First record of the genus *Leptanilloides* (Hymenoptera: Formicidae: Dorylinae) from the United States

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Abstract

We describe a new species of the Neotropical genus *Leptanilloides*, *L. chihuahuaensis* sp. n., based on male specimens from the Davis Mountains in western Texas. Known males of species of *Leptanilloides* are compared with *L. chihuahuaensis*. This is the first report of the genus from the United States and the Nearctic region. Previously, the *Leptanilloides* genus-group was only known to occur from southern Mexico to southeastern Brazil; and thus, this record from Texas represents a remarkable extension of the known range of the genus.

Key words: dorylomorph, army ants, taxonomy, Davis Mountains State Park, Texas, ants, Chihuahuan Desert, COI

Introduction

*Leptanilloides* Mann, 1923 is a genus of minute, rarely collected Neotropical ants related to army ants. Workers lack eyes and ocelli, although males have extraordinarily large eyes and obvious ocelli (for a full diagnosis of the genus see Borowiec & Longino 2011). Little is known about their biology, although most collections have been from cloud forests (Borowiec & Longino 2011).

Currently, twelve species of *Leptanilloides* are recognized. Mann (1923) originally placed *Leptanilloides* in the subfamily Dorylinae, but subsequent authors placed it in Cerapachyinae (Bolton 1990a, 1990b; Brown 1975). Later, it was placed in its own monotypic subfamily, Leptanilloidinae (Baroni Urbani et al. 1992; Bolton 1994). Two related genera, *Asphinctanilloides* Brandão et al., 1999, with three species, and *Amyrmex* Kusnezov, 1953, with one species, (Bolton 2014) were subsequently included in the Leptanilloidinae (Brandão et al. 1999; Ward & Brady 2009). Recently, Brady et al. (2014) transferred *Amyrmex, Asphinctanilloides, Leptanilloides*, and other dorylomorphs to the Dorylinae, which currently is not subdivided into tribes. However, the three genera that constituted the former Leptanilloidinae are clearly closely related (Ward & Brady 2009), and in this paper we refer to them as the *Leptanilloides* genus-group. The generic boundaries of these three genera are not well understood, and names in this genus-group will likely change in the future (Borowiec & Longino 2011).

Here, we describe the first *Leptanilloides* species from the United States and Nearctic region, which extends the known range of the genus approximately 2500 km north of previously reported collections.

Methods

Morphological observation. Measurements were made using an eyepiece micrometer placed in a 10× eyepiece of a Leica MZ16 stereomicroscope at a magnification of 100×. Photomicrographs were captured using a Leica DFC 495 digital camera mounted on a Leica Z16 macroscope with a motorized focus column, and image stacks were merged using Leica Application Suite V 4.1.0 with Montage Module. For describing wing venation we use the terminology of Brown & Nutting (1949), for genitalia we follow Boudinot (2013) and Yoshimura & Fisher (2012), and for mesosomal structure we use Yoshimura and Fisher (2012).
Measurements and indices. All measurements are given in mm.

HW: Head width. Maximum width of head including eyes in full-face view.
HL: Head length. Maximum length of head along midline in full-face view, measured medially from the anteriormost part of the head (anterior edge of frontal lobes) to the center of posterior margin.
MDL: Mandible length. Maximum length measured in full-face view from posterior margin of clypeus to apex of mandible.
SL: Scape length. Maximum length of scape (first antennal segment) measured without condyle and neck.
FlaLI, FlaLII, FlaLXI: Length of first, second, and terminal (11th) flagellomeres, respectively.
EL: Eye length. Maximum length of eye parallel to midline, measured in full-face view.
MH: Mesosoma height. Maximum height of mesosoma in lateral view measured perpendicular to long axis of mesosoma from the lowermost point of mesopleuron (in front of middle coxa) to dorsal edge of mesosoma.
ML: Mesosoma length. Maximum length of mesosoma in lateral view measured from farthest point on anterior face of pronotum, excluding the neck, to posteroventral corner of mesosoma.
PW: Petiole width. Maximum width of abdominal segment II (petiole) in dorsal view.
PL: Petiole length. Maximum length of abdominal segment II (petiole) in dorsal view, measuring only the length of the petiolar postergite.
AIIIW: Third abdominal tergite width. Maximum width in dorsal view.
AIIIL: Third abdominal tergite length. Maximum length in dorsal view measured medially, measuring only the length of the postergite, excluding pretergite III (helcium).
AIVL: Fourth abdominal tergite length. Maximum length in dorsal view measured medially, excluding pretergite.
FFeW: Fore femur width. Maximum width in lateral view.
FFeL: Fore femur length.
HFeL: Hind femur length.
HTiL: Hind tibia length.
FWL: Forewing length.
CI: Cephalic index. HW/HL×100.
MI: Mesosomal index. MH/ML×100.
PI: Petiolar index. PW/PL×100.

