarginate, in full-face view head appearing cordate in larger workers (Figure [**17B**]). Propodeal spines longer than the distance separating their bases. Color black to blackish red (Figure 17) ..... ***smithi***

- Head shape variable, usually more or less square, sometimes broader than long. Posterior border weakly to moderately emarginate, but head *never* appearing cordate in full-face view—even in larger workers (Figure [**3B**]). Propodeal spines or teeth variable in length, often as long as or shorter than the distance separating their bases. Color never black or blackish (Figures 3, 5, 6, 12, 13 & 15)..... **6**

6 Combining the following: median anterior pronotal tubercles well-developed, in anterior view nearly always upright and toothlike, the apices often with 2–3 small "peaks." Preocular carina never closely approaching the frontal carina in full-face view. First gastric tergite tuberculate (Figure 15) ..... ***septentrionalis***

- Median anterior tubercles poorly developed or absent altogether, not upright or toothlike in anterior view, when present taking the form of small denticles or low, broadly pyramidal mounds. Preocular carinae variable, sometimes closely approaching the frontal carinae in full face view. Tuberculi on first gastric tergite sometimes absent or minute (Figures 3, 5, 6, 12 & 13)..... **7**

7 Preocular carinae traversing nearly the entire antennal scrobe as it curves towards the frontal carina, closely approaching or sometimes even appearing to touch the frontal carinae in full-face view. Frontal lobes usually more or less symmetric (evenly rounded). First gastric tergite conspicuously tuberculate (Figure 3) ..... ***carinatus***

- Preocular carinae shorter, in full-face view never closely approaching or appearing to touch the frontal carinae in full-face view. Frontal lobes variable, sometimes asymmetric with the anterior margin longer

than the posterior margin. Tubercules miniscule or absent on first gastric tergite (Figures 5, 6, 12 & 13) .8

8 In full-face view, frontal lobes rounded (rarely subtriangular), more or less symmetrical, anterior and posterior sides equal in length or anterior side slightly longer than posterior (Figures 5 & 6)..... ***desertorum***

- In full-face view, frontal lobes subtriangular (rarely rounded), strongly asymmetric, the anterior side of the lobe often 2x as long as the posterior side or more (Figures 12 & 13)..... ***pomonae***

Key to the males of *Trachymyrmex* species occuring in the United States

Trachymyrmex nogalensis is not included in this key because the male of this species is unknown.

1 Ventrolateral pronotal tooth absent and dorsolateral pronotal tooth well-developed (Figures 9 & 20) **2**

- Ventrolateral pronotal tooth often clearly present, if indistinct or absent then the dorsolateral pronotal tooth is also indistinct or absent (Figures 2, 4, 7, 14, 16 & 18)..... **3**

2 In dorsal view, dorsolateral pronotal tooth short, sharp, and triangular. Setae on first gastric tergite sparse, decumbent or appressed (Figure 20)..... ***turrifex***

- In dorsal view, dorsolateral pronotal tooth a needlelike spine. Setae on first gastric tergite short, moderately abundant, more or less recurved, and mostly erect (Figure 9)..... ***jamaicensis***

3 In dorsal view, dorsolateral pronotal tooth distinct, sometimes even forming a short spine (Figures 2, 7 & 16)..... **4**

- In dorsal view, dorsolateral pronotal tooth very small or entirely absent, sometimes reduced to an angulate ridge, but not present as a tooth or spine (Figures 4, 14 & 18) **6**

4 In lateral view, irregular rugulae present on all surfaces of pronotum; interrugal spaces granulate. Antennal scrobe granulate, with at least several transverse rugulae distributed over the anterior ¾ (Figure 7)..... ..... ***desertorum***

- Pronotum generally lacking irregular rugulae, sometimes a few inconspicuous rugulae present near dorsolateral pronotal teeth. Antennal scrobe granulate, with 1–4 transverse rugulae near anterior margin or rugulae absent altogether **5**

5 Surface of first gastric tergite bumpy due to the presence of numerous small tubercles; each tubercle bears a decumbent, recurved setae. Dorsoventral pronotal teeth large, narrowly triangular in dorsal view (Figure 2)..... ***arizonensis***

- Surface of first gastric tergite finely granulate, lacking small tubercles, short, suberect somewhat recurved setae moderately abundant. Dorsoventral pronotal teeth short, broadly triangular in dorsal view (Figure 16)..... ***septentrionalis***

6 Small species (HL 0.6–0.75; HW 0.6–0.75). In full-face view, preocular carinae weakening rapidly as it passes the posterior border of the eye and turns towards the midline, past the eye the carina not more prominent than adjacent rugulose sculpture on the posterior half of the head, rear border of scrobe sometimes indistinct (Figure 14)..... ***pomonae***

- Larger species (HL 0.72–0.84; HW 0.75–0.87). In full face view, preocular carina remaining a distinctive vertical ridge as it passes the eye and turns towards the midline, past the eye the carina clearly more prominent than adjacent rugulose sculpture on the posterior half of the head, and remaining fully developed until reaching the midpoint of the posterior border of the scrobe (Figures 4 & 18)..... **6**

7 In dorsal view, mesoscutum slightly broader than long, sculpture coarsely and irregularly rugulose and granulate, sometimes a faint longitudinal pattern is discernable (Figure 4)..... ***carinatus***

- In dorsal view, mesoscutum about as long as broad, sculpture predominantly longitudinally rugulose, interrugal spaces finely granulose (Figure 18) ..... ***smithi***

SPECIES ACCOUNTS

T. arizonensis (Wheeler)

Atta (Trachymyrmex) arizonensis Wheeler, 1907: 710. Syntype queen and males, Palmerlee, Cochise County, Arizona, U.S.A. (MCZC, USNM) [examined]
Atta (Trachymyrmex) arizonensis Wheeler; Wheeler 1911: 93 [description of worker]
Trachymyrmex arizonensis (Wheeler); Gallardo 1916: 242 [Combination in *Trachymyrmex*]

Diagnosis

Worker: HL 0.88–1.20, HW 0.88–1.28, CI 96–107, SL 0.92–1.4, SI 103–113, ML 1.28–1.8. Large species (HL 0.88–1.20, HW 0.88–1.28) with relatively long legs and antennae (SI 103–113). Head as long as broad or slightly longer than broad (CI 96–107), gradually tapering anteriorly, widest at midpoint between eye and posterior margin. Frontal lobes well developed and strongly asymmetric, with a long, curving anterior margin that meets the much shorter posterior margin to form an acute angle. A broad notch is formed by the frontal lobe and the posterior continuation of the frontal carinae (Figure 1B). Preocular carinae sharply curving mesially and nearly always distinctly separated from the frontal carinae. Anterolateral promesonotal teeth often sharp, spinelike, directed laterally, not upwards. Propodeal teeth thin, spinelike, strongly divergent in dorsal view, shorter than the distance between their bases. Head, mesosoma and petiole moderately tuberculate, postpetiole and first gastric tergite strongly tuberulate. Color brownish yellow to medium reddish brown.

Queen: HL 1.19–1.38, HW 1.19–1.38, CI 100, SL 1.25–1.31, SI 96–105, ML 1.88–2.13. As in worker diagnosis, but mesosoma with caste-specific morphology related to wing-bearing and head with minute ocelli. Dorsolateral pronotal teeth large, robust, and tuberculate; ventrolateral pronotal teeth large, blunt, and lacking tuberculi.

Male: HL 0.98, HW 0.88, CI 93, SL 1.06, SI 121, ML 2.0–2.06. Legs and antennal scapes relatively long. Dorsolateral and ventrolateral pronotal teeth well-developed. Mesoscutum longer than broad, sculpture variable but longitudinal rugulae always present. First gastric tergite with "bumpy" surface. 1–3 toothlike tubercles present on each posterior corner of head and frontal lobes bluntly triangular, more or less symmetrical.

Discussion

Trachymyrmex arizonensis is often sympatric in central and southern Arizona with the slightly smaller *T. carinatus* and rarely sympatric with the larger *T. nogalensis*. It is easily distinguished from all other North American *Trachymyrmex* by the unusual shape of the frontal lobes in both workers and queens (Figure 1B).

Etymology

Since Wheeler (1907, 1911) collected both the type series and subsequently the workers of *T. arizonensis* in southeast Arizona, the collection locality clearly motivated the species name.

Biology

Trachymyrmex arizonensis is typically found at mid elevations (1000–2000 m) in mountainous areas within the Chihuahuan and Sonoran Deserts in central and southern Arizona, western New Mexico, and the Mexican states of Chihuahua and Sonora (Figure 22A). The species has also been reported from western Texas. Weber identified a single specimen of *T. arizonensis* from the Chisos Mountains (Van Pelt 1983). It is also reported from west Texas by O'Keefe *et al*. (2000), but as we have not been able to verify these records, the presence of *T. arizonensis* in western Texas remains uncertain. *Trachymyrmex arizonensis* occurs in a variety of habitats including arid Ocotillo- and *Acacia*-dominated scrub in mountain foothills, oak-juniper-pine woodlands, and relatively mesic mid elevation creek valley forests. Nests are found under rocks or logs or in open soil, frequently in areas that are partly or lightly shaded. A sloppy crater of excavated soil and a diagnostic yellowish-gray external refuse midden is often present near the nest entrance. *Trachymyrmex ari-*

zonensis and *T. smithi* are the only US species of *Trachymyrmex* that routinely have conspicuous external refuse middens near their nest entrances. Other species occasionally accumulate a small refuse pile close to the nest, but these are usually ephemeral. Colony-founding queens of *T. arizonensis* are frequently found under rocks. Older colonies often have 3–5 fungus garden chambers and may contain well over 1000 workers (R.A. Johnson pers. obs.; see also Wheeler 1911).

Trachymyrmex arizonensis is associated with *Pyramica arizonica* (Ward), a tiny dacetine ant that has been found only within or adjacent to *T. arizonensis* nests (Ward 1988; see also Yéo *et al*. 2006). Most species in the genus *Pyramica* are specialist predators on Collembola and strongly prefer relatively mesic habitats. We suspect that *P. arizonica* benefits from the controlled, moist microenvironment the *Trachymyrmex* provide for their fungal symbiont and feeds on the numerous collembolans that live in the chambers and refuse piles of the *Trachymyrmex* colony (Johnson & Cover, unpublished data).

In the mountains of southern Arizona, two army ant species, *Neivamyrmex nigrescens* and *N. rugulosus*, prey on *T. arizonensis* (Miranda *et al*. 1980, LaPolla *et al*. 2002). In Tamaulipas, Mexico, *N. texanus* was observed raiding a colony of *T. saussurei* (Rabeling & Sanchez-Peña, unpublished data). Based on these few observations, army ants seem to be important predators of at least some *Trachymyrmex* species, and their raids may result in a significant brood loss and partial destruction of the fungus garden (LaPolla *et al*. 2002).

ADDITIONAL MATERIAL EXAMINED: **U.S.A.**: ARIZONA, Cochise County: 1.6km NW Portal (RA Johnson), 5.5km W Portal (C Rabeling), 8.1mi SE Sunnyside (RR Snelling), Chiricahua Mtns. Southwestern Research Station (G Alpert, WS Creighton, RA Johnson, J LaPolla, RA Mendez, UG Mueller, C Rabeling & SP Cover), Dragoon (WM Wheeler), Huachuca Mtns. Sunnyside Canyon (SP Cover), Huachuca Mtns. Miller Canyon (WM Wheeler), Huachuca Mtns. Hunters Canyon (WM Wheeler); Coconino County: Hualpais Mtns. (DJ & JN Knull); Gila County: 12.1mi NE Globe (RA Johnson), Hwy 288 at 14.8mi N Salt River (RA Johnson, SP Cover), Sierra Ancha Pocket Creek (RA Johnson, C Strehl); Graham County: Graham Mtns, Post Canyon (WM Wheeler); Pima County: Baboquivari Mtns. (WS Creighton), Santa Catalina Mtns. Old Mt. Lemmon Rd. (RA Johnson), Tucson Sabino Canyon (DJ & JN Knull); Pinal County: USFS Rd. 287 at Pinto Creek (RA Johnson); Santa Cruz County: 1.5mi W Ruby on USFS Rd. 39 (RA Johnson), 1mi E Atascosa Lookout (RA Johnson), 3.8mi SE Jct FSR139 on FSR58 (SP Cover), Pajarito Mtns. 0.1mi W Jct. FSR 4181 on FSR39 (SP Cover), Pajarito Mtns. Sycamore Canyon (RA Johnson), Pajarito Mtns. Yanks Canyon (RA Johnson), Tumacacori Mtns. (DJ & KN Knull), 1.1mi W San Raphael Valley (RA Johnson), Pena Blanca Canyon (RA Johnson), Willow spring canyon (RA Johnson); NEW MEXICO, Grant County: 60km E Silver City (W Mackay); Texas, Brewster County: Big Bend National Park (A van Pelt); **MEXICO**: CHIHUAHUA: Hwy. 16 at 44 mi E Yecora (RA Johnson); SONORA: Sierra Mazatan (RA Johnson), without locality information (V Roth).

T. carinatus Mackay & Mackay

Trachymyrmex carinatus Mackay & Mackay, 1997: 43. Holotype worker (MCZC) [examined], paratype workers, paratype queens, and males, 15km W Bellavista, Municipio Riva Palacio, Chihuahua, Mexico (AMNH, WPMC, LACM, MCZC, USNM) [examined], (additional paratypes in MZSP, Universidad Nacional Autónoma de México: Instituto de Ecología)

Diagnosis

Worker: HL 0.8–1.0, HW 0.8–1.04, CI 96–108, SL 0.84–1.04, SI 100–105, ML 1.2–1.44. A relatively small species (HL 0.8–1, HW 0.8–1.04) with normally proportioned legs and antennal scapes (SI 100–105). Head more or less square (CI 96–108), sides subparallel posterior to the eyes, slightly tapering anteriorly between the eyes and mandibular insertions. Posterior margin weakly to moderately concave. Preocular carinae long, strongly curving mesially, and traversing nearly the entire distance between the eye and the frontal

carinae, sometimes nearly touching the frontal carinae or appearing to do so. In full-face view, frontal lobes more or less symmetrical. Anterolateral promesonotal teeth moderate in size, pointed in dorsal view, projecting horizontally, not vertically. Anterior median pronotal tubercles small or reduced to denticles, or if toothlike short and broadly pyramidal. Propodeal teeth usually acute, about as long as the distance between their bases. Dorsal surface of body moderately tuberculate, tuberculi generally moderate in size, bearing recurved setae. First gastric tergite coarsely and conspicuously tuberculate. Color brownish to yellow to medium reddish-brown.

Queen: HL 1.1–1.25, HW 1.15–1.4, CI 105–112, SL 1.1–1.15, SI 82–96, ML 1.9–2.1. As in worker diagnosis, except for typical caste-specific morphology of the mesosoma related to wing-bearing and head with minute ocelli. Dorsolateral pronotal teeth well-developed, tuberculate, sharply triangulate in dorsal view, often blunt-tipped in anterior view. Mesoscutum coarsely and irregularly rugulose, sometimes with faint longitudinal pattern, minutely tuberculate, and with abundant short, suberect, slightly recurved setae.

Male: HL 0.72–0.81, HW 0.75–0.84, CI 104, SL 0.81–0.9, SI 104–111, ML 1.6–1.8. Somewhat variable in size, but presenting the following characters: Dorsolateral pronotal tooth absent in dorsal view, ventrolateral pronotal tooth small, broadly to narrowly triangular. Mesoscutum irregularly rugulose, interrugal spaces coarsely granulose. Preocular carina a prominent vertical ridge, remaining strongly developed at least until it reaches the midpoint of the posterior border of the antennal scrobe. In full-face view, posterior corners of head more or less rounded, their outlines obscured by the presence of several conspicuous toothlike tuberculi on each corner.

Discussion

In southern Arizona, *T. carinatus* co-occurs with *T. arizonensis* in mid elevation habitats. Workers and queens of these two species are easily distinguished by the distinctive frontal lobes of *T. arizonensis* and the preocular carinae nearly touching the frontal carinae in *T. carinatus* (not closely approaching the frontal carinae in *T. arizonensis*). *T. carinatus* also sometimes co-occurs with *T. pomonae* from which it may be separated by its larger size and symmetrical frontal lobes (lobes notably asymmetric in *T. pomonae*). In addition, workers of *T. carinatus* are superficially very similar to those of the allopatric *T. septentrionalis,* from which they may be separated by the characters given in the key.

Etymology

The species name "carinatus" refers to the well-developed carinae on the vertex of the workers' and queens' heads.

Biology

Trachymyrmex carinatus was described by Mackay & Mackay (1997), based on specimens collected in Chihuahua, Mexico, and the Chiricahua Mountains of southeastern Arizona. *T. carinatus* occurs in central and southern Arizona, western New Mexico and the Mexican States of Sonora, Chihuahua and Coahuila, often in sympatry with *T. arizonensis*. A single collection from the Kofa Mountains in southwest Arizona marks its westernmost limit. So far, *T. carinatus* has been encountered most commonly in the mountains of southern and central Arizona in mid elevation habitats (800–1800m). Colonies may be found in open exposed areas with sparse ground cover, such as washes or road-sides, but are especially abundant in oak-juniper-pinyon woodlands. The Kofa Mountains specimens were collected from a nest next to a water seep shaded by palm trees on the wall of a canyon at ~800 m elevation (R. Snelling, personal communication). Nests are sometimes found under stones, but are more often encountered in open ground, where they can be recognized by the circular shape of the nest crater, which contrasts with the more amorphous nest excavations of *T. arizonensis*. Excavations by C. Rabeling reveal that nests in the Chiricahua Mountains of southern Arizona have one to three fungus garden chambers, with the shallowest chamber only 5 cm beneath the soil surface. Colo-

nies have fewer than 100 workers. Mating flights occur near dawn on mornings following summer rains (Mackay & Mackay 1997).

ADDITIONAL MATERIAL EXAMINED: **U.S.A.**: ARIZONA, Cochise County: 5.5km W Portal (C Rabeling), Chiricahua Mtns. Southwestern Research Station (RA Johnson, UG Mueller, C Rabeling & SP Cover), Huachuca Mtns. Carr Canyon (SP Cover), Huachuca Mtns. Sunnyside Canyon (RR Snelling), Peloncillo Mtns. Cottonwood Canyon (WS Creighton); Gila County: Jct. USFS Rd. 287 & 287A (RA Johnson), Sierra Ancha Mtns. Pocket Creek (RA Johnson), Sierra Ancha Mtns. 14.8 mi N Salt River on Rt. 288 (RA Johnson, SP Cover); Pinal Co: USFS Rd. 287 at 0.4 mi SE Pinto Creek (RA Johnson), Santa Cruz Co: 1mi E Atascosa Lookout (RA Johnson), 1mi S American Peak, Harshaw Creek Rd (RA Johnson), Pajarito Mtns 0.1mi W Jct FSR 4181 on FSR39 (SP Cover), Pajarito Mtns Yanks Canyon (RA Johnson), 8.8 mi W JctI-19 Rt92 on FSR368 (SP Cover); Yuma Co: Kofa Game Refuge, 2mi SE Jct24 (P Mehlhop & RR Snelling); NEW MEXICO, Sierra Co: Hillsboro (PS Ward); **MEXICO**: COAHUILA: Puerto de Ventanillas (E & WP Mackay).

T. desertorum (Wheeler)

Atta (Trachymyrmex) desertorum Wheeler, 1911: 98. Syntype workers, Carnegie Desert Botanical Laboratory, Tucson, Arizona, U.S.A. (MCZC, AMNH) [examined]
Trachymyrmex desertorum (Wheeler); Creighton 1950: 321 [Combination in *Trachymyrmex*]

Diagnosis

Worker: HL 0.8–1.12, HW 0.8–1.28, CI 100–114, SL 0.8–1.16, SI 91–100, ML 1.08–1.76. A medium-sized, relatively robust species (HL 0.8–1.12, HW 0.8–1.28) with relatively short antennal scapes (SI 91–100) that surpass the posterior corners of the head by at least their maximum diameter. Head broader than long in most workers, broad as long in some small workers (CI 100–114), gradually tapering anteriorly behind the eyes, more strongly tapering between the eyes and mandibular insertions. Posterior margin of head slightly to moderately concave. Preocular carinae short, traversing about half the distance between the eye and the frontal carinae. In full-face view, frontal lobes simple, rounded or subtriangular, more or less symmetrical in shape (anterior side sometimes slightly longer than posterior). Anterolateral promesonotal teeth short, thick, usually pointed, not blunt. Propodeal teeth sharply pointed, shorter than the distance between their bases. Dorsal surface of body moderately tuberculate, but tuberculi are generally small and their setae short and strongly recurved. Side of mesosoma sparsely tuberculate, tuberculi very small, scarcely visible. Color variable, ranging from brownish yellow to medium reddish-brown.

Queen: HL 1.2–1.25, HW 1.35–1.4, CI 89–113, SL 1.15, SI 82–85, ML 2.0–2.05. Generally as in worker diagnosis, except with typical caste-specific structures related to wing-bearing, and head with minute ocelli. Dorsolateral pronotal teeth prominent, broadly triangular, sharply pointed. Ventrolateral pronotal teeth short, triangular, and more or less pointed. Mesoscutum longitudinally rugulose, minutely tuberculate, setae abundant, short, straight, and suberect.

Male: HL 0.95, HW 1.0, CI 105, SL 0.9, SI 90, ML 2.05. In dorsal view, dorsolateral pronotal teeth short, sharp, and broadly triangular. Ventrolateral pronotal teeth small, more or less triangular. Irregular rugulae present on all surfaces of pronotum; mesoscutum covered with coarse, longitudinal, slightly reticulate rugulae. Antennal scrobe granulate, with at least several small transverse rugulae distributed over anterior ¾. First gastric tergite minutely tuberculate, with abundant short, weakly recurved, decumbent seta.

Discussion

Trachymyrmex desertorum is broadly sympatric throughout much of southern Arizona with the similar *T. carinatus* and *T. pomonae* (see distribution maps), but it generally occurs at lower elevations in true desert

habitats, rather than in mid elevation woodlands or forests. Females can be distinguished from those of *T. carinatus* by head shape (square to longer than broad in *T. carinatus*), short preocular carinae that do not closely approach the frontal carinae (closely approaching the frontal carinae in *T. carinatus*), and shorter antennal scapes. It may be distinguished from *T. pomonae* by its slightly asymmetric frontal lobes (lobes strongly asymmetric in *T. pomonae*). In the field this ant is most likely to be confused with small workers of *Acromyrmex versicolor* Pergande, which is common in many of the same habitats. In *Acromyrmex* the head is cordate, the mesosoma is spinose, rather than tuberculate, and the frontal lobes have two short laterally-directed teeth. None of these characters is present in *T. desertorum*.

