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# Taxonomic revision of the *Nylanderia guatemalensis* species complex (Hymenoptera: Formicidae) in the Neotropics, with implications for conservation and invasion biology

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## Abstract

The ant genus *Nylanderia* Emery comprises 138 known species and is common across most terrestrial regions worldwide. At least 15 species have spread beyond their native ranges, some becoming ecologically and economically destructive. Subtle morphology, unresolved taxonomy, and widespread distributions make these species difficult to identify, complicating conservation efforts in biodiversity hotspots like the Galápagos Islands. Here, based on a comprehensive examination of Neotropical *Nylanderia*, we revise the taxonomy of the *N. guatemalensis* complex, recognizing seven described species: *N. ambulator* Williams *et al.*; *N. coveri* LaPolla & Kallal; *N. docilis* (Forel); *N. guatemalensis* (Forel); *N. insularis* Williams **sp. nov.**; *N. nesiotis* (Wheeler) **stat. nov.**; and *N. silvestrii* (Emery); plus an undescribed eighth, *N.* sp. JKW1 (singleton). Among these, we confirm two in the Galápagos: the non-native *N. guatemalensis* and the endemic *N. nesiotis*. While eight other ant species in the Galápagos are considered probable endemics, *N. nesiotis* is the first confirmed as such. We synonymize *N. lietzi* (Forel), *N. steinheili* (Forel), *N. guatemalensis cocoensis* (Forel), *N. guatemalensis itinerans* (Forel), and *N. silvestrii kuenzleri* (Forel) with *N. guatemalensis*, and *N. guatemalensis edenensis* (Linsley & Usinger) with *N. nesiotis*. Species boundaries are supported by combined evidence from Ultraconserved Element (UCE) phylogenomics and morphology. We provide distributions, a worker-based key, and high-resolution images of available castes to facilitate species recognition, support biodiversity monitoring, and improve detection and management of invasive *Nylanderia*.

**Key words:** ants, cryptic species, endemism, phylogenomics, Ultraconserved Elements

## Introduction

Isolated island ecosystems are highly vulnerable to non-native species capable of outcompeting native species, and these impacts are exacerbated by climate change, habitat alteration, and human-mediated transport via tourism and cargo (Harter *et al.* 2015; Russell *et al.* 2017). Once established, invasive species can disrupt island ecosystems

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at all ecological levels, frequently causing population declines, species extinctions, and broader socioeconomic impacts (Reaser *et al.* 2007). Iconic examples of island invasions include the brown tree snake, *Boiga irregularis* (Merrem, 1802) on Guam, which decimated the island's native forest bird populations (Amand 2000; Richmond *et al.* 2015), and the yellow crazy ant, *Anoplolepis gracilipes* (F. Smith, 1857) on Christmas Island, which has caused widespread ecological collapse through predation on land crabs and disruption of food webs (Abbott 2006; Wetterer 2005). These examples demonstrate the ecological significance of holistically understanding biodiversity for both conservation and invasive species management. As native species, ants are key ecosystem engineers with disproportionately large positive effects on ecological processes and biodiversity worldwide, but invasive ants can have outsized impacts that displace native species and disrupt ecosystems (Bertelsmeier *et al.* 2017; Hölldobler & Wilson 1990; Parker & Kronauer 2021), with particularly severe ecological and economic consequences on islands (Krushelnycky *et al.* 2005). Globally, over 520 known ant species with non-native distributions exhibit distinct invasion capacities, source-sink dynamics, and substantial gaps in biosecurity detection (Wong *et al.* 2023).

The ant genus *Nylanderia* (Emery, 1906) exemplifies these challenges, and its relatively recent recognition as a valid genus (LaPolla *et al.* 2010) has prompted a series of regional revisions that have contributed to a more coherent and stable taxonomy for the group, with updated treatments of the Afrotropical, Nearctic, West Indian, and Indomalayan faunas (Ahmad & Bharti 2015; Kallal & LaPolla 2012; LaPolla *et al.* 2011; LaPolla & Kallal 2019; Punnath *et al.* 2026; Silva *et al.* 2023; Williams *et al.* 2025a, 2025b). With 138 described species and 19 subspecies (Bolton 2026), the genus is nearly cosmopolitan in distribution and includes at least 15 "globetrotting" species belonging to nine independent lineages—including the *Nylanderia guatemalensis* complex—that have spread globally over the past few centuries through human-mediated dispersal (Williams *et al.* 2020, 2022; Williams & Lucky 2020). These widespread invaders often occur in regions alongside morphologically similar native and endemic *Nylanderia* species, complicating the identification and detection of both native and non-native taxa. In the West Indies, several endemic species are restricted to particular islands or mountainous areas, including *Nylanderia lucayana* LaPolla & Kallal, 2019 (Lucayan Archipelago), *Nylanderia zaminyops* LaPolla & Kallal, 2019 (Trinidad), and *Nylanderia coveri* LaPolla & Kallal, 2019 (Grenada) (LaPolla & Kallal 2019). Nonetheless, improving the taxonomic stability of the genus remains essential. Non-native *Nylanderia* species have at times remained unrecognized for years after establishment and spread. For example, *Nylanderia fulva* (Mayr, 1862), an economically and ecologically impactful invasive ant in the southeastern United States, was misidentified from the 1990s until 2012 as *Nylanderia pubens* (Forel, 1893), a long-established nuisance species (Gotzek *et al.* 2012; Klotz *et al.* 1995).