Sequencing and Analysis of COI. DNA was extracted non-destructively from one male specimen using a Qiagen DNeasy Blood and Tissue Kit. A 658 bp fragment of the mitochondrial gene cytochrome c oxidase I (COI or cox1) was amplified using primers COI-1810F (5'-attcaaccaatcataaagatattgg-3') and COI-2518R2 (5'-taaacttctggatgtccaaaaatca-3') and the following PCR reaction mixture: 5 μL DNA, 10 μL Promega Master Mix, 0.8 μL forward and reverse primers, and 3.4 μL nuclease-free H2O. The PCR reaction was run on a thermal cycler using a standard program (5 min at 95C; then 40 cycles of 30 sec at 95C, 30 sec at 50C, 1.5 min at 72C; and 2 min at 72C). After amplification, the PCR product was cleaned using Affymetrix ExoSAP-IT and submitted for bidirectional sequencing at the University of Utah HSC Core facility.

Following sequencing, the forward and reverse reads were combined and cleaned using Sequencher v5.3 (Gene Codes Corp.) and the consensus sequence was exported as a fasta file. To compare the new sequence with already available COI sequences for Leptanilloides, all Leptanilloides data were downloaded from the Barcoding of Life Database (BOLD; http://www.boldsystems.org) and combined with the new sequence. The data were aligned using MAFFT v7.13 (Katoh 2002) and pairwise uncorrected (p) distances were calculated using PAUP* v4.0a144 (Swoford 2002).
**Taxonomy**

*Leptanilloides chihuahuaensis*

(Figs. 1, 2)


**Paratype males:** Two point-mounted specimens with the same data as the holotype but with unique specimen code: MEM 207972 and MEM 207973 [both specimens in Mississippi Entomological Museum (MEM), Mississippi State, MS, USA]; and three specimens, one point-mounted and two in 95% ethanol, with the following collection data: [United States] TEXAS, Jeff Davis Co., Davis Mts. St. Pk., 4915', 30°36'08"N 103°54'55"W, 21–25 July 2014, T.L. Schiefer, Malaise trap in riparian area in desert scrub/grassland, W.H. Cross Expedition with unique specimen codes: MEM 207974 [point mounted specimen deposited in MEM], MEM 207975 [preserved in 95% ethanol for DNA study, deposited in MEM] and MEM 207976 [preserved in 95% ethanol for DNA study, deposited in MEM].

**Holotype measurements and indices:** HW 0.24, HL 0.24, EL 0.11, MDL 0.13, SL 0.08, PedL 0.06, FlaL 0.04, FlaLI 0.04, FlaXI 0.12, MH 0.29, ML 0.46, PrW 0.20, PW 0.09, PL 0.07, AIIW 0.14, AIII 0.07, AIVW 0.20, AIVL 0.09, FFew 0.05, FFel 0.23, HHel 0.24, HHT 0.26, FWL 1.46, CI 100, MI 63, PI 128.