Etymology

Wheeler collected the *T. desertorum* types a few hundred meters from the Carnegie Desert Botanical Laboratory in Tucson, Arizona, on the bank of a dry arroyo that skirts Tumamoc hill in the "…feeble shade of the *Parkinsonia* and *Acacia* trees in the very hard, pebbly, desert soil…" (Wheeler 1910, p.100). This typical Sonoran Desert habitat no doubt inspired the species name.

Biology

Trachymyrmex desertorum is a Sonoran Desert species occurring at 530–840 m elevation in central and southern Arizona and the Mexican State of Sonora. A *Trachymyrmex* record from Willacy County, Texas (coll. Creighton 8-XI-1951) is erroneously cited as *T. desertorum* in the literature (Wheeler & Wheeler 1985; O'Keefe et al. 2000). The specimen belongs to *T. turrifex* and is currently deposited in the Jeanette Wheeler Collection at the University of Arizona. Therefore, there is no evidence that *T. desertorum* occurs in west Texas. Typically, *T. desertorum* occurs in Sonoran Desert habitats with palo verde (*Parkinsonia* spp.), creosote bush (*Larrea tridentata*), *Acacia*, jojoba (*Simmondsia chinensis*), honey mesquite (*Prosopis glandulosa*), and saguaro (*Carnegiea gigantea*). Nests are often in the shade under palo verde or mesquite trees, and are sometimes common in small washes. Foragers have been observed to collect green leaflets and fresh flower petals, but they have not been observed climbing plants and cutting live vegetation (C. Rabeling, personal observation). Nest craters are moderate in size (10–20 cm in diameter), conical in shape, and can be confused with the small craters of incipient *A. versicolor* nests. *Trachymyrmex desertorum* nests in very rocky soil, such that the limited excavatable space between the boulders often results in amorphously shaped fungus chambers. Nests contain 1 to 3 chambers that are placed up to 120 cm below the surface. Mating flights occur near dawn on mornings following summer rains. The single flight observed to date (J. Weser, pers. comm.) occurred on the same day as a mating flight of *A. versicolor*.

ADDITIONAL MATERIAL EXAMINED: **U.S.A.**: ARIZONA, Apache County: Santa Catalina Mtns. (WS Creighton), Cochise County: Chiricahua Mtns. Southwestern Research Station (HV Weems, Jr.), Dragoon (WS Creighton); Gila County: 6.3mi NNW Jct. Salt River on Rt. 288 (RA Johnson, UG Mueller, C Rabeling, A Rodrigues, SP Cover); Maricopa County: McDowell Mountain Park (RA Johnson); Pima County: Avra Valley (JH Hunt), Baboquivari Mtns. (WS Creighton), Oro Valley near First Ave. and Tangerine (RA Johnson), Tucson Tumamoc Hill (RA Johnson), **MEXICO**: SONORA, 10mi S Sonoyta (WS Creighton).

T. jamaicensis (André)

Atta (Acromyrmex) jamaicensis André, 1893: 149. Two syntype workers, Jamaica (repository unknown) [not examined];
Atta (Trachymyrmex) jamaicensis André; Wheeler 1907: 712 [Description of queen and male; combination in *Atta (Trachymyrmex)*];
Trachymyrmex jamaicensis (André); Gallardo 1916: 242 [Combination in *Trachymyrmex*]
Atta (Trachymyrmex) sharpii Forel, 1893: 372. Syntype worker(s) worker, near Brighton Estate, St. Vincent
Atta (Trachymyrmex) sharpii Forel; Wheeler 1907: 712 [Synonymy, under *Atta (T.) jamaicensis* (André)], [See Mayhé-Nunes and Brandão (2007: 15) for further discussion about synonymies of *Atta (T.) sharpii* Forel]

Atta (Trachymyrmex) maritima Wheeler, 1905: 107. Syntype workers, Andros and New Providence Islands, Bahamas
Atta (Trachymyrmex) maritima Wheeler; Wheeler 1907: 712 [Synonymy, under *Atta (T.) jamaicensis* (André)]
Acromyrmex (Trachymyrmex) jamaicensis var. *maritima* Mann, 1920: 428. Syntype workers, Mangrove Cay, Andros Island and Bluff, Eleuthera Island, Bahamas, [Mann revived *Atta (Trachymyrmex) maritima* Wheeler from synonymy as variety of *Acromyrmex (Trachymyrmex) jamaicensis* (André)]
Trachymyrmex jamaicensis var. *maritima* (Mann); Kempf 1972: 253 [Combination in *Trachymyrmex*]
Trachymyrmex jamaicensis var. *maritima* (Mann); Mayhé-Nunes and Brandão 2007: 13 [Synonymy, under *T. jamaicensis*]
Trachymyrmex jamaicensis var. *frontalis* Santschi, 1925: 238. Worker, Diquini, Haiti
Trachymyrmex jamaicensis var. *frontalis* Santschi; Mayhé-Nunes and Brandão 2007: 13 [Synonymy, under *T. jamaicensis*]
Trachymyrmex jamaicensis subsp. *cubaensis* Wheeler, 1937: 459. Syntype workers, coast below Pico Turquino, Sierra Maestra, Cuba
Trachymyrmex jamaicensis subsp. *cubaensis* Wheeler; Mayhé-Nunes and Brandão 2007: 13 [Synonymy, under *Trachymyrmex jamaicensis*]

Diagnosis

Worker: HL 1.2–1.35, HW 1.35–1.45, CI 107–113, SL 1.2–1.25, SI 86–89, ML 2–2.1. A large, relatively slender species with relatively long antennae and legs. Antennal scapes surpass posterior corners of head by 1–2 times their maximum diameter. Head shape slightly longer than broad (CI 107–113) in full-face view, sides subparallel behind the eyes, slightly tapering anteriorly between the eyes and mandibular insertions. Posterior margin moderately concave. Clypeus with row of coarse, long hairs on anterior margin, projecting forwards over the dorsal surface of the mandibles; in side view a few shorter erect hairs often present posterior to the anterior row. Preocular carinae relatively short, stopping at about 1/3 the distance between eye and posterior corner of head, always subparallel to frontal carinae, not traversing antennal scrobe. Frontal carinae long, reaching back to posterior corner of head. Antennal scrobe well developed but shallow, extending above the posterior margin of the head as a small tooth. In full-face view, frontal lobes broad, rounded, symmetrical in shape. Anterolateral promesonotal tooth long, thin, sharply pointed, projecting forward and upwards. Propodeal teeth sharply pointed, variable in size, approximately as long as the distance between their bases. Head and mesosoma sparsely tuberculate, with small tuberculi bearing short, fine, recurved setae. In full-face view, two ridges are present on the posterior third of head, between the frontal carinae. Gaster strongly tuberculate, in dorsal view tuberculi form four more or less distinct longitudinal ridges on first gastric tergite. Color dark reddish-black or gray-black, appendages and two petiolar segments usually a lighter reddish-brown.

Queen: HL 1.25, HW 1.6–1.7, CI 128–136, SL 1.15–1.2, SI 68–75, ML 2–2.05. As in worker diagnosis but with typical caste-specific mesosomal morphology related to wing-bearing and head with small ocelli. In dorsal view, dorsolateral pronotal teeth large and conspicuous, sharp, narrowly triangular. Ventrolateral pronotal teeth large, lobelike (rarely triangular). Mesoscutum with coarse, longitudinal, finely tuberculate rugulae; tuberculi bearing short, stiff, slightly recurved suberect setae. Posterior portion of scutellum bearing two prominent lobelike teeth projecting posteriorly. Pronotal sides, mesopleura, and propodeum with only a few miniscule tuberculi, if any.

Male: HL 0.72–0.75, HW 0.69–0.75, CI 96–100, SL 0.87–0.99, SI 121–139, ML 2.1–2.4. A comparatively large male with relatively long appendages and antennal scapes. Posterior corners of head much rounded in full-face view, ocelli very large, elevated above remainder of head, forming a short, vertical "turret" in side view. Dorsolateral pronotal teeth unique, taking the form of thin, needlelike spines. Ventrolateral teeth absent. Gaster finely tuberculate, each tubercle bearing a short erect to suberect more or less recurved seta.

Discussion

Trachymyrmex jamaicensis is a unique species in the context of the US American fauna. No other *Trachymyrmex* shows the combination of large body size, dark coloration, almost quadrate head shape, antennal scrobes extending to posterior corners of head, long scapes, and four tuberculate longitudinal ridges on the first gastric tergite.

Etymology

André (1893) described *T. jamaicensis* based on two worker specimens collected by M. Fox in Jamaica (no date given). The species name obviously refers to the Caribbean island on which the types were collected.

Biology

In the United States *T. jamaicensis* occurs only in southeast Florida and the Florida Keys, but it is also widely distributed through much of the Caribbean (see distribution map). Smith (1954) suggested that *Trachymyrmex jamaicensis* is a non-native species that was recently introduced from the Caribbean, whereas Deyrup (1994) argues for an early, natural introduction because of morphological differences between the Florida and Caribbean populations. A thorough study of population genetics and morphology would be required to test these hypotheses. In Florida, *T. jamaicensis* inhabits coastal tropical hardwood hammocks on shallow, sandy, coralline-rock-derived soils. Nests usually have several chambers; Weber (1967) found eight chambers in a colony excavated in the Bahamas. Based on partial nest excavations, Wheeler (1905, 1907) estimated that *T. jamaicensis* colonies contain 150 to several hundred workers. Due to the increasing urbanization of the coastline, Deyrup (1994) considers *T. jamaicensis* potentially endangered in Florida, which would give *T. jamaicensis* the distinction of being the first endangered fungus-growing ant species (IUCN 2006).

ADDITIONAL MATERIAL EXAMINED: **BAHAMAS**: Andros Island (WM Wheeler, WM Mann); Bimini Island (NA Weber); Eleuthera, Rainbow Bay (DB & RW Wiley, JR Wiley); San Salvador (Deyrup); **HAITI**: Diquini (WM Mann), Manneville (WM Mann), Port du Prince (WM Mann); **PUERTO RICO**: Culebra Island (WM Wheeler), Guánica State Forest (JT Longino); **U.S.A.**: FLORIDA, Broward County: Dania (WF Buren); Dade County: Elliot Key (M Deyrup); Martin County: Jonathan Dickinson State Park (M Deyrup, L Davis); Monroe County: Bahia Honda State Recreation Area (M Deyrup), Big Pine Key, Watson's Hammock (M Deyrup, EG Riley, PS Ward), Fat Deer Key (UG Mueller), Grassy Key (M Deyrup), Indian Key (M Deyrup), Key Largo (M Deyrup, UG Mueller), Long Key (M Deyrup, EO Wilson), John Pennekamp Coral Reef State Park (M Deyrup), Shark Key (N Carlin, M Deyrup).

T. nogalensis Byars

Trachymyrmex nogalensis Byars, 1951: 109. Holotype worker; Nogales, Arizona, U.S.A. (USNM) [examined]; Paratype workers, same locality (AMNH, MCZC, USNM) [examined].

Diagnosis

Worker: HL 1.1–1.35, HW 1.05–1.5, CI 96–112, SL 1.4–1.8, SI 117–133, ML 1.7–2.2. Large species (HL 1.1–1.35; HW 1.05–1.5), with relatively long legs and antennae (SI 117–133). Head generally longer than broad (CI 96–112), tapering slightly anterior to the eye, posterior border weakly concave. Antennal scape narrowing abruptly toward the antennal insertion, with a conspicuous lobe just distal to the narrowing. Frontal lobes well developed, evenly rounded, equilateral. Frontal carinae short, joining with preocular carinae to form short, distinctive "scrobes" that end just posterior to the level of the eye. Anterior terminus of the preocular carina forming a small tooth in full-face view. Anterolateral promesonotal teeth spinelike, sharply pointed, directed upwards and forward in side view. Propodeal spines toothlike, shorter than the distance between their bases. Body moderately tuberculate. Color yellowish brown.

Queen: HL 1.36–1.45, HW 1.4–1.45, CI 97–104, SL 1.64–1.8, SI 117–124, ML 2.25–2.4. Generally as in worker diagnosis, but mesosoma with caste-specific morphology relating to wing-bearing and the head bearing small ocelli. Dorsolateral pronotal teeth large, tuberculate and sharply pointed in dorsal view; ventrolateral pronotal teeth well-developed, resembling a blunt lobe. Mesoscutum lacking longitudinal rugulae but with numerous small tubercles, each bearing a short, sharply recurved seta.

Male: unknown.

Discussion

Trachymyrmex nogalensis is distinguished from other US *Trachymyrmex* species by the short, unique "scrobes" and the unusual basal lobe on the antennal scapes. In the field it can be confused only with the occasionally sympatric *T. arizonensis*, from which it is easily distinguished by the basal lobe on the antennal scape, (absent in *T. arizonensis*), and the distinctive frontal lobes of *T. arizonensis* (Figure 1B), (absent in *T. nogalensis*).

Etymology

Trachymyrmex nogalensis was described from Nogales, Arizona, based on workers that Byars collected from a colony nesting under his house. The species name clearly refers to the type locality.

Biology

Trachymyrmex nogalensis is rarely collected and is also the only *Trachymyrmex* species in the US whose male remains undiscovered. So far, it is known from only two locations in Arizona: the type locality, Nogales (in Santa Cruz County) and the Chiricahua Mountains (Cochise County) in the southeast corner of the state. All collections have been made in mid elevation habitats at 1200–1550 m. Byars (1951) collected workers and dealate queens on the porch of his house. Unfortunately, he provided no further information on the surrounding habitat or on any other nests. In the Chiricahua Mountains, we found *T. nogalensis* in creosote bush, mesquite-dominated desert habitats and on a rocky limestone outcrop dominated by Ocotillo, *Acacia, Agave* and *Mimosa*. Nests were cryptic and the entrances were located in cracks on rock-face. No information is available on nest architecture, fungus gardens, or number of workers in a colony because the extremely rocky ground makes excavation close to impossible. *Trachymyrmex nogalensis* is seldom encountered, probably because of it nocturnal foraging behavior and its cryptic nest sites. Studies of ecology, behavior and fungus cultivation would be fruitful areas for further research.

ADDITIONAL MATERIAL EXAMINED: **U.S.A.**: ARIZONA, Cochise County: Chiricahua Mtns. 0.8mi WNW Jct. FSR 42 on FSR42D (SP Cover), Chiricahua Mtns. 2km WNW Portal (G Alpert, RA Johnson, C Rabeling), Huachuca Mtns., Palmerlee (WM Wheeler); Santa Cruz County: Nogales (JN Kaiser, J Steward).

***T. pomonae* Rabeling & Cover, NEW SPECIES**

Diagnosis

Worker: HL 0.75–0.95, HW 0.78–0.95, CI 97–103, SL 0.73–0.88, SI 89–100, ML 1.0–1.28. The smallest species of *Trachymyrmex* in the US (HL 0.75–0.95; HW 0.78–0.95), with relatively short legs and antennal scapes (SI 89–100). Head quadrate (CI 97–103), sides subparallel behind the level of the eye, moderately tapering anteriorly between the eye and mandibular insertion. Posterior margin slightly to moderately concave. In full-face view, preocular carinae short, traversing only about half the distance between the eye and the frontal carinae. Frontal lobes subtriangular or rounded in full-face view, notably asymmetric with the anterior side of the lobe markedly longer than the posterior. Mesosomal teeth generally small in size, sometimes reduced to tubercles. Anterolateral promesonotal teeth short, usually pointed, projecting horizontally, not vertically. Propodeal teeth usually acute, shorter than the distance between the bases. Dorsal surface of the body moderately tuberculate, tuberculi small, tubercular setae short, recurved or straight and erect, tuberculi on sides of mesosoma minute, sometimes absent on sides of pronotum. Color medium reddish-brown.

Queen: HL 0.95–1.05, HW 1.05–1.1, CI 105–111, SL 0.9, SI 82–86, ML 1.5–1.55. As in worker diagnosis, but with caste-specific morphology of the mesosoma related to wing bearing and the presence of small ocelli on the head. Dorsoventral pronotal teeth present only as right angles in dorsal view, rather than as a triangular tooth. Ventrolateral pronotal teeth small, broadly triangular. Mesoscutum with coarse longitudinal

rugulae, tubercles absent, stiff, suberect setae moderately abundant, inclined posteriorly. First gastric tergite densely and minutely tuberculate, with abundant short, decumbent, slightly recurved setae.

Male: HL 0.6–0.75. HW 0.6–0.75, CI 100–108, SL 0.6–0.8, SI 93–107, ML 1.3–1.65. Somewhat variable in size, but smaller than other North American *Trachymyrmex* males (ML 1.3–1.65). Dorsolateral pronotal teeth absent. Ventrolateral pronotal teeth small, triangular. Preocular carinae as described in the key. Posterior corners of head angulate in full-face view and bearing only small tuberculi.

Description

HOLOTYPE WORKER: HL 0.81, HW 0.87, CI 107, SL 0.78, SI 90, ML 1.17. As in the diagnosis and as illustrated in Figure 12. Integument of head coarse, sandpaperlike, with curved setae, posterior corners rounded. Dorsal and lateral margins of head tuberculate, largest tuberculi on posterior corners, smaller tuberculi on lateral margin. In full-face view, frontal carinae almost reach dorsal margin of head. In lateral view, preocular carinae form straight line traversing the antennal scrobe by 1/3 its width. Antennal scrobe shallow, not tuberculate, with some short setae in dorsal half of scrobe. Frontal lobes subtriangular with anterior side twice as long as posterior one. Mandibles shiny, striate with 7 teeth/denticles. Antennal scape with abundant appressed setae, surpassing dorsal margin of head by 1.5x its maximum diameter. Mesosomal teeth short and rounded, median pronotal teeth reduced. Each tooth bears several erect, curved setae. Dorsal surface of propodeum with two tuberculate ridges, leading to propodeal teeth; each ridge bearing three tuberculi and several recurved setae. Anterior peduncle of petiole short, less than 1/3 the length of petiolar node. Petiole half as wide as postpetiole. Postpetiole oval in dorsal view, wider than long; posterior margin concave. First gasteric tergite tuberculate with recurved setae; tuberculi small. Color uniformly medium reddish-brown, with a faint, dark stripe on first gastric tergite. Paratype workers: HL 0.75–0.95, HW 0.78–0.95, CI 97–103, SL 0.73–0.88, SI 89–100, ML 1.0–1.28.

PARATYPE QUEEN: HL 0.96, HW 0.99, CI 103, SL 0.84, SI 85, ML 1.47. As in worker and queen diagnosis, with caste specific structure of mesosomal morphology, and as illustrated in Figure 13. Integument of head sandpaperlike, slightly irregular, fine-textured, dull with scattered minute tubercles. Head, tuberculation, frontal and preocular carinae, antennal scrobes and frontal lobes shaped as in worker. Mandibles shiny, striate with 9 teeth/denticles. Antennal scapes with many appressed setae, surpassing posterior corner of head 1x its maximum diameter. Mesosoma with typical morphology of the queen caste. In dorsal view, dorsolateral pronotal teeth short, broad, its peak almost forming a 90° angle, projecting horizontally not vertically. Posterior margin of scutellum slightly concave, edges do not form a distinct tooth. In lateral view, propodeal teeth very short and pointed, approximately ¾ as long as broad at its base. Petiole, postpetiole, and gaster shaped as in workers.

PARATYPE MALE: HL 0.65, HW 0.7, CI 108, SL 0.65, SI 93, ML 1.3. Head broader than long, mandibles short, apical and subapical tooth present, other teeth small to minute, sometimes indistinct or partly to entirely absent. Preocular carinae weakening posteriorly, becoming less conspicuous, broken, or sometimes incomplete as it forms the posterior border of the antennal scrobe. Dorsal surface of head coarsely granulate, finely rugulose, posterior margin with less than 15 small tuberculi, no tooth present on the corners. Posterolateral pronotal teeth short, broadly pyramidal, sometimes rounded. Anterolateral pronotal teeth absent. Sculpture on mesosoma, petiole, postpetiole and gaster coarsely granulate. Fine rugulae present on most of the mesosoma, primarily longitudinal on the mesoscutum, mostly reticulate on the scutellum and on the sides. Rugulae and tuberculi largely absent from the first gastric tergite, but numerous short, appressed, recurved setae present. Head dark blackish brown, scape lighter brown, mandibles and funiculus yellowish brown.

Discussion

Probably sympatric with *T. carinatus* and *T. arizonensis* in mid elevation woodland habitats throughout much of southern Arizona and northern Mexico, but workers and queens of *T. pomonae* are easily recognized

by their smaller size, shorter antennal scapes, notably asymmetric frontal lobes, and short preocular carinae that do not approach the frontal carinae. *T. pomonae* is most similar to *T. desertorum*, but is separable by its strongly asymmetric frontal lobes (weakly asymmetric at most in *T. desertorum*), smaller size, and different habitat preferences.

Etymology

In traditional Roman religion, Pomona was the goddess of fruit trees, gardens and orchards. *Trachymyrmex pomonae* therefore is Pomona's *Trachymyrmex*, because the ant's cultivation of fungus gardens is a highly developed form of "pomology" that would surely please the goddess.

Type locality

U.S.A., Arizona: Cochise County, Chiricahua Mountains 0.5 km north of Southwestern Research Station, 31°53.20'N 109°12.27'W, elevation 5600 feet (1707 m). Open Alligator Juniper, Emory Oak woodland to 6 m tall on south facing slope. Moderate groundcover with very rocky soil.

Type series: Holotype worker (SPC 6330) and the following paratypes: 15 workers, 1 queen [12-VIII-2001, SPC 6330]; 13 workers [12-VIII-2001, SPC 6328]; 48 workers, 8 queens, 1 male [14-VIII-2001, UGM010814-01]; 34 workers [10-VIII-2005, CR050810-01]. Holotypes and paratypes deposited in the Museum of Comparative Zoology (Cambridge, MA, USA). Additional paratypes deposited in: the Natural History Museum (London, UK), the Natural History Museum of Los Angeles County (Los Angeles, CA, USA), the National Museum of Natural History (Washington, DC, USA), the California Academy of Sciences (San Francisco, CA, USA), the Staatliches Museum für Naturkunde Karlsruhe (Germany), the Museu de Zoologia da USP (São Paulo, SP, Brazil), the Bohart Museum of Entomology, University of California at Davis (Davis, CA, USA), the collections of Robert A. Johnson (Tempe, AZ, USA), William P. Mackay (El Paso, TX, USA) and Christian Rabeling (Austin, TX, USA).

Additional material: R. A. Johnson collected specimens from two colonies of *T. pomonae* in Sonora, Mexico (5 km east San Pedro de la Cueva; 27-IV-2004). The nests had been found in the shade in a mesic canyon and had no nest mound. Deciduous thorn scrub produced an abundant leaf litter layer on the bottom of the canyon.