Species in this genus are notoriously difficult to distinguish using morphology alone, and even distantly related *Nylanderia* species can appear remarkably similar. Careful analysis and the use of male genital characters are often required to confirm the presence of cryptic invasive species and resolve long-standing misidentifications (Williams *et al.* 2024, 2025b). The importance of formally delimiting cryptic species is paramount to conservation, ecological monitoring, and invasive species management because assigning names and diagnostic characters to distinct lineages prevents taxonomic confusion and enables timely consideration of cryptic species in ecological assessments (Vivien *et al.* 2025).

The Galápagos Islands, a UNESCO World Heritage Site located 1,000 km off the coast of Ecuador, are under mounting pressure from increased tourism and the spread of invasive species (Harter *et al.* 2015; Herrera *et al.* 2024). These islands harbor a remarkable proportion of endemic species and fragile ecosystems that evolved in isolation, making them especially vulnerable to invasive taxa. Several invasive ant species, including *Wasmannia auropunctata* (Roger, 1863) and *Solenopsis geminata* (Fabricius, 1804), have already caused significant ecological damage to the archipelago's native arthropod and vertebrate fauna, representing direct impacts through predation and competition (Herrera *et al.* 2024; Wauters *et al.* 2018). Beyond these direct impacts, introduced ants now also make up a substantial portion of the diets of native Galápagos lava lizards, indicating that ant invasions are driving subtle yet meaningful trophic shifts and altering vertebrate food webs across the archipelago (Moreno-Buitrón *et al.* 2024). For instance, invasive ants, which are often abundant and nutritionally poor, can function as ecological 'junk food' that reduces growth and fitness of ant-specialist predators (e.g., in Californian horned lizards: Suarez & Case 2002). These cascading effects demonstrate the importance of understanding the diversity and ecological roles of ant taxa in the islands, including in genera such as *Nylanderia*, whose diversity and impacts remain poorly documented. However, knowledge of *Nylanderia* diversity in the Galápagos remains limited, reflecting a broader pattern in the Neotropics, where lack of standardized data collection, identification resources, and coordinated monitoring hinders comprehensive understanding of ant biodiversity (Oberski *et al.* 2025).

As part of a broader effort to clarify the taxonomy of Neotropical *Nylanderia*, we examined specimens from across the region, including the name-bearing types, and descriptions of all known species. Within this framework, we identified that all *Nylanderia* species occurring in the Galápagos belong to the *N. guatemalensis* complex. Taxonomic resolution of this complex has been particularly difficult due to the condition of historical type specimens from the late 1800s to early 1900s, many of which exhibit age-related deterioration, physical damage, and discoloration, making traditional morphological comparisons and molecular analysis of the types difficult. For specimens belonging to the *N. guatemalensis* complex, we used original species descriptions, morphometrics, qualitative morphological observations, Ultraconserved Element (UCE) phylogenomics from contemporary specimens, and historical distributional data to resolve long-standing questions about species boundaries.

Here, we revise the taxonomy of the *N. guatemalensis* complex based on a comprehensive, integrative examination of Neotropical material using morphological, molecular, and historical distribution data. We reconstruct phylogenetic relationships, delimit species boundaries, stabilize nomenclature, and provide a framework for identifying taxa within this widespread and taxonomically challenging group, including the description of a new species from the Lesser Antilles, *Nylanderia insularis* Williams **sp. nov.** We also clarify the identities of two *Nylanderia* species occurring in the Galápagos: the endemic *Nylanderia nesiotis* (Wheeler, 1919) and the non-native *Nylanderia guatemalensis* (Forel, 1885). We provide distributions, diagnostic characters, high-resolution images of available castes, and a worker-based key of the *N. guatemalensis* complex to facilitate accurate identification and support biodiversity monitoring, biosecurity, and invasive species management worldwide, including in fragile biodiversity hotspots such as the Galápagos.