**Additional paratype measurements and indices (two males):** HW 0.24, HL 0.22, EL 0.09–0.11, MDL 0.13, SL 0.09, PedL 0.06–0.07, FlaLI 0.04, FlaLII 0.04, FlaLXI 0.11–0.12, MH 0.30–0.31, ML 0.45–0.46, PrW 0.18, PW 0.07–0.08, PL 0.06–0.07, AIIW 0.15, AIII 0.07–0.10, AIVW 0.18–0.19, AIVL 0.01, FFew 0.05, FFel 0.21, HHel 0.23, HHT 0.26, FWL 1.38, CI 109, MI 65–69, PI 114–117.

**Etymology.** Named for the Chihuahuan Desert region where specimens were collected.

**Diagnosis (male).** Of the six males that have been described in the *Leptanilloides* genus-group, *L. chihuahuaensis* is most similar to "Leptanilloidinae male 1" from southern Mexico described by Borowiec & Longino (2011). *Leptanilloides chihuahuaensis* differs from "Leptanilloidinae male 1" by having finer and sparser pilosity, in dorsal view the petiole being widened anteriorly and posteriorly, parameres being narrower and incurved, and the hindwing having three hamuli (instead of two). Males of *L. chihuahuaensis* differ from males of *Amyrmex golbachi* Kusnezov, 1953 by lacking submarginal cells and a stigma in the forewing, possessing a free M vein, and having a larger paramere (about as long as petiole); from *L. mckennae* Longino 2003 by lacking submarginal cells and a stigma in forewing and having a much shorter paramere (in side view) (Ward 2007); from *L. nubecula* Donaso, Vieira & Wild, 2006 by being light to medium brown instead of dark brownish-black and being much smaller (HL 0.22–0.24 in *L. chihuahuaensis* vs. HL 0.32 in *L. nubecula*), and from both "Leptanilloidinae male 2 and male 3" (Borowiec & Longino 2011) by the much smaller size (HL 0.22–0.24 vs. HL 0.30–0.33 of "Leptanilloidinae male 2 and male 3") and by lacking submarginal cells and stigma in the forewing. Five other male morphotypes unassociated with workers were briefly discussed by Ward & Brady (2009). *Leptanilloides chihuahuaensis* differs from each of these by lacking submarginal cells and a stigma in the forewing. Geographically, *L. chihuahuaensis* is the only species thus far known to occur in the United States.

**Description (male):** Body size minute. Color light yellowish-brown, head and margins of abdominal segments IV–VII darker, appendages (antennae, mandibles, legs) lighter. Integument mostly smooth and shiny, with simple curved to strongly curved suberect to decumbent setae; pilosity on head, mesosoma, petiole, and first gastral tergite (AIII) scattered and not obscuring the shininess of the integument; pilosity denser on remainder of gaster and appendages.

Head in full-face view excluding eyes about as long as wide, widest above eyes; posterior corners of head evenly rounded. Eyes large, bulging, occupying almost half the side of head. Ocelli small, protruding slightly, arranged in almost an equilateral triangle, but with distance between lateral ocelli slightly greater than distance between lateral ocellus and median ocellus; distance between median ocellus and eye approximately the length of eye. Clypeus short, tranverse, lacking lamellae; lateroclypeal teeth and hypostomal teeth lacking. Mandible slender, falcate; apex blunt; masticatory margin edentate; external margin of mandible mostly evenly curved along its length; mandible tips overlap at closure.
FIGURE 1. Leptanilloides chihuahuensis, male, holotype (MEM 207971): (A) head in full-face view, (B) petiole in dorsal view, (C) tergite VIII and exposed male genitalia in dorsal view, (D) sternite IX and exposed male genitalia in ventral view, (E) lateral habitus, and (F) dorsal habitus. Abbreviations: ASIX = ninth abdominal sternite, ATVIII = eighth abdominal tergite, Ax = axilla, Msp = mesopleuron, MsScl = mesoscutellum, MsSct = mesoscutum, Mtn = metanotum, P = petiole, Ped = Pedicel, Pm = paramere, Prnt = pronotum, Prpd = propodeum, Pv = Penivalva, Sc = Scape, and Vol = volsella.