Biology

Trachymyrmex pomonae is the smallest *Trachymyrmex* species occurring in the United States. So far, this species is known only from southern Arizona (Cochise and Santa Cruz Counties) and the state of Sonora, Mexico. In Arizona, *T. pomonae* lives sympatrically with *T. carinatus* and *T. arizonensis* in the Chiricahua, Patagonia, and Pajarito Mountains at elevations of 1200–1700 m. The open woodland habitat in these mountains is dominated by Emory and Gray Oaks (*Quercus emoryi* and *Q. grisea*), pinyon pine (*Pinus edulis*), juniper (*Juniperus deppeana*), and in some places Chihuahua Pine (*Pinus leiophylla*). *Trachymyrmex pomonae* nests in very rocky soil. Nest craters are small, approximately 5 cm in diameter, or absent. When craters are absent, the nests are difficult to find, because the entrance is minute and the ants inconspicuous. Excavated nests had 1–3 fungus chambers distributed from 5–40 cm below the surface; fungus gardens were suspended from the ceiling of the chambers. The largest colony contained 183 workers, 2 dealate queens, 45 pupae and 31 larvae. Although a nuptial flight was not observed directly, winged queens and males were found from 9–25 August in the years 1999, 2001 and 2005. Males were encountered at nest entrances, whereas winged queens were found walking on the ground. The collection dates suggest that *T. pomonae* disperses in the monsoon season (July–September), after heavy rainfall has softened the clayey loam soil, a habit shared with the other *Trachymyrmex* in Arizona. Workers forage diurnally in the leaf litter to collect vegetable debris and caterpillar feces, which they use to nourish the fungus garden.

T. septentrionalis (McCook)

Oecodoma virginiana Buckley, 1867: 346. Syntype worker(s), near Aquia, Virginia, U.S.A. (repository unknown) [not examined]. Synonymy under *septentrionalis* by Wheeler, 1902: 29; here confirmed. Younger name valid under ICZN Article 23.9 (see discussion below)

Atta septentrionalis McCook, 1881: 362. Worker described; Island Heights, Pine Barrens, New Jersey, U.S.A. (repository unknown) [not examined]

Atta septentrionalis McCook; Wheeler 1907: 707 [description of queen and male]

Atta septentrionalis McCook; Forel 1912: 182 [combination in *Atta* (*Trachymyrmex*)]

Atta septentrionalis McCook; Gallardo 1916: 242 [combination in *Trachymyrmex*]

Atta (Trachymyrmex) septentrionalis var. *obscurior* Wheeler, 1907: 709. Syntype worker(s) described, Austin, Travis County, Texas, U.S.A.

Atta (Trachymyrmex) septentrionalis obscurior Wheeler; Wheeler 1911: 247 [raised to subspecies of *septentrionalis*]

Atta (Trachymyrmex) septentrionalis obscurior Wheeler; Wheeler 1911: 246 [description of queen]

Trachymyrmex septentrionalis obscurior (Wheeler); Creighton 1950: 324 [Combination in *Trachymyrmex*]

Trachymyrmex septentrionalis obscurior (Wheeler); Weber 1958: 53 [Synonymy, under *septentrionalis*]

Atta (Trachymyrmex) septentrionalis obscurior var. *crystallina* Wheeler, 1911: 247. Syntype workers, queens and males; Huntsville Walker County, Texas, U.S.A. [unavailable name]

Trachymyrmex septentrionalis obscurior var. *crystallina* Wheeler; Creighton 1950: 324 [material referred to *obscurior*]

Atta (Trachymyrmex) septentrionalis obscurior var. *irrorata* Wheeler, 1911: 247. Syntype workers; Huntsville, Walker County, Texas, U.S.A. [unavailable name]

Trachymyrmex septentrionalis obscurior var. *irrorata* Wheeler; Creighton 1950: 324 [material referred to *obscurior*]

Atta (Trachymyrmex) septentrionalis obscurior var. *seminole* Wheeler, 1911: 247. Syntype worker(s), queen(s) and male(s); Miami, Florida, U.S.A. [unavailable name]

Trachymyrmex septentrionalis seminole (Wheeler); Creighton 1950: 324 [subspecies of *septentrionalis*, first available use of *seminole*]

Trachymyrmex septentrionalis seminole (Wheeler); Weber 1958: 53 [Synonymy, under *septentrionalis*]

Atta (Trachymyrmex) septentrionalis var. *vertebrata* Wheeler, 1911: 246. Syntype workers and queens; Lakehurst, New Jersey, U.S.A.

Trachymyrmex septentrionalis var. *vertebrata* Wheeler; Creighton 1950: 323 [Synonymy, under *septentrionalis*]

Diagnosis

Worker: HL 0.84–0.96, HW 0.88–1.0, CI 104–105, SL 0.84–0.96, SI 96, ML 1.12–1.32. A relatively small (HL 0.84–0.96, HW 0.88–1.0), conspicuously tuberculate species with normally proportioned legs and antennal scapes (SI 96). Head slightly broader than long (CI 104–105), sides subparallel behind the eyes, gradually tapering anteriorly between the eyes and the mandibular insertion. Posterior margin moderately concave. Preocular carinae long, traversing 2/3 to ¾ of the distance between the eye and the frontal carina but not nearly touching the frontal carinae. In full-face view, frontal lobes rounded or subtriangular, usually somewhat asymmetric, with the anterior side longer than the posterior. Anterolateral promesonotal teeth well-developed, thin, sharply pointed in dorsal view, projecting somewhat upward as well as horizontally. Anterior median pronotal tubercles upright, toothlike in posterior view. Propodeal teeth usually longer than the distance separating their bases, often spinelike, pointed. Posterior margin of head, mesonotal dorsum, dorsal surfaces of petiole, postpetiole and gaster conspicuously tuberculate, tuberculi largest particularly on posterior corners of head and on the first gastric tergite. Color brownish yellow to medium reddish-brown.

Queen: HL 1.05–1.2, HW 1.1–1.25, CI 104–107, SL 1.05–1.15, SI 96–100, ML 1.55–1.85. As in worker diagnosis, but with caste-specific morphology the mesosoma related to wing-bearing. Dorsolateral pronotal teeth variable in size, but sharply triangulate in dorsal view, often blunt in anterior view. Ventrolateral pronotal teeth variable, but generally lobelike. Mesoscutum coarsely, longitudinally rugulose, finely tuberculate, tuberculi with short, sharply recurved hairs. First gastric tergite with numerous small tubercles bearing short, recurved, decumbent, recurved setae.

Male: HL 0.75, HW 0.8–0.9, CI 100–107, SL 0.9–1.1, SI 113–122, ML 1.5–1.85. In frontal view, posterior corners of the head angulate, angles formed by short, tuberculate ridges best seen in dorsal view; ocelli small and inconspicuous. Dorsoventral pronotal teeth, short, sharp, triangulate in dorsal view; ventrolateral

teeth short, triangular or lobelike. Sculpture of mesoscutum coarse, irregular, rugulose, sometimes weakly longitudinal. Tuberculi generally absent (miniscule, if present) on first gastric tergite.

Discussion

Trachymyrmex septentrionalis is disturbingly similar to the allopatric *T. carinatus,* but separable by the characters given in the key and by their non-overlapping distributions; *carinatus* occurs only in the desert southwest, *septentrionalis* occurs in Texas and the states north and east of there. Molecular evidence suggests the similarity is convergent (see Figure 21 & General Discussion). It is likely that collections identified in the literature as *T. septentrionalis* from Durango, Mexico may actually represent *T. carinatus* (Rojas Fernandez 1994).

Solely considering the publication date, *Oecodoma virginiana* Buckley (1867) would have seniority over McCook's (1881) *Atta septentrionalis*. But since Buckley's species description is insufficiently detailed to either recognize *T. septentrionalis* or distinguish between *septentrionalis* and its congeners, Wheeler (1902) proposed *Oocodoma virginiana* Buckley to be a junior synonym of *Atta septentrionalis* McCook. We agree with Wheeler and continue using the species name *septentrionalis*. Unfortunately, the locality of both types is unknown and we could not examine them.

Etymology

McCook (1881) described the worker of *T. septentrionalis* based on material collected from Island Heights in the New Jersey Pine Barrens. The species name *septentrionalis* refers to the seven plowing oxen, the brightest stars of the Great Bear constellation, which dominate the skies of the northern hemisphere. Thus, *septentrionalis* loosely translates to "northern" in the context of North American fungus-growing ants.

Biology

Trachymyrmex septentrionalis has the most extensive distribution of all attine ants in the US. It has been collected from Texas to Florida and as far north as central Illinois, southern Ohio and Long Island, New York. Like most fungus-growing ants, the distribution of *T. septentrionalis* is locally patchy. In part, this may be a consequence of the distribution of suitable soils. In the northern part of its range, *T. septentrionalis* occurs exclusively on pure sand soils in open habitats and open woodlands of the Pine Barrens. In the southern US, *T. septentrionalis* is abundant in a wide variety of similar oak and pine dominated habitat types, all characterized by very sandy soils and light (if any) shade. It has also occasionally been found nesting in sandy clay soils in well-developed forests with considerable shade, particularly in the southern part of its range.

During periods of high nest excavation activity in spring and fall, the crescent shaped mounds of *T. septentrionalis* are distinctive and conspicuous (Tschinkel & Bhatkar 1974). Older colonies may have several chambers, connected by one to few tunnels and inhabit a few hundred individuals (Weber 1972). As the northernmost distributed species of *Trachymyrmex*, colonies of *T. septentrionalis* hibernate during the winter and the fungus garden assumes a dormant condition. The length of hibernation varies considerably with respect to latitude. The northernmost populations in New York and New Jersey have short active periods from early May to September, whereas Florida populations remain active during the winter, as long as temperatures exceed 18ºC (Weber 1972). The army ant *Neivamyrmex nigrescens* and the ectatommine ant *Gnamptogenys hartmani* are known to raid colonies of *T. septentrionalis* (Cole 1939).

ADDITIONAL MATERIAL EXAMINED: **U.S.A.**: ALABAMA, Autauga County: Prattville (AS Mikheyev); Mobile County: Dauphin Island (WS Creighton), Theodore (EO Wilson); ARKANSAS, Miller County: State Line Rd. (UG Mueller); Washington County: Devil's Den State Park (AS Mikheyev); DISTRICT OF COLUMBIA, Washington (T Pergande, HS Barber); FLORIDA, Alachua County: Archer (M Deyrup), Gainesville (M Deyrup, KW Copper); Baker County: Osceola National Forest, East Tower, 250 (M Deyrup); Bay County: St. Andrews State Recreation Area (M Deyrup); Bradford County: Hampton (M Deyrup); Brevard County:

Micco 6mi W Micco Rd (M Deyrup), Melbourne Beach 2mi S Ecological Preserve (M Deyrup), Eau Gallie (M Deyrup), Indian River City, Dicerandra Preserve (M Deyrup), Titusville (M Deyrup); Broward County: Hollywood, Topeekeegee Yugnee Park (M Deyrup), Ft. Lauderdale (DE Read); Citrus County: 12mi NW Brooksville, Withlacoochee State Forest (M Deyrup), Pine Oak Estates, 488, 3mi NE 495 (M Deyrup); Clay County: Camp Blanding (M Deyrup); Collier County: Rookery Bay Preserve (M Deyrup); Columbia County: O'Leno State Park (M Deyrup), Ichetucknee Springs State Park (M Deyrup), I-75 & I-10, 0.5mi W (M Deyrup); Dade County: Coral Gables, Matheson Hammock (M Deyrup), Matheson State Park (EO Wilson); Desoto County: Arcadia, 13mi E, 2mi S of Headquarters (M Deyrup), Arcadia, W bank of Peace River (M Deyrup), Pine Level (M Deyrup); Dixie County: Jena (M Deyrup); Duval County: Jacksonville (M Deyrup), Fort George, Bis Talbot Is. State Park (Z Prusak); Escambia County: Pensacola (M Deyrup, EO Wilson); Franklin County: Carabelle Beach, 5mi W (M Deyrup); Gilchrist County: Trenton (M Deyrup); Glades County: Muse 2mi S (M Deyrup); Hardee County: Zolfo Springs (M Deyrup), Paynes Creek Historical Site (M Deyrup); Hendry County: 832 & 833, 3mi NE (M Deyrup); Hernando County: Bayport (M Deyrup); Highlands County: Archbold Biological Station (SP Cover, M Deyrup, UG Mueller, C Rabeling, TC Schneirla, NA Weber), Sebring (M Deyrup), Highlands Hammock State Park (M Deyrup), Lakemont (M Deyrup); Hillsborough County: Tampa (M Deyrup); Holmes County: Ponce de Leon Springs State Park (M Deyrup); Jackson County: Three Rivers State Recreation Area (M Deyrup), Florida Caverns State Park (M Deyrup); Lake County: Lake Louisa State Park (M Deyrup); Ocala National Forest (M Deyrup); Lee County: Koreshan State Historic Site (M Deyrup); Leon County: Apalachicola National Forest (M Deyrup), Tallahassee (AS Mikheyev); Levy County: Bronson (M Deyrup); Liberty County: Torreya State Park (M Deyrup); Madison County: I-10 & SR 53 (M. Deyrup); Manatee County: Lake Manatee Recreation Area (M Deyrup), Bradenton (M Deyrup, GD Reynolds); Marion County: Ocala National Forest (M Deyrup), Wiersdale (H Spencer); Martin County: Jonathan Dickinson State Park (WF Buren, M Deyrup, UG Mueller), Port Sewall (AL Melander); Miami-Dade County: Miami (WM Wheeler); Monroe County: Bahia Honda State Recreation Area (M Deyrup); Nassau County: Fort Clinch State Park (M Deyrup); Okaloosa County: Eglin Air Force Base (M Deyrup), Crestview (M Deyrup); Orange County: Orlando (M Deyrup), Wekiwa Springs State Park (M Deyrup, Z Prusak); Osceola County: Kenansville (M Deyrup), Kissimmee (M Deyrup); Pasco County: St. Leo (M Deyrup); Pinellas County: Fort Desoto Park (M Deyup), Belleair (AT Slosson); Polk County: Haines City (M Deyrup, DE Read), Winter Haven (C Dykes); Putnam County: Crescent (WM Mann); Santa Rosa County: Milton 10mi E (M Deyrup); Sarasota County: Venice (M Deyrup); Seminole County: Oviedo 1mi N (M Deyrup); St. Lucie County: Ft. Pierce (M Deyrup); Sumter County: Bay Hill (M Deyrup); Taylor County: Perry (M Deyrup); Volusia County: Blue Springs State Park (M Deyrup); Wakulla County: Wakulla Springs (M Deyrup); Walton County: DeFuniak Springs (M Deyrup); Washington County: Falling Water State Recreation Area (M Deyrup); GEORGIA, Lowndes County: Valdosta (AC Cole); Macon County: Marshallville (FJ Bartel); Richmond County: Ft. Gordon (RR Snelling); Ware County: Waycross (AS Mikheyev); ILLINOIS, Peoria County: Sand Ridge State Park (AS Mikheyev); Pope County: Dixon Springs State Park (AS Mikheyev); KENTUCKY, Marshall County: Kentucky Dam (WL Brown); LOUISIANA, Allen Parish, Reevers (AM Himler); Beauregard Parish: De Ridder (WF Buren); Rapides Parish: Alexandria (WF Buren); Hineston (UG Mueller); Red River Parish: Rt. 371, NE Hall Summit (UG Mueller); St. Tammany Parish: Sildell (J Mathew); Vernon Parish: LA10, mi 7 (UG Mueller); Walker County: Sam Houston National Forest (WL Brown); Webster Parish: Lake Bistineau St. Park (EG Riley), Sibley 3mi W (UG Mueller); MISSISSIPPI, Clarke County: Clarkco State Park (WP Mackay), Clay County: Cedar Bluff (AC Cole, LC Murphree); Forrest County: Hattisburg (AH Sturtevant); Hardin County: Mantee (UG Mueller); Harrison County: Gulfport (AC Cole); Lee County: Tupelo (MR Smith); Lowndes County: Columbus (MR Smith); Monroe County: Quincy (MR Smith); Oktibbeha County: Agricultural College (MR Smith), Starkville (AS Mikheyev); Stone County: Wiggins (AH Sturtevant); Wayne County: Waynesboro (AH Sturtevant); NORTH CAROLINA, Bladen County: White Oak (LR Sasser); Dare County: Roanoke Island (NA Weber); Richmond County: Hoffman

(AS Mikheyev); NEW JERSEY, Burlington County: Lebanon State Forest (AS Mikheyev), Moorestown (NJR White); Cumberland County: Bridgeton (FM Schott), Vineland (M Treat); Middlesex County: Bonhamtown (LB Woodruff); Ocean County: Howardsville (WL Brown), Lakehurst (WM Wheeler, WM Mann, R Crozier), Lakewood (FM Schott), Pine Barrens (NA Weber); NEW YORK, Suffolk County: Centereach, Long Island (AS Mikheyev); OKLAHOMA, Beckham County: Sayre (AC Cole); SOUTH CAROLINA, Dillon County: Lake View (DL Stephan); Florence County: Florence (MR Smith); Jasper County: Tillman (RA Mendez); Oconee County: Oconee State Park (MR Smith); Pickens County: Clemson College (MR Smith); TENNESSEE, Davidson County: Nashville (WS Creighton); Dickens County: Montgomery Bell Park (Pfitzer & Scott); Sevier County: Chilhowee Mtns. (AC Cole); Webster County: Shiloh National Military Park (UG Mueller); TEXAS, Anderson County: Palestine (FC Bishopp); Angelina County: Angelina National Forest (AS Mikheyev, C Rabeling); Bastrop County: Stengl Biological Station (UG Mueller, C Rabeling); Baylor County: at Brazos River, River Road (UG Mueller), 10km N Kurten (WP Mackay), College Station (EG Riley, NA Weber); Brown County: Brownwood (WD Pierce); Caldwell County: Powell Road (UG Mueller); Cass County: Atlanta State Park (JD Moody); Denton County: Denton (WH Long, WM Wheeler); Fannin County: Ivanhoe (E & G Wheeler); Fort Bend County: Sugarland, Cullinan Park (UG Mueller); Franklin County: Montichello Missionary Baptist Church (UG Mueller); Grimes County: Rt.30, 3.7mi E Carlos (UG Mueller), Shiro (WF Buren); Hardin County: Rt 327, crossing of Village Creek (UG Mueller); Lamar County: Paris (A Rucker, CJ Brues); Liberty County: Liberty (UG Mueller); Medina County: Benton, near Devine (WH Long); Milam County: Milano (WM Wheeler); Montague County: Bonita, rest area E Rt. 82 & Rt. 1815 (UG Mueller); Montgomery County: Willis (JC Bridwell); Sabine County: 9mi E Hemphill (Anderson, Riley & Moody); San Jacinto County: Rt. 2025, Lone Star Trail Head (UG Mueller); Smith County: Tyler State Park, Blackjack Nature Trail trailhead (UG Mueller); Travis County: Austin (UG Mueller, C Rabeling, WM Wheeler), Montopolis (WM Wheeler); Walker County: Huntsville (Hartman); Washington County: Washington-on-the-Brazos State Park (UG Mueller); Wise County: 7.5mi SW Bridgeport (JV Moody); Wood County: 9mi E Minneola on US 80 (JV Moody), Goodwin Woods, 3.5mi SW Hainsville (EG Riley); VIRGINIA, Appomattox County: Appomattox-Buckingham State Forest (S Rehner); Prince George County: Ft. Lee (RR Snelling); WEST VIRGINIA, Putnam County: Barcroft (JC Bridwell).

T. smithi Buren

Trachymyrmex smithi Buren, 1944: 5. Holotype worker, La Rosa, Coahuila, Mexico (LACM) [examined]. Paratype workers, same locality (AMNH, LACM, USNM) [examined]

Trachymyrmex smithi subsp. *neomexicanus* Cole, 1952: 159. Holotype worker, 6 mi N Las Cruces along Hwy US 85, New Mexico, U.S.A. (LACM) [examined], Paratype workers (AMNH, LACM, MCZC, USNM) [examined] **syn. nov.**

Trachymyrmex smithi subsp. *neomexicanus* Cole; Cole 1953: 300 [description of queen and male]

Diagnosis

Worker: HL 0.94–1.25, HW 1.0–1.375, CI 100–111, SL 0.86–1.19, SI 84–89, ML 1.25–1.69. A large, dark colored species. Head trapezoidal, almost cordate; always broader than long (HW > HL) even in the smallest workers, widest at midpoint between the eye and the posterior corner, and strongly tapering anteriorly. Posterior margin of head moderately concave, more so in larger workers. Antennal scapes short, surpassing the posterior corner of the head by its maximum diameter or less. In full-face view, frontal carinae extending almost to the posterior corners, but weakening before they reach the vertex. Preocular carinae variably developed, traversing approximately half the distance between eye and frontal carina, never touching the frontal carinae. Antennal scrobes weakly developed. In full-face view, frontal lobes small, broadly triangular, usually asymmetrical, with anterior side longer than the posterior. In dorsal view, anterolateral promesonotal

tooth thick, sharply pointed, projecting horizontally, not vertically. Anterior median promesonotal tubercles short, vertical, toothlike in frontal or posterior view. Propodeal teeth strongly divergent, spinelike and longer than the distance separating their bases. Vertex of head and gaster strongly tuberculate, remainder of body moderately tuberculate, tuberculi small, tubercular setae weakly to strongly recurved; tuberculi on sides of mesosoma miniscule and sparse. Texture of entire body surface coarse, sandpaperlike. *Trachymyrmex smithi* displays considerable color variation, ranging from grayish black or blackish brown to rarely dark red or reddish-brown.

Queen: HL 1.2, HW 1.35–1.4, CI 113–114, SL 1.05–1.1, SI 78–79, ML 1.9–2.0. As in worker diagnosis but with typical caste-specific mesosomal morphology related to wing-bearing and head with small ocelli. Dorsolateral pronotal teeth well developed, tuberculate and sharply triangulate in dorsal view. Ventrolateral pronotal teeth short, triangular, not tuberculate and pointed. Mesoscutum longitudinally rugulose, not tuberculate. Pronotal sides, mesopleura and propodeum with only a few minute tuberculi, if any. Setae abundant, short, straight and suberect. Dorsum of mesosoma, petiole, postpetiole and gaster distinctly bicolored.

Male: HL 0.81–0.84, HW 0.84–0.87, CI 100–107, SL 0.93–0.99, SI 107–118, ML 1.9–2.05. A large male with relatively long appendages and antennal scapes. Preocular carina a distinctive vertical ridge as it passes the eye and curves towards the midline, remaining strongly developed until the posteriormost portion of the "scrobe." Ocelli moderately large, slightly elevated above the remainder of the head in side view. Dorsolateral pronotal teeth very short, indistinct, or absent. Ventrolateral pronotal teeth short, triangular. Mesoscutum with weakly reticulate longitudunal rugluae, interrugal spaces granulate. First gastric tergite minutely tuberculate, with numerous, short, decumbent or suberect recurved setae.

