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Three new species of *Leptanilloides* Mann from Andean Ecuador (Formicidae: Leptanilloidinae)

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Abstract

We report three new species of the ant genus *Leptanilloides* from Andean Ecuador. *Leptanilloides nomada* **sp. n.** and *L. caracola* **sp. n.** are described from the worker caste, the latter from a unique specimen; *L. nubecula* **sp. n.** is described from workers, males, and two gyne subcastes previously unknown for the entire subfamily. Phenotypic variation in morphological characters in the new species *L. nomada* and *L. nubecula* is more plastic than suggested by the traditional generic diagnosis. These records represent the first case of three *Leptanilloides* species occurring in sympatry. We discuss aspects of the army ant syndrome and its relevance to the genus *Leptanilloides*.

Resumen

Tres nuevas especies del género de hormigas *Leptanilloides* son descritas a partir de especimenes encontrados en Los Andes ecuatorianos. *Leptanilloides nomada* **sp. n.** y *L. caracola* **sp. n.** son descritas en base a obreras, ésta última es descrita a partir de un sólo espécimen. *L. nubecula* **sp. n.** es descrita en base a obreras, machos y dos subcastas de ginas previamente desconocidas para toda la subfamilia. La variación fenotípica encontrada en algunos caracteres morfológicos de las nuevas especies *L. nomada* y *L. nubecula* es más plástica de lo que sugiere la diagnosis genérica tradicional. Estos registros constituyen el primer ejemplo de tres especies de *Leptanilloides* viviendo en simpatría. Discutimos aspectos del síndrome de las hormigas legionarias y su aplicación al género *Leptanilloides*.

Key words: Army Ants, Cloud Forest, Conservation, Ecuador, Leptanilloidinae, Otonga, Systematics, Taxonomy.

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Introduction

Leptanilloides is an uncommonly collected ant genus with subterranean habits in the New World Andean and sub-Andean tropics. With cryptic and eyeless worker ants, the genus was included in the ant subfamily Cerapachyinae (Brown 1975; Bolton 1990a, b) until Baroni Urbani *et al.* (1992) justified the establishment of a separate subfamily, Leptanilloidinae, hypothesized as the sister group to Cerapachyinae and all other members of the dorylomorphs. The only apomorphy for the new subfamily provided by Baroni Urbani *et al*. (l. c.) was the extremely reduced pygidium, represented by a small U-shaped sclerite.

Brandão, Diniz *et al*. (1999) expanded our understanding of Leptanilloidinae and described six new species that were arranged in two genera, *Leptanilloides* and *Asphinctanilloides*. The reassessment, based on external and sting characters, added five apomorphies supporting the subfamily: lateral blunt teeth on genae, metatibial gland absent, gonostylus fused to the posterior arm of the oblong plate, several microtrichia plus two longer sensillae at the presumed junction of gonostylus with posterior arm of oblong plate, and base of sting shaft with a pair of long setae. Brandão, Diniz *et al.* (l. c.) also established several apomorphies for both leptanilloidine genera. For *Leptanilloides*, two apomorphies were proposed: propodeal dorsum at least two times longer than declivity and abdominal segments 4 and 5 separated by a deep incision; while for *Asphinctanilloides*, five apomorphies were established: postpetiole extremely reduced in size with spiracle at midlength, spiracular plate median connection of the sting apparatus with bilobed anterior region, quadrate plate apodeme wider than body of the plate, fulcral arms absent, and basal ridge of sting not visible. Recently, Longino (2003) described a new species, *Leptanilloides mckennae* Longino, from Costa Rica. *Leptanilloides mckennae* expands the geographic distribution of the subfamily and also presents some characters (i.e. very small postpetiole and posterior shifted postpetiolar spiracle) that have been considered apomorphic for *Asphinctanilloides*.

The male caste of Leptanilloidinae was described recently by Ward (2006), who linked an unassociated male ant from a montane Costa Rican forest to *L. mckennae* workers using molecular data. Ward (l. c.) also discussed the molecular similarities of leptanilloidines to other dorylomorphs and the evolution and morphological convergences of ant assemblages living in subterranean habitats (see also Ward 1994; López *et al.* 1994; Brady & Ward 2005). Brandão, Silva *et al.* (1999) review some aspects of the biology of this subfamily, including observations suggestive of nomadic habits.

A recent discovery of two living colonies of *Leptanilloides* in Ecuador provided an opportunity to observe aspects of their behavior and motivated the present work. In this paper we describe three new sympatric species of *Leptanilloides* from an Andean cloud forest in western Ecuador. In addition, we describe two distinct gyne subcastes of *L. nubecula* **sp. n.** for the first time in the subfamily and provide a discussion of some biological aspects of this subfamily.

Materials and Methods

The type series of *L. nomada* **sp. n.** was collected in December 2003 by ALW and JMV in a private forest reserve, the *Bosque Integral Otonga*, on the western slopes of Ecuadorian Andes. In June 2004 a second species, *L. nubecula* **sp. n.**, was collected in the reserve by DAD as part of an ant diversity survey. Finally, a single worker specimen of *L. caracola* **sp. n.** was discovered while reviewing the ant collection at QCAZ museum.