## Material and methods

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

| | |
|---|---|
| **ABS** | Archbold Biological Station, Venus, Florida, U.S.A. |
| **ALWC** | Alex L. Wild Collection, Austin, Texas, U.S.A. |
| **CASC** | California Academy of Sciences, San Francisco, California, U.S.A. |
| **CDRS** | Charles Darwin Research Station, Puerto Ayora, Santa Cruz, Galápagos Islands, Ecuador |
| **DBBC** | Doug Booher Collection, Athens, Georgia, U.S.A. |
| **FSCA** | Florida State Collection of Arthropods, Gainesville, Florida, U.S.A. |
| **ICN** | National Insect Collection, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá D.C. |
| **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 de la Ville de Genève, Geneva, Switzerland |
| **MNCR** | Museo Nacional de Costa Rica, San José, Bella Vista, Costa Rica |
| **MSNG** | Museo di Storia Naturale Giacomo Doria, Genoa, Italy |
| **NHMB** | Museum für Naturkunde Berlin, Berlin, Germany |
| **NHMUK** | Natural History Museum of London, London, UK |
| **PSWC** | Phil S. Ward Collection, Davis, California, U.S.A. |
| **USNM** | National Museum of Natural History, Washington, D.C., U.S.A. |
| **UTIC** | University of Texas Insect Collection, Austin, Texas, U.S.A. |

**Sample selection.** We examined over 2,000 *Nylanderia* specimens from across the Neotropics, representing approximately 75 putative species, about 25 of which remain undescribed. This broad sampling, spanning Central and South America and the Caribbean, provides essential context for assessing the known diversity of *Nylanderia* in the region and for recognizing undescribed Neotropical species. Specimens encompass a wide range of habitats and elevations and include recent survey material, historical holdings from museum collections, and publicly available images of specimens on AntWeb (2026). Together, these data capture broad geographic, morphological, and ecological variation within the genus, providing a robust comparative framework for evaluating species boundaries. Additional information on the extent and scope of material examined is documented across previous studies (LaPolla & Kallal 2019; Williams *et al.* 2020, 2022, 2024, 2025a; 2025b).

Within this broader context, we focused our analyses primarily on two key subsets of material: (1) members of the *N. guatemalensis* complex spanning Mesoamerica, northern South America, and the West Indies, and (2) *Nylanderia* specimens collected from across the Galápagos Islands, including material previously identified as *N. fulva* and *Nylanderia vaga* (Forel, 1901) to verify whether those species have historically been present in the archipelago. Samples included those collected from three large-scale leaf litter surveys conducted across Mexico and Mesoamerica between 2001 and 2016: (1) Project ALAS (Longino & Colwell 2011), (2) Project LLAMA (Longino *et al.* 2014), and (3) Project ADMAC (Longino & Branstetter 2019). See Table S1 for collection information for the Galápagos and *N. guatemalensis* complex specimens described above.

**Species delimitation criteria.** Species in this study were delimited following recommendations for the treatment of cryptic taxa (Vivien *et al.* 2025) and using a combination of operational criteria: (1) phylogenetic results, (2) morphology of workers, queens, and males, and (3) geographical distribution and habitat. Phylogenetic evidence was given priority and was corroborated by morphological data. Sequenced specimens were linked to historical types by comparing distributional information and diagnostic morphological and morphometric characters identified in this study.

**DNA extraction, UCE library preparation, and sequencing.** A total of 123 sequences were included in this study, comprising 116 from previous studies (Williams *et al.* 2020, 2022, 2024) and seven newly generated sequences of *N. nesiotis* from the Galápagos Islands. DNA was non-destructively extracted from the *N. nesiotis* specimens using DNeasy Blood & Tissue Kits (Qiagen), and specimens were retained as vouchers for deposition at USNM. UCE sequence statistics for the unaligned fasta files are presented in Table 1. Specimens were selected to encompass the known diversity of species in the *N. fulva* and *N. guatemalensis* complexes. Outgroups were comprised of 16 additional Neotropical *Nylanderia* species, ten *Nylanderia* species from other regions, and *Paratrechina longicornis* (Latreille, 1802). Specimen data for all sequences used in this study can be found in Table S2, and summary statistics for all fasta files are in Tables 1 and S3. All sequences are available from the National Center for Biotechnology Sequence Read Archive (http://www.ncbi.nlm.nih.gov/sra; PRJNA1105377, PRJNA728185, PRJNA553590, PRJNA1375855).

