



Nylanderia of the World, Part IV: Taxonomic contributions to the American Clade I of New World *Nylanderia* (Hymenoptera: Formicidae)



JASON L. WILLIAMS^{1,*,}, JOHN F. WILLIAMS^{1,†}, JOHN S. LAPOLLA² & ANDREA LUCKY¹

¹Entomology & Nematology Department, University of Florida, Gainesville, Florida, U.S.A.

 jfwilliams@ufl.edu;  <https://orcid.org/0000-0001-7605-3596>

 alucky@ufl.edu;  <https://orcid.org/0000-0001-8397-7498>

²Department of Biological Sciences, Towson University, Towson, Maryland, U.S.A.

 jlapolla@towson.edu;  <https://orcid.org/0000-0001-7602-1527>

[†]Co-first author

*Corresponding author:  jleewill@gmail.com;  <https://orcid.org/0000-0002-9834-3348>

Abstract

Globally, potentially hundreds of *Nylanderia* species remain undescribed, hidden within several broadly distributed complexes of morphologically cryptic species. By integrating phylogenomics, geography, and morphology, we describe eight new *Nylanderia* species from southern Mexico and Mesoamerica, increasing the total number of known species in the genus to 131. In the Americas, *Nylanderia* is divided into two distantly related clades: American Clade I (AC1) and American Clade II (AC2). Within AC1, *Nylanderia austroccidua* (Trager) was originally described as a widespread and morphologically variable species distributed from Utah to Costa Rica. This species was diagnosed by a slight concavity in the anterior face of the pronotum and varying degrees of fine cuticular microsculpturing across the body that causes blue cuticular iridescence under microscopic examination. Using Ultraconserved Elements (UCEs) for molecular phylogenetic analysis, we found that taxa matching the original description of *N. austroccidua* are paraphyletic with respect to Nearctic *Nylanderia* species. We also found that AC1 includes a Neotropical subclade extending into Mesoamerica, the distribution of which overlaps with AC2, which is exclusively Neotropical. Along with an updated description of *N. austroccidua*, we also describe the following new species belonging to clade AC1: *N. breviscapa*, **sp. nov.**, *N. contraria*, **sp. nov.**, *N. lazulina*, **sp. nov.**, *N. luceata*, **sp. nov.**, *N. mendax* **sp. nov.**, *N. mosaica* **sp. nov.**, *N. polita* **sp. nov.**, and *N. usul*, **sp. nov.** A dichotomous key and images of the worker caste of these species are included and, where available, images of queens and males are provided.

Key words: ant, Central America, Formicinae, Mesoamerica, Mexico, new species, phylogenomics

Introduction

Nylanderia Emery is one of the most commonly collected ant genera from leaf litter across the world (Ward 2000). In addition to the eight new species described in this study, there are currently 123 known species and 25 subspecies (Bolton 2024), with estimates suggesting that hundreds more remain undescribed (LaPolla *et al.* 2011). Originating in Southeast Asia during the mid-Eocene, *Nylanderia* has since undergone a rapid radiation across much of the globe, with two distinct dispersals to the Americas represented by two distantly related clades (Fig. 1)—one centered in the Nearctic (herein referred to as ‘American Clade I’, or ‘AC1’) and the other in the Neotropics (‘American Clade II’, or ‘AC2’) (Williams *et al.* 2020). *Nylanderia* species are generally characterized as small to medium-sized formicines with subtle morphological differences, making them difficult to distinguish from each other. Species-level identification is additionally hampered by the frequent, inadvertent arrival of at least 15 different ‘globetrotting’ *Nylanderia* species at ports of entry across the world (Williams & Lucky 2020). *Nylanderia* also includes numerous morphologically cryptic species complexes in which intraspecific variation in the worker caste blends near-seamlessly with interspecific variation, making taxonomy of the group particularly challenging without integration of phylogenomic data (Williams *et al.* 2020, 2022) and inviting the evaluation of male character sets for taxonomic utility (Williams *et al.* 2024).

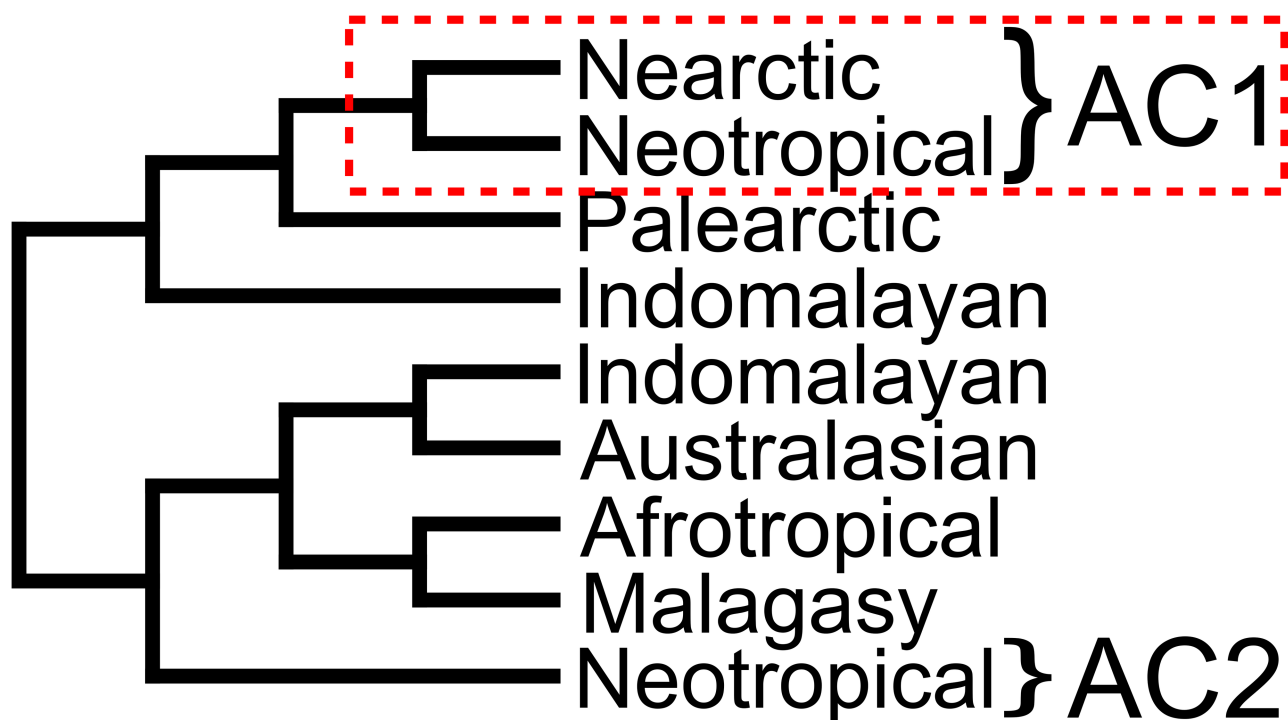


FIGURE 1. Simplified cladogram depicting relationships between major biogeographically defined lineages of *Nylanderia* (Williams *et al.* 2020, 2022), including American Clade I (AC1) and American Clade II (AC2). Focal taxa of this study all belong to clade AC1.

A taxonomic revision of *Nylanderia* in the Nearctic recognized 14 native species (Kallal & LaPolla 2012), with subsequent studies of socially parasitic species adding three more (Messer *et al.* 2016, 2020), bringing the total to 17 species known in the region. In both its initial description and subsequent retreatment in the Nearctic revision (Kallal & LaPolla 2012), *Nylanderia austroccidua* (Trager 1984) was regarded as a probable species complex based on its broad distribution and extensive morphological variation. Many specimens matching the description of *N. austroccidua* are found across Mexico and Mesoamerica, where extensive morphological diversity appears to be concentrated. These specimens are found primarily in montane, moderate to high elevation forests ranging from Utah, across the southwestern United States, and throughout Central America as far south as Costa Rica (Kallal & LaPolla 2012).

This study serves as an addendum to the Nearctic revision, focusing specifically on the taxonomic treatment of the lineages within clade AC1 that align with the description of *N. austroccidua* and extend into Mesoamerica as far south as Costa Rica. By integrating phylogenomics, geography, and morphology, we aim to test the monophyly of a group of morphologically similar species herein provisionally referred to as the ‘*N. austroccidua* complex,’ provide an updated description of *N. austroccidua* (*sensu stricto*), and formally describe eight additional species as new. One more species, identified within the Neotropical subclade of clade AC1, is tentatively classified as ‘*N. cf. docilis*’ due to its superficial similarity to the South American species, *Nylanderia docilis* (Forel 1908). This classification indicates that it is neither formally described as a new species nor definitively identified as *N. docilis*, as our understanding of the South American taxonomy is currently insufficient without further revisionary work. Additionally, we present a phylogeny of clade AC1, a dichotomous key, distribution maps, and images of workers, queens, and males.

Material and methods

Sources of material. Specimens examined for this study are deposited at the following institutions and private collections:

CASC	California Academy of Sciences, San Francisco, California, U.S.A.
JTLC	John (Jack) T. Longino Collection, Salt Lake City, Utah, U.S.A.
MCZC	Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland
MNCR	Museo Nacional de Costa Rica, San José, Bella Vista, Costa Rica
USNM	National Museum of Natural History, Washington, D.C., U.S.A.
SWRS	Southwestern Research Station, Portal, Arizona, U.S.A.

Sample selection. Most of the samples examined for this study ($n=403$) were subsampled and processed from three extensive leaf litter sampling surveys conducted between 2001 and 2016: (1) Project ALAS (Longino & Colwell 2011), (2) Project LLAMA (Longino *et al.* 2014; Longino & Anderson 2008), and (3) Project ADMAC (Longino & Branstetter 2019). Subsampling for this study was conducted systematically to maximize coverage across geographic range, habitat type, elevational gradients, and morphological diversity. Priority was given to samples that included queens or males in addition to workers. Since *Nylanderia* species typically nest in leaf litter (LaPolla *et al.* 2011; Ward 2000), Winkler extractions often capture large portions of colonies, facilitating associations between the different castes and sexes when present.

Species delimitation criteria. We used the combination of the following operational criteria to classify and delimit species in this study: (1) phylogenetic results; (2) worker, queen, and male morphology; and (3) geographical distribution patterns and habitat. Priority was given to interpretation of phylogenetic results, which was corroborated in all cases by morphological evidence. Species were determined to be strongly-supported monophyletic lineages with unique morphological features.

DNA extraction, UCE library preparation, and sequencing. All 104 sequences used in this study were previously generated for three other projects (Williams *et al.* 2020, 2022, 2024) and selected from a globally representative dataset to encompass the known diversity of clade AC1. Collection information for each specimen sequenced can be found in Table S1 and sample quality data are in Table S2. Quality-trimmed reads are available from the National Center for Biotechnology Sequence Read Archive (<http://www.ncbi.nlm.nih.gov/sra>; PRJNA1105377, PRJNA728185, PRJNA553590).

UCE data processing and alignment. We used the PHYLUCE v1.7.3 pipeline (Faircloth 2015) to process UCE sequences and assembled the clean-fastq reads using SPAdes (Bankevich *et al.* 2012). We Aligned the UCE loci using MAFFT (Katoh & Standley 2013) and trimmed the alignments using GBLOCKS (Castresana 2000). We selected a 90% complete matrix retaining 1,977 loci for the final dataset. We removed poorly aligned sequence fragments using the ‘spruceup’ Python script (Borowiec 2019) and selected the 97% cutoff for downstream analysis. Summary statistics were calculated using the Alignment Manipulations and Summary (AMAS) Python script (Borowiec 2016): alignment length = 1,422,207; total matrix cells = 147,909,528; missing % = 8.9; proportion variable sites = 0.24; and proportion parsimony informative = 0.08. See Table 1 for more UCE sequencing statistics.

TABLE 1. Ultraconserved element sequencing statistics.

	Extract conc. (ng/μL)	Post-PCR conc. (ng/μL)	Contigs	Total bp	Mean length	Min length	Max length	Median length
Mean	0.66	26.70	2249.15	2277599.59	999.96	5.90	181.33	2572.63
Min	0.11	0.30	309.00	90372.00	292.47	2.84	56.00	563.00
Max	2.03	57.70	2366.00	2841873.00	1232.92	7.20	247.00	5853.00
SD	0.33	11.83	226.07	546186.79	210.75	1.01	50.27	676.87
95% CI	0.06	2.27	43.45	104971.79	40.50	0.19	9.66	130.09

Phylogenetic analysis. We used site entropy information from Sliding-Window Site Characteristics SWSC-EN; Tagliacollo & Lanfear 2018) to inform the partition scheme for the 90% complete matrix. Partitioning was completed in PartitionFinder2 (Lanfear *et al.* 2017) under the GTR+G model using the ‘recluster’ algorithm. Using this partition scheme, we reconstructed phylogeny under maximum-likelihood (ML) criterion in IQ-TREE 2 (Minh *et al.* 2020). The best-fit substitution model for each partition was determined using ‘-m MFP+MERGE’ (ModelFinder; Kalyaanamoorthy *et al.* 2017). Nodal support was assessed using a Shimodaira-hasegawa approximate likelihood-

rate test (SH-aLRT; Guindon *et al.* 2010) with 1,000 replicates ('-alrt 1000') and 1,000 ultrafast bootstrap (UFBoot; Hoang *et al.* 2017) replicates ('-bb 1000') using the '-bnni' algorithm. Only nodes with values of SH-aLRT ≥ 0.90 and UFBoot ≥ 0.95 were considered strongly supported.

Imaging and measurements. Specimen images were taken using a Canon EOS 6D Mark II camera mounted on a Macropod Pro 3D and Micro Kit System (Macroscopic Solutions, East Hartford, CT, USA). Profile, full-face, and dorsal views of specimens were imaged using a Canon MP-E 65mm lens. Male genitalia in ventral and in dorsal view were imaged using a Canon EF 200mm lens mounted with a 10x objective. For each view, up to 60 images were taken and then focus-stacked using Zerene Stacker. Focus-stacked images taken as part of this study are also made available via AntWeb (AntWeb 2024). Measurements (to the nearest 0.001 mm) were taken from pinned specimens at 200x magnification using a Mitutoyo IT-012U digital stage micrometer mounted to a Leica S8 APO dissecting stereomicroscope. See Table S3 for all specimen measurements recorded in this study. Measurements and indices are defined as:

EL	(Eye Length): In full-face view, maximum anteroposterior length of the compound eye.
EW	(Eye Width): In oblique lateral view, maximum width of the compound eye.
GL	(Gaster Length): In lateral view, maximum length from the anteriormost point of the third abdominal segment (first gastral segment) to the posteriormost point of the terminal abdominal segment.
HE	(Head Emargination): In full-face view, depth of the medial concavity in the posterior margin of the head, from a line drawn across the posterior margin to the medial point of the concavity (HE=0 when posterior margin is not concave).
HL	(Head Length): In full-face view, maximum length from a line drawn across the posterior margin of the head to a parallel line drawn across the anterior margin of the clypeus.
HLA	(Head Length Anterior): In full-face view, length from a line drawn across the anteriormost points of the compound eyes to a line drawn across the anterior margin of the clypeus.
HLP	(Head Length Posterior): In full-face view, length from a line drawn across the posteriormost points of the compound eyes to a line drawn across the posterior margin of the head.
HW	(Head Width): In full-face view, maximum width of the head between the lateral margins, excluding the compound eyes.
IOD	(Interocular Distance): In full-face view, minimum distance between the medial points of the compound eyes.
LHT	(Length of Hind Tibia): In a view perpendicular to the long axis of the metatibia, length of the metatibia, excluding the proximomedial part of the articulation with the metafemur.
MMC	(Mesonotal Macrosetae Count): Number of erect macrosetae on mesonotum found on one side of the sagittal plane.
MW	(Mesonotum Width): In dorsal view, maximum width of the mesonotum.
PDH	(Propodeum Height): In lateral view, distance between the base of the metapleuron and the highest point of the propodeum.
PMC	(Pronotal Macrosetae Count): Number of erect macrosetae on pronotum found on one side of the sagittal plane.
PrW	(Propodeum Width): In dorsal view, maximum width of the propodeum.
PTW	(Petiole Width): In dorsal view, maximum width of the petiole.
PW	(Pronotum Width): In dorsal view, maximum width of the pronotum.
SL	(Scape Length): In a view perpendicular to the long axis of the scape, maximum length of the scape, excluding the condyle.
SMC	(Scape Macrosetae Count): Total number of erect macrosetae on the scape, excluding the terminal cluster often found around the joint of the scape and the funiculus. View of scape may need to be rotated to get an accurate count.
TL	(Total Length): HL + WL + GL
WL	(Weber's Length): In lateral view, maximum length from the point at which the pronotum meets the cervical shield to the posterior basal angle of the metapleural lobe.
BLI	(Body Length Index): $(WL/HW) \times 100$
CI	(Cephalic Index): $(HW/HL) \times 100$
EPI	(Eye Position Index): $(HLA/HLP) \times 100$

HTI	(Hind Tibia Index): (LHT/HW) x 100
REL	(Relative Eye Length): (EL/HL) x 100
SI	(Scape Index): (SL/HW) x 100

Results

Synopsis of species

N. austroccidua (Trager 1984), southwestern North America, from Utah, U.S.A to Tamaulipas, Mexico
N. breviscapa, **sp. nov.**, southern Mexico
N. contraria, **sp. nov.**, southern Mexico
N. cf. docilis, widespread from southern Mexico to Honduras
N. lazulina, **sp. nov.** widespread from southern Mexico to Honduras
N. luceata, **sp. nov.**, Guatemala and Honduras
N. mendax, **sp. nov.**, Guatemala
N. mosaica, **sp. nov.**, Costa Rica
N. polita, **sp. nov.**, southern Mexico
N. usul, **sp. nov.**, Costa Rica

Phylogenetic analysis

Clade AC1 is strongly supported and comprises two well-defined subclades: a Nearctic subclade, which contains all known Nearctic *Nylanderia* species, and a Neotropical subclade (Fig. 2). These two subclades overlap in distribution around the Isthmus of Tehuantepec in southern Mexico. Strong support was found for paraphyly of the *N. austroccidua* complex. Within the Nearctic subclade of clade AC1, *N. austroccidua* (*sensu stricto*), *N. contraria*, and *N. polita* were resolved as more closely related to other Nearctic species, with *N. contraria* and *N. polita* strongly supported as sister species. The remaining seven species in the complex—*N. breviscapa*, *N. cf. docilis*, *N. lazulina*, *N. luceata*, *N. mendax*, *N. mosaica*, and *N. usul*—resolved within the Neotropical subclade of AC1.

Morphological diagnosis of clade AC1 species in southern Mexico and Mesoamerica

Workers of species in clade AC1 are most readily distinguished from other *Nylanderia* species by their relatively sparse overall pilosity (Kallal & LaPolla 2012). While cephalic pubescence can be highly variable, ranging from sparse to dense, mesosomal pubescence is often lacking entirely or limited to small patches on the pronotum or the dorsal face of the propodeum. Gaster pubescence is absent or sparse, except in *Nylanderia bruesii* (Wheeler 1903), which has dense pubescence on the gaster (Kallal & LaPolla 2012).

Workers of clade AC1 species found in Mexico and Mesoamerica that were previously diagnosed as *N. austroccidua* share a combination of the following characters. They are relatively small (TL: 1.62–2.52 mm). The head is longer than broad (CI: 76–91; Fig. 71A), quadrate, and often with emargination of the posterior margin (HE: 0–0.03 mm). All have a similar overall shape of the mesosoma, with an angular pronotum bearing a slight concavity on the anterior face. All species in this complex except for *N. lazulina* have a pair of small, erect setae on the apex of the petiole. All species except for *N. polita* have cuticular microsculpture that reflects varying degrees of blue iridescence, visible under microscopy specifically with diffuse LED or fiber optic lights but difficult to consistently capture in images (e.g., see medial head surface of *N. austroccidua* in Figs. 4 and 5). Blue cuticular iridescence is not unique to this clade and can be found in many other *Nylanderia* species. However, *Nylanderia faisonensis* (Forel 1922) is the only other species in American Clade I that has blue cuticular iridescence.

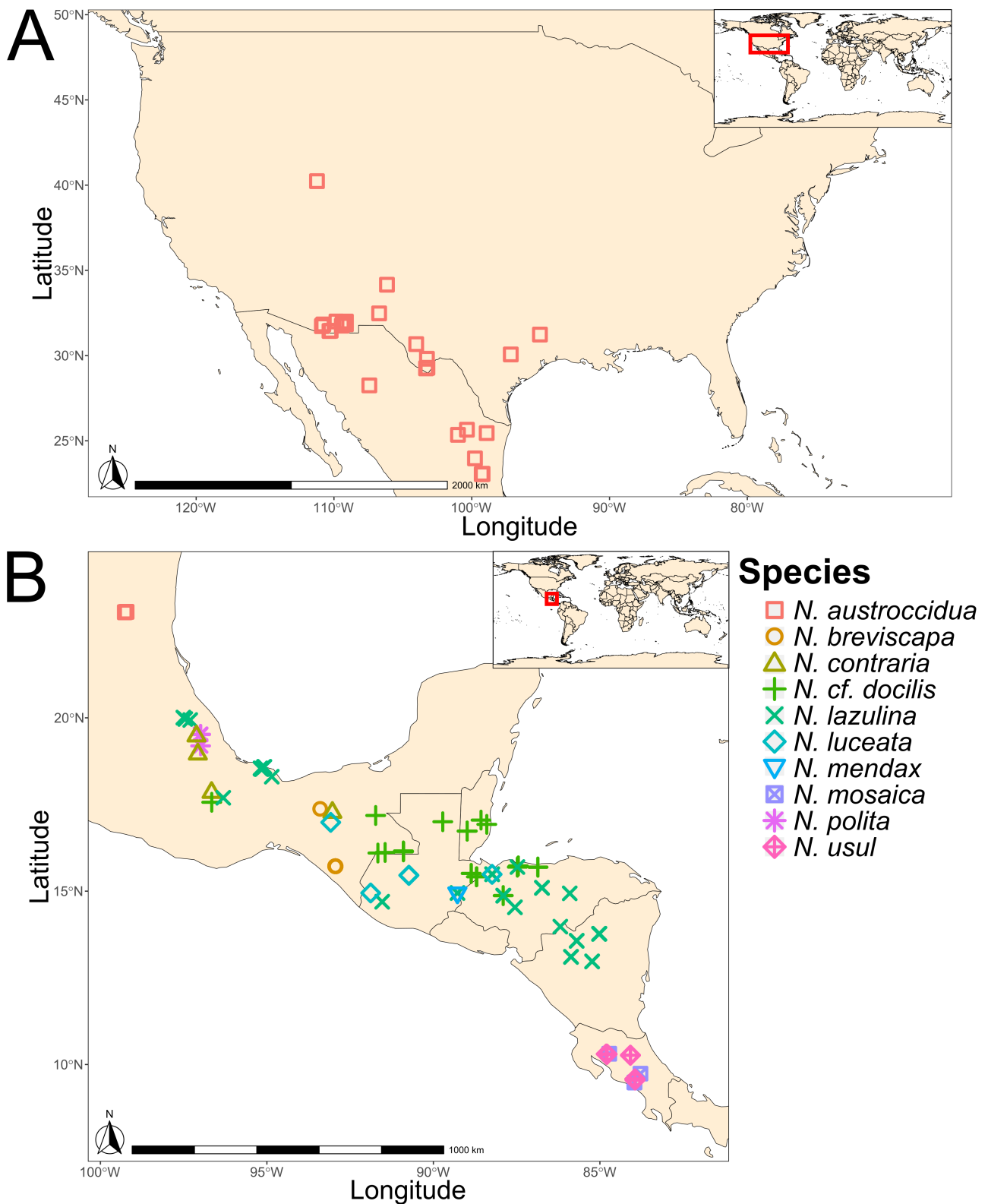


FIGURE 2. Distributions of species: (A) *N. austroccidua* in the United States and northern Mexico, (B) species found across southern Mexico and Mesoamerica, and (C) *N. docilis* in South America. Maps were created using GPS coordinates listed in Table S1 and from the Global Ant Biodiversity Informatics (GABI; Guénard *et al.* 2017) database.