Institutions mentioned in this study are abbreviated as follows: ALWC—Alexander L. Wild personal collection, Tucson, Arizona, USA; BMNH—British Museum of Natural History, London, United Kingdom; CASC—California Academy of Sciences, San Francisco, CA, USA; LACM—Natural History Museum of Los Angeles County, Los Angeles, California, USA; MCZC—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MHNG—Muséum d'Histoire Naturelle, Geneve, Switzerland; MZSP—Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; NHMB—Naturhistorisches Museum, Basel, Switzerland; NHMW—Naturhistorisches Museum Wien, Vienna, Austria; QCAZ—Museo de Zoología de la Pontificia Universidad Católica del Ecuador; UCDC—Bohart Museum of Entomology, Davis, California, USA; USNM—National Museum of Natural History, Washington, DC, USA.

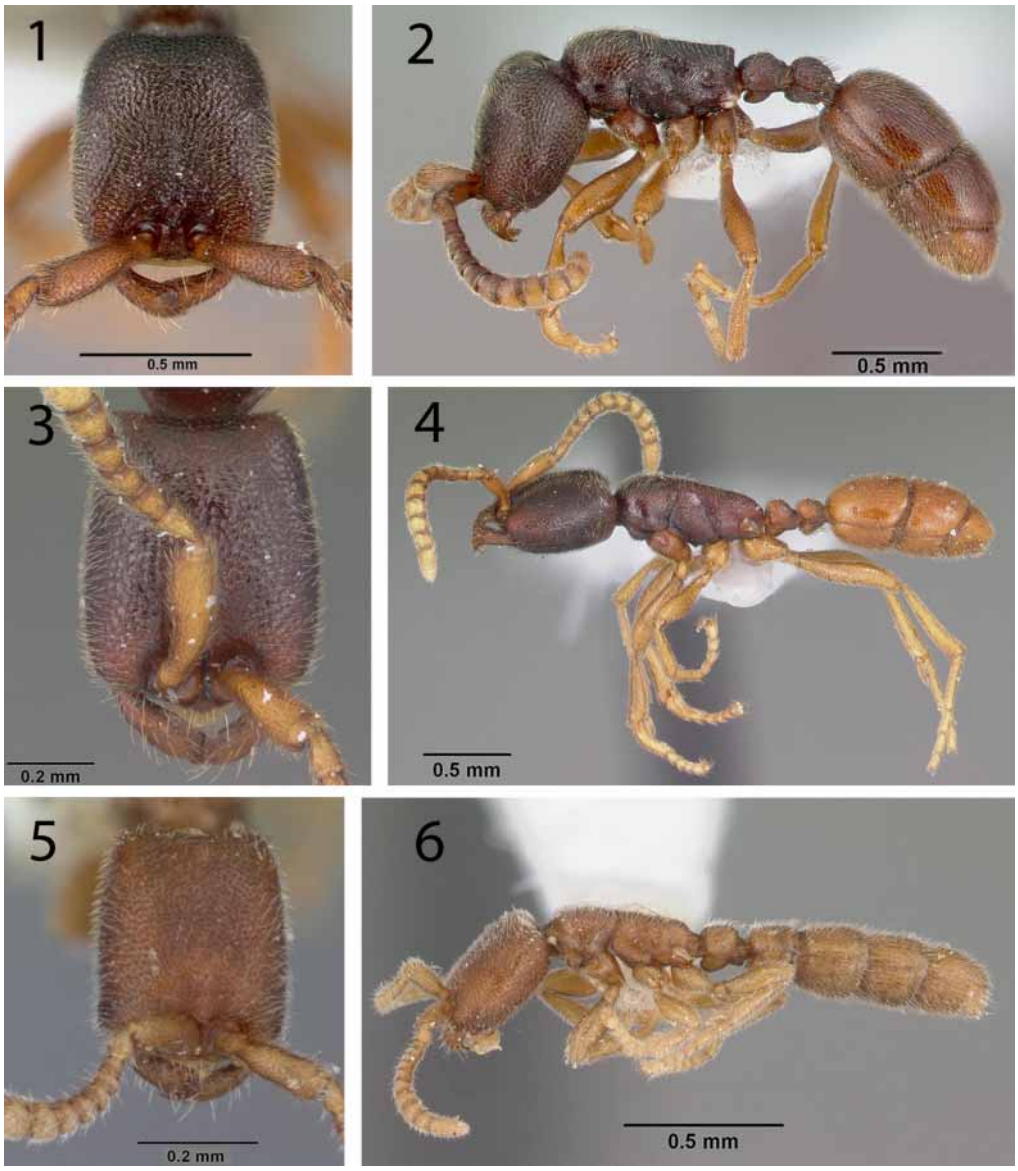
Observations were made at 50x magnification with a Wild M5A dissecting microscope at UCDC by ALW to the nearest .01 mm and at 66x on a Zeiss Stemi SV11 dissecting microscope at QCAZ by DAD to the nearest .02 mm. Worker measurements and indices are based on Brandão, Diniz *et al*. (1999) but include some others from Longino (2003) and Ward (2006): HL—head length, measured in full-face view, from the anterior median clypeal border (not including the lamellate apron) to the median occipital border; HW—maximum head width in full-face view; SL—scape length excluding the condylar bulb; WL—mesosoma length from the base of anterior slope of pronotum to the lower posterior angle of propodeum; FL—length of the fore femur; EL—length of compound eye, as seen in full-face view; LHT—length of the metatibia in dorsal view, excluding the medioproximal lobe; PL—petiole length, measured along line parallel to tergosternal suture, from anterior-most to posterior-most visible portions of tergite; PPL—postpetiole length, measured along line parallel to tergosternal suture, from anterior-most to posterior-most visible portions of tergite; CI—cephalic index (HW × 100/HL); SI—scape index (SL × 100/HW); REL—relative eye length (EL × 100/HL).