**TABLE 1.** Ultraconserved Element sequence statistics.

| | Extract conc. (ng/μL) | Post-PCR conc. (ng/μL) | Contigs | Total bp | Mean length | Min length | Max length | Median length |
|---|---|---|---|---|---|---|---|---|
| Mean | 0.73 | 23.23 | 1945 | 1553886 | 743 | 141 | 2618 | 738 |
| Min | 0.05 | 0.25 | 360 | 100165 | 248 | 55 | 538 | 244 |
| Max | 3.83 | 64.50 | 2356 | 2719013 | 1167 | 239 | 10262 | 1207 |
| SD | 0.61 | 17.02 | 519 | 813711 | 295 | 68 | 1469 | 317 |
| 95% CI | 0.16 | 2.98 | 88 | 162888 | 59 | 15 | 275 | 65 |

**UCE data processing and alignment.** We processed UCE sequences using the PHYLUCE v1.7.3 pipeline (Faircloth 2015) and assembled clean FASTQ reads with SPAdes (Bankevich *et al.* 2012). UCE loci were aligned with MAFFT (Katoh & Standley 2013) and trimmed using GBLOCKS (Castresana 2000). An 80% complete matrix was selected, retaining 1,784 loci for the final dataset. Poorly aligned fragments were removed with the 'spruceup' Python script (Borowiec 2019) using a 97% cutoff for downstream analyses. Summary statistics were calculated with the Alignment Manipulation and Summary (AMAS) Python script (Borowiec 2016): alignment length = 685–894 bp; total matrix cells = 84,364,962; percentage of missing data = 18.58; proportion of variable sites = 0.396; and proportion of parsimony-informative sites = 0.14.

**Phylogenetic analysis.** We used site entropy from Sliding-Window Site Characteristics (SWSC-EN; Tagliacollo & Lanfear 2018) to guide partitioning of the 80% complete matrix. Partitioning was performed in PartitionFinder2 (Lanfear *et al.* 2017) under the GTR+G model using the 'rcluster' algorithm. Using this scheme, we reconstructed phylogeny under a maximum-likelihood framework in IQ-TREE 2 v3.0.1 (Minh *et al.* 2020), with the best-fit substitution model for each partition selected via ModelFinder ('-m MFP+MERGE'; Kalyaanamoorthy *et al.* 2017). Nodal support was evaluated using 1,000 replicates of both the Shimodaira-Hasegawa approximate likelihood ratio test (SH-aLRT; Guindon *et al.* 2010) and the ultrafast bootstrap (UFBoot; Hoang *et al.* 2017) with the '-bnni' option to reduce bias. Nodes were considered strongly supported if SH-aLRT ≥ 0.90 and UFBoot ≥ 0.95.

We also used the '-S' flag in IQ-TREE 2 to reconstruct individual gene trees for each UCE locus in the 80% complete matrix, and collapsed all branches with <10% bootstrap support using the 'nw_ed' function in Newick Utilities v1.6 (Junier & Zdobnov 2010). These collapsed gene trees were used as the input for species tree reconstruction in ASTRAL-III v5.7.4 (Zhang *et al.* 2018) under the multispecies coalescent (MSC) model. Local posterior probabilities (Sayyari & Mirarab 2016) were used to assess nodal support, with ≥0.95 indicating strong support.

**Imaging and morphometrics.** 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, as well as male genitalia in ventral and dorsal views, were imaged using a Canon EF 200mm lens mounted with a 10x objective. For each view, up to 80 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 (2025). 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 S4 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) x 100 |
| **CI** | (Cephalic Index): (HW/HL) x 100 |
| **EPI** | (Eye Position Index): (HLA/HLP) x 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 *N. guatemalensis* complex species

*Nylanderia ambulator* Williams *et al.,* 2025, Mesoamerica, northern South America
*Nylanderia coveri* LaPolla & Kallal, 2019, Grenada
*Nylanderia docilis* (Forel, 1908), South America
*Nylanderia guatemalensis* (Forel, 1885), widespread across the Neotropics
=*Nylanderia guatemalensis* cocoensis (Forel, 1902) **syn. nov.**
=*Nylanderia guatemalensis itinerans* (Forel, 1901) **syn. nov.**
=*Nylanderia lietzi* (Forel, 1908) **syn. nov.**
=*Nylanderia silvestrii kuenzleri* (Forel, 1909) **syn. nov.**
=*Nylanderia steinheili* (Forel, 1893) **syn. nov.**
=*Nylanderia steinheili minuta* (Forel, 1893)
*Nylanderia insularis* Williams **sp. nov.**, Lesser Antilles, northern coast of South America
*Nylanderia nesiotis* (Wheeler, 1919) **stat. nov.**, widespread across the Galápagos
=*Nylanderia guatemalensis edenensis* (Linsley & Usinger, 1966) **syn. nov.**[1]
*Nylanderia silvestrii* (Emery, 1906), South America
*Nylanderia* sp. JKW1, undescribed[2], Montserrat