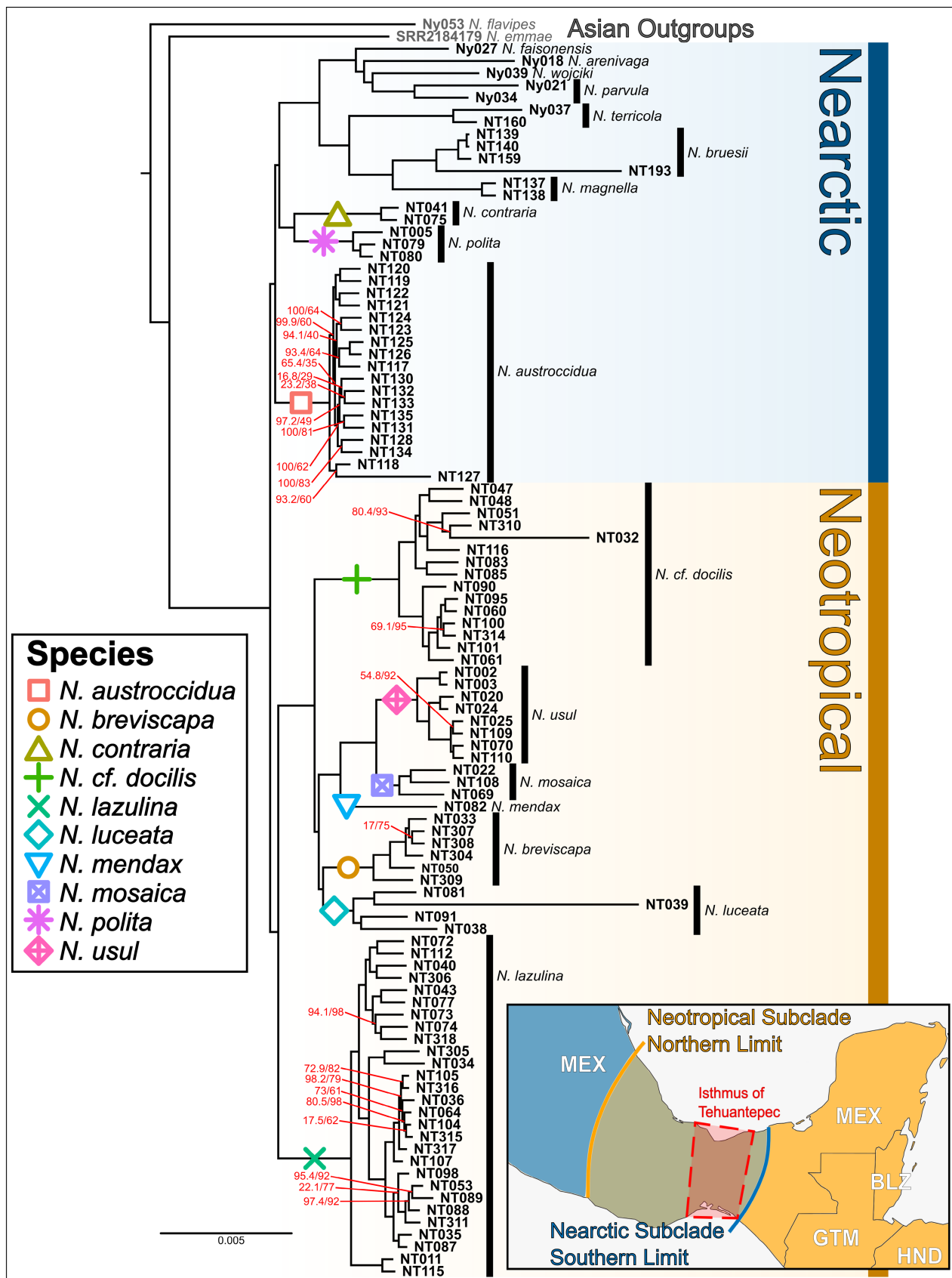


FIGURE 3. Maximum likelihood phylogeny of clade AC1 reconstructed using the 90% complete SWSC partitioned matrix. Nodal support (SH-aLRT/UFBoot) is displayed only for nodes with <95% support for either measure. The map inset in the bottom-right indicates the extent of geographical overlap between the Nearctic and Neotropical subclades around the Isthmus of Tehuantepec.

Key to *Nylanderia* clade AC1 species of southern Mexico and Mesoamerica

1. Cephalic pubescence moderate to dense (Figs. 4A, 4B); overall color variable 2
 - Cephalic pubescence absent to sparse (Fig. 4C); often uniformly yellow with thick, black setae, with specimens from Belize sometimes light to medium brown *cf. docilis*
2. Overall color light to dark brown; dense cephalic pubescence (Fig. 4A); scapes relatively short, surpassing posterior margin by no more than a third of their length ($SI < 133$) 3
 - Overall color variable; if overall color is brown or reddish-brown, then cephalic pubescence moderate (Fig. 4B); if overall color is yellow, then cephalic pubescence moderate (Fig. 4B) to dense (Fig. 4A); scape length variable 6
3. Posterior face of propodeum about as long as or slightly longer than dorsal face; ranging across southern Mexico and Central America 4
 - Posterior face of propodeum about twice as long as dorsal face; ranging across southwestern North America from central Mexico to Utah (Fig. 2) *austroccidua*
4. Medium to dark brown with antennae, mandibles, and tarsi yellow in contrast to body; head and gaster concolorous with mesosoma; meso- and metacoxae lighter in color than mesosoma; scapes surpassing posterior margin by about a third of their length ($SI \geq 130$) 5
 - Light brown with antennae, mandibles, and tarsi concolorous with body; sometimes bicolored with medium brown head and gaster; meso- and metacoxae concolorous with mesosoma; scapes surpassing posterior margin by less than a quarter of their length ($SI < 130$) *breviscapa*
5. Dark brown, with whitish meso- and metacoxae strongly contrasting with mesosoma; fine cuticular microsculpture resulting in moderate to strong blue iridescence on head and mesosoma *contraria*
 - Medium to dark brown, with meso- and metacoxae somewhat lighter than mesosoma; cuticle smooth and shiny, with no microsculpture and without blue iridescence *polita*
6. Overall color variable, but with head and mesosoma concolorous with gaster; cephalic pubescence dense (Fig. 4A) if overall color is yellow, cephalic pubescence moderate (Fig. 4B) if overall color is brown 7
 - Strongly bicolored, with yellow to yellow-brown head and mesosoma and medium to dark brown gaster; cephalic pubescence moderate (Fig. 4B) *mosaica*
7. meso- and metacoxae at most somewhat lighter than mesosoma, not whitish 8
 - Meso- and metacoxae whitish, strongly contrasting with mesosoma 9
8. Medium to dark reddish-brown; scapes relatively long, surpassing posterior margin by more than a third to nearly half their length ($SI \geq 140$); moderate cephalic pubescence (Fig. 4B); propodeum low and evenly rounded, with posterior face at most slightly longer than dorsal face; found in Guatemala, possibly Honduras *mendax*
 - Color variable; scapes relatively short, surpassing posterior margin by about a quarter to a third of their length ($SI < 140$); cephalic pubescence moderate (Fig. 4B) in dark specimens and dense (Fig. 4A) in yellow specimens; propodeum high and evenly rounded, with posterior face steep and at most slightly longer than dorsal face; found in Costa Rica *usul*
9. Medium to dark reddish-brown; macrosetae relatively thick and black, strongly contrasting in color with body; antennae, mandibles, and tarsi concolorous with body; overall cuticle finely microsculptured, giving matte appearance and strong blue iridescence; erect setae on scapes relatively sparse ($SMC < 7$); apex of petiole scale without pair of small, erect setae; compound eyes relatively large ($REL > 19$); scapes relatively long, surpassing posterior margin by nearly half their length ($SI \geq 140$); metatibiae relatively long ($HTI \geq 125$); mesosoma relatively long ($BLI > 146$); relatively large in overall size ($TL = 1.99-2.52$) *lazulina*
 - Light to medium reddish-brown; macrosetae relatively thin and concolorous with body; antennae, mandibles, and tarsi yellow to yellow-brown, contrasting with body; overall cuticle lightly microsculptured and with subtle blue iridescence; erect setae on scapes relatively abundant ($SMC \geq 7$); apex of petiole scale bearing a pair of small, erect setae; compound eyes relatively small ($REL \leq 19$); scapes relatively short, surpassing posterior margin by less than a quarter of their length ($SI < 130$); metatibiae relatively short ($HTI < 115$); mesosoma relatively short ($BLI \leq 146$); relatively small in overall size ($TL = 1.71-2.24$) *luceata*

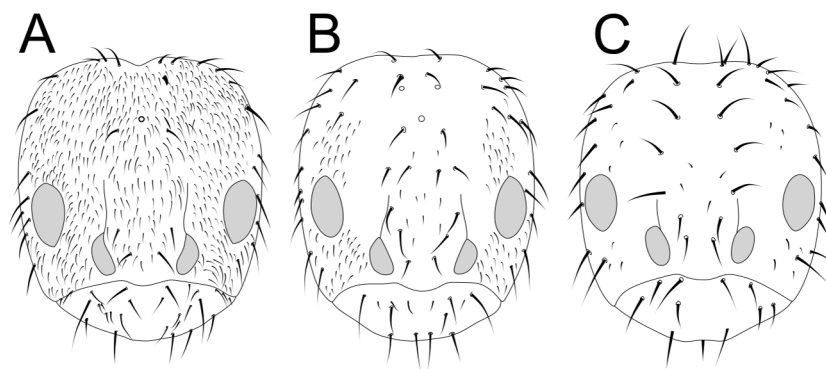


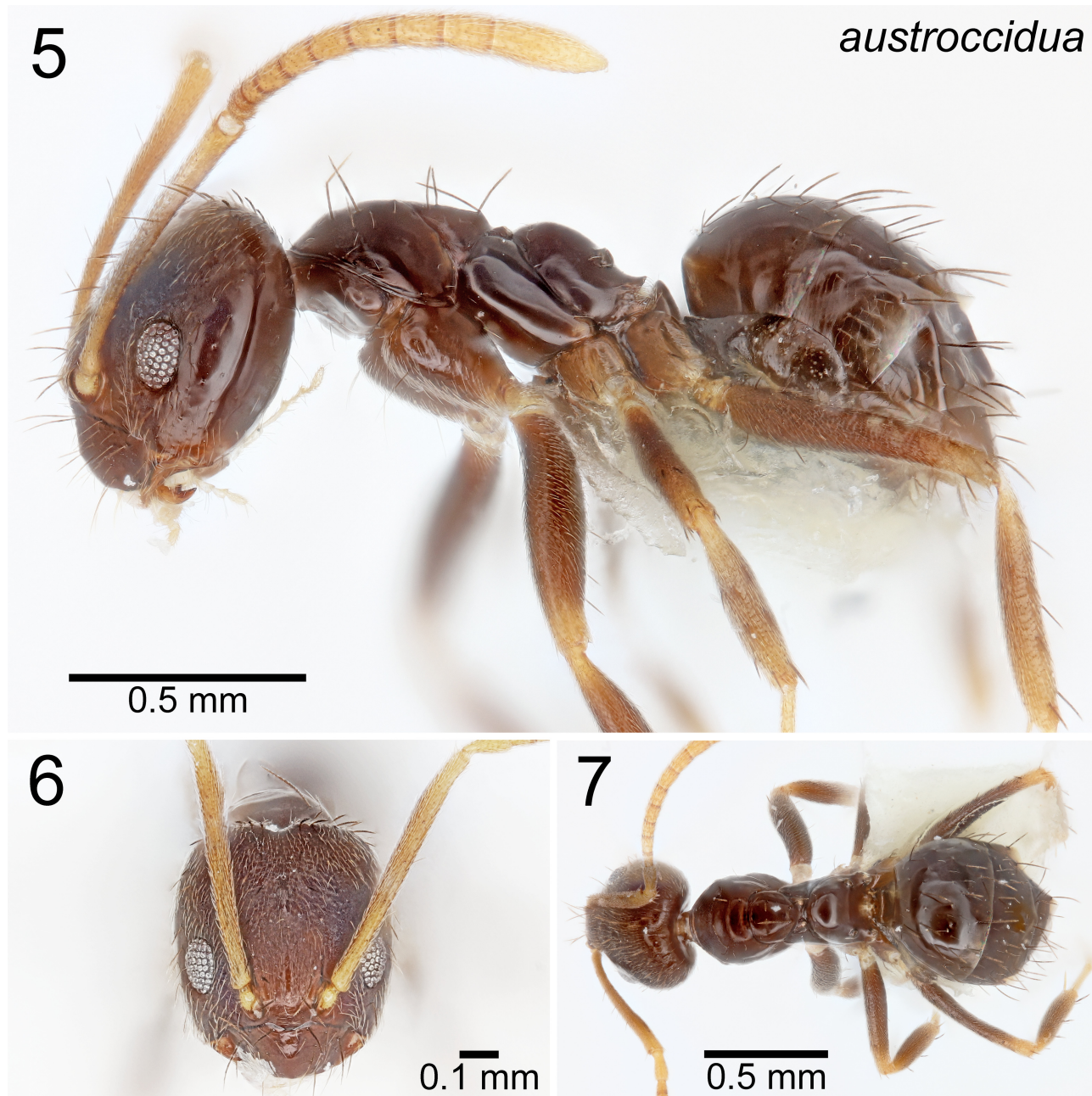
FIGURE 4. Line drawings depicting examples of cephalic pubescence patterns in full-face view: (A) *N. austroccidua* with uniformly dense cephalic pubescence; (B) *N. lazulina* with moderate pubescence, concentrated primarily in areas anterior and posterior to the compound eyes; and (C) *N. cf. docilis* with sparse cephalic pubescence.

Species Accounts

Nylanderia austroccidua (Trager 1984)

Figs. 5–7 (worker)

Paratrechina austroccidua Trager 1984: 113 (w.q.m.). Holotype worker, U.S.A.: Texas, Boot Springs, Chisos Mts., elev. 2040m, 26.vii.1979, P.S. Ward #3771 (LACM) (examined). 12 paratype workers and 2 paratype males, same locality data as holotype (LACM, MCZC). Combination in *Nylanderia*: LaPolla *et al.* 2010: 127.



FIGURES 5–7. *Nylanderia austroccidua* worker (USNMENT01131945). Lateral, full-face, and dorsal view of the body.

Worker diagnosis: Antennae relatively short, with scapes surpassing posterior margin of head by about a third of their length (SI = 113–128); medium to dark brown and sometimes bicolored with darker head and gaster; antennae, mandibles, leg joints, and tarsi yellow in contrast to body; meso- and metacoxae usually somewhat lighter than mesosoma; fine cuticular microsculpture resulting in moderate to strong blue iridescence on head and mesosoma; dense cephalic pubescence; posterior emargination of head strongly variable, from lacking emargination entirely to deep and notch-like.

Compare with: *N. contraria*, *N. polita*

WORKER. *Measurements* ($n=12$): TL: 1.66–2.22; EL: 0.11–0.14; EW: 0.09–0.10; IOD: 0.29–0.34; HE: 0.00–0.03; HL: 0.52–0.61; HW: 0.44–0.52; HLA: 0.17–0.21; HLP: 0.24–0.29; SL: 0.56–0.63; PW: 0.32–0.38; MW: 0.17–0.20; PrW: 0.22–0.28; PDH: 0.18–0.22; PTW: 0.09–0.14; LHT: 0.47–0.55; WL: 0.55–0.72; GL: 0.48–0.95; SMC: 4–7; PMC: 2–3; MMC: 2–3. *Indices*: BLI: 125–143; CI: 84–85; EPI: 58–79; HTI: 101–110; REL: 19–23; SI: 113–128.

Color: medium to dark brown with yellow to yellow-brown antennae, mandibles, and tarsi; meso- and metacoxae often somewhat lighter than mesosoma; sometimes bicolored with mesosoma lighter than head and gaster; overall cuticle with fine microsculpture resulting in moderate to strong blue iridescence on head and mesosoma. *Pilosity*: dense cephalic pubescence covering all surfaces of head in full-face view; mesosoma pubescence sparse to absent, limited at most to scattered hairs on pronotum and propodeum, and a fringe of hairs concentrated just posterior to the metanotal groove; gaster pubescence sparse to absent; pair of small, erect setae on apex of petiole. *Head*: longer than broad and quadrate with distinct posterolateral corners and flattened posterior margin, usually with moderate to strong emargination but sometimes with little to no emargination ($HE = 0.00–0.03$); scapes surpass posterior margin of head by about a third of their length ($SI = 113–128$); median ocellus often large and apparent; lateral ocelli small and often absent or not apparent. *Mesosoma*: promesonotal area flat to evenly convex in profile view, with posterior margin of pronotum continuous or nearly continuous with anterior margin of mesonotum; propodeum low and unevenly rounded, with posterior face about twice as long as dorsal face.

QUEEN. *Measurements* ($n=2$): TL: 3.73–4.26; EL: 0.27; HL: 0.76–0.79; HW: 0.67–0.75; SL: 0.77–0.83; WL: 1.25–1.27; GL: 1.71–2.21. *Indices*: CI: 97–99; REL: 34–36; SI: 102–105.

Relatively large ($TL = 3.73–4.26$). *Color*: medium to dark brown with yellow to yellow-brown antennae, mandibles, and tarsi; meso- and metacoxae at most somewhat lighter than mesosoma. *Pilosity*: most of body covered in moderate to dense pubescence; lacking pubescence on posterior face of propodeum; 1–3 small, erect setae on anepisternum. *Head*: as broad as long; scapes surpass posterior margin of head by about a third of their length.

MALE. *Measurements* ($n=4$): TL: 1.74–2.27; EL: 0.19–0.22; HL: 0.48–0.57; HW: 0.40–0.53; SL: 0.59–0.64; WL: 0.59–0.86; GL: 0.65–0.88. *Indices*: CI: 83–97; REL: 35–39; SI: 110–122.

Color: medium to dark brown with yellow to yellow-brown antennae, mandibles, and tarsi; meso- and metacoxae at most somewhat lighter than mesosoma. *Pilosity*: dense pubescence on head, mesoscutum, and mesoscutellum; pubescence sparse to absent on pronotum, anepisternum, katapisternum, propodeum, and gaster; lacking pubescence on posterior face of propodeum. *Head*: as broad as long; compound eyes surpass lateral margins of head in full-face view; scapes surpass posterior margin of head by about a third of their length. *Mesosoma*: In profile view, propodeum gently rounded with dorsal face about twice as long as posterior face. *Genitalia*: gonopod narrow and evenly triangular, with nearly straight edges and apex coming to a point (Fig. 71); in ventral view, ventromedial edge of basivolsella weakly and evenly curved (Fig. 91 of Kallal & LaPolla 2012); gonosticulus straight and only slightly longer than cuspis.

Other material examined: **MEXICO:** Tamaulipas, El Cielo, Gómez Farías, 23.05216 -99.24252, 7.ix.2019, cloud forest, bait trap, Sandoval-Becerra *et al.* #MXFOR/0062; Tamaulipas, El Cielo, Gómez Farías, 23.05819 -99.22366, 12.ix.2019, oak-pine forest, hand, Sandoval-Becerra *et al.* #MXFOR/0102; Tamaulipas, El Cielo, Gómez Farías, 23.0561 -99.2151, 22.x.2019, Sandoval-Becerra *et al.* #MXFOR/1387; Tamaulipas, El Cielo, Gómez Farías, 23.0561 -99.2151, 22.x.2019, Sandoval-Becerra *et al.* #MXFOR/1417; Tamaulipas, El Cielo, Gómez Farías, 23.0561 -99.2151, 22.x.2019, Sandoval-Becerra *et al.* #MXFOR/1433; Tamaulipas, El Cielo, Gómez Farías, 23.0561 -99.2151, 22.x.2019, Sandoval-Becerra *et al.* #MXFOR/1473; Tamaulipas, El Cielo, Gómez Farías, 23.0521 -99.2425, 7.ix.2019, Sandoval-Becerra *et al.* #MXFOR/1617; Tamaulipas, El Cielo, Gómez Farías, 23.0486 -99.2455, 8.ix.2019, Sandoval-Becerra *et al.* #MXFOR/1712; Tamaulipas, El Cielo, Gómez Farías, 23.0521 -99.2425, 7.ix.2019, Sandoval-Becerra *et al.* #MXFOR/1618; Tamaulipas, El Cielo, Gómez Farías, 23.0486 -99.2455, 8.ix.2019, Sandoval-Becerra *et al.* #MXFOR/1714; Tamaulipas, El Cielo, Gómez Farías, 23.0455 -99.2635, 9.ix.2019, Sandoval-Becerra *et al.* #MXFOR/1739; Tamaulipas, El Cielo, Gómez Farías, 23.0413 -99.2671, 10.ix.2019, Sandoval-Becerra *et al.* #MXFOR/1781; Tamaulipas, El Cielo, Gómez Farías, 23.0486 -99.2671, 30.x.2019, Sandoval-Becerra *et al.* #MXFOR/1805; Tamaulipas, El Cielo, Gómez Farías, 30.x.2019, Sandoval-Becerra *et al.* #MXFOR/1806; Tamaulipas, El Cielo, Gómez Farías, 23.0486 -99.2644, 30.x.2019, Sandoval-Becerra *et al.* #MXFOR/1810; Tamaulipas, El Cielo, Gómez Farías, 23.0486 -99.2644, 30.x.2019, Sandoval-Becerra *et al.* #MXFOR/1824; Tamaulipas, El Cielo, Gómez Farías, 23.0462 -99.2649, 31.x.2019, Sandoval-Becerra *et*

al. #MXFOR/1853; Tamaulipas, El Cielo, Gómez Farías, 23.0462 -99.2649, 31.x.2019, Sandoval-Becerra *et al.* #MXFOR/1856; Tamaulipas, El Cielo, Gómez Farías, 23.04555 -99.26355, pine forest, bait trap, 9.ix.2019, Sandoval-Becerra *et al.* #MXFOR/0036; Tamaulipas, El Cielo, Gómez Farías, 23.048673 -99.264491, cloud-pine forest, hand, 30.x.2019, Sandoval-Becerra *et al.* #MXFOR/0939; Tamaulipas, El Cielo, Gómez Farías, 23.05613 -99.21519, deciduous forest, bait trap, 22.x.2019, Sandoval-Becerra *et al.* #MXFOR/0124; Tamaulipas, El Cielo, Gómez Farías, 23.0581 -99.2236, 12.ix.2019, Sandoval-Becerra *et al.* #MXFOR/1580; Tamaulipas, El Cielo, Gómez Farías, 23.0561 -99.2151, 22.x.2019, Sandoval-Becerra *et al.* #MXFOR/1382; Tamaulipas, El Cielo, Gómez Farías, 23.0561 -99.2151, 22.x.2019, Sandoval-Becerra *et al.* #MXFOR/1465; Tamaulipas, El Cielo, Gómez Farías, 23.0521 -99.2425, 7.ix.2019, Sandoval-Becerra *et al.* #MXFOR/1635; Tamaulipas, El Cielo, Gómez Farías, 23.0521 -99.2425, 7.ix.2019, Sandoval-Becerra *et al.* #MXFOR/1674; Tamaulipas, El Cielo, Gómez Farías, 23.0581 -99.2236, 12.ix.2019, Sandoval-Becerra *et al.* #MXFOR/1564; Tamaulipas, El Cielo, Gómez Farías, 23.0455 -99.2635, 9.ix.2019, Sandoval-Becerra *et al.* #MXFOR/1737; **U.S.A.:** Arizona, Cochise Co., Chiricahua Mts., Pinery Canyon, 6.9km W Onion Saddle, elev. 1890m, 11.viii.1989, S.P. Cover #2092 (SWRS: CASENT0102818); Arizona, Cochise Co., Huachuca Mts., Upper Ramsey Canyon, 31.4333 -110.3167, elev. 1910m, 18.viii.2002, under stone, *Quercus/Pinus/Pseudotsuga* forest, P.S. Ward #14739 (MCZC: MCZ-ENT00531422).

Notes: Workers of *N. austroccidua* most closely resemble those of *N. contraria* and *N. polita*. However, this species can be most readily distinguished from *N. contraria* by the color of its meso- and metacoxae, which are at most only slightly lighter brown than the rest of the body in *N. austroccidua*. In contrast, *N. contraria* has whitish meso- and metacoxae that strongly contrast with the rest of the body, which is dark brown. *Nylanderia austroccidua* is most readily differentiated from *N. polita* by the latter's smooth and shiny surface, which lacks the cuticular microsculpture and blue iridescence that is readily observable under microscopy in all other species of this complex. This species does not overlap in range with *N. contraria* or *N. polita* and is primarily found in high elevation forests ranging across southwestern North America from central Mexico to Utah (Figs. 2A, 2B).

Nylanderia breviscapa, sp. nov.

Figs. 8–10 (worker); Figs. 11–12 (queen); Figs. 13–16 (male)

Holotype worker, **MEXICO:** Chiapas, 2km SE Custepec, 15.72197 -92.94163 ±100m, elev. 1850m, 17.v.2008, ridge oak forest, sifted litter, R.S. Anderson #RSA2008-010 (USNM: USNMMENT01131317). 6 paratype workers, 1 paratype queen, and 4 paratype males with same locality data as holotype (USNM: USNMMENT01130960, USNMMENT01131318, USNMMENT01131319, USNMMENT01131868, USNMMENT01131869, USNMMENT01131870; MNCR: USNMMENT01131320, USNMMENT01131321, USNMMENT01131322, USNMMENT01131962, USNMMENT01132155).

Worker diagnosis: Antennae relatively short, scapes surpassing posterior margin by less than a quarter of their length; light brown and sometimes bicolored with medium brown head and gaster; meso- and metacoxae about same color as mesosoma; microsculpture and blue iridescence subtle, most visible on head; dense cephalic pubescence.