Specimens were imaged in an Auto-montage system (http://www.syncroscopy.com) by April Nobile at CASC and by ALW at UCDC, and images have been placed online as part of the Antweb database (http://www.antweb.org). For scanning electron microscopy (SEM) of *L. nubecula* **sp. n.** ergatogyne, a specimen was washed in graded series of acetone and critical point dried before metallization and observation in the MZSP SEM lab by Lara Guimarães. Images were processed as TIFF files in Adobe Photoshop.

Results

Leptanilloides nomada Donoso, Vieira & Wild

Holotype worker deposited at QCAZ. Type locality: Ecuador, Cotopaxi Province, Bosque Integral Otonga, 1960m, 79°0.197'W; 00°25.158'S, 02-Dec-2003, A. L. Wild & J. M. Vieira, leg # AW2146. Pinned paratypes were deposited in the following museums: ALWC, BMNH, CASC, LACM, MCZC, MHNG, MZSP, NHMB, NHMW, UCDC and USNM. Additional paratypes are pinned or stored in 95% ethanol at ambient temperature at QCAZ museum. See Figures 1, 2, 7–10.



FIGURES 1–6. Head in full-face view and lateral view of the body of *Leptanilloides nomada* (1–2), *L. nubecula* (3–4) and *L. caracola* (5–6).

Etymology: We chose the word *nomada* in allusion to the nomadic habits of traditional shepherds (nom = to graze; nomad = shepherd; -a, gives a feminine ending to the derivation [latin]).

WORKER

Diagnosis: Relatively large and slender. Genal teeth lacking. Clypeal lamella apron straight. Antenna stout. Mesosoma prominent. Postpetiole relatively small. Hypostomal teeth conspicuous, seen with head in ventral view. Abdominal segment 4 about the same length as following segments combined. Dark reddish coloration.

Description: Head, in full frontal view, subquadrate and somewhat wider anteriorly (CI 85–88). Lateral margins nearly straight and parallel. Posterior corners rounded and posterior margin slightly concave. Clypeus short with anterior border almost straight and bearing a concave translucent lamellae; with some setae projecting anteriorly. Frontal carina short. Frontal lobes well developed and contiguous between antennal insertions. Gena lacking carina. Mandibles slender, masticatory margin edentate, with distinct basal and apical portions separated by a rounded angle. Eyes absent. Antenna stout and 12 segmented. Torulus conspicuous. Scape long and clavate, extending further than medial distance to posterior margin. First funicular segment longer than broad, submoniliform, gradually increasing in size toward apex but without forming a distinct antennal club. Head in full face view bearing two hypostomal teeth, easily seen under clypeal translucent lamella on ventrum.

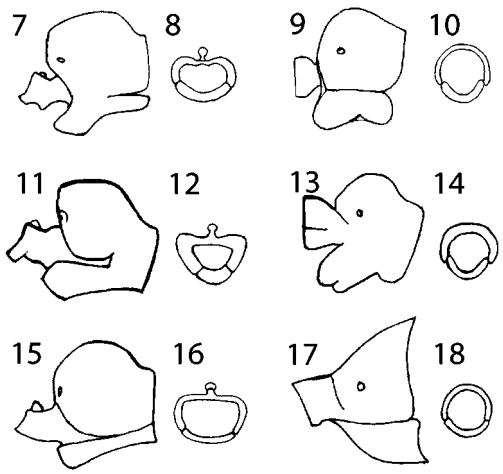
Mesosomal dorsum long, slender and flattened. Pronotum stout, with a conspicuous and flexible promesonotal suture. Metanotal groove obsolete. Mesonotum with large and sclerotized lateral lamella. Propodeum long and unarmed. Propodeal declivity very short and rounding into dorsal face. Propodeal spiracle conspicuous and rounded, in middle of the sclerite. Metapleural gland evident but located under translucent (yellow) flanges which are straight but rounded (not sharp) in posterior angle.

Petiole longer than postpetiole and as wide as long in dorsal view. Petiole with straight sides and slightly narrowed from front to rear. In profile, petiolar tergite with two dorsal portions (Figures 7–8). Anterior portion concave and the posterior portion convex. Postpetiole with dorsal edge almost rounded (Figures 9–10). Anterior-ventral portion of petiolar and postpetiolar sternite bearing a deep and rounded process. Petiolar spiracle situated in anterior part of tergite. Postpetiolar spiracle situated anterior to midlength of tergite in lateral view.

Metasoma robust. Abdominal segment 4 about the same length as following segments combined. Tergite of abdominal segment 5 not ring-like but appearing to conceal abdominal segment 6. Abdominal segments 4–5 and 5–6 separated by deep incisions. Spiracle of abdominal segment 4 conspicuous and located at 2/5 length of tergite. Spiracle of abdominal segment 5 and 6 less conspicuous and located more anteriorly than spiracle of abdominal segment 4. Pygidium concealed by the preceding segment and U-shaped.