**Remarks.** [1]Wheeler (1924) originally described *Prenolepis (Nylanderia) vividula guatemalensis edenensis* as a variety of a subspecies (a quadrinomial), rendering the name as infrasubspecific, and therefore unavailable under ICZN Article 45.6.4. However, Linsley & Usinger (1966) explicitly adopted the name *Paratrechina vividula edenensis* at subspecific rank and provided a bibliographic reference to Wheeler's earlier description. This satisfies the conditions of Article 13.1 for availability via reference to a prior description. Consequently, authorship of the available name is attributed to Linsley & Usinger (1966), and *Nylanderia guatemalensis edenensis* is herein treated as a junior synonym of *Nylanderia nesiotis*. The name *Paratrechina* (*Nylanderia*) *vividula* var. *galapageia* was also used by Wheeler for this species and appears in a ledger of type specimens housed in the Ernst Mayr Library, Museum of Comparative Zoology (Fig. 1); it is treated here as a naked name (*nomen nudum*) with no nomenclatural standing. [2]The undescribed species *N.* sp. JKW1 is represented by a single worker specimen and is therefore not formally described here.

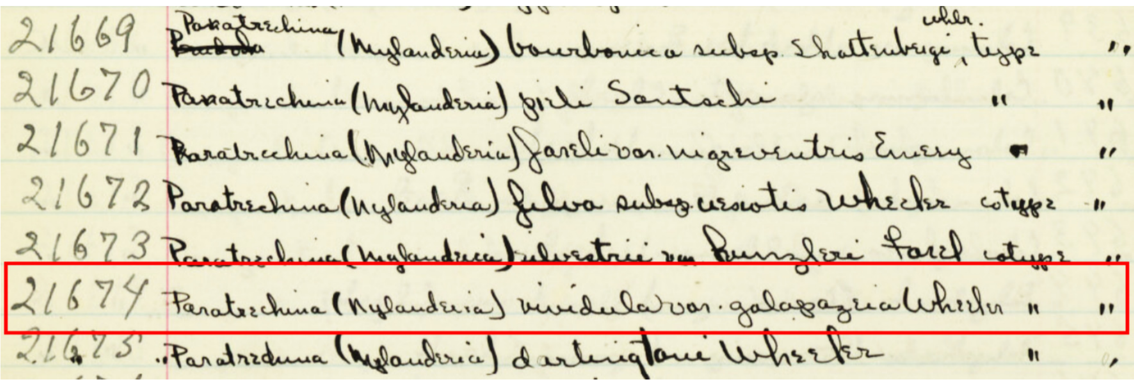

21669 Paratrechina (Nylanderia) bourbonica subsp. skottsbergi, type
21670 Paratrechina (Nylanderia) Santschi
21671 Paratrechina (Nylanderia) var. nigriventris Emery
21672 Paratrechina (Nylanderia) fulva subsp. nesiotis Wheeler cotype
21673 Paratrechina (Nylanderia) silvestrii var. kuenzleri Forel cotype
21674 Paratrechina (Nylanderia) vividula var. galapageia Wheeler
21675 Paratrechina (Nylanderia) darlingtoni Wheeler

**FIGURE 1.** Excerpt of a ledger page from the Ernst Mayr Library, Museum of Comparative Zoology (MCZ), Harvard University, showing the name *Paratrechina* (*Nylanderia*) *vividula* var. *galapageia*, a manuscript name (unavailable) associated with the *N. guatemalensis edenensis* type series.

## Species distributions

*Nylanderia guatemalensis* is the most widespread species of the *N. guatemalensis* complex, occurring in Mesoamerica, Florida, the West Indies, the Galápagos, on Cocos Island, and across South America as far south as Buenos Aires, Argentina (Fig. 2). *Nylanderia ambulator* is less widespread and occurs across Mesoamerica and northern South America (Venezuela). In the West Indies, *Nylanderia coveri* is known only from Grenada and *N.* sp. JKW1 is known only from Montserrat. *Nylanderia insularis* is found primarily in the Lesser Antilles, with some records on the northern coast of South America (Trinidad and French Guiana). *Nylanderia docilis* and *N. silvestrii* range across most of South America.