Compare with: *N. austroccidua*

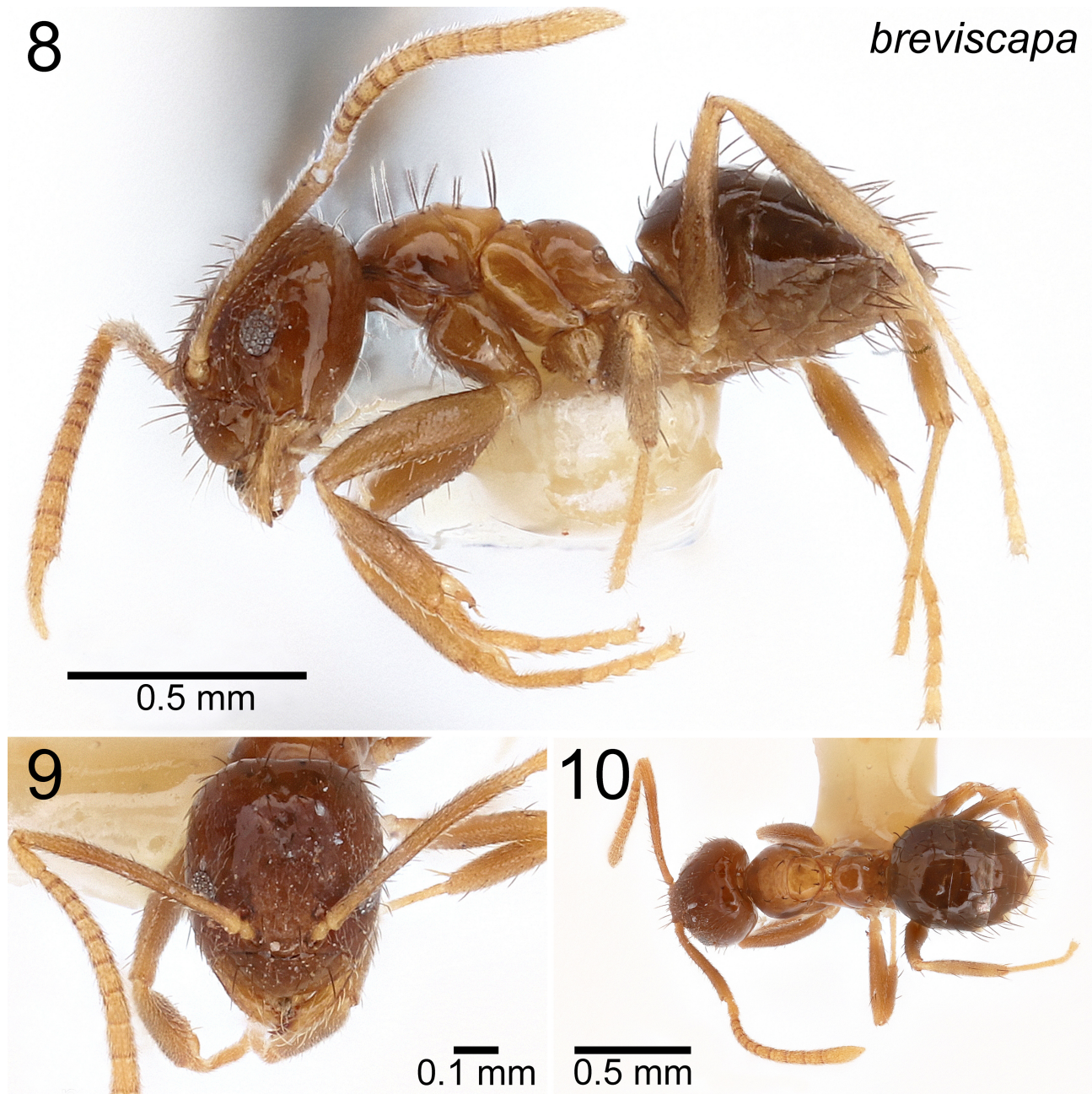
WORKER. Measurements ($n=12$): TL: 1.71–2.08; EL: 0.10–0.11; EW: 0.07–0.09; IOD: 0.30–0.33; HE: 0.00–0.01; HL: 0.53–0.58; HW: 0.44–0.48; HLA: 0.18–0.21; HLP: 0.23–0.27; SL: 0.53–0.59; PW: 0.32–0.35; MW: 0.18–0.21; PrW: 0.23–0.29; PDH: 0.17–0.25; PTW: 0.11–0.15; LHT: 0.40–0.50; WL: 0.61–0.66; GL: 0.57–0.91; SMC: 6–8; PMC: 2–4; MMC: 2–3. **Indices:** BLI: 134–146; CI: 81–85; EPI: 70–84; HTI: 93–113; REL: 18–20; SI: 114–128.

Color: Light brown, sometimes bicolored with medium brown head and gaster; meso- and metacoxae about same color as mesosoma; overall cuticle with some microsculpture resulting in subtle blue iridescence on head and mesosoma. **Pilosity:** dense cephalic pubescence covering all surfaces of head in full-face view; mesosoma pubescence sparse to absent, at most limited to scattered hairs on pronotum; gaster pubescence sparse to absent; pair of small, erect setae on apex of petiole. **Head:** longer than broad and quadrate with distinct posterolateral corners and flattened posterior margin, usually with no medial emargination; scapes surpass posterior margin of head by less than a quarter of their length; median ocellus small and not always apparent; lateral ocelli absent or not apparent. **Mesosoma:** posterior margin of pronotum forming obtuse angle with anterior margin of mesonotum in profile view; propodeum low and evenly rounded, with posterior face about same length as dorsal face.

QUEEN. Measurements ($n=1$): TL: 2.69; EL: 0.18; HL: 0.60; HW: 0.57; SL: 0.61; WL: 0.92; GL: 1.18. **Indices:** BLI: 154; CI: 96; REL: 29; SI: 106.

Relatively small (TL < 3) *Color*: Uniformly yellow-brown to light brown; *Pilosity*: most of body covered in moderate to dense pubescence; lacking pubescence on posterior face of propodeum; 5-6 small, erect setae on anepisternum. *Head*: As broad as long; scapes surpass posterior margin of head by about a third of their length.

MALE. *Measurements* (n=2): TL: 1.79–1.92; EL: 0.15–0.16; HL: 0.47–0.48; HW: 0.41–0.43; SL: 0.49–0.51; WL: 0.63–0.66; GL: 0.69–0.78. *Indices*: BLI: 154–155; CI: 87–90; REL: 32–34; SI: 119–120.



FIGURES 8–10. *Nylanderia breviscapa* holotype worker (USNMENT01131317). Lateral, full-face, and dorsal view of the body.

Color: uniformly light to medium brown; meso- and metacoxae concolorous with mesosoma. *Pilosity*: dense pubescence on head, mesoscutum, and mesoscutellum; pubescence sparse to absent on pronotum, anepisternum, katepisternum, propodeum, and gaster. *Head*: as broad as long; compound eyes surpass lateral margins of head in full-face view; scapes surpass posterior margin of head by about a third of their length. *Mesosoma*: In profile view, propodeum gently and evenly rounded, with dorsal face about as long as posterior face. *Genitalia*: gonopod broad at base, taper strongly to a narrow, digitiform shape, with the apex rounded and slightly turned upward (Fig. 71); in ventral view, ventromedial edge of basivolsella strongly curved (Fig. 15); gonossiculus mostly straight, gradually curved medially toward penial sclerite, and nearly three times as long as cuspis.

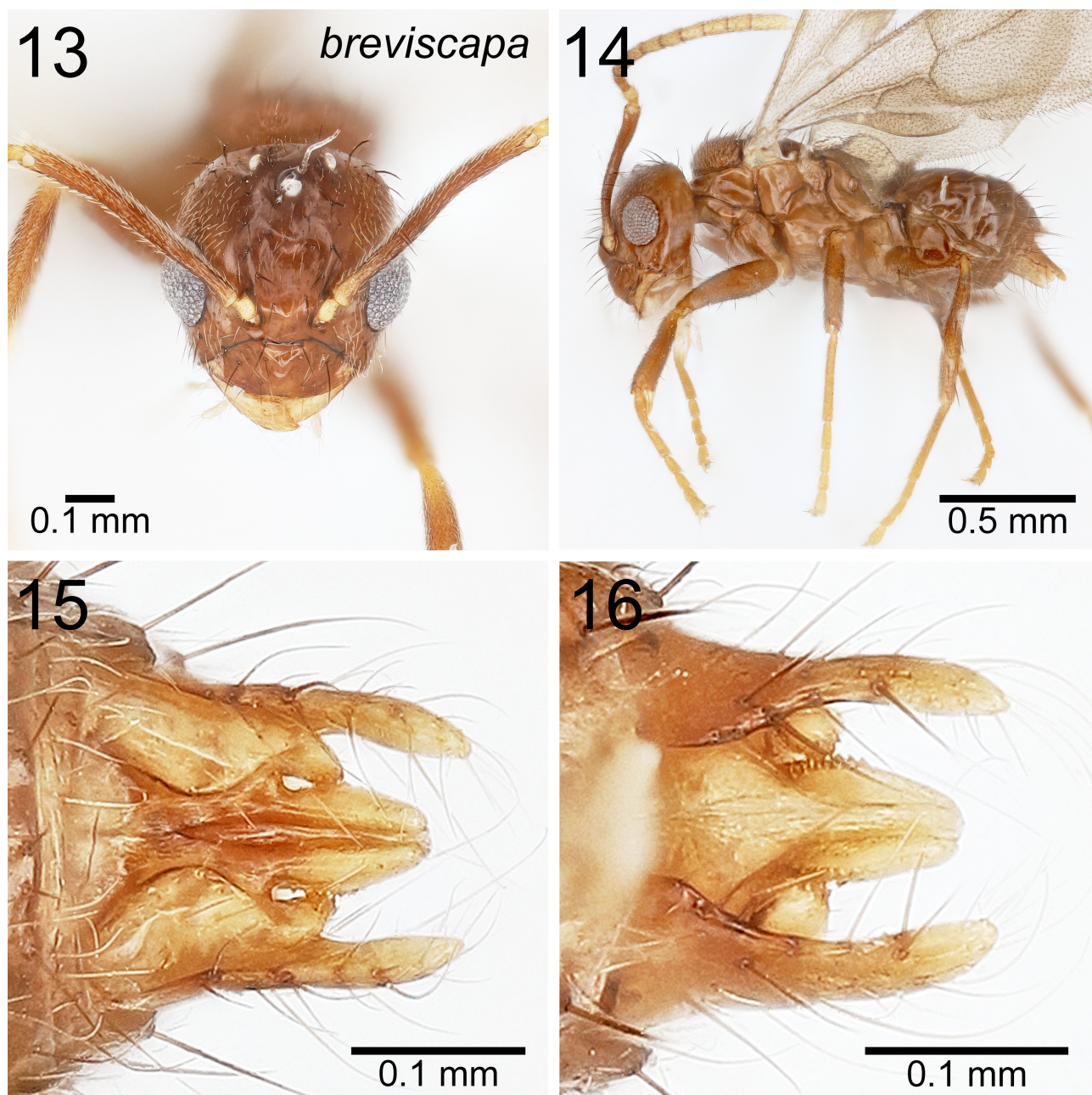
Other material examined: MEXICO: Chiapas, 2km SE Custepec, 15.72188 -92.93677 ±100m, elev. 1900m, 19.v.2008, oak-pine forest, sifted litter, R.S. Anderson #RSA2008-016; Chiapas, 2km SE Custepec, 15.72216 -92.94298 ±100m, elev. 1820m, 20.v.2008, oak forest, sifted litter, R.S. Anderson #RSA2008-020; Chiapas, 2km SE Custepec, 15.7214 -92.93909 ±100m, elev. 1830m, 20.v.2008, hardwood forest, sifted litter, R.S. Anderson #RSA2008-023; Chiapas, 3km SE Custepec, 15.71578 -92.93847 ±50m, elev. 1700m, 17.v.2008, 2° mesophil forest, sifted litter, LLAMA#Wa-A-02-2-07; Chiapas, 2km SE Custepec, 15.7208 -92.95097 ±50m, elev. 1520m, 17.v.2008, mesophil forest, sifted litter, LLAMA#Wa-A-02-1-35; Chiapas, 2km SE Custepec, 15.72085 -92.95097 ±50m, elev. 1520m, 17.v.2008, mesophil forest, sifted litter, LLAMA#Wa-A-02-1-34; Chiapas, 2km SE Custepec, 15.72098 -92.95095 ±50m, elev. 1520m, 17.v.2008, mesophil forest, sifted litter, LLAMA#Wa-A-02-1-31; Chiapas, 2km SE Custepec, 15.72098 -92.95054 ±50m, elev. 1520m, 17.v.2008, mesophil forest, sifted litter, LLAMA#Wa-A-02-1-22; Chiapas, 2km SE Custepec, 15.72096 -92.9502 ±50m, elev. 1520m, 17.v.2008, mesophil forest, sifted litter, LLAMA#Wa-A-02-1-11; Chiapas, 2km SE Custepec, 15.721 -92.95036 ±50m, elev. 1520m, 17.v.2008, mesophil forest, sifted litter, LLAMA#Wa-A-02-1-04; Chiapas, 3km SE Custepec, 15.71603 -92.93808 ±50m, elev. 1700m, 17.v.2008, 2° mesophil forest, sifted litter, LLAMA#Wa-A-02-2-19; Chiapas, 3km SE Custepec, 15.71569 -92.93849 ±50m, elev. 1700m, 17.v.2008, 2° mesophil forest, sifted litter, LLAMA#Wa-A-02-2-09; Chiapas, 3km SE Custepec, 15.71607 -92.93812 ±50m, elev. 1700m, 17.v.2008, 2° mesophil forest, sifted litter, LLAMA#Wa-A-02-2-17; Chiapas, 3km SE Custepec, 15.71585 -92.93811 ±50m, elev. 1700m, 17.v.2008, 2° mesophil forest, sifted litter, LLAMA#Wa-A-02-2-23; Chiapas, 5km NNW Coapilla, 17.18326 -93.15208 ±50m, elev. 1915m, 25.v.2008, 2° mesophil forest, sifted litter, LLAMA#Wa-A-04-2-08; Chiapas, 3km SE Custepec, 15.71485 -92.93823 ±50m, elev. 1700m, 17.v.2008, 2° mesophil forest, sifted litter, LLAMA#Wa-A-02-2-50; Chiapas, 3km SE Custepec, 15.71494 -92.93823 ±50m, elev. 1700m, 17.v.2008, 2° mesophil forest, sifted litter, LLAMA#Wa-A-02-2-48; Chiapas, 3km SE Custepec, 15.71554 -92.93815 ±50m, elev. 1700m, 17.v.2008, 2° mesophil forest, sifted litter, LLAMA#Wa-A-02-2-30; Chiapas, 3km SE Custepec, 15.71576 -92.93812 ±50m, elev. 1700m, 17.v.2008, 2° mesophil forest, sifted litter, LLAMA#Wa-A-02-2-25; Chiapas, 3km SE Custepec, 15.7158 -92.93811 ±50m, elev. 1700m, 17.v.2008, 2° mesophil forest, sifted litter, LLAMA#Wa-A-02-2-24; Chiapas, 3km SE Custepec, 15.71528 -92.938 ±50m, elev. 1700m, 17.v.2008, 2° mesophil forest, sifted litter, LLAMA#Wa-A-02-2-37.



FIGURES 11–12. *Nylanderia breviscapa* paratype queen (USNMENT01131869). Full-face and lateral view of the body.

Etymology: The species epithet combines ‘*brevis*’ (L. = short) and ‘*scapus*’ (L. = stalk), referring to the relatively short antennal scapes of this species.

Notes: *Nylanderia breviscapa* workers most closely resemble those of *N. austroccidua* but with a more compact overall appearance, relatively shorter scapes that barely surpass the posterior margin of the head, and meso- and metacoxae that are about the same color as the mesosoma. The known range of this species is limited to high elevation forests in the southern state of Chiapas, Mexico (Fig. 2B).



FIGURES 13–16. *Nylanderia breviscapa* paratype male (USNMENT01131870). Full-face and lateral view of the body; ventral and dorsal view of the genital capsule.

***Nylanderia contraria*, sp. nov.**

Figs. 17–19 (worker); Figs. 20–21 (queen); Figs. 22–25 (male)

Holotype worker, **MEXICO**: Oaxaca, Cafetal Carlota, 18.04802 -96.69164 ±30m, elev. 1028m, 12.vi.2016, liquidambar/ cloud forest, sifted litter, R.S. Anderson #RSA2016-136 (USNM: USNMENT01130973). 5 paratype workers, 3 paratype queens, and 2 paratype males with same locality data as holotype (USNM: USNMENT01131808, USNMENT01131970, USNMENT01131971, USNMENT01131974, USNMENT01131975, USNMENT01131977; MNCR: USNMENT01131972, USNMENT01131973, USNMENT01131976, USNMENT01131978).

Worker diagnosis: Antennae relatively short, with scapes surpassing posterior margin of head by about a third of their length; dark brown, with antennae, mandibles, leg joints, and tarsi yellow in contrast to body; meso- and metacoxae whitish, strongly contrasting with mesosoma; fine cuticular microsculpture resulting in moderate to

strong blue iridescence on head and mesosoma; dense cephalic pubescence; posterior margin of head slightly to moderately emarginate.

Compare with: *N. austroccidua*, *N. polita*.



FIGURES 17–19. *Nylanderia contraria* holotype worker (USNMENT01130973). Lateral, full-face, and dorsal view of the body.

WORKER. *Measurements* ($n=11$): TL: 1.67–2.19; EL: 0.10–0.12; EW: 0.08–0.09; IOD: 0.26–0.33; HE: 0.01; HL: 0.52–0.58; HW: 0.43–0.50; HLA: 0.18–0.20; HLP: 0.23–0.27; SL: 0.55–0.62; PW: 0.29–0.36; MW: 0.17–0.20; PrW: 0.23–0.26; PDH: 0.12–0.21; PTW: 0.10–0.24; LHT: 0.45–0.51; WL: 0.58–0.68; GL: 0.57–0.95; SMC: 5–7; PMC: 2–3; MMC: 2. *Indices*: BLI: 130–144; CI: 81–85; EPI: 69–78; HTI: 101–109; REL: 18–22; SI: 118–132.

Color: dark brown with yellow to yellow-brown antennae, mandibles, leg joints, and tarsi; meso- and metacoxae whitish, strongly contrasting with rest of body; overall cuticle with fine microsculpture resulting in moderate to strong blue iridescence on head and mesosoma. *Pilosity*: dense cephalic pubescence covering all surfaces of head in full-face view; mesosoma pubescence sparse to absent, limited at most to scattered hairs on pronotum and propodeum, and a fringe of hairs concentrated just posterior to the metanotal groove; gaster pubescence sparse to absent; pair of

small, erect setae on apex of petiole. *Head*: longer than broad and quadrate with distinct posterolateral corners and flattened posterior margin, usually with slight to moderate emargination; scapes surpass posterior margin of head by about a third of their length; median ocellus often large and apparent; lateral ocelli small and often absent or not apparent. *Mesosoma*: promesonotal area flat to evenly convex in profile view, with posterior margin of pronotum continuous or nearly continuous with anterior margin of mesonotum; propodeum low and evenly rounded, with posterior face at most slightly longer than dorsal face.



FIGURES 20–21. *Nylanderia contraria* paratype queen (USNMENT01131974). Full-face and lateral view of the body.

QUEEN. *Measurements* ($n=3$): TL: 3.36–3.61; EL: 0.18–0.19; HL: 0.62–0.64; HW: 0.62–0.63; SL: 0.62–0.64; WL: 1.03–1.10; GL: 1.70–1.90. *Indices*: BLI: 164–177; CI: 97–100; REL: 29–30; SI: 100–102.

Moderately sized. *Color*: Medium to dark brown, with whitish meso- and metacoxae. *Pilosity*: most of body covered in moderate to dense pubescence; lacking pubescence on posterior face of propodeum; 1–4 small, erect setae on anepisternum.

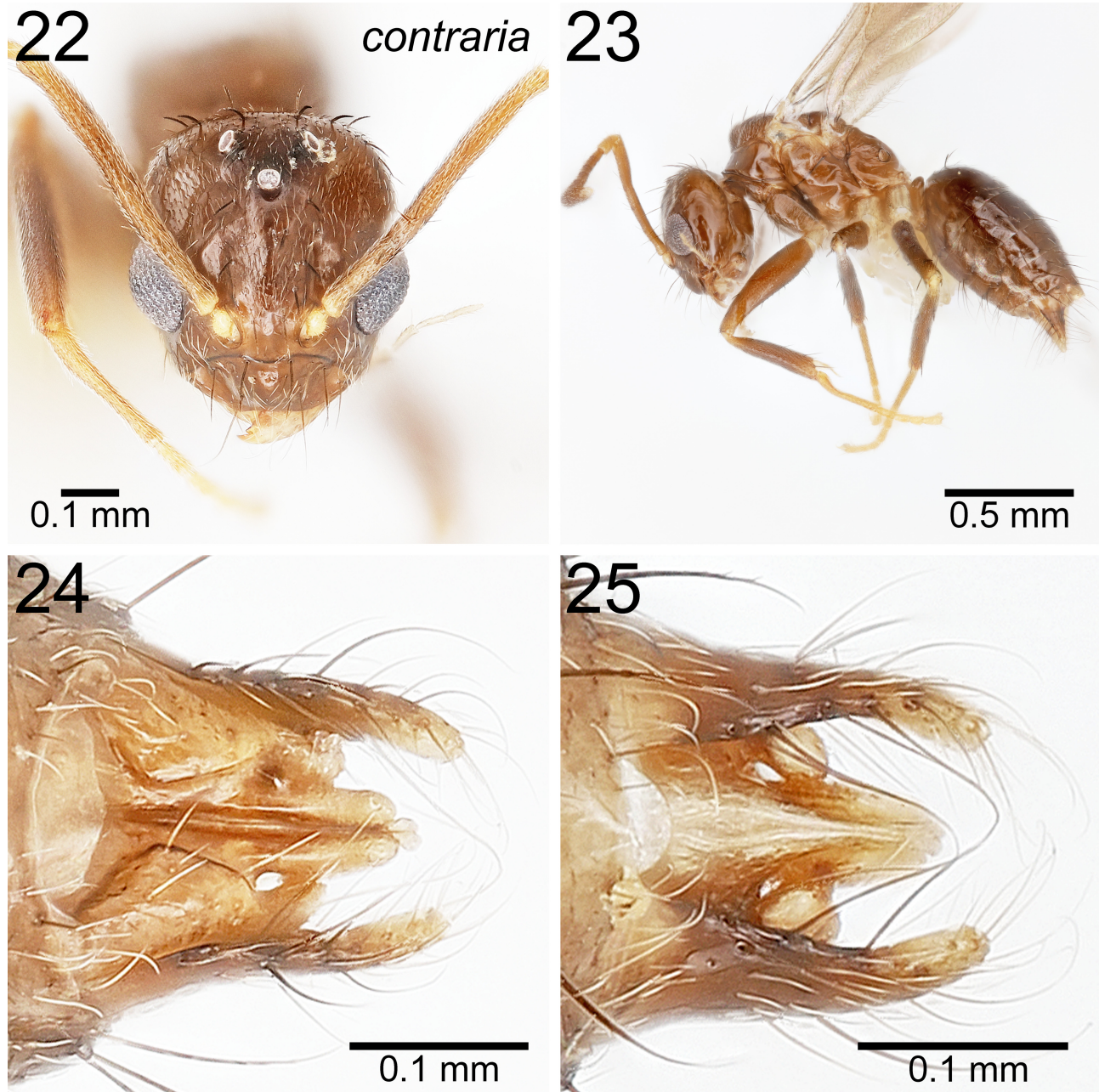
MALE. *Measurements* ($n=2$): TL: 1.90–1.95; EL: 0.16; HL: 0.47; HW: 0.41–0.43; SL: 0.51–0.52; WL: 0.66–0.69; GL: 0.77–0.79. *Indices*: BLI: 152–167; CI: 88–91; REL: 33–35; SI: 121–123.

Color: medium to dark brown with yellow to yellow-brown antennae, mandibles, and tarsi; whitish meso- and metacoxae. *Pilosity*: dense pubescence on head, mesoscutum, and mesoscutellum; pubescence sparse to absent on pronotum, anepisternum, katapisternum, propodeum, and gaster. *Head*: as broad as long; compound eyes surpass lateral margins of head in full-face view; scapes surpass posterior margin of head by about a third of their length. *Mesosoma*: In profile view, propodeum gently and evenly rounded, with dorsal face about as long as posterior face. *Genitalia*: gonopod narrow and triangular, with apex coming to a point and slightly turned upward (Fig. 71); in ventral view, ventromedial edge of basivolsella strongly angled at base and sloping laterally toward cuspis (Fig. 24); gonossiculus mostly straight and about twice as long as cuspis.

Other material examined: MEXICO: Veracruz, 8km WSW Xalapa, 19.52123 -96.99372 \pm 100m, elev. 1570m, 24.vi.2016, cloud forest, baiting, ADMAC#Ba-F-05-4-01-11; Oaxaca, Cafetal Carlota, 18.0479 -96.69193 \pm 30m, elev. 1021m, 12.vi.2016, liquidambar/cloud forest, sifted litter, R.S. Anderson #RSA2016-137; Oaxaca, Cafetal Carlota, 18.04756 -96.69252 \pm 30m, elev. 1011m, 12.vi.2016, liquidambar/cloud forest, sifted litter, R.S. Anderson #RSA2016-138; Oaxaca, Cafetal Carlota, 18.04773 -96.68953 \pm 30m, elev. 1041m, 14.vi.2016, liquidambar/cloud forest, sifted litter, R.S. Anderson #RSA2016-145; Oaxaca, Cafetal Carlota, 18.04784 -96.69198 \pm 30m, elev. 1019m, 14.vi.2016, liquidambar/cloud forest, sifted litter, R.S. Anderson #RSA2016-146; Oaxaca, above Cafetal Carlota, 18.05241 -96.69106 \pm 30m, elev. 1374m, 14.vi.2016, mixed hardwood forest, sifted litter, R.S. Anderson #RSA2016-148; Oaxaca, above Cafetal Carlota, 18.05367 -96.69183 \pm 30m, elev. 1459m, 14.vi.2016, mixed hardwood forest, sifted litter, R.S. Anderson #RSA2016-149; Oaxaca, above Cafetal Carlota, 18.05419 -96.69207 \pm 30m, elev. 1508m, 14.vi.2016, mixed hardwood forest, sifted litter, R.S. Anderson #RSA2016-150; Oaxaca, near Cerro 71, 18.11476 -96.76884 \pm 30m, elev. 1437m, 15.vi.2016, mixed hardwood forest, sifted litter, R.S. Anderson #RSA2016-152; Oaxaca, Agua de Hueso, 18.14653 -96.7934 \pm 30m, elev. 1915m, 15.vi.2016, scrubby cloud forest,

sifted litter, R.S. Anderson #RSA2016-153; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04847 -96.69065 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-1-18; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04879 -96.69065 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-1-25; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04892 -96.69065 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-1-28; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04901 -96.69065 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-1-30; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.0486 -96.6907 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-1-32; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.0486 -96.69101 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-1-38; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.0486 -96.69106 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-1-39; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.0486 -96.69116 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-1-41; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.0486 -96.69121 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-1-42; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.0486 -96.69132 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-1-44; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.0486 -96.69147 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-1-47; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04736 -96.6903 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-01; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04745 -96.69018 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-04; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04748 -96.69014 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-05; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04756 -96.69002 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-08; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04759 -96.68999 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-09; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04762 -96.68995 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-10; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04765 -96.68991 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-11; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04804 -96.68954 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-24; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04818 -96.68967 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-28; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04825 -96.68974 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-30; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04828 -96.68977 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-31; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04835 -96.68984 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-33; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04839 -96.68987 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-34; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04846 -96.68994 ±20m, 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-36; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04846 -96.69027 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-46; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04835 -96.69037 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-49; Veracruz, 8km WSW Xalapa, 19.5213 -96.99184 ±20m, elev. 1520m, 22.vi.2016, cloud forest, sifted litter, ADMAC#Wa-F-05-1-25; Veracruz, 8km WSW Xalapa, 19.52107 -96.99216 ±20m, elev. 1530m, 22.vi.2016, cloud forest, sifted litter, ADMAC#Wa-F-05-1-33; Veracruz, 8km WSW Xalapa, 19.52092 -96.99236 ±20m, elev. 1530m, 22.vi.2016, cloud forest, sifted litter, ADMAC#Wa-F-05-1-38; Veracruz, 8km WSW Xalapa, 19.5219 -96.99063 ±20m, elev. 1500m, 22.vi.2016, cloud forest, sifted litter, ADMAC#Wa-F-05-2-09; Veracruz, 8km WSW Xalapa, 19.52245 -96.99086 ±20m, elev. 1500m, 22.vi.2016, cloud forest, sifted litter, ADMAC#Wa-F-05-2-22; Chiapas, 5km NE Coapilla, 17.17602 -93.13293 ±300m, elev. 1990m, 25.v.2008, mesophil forest, sifted litter, LLAMA#Wm-A-04-1; Oaxaca, 1km E San Jerónimo Tecuatl, 18.16841 -96.90282 ±10m, elev. 1800m, 12.vi.2016, 2° alder forest, sifted litter, ADMAC#Wm-F-04-1-02; Oaxaca, 1km SE Huautla, 18.12357 -96.83419 ±10m, elev. 1650m, 12.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wm-F-04-1-03; Oaxaca, 6km WNW Ayautla, 18.05281 -96.72518 ±10m, elev. 1570m, 12.vi.2016, 2° mixed hardwood forest, sifted litter, ADMAC#Wm-F-04-1-04; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.05175 -96.69096 ±20m, elev. 1320m, 14.vi.2016, 2° wet forest, sifted litter, ADMAC#Wm-F-04-1-06; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.05369 -96.69192 ±20m, elev. 1460m, 14.vi.2016, 2° wet forest, sifted litter, ADMAC#Wm-F-04-1-07; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.05543 -96.69253 ±20m, elev.