Legs long (FL 0.50–0.52). Tibia enlarged apically. Tibia of foreleg with a long pectinate spur. Metatibial gland absent. Tarsal claws simple.

Head and mesosoma dark reddish. Gaster lighter in color, to yellowish red. Body bearing abundant white pilosity, denser dorsally than ventrally. Head, mesosoma, petiole, and post-petiole densely foveolate. Body shining.



FIGURES 7–18. Petiole and postpetiole in lateral and frontal views. Worker of *Leptanilloides nomada* (7–10). Worker (11–14) and ergatogyne (15–18) of *L. nubecula*.

Measurements (in mm) and indices: (**holotype**, min.-max. of 13 specimens): HL **0.68**, 0.65–0.68; HW **0.59**, 0.56–0.59; SL **0.42,** 0.39–0.42; FL **0.51**, 0.50–0.52; LHT **0.54**, 0.53–0.57; WL **0.75**, 0.72–0.77; PL **0.20**, 0.19–0.21; PPL **0.17**, 0.17–0.20; CI **87**, 85–88; SI **72**, 68–73.

***Comments*:** Known only from workers at the type locality. This species is reported as *Leptanilloides* sp. EC1 in Ward (2006).

The type colony was collected at night from a series of subterranean trails and small chambers along a trail-cut in a cloud forest. The trails emerged above ground for short sections spanning several centimeters. Workers flicked their antennae in a manner similar to that observed in ecitonine army ants. The colony contained numerous larvae at the same stage of development, and workers carried the larvae slung underneath their bodies in the same manner commonly observed among army ants (Gotwald 1995) and suspected for other *Leptanilloides* species (Figure 6 in Brandão, Diniz *et al*. 1999).

Holotype worker, male and gyne deposited at QCAZ. Type locality: Ecuador, Cotopaxi Province, Bosque Integral Otonga, 1978m, 79°0.197'W; 00°25.158'S, 24-Jun-2004, D.A. Donoso Leg. Under log. Some paratypes pinned and stored in the following museums: CASC, MCZC, MZSP and UCDC. Additional paratypes are stored in 95% ethanol at ambient temperature at QCAZ museum. See Figures 3–4, 11–28.

Etymology: The Latin word *nubecula* literally means *little cloud* and was chosen in reference to the cloud forest where this species was first collected. This is a noun in apposition.

WORKER

Diagnosis: Relatively large and slender ants. Polymorphic in color pattern. Without genal teeth. Anterior clypeal margin and the lamella apron triangular. Hypostomal teeth inconspicuous. Postpetiole relatively small. Abdominal segment 4 about the same length as following segments combined.

Description: Head elongate and subrectangular (CI 75–79), slightly wider anteriorly. Lateral margins of head nearly straight and parallel. Posterior corners rounded and posterior border concave. Clypeus short with anterior margin triangular. Clypeal apron translucent and triangular pointed anteriorly projecting some setae. Frontal carina very short. Frontal lobes distinct, merging between antenna. Gena without teeth. Hypostomal teeth present but inconspicuous on ventrum of head. Mandibles slender, with distinct basal and apical portions separated by a rounded angle. Masticatory margin edentate, although bearing several small denticles. Eyes absent. Antenna 12 segmented. Antennal scape slender and extending further than medial distance to posterior margin. First funicular segment longer than broad, submoniliform. Antenna gradually increases in size toward apex but without forming a distinctive antennal club.