In the Galápagos, *N. nesiotis* occurs on all major islands, including Fernandina, Floreana, Isabela, Rábida, San Cristóbal, Santa Cruz, Santa Fé, and Santiago. *Nylanderia guatemalensis* occurs on San Cristóbal and Santa Cruz. Specimens historically identified as *N. fulva* or *N. vaga* were found to be misidentifications and instead correspond to either *N. guatemalensis* or *N. nesiotis*. No evidence supports that *N. fulva* or *N. vaga* have ever occurred in the Galápagos Islands.

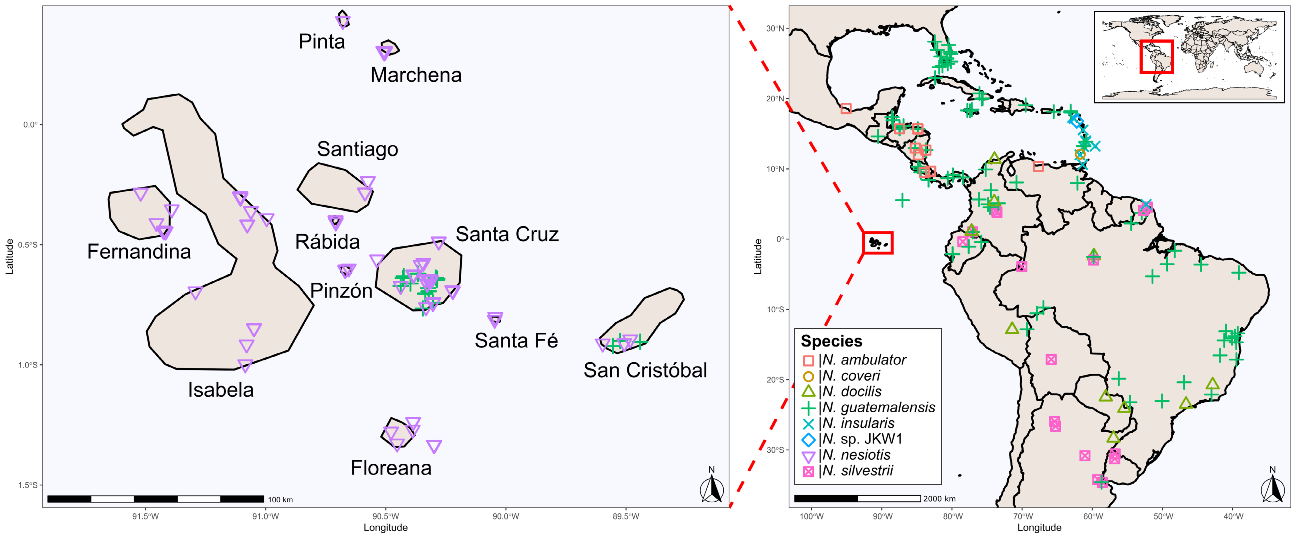



**FIGURE 2.** Distributions of *N. guatemalensis* complex species across the Neotropics, with the Galápagos archipelago magnified on the left for finer resolution. Maps were created using GPS coordinates listed in Table S1, including both newly sequenced specimens from this study and additional occurrence records, and also using data from the Global Ant Biodiversity Informatics (GABI; Guénard *et al.* 2017) database.

## Phylogenetic analysis

The maximum likelihood analysis weakly supports the monophyly of the *N. guatemalensis* complex (Fig. 3), while the multispecies coalescent provides relatively strong, but not maximal support (LPP = 92%). This complex is sister to the *N. fulva* complex and comprises eight total species: *N. ambulator, N. coveri, N. docilis, N. guatemalensis, N. insularis, N. nesiotis, N. silvestrii,* and *N.* sp. JKW1 (undescribed). Within this complex, two major subclades are strongly supported: (1) *N. ambulator* + *N. docilis* + *N. insularis* + *N. silvestrii*, and (2) *N. coveri* + *N. guatemalensis* + *N. nesiotis* + *N.* sp. JKW1. Sequences now treated as the newly described *N. insularis* were misidentified as *N. guatemalensis* in prior systematic treatments of this genus (LaPolla & Kallal 2019; Williams *et al.* 2020, 2022, 2024). This new species is strongly supported by all analyses as most closely related to a clade including *N. ambulator, N. docilis,* and *N. silvestrii*. The Galápagos endemic *N. nesiotis* is most closely related to *N.* sp. JKW1 from Montserrat in the West Indies. Together, these two species comprise a clade that is sister to the clade comprised of *N. guatemalensis* and *N. coveri*. Sequences treated here as *N. guatemalensis* were previously identified as *N. steinheili* (LaPolla & Kallal 2019; Williams *et al.* 2020, 2022, 2024), which is herein synonymized with *N. guatemalensis* (syn. nov.).