Discussion

Trachymyrmex smithi might be confused with *T. jamaicensis* due to its large size and dark coloration, but the species are allopatric; *T. jamaicensis* is only known from southwest Florida, the Florida Keys, and the Caribbean, whereas *T. smithi* occurs in the deserts of western Texas, New Mexico, and the State of Coahuila in northern Mexico (see distribution maps). In addition, the frontal and preocular carina of *T. smithi* do not form a well developed antennal scrobe that extends back to the preoccipital margin as in *T. jamaicensis,* and the frontal lobes are triangular in *T. smithi*, not rounded, as in *T. jamacensis*.

Buren (1944) described *T. smithi* from Mexico (La Rosa, Coahuila) and Cole (1952) later based the subspecies *T. smithi neomexicanus* on workers from the United States (Las Cruces, New Mexico). Cole separated *neomexicanus* from *smithi* because it possessed larger and less tuberculate spines, a more concave posterior margin of the postpetiole, larger body size, darker color, and more abundant gray "granulation" on the integument. For a *Trachymyrmex*, *T. smithi* workers show considerable size variation and all characters, except color and the presence of granulation, vary proportionally to size. The morphological differences cited by Cole for *neomexicanus* fall well within the range of variation shown by this widely distributed species. Likewise, black, reddish-brown and intermediate color morphs are distributed over the species entire range, including the type locality (C. Rabeling personal observation). Molecular evidence also supports our contention that in *T. smithi* we are dealing with a single variable species. The short branch lengths in the molecular phylogenetic analysis (see below) show that the sequence diversity is minimal and similar for both *smithi* and *neomexicanus* (Figure 21). The more abundant gray granulation of *neomexicanus* mentioned by Cole (1952) is most likely caused by actinomycete bacteria of the genus *Pseudonocardia* (Cafaro & Currie 2005), which grow on the ant's exoskeleton. Actinomycete load on the worker's body surface varies among individuals of the same nest and is affected by worker age, characteristic activity (foraging versus garden-tending), or the health of the fungus garden. This coating is therefore of no taxonomic importance. To remove the sometimes confusing actinomycete coating, specimens can be washed with acidic acid (vinegar).

To our great surprise we encountered two holotypes of *T. smithi* Buren; one deposited in the LACM and the other in the USNM collection. Most likely, the USNM specimen was mislabeled and actually represents a

paratype, because Buren (1944, p. 6) stated that the single holotype would remain in his personal collection and paratypes would be deposited in the National Museum and his personal collection. Since the LACM accessioned the W. F. Buren collection in 1983, we here designate the holotype of *T. smithi* as the specimen deposited at the LACM.

Etymology

Buren (1944) named this species after Marion R. Smith, myrmecologist and curator of Hymenoptera at the National Museum of Natural History in Washington, DC for many years during the mid twentieth century.

Biology

Trachymyrmex smithi is a Chihuahuan Desert species that occurs in southwest Texas, south-central New Mexico, and the Mexican states of Chihuahua and Coahuila. It inhabits creosote bush bajadas (alluvial fans), mesquite/*Yucca* grassland playas (dry lakebeds) and mesquite coppice dune habitats at elevations of 1100–1500 m. Nests are often in the shade of creosote bush or Mormon tea (*Ephedra trifurca*). Older nests may have large nest mounds (~30 cm diameter) with conspicuous middens consisting of dried leaves and exhausted fungus substrate. The subterranean nests of *T. smithi* are the largest of all *Trachymyrmex* species occurring in the US. Older nests consist of more than 20–30 chambers (Johnson *et al*. 2006; Rabeling & Mueller, unpublished data) of which 50–60% contain fungus gardens in the summer. Near El Paso, Texas, the fungus gardens are nourished with entire mesquite leaflets (Johnson *et al*. 2006; Rabeling, unpublished data), and resemble the fragile fungus gardens of grass-cutting *Acromyrmex* species in South America. Colonies can be very populous; Johnson *et al*. (2006) report up to 786 workers and 6 dealate queens in one nest, and Schuhmacher and Whitford (1974) estimate 1250 workers for one colony based on mark-recapture experiments. Colony activity and the number of fungus gardens decrease from November through May (Schuhmacher & Whitford 1976). Two nests, which we partially excavated during winter, had 26 chambers per colony, reaching down to 180 and 130 cm depth, respectively. None of the chambers contained a fungus garden in December, suggesting that *T. smithi* moves its gardens to deeper layers in winter. During springtime the excavation of two adjacent colonies showed, that in April the ants already moved the fungus garden to shallower nest chambers. Numerous fungus gardens were encountered hanging from the chambers' ceilings in 25–130 cm depth. From the partially excavated winter colonies, 212 and 362 workers were collected (Rabeling & Mueller, unpublished data). *Trachymyrmex smithi* forages mostly at night during the summer months, to avoid soil temperatures exceeding 50°C during the day (Whitford 1978).

ADDITIONAL MATERIAL EXAMINED: **U.S.A.**: NEW MEXICO, Dona Ana County: 3mi NNE Las Cruces (C Rabeling), 10mi NNW Las Cruces on Hwy 185 (UG Mueller, C Rabeling, A Rodrigues), 25km NE Las Cruces, LTER site (WP Mackay), 45km NW Las Cruces (E & WP Mackay), Dona Ana Range (P Lenhart), Las Cruces (AC Cole), Mesilla Park (J Bequaert, AC Cole, WM Wheeler); Otero County: Tularosa (AC Cole); TEXAS, Brewster County: 6mi SE Panther Junction (JV Moody), Rio Grande Village (UG Mueller); El Paso County: 4.3mi NE Farbens (OF Francke, JV Moody & TB Hall), Anthony (OF Francke, JV Moody & TB Hall), Horizon City (P Lenhart), SW Hueco Mtns. (P Lenhart), UTEP campus (P Lenhart); Pecos County: Fort Stockton (AC Cole); Presidio County: 22mi N Candelaria (OF Francke, JV Moody & TB Hall), Presidio County: 26.2mi N Candelaria (OF Francke, JV Moody & TB Hall), Presidio Co: 34mi SE Presidio (OF Francke, JV Moody & TB Hall); **MEXICO**: CHIHUAHUA, Chihuahua (E & WP Mackay); COAHUILA, La Rosa (C Rabeling).

***T. turrifex* (Wheeler)**

Atta (Trachymyrmex) turrifex Wheeler, 1903: 100. Syntype workers and queens, Marfa, Presidio County; Fort Stockton, Pecos County; Del Rio and Langtry, Valverde County; Marble Falls, Burnet County; Austin, Travis County; Texas,

U.S.A. (AMNH, MCZC, USNM) [examined]
Trachymyrmex turrifex Wheeler; Gallardo 1916: 242 [Combination in *Trachymyrmex*]
Atta (Trachymyrmex) turrifex subsp. *caroli* Wheeler, 1911: 248. Syntype workers, Huntsville, Walker County, Texas, U.S.A. (repository unknown) [not examined] **syn. nov.**
Trachymyrmex turrifex caroli (Wheeler), Creighton 1950: 324 [Combination in *Trachymyrmex*]

Diagnosis

Worker: HL 0.88–1.0, HW 0.8–0.96, CI 91–96, SL 0.72–0.8, SI 83–91, ML 1.2–1.4. A medium sized, species (HL 0.88–1.0, HW 0.8–0.96) with the shortest antennal scapes (SI 83–91) relative to head width of all US *Trachymyrmex* species. The scapes reach or pass the posterior corner of the head by half its maximum diameter at most. Head slightly longer than broad (CI 91–96) with its maximum width close to the posterior border of head, tapering gradually from point of broadest width to mandibular insertion. Posterior margin moderately concave. Both preocular and frontal carinae long and subparallel, reaching back towards the posterior margin of head, forming well-developed antennal scrobes. In full face view, frontal lobes broad, rounded, describing a half circle. Anterolateral promesonotal teeth short, thin, in dorsal view sharply pointed, directed anterolaterally and upwards. Bases of median pronotal teeth fused, but the peaks of each tooth still distinguishable. Propodeal teeth pointed, almost twice as long as the distance between their bases. Dorsal body surface strongly tuberculate, tuberculi well developed, on first gastric tergite, sometimes connected through ridges. Tuberculi bearing long, dark, strongly recurved setae. Side of mesosoma less tuberculate, tuberculi smaller. Color is variable from yellowish brown to medium reddish brown.

Queen: HL 1.1–1.2, HW 1.1–1.2, CI 100, SL 0.85–1.0, SI 71–87, ML 1.7–1.8. As in the worker diagnosis, except for case-specific structures of the mesosoma related to wing-bearing. Dorsoventral pronotal teeth pointed, broadly triangular in dorsal view; ventrolateral pronotal teeth small, lobelike. Mesoscutum with moderately abundant, short, coarse, longitudinal rugulae and abundant small tuberculi, each bearing a stiff, more or less recurved suberect or decumbent seta. Rear border of scutellum projecting posteriorly as two lobelike teeth. First gastric tergite covered with small tubercles interconnected by a network of fine rugulae forming an almost geometric pattern; each tubercle bearing a stiff, recurved, decumbent setae.

Male: HL 0.7–0.75, HW 0.6, CI 80–86, SL 0.7–0.75, SI 117–125, ML 1.5–1.6. A distinctive *Trachymyrmex* male easily recognized by the general lack of tuberculi on all body surfaces. In addition, the rear border of the antennal scrobe is poorly defined or absent. Dorsoventral pronotal teeth small, triangular, usually sharply pointed; ventrolateral pronotal teeth absent. Mesoscutum sparsely to moderately longitudinally rugulose, interrugal spaces finely granulate. In dorsal view, rear border of scutellum forming two triangular teeth that project posteriorly. First gastric tergite finely granulate with scattered punctures bearing fine, appressed recurved setae.

Discussion

Trachymyrmex turrifex is distinguished from other North American species by its well-developed antennal scrobes. Only the allopatric *T. jamaicensis* has comparably developed antennal scrobes, but it may be easily distinguished from *T. turrifex* by its larger size, reddish-black coloration and shorter clypeal pilosity (as described in the key).

Trachymyrmex turrifex is distributed throughout Texas, northeastern Mexico, western Louisiana, and barely reaches southern Oklahoma. Individuals are somewhat variable in size, and color varies from light yellowish brown to dark reddish-brown. Wheeler (1903) described *turrifex* from several localities in Central Texas, and *T. turrifex caroli* as a subspecies of *T. turrifex* from Huntsville, Texas (1911). Wheeler's reasoning was that *caroli* "represents a depauperate, arenicolous race ranging considerably eastwards of the typical *turrifex"* (Wheeler 1911, p. 248). Wheeler distinguished between these two "subspecies" based on the smaller body size, brownish yellow coloration, smaller tubercles, and lack of longitudinal impression on first gastric tergite in *T. turrifex caroli*. In our experience, all of these character states fall well within the variation observed within and among colonies of typical *turrifex*, as seen throughout its known geographic range,

which now extends to western Louisiana and places Huntsville towards the center of *T. turrifex*'s distribution (Figure 24C). Since we were not able to locate Wheeler's type specimens of *T. turrifex caroli*, we collected fresh material at the type locality in Huntsville, Texas. These specimens were morphologically not different from other examined *turrifex*. Lastly, our DNA sequence information indicates that *caroli* is also genetically not distinct from *turrifex* (Figure 21). We therefore synonymize *T. turrifex caroli* with *T. turrifex*.

Etymology

The epithet for *T. turrifex* is derived from its characteristic turretlike nest entrances, which are built from soil particles and leaf litter debris.

Biology

The geographic range of *T. turrifex* is centered in Texas and extends into southern Oklahoma, western Louisiana, and south into the Mexican States of Chihuahua and Tamaulipas (Figure 24C). *T. turrifex* is abundant in open desert habitats of west Texas, the black clay soils of central Texas and is somewhat less abundant in the sandy soils of eastern Texas and western Louisiana. Dense populations occur in southern Texas, particularly in the Rio Grande Valley. When occurring sympatrically in sandy soils with *T. septentrionalis*, *T. turrifex* is less abundant, but the reverse pattern occurs in black clay soils where *turrifex* is usually more common than *septentrionalis*. The characteristic turretlike nest entrances, which are built from soil particles and plant litter debris during the wetter parts of the year, are a diagnostic character for *turrifex* in the field. Turrets are absent during winter dormancy and are reduced or absent in summer, particularly after a period of drought. Nests consist of 1–5 chambers, which are connected by vertical tunnels. Colonies are monogynous and contain up to 300 workers.

ADDITIONAL MATERIAL EXAMINED: **U.S.A.**: LOUISIANA, Beauregard Parish: De Ridder (WF Buren); Rapides Parish: Alexandria (WF Buren); Vernon Parish: 7mi E Pickering (UG Mueller); Webster Parish: 3mi W Sibley (UG Mueller); OKLAHOMA, Love County: I35 & Red River, 200m N (UG Mueller); TEXAS, Austin County: Rt. 3013 crossing San Bernard River (UG Mueller); Bastrop County: Stengl Biological Station (UG Mueller, C Rabeling); Baylor County: Round Timber (UG Mueller); Blanco County: Rt. 3232, 3mi N Rt. 290 (UG Mueller), Pedernales State Park (UG Mueller, C Rabeling); Brewster County: 18mi NE Marathon (OF Francke, JV Moody & TB Hall), 6mi E Alpine (OF Francke, JV Moody & TB Hall), 6mi SE Panther Junction (OF Francke, JV Moody & TB Hall); Brooks County: Falfurrias (TFM McGehee); Burnet County: Inks Lake State Park (NA Weber), Cameron County: Brownsville (UG Mueller), Harlingen (WF Buren, BC Stephenson), La Feria (WS Creighton, PT Riherd, RR Snelling), Resaca de Palma State Park (UG Mueller), Santa Rosa (UG Mueller), South Padre Island, Isla Blanca State Park (UG Mueller); Crass County: Atlanta State Park (JV Moody); Colorado County: Columbus (WF Buren); Crockett County: 15mi S Rankin (OF Francke, JV Moody & TB Hall), Ozona (AC Cole); Crosby County: 10mi S Crosbytown (OF Francke, JV Moody & TB Hall); Culberson County: Guadalupe Mountains Nat. Park (OF Francke, JV Moody & TB Hall); Denton County: 8mi W Lewisville (JV Moody), Ray Roberts Lake State Park (UG Mueller); Dickens County: 13.5mi N Dickens (OF Francke, JV Moody & TB Hall); Dimmit County: 15mi NW Carrizo Springs (OF Francke, JV Moody & TB Hall); Donley County: 4mi N Clarendon (OF Francke, JV Moody & TB Hall); Fisher County: 5.2mi N Rotan (OF Francke, JV Moody & TB Hall); Floyd County: 4.5mi S Floydada (OF Francke, JV Moody & TB Hall); Franklin County: I-30 to Mt. Pleasant (UG Mueller); Garza County: 2mi SW Post (OF Francke, JV Moody & TB Hall); Gillespie County: 10.1mi N Fredericksburg (Bartell & Beckham); Grayson County: Eisenhower State Park (JV Moody); Hall County: 6mi SE Turkey (CW O'Brian); Hardeman County: Copper Breaks State Park (UG Mueller); Haskell County: 13.3mi NE Haskell (Bartell, Beckham, Cooper, Henderson & Neece); Henderson County: Walnut Creek (WM Wheeler); Hidalgo County: Bentsen-Rio Grande Valley State Park (UG Mueller, C Rabeling), Edinburgh (WL Sterling), Weslaco (WM Buren), Monte Cristo Tract (UG Mueller); Hood County: Granbury (UG Mueller); Howard County: 11mi NW Big Springs

(OF Francke, JV Moody & TB Hall); Irion County: 22mi N Barnhart (OF Francke, JV Moody & TB Hall); Jeff Davis County: 4mi S Fort Davis (OF Francke, JV Moody & TB Hall), Davis Mtns. (AC Cole); Kendall County: 3.9mi SW Boerne (Bartell & Beckham); Kenedy County: 2mi N Sarita (UG Mueller); Kent County: 5mi SW Clairemont (JV Moody); Knox County: Rt.266 & Brazos River (UG Mueller); Lee County: Lake Somerville State Park (UG Mueller); Llano County: Kingsland (UG Mueller); Lubbock County: Lubbock (JV Moody); Maverick County: 11.5mi SE Eagle Pass (OF Francke, JV Moody & TB Hall); Medina County: Natalia, I-35 Rest Area (UG Mueller); Midland County: 17mi S Midland (OF Francke, JV Moody & TB Hall); Montague County: Lake Nacona (UG Mueller); Motley County: 4mi NW Matador (OF Francke, JV Moody & TB Hall); Nolan County: 18.6mi S Sweetwater (OF Francke, JV Moody & TB Hall); Palo Pinto County: Oaks Crossing (UG Mueller); Pecos County: Fort Stockton (AC Cole); Refugio County: Refugio, Mission River Park (UG Mueller); Robertson County: 3.1mi NE Jct. OSR & FM1940 (SJ Merritt); Salle County: Millet (UG Mueller); Scurry County: 7.mi W Ira (WD Wisdom); Smith County: Tyler State Park (UG Mueller); Starr County: Falcon State Park (UG Mueller); Tom Green County: 15mi NW San Angelo (OF Francke, JV Moody & TB Hall); Travis County: Austin (MH Long, UG Mueller, C Rabeling, JJ Scott), Bull Creek Park (UG Mueller, C Rabeling), Hamilton Pool Reserve (UG Mueller, C Rabeling); Upshur County: Rhonesboro (UG Mueller); Uvalde County: Uvalde (ACF Hung, UG Mueller), Val Verde County: Del Rio (UG Mueller); Walker County: Huntsville (C Rabeling & UG Mueller); Washington County: Washington-on-the-Brazos State Park (UG Mueller); Webb County: 52.5mi N Laredo (OF Francke, JV Moody & TB Hall); Willacy County: 0.7mi S Kenedy County border (UG Mueller); Wise County: 7.5mi SW Bridgeport (JV Moody); Wood County: 9mi E Minneola on US 80 (JV Moody); Young County: Fort Belknap (UG Mueller); Zapata County: Falcon State Park (UG Mueller); Zava County: Pryor (UG Mueller); **MEXICO**: NUEVO LEON, Vallecillo (E Buren); TAMAULIPAS, near Cuidad Victoria (Flores-Maldonado).

GENERAL DISCUSSION

The taxonomy of the genus *Trachymyrmex* is slowly being clarified (Mayhé-Nunes & Brandão 2002, 2005, 2007), following years of confusion caused in part by insufficient collections of most taxa and by the failure to discover reliable species-level characters, a task made difficult by the notable variation in morphology and color seen within many *Trachymyrmex* species. The present study identifies nine *Trachymyrmex* species occurring in North America north of the Mexican border. Reliable delineation of species boundaries was possible due to the collection of large numbers of nest series in recent years by several collectors, including the authors. The new material has enabled us to re-evaluate the morphology of each species and to assemble an independent molecular dataset addressing between- and within-species variation.

The molecular data confirms the genetic distinctness of each of the nine species in the context of the North American fauna (Fig. 21). It also reveals that morphological similarity is not necessarily an indicator of a close genetic relationship. Of the *Trachymyrmex* covered in this study, there are two pairs of species (*carinatus*/*septentrionalis* and *pomonae*/*desertorum*) that show close overall morphological similarity. The molecular information reveals, however, that the species within each of the two pairs are not closely related.

We purposely analyzed our molecular data without choosing an outgroup for two reasons. *Trachymyrmex* may not be monophyletic (Schultz & Meier 1995), and our sampling is paraphyletic by definition because we studied only a fraction of the total number of species in the genus occurring at the northern limit of its distribution. A phylogenetic analysis of the tribe Attini based on several protein-coding genes by Schultz and coworkers (Schultz personal communication) suggests that *Trachymyrmex* is polyphyletic and paraphyletic with respect to *Sericomyrmex*. On the other hand Mayhé-Nunes and Brandão (2002) interpret the tubercular mesosomal projections as an autapomorphy of *Trachymyrmex*, suggesting monophyly of the genus. Our data cannot resolve these conflicting hypotheses; a more extensive study combining molecular and morphological

data for a representative sampling of both *Trachymyrmex* and *Sericomyrmex* will be necessary to resolve this problem. North American *Trachymyrmex* are clearly thermophilic and are adapted to life in warm, arid climates. Seven of nine species occur in the deserts of southwest USA, including Arizona, New Mexico, Texas, and extending into northern Mexico. All these *Trachymyrmex* species occur in warm desert, desert-scrub, or seasonally dry mid-elevation habitats. Winters are short, mild, and usually dry. As one might expect, these *Trachymyrmex* show life-history features similar to those of many other dry climate ants. They construct moderately deep nests that buffer the ants and their gardens from surface temperature changes and the effects of prolonged dry spells. During periods of severe drought and low foraging success, these *Trachymyrmex* species often become inactive and seal their nests for extended periods. The ants also respond strongly to the return of favorable conditions, foraging and excavating vigorously while soil is moist. Lastly, mating flights are triggered by summer rains, when conditions become favorable for founding queens to start new nests. The two *Trachymyrmex* species found in the eastern US are also associated with warm, seasonally dry habitats. *Trachymyrmex jamaicensis* is a tropical species that extends into southern Florida from the Caribbean region. It occurs primarily in coastal scrub or hammock vegetation on soils derived from coralline rock. These soils are extremely well-drained and are very dry for much of the year. In this respect, they provide conditions broadly similar to those encountered by the *Trachymyrmex* in the southwest.

In *T. septentrionalis*, however, we encounter something quite different. This ant is unique within the genus in that it is fully adapted for life in temperate climates. During the winter, the ants become completely dormant and brood production ceases. Likewise, the fungus garden assumes a dormant state and gradually decreases in size as the ants cease to add substrate. The ants may even collapse the gardens to a few fungus fragments that the ants hold in their mandibles and which are used as starter cultures for spring gardens. As far as we know, this phenomenon is unique among the Attini. Despite this unique response to cold conditions, *T. septentrionalis* shows a strong preference for warm, well-drained soils and seasonally dry habitats; in this respect, *T. septentrionalis* behaves like the desert-adapted *Trachymyrmex* discussed above.