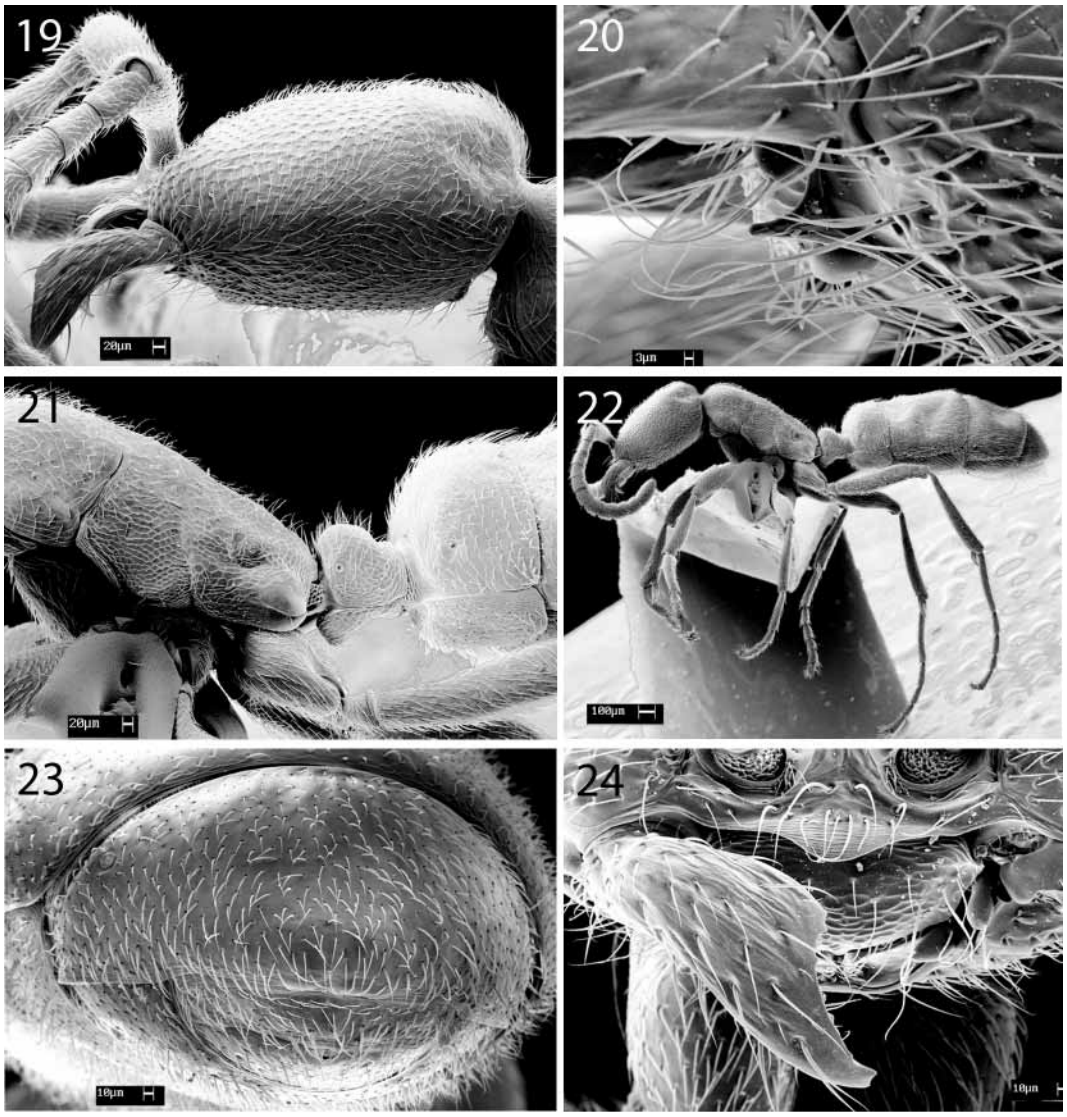
Mesosoma elongate, not slender and flattened. Pronotal suture conspicuous and flexible. Metanotal groove obsolete. Propodeum unarmed, rounded and long. Propodeal declivity very short and rounding into dorsal face. Propodeal spiracle conspicuous and rounded, slightly below the middle of the sclerite. Metapleural gland noticeable, with flanges rounded posteriorly.

Petiole in dorsal view longer than postpetiole, both segments subequal in width and slightly narrowed from front to rear, lateral borders straight. In profile, segments heart shaped, tergites always bigger than sternites. Petiolar sternite bearing large rounded process. Postpetiole ventral process not as large as petiole process. Petiolar spiracle situated at the anterior margin of the tergite (Figures 11–14).

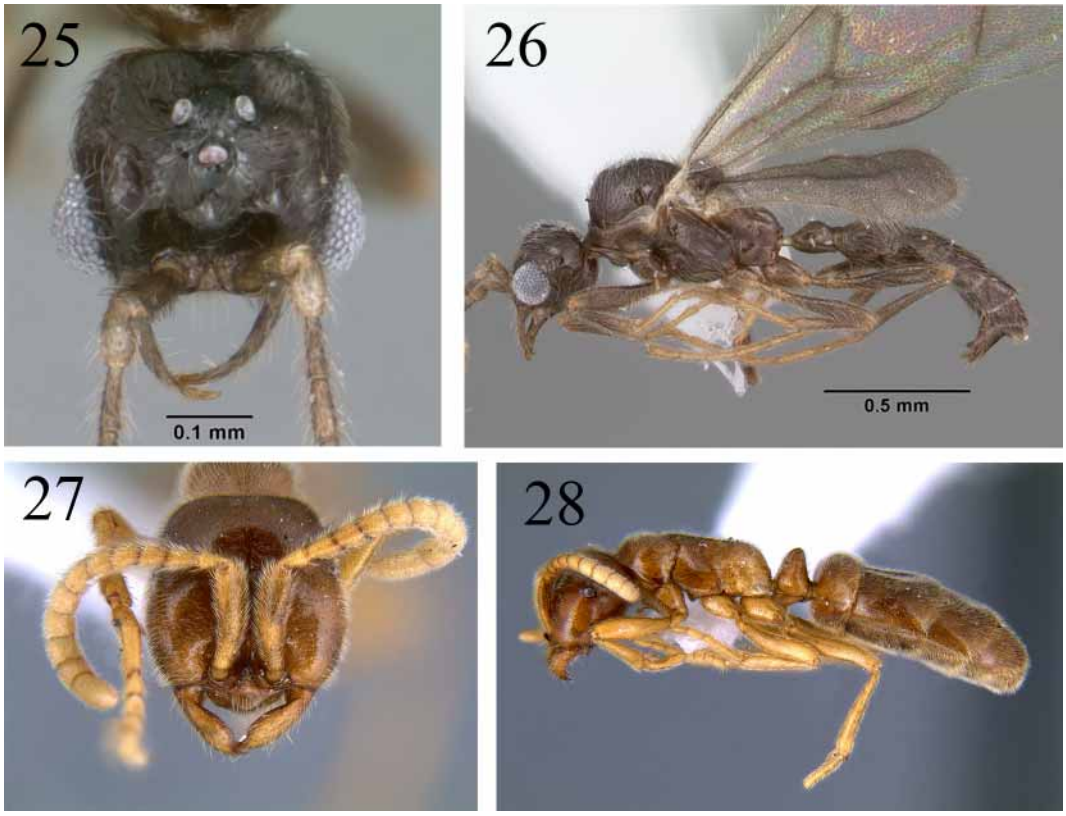
Metasoma short and compact. Abdominal segment 4 about the same length as following abdominal segments combined. Abdominal segment 5 not ring-like but conceals abdominal segment 6. Abdominal segments 4–5 and 5–6 separated by constrictions. Spiracle of abdominal segment 4 conspicuous and located at 1/3 length of

tergite. Spiracle of abdominal segment 5 conspicuous and located more anteriorly. Spiracle of abdominal segment 6 easily seen and located very anterior in the tergite. Pygidium concealed by preceding segment and displaying typical U-shape.