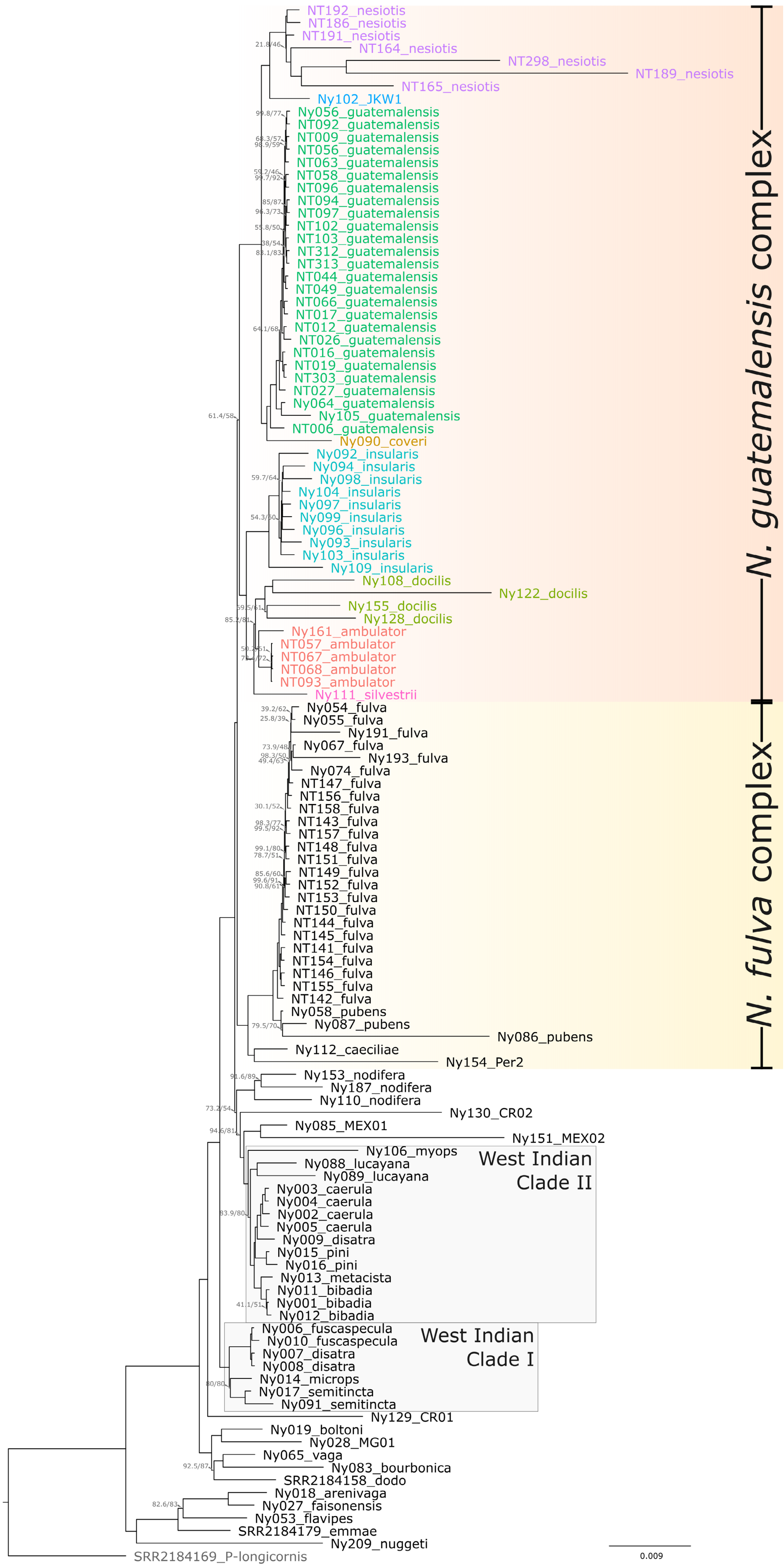



**FIGURE 3.** Maximum likelihood phylogeny of the *N. fulva* and *N. guatemalensis* complexes reconstructed using the 80% complete SWSC partitioned matrix. Nodal support (SH-aLRT/UFBoot) is displayed only for nodes with < 95% support for either measure.