1610m, 14.vi.2016, montane wet forest, sifted litter, ADMAC#Wm-F-04-1-08; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.05602 -96.69274 ±20m, elev. 1660m, 14.vi.2016, montane wet forest, sifted litter, ADMAC#Wm-F-04-1-09; Oaxaca, 5km ENE Huautla, 18.14453 -96.79799 ±20m, elev. 1890m, 15.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wm-F-04-2-02; Veracruz, 8km WSW Xalapa, 19.52265 -96.9909 ±125m, elev. 1500m, 22.vi.2016, cloud forest, sifted litter, ADMAC#Wm-F-05-2-01; Veracruz, Las Cañadas, 19.18823 -96.99155 ±20m, elev. 1410m, 1.vii.2016, montane wet forest, sifted litter, ADMAC#Wm-F-07-1-06; Veracruz, Las Cañadas, 19.19018 -96.99164 ±20m, elev. 1400m, 1.vii.2016, montane wet forest, sifted litter, ADMAC#Wm-F-07-1-08.



FIGURES 22–25. *Nylanderia contraria* paratype male (USNMMENT01131977). Full-face and lateral view of the body; ventral and dorsal view of the genital capsule.

Etymology: The species epithet is derived from ‘*contrarius*’ (L. = contrary), referring to the strong color contrast observed in this species between the white meso- and metacoxae and the medium to dark brown of the rest of the body.

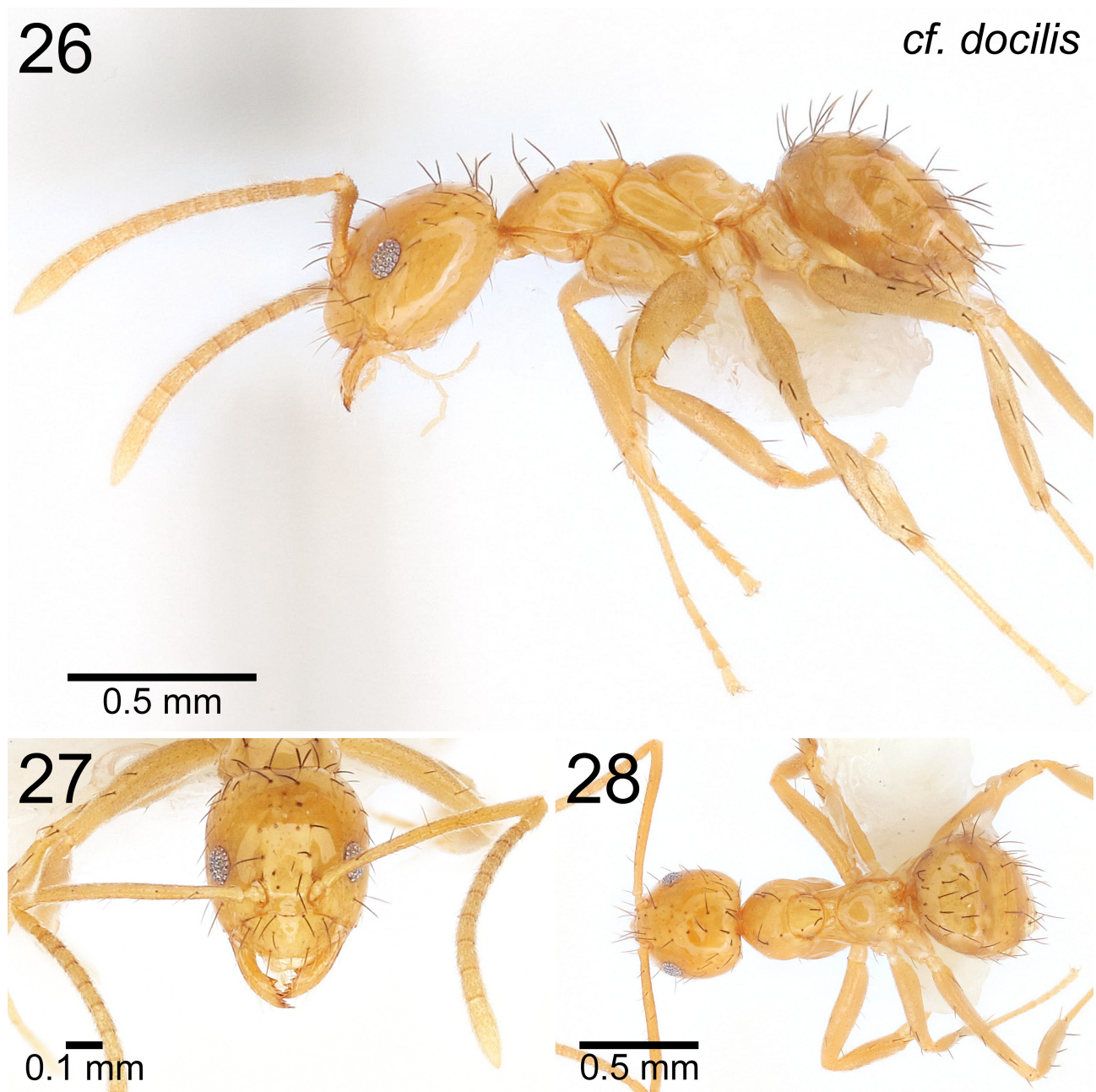
Notes: While the overall habitus of *N. contraria* workers most strongly resembles that of *N. austroccidua* and *N. polita* workers, they are most readily distinguished from both of those species by the stark contrast in color

between its whitish meso- and metacoxae and dark brown mesosoma. This species is more likely to be confused with *N. austroccidua*, as these two species have similar cuticular microsculpture that causes a similar amount of blue iridescence, which *N. polita* lacks entirely. *Nylanderia contraria* can be found in moderate to high elevation forests in southern Mexico, and its known range is limited to the states of Oaxaca and Veracruz (Fig. 2B).

Nylanderia cf. docilis

Figs. 26–28 (worker); Figs. 29–30 (queen); Figs. 31–34 (male)

Worker diagnosis: Antennae relatively long, with scapes surpassing posterior margin of head by nearly half their length; usually uniformly yellow with black macrosetae strongly contrasting with overall color; microsculpture and blue iridescence subtle, most visible on head; cephalic pubescence sparse to absent; metatibiae relatively long (HTI > 125).



FIGURES 26–28. *Nylanderia cf. docilis* worker (USNMENT01131072). Lateral, full-face, and dorsal view of the body.



FIGURES 29–30. *Nylanderia cf. docilis* queen (USNMENT01132074). Full-face and lateral view of the body.

Compare with: *N. mosaica*, *N. usul*

WORKER. *Measurements* ($n=26$): TL: 1.68–2.33; EL: 0.09–0.13; EW: 0.07–0.10; IOD: 0.27–0.32; HE: 0.00–0.01; HL: 0.48–0.60; HW: 0.40–0.49; HLA: 0.18–0.22; HLP: 0.22–0.25; SL: 0.53–0.69; PW: 0.29–0.37; MW: 0.15–0.21; PrW: 0.22–0.26; PDH: 0.16–0.22; PTW: 0.09–0.13; LHT: 0.50–0.62; WL: 0.58–0.74; GL: 0.61–1.02; SMC: 6–9; PMC: 2–3; MMC: 2–3. *Indices*: BLI: 124–152; CI: 81–90; EPI: 76–90; HTI: 121–132; REL: 18–22; SI: 124–147.

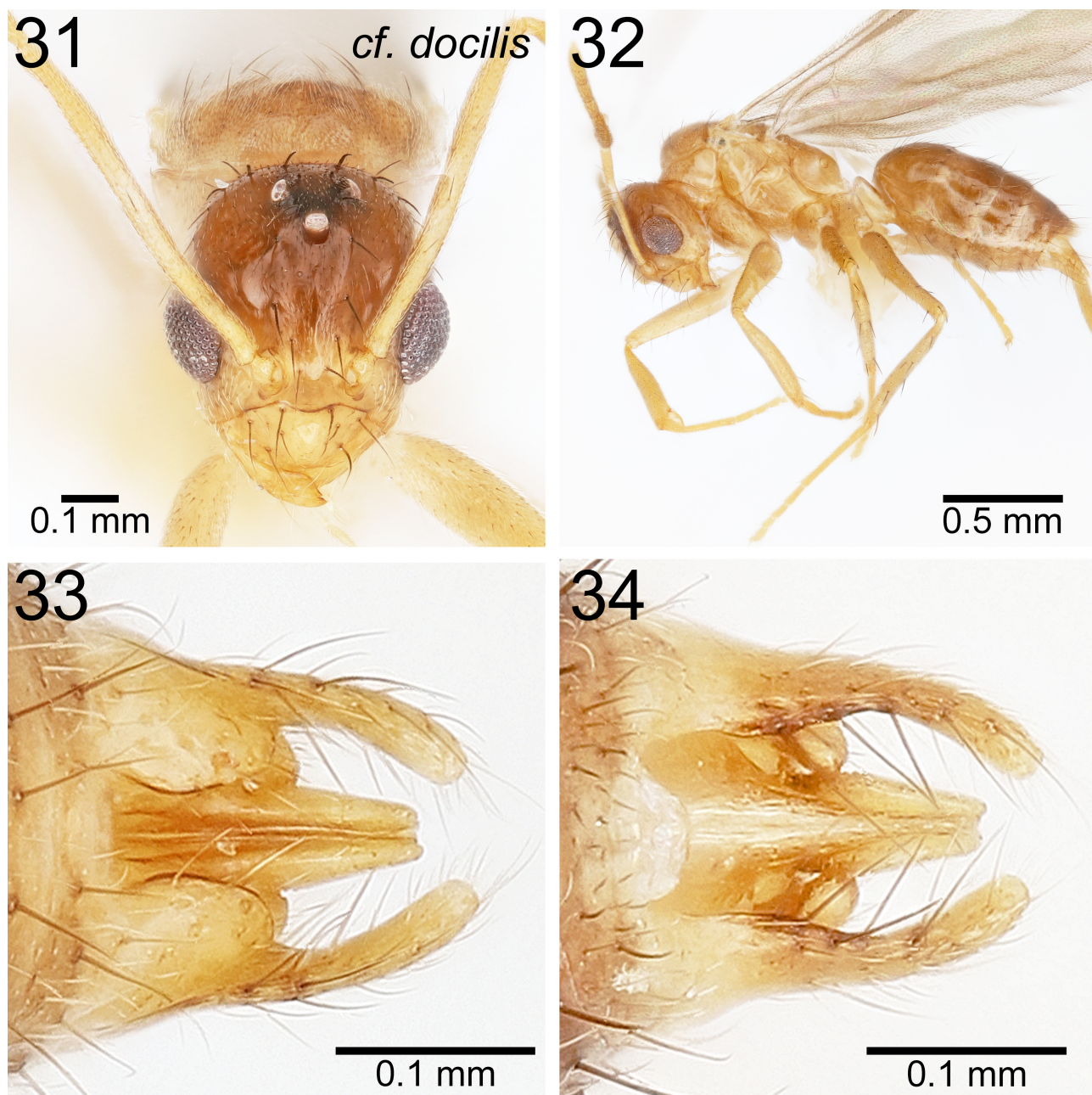
Color: usually uniformly yellow with thick, black macrosetae strongly contrasting with overall color, but sometimes light to medium brown with somewhat lighter meso- and metacoxae; overall cuticle with light microsculpture resulting in subtle blue iridescence on head and mesosoma. *Pilosity*: sparse cephalic pubescence; mesosoma and gaster pubescence sparse to absent; pair of small, erect setae on apex of petiole. *Head*: longer than broad and quadrate with distinct posterolateral corners and flattened posterior margin, usually with slight to moderate emargination; scapes long, surpassing posterior margin by nearly half their length; all three ocelli absent or not apparent. *Mesosoma*: posterior margin of pronotum forming obtuse angle with anterior margin of mesonotum in profile view; propodeum low and evenly rounded, with posterior face about same length as dorsal face.

QUEEN. *Measurements* ($n=2$): TL: 3.13–3.28; EL: 0.18–0.20; HL: 0.66–0.67; HW: 0.63; SL: 0.79–0.81; WL: 1.21–1.24; GL: 1.22–1.41. *Indices*: BLI: 183–185; CI: 94–96; REL: 27–29; SI: 125–128.

Moderately sized. *Color*: Uniformly yellow-brown. *Pilosity*: most of body covered in moderate to dense pubescence; lacking pubescence on posterior face of propodeum; 4–5 small, erect setae on anepisternum.

MALE. *Measurements* ($n=2$): TL: 1.95–2.14; EL: 0.16; HL: 0.46–0.47; HW: 0.41; SL: 0.59–0.61; WL: 0.74–0.77; GL: 0.75–0.90. *Indices*: BLI: 181–189; CI: 86–88; REL: 35; SI: 144–149.

Color: yellow to yellow-brown, with posterior half of head somewhat darker in contrast; metacoxae concolorous with mesosoma. *Pilosity*: dense pubescence on head, mesoscutum, and mesoscutellum; small patch of pubescence found medially on pronotum, but absent laterally; pubescence sparse to absent on anepisternum, katapisternum, propodeum, and gaster; 1–2 small, erect setae on anepisternum. *Head*: as broad as long; compound eyes surpass lateral margins of head in full-face view; scapes surpass posterior margin of head by about a third of their length. *Mesosoma*: In profile view, propodeum angled with dorsal face somewhat longer than posterior face. *Genitalia*: gonopod narrow and triangular, with apex rounded and slightly turned upward (Fig. 71); in ventral view, ventromedial edge of basivolsella lobate and strongly rounded, with cuspis strongly curved dorsally and almost entirely obscured by basivolsella (Fig. 33); gonossiculus mostly straight and more than three times as long as cuspis.



FIGURES 31–34. *Nylanderia* cf. *docilis* male (USNMENT01131834). Full-face and lateral view of the body; ventral and dorsal view of the genital capsule.

Other material examined: **BELIZE:** Cayo, Los Cuevas Field Station, ca. 15km E Caracol, 16.733 -88.986 ±500m, elev. 581m, 29.vi.2019, montane forest, sifted litter, R.S. Anderson #RSA2019-009; Stann Creek, Bocawina, ca. 15km W Dangriga, 16.927 -88.397 ±500m, elev. 86m, 3.vii.2019, rainforest, sifted litter, R.S. Anderson #RSA2019-011; Stann Creek, TREES Field Station, ca. 37km W Dangriga, 17.05 -88.57 ±500m, elev. 222m, 25.vi.2019, 2° rainforest, sifted litter, R.S. Anderson #RSA2019-005; **COSTA RICA:** San José, 8km S Santa María, 9.58121 -83.9525 ±1000m, elev. 1470m, 30.vi.2015, cloud forest, Krissy Dominguez #KD15-11-09; **GUATEMALA:** Izabal, 5km NW Morales, 15.51214 -88.8662 ±58m, elev. 215m, 18.v.2009, 2° lowland rainforest, sifted litter, LLAMA#Wm-B-04-1-10; Izabal, 5km NW Morales, 15.51077 -88.8648 ±38m, elev. 190m, 18.v.2009, 2° lowland rainforest, sifted litter, LLAMA#Wm-B-04-2-01; Izabal, 5km NW Morales, 15.5103 -88.86326 ±45m, elev. 170m, 18.v.2009, 2° lowland rainforest, sifted litter, LLAMA#Wm-B-04-2-02; Izabal, 16km ESE Morales, 15.41307 -88.70953 ±30m, elev. 410m, 19.v.2009, 2° lowland rainforest, sifted litter, LLAMA#Wm-B-04-2-06;

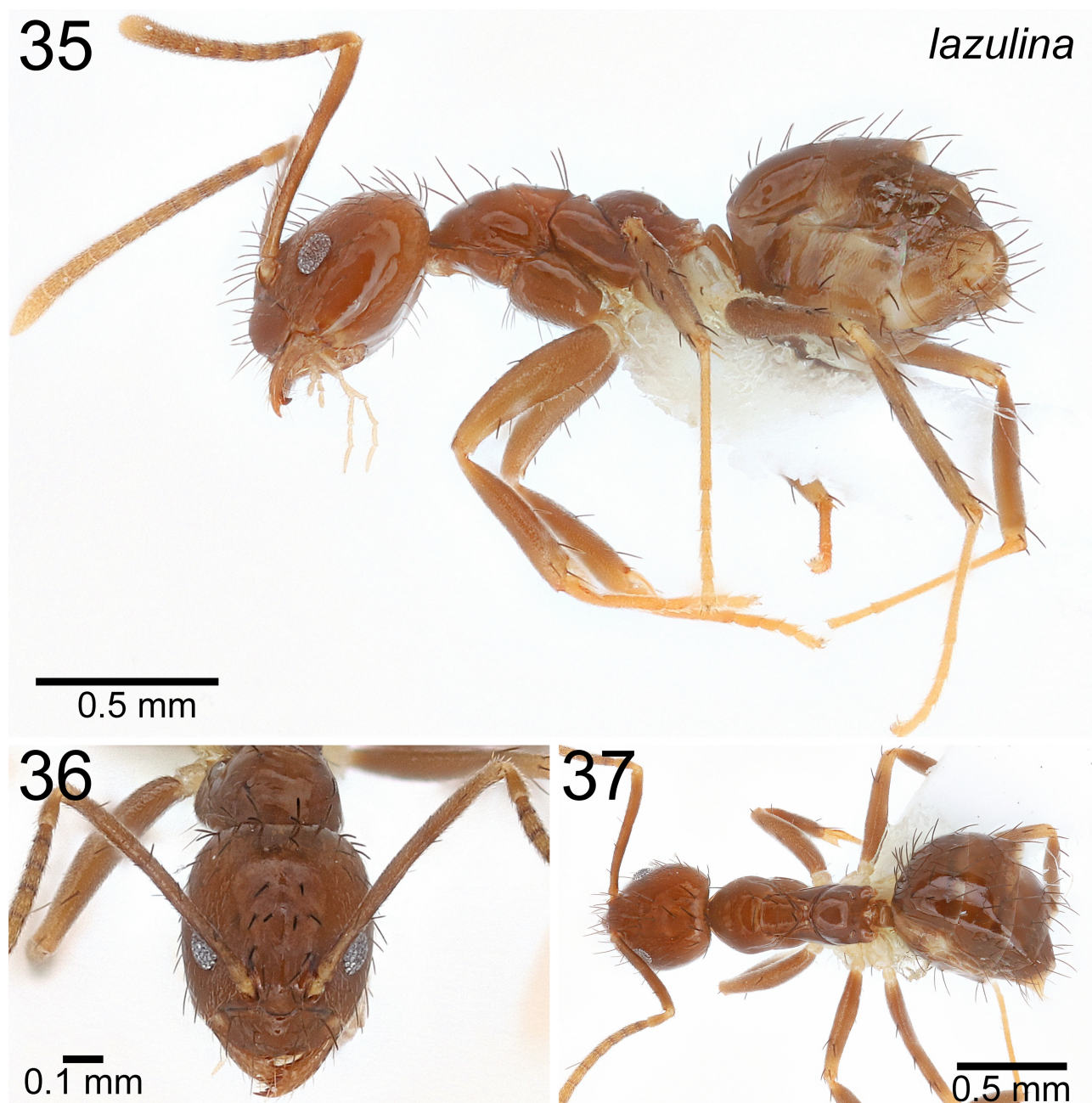
Izabal, 16km ESE Morales, 15.41764 -88.69683 \pm 70m, elev. 410m, 19.v.2009, 2° lowland rainforest, sifted litter, LLAMA#Wm-B-04-2-09; Petén, Cerro Cahuí, 17.00266 -89.7187 \pm 8m, elev. 290m, 21.v.2009, tropical moist forest at night, sifted litter, LLAMA#Wx-B-05-1-01; **HONDURAS:** Atlántida, 7km SSW Tela, 15.72521 -87.452 \pm 20m, elev. 190m, 15.vi.2010, tropical rainforest, sifted litter, LLAMA#Wa-C-08-2-02; Atlántida, 7km SSW Tela, 15.72417 -87.45187 \pm 20m, elev. 190m, 15.vi.2010, tropical rainforest, sifted litter, LLAMA#Wa-C-08-2-25; Atlántida, 12km SW La Ceiba, 15.69449 -86.86436 \pm 20m, elev. 200m, 19.vi.2010, tropical rainforest, sifted litter, LLAMA#Wa-C-09-1-04; Atlántida, 12km SW La Ceiba, 15.69449 -86.86348 \pm 20m, elev. 200m, 19.vi.2010, tropical rainforest, sifted litter, LLAMA#Wa-C-09-1-23; Atlántida, 12km SW La Ceiba, 15.69449 -86.86334 \pm 20m, elev. 200m, 19.vi.2010, tropical rainforest, sifted litter, LLAMA#Wa-C-09-1-26; Atlántida, 12km SW La Ceiba, 15.69449 -86.86279 \pm 20m, elev. 200m, 19.vi.2010, tropical rainforest, sifted litter, LLAMA#Wa-C-09-1-38; Atlántida, 12km SW La Ceiba, 15.69108 -86.86084 \pm 20m, elev. 280m, 19.vi.2010, tropical rainforest, sifted litter, LLAMA#Wa-C-09-2-24; Atlántida, 12km SW La Ceiba, 15.69112 -86.86107 \pm 20m, elev. 280m, 19.vi.2010, tropical rainforest, sifted litter, LLAMA#Wa-C-09-2-29; Atlántida, 12km SW La Ceiba, 15.6913 -86.86138 \pm 20m, elev. 280m, 19.vi.2010, tropical rainforest, sifted litter, LLAMA#Wa-C-09-2-39; Atlántida, 12km SW La Ceiba, 15.6916 -86.86122 \pm 20m, elev. 280m, 19.vi.2010, tropical rainforest, sifted litter, LLAMA#Wa-C-09-2-47; Atlántida, 12km SW La Ceiba, 15.69164 -86.86119 \pm 20m, elev. 280m, 19.vi.2010, tropical rainforest, sifted litter, LLAMA#Wa-C-09-2-48; Atlántida, 12km SW La Ceiba, 15.69167 -86.86116 \pm 20m, elev. 280m, 19.vi.2010, tropical rainforest, sifted litter, LLAMA#Wa-C-09-2-49; Atlántida, 7km SSW Tela, 15.72792 -87.4497 \pm 20m, elev. 120m, 16.vi.2010, tropical rainforest, sifted litter, LLAMA#Wm-C-08-1-04; Atlántida, 7km SSW Tela, 15.72792 -87.4497 \pm 20m, elev. 120m, 16.vi.2010, tropical rainforest, sifted litter, LLAMA#Wm-C-08-1-05; Atlántida, 10km SSW Tela, 15.6937377 -87.47797 \pm 20m, elev. 770m, 17.vi.2010, tropical wet forest, sifted litter, LLAMA#Wm-C-08-1-09; Atlántida, 10km SSW Tela, 15.69714 -87.47451 \pm 20m, elev. 610m, 17.vi.2010, tropical wet forest, sifted litter, LLAMA#Wm-C-08-2-02; Atlántida, 10km SSW Tela, 15.69914 -87.47202 \pm 20m, elev. 520m, 17.vi.2010, tropical wet forest, sifted litter, LLAMA#Wm-C-08-2-04; Atlántida, 9km SSW Tela, 15.70207 -87.47304 \pm 20m, elev. 450m, 17.vi.2010, tropical rainforest, sifted litter, LLAMA#Wm-C-08-2-05; Atlántida, 9km SSW Tela, 15.70493 -87.47291 \pm 20m, elev. 410m, 17.vi.2010, tropical rainforest, sifted litter, LLAMA#Wm-C-08-2-06; Atlántida, 8km SSW Tela, 15.70914 -87.46623 \pm 20m, elev. 330m, 17.vi.2010, tropical rainforest, sifted litter, LLAMA#Wm-C-08-2-08; Atlántida, 12km SW La Ceiba, 15.69445 -86.86338 \pm 300m, elev. 140m, 19.vi.2010, tropical rainforest, sifted litter, LLAMA#Wm-C-09-1-01; Atlántida, 12km SW La Ceiba, 15.69445 -86.86338 \pm 300m, elev. 140m, 19.vi.2010, tropical rainforest, sifted litter, LLAMA#Wm-C-09-2-01; Comayagua, PN Cerro Azul Meambar, 14.87314 -87.90297 \pm 30m, elev. 890m, 22.v.2010, montane rainforest, sifted litter, LLAMA#Wm-C-04-1-07; Comayagua, PN Cerro Azul Meambar, 14.87238 -87.90332 \pm 20m, elev. 870m, 22.v.2010, montane rainforest, sifted litter, LLAMA#Wm-C-04-1-08; Comayagua, PN Cerro Azul Meambar, 14.86993 -87.90479 \pm 110m, elev. 770m, 21.v.2010, montane rainforest, sifted litter, LLAMA#Wm-C-04-2-01; **MEXICO:** Chiapas, 13.7km NW Metzabok, 17.18333 -91.73333, elev. 540m, 14.vii.2007, J.T. Longino #JTL6046-s; Chiapas, Lagos de Montebello, Cinco Lagos, 16.1 -91.66667, elev. 1600m, 21.vii.2007, R.S. Anderson #RSA2007-023; Chiapas, 2km S Playón de la Gloria, 16.13853 -90.90146 \pm 50m, elev. 170m, 22.vii.2007, rainforest, sifted litter, R.S. Anderson #RSA2007-025; Chiapas, 2km S Playón de la Gloria, 16.13333 -90.9, elev. 170m, 22.vii.2007, R.S. Anderson #RSA2007-026; Chiapas, 2.5km S Nuevo San Juan Chamula, 16.11667 -91.45, elev. 750m, 22.vii.2007, R.S. Anderson #RSA2007-028; Chiapas, Playón de la Gloria, 16.16095 -90.90142 \pm 50m, elev. 160m, 24.vi.2008, mature wet forest, sifted litter, LLAMA#Wa-A-09-1-39; Chiapas, Playón de la Gloria, 16.14721 -90.89549 \pm 50m, elev. 170m, 24.vi.2008, 2° wet forest, sifted litter, LLAMA#Wa-A-09-2-39; Oaxaca, Cafetal Carlota, 18.04802 -96.69164 \pm 30m, elev. 1028m, 12.vi.2016, liquidambar/cloud forest, sifted litter, R.S. Anderson #RSA2016-136.