Why are all North American *Trachymyrmex* associated with well-drained soils and relatively open habitats? This preference is clearly not characteristic of the genus as a whole, and appears to have been derived during the northward expansion of the genus throughout Mexico and into the US. In the Neotropics, in contrast, *Trachymyrmex* species reach their highest diversity in lowland rainforests with weak seasonality, relatively constant moisture, and water-retentive, clay soils (Rabeling, unpublished data). We offer the following tentative reflections on the biogeography of the North American *Trachymyrmex* species, and the evolutionary changes during the northward expansion from the Neotropics into subtropical and temperate zones:

1) If high temperatures are sufficiently stable for uninterrupted fungiculture and brood rearing, as is true for most of the lowland Neotropics, *Trachymyrmex* apparently have little difficulty coping with abundant soil moisture.

2) *Trachymyrmex* are successful in drier climates, as in the southwestern US, because they evolved behavioral adaptations to regulate the microclimate within their nest chambers (e.g. by placing chambers deep in the soil, as in *T. desertorum* and *T. smithi*), thereby reducing mortality when soil moisture levels are low at the surface. It is even possible that the fungus cultivars evolved physiological adaptations for temperate conditions, like cold-hardiness or desiccation tolerance, enhancing survival during unfavorable seasons. Perhaps because of such adaptations, aridity has been no barrier to the radiation of the genus into subtropical and temperate regions, like northern Mexico and the southern United States.

3) As *Trachymyrmex* moved north and colonized areas with an ever more pronounced winter season, their preference for arid habitats and well-drained soils may have been an adaptive advantage, maximizing the length of the warm, active season while simultaneously minimizing the period during the year when soil temperatures are cool (or cold) and soil moisture is high.

4) Colonization of truly temperate areas with long, cold winters (e.g.: Illinois) was made possible by the evolution of the unique garden reduction seen in winter in the fungus gardens of *T. septentrionalis*. This win-

ter dormancy apparently serves to preserve the fungus culture when the ants are torpid themselves, and thus are unable to care for full-grown gardens. These behavioral adaptations of the ants and possible physiological adaptations of the cultivars during winter may enable the fungus to endure cold and wet conditions that might be lethal to actively growing gardens.

With this taxonomic revision, we hope to make the North American *Trachymyrmex* species accessible for further studies by other biologists. Experimental research testing the hypothesis of cold-hardiness and/or desiccation resistance of *Trachymyrmex* fungi would be particularly interesting areas of research; or to say it with the timeless words of W. M. Wheeler: "The study of the Attini [...] has only just begun, and further advances in this fascinating subject will be more difficult for the mycologist than for the entomologist" (Wheeler 1910, p. 338).

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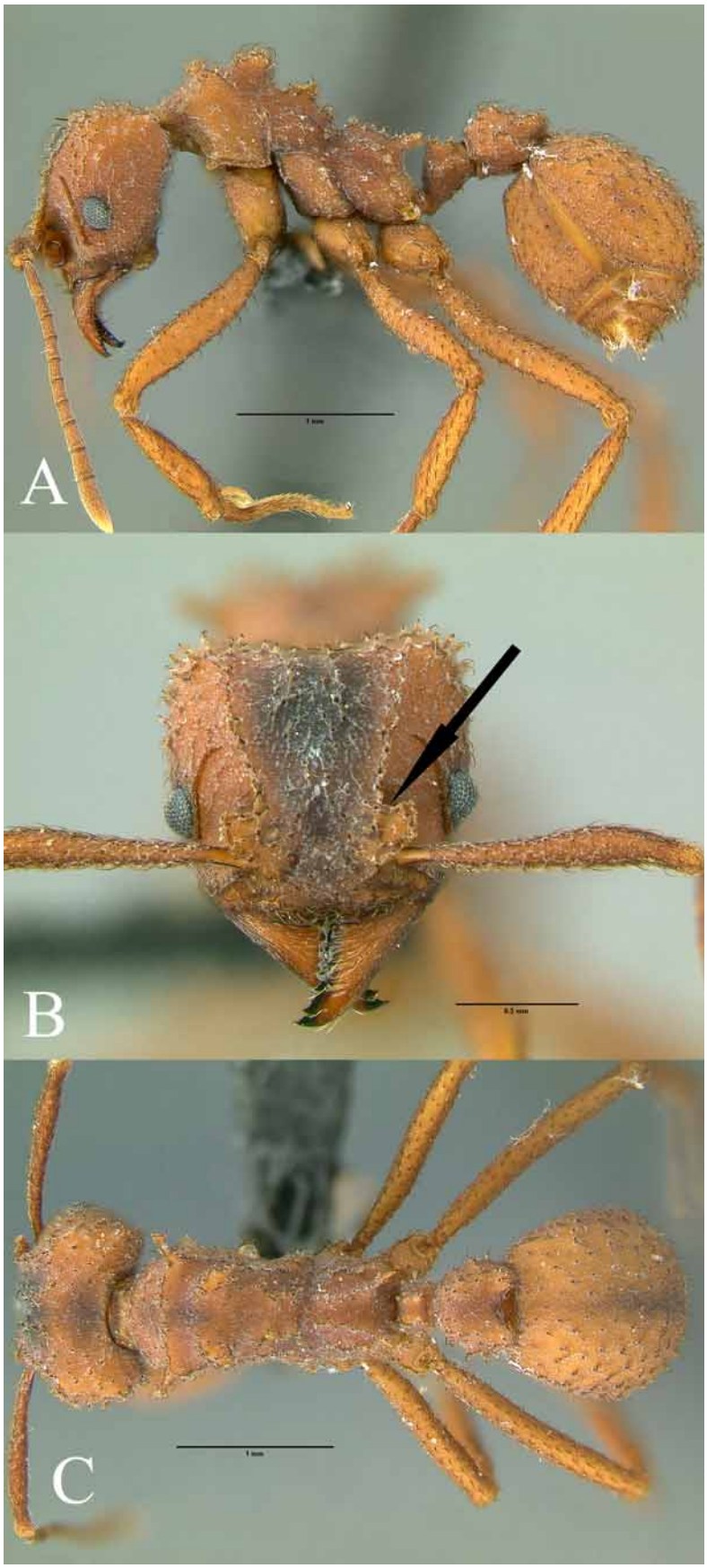

FIGURE 1: *Trachymyrmex arizonensis* worker in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 1 mm, 0.5 mm and 1 mm in part (a), (b) and (c), respectively.

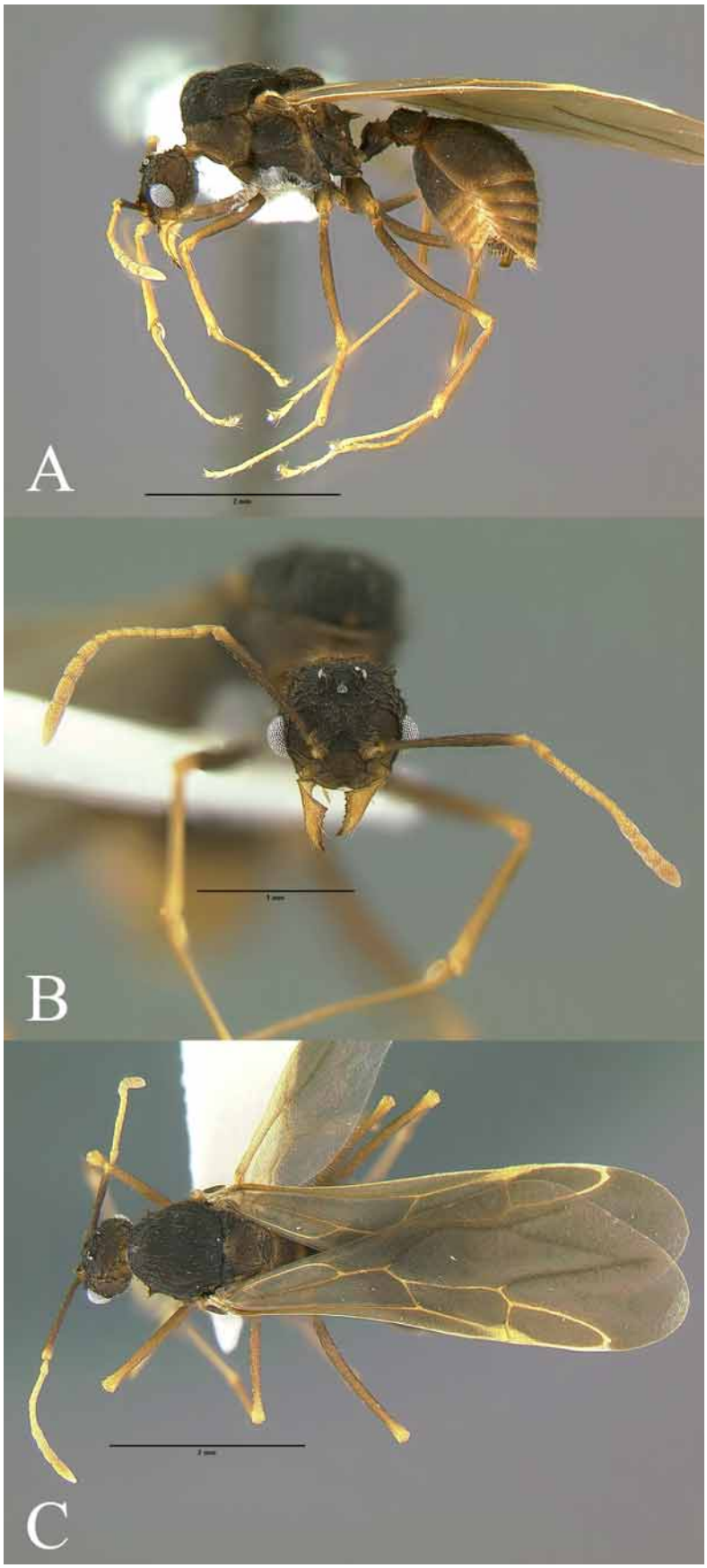

FIGURE 2: *Trachymyrmex arizonensis* male in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 2 mm, 1 mm and 2 mm in part (a), (b) and (c), respectively.

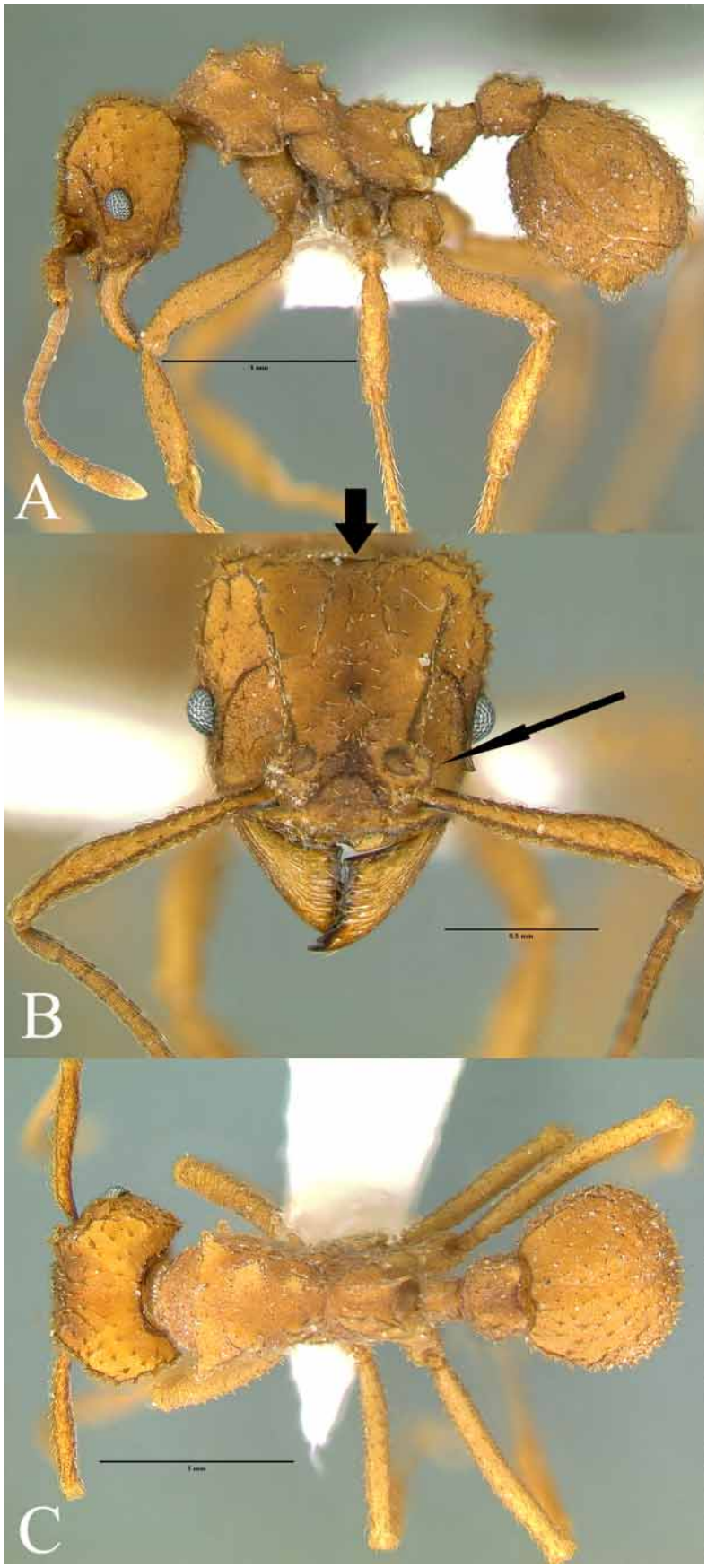

FIGURE 3: *Trachymyrmex carinatus* worker in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 1 mm, 0.5 mm and 1 mm in part (a), (b) and (c), respectively.

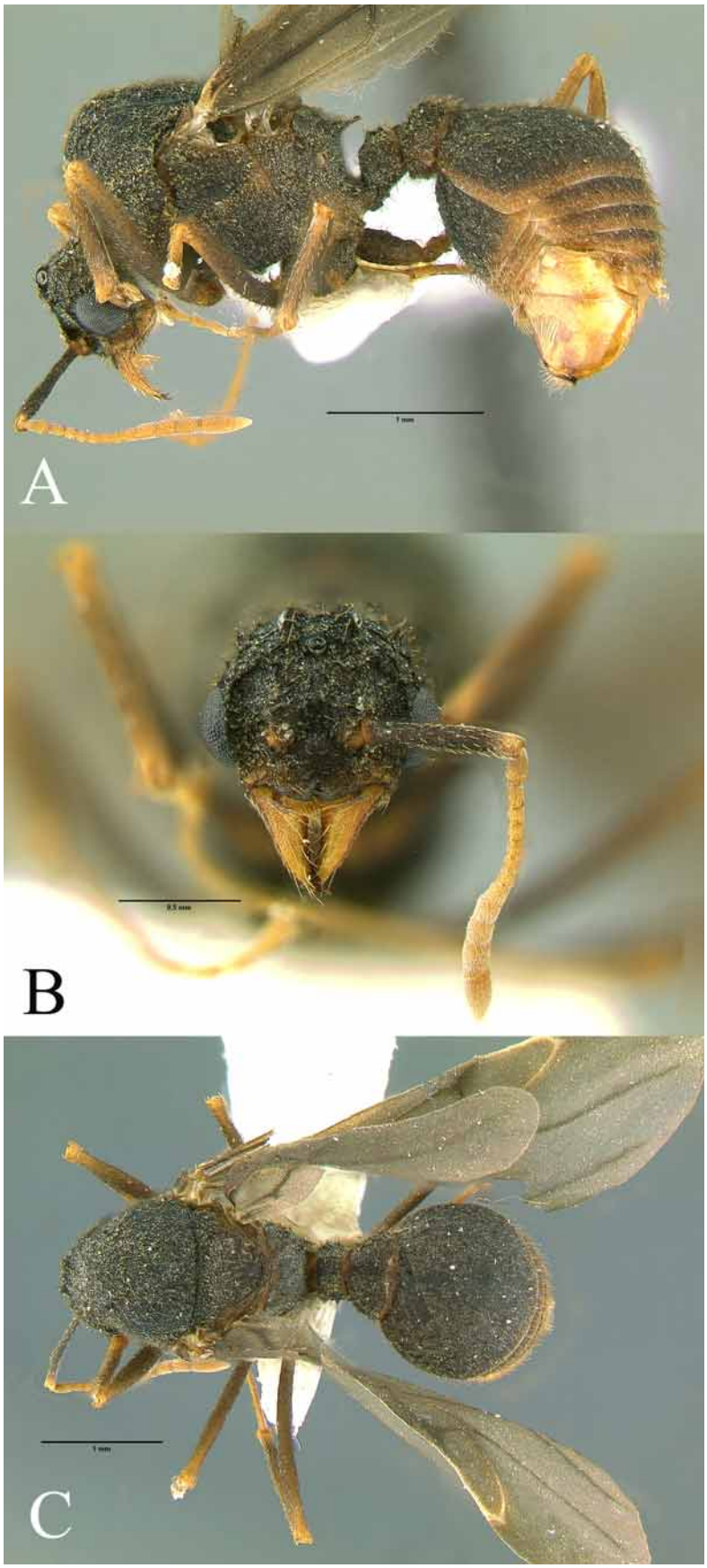

FIGURE 4: *Trachymyrmex carinatus* male in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 1 mm, 0.5 mm and 1 mm in part (a), (b) and (c), respectively.

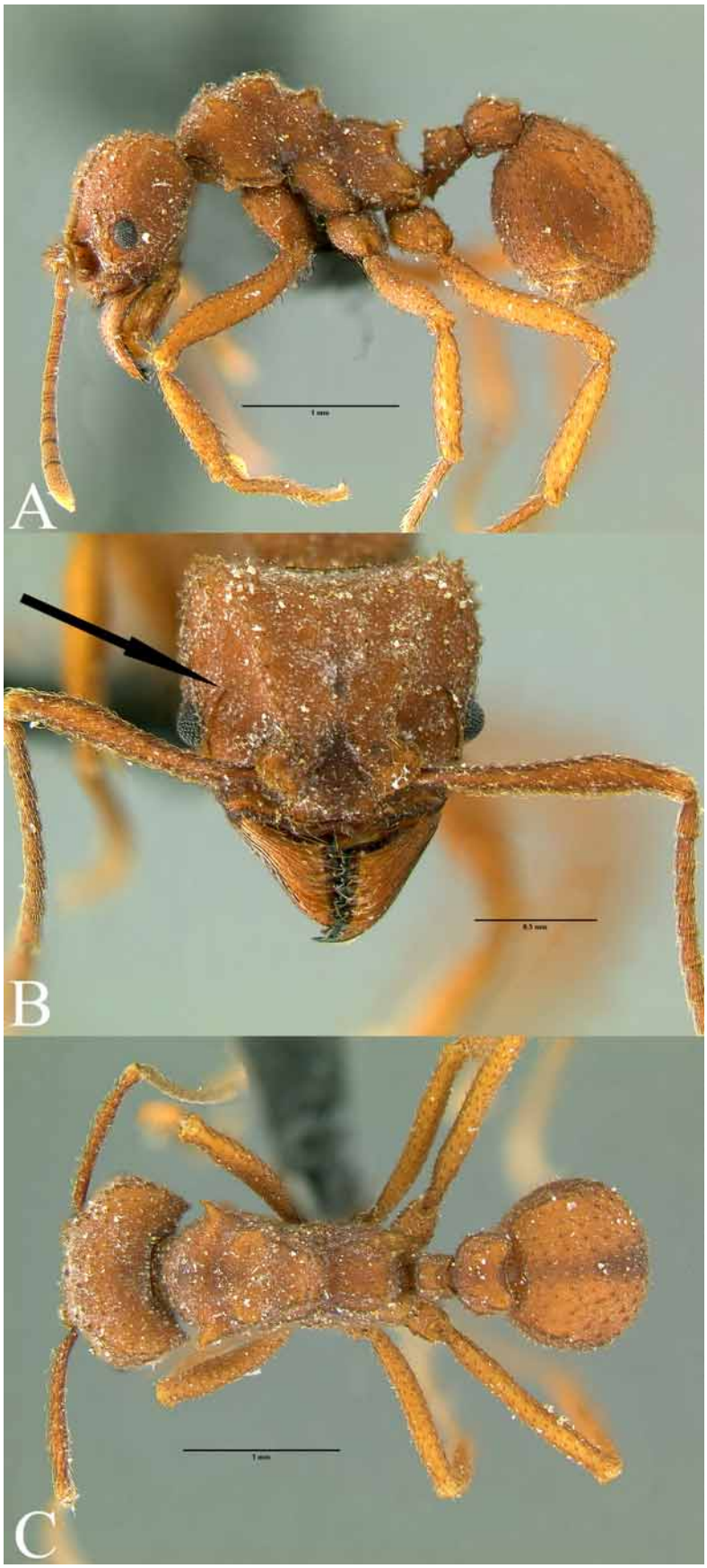

FIGURE 5: *Trachymyrmex desertorum* worker in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 1 mm, 0.5 mm and 1 mm in part (a), (b) and (c), respectively.

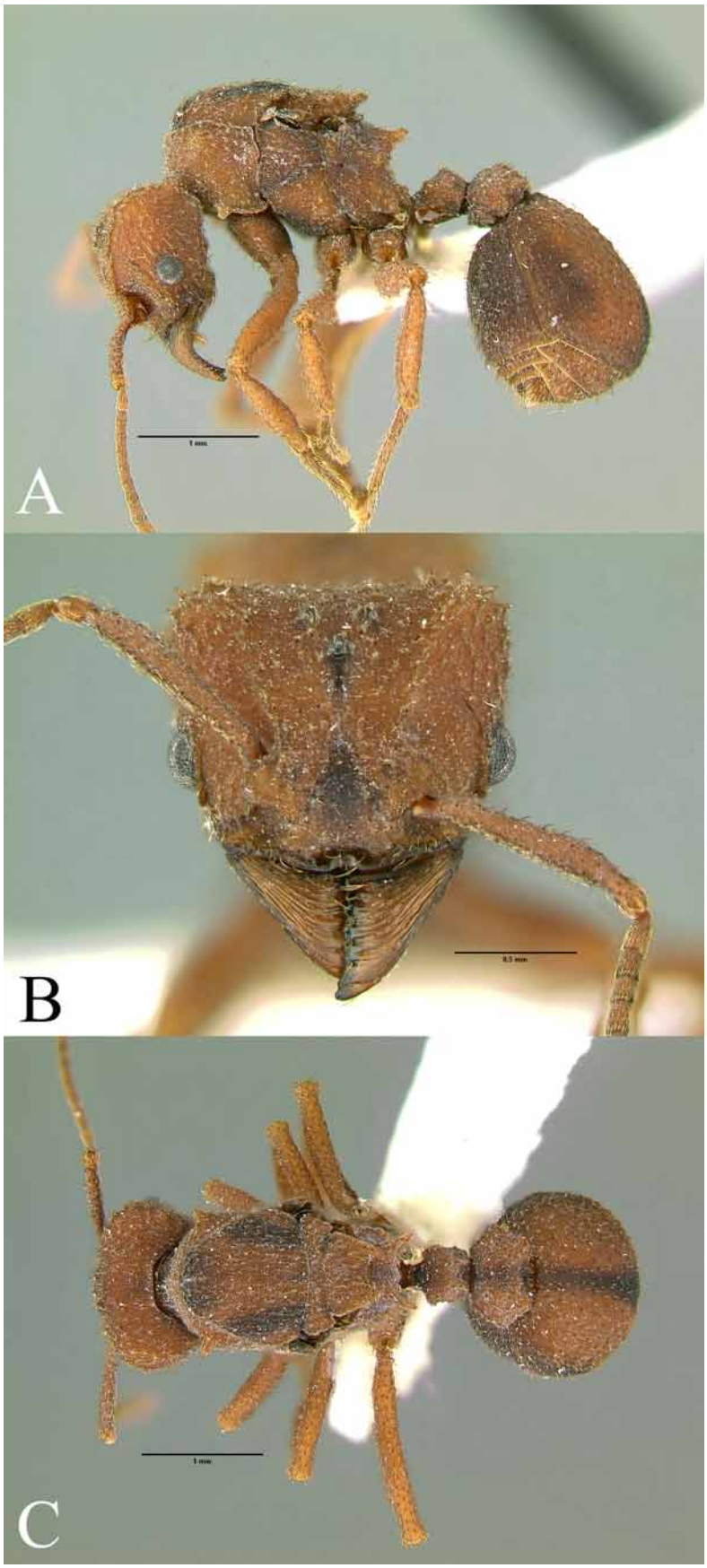

FIGURE 6: *Trachymyrmex desertorum* queen in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 1 mm, 0.5 mm and 1 mm in part (a), (b) and (c), respectively.