Antennal sockets circular and exposed, located at the anterior clypeal margin with anterior edge of sockets slightly overlapping anterior clypeal margin. Antenna 13-merous; scape, pedicel, and each flagellomere longer than wide. Scape length about twice the length of the first flagellomere, and about the combined length of the first and second flagellomere; scape subequal to the length of ultimate flagellomere; pedicel thickened, length about 1.5 times width; flagellomeres 1-11 each at least twice as long as wide; first and second flagellomeres subequal in length.

Pronotum U-shaped in dorsal view, reduced anteromedially to a thin horizontal strip, set below the level of the dorsally protruding mesonotum; pronotum triangular in lateral view, with pointed posterior apex directed toward wing base. Mesoscutum lacking notauli; parapsidal lines not discernable. Axillae depressed, not meeting medially,
FIGURE 2. *Leptanilloides chihuahuensis*, male, holotype (MEM 207971): (A) lateral habitus and (B) forewing and hindwing showing labeled veins. Abbreviations: 2r-rs = second radial sector cross-vein, A = anal vein, C = costal vein, Cu = cubital vein, cu-a = cubital-anal cross-vein, ha = hamuli, M = medial vein, M+Cu = merged medial-cubital veins, Rs+M = merged medial and radial sector plus medial veins, Rs = radial sector, Sc+R = merged subcostal and radial veins.
connected by a narrow furrow. Tegula, or tegula-like structure present at wing base, minute, inconspicuous, with 2-3 erect setae. Mesopleuron lacking oblique transverse sulcus, not divided into anepisternum and katepisternum. Mesoscutellum prominently bulging, as seen in lateral view. Metapleural gland not discernable. Propodeum with dorsal and declivious surfaces not differentiated, evenly rounded. Propodeal spiracle small, ovate, positioned slightly below midheight of propodeum and slightly posterior to the midlength. Legs slender, mesotibia and metatibia each with two simple spurs, pretarsal claw lacking preapical tooth.

Wings with reduced venation; clear; fringed with short to longer fine setae; with numerous short, fine microsetae evenly distributed across wing surfaces and with scattered longer setae present. Fore wing: Costal (C) vein present, about ½ the length of wing, tubular basally for less than ¼ the length of wing, then becoming nebulus before fading out completely. Pterostigma not present. Subcostal and radial veins fused forming Sc+R; located just below and parallel to costal vein, approximately the same length as costal vein and similarly tubular for about ½ of its length before becoming nebulus. Medial (M) and cubital (Cu) veins fused (M+Cu), nebulus, slightly less than ¼ of the wing length. Anal (A) vein present beneath M+Cu, about the same length as M+Cu, tubular for slightly more than half of its length before becoming nebulus; apically M+Cu connected to A by nebulus crossvein cu-a; subbasal cell present between M+Cu and A. Branching upward from the top of Cu-a is the tubular abscissa Rs+M (the joined veins M·f1 and Rs+M). Radial sector (Rs), tubular, branches upward from Rs+M, then becomes nebulus just past the nebulus/spectral crossvein 2r-rs (1r-rs is absent). M branches off of Rs+M just before Rs, appearing spectral basally then continuing as a nebulus vein that does not reach the wing margin. Cu is present as a nebulus vein that branches off near the apex of A; Cu does not reach the wing margin. Posterior margin of fore wing with narrow, conspicuous fold where hamuli attach.

Hind wing with Sc+R present, tubular basally becoming nebulus, less than ¼ the length of wing. No other veins present. Anterior margin of hind wing past midlength with a thin, but conspicuous dark stigma. Three hamuli present in the region of the stigma. Jugal lobe absent.