Notes: Workers of this species exhibit some variability in overall color, ranging from uniformly yellow across most of its range to light brown with somewhat lighter meso- and metacoxae in some specimens collected from Belize. Because of its uniform yellow color, *N. cf. docilis* most readily resembles *N. mosaica* and the lighter form *N. usul*. However, cephalic pubescence is sparse in *N. cf. docilis*, moderate in *N. mosaica*, and moderate to dense in *N. usul*. The gaster is also about the same color as the rest of the body in *N. cf. docilis*, while in *N. mosaica*, the gaster is distinctly darker. Compared to all other species examined in this study, *N. cf. docilis* also has the longest metatibiae relative to its head width (HTI > 125; Fig. 72D). *Nylanderia cf. docilis* has a distribution across low to moderate elevation forests from southern Mexico to Honduras.

Nylanderia lazulina, sp. nov

Figs. 35–37 (worker); Figs. 38–39 (queen); Figs. 40–43 (male)

Holotype worker, **MEXICO**: Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.05817 -96.64624 ±20m, elev. 390m, 9.vi.2016, lowland rainforest, sifted litter, ADMAC#Wa-F-03-2-36, (USNM: USNMENT01131154). 5 paratype workers with same locality data as holotype (USNM: USNMENT01131308, USNMENT01131309; MNCR: USNMENT01131310, USNMENT01131311, USNMENT01131312). 1 paratype worker, 2 paratype males, and 1 paratype queen, **MEXICO**: Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.0593 -96.64624 ±20m, elev. 420m, 9.vi.2016, lowland rainforest, sifted litter, ADMAC#Wa-F-03-2-13, (USNM: USNMENT01131339, USNMENT01131866; MNCR: USNMENT01131865).



FIGURES 35–37. *Nylanderia lazulina* holotype worker (USNMENT01131154). Lateral, full-face, and dorsal view of the body.

Worker diagnosis: Antennae relatively long, with scapes surpassing posterior margin by nearly half their length; medium to dark reddish-brown and with strongly contrasting whitish meso- and metacoxae; microsculpture very finely matte, causing intense blue iridescence on head, mesosoma, and gaster; erect setae on all parts of body thick,

long, and dark; sparse thick erect setae on scapes that strongly contrast with relatively fine appressed pubescence; moderate cephalic pubescence; metatibiae relatively long (HTI > 125).

Compare with: *N. contraria*, *N. luceata*

WORKER. *Measurements* ($n=12$): TL: 1.99–2.52; EL: 0.12–0.16; EW: 0.09–0.12; IOD: 0.29–0.33; HE: 0.00–0.01; HL: 0.56–0.69; HW: 0.46–0.55; HLA: 0.17–0.25; HLP: 0.25–0.29; SL: 0.68–0.83; PW: 0.35–0.42; MW: 0.18–0.28; PrW: 0.24–0.31; PDH: 0.22–0.25; PTW: 0.11–0.15; LHT: 0.60–0.76; WL: 0.71–0.88; GL: 0.69–1.00; SMC: 3–6; PMC: 2–4; MMC: 2. *Indices*: BLI: 147–162; CI: 80–83; EPI: 65–87; HTI: 125–146; REL: 20–24; SI: 143–156.



FIGURES 38–39. *Nylanderia lazulina* paratype queen (USNMENT01131866). Full-face and lateral view of the body.

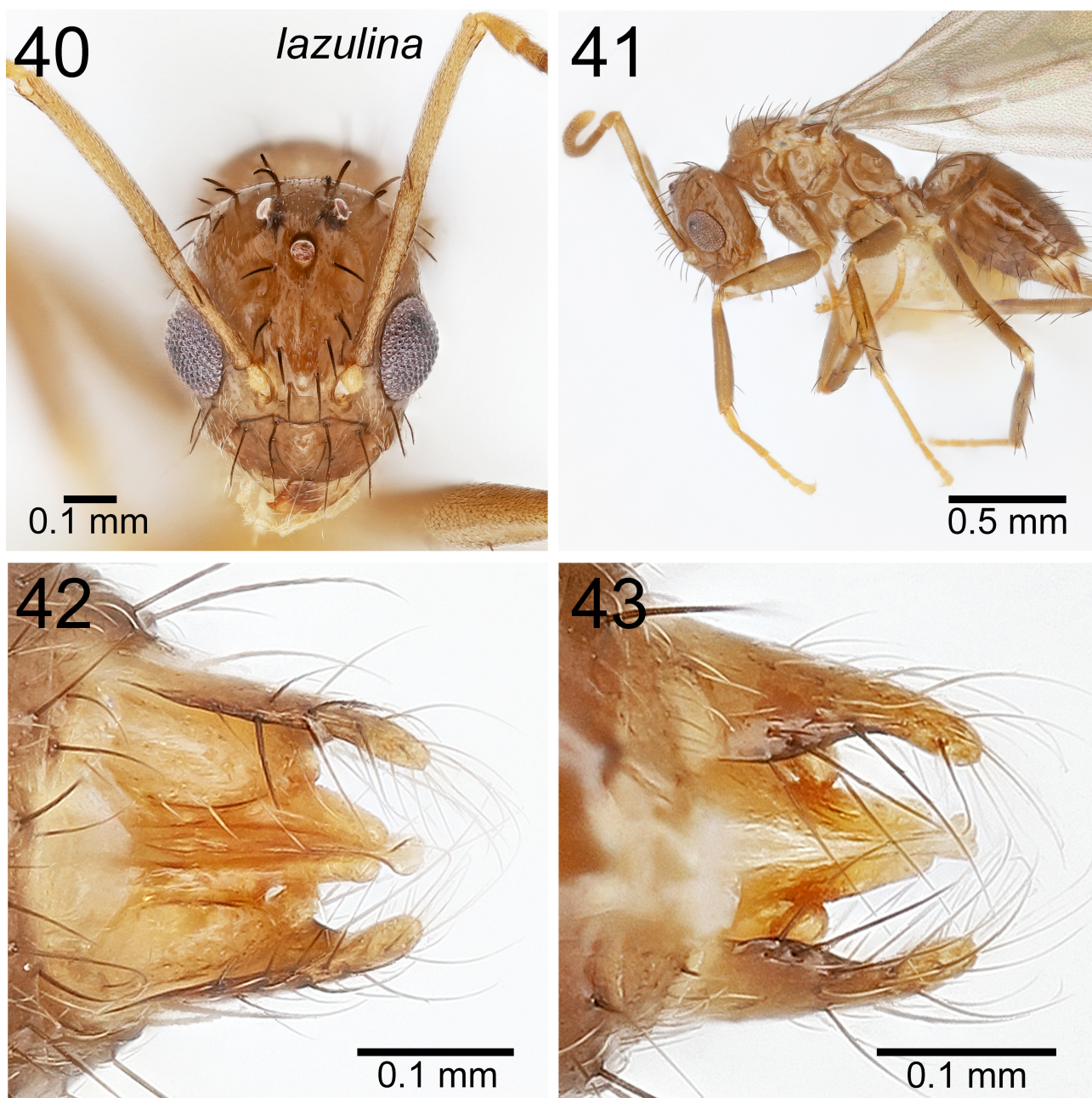
Color: medium to dark reddish-brown and with strongly contrasting whitish meso- and metacoxae; black macrosetae strongly contrasting with overall color; overall cuticle with very fine microsculpture, giving cuticle matte appearance and resulting in strong blue iridescence on head, mesosoma, and gaster. **Pilosity:** erect setae on all parts of body thick, long, and dark; moderate cephalic pubescence, found laterally and concentrated around compound eyes; pubescence sparse to absent between compound eyes; mesosoma pubescence sparse to absent, limited at most to scattered hairs on pronotum and propodeum, and a fringe of hairs concentrated just posterior to the metanotal groove; gaster pubescence sparse to absent; no erect setae on apex of petiole. **Head:** longer than broad and quadrate with distinct posterolateral corners and flattened posterior margin, with little to no medial emargination; scapes long, surpassing posterior margin by nearly half their length; median ocellus small, but often apparent; lateral ocelli small and often absent or not apparent. **Mesosoma:** posterior margin of pronotum forming obtuse angle with anterior margin of mesonotum in profile view; propodeum low and evenly rounded, with posterior face about same length as dorsal face.

QUEEN. *Measurements* ($n=1$): TL: 3.74; EL: 0.21; HL: 0.71; HW: 0.71; SL: 0.81; WL: 1.18; GL: 1.85. *Indices*: BLI: 165; CI: 99; REL: 30; SI: 114.

Relatively large. **Color:** Dark brown, with meso- and metacoxae somewhat lighter. **Pilosity:** most of body covered in moderate to dense pubescence; lacking pubescence on posterior face of propodeum; 1–2 small, erect setae on anepisternum.

MALE. *Measurements* ($n=2$): TL: 1.98–2.06; EL: 0.17–0.18; HL: 0.50–0.51; HW: 0.44–0.45; SL: 0.62–0.63; WL: 0.74; GL: 0.74–0.82. *Indices*: BLI: 165–167; CI: 87–89; REL: 33–35; SI: 140–142.

Color: uniformly medium brown with meso- and metacoxae at most somewhat lighter than mesosoma. **Pilosity:** dense pubescence on head, mesoscutum, and mesoscutellum; pubescence sparse to absent on pronotum, anepisternum, katepisternum, propodeum, and gaster. **Head:** as broad as long; compound eyes surpass lateral margins of head in full-face view; scapes surpass posterior margin of head by about half their length. **Mesosoma:** In profile view, propodeum angled with dorsal face twice as long as posterior face. **Genitalia:** gonopod triangular and very broad at base, tapering strongly with apex steeply upturned and coming to a point (Fig. 71); in ventral view, ventromedial edge of basivolsella weakly and evenly curved (Fig. 42); gonossiculus straight and nearly three times longer than cuspis.



FIGURES 40–43. *Nylanderia lazulina* paratype male (USNMENT01131339). Full-face and lateral view of the body; ventral and dorsal view of the genital capsule.

Other material examined: GUATEMALA: Retalhuleu, Finca los Chicharros, SW Zunil, 14.6946 -91.53792 \pm 50m, elev. 1273m, 3.vi.2015, mixed hardwood, sifted litter, R.S. Anderson #RSA2015-102; Zacapa, 2km SE La Unión, 14.94654 -89.276 \pm 55m, elev. 1550m, 12.v.2009, 2° cloud forest, sifted litter, LLAMA#Wm-B-03-1-01; Zacapa, 2km SE La Unión, 14.94758 -89.27751 \pm 28m, elev. 1530m, 12.v.2009, cloud forest, sifted litter, LLAMA#Wm-B-03-1-02; Zacapa, 2km SE La Unión, 14.94654 -89.276 \pm 305m, elev. 1550m, 12.v.2009, cloud forest, sifted litter, LLAMA#Wm-B-03-1-06; **HONDURAS:** Comayagua, Montana Comayagua, 14.53448 -87.55155 \pm 100m, elev. 1360m, 16.v.2009, mixed liquidambar forest, sifted litter, R.S. Anderson #RSA2009-031; Olancho, Parque Nacional La Muralla, 15.0943 -86.7387 \pm 50m, elev. 1420m, 2.v.2010, cloud forest, sifted litter, R.S. Anderson #RSA2010-002; Olancho, Parque Nacional La Muralla, 15.09387 -86.73934 \pm 50m, elev. 1410m, 2.v.2010, cloud forest, sifted litter, R.S. Anderson #RSA2010-003; Olancho, 9km N Catacamas, 14.93693 -85.90535 \pm 20m, elev. 1360m, 10.v.2010, mixed hardwood forest, sifted litter, R.S. Anderson #RSA2010-020; Comayagua,

PN Cerro Azul Meambar, 14.86937 -87.89583 \pm 20m, elev. 1140m, 20.v.2010, ridgetop cloud forest, sifted litter, LLAMA#Wa-C-04-2-48; Comayagua, PN Cerro Azul Meambar, 14.86932 -87.89576 \pm 20m, elev. 1140m, 20.v.2010, ridgetop cloud forest, sifted litter, LLAMA#Wa-C-04-2-50; Cortés, PN Cusuco, 15.48683 -88.2343 \pm 20m, elev. 1330m, 30.v.2010, mesophyll forest, sifted litter, LLAMA#Wa-C-06-1-24; Cortés, PN Cusuco, 15.48683 -88.23425 \pm 20m, elev. 1330m, 30.v.2010, mesophyll forest, sifted litter, LLAMA#Wa-C-06-1-25; Cortés, PN Cusuco, 15.48686 -88.23402 \pm 20m, elev. 1330m, 30.v.2010, mesophyll forest, sifted litter, LLAMA#Wa-C-06-1-30; Cortés, PN Cusuco, 15.48686 -88.23398 \pm 20m, elev. 1330m, 30.v.2010, mesophyll forest, sifted litter, LLAMA#Wa-C-06-1-31; Cortés, PN Cusuco, 15.4894 -88.2363 \pm 20m, elev. 1290m, 30.v.2010, mesophyll forest, sifted litter, LLAMA#Wa-C-06-2-14; Cortés, PN Cusuco, 15.4894 -88.23639 \pm 20m, elev. 1290m, 30.v.2010, mesophyll forest, sifted litter, LLAMA#Wa-C-06-2-16; Cortés, PN Cusuco, 15.48932 -88.23752 \pm 20m, elev. 1290m, 30.v.2010, mesophyll forest, sifted litter, LLAMA#Wa-C-06-2-43; Cortés, PN Cusuco, 15.48915 -88.23745 \pm 20m, elev. 1290m, 30.v.2010, mesophyll forest, sifted litter, LLAMA#Wa-C-06-2-47; Olancho, PN La Muralla, 15.09734 -86.73912 \pm 20m, elev. 1490m, 2.v.2010, cloud forest, sifted litter, LLAMA#Wm-C-01-1-01; Olancho, PN La Muralla, 15.09803 -86.7399 \pm 20m, elev. 1500m, 2.v.2010, cloud forest, sifted litter, LLAMA#Wm-C-01-1-02; Olancho, PN La Muralla, 15.09859 -86.74216 \pm 10m, elev. 1510m, 2.v.2010, cloud forest, sifted litter, LLAMA#Wm-C-01-1-03; Olancho, PN La Muralla, 15.09911 -86.74067 \pm 125m, elev. 1530m, 2.v.2010, cloud forest, sifted litter, LLAMA#Wm-C-01-1-05; Olancho, PN La Muralla, 15.09489 -86.73944 \pm 125m, elev. 1420m, 2.v.2010, cloud forest, sifted litter, LLAMA#Wm-C-01-2-01; Comayagua, PN Cerro Azul Meambar, 14.87112 -87.89938 \pm 300m, elev. 1100m, 20.v.2010, ridgetop cloud forest, sifted litter, LLAMA#Wm-C-04-1-01; Comayagua, PN Cerro Azul Meambar, 14.86951 -87.89701 \pm 300m, elev. 1150m, 20.v.2010, ridgetop cloud forest, sifted litter, LLAMA#Wm-C-04-1-02; Comayagua, PN Cerro Azul Meambar, 14.87236 -87.90098 \pm 20m, elev. 1040m, 22.v.2010, cloud forest, sifted litter, LLAMA#Wm-C-04-1-05; Comayagua, PN Cerro Azul Meambar, 14.87209 -87.90187 \pm 20m, elev. 1000m, 22.v.2010, montane rainforest, sifted litter, LLAMA#Wm-C-04-1-06; Comayagua, PN Cerro Azul Meambar, 14.87314 -87.90297 \pm 30m, elev. 890m, 22.v.2010, montane rainforest, sifted litter, LLAMA#Wm-C-04-1-07; Comayagua, PN Cerro Azul Meambar, 14.87238 -87.90332 \pm 20m, elev. 870m, 22.v.2010, montane rainforest, sifted litter, LLAMA#Wm-C-04-1-08; Comayagua, PN Cerro Azul Meambar, 14.86993 -87.90479 \pm 110m, elev. 770m, 21.v.2010, montane rainforest, sifted litter, LLAMA#Wm-C-04-2-01; Atlántida, 10km SSW Tela, 15.69652 -87.47636 \pm 20m, elev. 660m, 17.vi.2010, tropical wet forest, sifted litter, LLAMA#Wm-C-08-2-01; **MEXICO:** Puebla, 1.4km WSW Hueytamalco, 19.93725 -97.30273 \pm 50m, elev. 760m, 12.vi.2019, mesophyll forest, sifted litter, J.T. Longino #JTL10644-s; Veracruz, 10km NNW Sontecomapan, 18.58333 -95.08333 \pm m, elev. 500m, 21.iii.1985, rainforest, P.S. Ward #PSW7369-41; Veracruz, 10km NNW Sontecomapan, 18.58333 -95.08333 \pm m, elev. 500m, 21.iii.1985, rainforest, sifted litter, P.S. Ward #PSW7369-41; Veracruz, Road to Ruiz Cortínez, 18.51999 -95.16196 \pm 30m, elev. 1054m, 5.vi.2016, liquidambar forest, sifted litter, R.S. Anderson #RSA2016-104; Veracruz, Road to Ruiz Cortínez, 18.5229 -95.15441 \pm 30m, elev. 1114m, 5.vi.2016, mixed hardwood forest, sifted litter, R.S. Anderson #RSA2016-105; Veracruz, hills above Ruiz Cortínez, 18.5304 -95.14127 \pm 30m, elev. 1239m, 7.vi.2016, hilltop hardwood forest, sifted litter, R.S. Anderson #RSA2016-110; Oaxaca, Cafetal Carlota, 18.04756 -96.69252 \pm 30m, elev. 1011m, 12.vi.2016, liquidambar/cloud forest, sifted litter, R.S. Anderson #RSA2016-138; Oaxaca, Cafetal Carlota, 18.04773 -96.68953 \pm 30m, elev. 1041m, 14.vi.2016, liquidambar/cloud forest, sifted litter, R.S. Anderson #RSA2016-145; Oaxaca, Cafetal Carlota, 18.04784 -96.69198 \pm 30m, elev. 1019m, 14.vi.2016, liquidambar/cloud forest, sifted litter, R.S. Anderson #RSA2016-146; Oaxaca, Cafetal Carlota, 18.04791 -96.69076 \pm 30m, elev. 1035m, 14.vi.2016, liquidambar/cloud forest, sifted litter, R.S. Anderson #RSA2016-147; Veracruz, Est. Biol. Los Tuxtlas, 18.5863 -95.07665 \pm 20m, elev. 180m, 29.v.2016, tropical rainforest, sifted litter, ADMAC#Wa-F-01-2-17; Veracruz, Est. Biol. Los Tuxtlas, 18.58557 -95.07665 \pm 20m, elev. 180m, 29.v.2016, tropical rainforest, sifted litter, ADMAC#Wa-F-01-2-33; Veracruz, Est. Biol. Los Tuxtlas, 18.58539 -95.07665 \pm 20m, elev. 180m, 29.v.2016, tropical rainforest, sifted litter, ADMAC#Wa-F-01-2-37; Veracruz, Ruiz Cortínez, 12 km NE San Andrés Tuxtla, 18.53399 -95.14888 \pm 20m, elev. 1130m, 3.vi.2016, montane wet forest, sifted litter, ADMAC#Wa-F-02-1-10; Veracruz, Ruiz Cortínez, 12 km NE San Andrés Tuxtla, 18.53412 -95.14974 \pm 20m, elev. 1130m, 3.vi.2016, montane wet forest, sifted litter, ADMAC#Wa-F-02-1-27; Veracruz, Ruiz Cortínez, 12 km NE San Andrés Tuxtla, 18.53399 -95.14765 \pm 20m, elev. 1130m, 3.vi.2016, montane wet forest, sifted litter, ADMAC#Wa-F-02-1-44; Veracruz, Ruiz Cortínez, 12 km NE San Andrés Tuxtla, 18.53399 -95.14734 \pm 20m, elev. 1130m, 3.vi.2016, montane wet forest, sifted litter, ADMAC#Wa-F-02-1-50; Veracruz, Ruiz Cortínez, 12 km NE San Andrés Tuxtla, 18.53231 -95.14302 \pm 20m, elev. 1130m, 3.vi.2016, montane wet forest, sifted litter, ADMAC#Wa-F-02-2-

23; Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.06001 -96.64345 ±20m, elev. 430m, 9.vi.2016, lowland rainforest, sifted litter, ADMAC#Wa-F-03-1-02; Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.06001 -96.6435 ±20m, elev. 430m, 9.vi.2016, lowland rainforest, sifted litter, ADMAC#Wa-F-03-1-03; Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.06001 -96.64355 ±20m, elev. 430m, 9.vi.2016, lowland rainforest, sifted litter, ADMAC#Wa-F-03-1-04; Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.06001 -96.64458 ±20m, elev. 430m, 9.vi.2016, lowland rainforest, sifted litter, ADMAC#Wa-F-03-1-24; Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.06001 -96.64463 ±20m, elev. 430m, 9.vi.2016, lowland rainforest, sifted litter, ADMAC#Wa-F-03-1-25; Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.05957 -96.64579 ±20m, elev. 430m, 9.vi.2016, lowland rainforest, sifted litter, ADMAC#Wa-F-03-2-02; Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.05952 -96.64588 ±20m, elev. 430m, 9.vi.2016, lowland rainforest, sifted litter, ADMAC#Wa-F-03-2-04; Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.05939 -96.64615 ±20m, elev. 420m, 9.vi.2016, lowland rainforest, sifted litter, ADMAC#Wa-F-03-2-10; Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.05936 -96.64619 ±20m, elev. 420m, 9.vi.2016, lowland rainforest, sifted litter, ADMAC#Wa-F-03-2-11; Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.05934 -96.64624 ±20m, elev. 420m, 9.vi.2016, lowland rainforest, sifted litter, ADMAC#Wa-F-03-2-12; Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.05925 -96.64624 ±20m, elev. 420m, 9.vi.2016, lowland rainforest, sifted litter, ADMAC#Wa-F-03-2-14; Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.05889 -96.64624 ±20m, elev. 410m, 9.vi.2016, lowland rainforest, sifted litter, ADMAC#Wa-F-03-2-22; Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.05866 -96.64624 ±20m, elev. 400m, 9.vi.2016, lowland rainforest, sifted litter, ADMAC#Wa-F-03-2-25; Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.0583 -96.64624 ±20m, elev. 400m, 9.vi.2016, lowland rainforest, sifted litter, ADMAC#Wa-F-03-2-33; Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.05821 -96.64624 ±20m, elev. 390m, 9.vi.2016, lowland rainforest, sifted litter, ADMAC#Wa-F-03-2-35; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.0486 -96.69106 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-1-39; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.0486 -96.69127 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-1-43; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.0486 -96.69147 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-1-47; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04736 -96.6903 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-01; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04745 -96.69018 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-04; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04753 -96.69006 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-07; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04762 -96.68995 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-10; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04804 -96.68954 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-24; Oaxaca, Cafetal Carlota, 3km NW Ayautla, 18.04807 -96.68957 ±20m, elev. 1040m, 13.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wa-F-04-2-25; Veracruz, Est. Biol. Los Tuxtlas, 18.5862 -95.07964 ±20m, elev. 260m, 30.v.2016, tropical rainforest, sifted litter, ADMAC#Wm-F-01-1-02; Veracruz, Est. Biol. Los Tuxtlas, 18.583 -95.08223 ±20m, elev. 360m, 30.v.2016, tropical rainforest, sifted litter, ADMAC#Wm-F-01-1-04; Veracruz, 8km NNE Sotepan, 18.30208 -94.85354 ±20m, elev. 1020m, 30.v.2016, liquidamber-oak forest, sifted litter, ADMAC#Wm-F-01-1-07; Veracruz, Ruiz Cortínez, 12 km NE San Andrés Tuxtla, 18.53456 -95.13976 ±20m, elev. 1070m, 2.vi.2016, montane wet forest, sifted litter, ADMAC#Wm-F-02-1-01; Veracruz, Volcan San Martín, 18.53438 -95.19025 ±20m, elev. 1020m, 5.vi.2016, mature forest edge near pasture, sifted litter, ADMAC#Wm-F-02-1-04; Veracruz, Volcan San Martín, 18.54332 -95.19177 ±20m, elev. 1110m, 5.vi.2016, mature wet forest, sifted litter, ADMAC#Wm-F-02-1-05; Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.05845 -96.64414 ±20m, elev. 380m, 8.vi.2016, lowland rainforest, sifted litter, ADMAC#Wm-F-03-1-01; Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.05678 -96.64841 ±20m, elev. 540m, 8.vi.2016, lowland rainforest, sifted litter, ADMAC#Wm-F-03-1-02; Oaxaca, Uluapan, 4km NE San Bartolomé Ayautla, 18.06188 -96.64635 ±20m, elev. 640m, 11.vi.2016, lowland rainforest, sifted litter, ADMAC#Wm-F-03-1-05; Oaxaca, 8km E Huautla, 18.11663 -96.7695 ±20m, elev. 1380m, 15.vi.2016, 2° liquidambar forest, sifted litter, ADMAC#Wm-F-04-1-10; Oaxaca, 10km ENE Huautla, 18.15269 -96.75035 ±20m, elev. 1150m, 15.vi.2016, vegetated karst pinnacle, sifted litter, ADMAC#Wm-F-04-2-01; Puebla, Cascada Las Brisas, 2km SE Cuetzalan, 20.00549 -97.50801 ±20m, elev. 930m, 2.vii.2016, montane wet forest, sifted litter, ADMAC#Wm-F-08-1-02; Puebla, Cascada Las Brisas, 2km SE Cuetzalan, 20.00545 -97.50789 ±20m, elev. 930m, 2.vii.2016, montane wet forest, sifted litter, ADMAC#Wm-F-08-1-03; Puebla, Presa La Soledad; 11km SE Cuetzalan, 19.96599 -97.45082 ±20m, elev. 760m, 3.vii.2016, mixed pine-hardwood forest,

sifted litter, ADMAC#Wm-F-08-1-04; **NICARAGUA:** Matagalpa, RN Cerro Musún, 12.97283 -85.23419 ±50m, elev. 1170m, 2.v.2011, wet montane forest, sifted litter, R.S. Anderson #RSA2011-011; Matagalpa, RN Cerro Musún, 12.97608 -85.23299 ±50m, elev. 1250m, 2.v.2011, wet montane forest, sifted litter, R.S. Anderson #RSA2011-012; Jinotega, PN Cerro Saslaya, 13.77172 -85.01277 ±10m, elev. 1110m, 12.v.2011, ridgetop cloud forest, sifted litter, LLAMA#Wa-D-03-1-05; Jinotega, PN Cerro Saslaya, 13.76689 -85.02472 ±10m, elev. 1040m, 12.v.2011, montane wet forest, sifted litter, LLAMA#Wa-D-03-2-10; Jinotega, PN Cerro Saslaya, 13.76749 -85.02452 ±13m, elev. 1040m, 12.v.2011, montane wet forest, sifted litter, LLAMA#Wa-D-03-2-24; Jinotega, PN Cerro Saslaya, 13.76792 -85.02438 ±10m, elev. 1040m, 12.v.2011, montane wet forest, sifted litter, LLAMA#Wa-D-03-2-34; Jinotega, PN Cerro Saslaya, 13.76818 -85.02429 ±10m, elev. 1040m, 12.v.2011, montane wet forest, sifted litter, LLAMA#Wa-D-03-2-40; Jinotega, RN Datanlí El Diablo, 13.10417 -85.86806 ±10m, elev. 1400m, 18.v.2011, cloud forest, sifted litter, LLAMA#Wa-D-04-2-14; Jinotega, RN Datanlí El Diablo, 13.10436 -85.86787 ±10m, elev. 1400m, 18.v.2011, cloud forest, sifted litter, LLAMA#Wa-D-04-2-20; Jinotega, RN Datanlí El Diablo, 13.10474 -85.86748 ±10m, elev. 1400m, 18.v.2011, cloud forest, sifted litter, LLAMA#Wa-D-04-2-32; Jinotega, RN Cerro Kilambé, 13.56942 -85.69745 ±10m, 1500m, 23.v.2011, cloud forest, sifted litter, LLAMA#Wa-D-05-1-07; Jinotega, RN Cerro Kilambé, 13.56755 -85.69695 ±10m, elev. 1420m, 23.v.2011, cloud forest, sifted litter, LLAMA#Wa-D-05-2-06; Jinotega, RN Cerro Kilambé, 13.56746 -85.69746 ±10m, elev. 1400m, 23.v.2011, cloud forest, sifted litter, LLAMA#Wa-D-05-2-18; Jinotega, RN Cerro Kilambé, 13.56745 -85.69676 ±10m, elev. 1440m, 23.v.2011, cloud forest, sifted litter, LLAMA#Wa-D-05-2-32; Jinotega, RN Cerro Kilambé, 13.56747 -85.69667 ±10m, elev. 1440m, 23.v.2011, cloud forest, sifted litter, LLAMA#Wa-D-05-2-34; Jinotega, RN Cerro Kilambé, 13.5675 -85.69644 ±15m, elev. 1440m, 23.v.2011, cloud forest, sifted litter, LLAMA#Wa-D-05-2-39; Jinotega, RN Cerro Kilambé, 13.56751 -85.6964 ±10m, elev. 1440m, 23.v.2011, cloud forest, sifted litter, LLAMA#Wa-D-05-2-40; Jinotega, RN Cerro Kilambé, 13.56754 -85.69621 ±10m, elev. 1440m, 23.v.2011, cloud forest, sifted litter, LLAMA#Wa-D-05-2-44; Jinotega, PN Cerro Saslaya, 13.771 -85.02538 ±30m, elev. 1140m, 13.v.2011, montane wet forest, sifted litter, LLAMA#Wm-D-03-2-08; Jinotega, RN Datanlí El Diablo, 13.10754 -85.86831 ±40m, elev. 1450m, 19.v.2011, cloud forest, sifted litter, LLAMA#Wm-D-04-1-07; Jinotega, RN Datanlí El Diablo, 13.10436 -85.86787 ±150m, elev. 1400m, 18.v.2011, cloud forest, sifted litter, LLAMA#Wm-D-04-2-01; Nueva Segovia, 9km NW Jalapa, 13.97735 -86.18887 ±20m, elev. 1420m, 29.v.2011, oak cloud forest, sifted litter, LLAMA#Wm-D-06-1-05.

Etymology: The species epithet is derived from ‘*lazulum*’ (L. = sky), referring to the intensity of the brilliant blue iridescence found across the entire cuticle of this species.

Notes: *Nylanderia lazulina* workers have whitish meso- and metacoxae like those of *N. contraria* and *N. luceata* but are otherwise distinct and not likely to be confused with other species. Unlike all other species, it is medium to dark reddish brown with dense microsculpture that gives the overall surface of the cuticle a matte appearance. It also has a very strong blue iridescence, perhaps more intense than any other known *Nylanderia* species. This species is primarily found in moderate to high elevation forests ranging from Veracruz, Mexico to Nicaragua (Fig. 2B), and is relatively common across this range compared to other *Nylanderia* species.

Nylanderia luceata, sp. nov.

Figs. 44–46 (worker); Figs. 47–48 (queen)

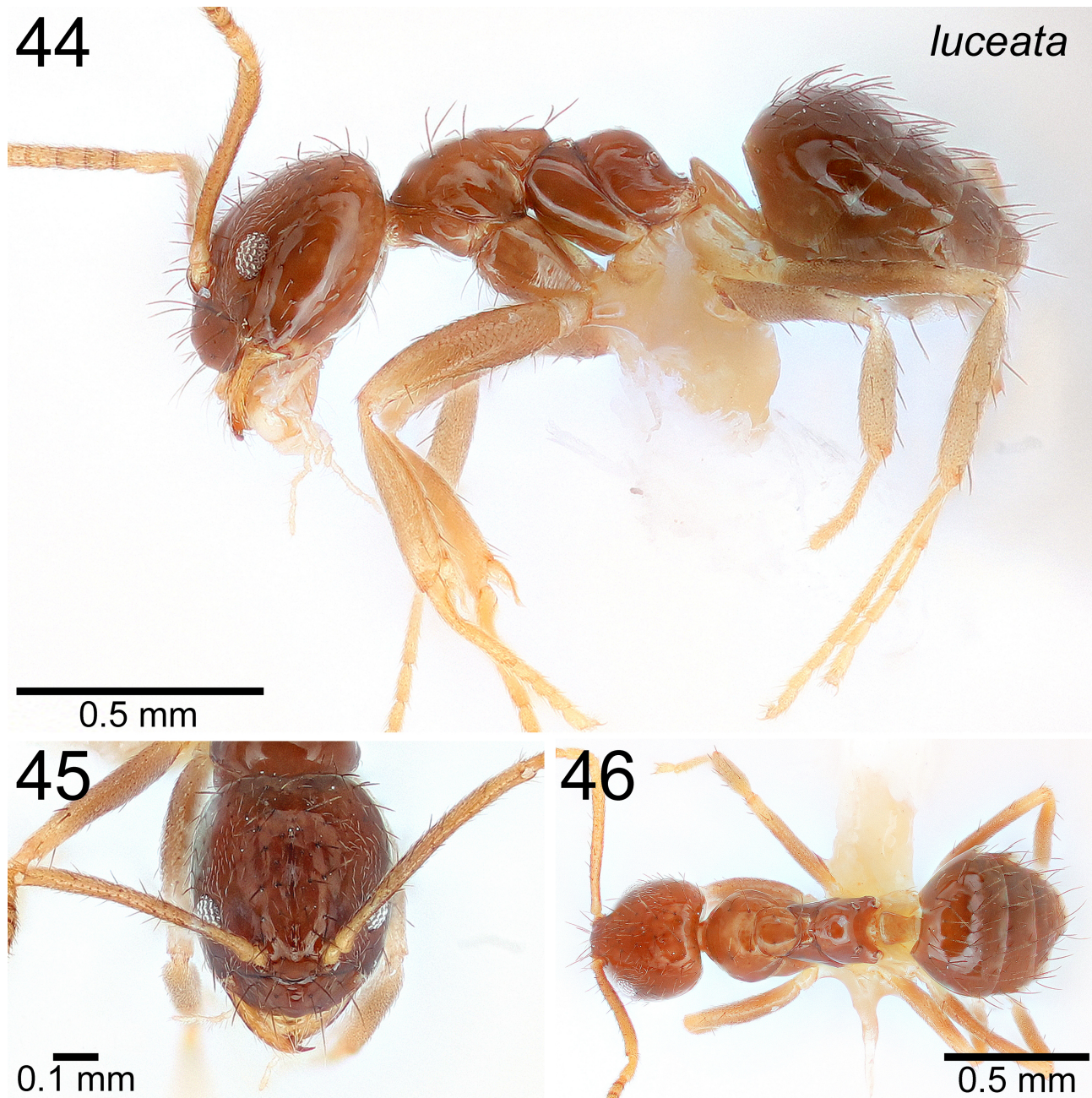
Holotype worker, **HONDURAS:** Cortés, PN Cusuco, 15.48572 -88.23746 ±60m, elev. 1210m, 31.v.2010, mesophyll forest, sifted litter, LLAMA#Wm-C-06-2-04 (USNM: USNMENT01131824). 5 paratype workers and 1 paratype queen with same locality data as holotype (USNM: USNMENT01131241, USNMENT01131816, USNMENT01131817, USNMENT01131867; MNCR: USNMENT01131821, USNMENT01131822).

Worker diagnosis: Antennae relatively short, with scapes surpassing posterior margin by less than a quarter of their length; light to medium reddish-brown and with meso- and metacoxae lighter than mesosoma; microsculpture and blue iridescence subtle, most visible on head; moderate cephalic pubescence.

Compare with: *N. contraria*, *N. lazulina*

WORKER. Measurements ($n=8$): TL: 1.71–2.24; EL: 0.09–0.11; EW: 0.08–0.09; IOD: 0.31–0.34; HE: 0.00–0.02; HL: 0.53–0.61; HW: 0.45–0.51; HLA: 0.18–0.21; HLP: 0.25–0.29; SL: 0.56–0.62; PW: 0.31–0.37; MW: 0.17–0.20; PrW: 0.24–0.28; PDH: 0.18–0.23; PTW: 0.11–0.13; LHT: 0.50–0.55; WL: 0.62–0.72; GL: 0.55–0.96;

SMC: 9–13; PMC: 2–4; MMC: 2–3. *Indices*: BLI: 131–146; CI: 83–87; EPI: 71–78; HTI: 106–112; REL: 17–19; SI: 119–129.

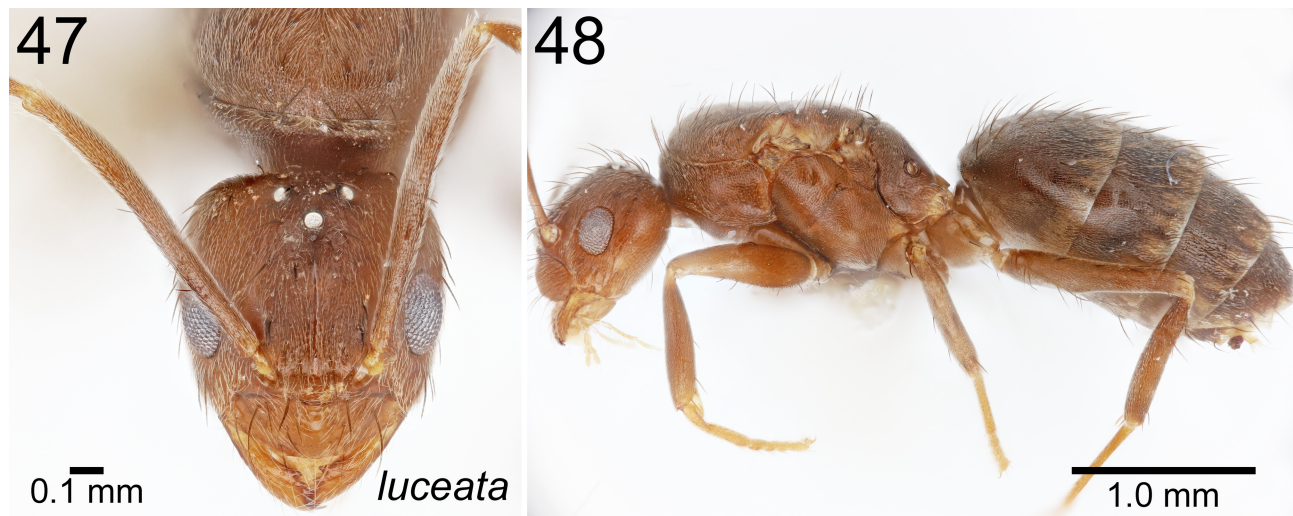


FIGURES 44–46. *Nylanderia luceata* holotype worker (USNMMENT01131824). Lateral, full-face, and dorsal view of the body.

Color: light to medium reddish-brown with antennae, mandibles, leg joints, and tarsi yellow to yellow-brown in contrast to body; meso- and metacoxae yellow to whitish and lighter than mesosoma; overall cuticle lightly microsculptured, resulting in subtle blue iridescence on head, mesosoma, and gaster. *Pilosity*: erect macrosetae on all parts of body thick, long, and dark; moderate cephalic pubescence, found laterally and concentrated around compound eyes; pubescence sparse to absent between compound eyes; mesosoma pubescence sparse to absent, limited at most to scattered hairs on pronotum and propodeum, and a fringe of hairs concentrated just posterior to the metanotal groove; gaster pubescence sparse to absent; pair of small, erect setae on apex of petiole. *Head*: longer than broad and quadrate with distinct posterolateral corners and flattened posterior margin, with slight to moderate medial emargination; scapes surpass posterior margin of head by less than a quarter of their length; compound eyes relatively small (REL:<19); median ocellus small, but often apparent; lateral ocelli absent or not apparent.

Mesosoma: posterior margin of pronotum forming obtuse angle with anterior margin of mesonotum in profile view; propodeum low and evenly rounded, with posterior face about same length as dorsal face.

QUEEN. *Measurements* ($n=1$): TL: 3.98; EL: 0.23; HL: 0.77; HW: 0.72; SL: 0.91; WL: 1.41; GL: 1.80. *Indices*: BLI: 183; CI: 94; REL: 30; SI: 126.



FIGURES 47–48. *Nylanderia luceata* paratype queen (USNMENT01131867). Full-face and lateral view of the body.

Relatively large. *Color*: uniformly medium reddish-brown. *Pilosity*: most body covered in moderate to dense pubescence; lacking pubescence on posterior face of propodeum; 1-2 small, erect setae on anepisternum.

Other material examined: **GUATEMALA**: San Marcos, Bojonal Road, 14.94786 -91.8837 \pm 50m, elev. 1618m, 4.vi.2015, cloud forest, leaf litter, R.S. Anderson #RSA2015-105; **MEXICO**: Chiapas, 5km NE Coapilla, 17.17602 -93.13293 \pm 300m, elev. 1990m, 25.v.2008, mesophil forest, leaf litter, LLAMA#Wm-A-04-1.

Etymology: The species epithet is derived from ‘luceo’ (L. = to shine).

Notes: *Nylanderia luceata* workers, like those of *N. lazulina* and *N. contraria*, have whitish meso- and metacoxae that strongly contrast with the color of the mesosoma. However, the body of *N. luceata* is lighter in overall color, its cuticle is much less microsculptured, and its blue iridescence is much more subtle than both of those species.. Unlike *N. contraria*, both this species and *N. lazulina* have only moderate cephalic pubescence, existing mostly as patches around the compound eyes and absent to sparse medially (Fig. 4B). Though subtle, the compound eyes of *N. luceata* are often slightly smaller than those of all other species in examined in this study. *Nylanderia luceata* is found in high elevation forests ranging from Chiapas in southern Mexico to the western edge of Honduras (Fig. 2B).

Nylanderia mendax, sp. nov.

Figs. 49–51 (worker)

Holotype worker, **GUATEMALA**: Zacapa, 2km SE La Unión, 14.95039 -89.27894 \pm 53m, elev. 1440m, cloud forest, sifted litter, 12.v.2009, cloud forest, sifted litter, LLAMA#Wm-B-03-1-04 (USNM: USNMENT01131331). 8 paratype workers with same locality data as holotype (USNM: USNMENT01131210, USNMENT01131328, USNMENT01131329, USNMENT01131330, USNMENT01131332; MNCR: USNMENT01131876, USNMENT01131877, USNMENT01131878).

Worker diagnosis: Antennae relatively long, with scapes surpassing posterior margin by nearly half their length; medium to dark reddish-brown with yellow to yellow-brown mandibles, antennae, and leg; meso- and metacoxae about same color or somewhat lighter than mesosoma; moderate to fine cuticular microsculpture resulting in moderate to strong blue iridescence on head, mesosoma, and gaster; erect setae on scapes long and dark, strongly contrasting with appressed pubescence; moderate cephalic pubescence; metatibiae relatively long (HTI > 125).

Compare with: *N. mosaica*, *N. usul*.

49

mendax

FIGURES 49–51. *Nylanderia mendax* holotype worker (USNMENT01131331). Lateral, full-face, and dorsal view of the body.

WORKER. *Measurements* ($n=6$): TL: 2.16–2.52; EL: 0.12–0.14; EW: 0.10–0.11; IOD: 0.32–0.35; HE: 0.00–0.01; HL: 0.59–0.63; HW: 0.48–0.53; HLA: 0.20–0.23; HLP: 0.24–0.28; SL: 0.70–0.75; PW: 0.36–0.40; MW: 0.19–0.21; PrW: 0.28–0.31; PDH: 0.19–0.26; PTW: 0.12–0.13; LHT: 0.64–0.68; WL: 0.77–0.83; GL: 0.71–1.07; SMC: 11–13; PMC: 2–3; MMC: 2. *Indices*: BLI: 151–160; CI: 82–85; EPI: 76–95; HTI: 127–134; REL: 20–23; SI: 140–146.

Color: medium to dark reddish-brown with yellow to yellow-brown mandibles, antennae, and leg joints; meso- and metacoxae about same color or somewhat lighter than mesosoma; overall cuticle moderately to finely microsculptured, resulting in moderate to strong blue iridescence on head, mesosoma, and gaster. *Pilosity*: erect macrosetae on scapes abundant, long, and dark, strongly contrasting with fine, appressed pubescence; moderate cephalic pubescence, found laterally and concentrated around compound eyes; pubescence sparse to absent between compound eyes; mesosoma pubescence sparse to absent, limited at most to scattered hairs on pronotum and

propodeum, and a fringe of hairs concentrated just posterior to the metanotal groove; gaster pubescence sparse to absent; pair of small, erect setae on apex of petiole. *Head*: longer than broad and quadrate with distinct posterolateral corners and flattened posterior margin, with little to no medial emargination; scapes long, surpassing posterior margin by nearly half their length; median ocellus small, but often apparent; lateral ocelli absent or not apparent. *Mesosoma*: promesonotal area evenly convex in profile view, with posterior margin of pronotum continuous or nearly continuous with anterior margin of mesonotum; propodeum low and evenly rounded, with posterior face at most slightly longer than dorsal face.

Etymology: The species epithet is derived from ‘*mendax*’ (L. = deceptive), referring to the species’ strong morphological similarity to *N. usul*.

Notes: *Nylanderia mendax* workers most strongly resemble those of *N. usul* and are also somewhat like those of *N. mosaica*. This species’ overall color, which is medium to dark reddish-brown, is much different than that of *N. mosaica*, which is overall yellow to yellow-brown with a medium to dark brown gaster. Both *N. usul* and *N. mendax* also tend to be larger in overall body size than *N. mosaica*. *Nylanderia mendax* is most readily separable from *N. usul* by the relative length of its scapes, which surpass the posterior margin of the head by nearly half their length. In *N. usul*, the scapes are much shorter, only surpassing the posterior margin by a quarter to a third of their length. *Nylanderia mendax* is known from only one locality in Zacapa, Guatemala (Fig. 2B), where it occurs in high elevation cloud forest.

Nylanderia mosaica, sp. nov.

Figs. 52–54 (worker); Figs. 55–56 (queen)

Holotype worker, **COSTA RICA**: Alajuela, 10km E of Monteverde, 10.30971 -84.72004, ±50m, elev. 890m, wet forest, sifted litter, 18.v.2014, J.T. Longino #JTL8692-s (USNM: USNMMENT01131335). 1 paratype worker and 1 paratype queen with same locality data as holotype (USNM: USNMMENT01130940, USNMMENT01131335). 3 paratype workers, **COSTA RICA**: San José, Cerro Plano, 9.48264 -83.96259 ±10m, elev. 1070m, 4.vii.2015, ridgetop cloud forest, isolated peak with oak trees, leaf litter, ADMAC#Wa-E-06-2-25 (MNCR: USNMMENT01131333, USNMMENT01131334, USNMMENT01131848).

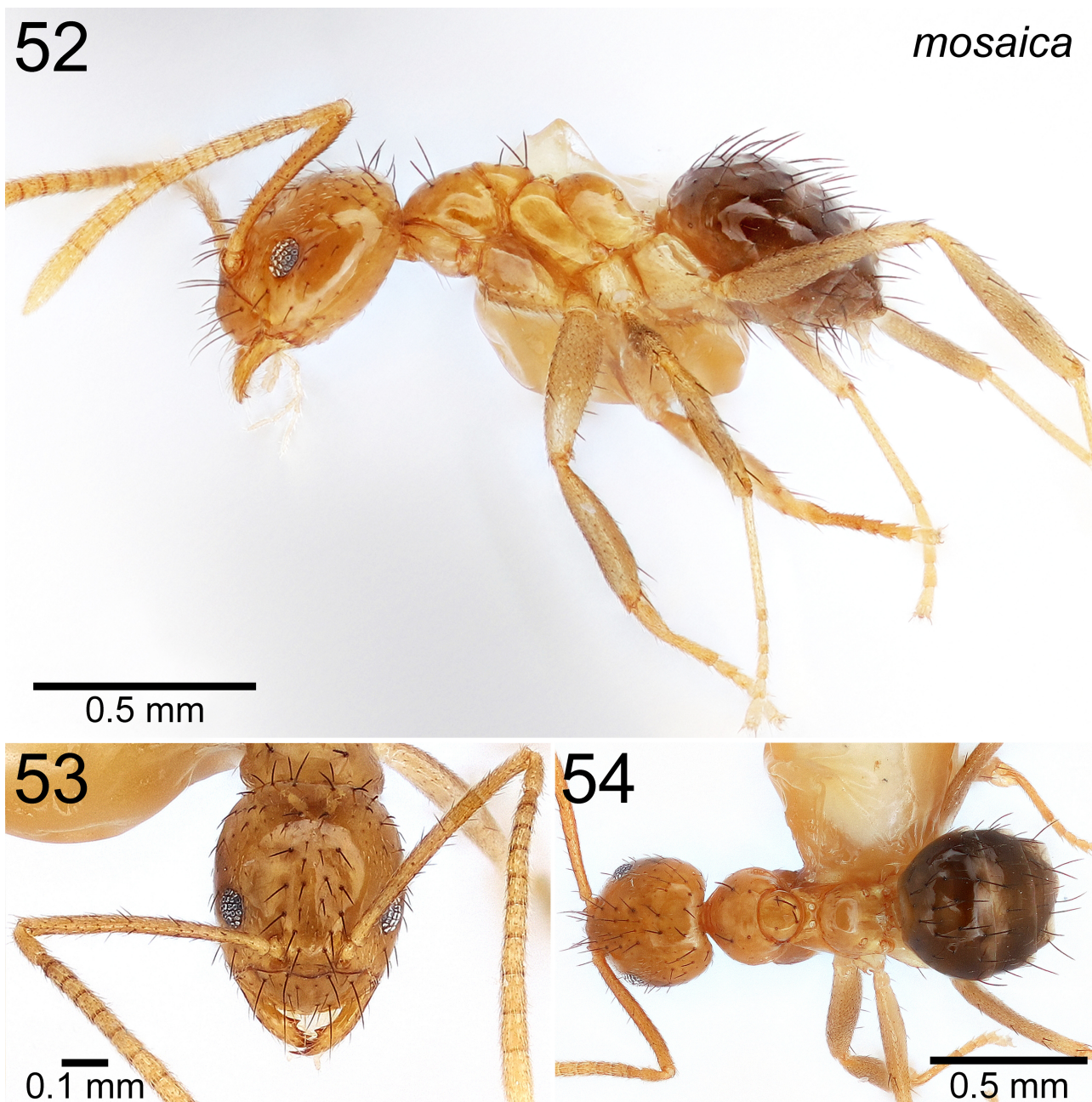
Worker diagnosis: Antennae relatively short, with scapes surpassing posterior margin by about a quarter of their length; bicolored, with yellow to yellow-brown head and mesosoma and medium to dark brown gaster; meso- and metacoxae yellow and at most somewhat lighter than mesosoma; light cuticular microsculpture resulting in subtle blue iridescence on head, mesosoma, and gaster; moderate cephalic pubescence.