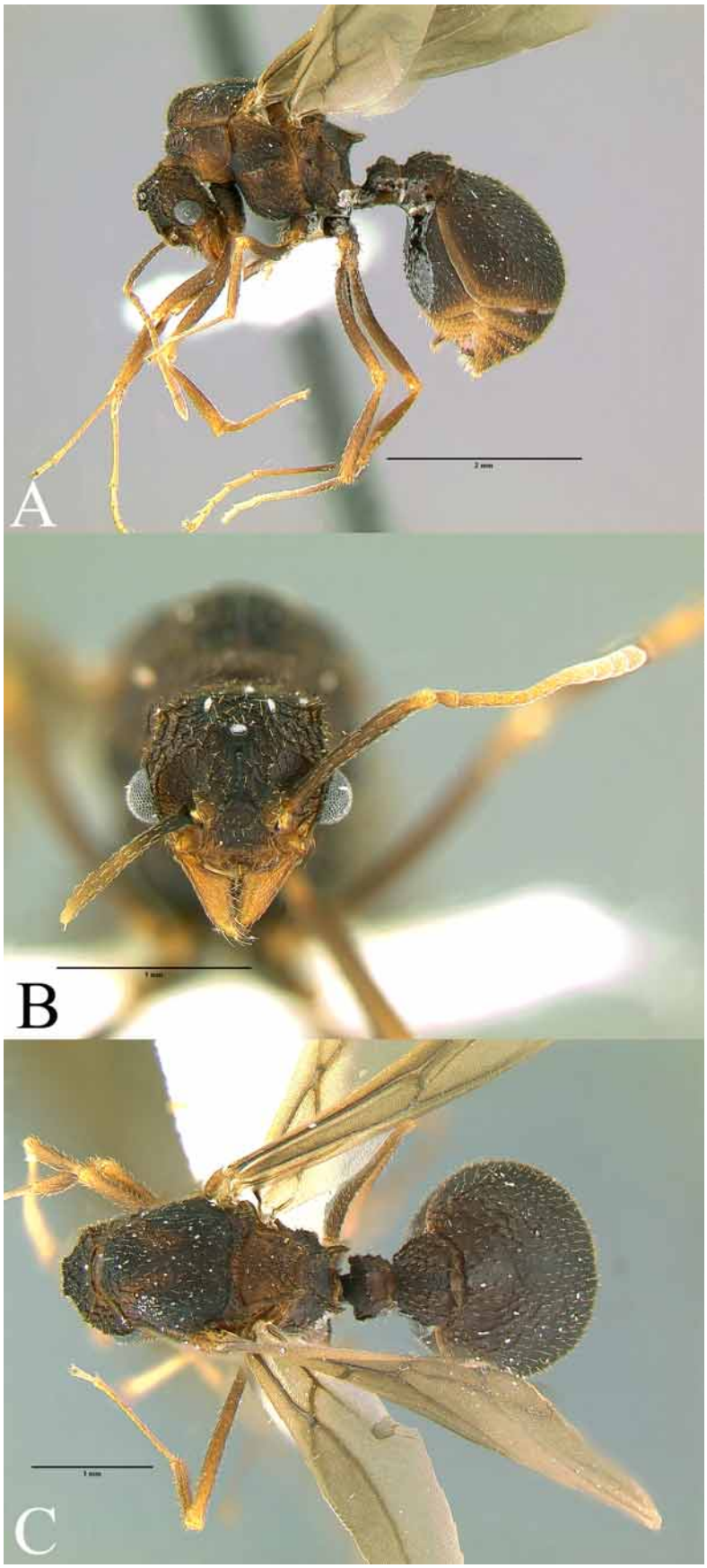

FIGURE 7: *Trachymyrmex desertorum* male in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 2 mm, 1 mm and 1 mm in part (a), (b) and (c), respectively.

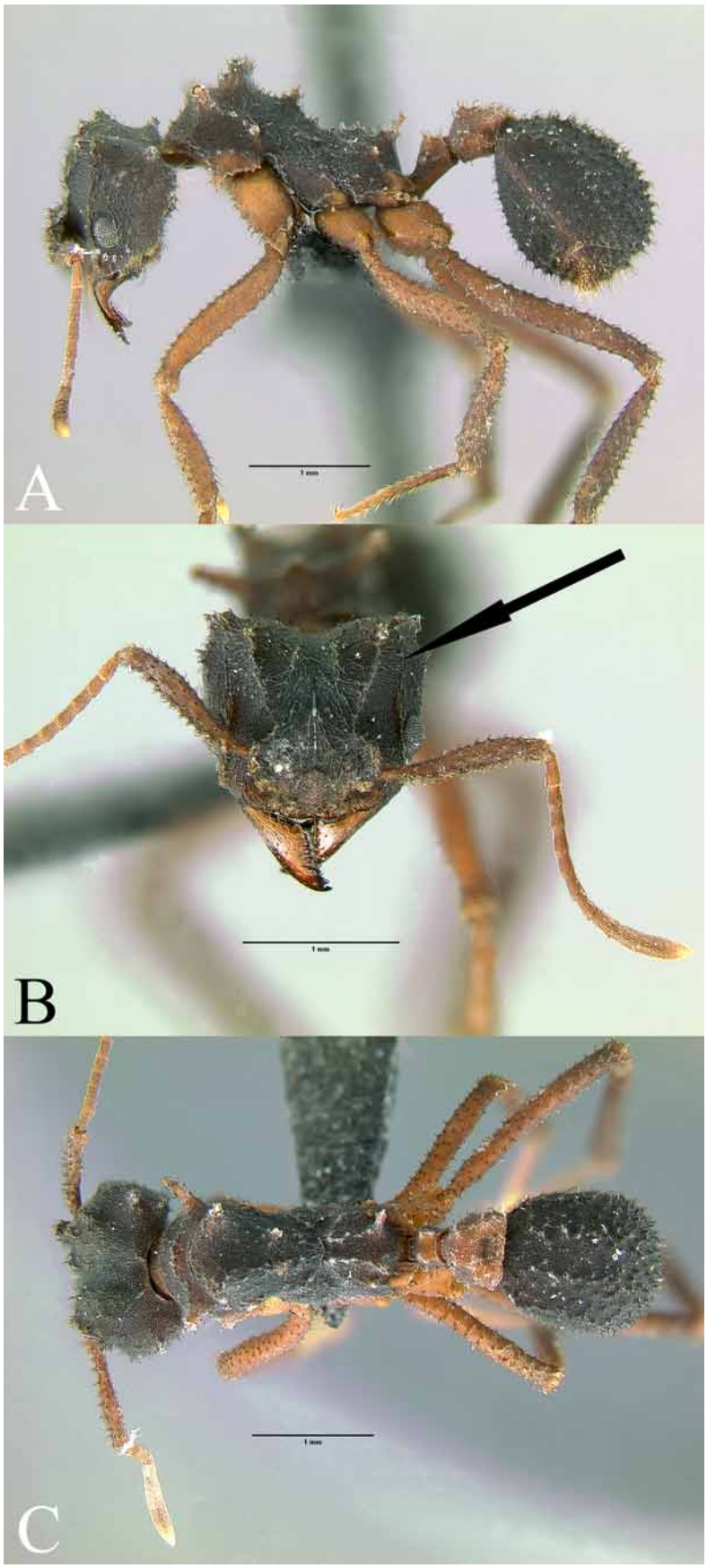

FIGURE 8: *Trachymyrmex jamaicensis* worker in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 1 mm in each part of the figure.

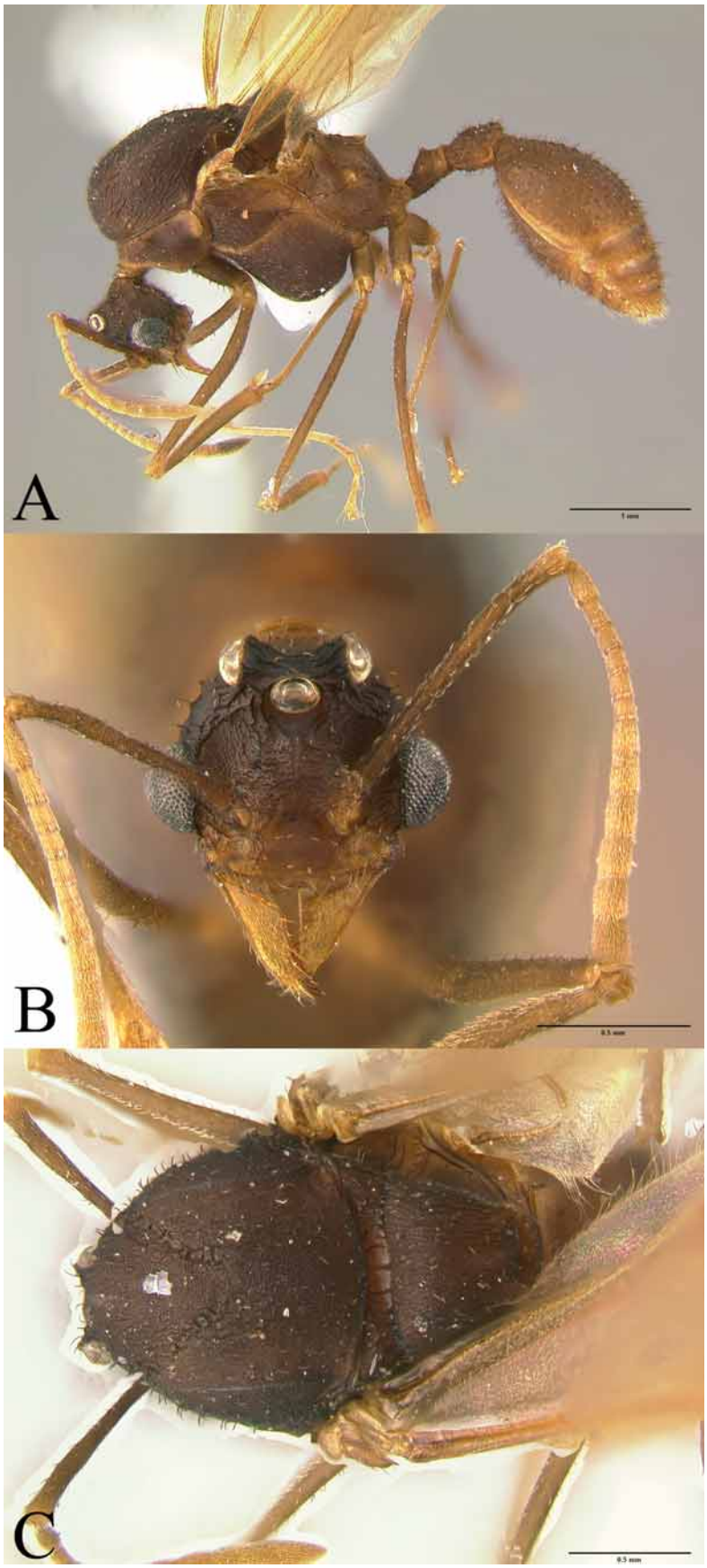

FIGURE 9: *Trachymyrmex jamaicensis* male in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 1 mm, 0.5 mm and 0.5 mm in part (a), (b) and (c), respectively.

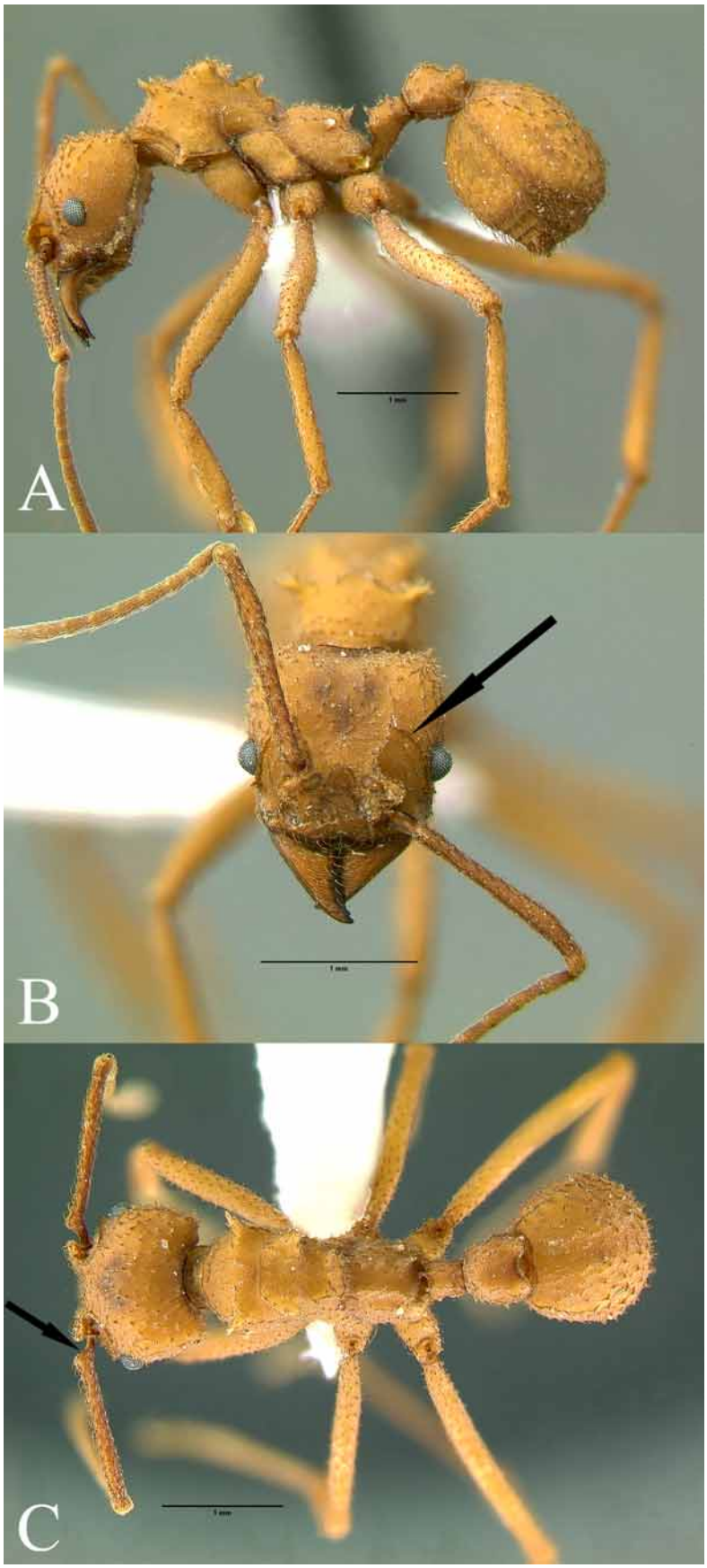

FIGURE 10: *Trachymyrmex nogalensis* worker in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 1 mm in each part of the figure.

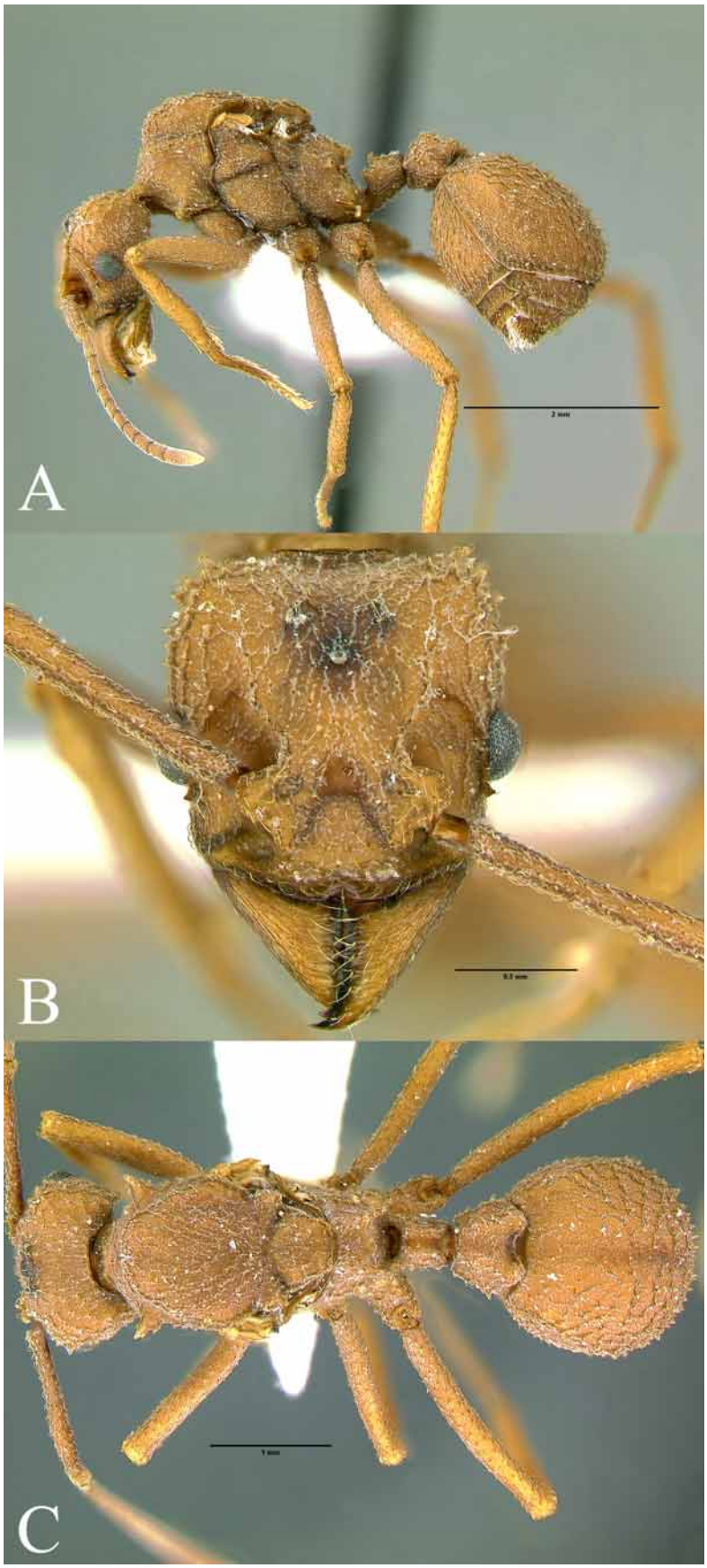

FIGURE 11: *Trachymyrmex nogalensis* queen in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 2 mm, 0.5 mm and 1 mm in part (a), (b) and (c), respectively.

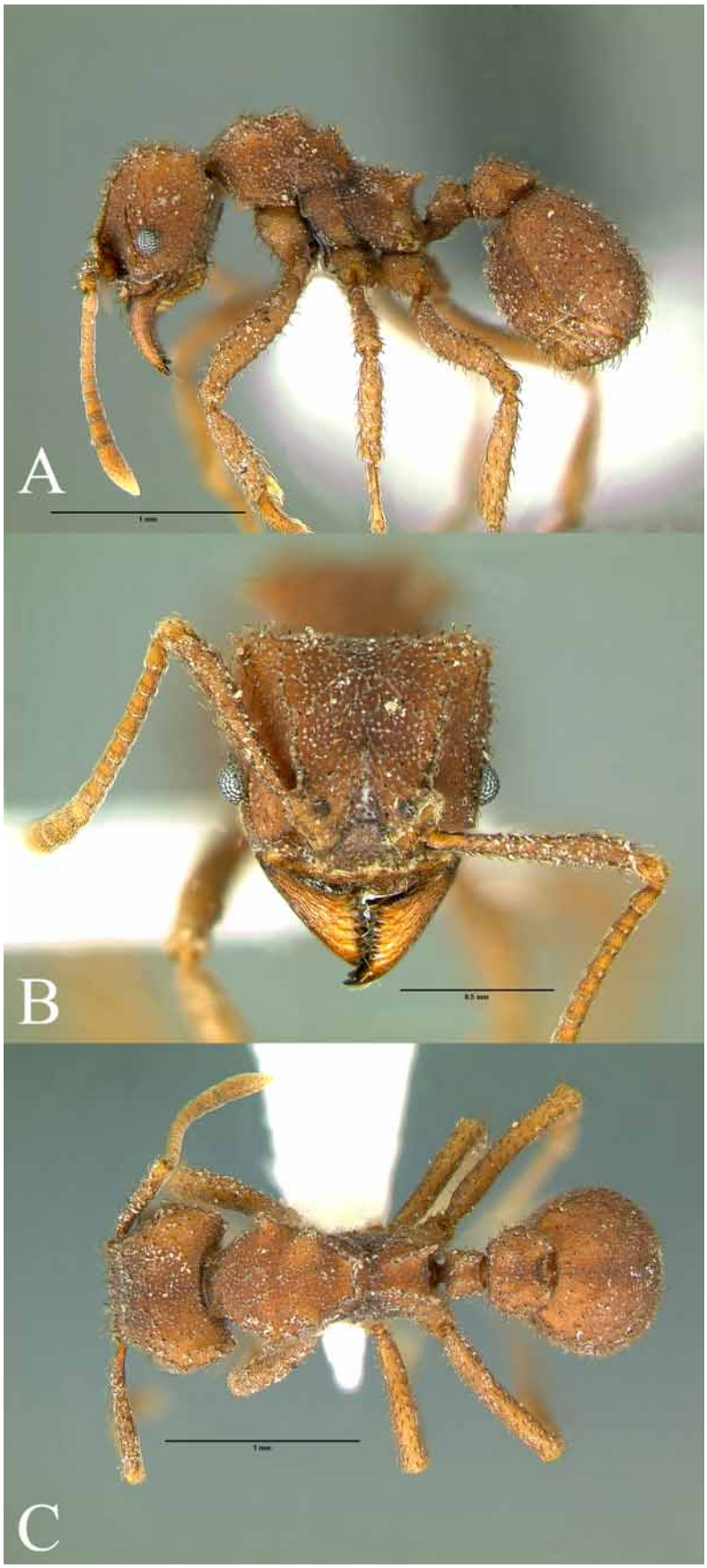

FIGURE 12: *Trachymyrmex pomonae* Holotype worker in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 1 mm, 0.5 mm and 1 mm in part (a), (b) and (c), respectively.