Legs long (FL 0.53–0.56). Tibia enlarged apically. Tibia of foreleg with a long and pectinate spur. Metatibial gland absent. Claws simple.



FIGURES 19–24. *Leptanilloides nubecula* ergatogyne. Head in lateral view and a close up of the hypostomal teeth (19–20). Lateral detail of the petiole, note the shape of the postpetiole (21). Lateral view of the body (22). Tergite of abdominal segment 7 (23). A detail of the clypeus (24).



FIGURES 25–28. Full face view of head and lateral view of body of the male (25-26) and gyne (27–28) of *Leptanilloides nubecula*.

Body color varies from testaceus to reddish brown, always shining. Head and mesosoma always darker than gaster. Head foveolate. Mesosoma and abdomen finely and sparsely foveolate. Head, body and appendages with abundant short, erect, light hairs.

Measurements (in mm) and indices: (**holotype**, min.-max. of 5 specimens): HL **0.69**, 0.69–0.72; HW **0.54**, 0.54–0.56; SL **0.42**, 0.42–0.44; FL **0.54**, 0.53–0.56, LHT **0.60**, 0.59–0.65; WL **0.87**, 0.86–0.90; PL **0.17**, 0.15–0.17; PPL **0.11**, 0.11–0.15; CI **78**, 75–79; SI **78**, 76–81.

GYNE

Diagnosis: Subdichtadiigyne. Approximately 1/4 larger than workers. Head rounded, lateral borders convex. Compound eyes present and comprised of about 10 facets. Mandibles subtriangular, masticatory margin edentate. Clypeal lamella apron present. Apterous, wings and wing buds absent. Petiole enlarged, taller and broader but similarly proportioned to worker petiole but without dorsal or lateral horns typical of ecitonine and doryline gynes. Distinct postpetiole absent, third abdominal segment broadly attached to following segments, with tergosternal fusion. Petiolar and postpetiolar spiracles located as in workers. Promesonotal suture present and articulated. All segments covered with dense pubescence. See Figures 27–28.

Measurements (in mm) and indices: (one gyne measured): HL 0.78; HW 0.74; SL 0.44; LHT 0.75; WL 1.08; PL 0.20; CI 94; SI 59.

ERGATOID GYNE

Diagnosis: Similar to workers but lighter in color and lacking a separate postpetiole (Figure 21–22). Gaster enlarged. Ovarioles present but not active. See Figures 15–24.

Measurements (in mm) and indices: (min.-max. of 3 specimens measured): HL 0.62–0.65; HW 0.53; SL 0.41–0.42; LHT 0.59–0.60; WL 0.78–0.81; PL 0.11–0.12; CI 85–81; SI 77–80.

MALE

Diagnosis: Mandibles falcate and overlapping at closure. The masticatory margin edentate. Genal teeth and hypostomal teeth lacking. Pronotum U-shaped in dorsal view and reduced anteromedially to a thin horizontal strip, set well below the level of the mesonotum. Pronotum triangular in profile, with pointed posterior apex; metapleural gland reduced and inconspicuous; propodeal spiracle small, circular, positioned at about midheight of propodeum. Medial vein diverging from radial vein more anteriorly than in *L. mckennae*; hindwing lacking closed cells. Integument mostly smooth and shiny, with scattered piligerous punctures; pilosity common on most of body, head and mandibles, suberect to decumbent. See Figures 25–26.

Measurements (in mm) and indices: (One male measured): HL 0.32; HW 0.32; SL 0.14; EL 0.14; FL 0.36; LHT 0.40; WL 0.64; PL 0.11; CI 100; SI 41; REL 45.

Comments: The type series was a colony found at 2000 hr under a rotten log. A second colony, with males, was found on a second excursion to the same study site. The diagnosis of the ergatogynes may be incomplete in reference to color and other age-related traits, as the collected ergatogyne individuals were teneral, showing pale coloration, absence of abdominal fat bodies, and undeveloped ovaries.

Leptanilloides caracola Donoso, Vieira & Wild

Holotype worker deposited at MCZC. Type locality: Ecuador, Cotopaxi Province, Bosque Integral Otonga, 2200m, 78°0.95'W; 00°0.32'S, 04-Abr-1997, EX: D3, I. G. Tapia & P. Ponce Leg. Only one specimen examined. See Figures 5–6.

Etymology: Name in reference to a popular character in local folklore. Noun in apposition.

WORKER

Diagnosis: This species can be recognized by its minute size, light brown color, absence of genal teeth and large postpetiole.