Compare with: *N. mendax*, *N. usul*

WORKER. Measurements ($n=9$): TL: 1.70–2.01; EL: 0.09–0.12; EW: 0.07–0.10; IOD: 0.30–0.34; HE: 0.00–0.01; HL: 0.52–0.57; HW: 0.42–0.49; HLA: 0.18–0.20; HLP: 0.23–0.27; SL: 0.59–0.65; PW: 0.32–0.36; MW: 0.17–0.19; PrW: 0.24–0.28; PDH: 0.17–0.30; PTW: 0.10–0.14; LHT: 0.50–0.56; WL: 0.60–0.70; GL: 0.58–0.76; SMC: 9–12; PMC: 2–3; MMC: 2–3. **Indices:** BLI: 139–148; CI: 82–88; EPI: 72–81; HTI: 112–119; REL: 17–21; SI: 127–139.

Color: bicolored, with yellow to yellow-brown head and mesosoma and medium to dark brown gaster; black macrosetae strongly contrasting with overall color; meso- and metacoxae yellow and at most somewhat lighter than mesosoma; overall cuticle lightly microsculptured, resulting in subtle blue iridescence on head, mesosoma, and gaster. **Pilosity:** erect macrosetae on scapes abundant, long, and dark, strongly contrasting with fine, appressed pubescence; moderate cephalic pubescence, found laterally and concentrated around compound eyes; pubescence sparse to absent between compound eyes; mesosoma pubescence sparse to absent, limited at most to scattered hairs on pronotum and propodeum, and a fringe of hairs concentrated just posterior to the metanotal groove; gaster pubescence sparse to absent; pair of small, erect setae on apex of petiole. *Head*: longer than broad and quadrate with distinct posterolateral corners and flattened posterior margin, with little to no medial emargination; scapes surpass posterior margin of head by about a quarter of their length; all three ocelli absent or not apparent. *Mesosoma*: posterior margin of pronotum forming obtuse angle with anterior margin of mesonotum in profile view; propodeum low and evenly rounded, with posterior face about same length as dorsal face.

QUEEN. Measurements ($n=1$): TL: 3.51; EL: 0.21; HL: 0.68; HW: 0.68; SL: 0.80; WL: 1.29; GL: 1.54. **Indices:** BLI: 190; CI: 99; REL: 30; SI: 119.



FIGURES 52–54. *Nylanderia mosaica* holotype worker (USNMENT01131335). Lateral, full-face, and dorsal view of the body.

Moderately sized. *Color*: bicolored, with light yellow-brown mesosoma and medium to dark yellow-brown head and gaster; meso- and metacoxae concolorous with mesosoma. *Pilosity*: most of body covered in moderate to dense pubescence; lacking pubescence laterally on pronotum, on most of anepisternum except for dorsal edge, and posterior face of propodeum; 8-10 small, erect setae on anepisternum.

Other material examined: COSTA RICA: San José, Cerro Plano, 9.48264 -83.96259 ±10m, elev. 1070m, 4.vii.2015, ridgetop cloud forest, isolated peak with oak trees, leaf litter, ADMAC#Wa-E-06-2-25; Cartago, PN Tapantí, 9.73699 -83.78176 ±20m, elev. 1330m, 6.vi.2015, cloud forest, old 2nd growth, riparian, leaf litter, ADMAC#Wm-E-01-1-02.

Etymology: The species epithet is derived from ‘*musaicum*’ (L. = mosaic), referring to this species’ bicolored appearance.



FIGURES 55–56. *Nylanderia mosaica* paratype queen (USNMMENT01131336). Full-face and lateral view of the body.

Notes: *Nylanderia mosaica* workers most strongly resemble those of *N. mendax* and *N. usul* in appearance, though *N. mosaica* workers are easily separable based on their relatively small body size and bicolored appearance, with a yellow to yellow-brown head and mesosoma and medium to dark brown gaster. This species is only known to moderate to high elevation forests in Costa Rica (Fig. 2B), where it is sympatric with only *N. usul* and no other species in American Clade I.

***Nylanderia polita*, sp. nov.**

Figs. 57–59 (worker); Figs. 60–61 (queen)

Holotype worker, **MEXICO:** Veracruz, 8km WSW of Xalapa, 19.52081 -96.9917 ±20m, elev. 1530m, cloud forest, leaf litter (MiniWinkler), 22.vi.2016, ADMAC#Wa-F-05-1-41 (USNM: USNMMENT01131180); 4 paratype workers with same locality data as holotype (USNM: USNMMENT01131313, USNMMENT01131314; MNCR: USNMMENT01131315, USNMMENT01131316). 1 paratype queen, **MEXICO:** Veracruz, 8km WSW of Xalapa, 19.52283 -96.99102 ±20m, elev. 1500m, cloud forest, leaf litter (MiniWinkler), 22.vi.2016, ADMAC#Wa-F-05-2-31 (USNM: USNMMENT01131789).

Worker diagnosis: Antennae relatively short, with scapes surpassing posterior margin of head by about a third of their length; medium to dark brown with antennae, mandibles, leg joints, and tarsi yellow in contrast to body; meso- and metacoxae somewhat lighter than mesosoma; entire cuticle smooth and shiny, with microsculpture, and completely lacking blue iridescence; dense cephalic pubescence; posterior margin of head with little to no emargination.

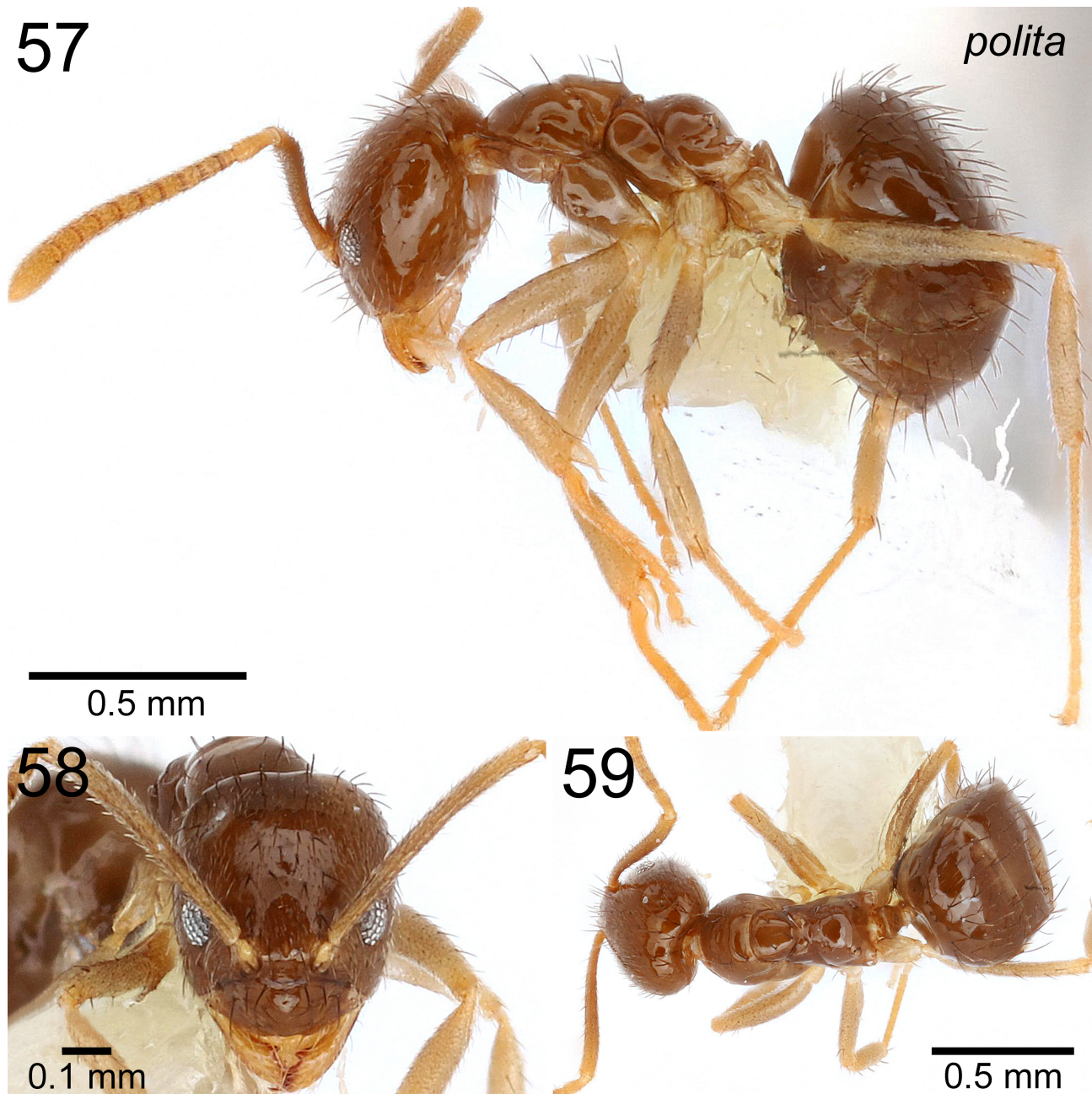
Compare with: *N. austroccidua*, *N. contraria*

WORKER. Measurements ($n=10$): TL: 1.81–2.13; EL: 0.09–0.12; EW: 0.08–0.10; IOD: 0.29–0.32; HE: 0.01; HL: 0.52–0.58; HW: 0.44–0.49; HLA: 0.18–0.20; HLP: 0.26–0.28; SL: 0.31–0.35; PW: 0.31–0.35; MW: 0.17–0.20; PrW: 0.24–0.32; PDH: 0.17–0.22; PTW: 0.09–0.16; LHT: 0.49–0.53; WL: 0.59–0.68; GL: 0.64–0.94; SMC: 7–10; PMC: 2–3; MMC: 2. **Indices:** BLI: 130–149; CI: 79–86; EPI: 67–72; HTI: 109–116; REL: 18–22; SI: 122–129.

Color: medium to dark brown with yellow to yellow-brown antennae, mandibles, and tarsi; meso- and metacoxae often somewhat lighter than mesosoma but sometimes concolorous; overall cuticle smooth and shiny, with no cuticular microsculpture and no blue iridescence **Pilosity:** dense cephalic pubescence covering all surfaces of head in full-face view; mesosoma pubescence sparse to absent, limited at most to scattered hairs on pronotum and propodeum, and a fringe of hairs concentrated just posterior to the metanotal groove; gaster pubescence sparse to absent; pair of small, erect setae on apex of petiole. **Head:** longer than broad and quadrate with distinct posterolateral corners and flattened posterior margin, with little to no medial emargination; scapes surpass posterior margin of head by about a third of their length; median ocellus small, but often apparent; lateral ocelli absent or not apparent.

Mesosoma: posterior margin of pronotum forming obtuse angle with anterior margin of mesonotum in profile view; propodeum evenly rounded with dorsal face about as long as posterior face.

QUEEN. *Measurements* ($n=1$): TL: 3.19; EL: 0.16; HL: 0.64; HW: 0.61; SL: 0.63; WL: 1.02; GL: 1.53. *Indices*: BLI: 160; CI: 96; REL: 25; SI: 102.



FIGURES 57–59. *Nylanderia polita* holotype worker (USNMENT01131180). Lateral, full-face, and dorsal view of the body.

Moderately sized. *Color*: medium to dark brown, with meso- and metacoxae lighter than mesosoma. *Pilosity*: most of body covered in moderate to dense pubescence; lacking pubescence on posterior face of propodeum; 1-2 small, erect setae on anepisternum.

Other material examined: MEXICO: Veracruz, Las Cañadas, 19.1906 -96.99055 ±60m, 1390m, 1.vii.2016, montane wet forest, baiting, ADMAC#Ba-F-07-1-04-11; Veracruz, 8km WSW Xalapa, 19.52177 -96.99121 ±20m, elev. 1500m, 22.vi.2016, cloud forest, sifted litter, ADMAC#Wa-F-05-1-09; Veracruz, 8km WSW Xalapa, 19.52165 -96.99137 ±20m, elev. 1510m, 22.vi.2016, cloud forest, sifted litter, ADMAC#Wa-F-05-1-13; Veracruz, 8km WSW Xalapa, 19.52181 -96.9906 ±20m, elev. 1500m, 22.vi.2016, cloud forest, sifted litter, ADMAC#Wa-F-05-2-07; Veracruz, 8km WSW Xalapa, 19.52275 -96.99098 ±20m, elev. 1500m, 22.vi.2016, cloud forest, sifted litter,

ADMAC#Wa-F-05-2-29; Veracruz, 8km WSW Xalapa, 19.52283 -96.99102 ±20m, elev. 1500m, 22.vi.2016, cloud forest, sifted litter, ADMAC#Wa-F-05-2-31; Veracruz, 8km WSW Xalapa, 19.5236 -96.99123 ±20m, elev. 1500m, 22.vi.2016, cloud forest, sifted litter, ADMAC#Wa-F-05-2-50.



FIGURES 60–61. *Nylanderia polita* paratype queen (USNMENT01131789). Full-face and lateral view of the body.

Etymology: The species epithet is derived from ‘*politus*’ (L. = polished), referring to the smooth, shining appearance of the species’ cuticle.

Notes: *Nylanderia polita* workers most strongly resemble those of *N. austroccidua* and *N. contraria* but are easily separable from the latter two by their overall smooth cuticle with no microsculpture and complete lack of blue iridescence. Unlike *N. austroccidua*, this species has an evenly rounded propodeum with the posterior face about as long as the dorsal face in profile view. Unlike *N. contraria*, the meso- and metacoxae of *N. polita* are never whitish and at most only somewhat lighter in color than the mesosoma. The known range of this species is limited only to high elevation forests in Veracruz, Mexico (Fig. 2B).

Nylanderia usul, sp. nov.

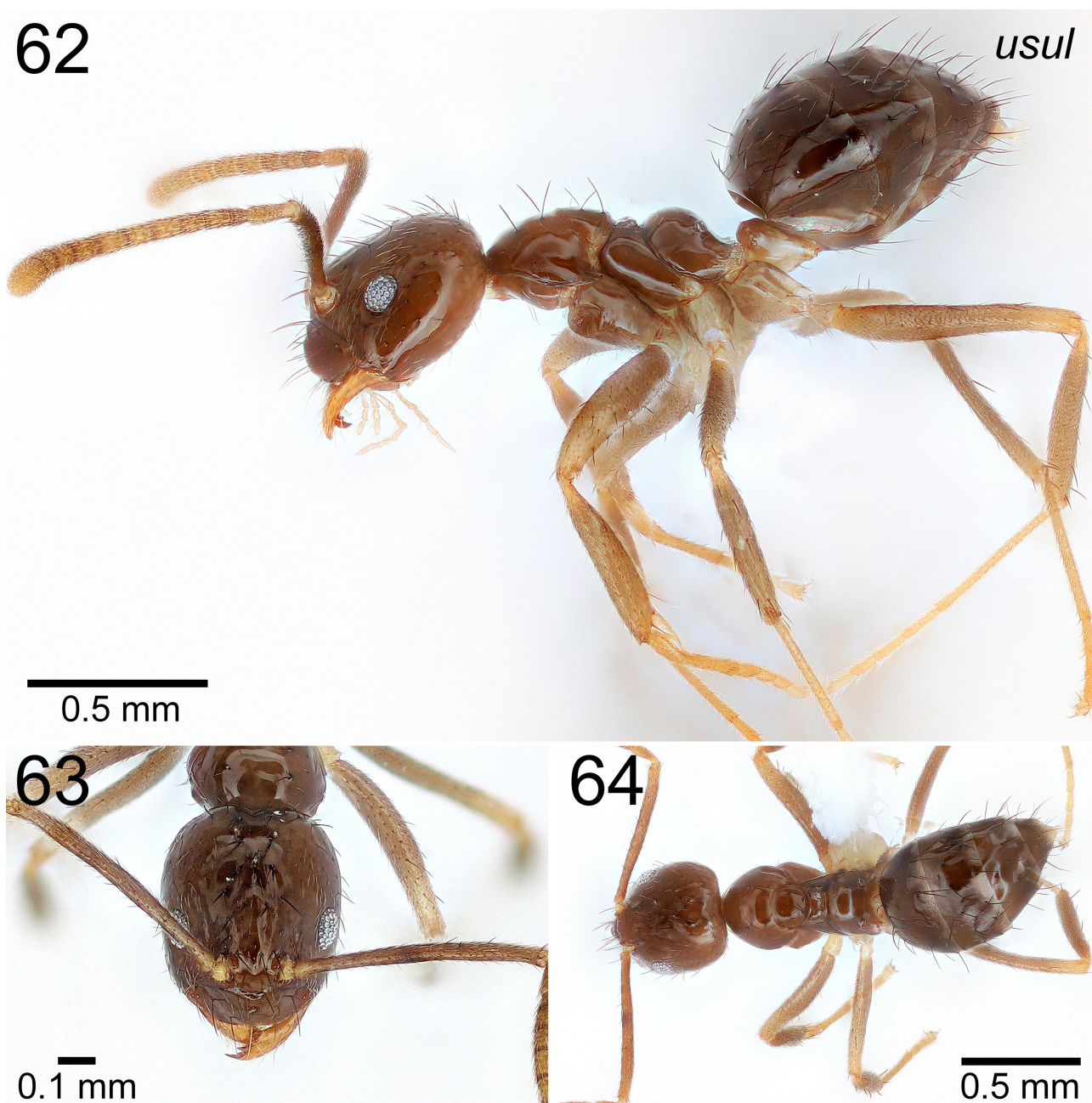
Figs. 62–64 (worker); Figs. 65–66 (queen); Figs. 67–70 (male)

Holotype worker, **COSTARICA**: San José, 11km SSE Santa María, 9.55301 -83.94523 ±10m, elev. 1950m, 24.vi.2015, cloud forest, sifted litter, ADMAC#Wa-E-04-1-49 (USNM: USNMENT01131798). 5 paratype workers, 1 paratype queen, and 1 paratype male with same locality data as holotype (USNM: USNMENT01131109, USNMENT01131799, USNMENT01131800, USNMENT01131819, USNMENT01131831; MNCR: USNMENT01131802, USNMENT01131804).

Worker diagnosis: Antennae relatively short, with scapes surpassing posterior margin by about a quarter to a third of their length; color variable from yellow to dark brown, with meso- and metacoxae at most somewhat lighter than mesosoma; fine cuticular microsculpture resulting in moderate to strong blue iridescence on head, mesosoma, and gaster; moderate to dense cephalic pubescence; propodeum high and evenly rounded, with posterior face steep and at most slightly longer than dorsal face.

Compare with: *N. mendax*, *N. mosaica*

WORKER. Measurements ($n=11$): TL: 2.00–2.35; EL: 0.11–0.13; EW: 0.08–0.10; IOD: 0.32–0.39; HE: 0.01–0.02; HL: 0.58–0.65; HW: 0.47–0.53; HLA: 0.18–0.23; HLP: 0.27–0.30; SL: 0.65–0.74; PW: 0.36–0.40; MW: 0.18–0.21; PrW: 0.26–0.32; PDH: 0.18–0.27; PTW: 0.13–0.15; LHT: 0.58–0.69; WL: 0.69–0.80; GL: 0.70–0.94; SMC: 9–12; PMC: 2–3; MMC: 2–3. **Indices:** BLI: 144–154; CI: 81–84; EPI: 67–80; HTI: 113–131; REL: 18–21; SI: 128–140.



FIGURES 62–64. *Nylanderia usul* holotype worker (USNMENT01131798). Lateral, full-face, and dorsal view of the body.

Color: variable, from yellow to dark brown; darker specimens often with yellow to yellow-brown mandibles and leg joints; in darker specimens, meso- and metacoxae somewhat lighter than mesosoma; overall cuticle moderately to finely microsculptured, resulting in moderate to strong blue iridescence on head, mesosoma, and gaster. *Pilosity*: moderate to dense cephalic pubescence; mesosoma pubescence sparse to absent, limited at most to scattered hairs on pronotum and propodeum, and a fringe of hairs concentrated just posterior to the metanotal groove; gaster pubescence sparse to absent; pair of small, erect setae on apex of petiole. *Head*: longer than broad and quadrate with distinct posterolateral corners and flattened posterior margin, with moderate medial emargination; scapes surpass posterior margin of head by about a quarter to a third of their length; median ocellus small, but often apparent; lateral ocelli absent or not apparent. *Mesosoma*: promesonotal area evenly convex in profile view, with posterior margin of pronotum continuous or nearly continuous with anterior margin of mesonotum; propodeum high and evenly rounded, with posterior face steep and at most slightly longer than dorsal face.



FIGURES 65–66. *Nylanderia usul* paratype queen (USNMENT01131819). Full-face and lateral view of the body.

QUEEN. *Measurements* ($n=1$): TL: 3.73; EL: 0.19; HL: 0.72; HW: 0.69; SL: 0.86; WL: 1.44; GL: 1.58. *Indices*: BLI: 200; CI: 97; REL: 26; SI: 125.

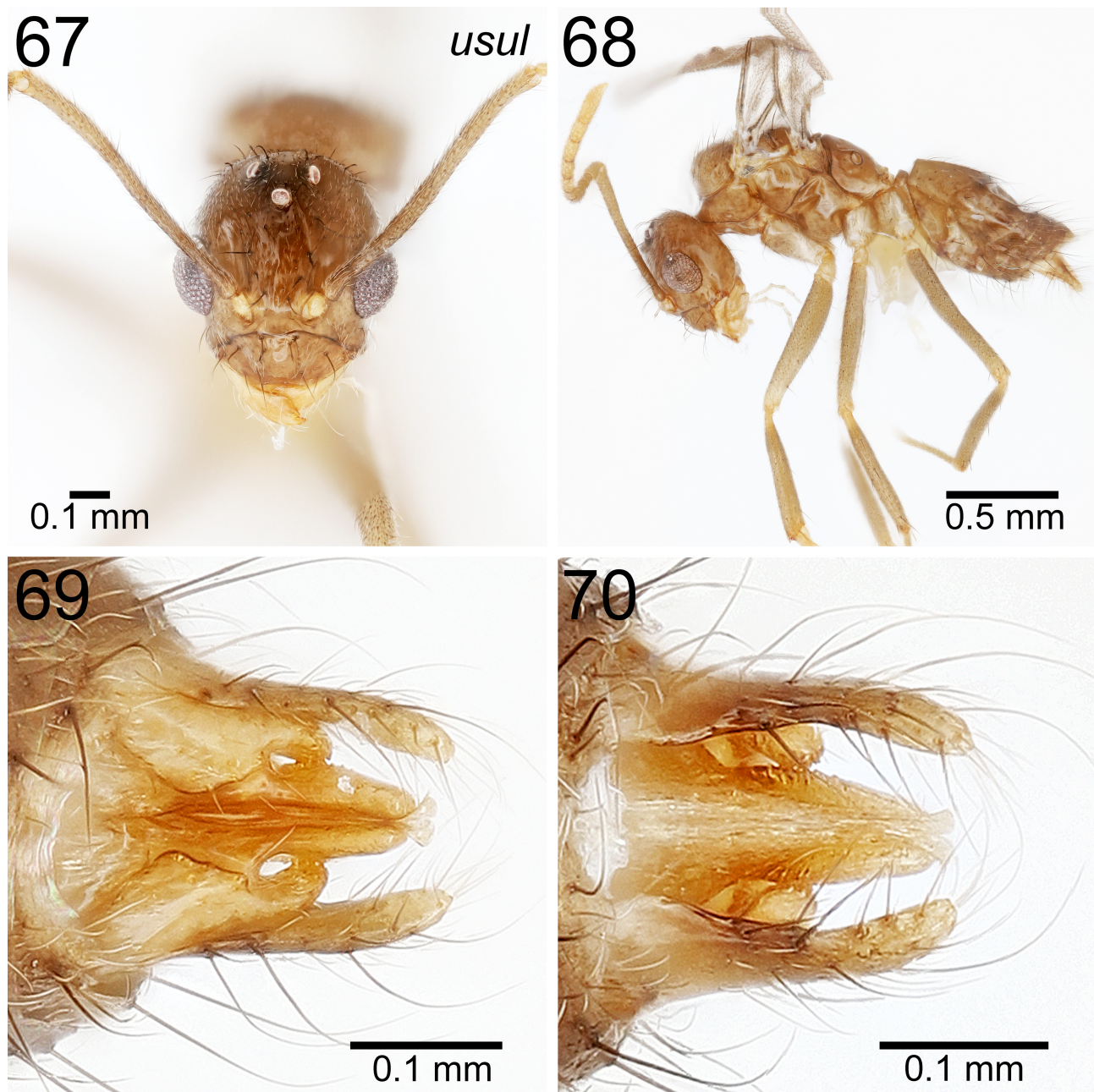
Relatively large. *Color*: medium to dark brown, with meso- and metacoxae at most somewhat lighter than mesosoma. *Pilosity*: most of body covered in moderate to dense pubescence; pubescence sparse to absent laterally on pronotum, sparse on most of anepisternum, absent on dorsal half of katepisternum, and absent on posterior face of propodeum; 4–5 small, erect setae on anepisternum.

MALE. *Measurements* ($n=1$): TL: 2.20; EL: 0.18; HL: 0.53; HW: 0.46; SL: 0.70; WL: 0.82; GL: 0.85. *Indices*: BLI: 180; CI: 86; REL: 34; SI: 154.