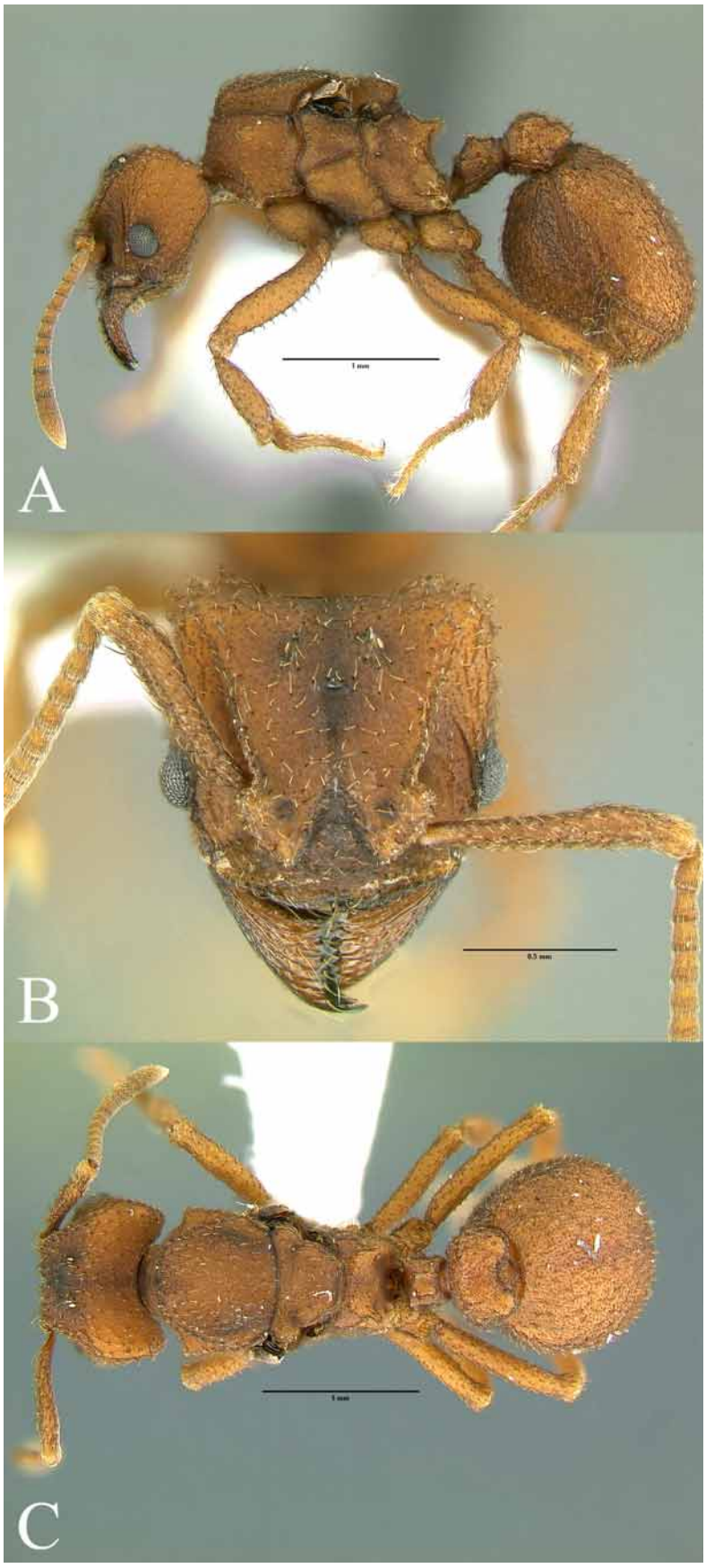

FIGURE 13: *Trachymyrmex pomonae* Paratype queen in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 1 mm, 0.5 mm and 1 mm in part (a), (b) and (c), respectively.

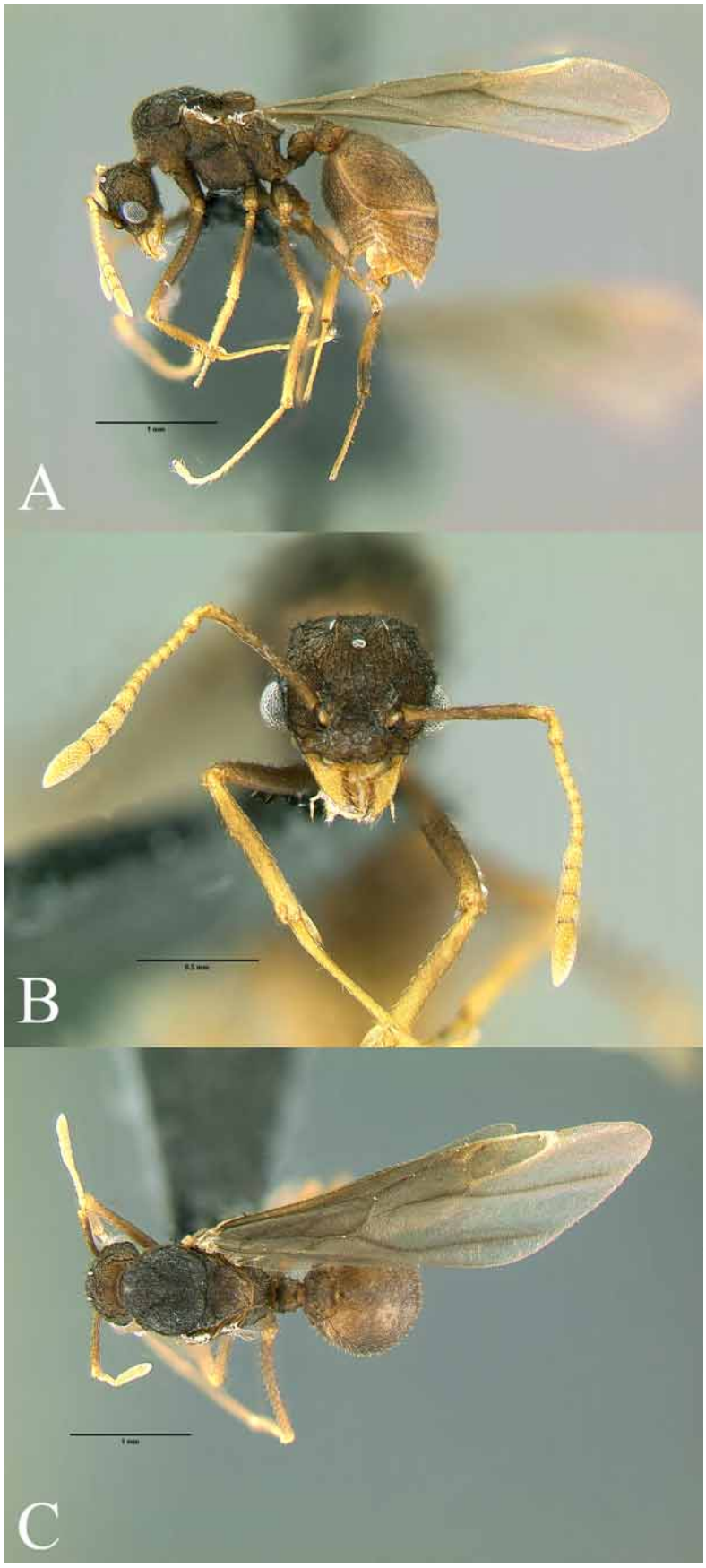

FIGURE 14: *Trachymyrmex pomonae* Paratype male in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 1 mm, 0.5 mm and 1 mm in part (a), (b) and (c), respectively.

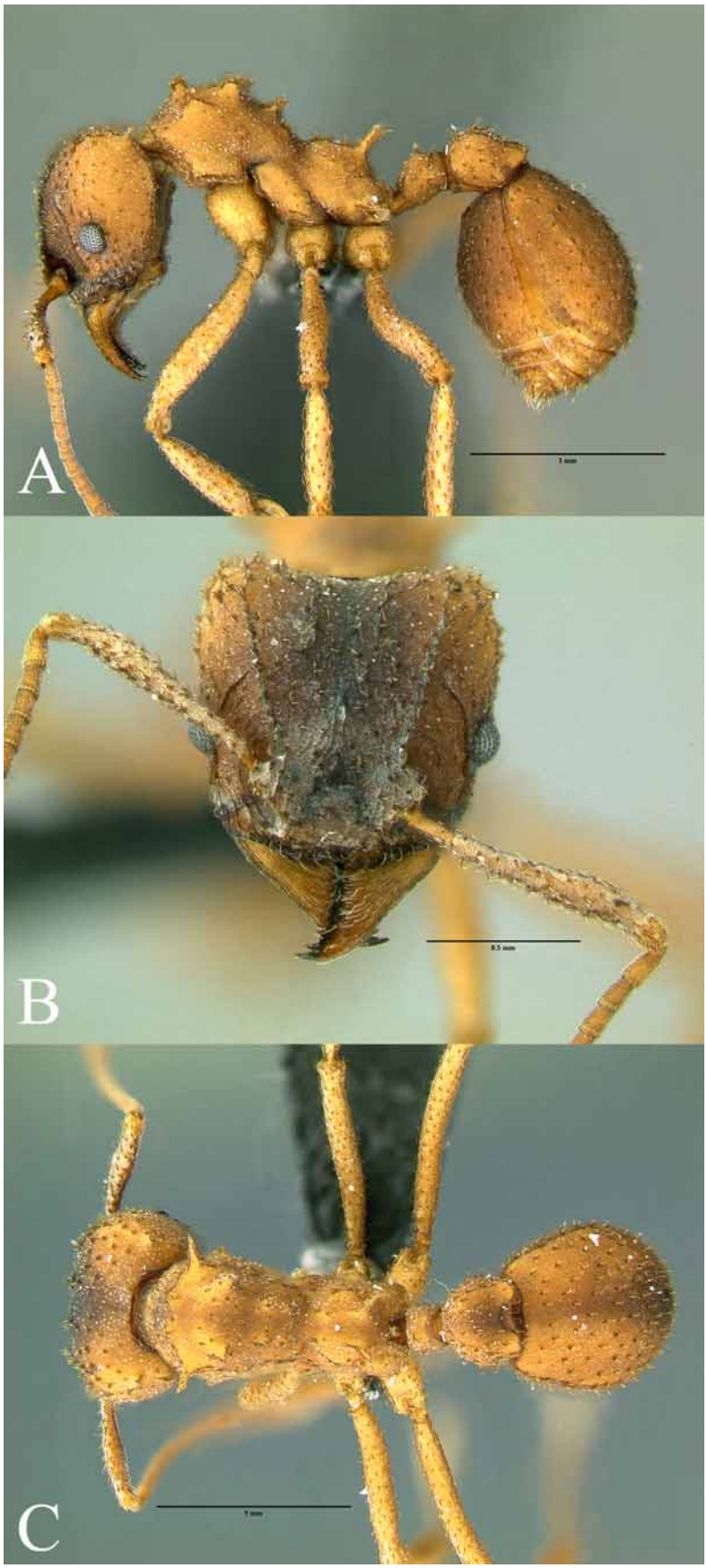

FIGURE 15: *Trachymyrmex septentrionalis* worker in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 1 mm, 0.5 mm and 1 mm in part (a), (b) and (c), respectively.

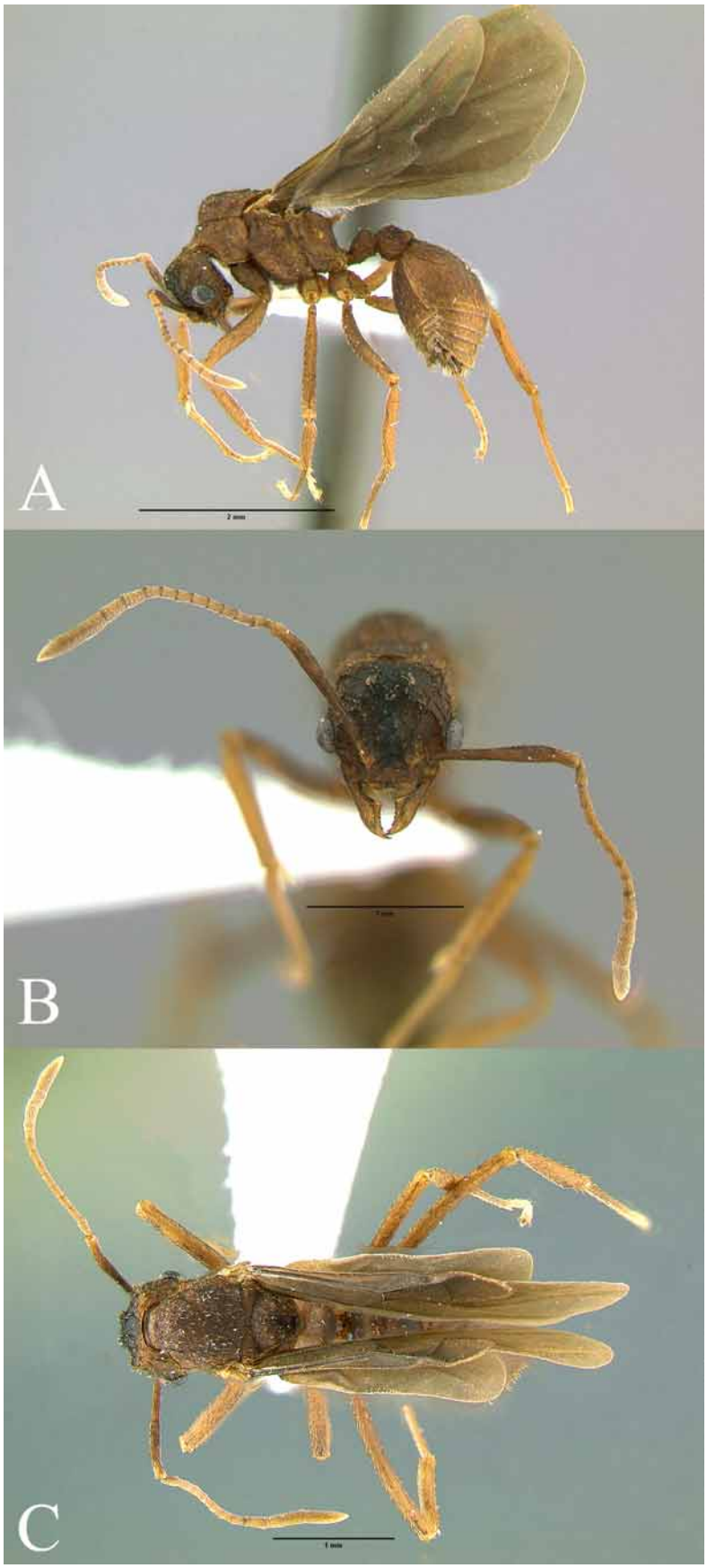

FIGURE 16: *Trachymyrmex septentrionalis* male in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 2 mm, 1 mm and 1 mm in part (a), (b) and (c), respectively.

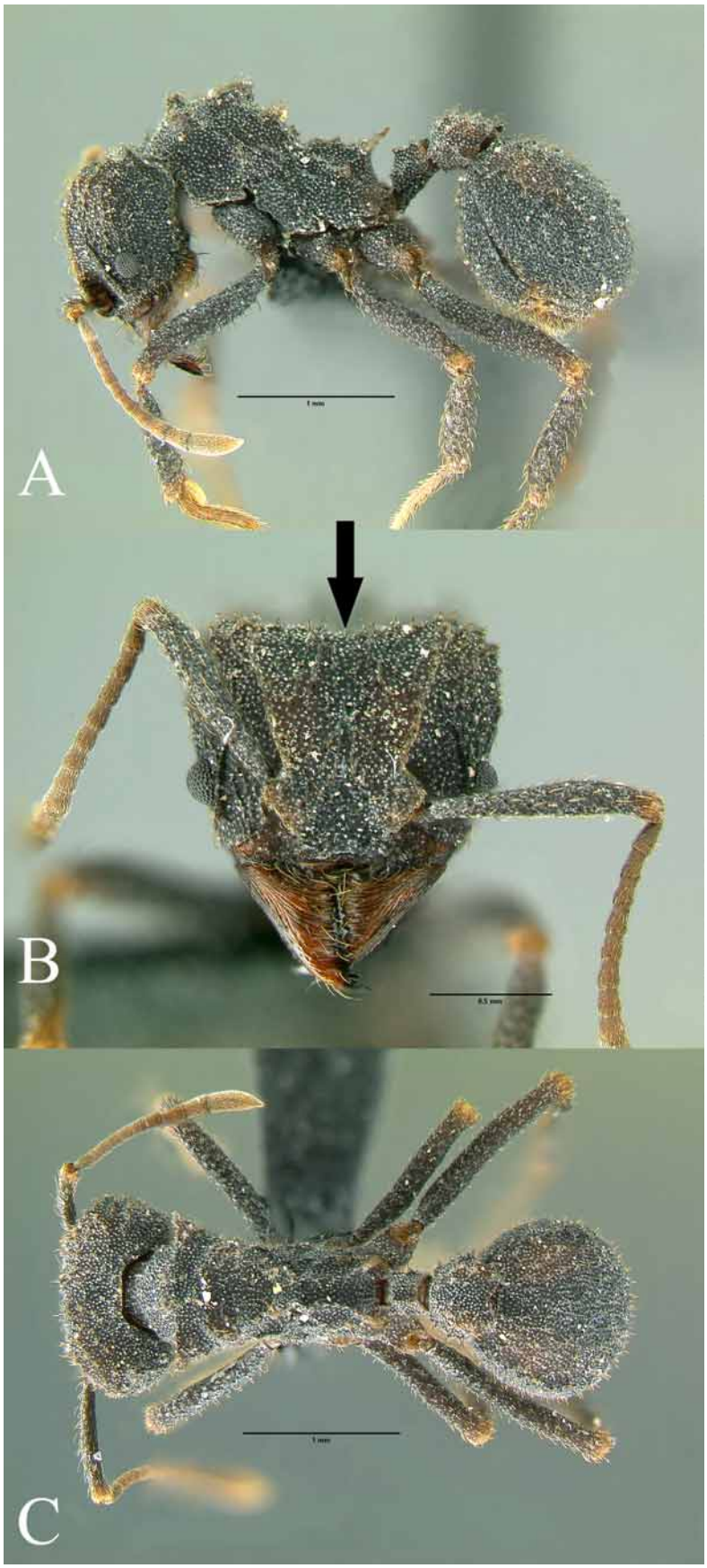

FIGURE 17: *Trachymyrmex smithi* worker in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 1 mm, 0.5 mm and 1 mm in part (a), (b) and (c), respectively.

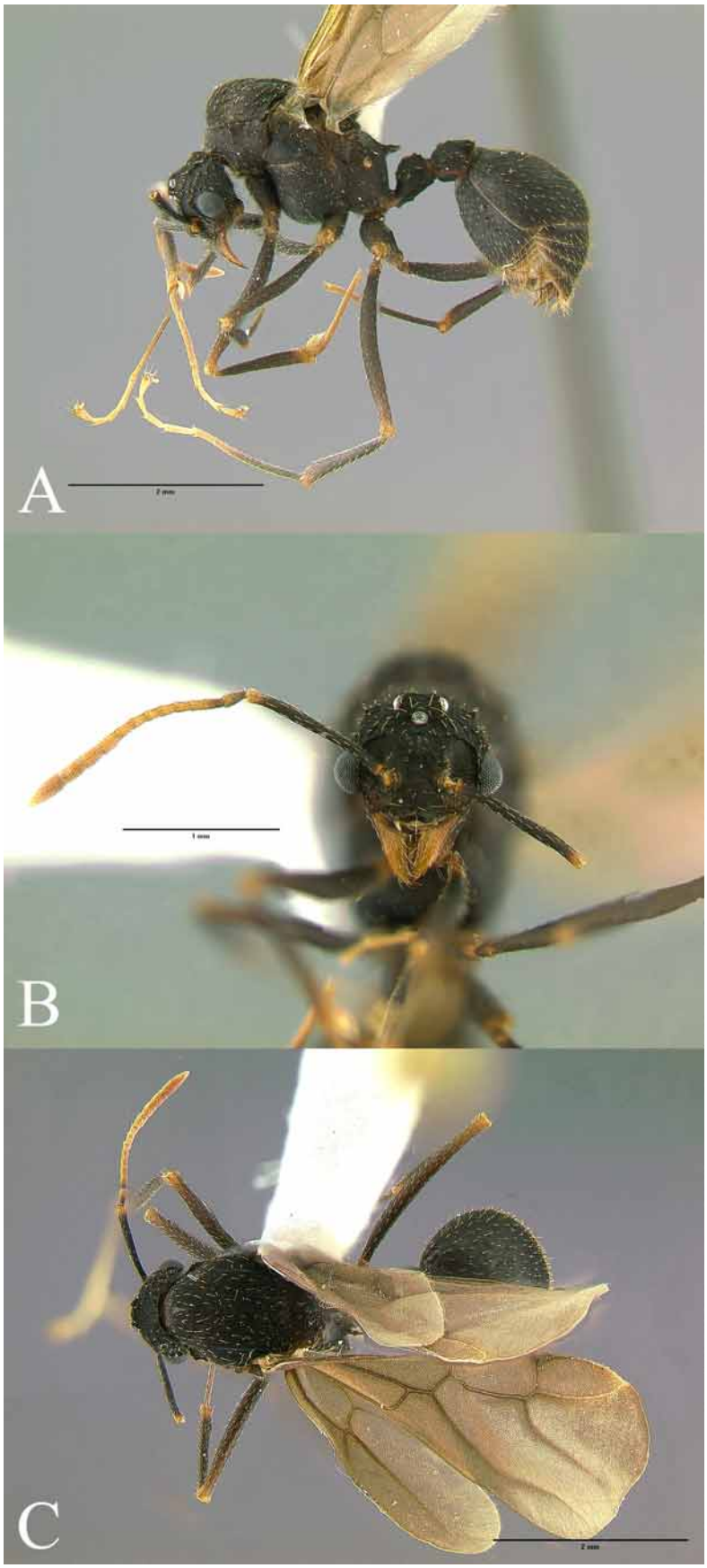

FIGURE 18: *Trachymyrmex smithi* male in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 2 mm, 1 mm and 2 mm in part (a), (b) and (c), respectively.