Description: Head elongate and subquadrate (CI 78), slightly wider anteriorly. Lateral margins of head nearly straight and parallel. Posterior corners rounded and posterior border slightly concave. Clypeus short with anterior border straight, lamella apron triangular. Frontal carina very short, fused between the antenna, separated anteriorly and bordering the antennal fossa. Gena without blunt teeth. Mandibles short, masticatory margin edentate, with distinct basal and apical portions separated by a rounded angle. Eyes absent. Antenna stout, 12 segmented. Scape short and clavate, extending about 3/8 the distance to occipital borders. Funiculus moderately narrow. First funicular joint rounded, broader and longer than the second. Antennal joints submoniliform, gradually increasing in size toward apex but not forming an antennal club.

Mesosoma long, slender and flattened. Pronotum conspicuous, with a flexible promesonotal suture. Metanotal groove obsolete. Sides of mesonotum sclerotized. Propodeum unarmed. Propodeal declivity very short and rounding into the dorsal face. Propodeal spiracle round, situated in the middle of the sclerite. Metapleural gland flanges conspicuous, translucent and posteriorly rounded.

Petiole distinct. Petiole smaller than postpetiole in dorsal view. Petiole very slightly narrowed from front to rear and with straight sides. Postpetiole more narrowed from front to rear. In profile, petiolar tergite with two dorsal portions. Anterior portion large and concave and posterior portion convex. Postpetiole in profile with dorsal edge rounded. Antero-ventral portion of the petiolar sternite with a deep and rounded process. Postpetiole without anteroventral process. Petiolar and postpetiolar spiracle not easily seen.

Metasoma long and slender. Abdominal segments 4–6 subequal in length in dorsal view and separated by strong constrictions. Pygidium concealed by the preceding segment and U-shaped.

Tibia enlarged apically. Tibial spur of foreleg long and pectinate. Metatibial gland absent. Claws simple.

Body color shining light yellowish brown. Head with abundant punctures. Mesosoma and abdomen more finely and sparsely punctate. Head, body and appendages with abundant, rather coarse, short and erect, brownish hairs.

Measurements (in mm) and indices: *(only holotype measured)*: HL 0.40; HW 0.31; SL 0.18; FL 0.22; LHT 0.24; WL 0.47; PL 0.12; PPL 0.16; CI 78; SI 58.

Comments: Data found on the label (i.e. EX:D3) indicates the specimen was collected in a pitfall trap in second growth forest (I. G. Tapia, pers. com.).

Discussion

Few phenomena have attracted such attention from myrmecologists as the *army ant syndrome* (Wilson 1958, 1971; Gotwald 1995; Brady 2003; Brady and Ward 2005). The army ant syndrome is defined as a combination of three discrete features: nomadism, obligate group-predation and queen dichthadiigyny. Brandão, Silva *et al.* (1999) provided

indirect evidence that army-ant like behavior occurs in the subfamily Leptanilloidinae. First, they observed synchrony in larva production, which suggests nomadism. Second, two observations suggested group predatory behavior: 1) direct observation of group-predation by an *Asphinctanilloides anae* Brandão *et al.* colony on an arthropod and 2) presence on larvae of mandibles with slender, sharp pointed teeth that facilitate being carried by workers. One of the worker paratypes of *L. legionaria* Brandão *et al*. was preserved holding a larva in the fashion typical of army ants, with the larva slung ventrally under the body of the worker (Figure 6 in Brandão, Diniz *et al*. 1999), and our field observations confirm this behavior in *L. nomada* and *L. nubecula*. Our observations provide further evidence for synchrony in brood production, as noted by the presence of numerous (>100) larvae in a single growth stage during collections of *L. nomada* and *L. nubecula*. Also, our observations demonstrate for *Leptanilloides* subterranean habits, trail-following behavior, and nocturnal activity.

The discovery of the *L. nubecula* gyne with a subdichtadiigyne habitus brings new data to the discussion of army ant origins. The leptanilloidine queen differs from true army ants in at least two respects: the gaster is not fully physogastric (maybe due to the relatively small number of workers in a normal leptanilloidine colony, or to a particular colony stage when collected), and the presence of eyes. However, in common with true army ants, leptanilloidine gynes are apterous and have an enlarged postpetiole and falcate mandibles. These characteristics suggest obligate fission as the reproductive strategy for *Leptanilloides* (see discussion in Gotwald 1995; Peeters & Ito 2001). Workers also show variable expression of typical army ant characters. Unlike true army ants, the colonies are not extraordinarily large, and there is no extreme polymorphism like some of the army ants. The Leptanilloidinae suggest a scenario for what the early stages of army ant evolution might have been.

The queen polymorphism (one true gyne plus several ergatogynes) found in *L. nubecula* is not new in the dorylomorphs (see Peeters & Ito 2001). Polygyny was reported for *Neivamyrmex carolinensis* (Emery) (Rettenmeyer & Watkins 1978). In this species, polygyny was presumed to be correlated with special ecological limitations imposed by the tough environment in which the ants live. They occur at the northern limit of the range of army ants, and there may be a high rate of gyne death due to cold winters (Gotwald 1995). The cold conditions of the high Andean cloud forest may similarly favor polygyny in *Leptanilloides*.