Petiole (abdominal segment II) subquadrate in lateral view, about as long as high or wide, not constricted posteriorly; in dorsal view anterior corners widened, sides slightly constricted, appearing shallowly concave before widening posteriorly; petiole broadly joined to abdominal segment III; petiolar spiracle located on anterior third of the segment, near anterodorsal extremity. Abdominal segment III larger than petiole, not developed as postpetiole, and not separated from abdominal segment IV by a constriction. Abdominal spiracles III, IV, V, and VI located on anterior third of tergites (abdominal spiracle VII not visible in examined specimens). Abdominal tergite VIII (pygidium) small, simple and visible dorsally, not entirely covered by abdominal tergite VII. Pygostyli absent. Abdominal sternite IX (subgenital plate) with posterior margin broadly concave, but with a median subtriangular process. Paramere (basimere + telomere) small (about the length of petiole); basimere roughly triangular, widest at base, narrowing to incurved falcate telomere that terminates in a blunt apex. Volsella triangular, with slightly rounded apex; volsella not differentiated into digitus and cuspis. Penisvalva elongate triangular, extending to about as far as paramere apex.

### TABLE 1.

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**Analysis of COI.** A 658 bp region of the mitochondrial gene COI, the barcode region, was sequenced successfully and the resulting consensus sequence was submitted to GenBank (Table 1). Five additional COI sequences for *Leptanilloides* were found and downloaded from the BOLD database (Table 1), including three for *L.
gracilis Borowiec & Longino (southern Mexico, Honduras), one for L. nubecula Donoso et al. (Ecuador), and one for an undescribed species L. MAS001 (Costa Rica). Comparing L. chihuahuaensis to the other specimens, pairwise genetic distances were all above 8.0%, ranging from 8.2% (L. gracilis, Honduras) to 20.1% (L. nubecula, Ecuador).

Discussion

Of the 16 species in the Leptanilloides genus-group, males of only three have been given species names, and of those three, only males of L. nubecula Donoso, Vieira & Wild and L. meckemae Longino were associated with their respective worker castes (Donosa et al. 2006, Ward 2007). The description of Amyrmez golbachi was based solely on the male caste (Kusnezov 1953). Three other male morphotypes were described by Borowiec & Longino (2011), but, because they were unassociated with workers, they could not be certain of their specific identities. Therefore, Borowiec & Longino (2011) simply referred to these male morphotypes as Leptanilloidinae male 1, male 2, and male 3. Borowiec & Longino (2011) stated that "Leptanilloidinae male 1" was likely conspecific with L. gracilis Borowiec & Longino, 2011 based on various shared morphological features, the relatively small size, and the largely sympatric distribution of "Leptanilloidinae male 1" and workers of L. gracilis. The status of Leptanilloidinae males 2 and 3 is less clear. These male morphotypes might represent the males of described species in the group or they may be new species. While searching unidentified material in the Bohart Museum of Entomology collection (UCDC), Ward & Brady (2009) discovered several male Leptanilloides genus-group males that represent at least five more species in the group. These appeared to belong to Amyrmez and possibly Asphinctanilloides, although it is not clear whether they represented new species or were the males of described species in the group.

All of the described species and even the undescribed males discussed by Ward & Brady (2009) in the Leptanilloides genus-group have exclusively Neotropical distributions ranging from Chiapas, Mexico (Borowiec & Longino 2011) to southeastern Brazil (Silva et al. 2013). Based on reported specimen data, members of this genus group have been collected mostly in cloud forests (Borowiec & Longino, 2011; Brandão et al. 1999; Donoso et al. 2006; Longino 2003, Silva et al. 2013). The new species described here, however, was collected in semiarid grassland habitat in the southern foothills of the Davis Mountains in western Texas, approximately 2500 km north of the next closest collection of the genus-group in Chiapas, Mexico.

The specimens of L. chihuahuaensis were collected in Townes style Malaise traps (Townes 1972) at two locations within Davis Mountains State Park. The first location was on the south (north-facing) slope of Keesey Canyon adjacent to a hillside drainage area. The vegetation at this site was dominated by short grasses but also included scattered forbs and a few low trees and shrubs. The noncalcareous soil, of igneous origin, was shallow, well drained, and extremely rocky (Turner 1977). The second location was in Limpia Canyon on the dry floodplain of the intermittent Limpia Creek. The soils here were similar to the first site, but the vegetation differed in having taller grasses and forbs, with grasses being less dominant, and with forbs, shrubs, and small trees being more numerous. Many rocky, unvegetated areas were also scattered through this habitat. The Malaise trap at this site was located only 20 m from the north (south-facing) slope of Limpia Canyon, which had similar habitat to the first site, so it is possible that the ants in this trap originated from the canyon slope rather than the floodplain.