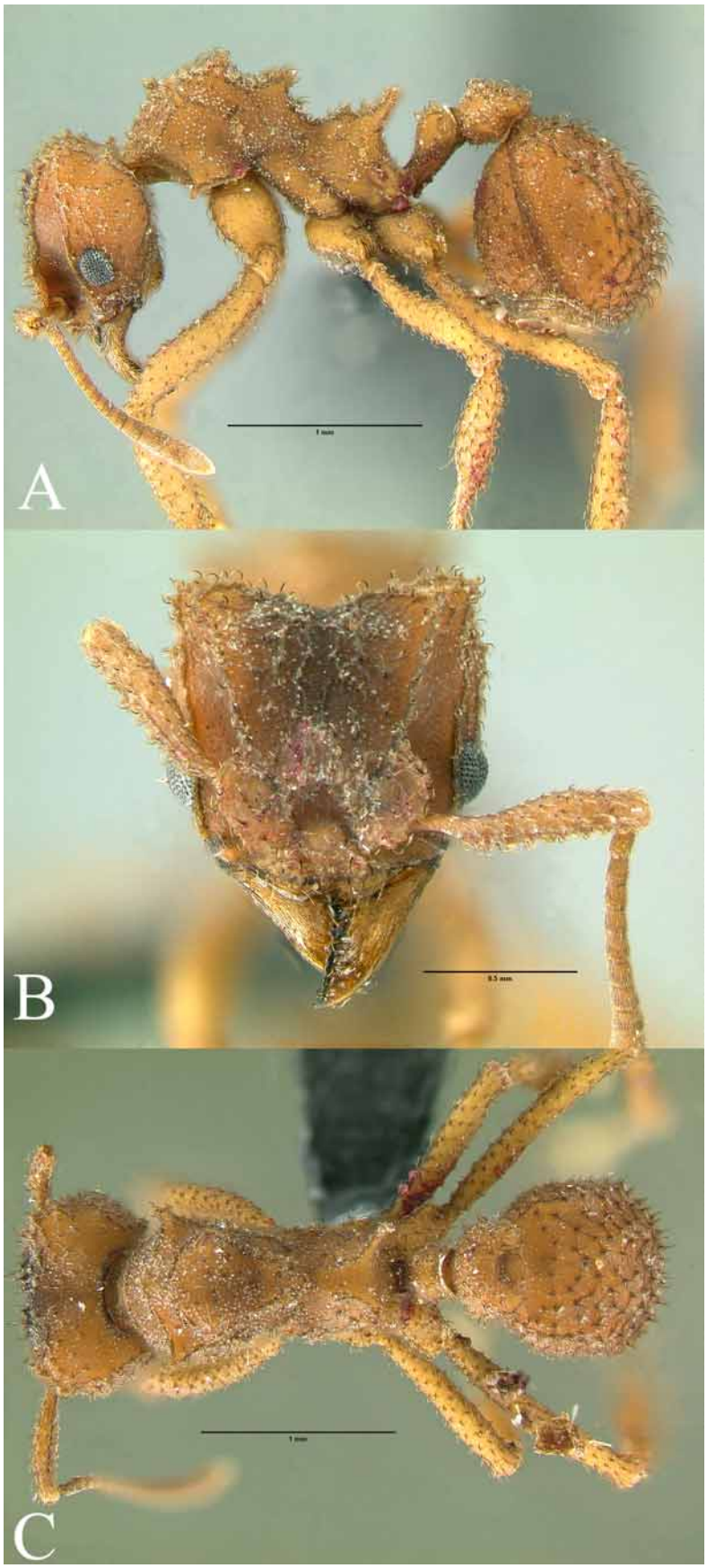

FIGURE 19: *Trachymyrmex turrifex* worker in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 1 mm, 0.5 mm and 1 mm in part (a), (b) and (c), respectively.

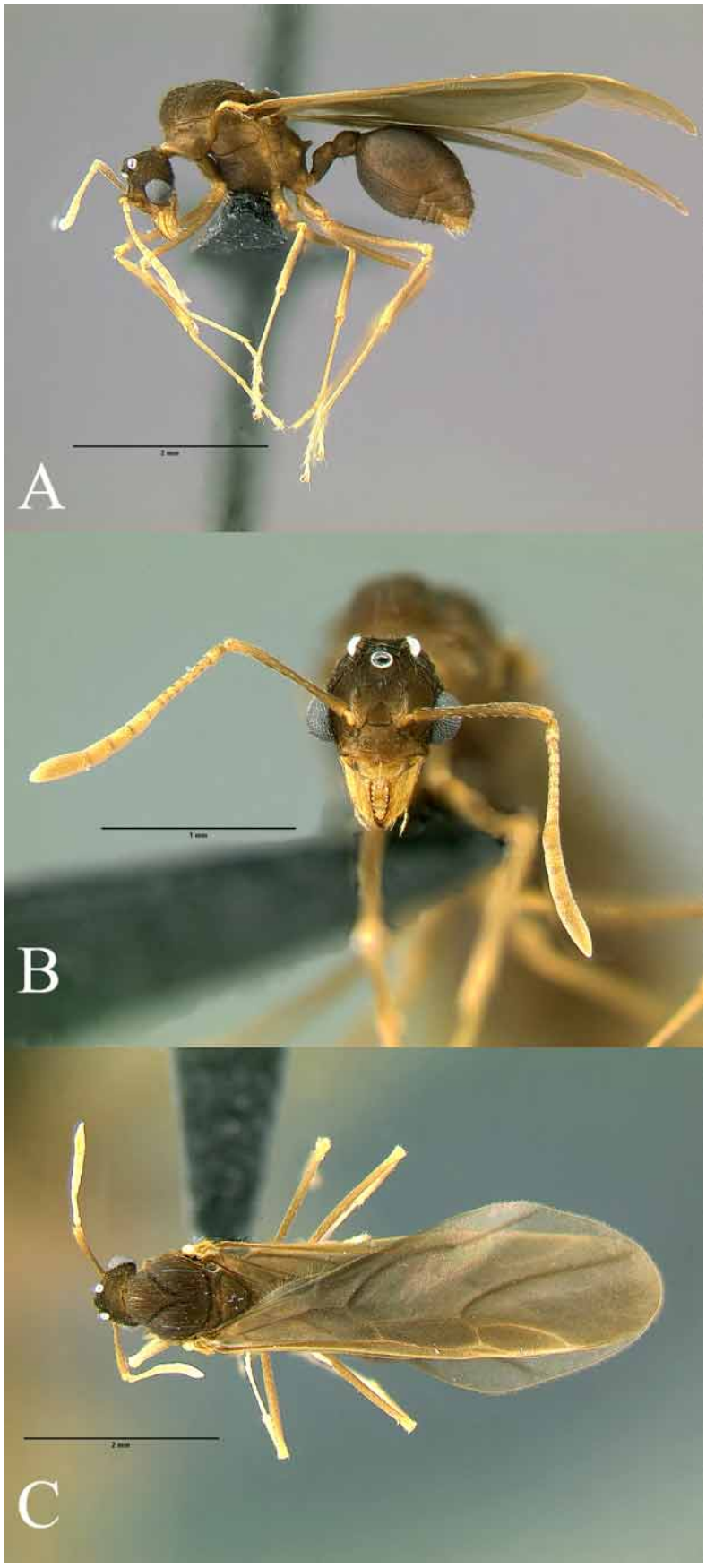

FIGURE 20: *Trachymyrmex turrifex* male in (a) lateral, (b) full face and (c) dorsal view. Scale bar represents 2 mm, 1 mm and 2 mm in part (a), (b) and (c), respectively.

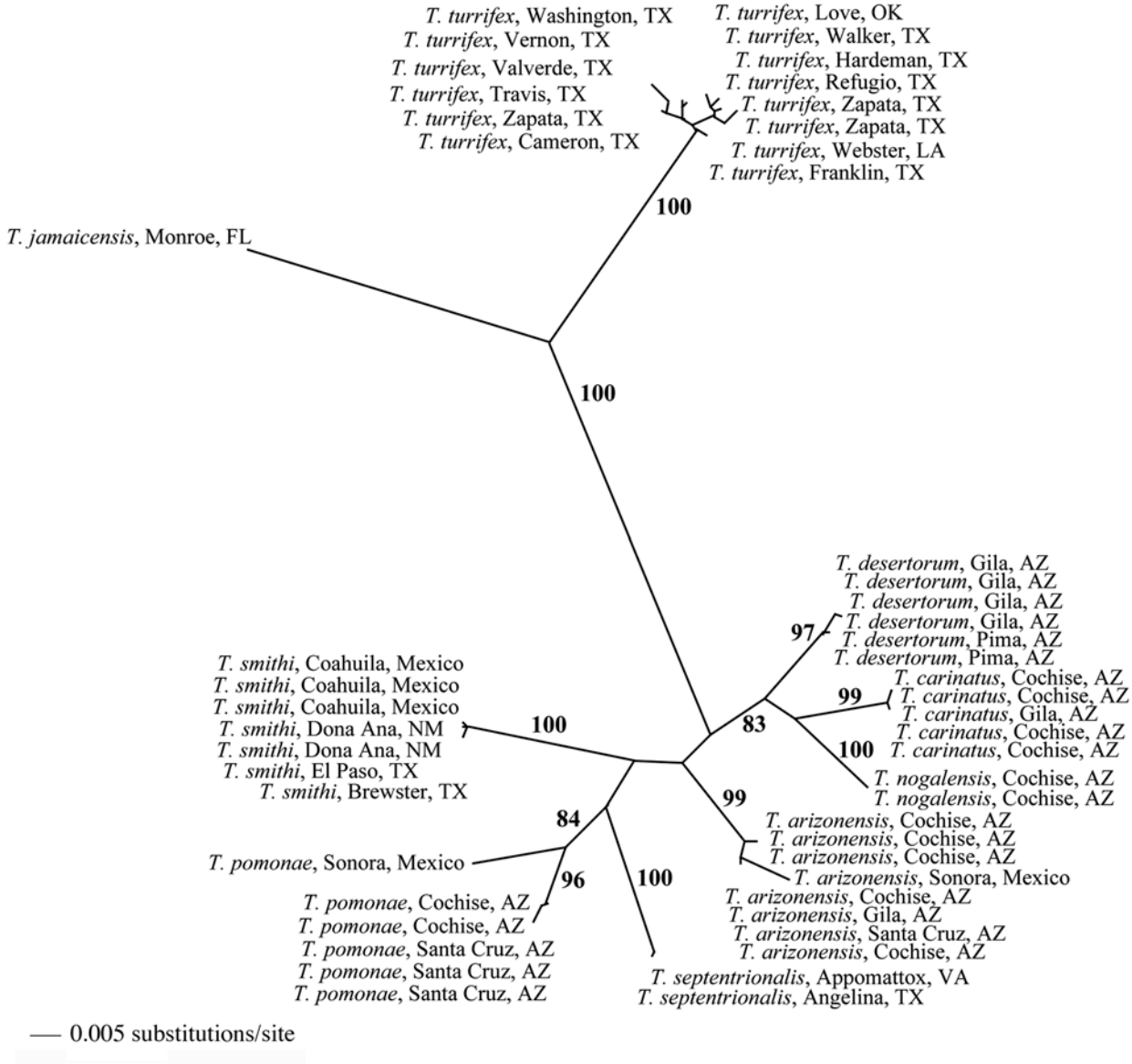

FIGURE 21: Maximum Likelihood phylogram of surveyed populations of the *Trachymyrmex* species occurring in the United States, with branch lengths, calculated under GTR+R model. Numbers on branches represent bootstrap values based on 560 pseudoreplications. The scale bar depicts expected rate of substitutions per site. County/Parish, State and Country names (for Mexican samples) are given behind the species name. Note: the taxon sampling for the genus *Trachymyrmex* is incomplete, thus two species appearing adjacently in this phylogram are not necessarily sister taxa.

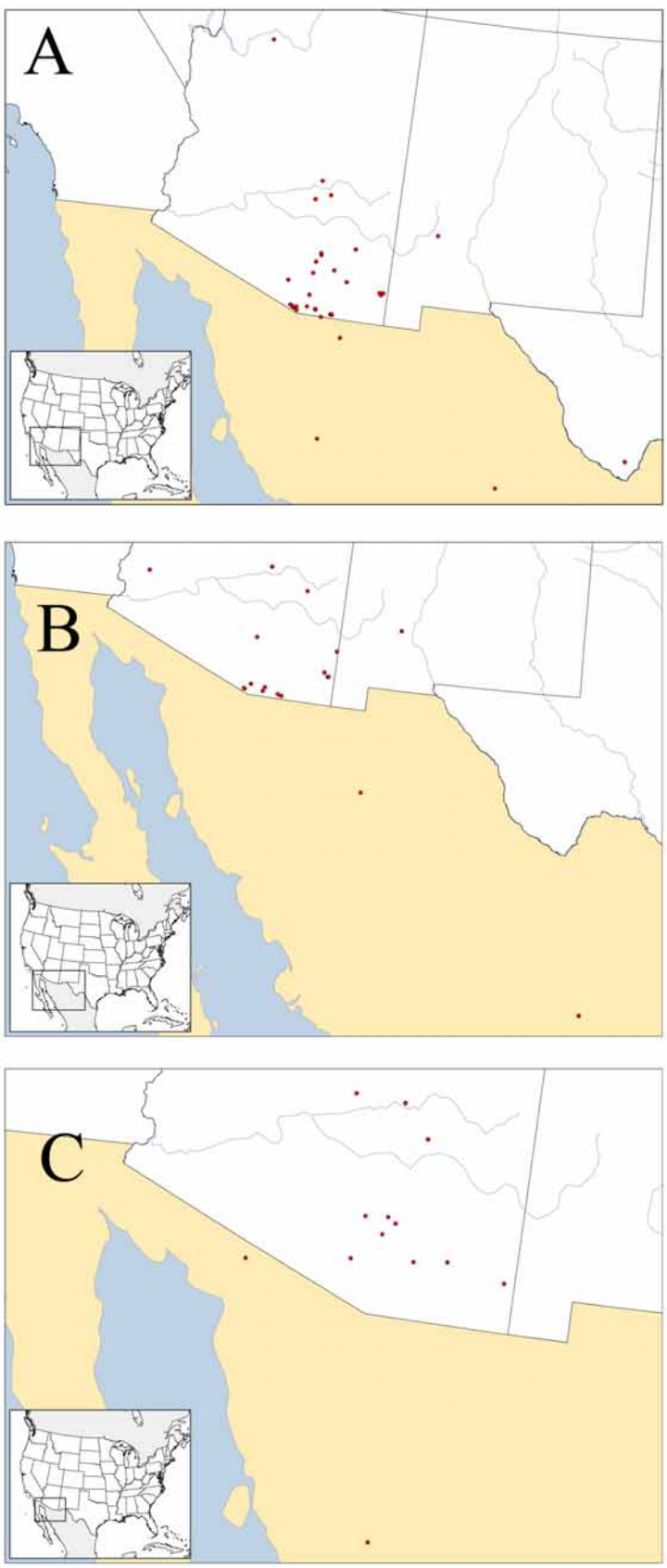

FIGURE 22: Distribution of (a) *T. arizonensis*, (b) *T. carinatus* and (c) *T. desertorum*.

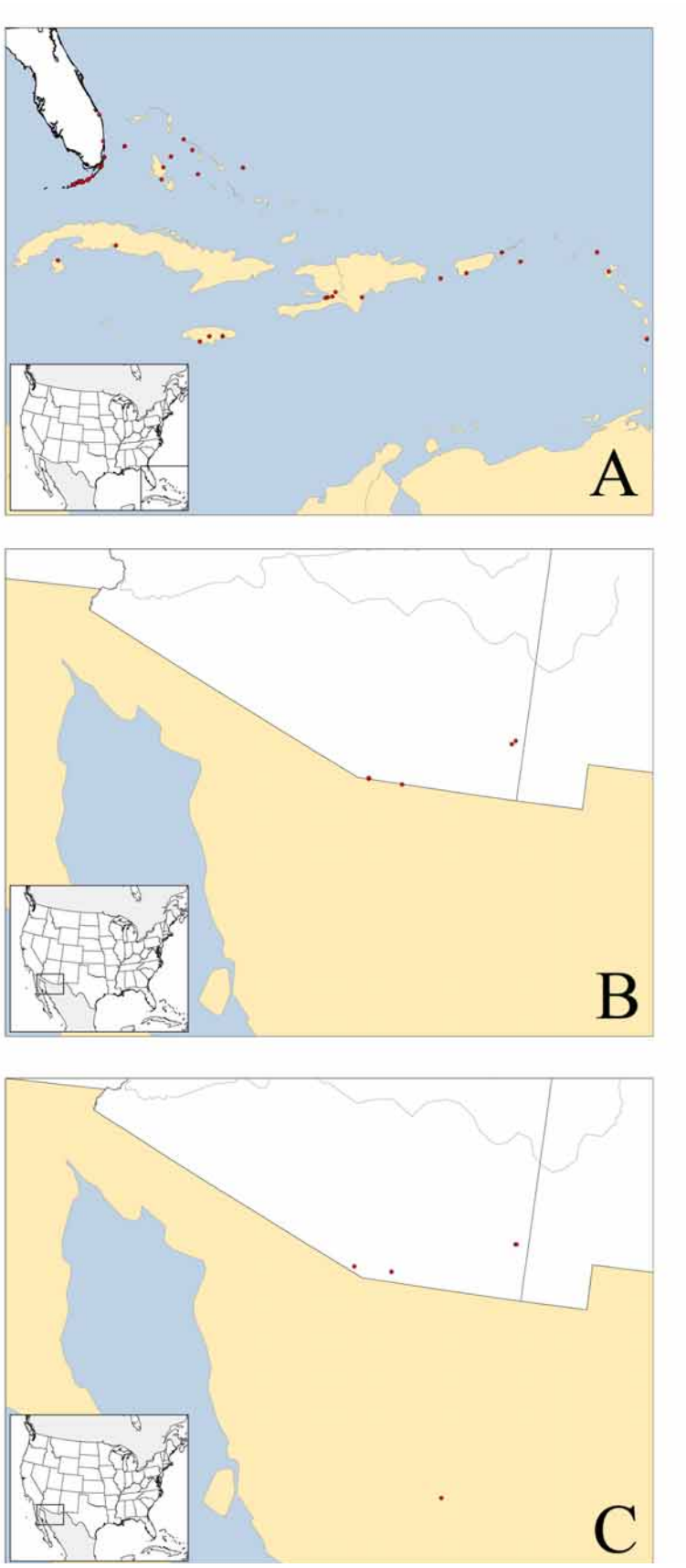

FIGURE 23: Distribution of (a) *T. jamaicensis*, (b) *T. nogalensis* and (c) *T. pomonae*.

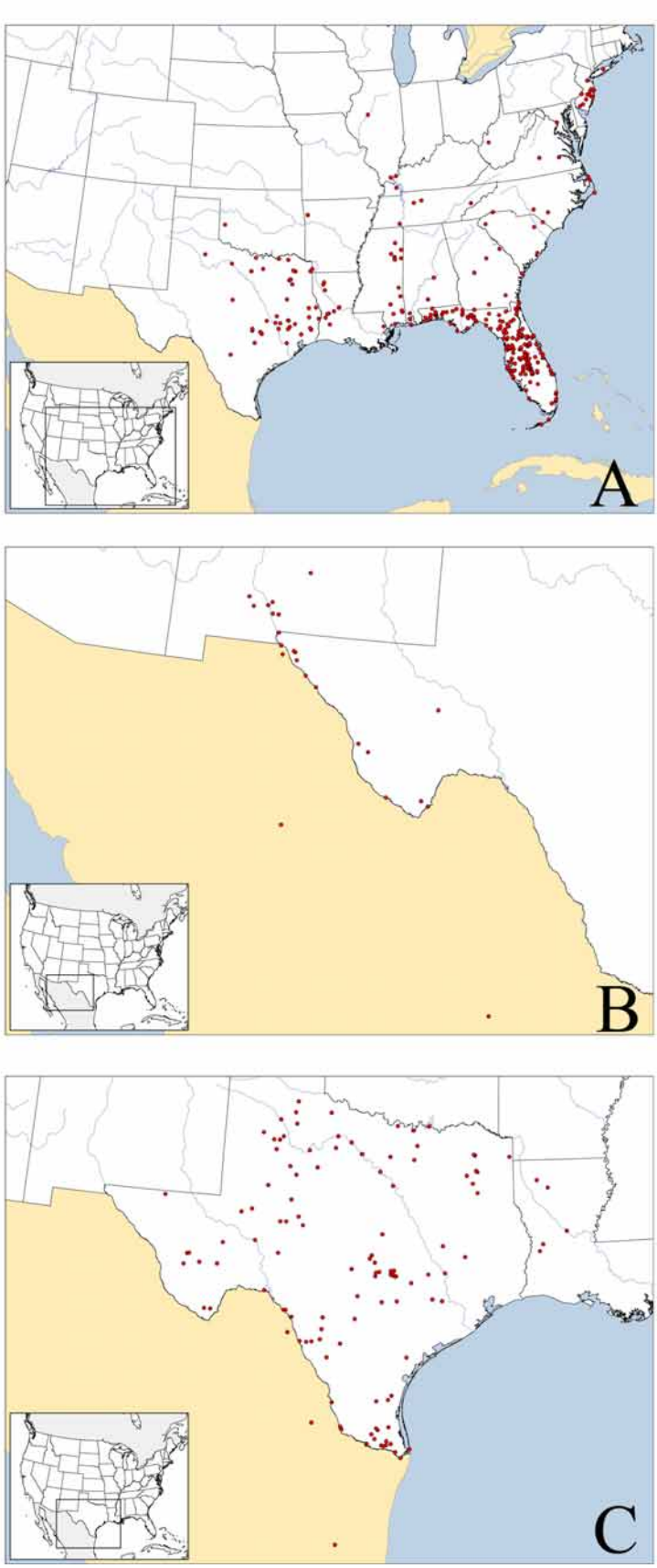

FIGURE 24: Distribution of (a) *T. septentrionalis*, (b) *T. smithi* and (c) *T. turrifex*.