The new species *L. nomada* and *L. nubecula* share strikingly similar character states with *L. mckennae* Longino and *L. legionaria* Brandão *et al.* with respect to external morphology. Shared characters include: 1) high reduction or lack of genal teeth, 2) petiolar form intermediate between *Asphinctanilloides* and *Leptanilloides*, 3) postpetiole smaller than petiole, 4) postpetiolar spiracle shifted backwards on anteromedian side of tergite, and 5) blunt flange over metapleural gland opening. These characters blur the distinction between *Leptanilloides* and *Asphinctanilloides*, an observation previously noted by Longino (2003) and Ward (2006). It is noteworthy that the males of the two

species for which males are known differ greatly in mandible shape. The mandible of *L. nubecula* males are falcate while those of *L. mckennae* are subtriangular. The presence of sickle-shaped mandibles in *L. nubecula* males provides additional evidence that at least some *Leptanilloides* show trends toward stereotypical army ant morphology (see Ward 2006).

The character states shown by *Leptanilloides* have important consequences for the reconstruction of army ant evolution. Dorylomorphs comprise a well-supported group of ant subfamilies which includes army ants and relatives (Bolton 2003). The current view sets Leptanilloidinae as the sister group to the remainder of the dorylomorphs [Cerapachyinae + (true army ants)] (Brady and Ward 2005). This phylogenetic placement makes Leptanilloidinae an important taxon of reference for studies on the evolution of cerapachyines and of the more highly specialized true army ants, especially under some models of character evolution (Cunningham 1999). In particular, the observations reported here imply that some army ant traits, including eyelessness in the worker, specialized gyne morphology, and the form of brood carrying, may have been present in the ancestral dorylomorph. However, the presence of large eyes and small, unspecialized gynes in some *Cerapachys* species (Brown 1975) raise the alternate scenario, that *Leptanilloides* may represent a case of parallel evolution and convergence on true army ants. Ward (2006) suggests that the leptanilloidine lineage is older than the approximately 105 million year old army ant lineage, as estimated from molecular dating analysis (Brady 2003). If true, they predate the complete fragmentation of Gondwana. Since leptanilloidine ants have not been recorded outside of the Neotropics, the group may well have gone extinct elsewhere.

The discovery of three *Leptanilloides* species living in sympatry provides evidence of considerably more ecological diversity than was previously thought. The different *Leptanilloides* species may well be occupying distinct subterranean ecological niches. True army ants usually also occur as diverse communities of sympatric species (Gotwald 1995), although in that group as well little is known about how the different species partition local resources It is unknown whether these sympatric *Leptanilloides* speciated in sympatry or whether they co-occur as a result of secondary contact. In any case, the Otonga reserve and other Andean cloud forests are of extremely high importance for the study and conservation of *Leptanilloides* ants, a significance noted more generally by Myers *et al.* (2000) and documented for mammals (Jarrin 2001) and vascular plants (Jaramillo 2001).

Key to species of *Leptanilloides* based on the worker caste

1 Postpetiole in profile much shallower dorsoventrally than adjoining fourth abdominal segment (Figures 2, 4); postpetiolar spiracle shifted posteriad on anteromedian side of tergite (Figures 9, 13); genal teeth absent or very reduced in size (Figure 3), body size relatively large [HL 0.68–0.70] 2

- Postpetiole in profile nearly as deep dorsoventrally as fourth abdominal segment (Figure 6); postpetiolar spiracle situated forward on the tergite; genal teeth usually present and large (except in *L. caracola*), body size relatively small [HL 0.40–0.50] 5

2 Head subquadrate [CI 85–88]; lateral margins nearly straight and parallel (Figure 1); propodeal declivity short and straight, propodeum with dorsal and posterior faces clearly differentiated (Figure 2) ..... *L. nomada* (Ecuador)

- Head subrectangular [CI 75–80]; lateral margins rounded (Figure 3); propodeal declivity usually rounded without clear distinction between dorsal and posterior face (Figure 4) 3

3 Lateral margins of the head rounded; posterior margin of the head slightly concave; head sculpture fine, at most 10-12 shallow foveolae across face at midlength (Figure 5 in Brandão, Diniz *et al.* 1999)..... *L. legionaria* (Colombia)

- Lateral margins of the head slightly rounded; posterior margin of the head deeply concave; head sculpture more coarse, with at least 15 foveolae across face at midlength . 4

4 Without hypostomal teeth..... *L. mckennae* (Costa Rica)

- With hypostomal teeth (Figures 19–20)..... *L. nubecula* (Ecuador)

5 Flange over metapleural gland opening rounded posteriorly; head sculpture coarse, about 20 deep foveolae across face at midlength 7

- Flange over the metapleural gland opening sharply pointed posteriorly; head sculpture variable 6

6 Petiole, in lateral view, longer than postpetiole; head sculpture shallow, with 15 foveolae across face at midlength (Figure 7 in Brandão, Diniz *et al.* 1999)..... ..... *L. biconstricta* (Bolivia)

- Petiole, in lateral view, as long as postpetiole; head sculpture deeper, with 25 foveolae across face at midlength (Figure 1 in Brandão, Diniz *et al.* 1999) .... *L. sculpturata* (Colombia)

7 Genal teeth very small or reduced; mandibular teeth not developed, masticatory margin edentate (Figure 5) ..... *L. caracola* (Ecuador)

- Genal teeth present (Figure 16 in Brandão, Diniz *et al.* 1999); mandibular teeth well developed (Figure 16 in Brandão, Diniz *et al.* 1999)..... *L. improvisa* (Ecuador)

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