Other ant species collected by MEM researchers in the same localities and during the same time period that L. chihuahuaensis was collected were typical species for this arid region. Other species collected in the same Malaise traps included Doromyrmex flavus McCook, Forelius pruinosis (Roger), Formica gnava Buckley, Myrmecina americana Emery, and Myrmecocystus melliger Forel, as well as unidentified males of Crematogaster, Pheidole, Solenopsis, and Strumigenys. General collections in the same area yielded species including Camponotus festinatus (Buckley), C. semitestaceus Snelling (found in higher elevations), Forelius mccooki (McCook), Liometopum apiculatum Mayr, Odontomachus clarus Roger, Neivamyrmex minor (Cresson), N. texanus Watkins, Novomessor cockerelli (André), Pheidole hyatti Emery, P. titanis Wheeler, P. spp., Pogonomyrmex barbatus (F. Smith), P. imberbiculus Wheeler, P. rugosus Emery, and Trachymyrmex septentrionalis (McCook).

The climate in the vicinity of Davis Mountains State Park is marked by hot summers and cool, dry winters (Bell et al. 2014), with over 80% of annual precipitation occurring from May through October (NOAA 2014). The average annual precipitation at nearby Fort Davis is 44.4 cm, compared to the 20.4 to 30.5 cm of rainfall received by the surrounding lower elevation areas of Trans-Pecos Texas (NOAA 2014; Texas State Historical Association
2010). This difference in precipitation is due to the pronounced orographic lifting caused by the Davis Mountains, which results in an approximately 5 cm increase in annual rainfall for each 305 m increase in elevation (DeBaca 2008; Turner 1977).

The Davis Mountain range is located within the Chihuahuan Desert ecoregion, which occupies almost 650,000 square kilometers extending from central Mexico into western Texas, central and southern New Mexico, and southeastern Arizona (Commission for Environmental Cooperation 2006; Griffith et al. 2007; Hoyt 2007). The isolating effect of the complex topography of this extensive ecoregion, which is characterized by low-lying basins and isolated mountain ranges, contributes to the Chihuahuan Desert being one of the most diverse arid regions in the world (Bell et al. 2014; Hernández & Gómez-Hinostrosa 2005). This diversity is threatened by overgrazing, water diversion, excessive groundwater pumping, introduced species, and overcollecting of animals and plants, such as cacti, for the commercial trade (Hoyt 2002). The collection of Leptanilloides from this region is surprising both because of the remarkable range extension it represents for the genus-group as well as the significantly different type of habitat the specimens were collected in compared to other collections of the genus-group.

Despite the fact that males of all species in the Leptanilloides genus-group have not been described and that males collected in Texas were unassociated with a colony, we believe there is sufficient evidence for describing L. chihuahuensis as a new species. First, L. chihuahuensis has a very disjunct distribution and occurs in a markedly different habitat than other species. Second, there are obvious morphological features that distinguish L. chihuahuensis from other described males. And lastly, COI sequence divergence, as compared to several other species with data in GenBank, including L. gracilis, exceeds 8%. Although we do not think that this divergence level by itself is sufficient for species status - it has been shown that intraspecific divergence can be quite high (e.g. Meyer and Paulay 2005, Wiemers and Fiedler 2007) – we do believe that the result strengthens our argument. We also feel confident in using the generic name Leptanilloides because specimens of L. chihuahuensis most closely match Borowiec & Longino's (2011) description and figures of "Leptanilloidinae male 1," which they believed to be conspecific with L. gracilis. Additionally, the taxonomic status of the genera in the Leptanilloides genus-group remains unresolved with a strong likelihood that Amyrmex, Asphinctanilloides, and Leptanilloides might be synonymized with one another. If these genera were synonymized, the name Leptanilloides would have priority.

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