Color: medium brown with yellow mandibles; meso- and metacoxae lighter than mesosoma. *Pilosity*: dense pubescence on head, mesoscutum, and mesoscutellum; pubescence sparse to absent on pronotum, anepisternum, katepisternum, propodeum, and gaster; 1–2 small, erect setae on anepisternum. *Head*: as broad as long; compound eyes surpass lateral margins of head in full-face view; scapes curve sinuously and surpass posterior margin of head by about a third of their length. *Mesosoma*: In profile view, propodeum gently curved with dorsal face somewhat longer than posterior face. *Genitalia*: gonopod long, narrow, and evenly triangular to weakly digitiform, with apex tapered and coming to a point (Fig. 71); in ventral view, ventromedial edge of basivolsella unevenly bracket-shaped and crenate, with edge at base of cuspis forming a right angle (Fig. 69); gonosticulus straight and nearly three times longer than cuspis.

Other material examined: COSTA RICA: Heredia, 16km SSE La Virgen, 10.26667 -84.08333 ±m, elev. 1100m, 8.ii.2001, montane wet forest, leaf litter, ALAS#11/B/all; Heredia, 16km SSE La Virgen, 10.26863 -84.08287 ±200m, elev. 1110m, 14.iii.2001, montane wet forest, leaf litter, ALAS#11/WF/02; Heredia, 16km SSE La Virgen, 10.26863 -84.08287 ±200m, elev. 1110m, 14.iii.2001, montane wet forest, leaf litter, ALAS#15/WF/02; Puntarenas, Monteverde, 10.30327 -84.81099 ±50m, elev. 1400m, 6.i.2020, moist forest, leaf litter, J.T. Longino #JTL10993-s; Puntarenas, Monteverde, 10.30259 -84.79269 ±50m, elev. 1590m, 13.v.2014, cloud forest, leaf litter, J.T. Longino #JTL8625-s; Puntarenas, Monteverde, 10.28987 -84.79322 ±50m, elev. 1310m, 13.v.2014, moist forest, leaf litter, J.T. Longino #JTL8631-s; Puntarenas, Monteverde, 10.28744 -84.79266 ±50m, elev. 1180m, 13.v.2014, moist forest, leaf litter, J.T. Longino #JTL8632-s; Alajuela, 5km E Monteverde, 10.29824 -84.78163 ±50m, elev. 1495m, 18.v.2014, cloud forest, leaf litter, J.T. Longino #JTL8698-s; San José, 7.5km SSE Santa María de Dota, 9.58689 -83.94758 ±50m, elev. 1520m, 27.v.2014, 2nd growth cloud forest, leaf litter, T. Sumnicht & J.T. Longino #JTL8704-s; San José, 11km SSE Santa María, 9.55387 -83.94547 ±10m, elev. 1940m, 24.vi.2015, cloud forest, leaf litter, ADMAC#Wa-E-04-1-21; San José, 11km SSE Santa María, 9.55378 -83.94551 ±10m, elev. 1940m, 24.vi.2015, cloud forest, leaf litter, ADMAC#Wa-E-04-1-24; San José, 11km SSE Santa María, 9.55296 -83.94551 ±10m, elev. 1940m, 24.vi.2015, cloud forest, leaf litter, ADMAC#Wa-E-04-1-42; San José, 8km SSE Santa María, 9.58425 -83.94826 ±20m, elev. 1580m, 23.vi.2015, cloud forest, leaf litter, ADMAC#Wm-E-04-1-02; San José, 8km SSE Santa María, 9.57877 -83.95085 ±20m, elev. 1620m, 25.vi.2015, cloud forest, leaf litter, ADMAC#Wm-E-04-1-

06; San José, 9km SSE Santa María, 9.56191 -83.94807 ±20m, elev. 1830m, 25.vi.2015, cloud forest, leaf litter, ADMAC#Wm-E-04-1-09; San José, 10km SSE Santa María, 9.55908 -83.94646 ±20m, elev. 1870m, 25.vi.2015, cloud forest, leaf litter, ADMAC#Wm-E-04-1-10.



FIGURES 67–70. *Nylanderia usul* paratype male (USNMENT01131831). Full-face and lateral view of the body; ventral and dorsal view of the genital capsule.

Etymology: The species epithet is derived from Frank Herbert’s science fiction novel *Dune*. In the novel, “Usul” is the secret name given to the protagonist, Paul Atreides, by the Fremen, the desert dwellers of the planet Arrakis. This name references the species’ moderate to intense blue iridescence, alluding to the “blue-within-blue” eyes that Paul acquires after joining the Fremen and consuming the spice melange. The term “Usul” translates to “the strength of the base of the pillar” and is derived from the Arabic word *usul*, the plural form of *asl*, which means “origin,” “root,” or “principle.”

Notes: *Nylanderia usul* workers most strongly resemble those of *N. mendax* and *N. mosaica*. This species is most readily separable from *N. mendax* by its relatively short scapes, which only surpass the posterior margin of the head by a quarter to a third of their length, whereas in *N. mendax* they surpass the posterior margin by nearly half

their length. There are two distinct color morphs of this species. The dark form is dark brown with yellow to yellow-brown mandibles and tarsi, meso- and metacoxae somewhat lighter than the mesosoma, and has moderate cephalic pubescence, concentrated mostly as patches around the compound eyes (Fig. 4B). The light form is uniformly yellow, with dense cephalic pubescence (Fig. 4A). The light form is more likely to be confused with *N. mosaica*, but the latter is smaller in overall size and bicolored with a yellow to yellow-brown head and mesosoma and medium to dark brown gaster. Interestingly, the light form, represented by NT002, NT003, NT020, and NT024 in the phylogeny (Fig. 3), resolved as paraphyletic with respect to the dark form. This pattern may indicate a case of incipient speciation, in which one is beginning to diverge from the other but has not yet achieved full reproductive isolation. Consequently, the two forms may be interpretable as two distinct species based on their morphology. However, for now we conservatively treat them all as a single species. If someday these two forms are split into separate species, the dark form will keep the name *N. usul* and the light form will take a new name. *Nylanderia usul* is only known from moderate to high elevation forests in Costa Rica (Fig. 2B), where it is sympatric with only *N. mosaica* and no other species in American Clade I.

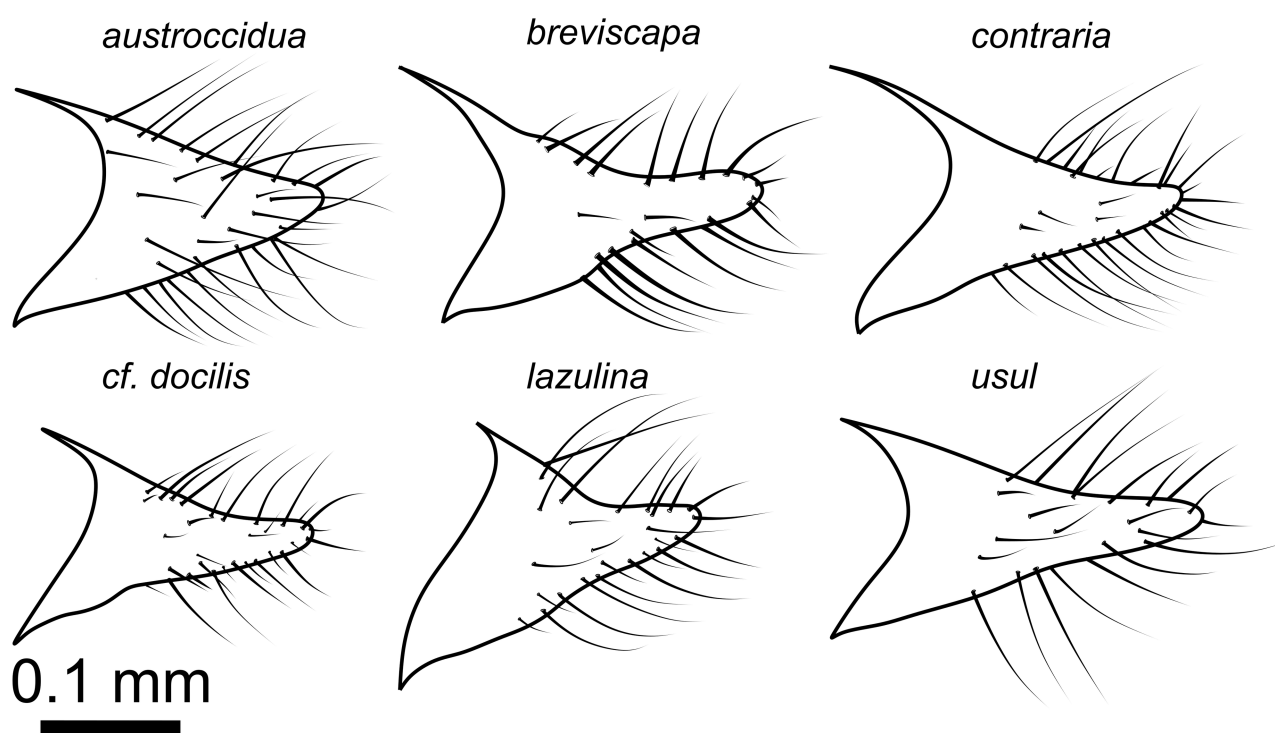


FIGURE 71. Line drawings of male gonopods of *N. austroccidua*, *N. breviscapa*, *N. contraria*, *N. cf. docilis*, *N. lazulina*, and *N. usul*.

Discussion

We used a combination of evidence from phylogenomics, morphology, and geographic distributions to reconstruct phylogeny of a major American clade of *Nylanderia*—clade AC1—and describe eight new species within. *Nylanderia* is a rapidly and recently radiated and diverse genus of ants, with two distantly related clades (AC1 and AC2) representing two independent dispersals to the Americas within the last 30 million years (Williams *et al.* 2020). Genera of ants that have rapidly and recently radiated across large geographic areas present significant challenges to taxonomy, complicating species identification and delimitation due to the emergence of cryptic species and the prevalence of homoplasious traits that obscure evolutionary relationships among divergent lineages. Other similar examples of rapid and recent radiations of ant lineages in the Americas, where studies have led to the discovery and description of new species, include *Dorymyrmex* (Oberski 2022), *Sericomyrmex* (Ješovnik *et al.* 2017), and *Strumigenys* (Booher 2021).

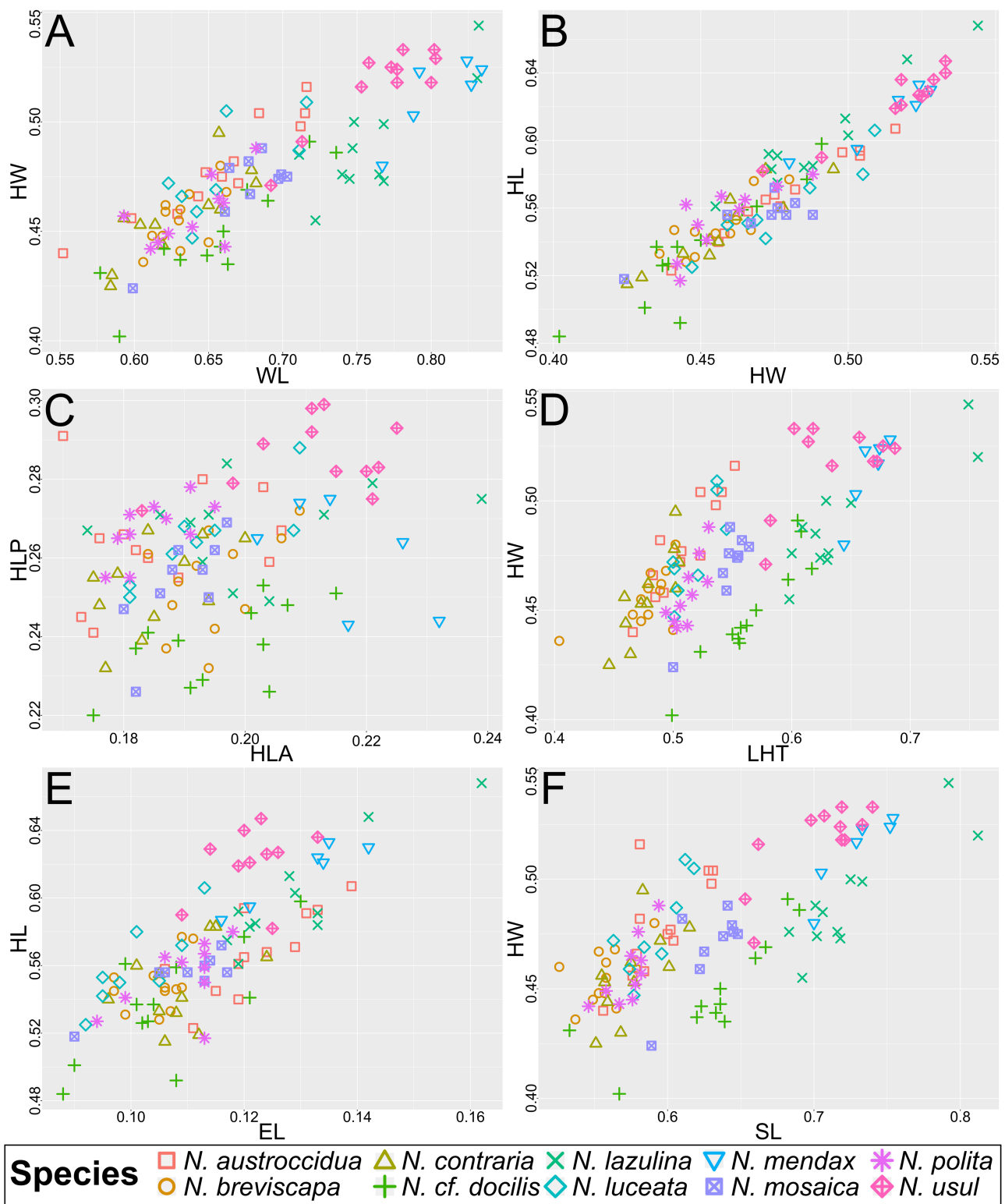


FIGURE 72. Bivariate plots of measurements: (A) Body Length Index (WL/HW), (B) Cephalic Index (HW/HL), (C) Eye Position Index (HLA/HLP), (D) Hind Tibia Index (LHT/HW), (E) Relative Eye Length (EL/HL), and (F) Scape Index (SL/HW).

Clade AC2 represents an exclusively Neotropical lineage. However, we now provide evidence of a previously unknown Neotropical lineage, which is most closely related to the Nearctic subclade of clade AC1. This newly identified lineage of Neotropical *Nylanderia* represents a significant piece of biodiversity across southern Mexico

and Mesoamerica, ‘hidden’ under the guise of what was once considered intraspecific variation within the single species *N. austroccidua*. This subclade alone comprises at least seven species, six of which are formally described here. In addition to these six species, we also describe two more that strongly resemble *N. austroccidua* but belong to the Nearctic subclade of clade AC1.

The previously undiscovered diversity within this lineage exemplifies the broader richness and complexity of the genus, which, though not immediately apparent, becomes evident upon detailed examination. By integrating molecular data with morphological analysis, we have been able to more accurately delimit species boundaries. Our phylogenomic analyses provide a robust framework for classification based on topology and node support, while morphological taxonomic characters enable us to make universal diagnoses and contingent statements regarding worker, queen, and male specimens. This dual approach has revealed hidden diversity that might otherwise have gone unrecognized. Many species within this group inhabit regions that are increasingly threatened by habitat loss due to forest conversion, agricultural expansion, urban encroachment, and climate change. A more comprehensive understanding of these and other poorly characterized species, facilitated by molecular insights, is essential for effective biodiversity conservation in vulnerable areas worldwide. We hope that this taxonomic contribution to a major American clade of *Nylanderia* species enhances the identification and protection of this diversity.

Acknowledgments

We thank Drs. Jack T. Longino, Robert S. Anderson, and Milan Janda for providing most of the specimens used in this study. We also thank Dr. Thiago S. R. da Silva and one anonymous reviewer for their insightful feedback, which helped improve the clarity and rigor of this manuscript. Computational resources (‘HiPerGator’) for molecular bioinformatics were provided by University of Florida Research Computing (<http://researchcomputing.ufl.edu>). This study was supported by the National Science Foundation (NSF) under grant DEB-2026772. Additional funding for JFW was awarded by the UF University Scholars Program.

References

- AntWeb (2024) Available from: <http://www.antweb.org> (accessed 15 October 2024)
- Bankevich, A., Nurk, S., Antipov, D., Gurevich, A.A., Dvorkin, M., Kulikov, A.S., Lesin, V.M., Nikolenko, S.I., Pham, S., Prjibelski, A.D., Pyshkin, A.V., Sirotkin, A.V., Vyahhi, N., Tesler, G., Alekseyev, M.A. & Pevzner, P.A. (2012) SPAdes: A new genome assembly algorithm and its applications to single-cell sequencing. *Journal of Computational Biology*, 19, 455–477.
<https://doi.org/10.1089/cmb.2012.0021>
- Bolton, B. (2024) An online catalog of the ants of the world. Available from: <http://antcat.org> (accessed 7 March 2024)
- Booher, D.B. (2021) The ant genus *Strumigenys* Smith, 1860 (Hymenoptera: Formicidae) in western North America North of Mexico. *Zootaxa*, 5061 (2), 201–248.
<https://doi.org/10.11646/zootaxa.5061.2.1>
- Borowiec, M. (2016) AMAS: A fast tool for alignment manipulation and computing of summary statistics. *PeerJ*, 4, e1660.
<https://doi.org/10.7717/peerj.1660>
- Borowiec, M. (2019) Spruceup: fast and flexible identification, visualization, and removal of outliers from large multiple sequence alignments. *Journal of Open Source Software*, 4 (42), 1635.
<https://doi.org/10.21105/joss.01635>
- Castresana, J. (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution*, 17, 540–552.
- Emery, C. (1906) Note sur *Prenolepis vividula* Nyl. et sur la classification des espèces du genre *Prenolepis*. *Annales de la Société Entomologique de Belgique*, 50, 130–134.
- Faircloth, B.C. (2015) PHYLUCE is a software package for the analysis of conserved genomic loci. *Bioinformatics* 32, 786–788.
<https://doi.org/10.1093/bioinformatics/btv646>
- Forel, A. (1908) Ameisen aus Sao Paulo (Brasilien), Paraguay etc. gesammelt von Prof. Herm. v. Ihering, Dr. Lutz, Dr. Fiebrig, etc. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien*, 58, 340–418.
- Forel, A. (1922) Glanures myrmécologiques en 1922. *Revue suisse de zoologie*, 30, 87–102.
<https://doi.org/10.5962/bhl.part.144519>
- Guénard, B., Weiser, M.D., Gómez, K., Narula, N. & Economo, E.P. (2017) The Global Ant Biodiversity Informatics (GABI)

- database: Synthesizing data on the geographic distribution of ant species (Hymenoptera: Formicidae). *Myrmecological News*, 24, 83–89.
- Guindon, S., Dufayard, J.F., Lefort, V., Anisimova, M., Hordijk, W. & Gascuel, O. (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. *Systematic Biology*, 59, 307–321. <https://doi.org/10.1093/sysbio/syq010>
- Hoang, D.T., Chernomor, O., Haeseler, A.V., Minh, B.Q. & Vinh, L.S. (2017) UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, 35, 518–522. <https://doi.org/10.5281/zenodo.854445>
- Ješovnik, A., Sosa-Calvo, J., Lloyd, M.W., Branstetter, M.G., Fernández, F. & Schultz, T.R. (2017) Phylogenomic species delimitation and host-symbiont coevolution in the fungus-farming ant genus *Sericomyrmex* Mayr (Hymenoptera: Formicidae): Ultraconserved elements (UCEs) resolve a recent radiation. *Systematic Entomology*, 42, 523–542. <https://doi.org/10.1111/syen.12228>
- Kallal, R.J. & LaPolla, J.S. (2012) Monograph of *Nylanderia* (Hymenoptera: Formicidae) of the World, Part II: *Nylanderia* in the Nearctic. *Zootaxa*, 3508 (1), 1–64. <https://doi.org/10.11646/zootaxa.3508.1.1>
- Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K.F., Von Haeseler, A. & Jermini, L.S. (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods*, 14, 587–589. <https://doi.org/10.1038/nmeth.4285>
- Katoh, K. & Standley, D.M. (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution*, 30 (4), 772–780. <https://doi.org/10.1093/molbev/mst010>
- Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T. & Calcott, B. (2017) Partitionfinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution*, 34, 772–773. <https://doi.org/10.1093/molbev/msw260>
- LaPolla, J.S., Brady, S.G. & Shattuck, S.O. (2010) Phylogeny and taxonomy of the *Prenolepis* genus-group of ants (Hymenoptera: Formicidae). *Systematic Entomology*, 35, 118–131. <https://doi.org/10.1111/j.1365-3113.2009.00492.x>
- LaPolla, J.S., Brady, S.G. & Shattuck, S.O. (2011) Monograph of *Nylanderia* (Hymenoptera: Formicidae) of the World: Introduction. *Zootaxa*, 3110 (1), 1–9. <https://doi.org/10.11646/zootaxa.3110.1.1>
- Longino, J.T. & Anderson, R.S. (2008) *Leaf Litter Arthropods of Mesoamerica: LLAMA*. Available from: <https://archives.evergreen.edu/webpages/projects/llama/> (accessed 19 November 2024)
- Longino, J.T. & Branstetter, M.G. (2019) The truncated bell: an enigmatic but pervasive elevational diversity pattern in Middle American ants. *Ecography*, 42, 272–283. <https://doi.org/10.1111/ecog.03871>
- Longino, J.T., Branstetter, M.G. & Colwell, R.K. (2014) How Ants Drop Out: Ant Abundance on Tropical Mountains. *PLoS ONE*, 9, e104030. <https://doi.org/10.1371/journal.pone.0104030>
- Longino, J.T. & Colwell, R.K. (2011) Density compensation, species composition, and richness of ants on a neotropical elevational gradient. *Ecosphere*, 2, Art29. <https://doi.org/10.1890/ES10-00200.1>
- Messer, S.J., Cover, S.P. & Lapolla, J.S. (2016) *Nylanderia deceptrix* sp. n., a new species of obligately socially parasitic formicine ant (Hymenoptera, Formicidae). *ZooKeys*, 2016, 49–65. <https://doi.org/10.3897/zookeys.552.6475>
- Messer, S.J., Cover, S.P. & Rabeling, C. (2020) Two new species of socially parasitic *Nylanderia* ants from the southeastern United States. *ZooKeys*, 48, 23–48. <https://doi.org/10.3897/zookeys.921.46921>
- Minh, B.Q., Schmidt, H.A., Chernomor, O., Schrempf, D., Woodhams, M.D., von Haeseler, A. & Lanfear, R. (2020) IQ-TREE 2: New Models and Efficient Methods for Phylogenetic Inference in the Genomic Era. *Molecular biology and evolution*, 37, 1530–1534. <https://doi.org/10.1093/molbev/msaa015>
- Oberski, J.T. (2022) Molecular phylogenetics, phylogenomics, and phylogeography First Phylogenomic Assessment of the Amphitropical New World Ant Genus *Dorymyrmex* (Hymenoptera: Formicidae), a Longstanding Taxonomic Puzzle. *Insect Systematics and Diversity*, 6, 1. <https://doi.org/10.1093/isd/ixab022>
- Tagliacollo, V.A. & Lanfear, R. (2018) Estimating improved partitioning schemes for Ultraconserved Elements. *Molecular Biology and Evolution*, 35, 1798–1811. <https://doi.org/10.1093/molbev/msy069>
- Trager, J. (1984) A revision of the genus *Paratrechina* (Hymenoptera: Formicidae) of the continental United States. *Sociobiology*, 9, 51–162.

<https://doi.org/10.5281/zenodo.24910>

- Ward, P.S. (2000) Broad-scale patterns of diversity in leaf litter ant communities. *In*: Agosti, D., Majer, J.D., Alonso, L.E. & Schultz, T.R. (Eds), *Ants. Standard methods for measuring and monitoring biodiversity*. Smithsonian Institution, Washington, D.C., pp. 99–121.
- Wheeler, W.M. (1903) A Decade of Texan Formicidae. *Psyche: A Journal of Entomology*, 10, 93–111.
<https://doi.org/10.1155/1903/67840>
- Williams, J.L. & Lucky, A. (2020) Non-native and invasive *Nylanderia* crazy ants (Hymenoptera: Formicidae) of the world: Integrating genomics to enhance taxonomic preparedness. *Annals of the Entomological Society of America*, 113, 318–336.
<https://doi.org/10.1093/aesa/saz039>
- Williams, J.L., Punath, A., Fernández, M.B., Calcaterra, L.A., LaPolla, J.S. & Lucky, A. (2024) “Picking up signals” in male genital morphospace and integrating phylogenomics to delimit Neotropical *Nylanderia* Emery species (Hymenoptera: Formicidae). *In*: Hines, H. (Ed.), *Insect Systematics and Diversity*, 8 (5), 6.
<https://doi.org/10.1093/isd/ixae028>
- Williams, J.L., Zhang, Y.M., LaPolla, J.S., Schultz, T.R. & Lucky, A. (2022) Phylogenomic delimitation of morphologically cryptic species in globetrotting *Nylanderia* (Hymenoptera: Formicidae) species complexes. *Insect Systematics and Diversity*, 6, 10.
<https://doi.org/10.1093/isd/ixab027>
- Williams, J.L., Zhang, Y.M., Lloyd, M.W., LaPolla, J.S., Schultz, T.R. & Lucky, A. (2020) Global domination by crazy ants: Phylogenomics reveals biogeographical history and invasive species relationships in the genus *Nylanderia* (Hymenoptera: Formicidae). *Systematic Entomology*, 45, 730–744.
<https://doi.org/10.1111/syen.12423>

Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper.

File S1. Alignment file (.nex) for the 90% complete SWSC-partitioned UCE data matrix.

Table S1. Locality information for all specimens used in this study.

Table S2. Sample quality data for all specimens used for UCE sequencing.

Table S3. All specimen measurements recorded in this study.