### Morphological diagnosis of the *N. guatemalensis* complex

Workers are small to medium-sized (TL = 1.8–3.2; HW = 0.40–0.65; WL = 0.62–1.01) with abundant erect macrosetae on the scape (SMC > 10), and usually with dense pubescence across the head, scape, dorsal mesosoma, and gaster (except in *N. silvestrii*, which has sparse cephalic and mesosomal pubescence, and at most a patch of pubescence found anterodorsally on abdominal tergite III). These features are common to members of clade AC2, which includes both the *N. guatemalensis* complex and the closely related *N. fulva* complex. In contrast, workers of clade AC1 species (see Williams *et al.* 2025a) have a glabrous or sparsely pubescent mesosoma and lack gastral pubescence—except for *Nylanderia bruesii* from Mexico and the southwestern United States, which has dense gastral pubescence—and usually have fewer erect scape macrosetae (SMC < 10).

Within AC2, *N. guatemalensis* complex species differ from those of the *N. fulva* complex in several ways. Pubescence on the lateral mesosoma is generally sparse or absent (Fig. 4A), except in *N. nesiotis*, which ranges from having moderate to dense mesopleural pubescence (Fig. 4B). Body color varies from light yellow to dark brown, and most species (except *N. coveri*) show contrasting coloration between the lighter protrochanter, mesocoxa, and metacoxa and the overall darker body (Figs. 4A, 4B); similar lightening of these segments occurs convergently in other groups, including some AC1 species. However, this pattern is not seen in the uniformly colored *N. fulva* complex, in which these leg segments are typically concolorous with the body (Fig. 4C). Although *N. nesiotis* was previously treated as a subspecies of *N. fulva* due to its dense mesosomal pubescence, its contrasting color pattern is more consistent with what is observed in the *N. guatemalensis* complex.


**FIGURE 4.** Diagnostic comparison of the mesosoma (lateral view) of members of the *N. guatemalensis* complex and the *N. fulva* complex: (A) *N. insularis*, (B) *N. nesiotis*, and (C) *N. fulva*. In the *N. guatemalensis* complex (A and B), the mesopleuron is glabrous except in *N. nesiotis*, which exhibits moderate to dense pubescence, and the protrochanter, mesocoxa, and metacoxa are lighter-colored than the body. In contrast, the *N. fulva* complex (C) has dense mesosomal pubescence and the protrochanter, mesocoxa, and metacoxa are concolorous with the mesosoma. Image of *N. fulva* mesosoma adapted from AntWeb.org (CASENT0911029; photo credit Will Ericson).

In the *N. guatemalensis* complex, the mesosoma in profile also has a flat to weakly rounded mesonotum that does not decline posteriorly, and with the posterior margin clearly discontinuous from the metanotal area (Fig. 5A). This contrasts with some other Neotropical species, such as *Nylanderia acuminata* (Forel, 1911), *Nylanderia aurantia* Williams *et al.*, 2025, *Nylanderia caeciliae* (Forel, 1899), *Nylanderia collaborans* Williams *et al.*, 2025, *Nylanderia goeldii* (Forel, 1912), and *Nylanderia nodifera* (Mayr, 1870), in which the mesonotum declines into a deeply impressed metanotal groove, producing a profile in which the mesonotum and metanotal area are nearly continuous (Fig. 5B).

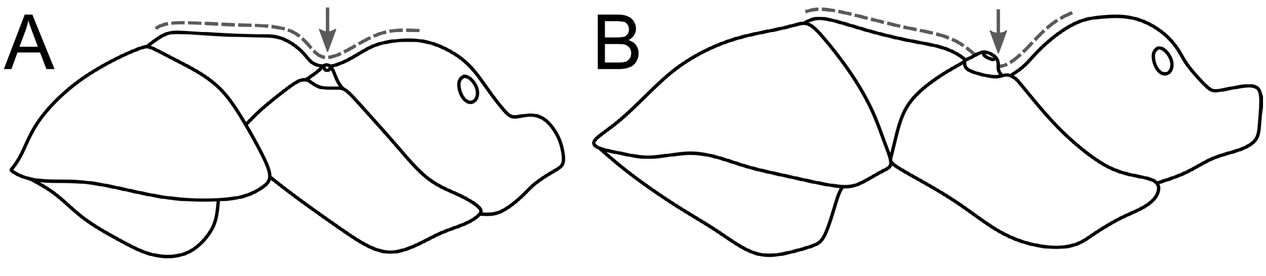
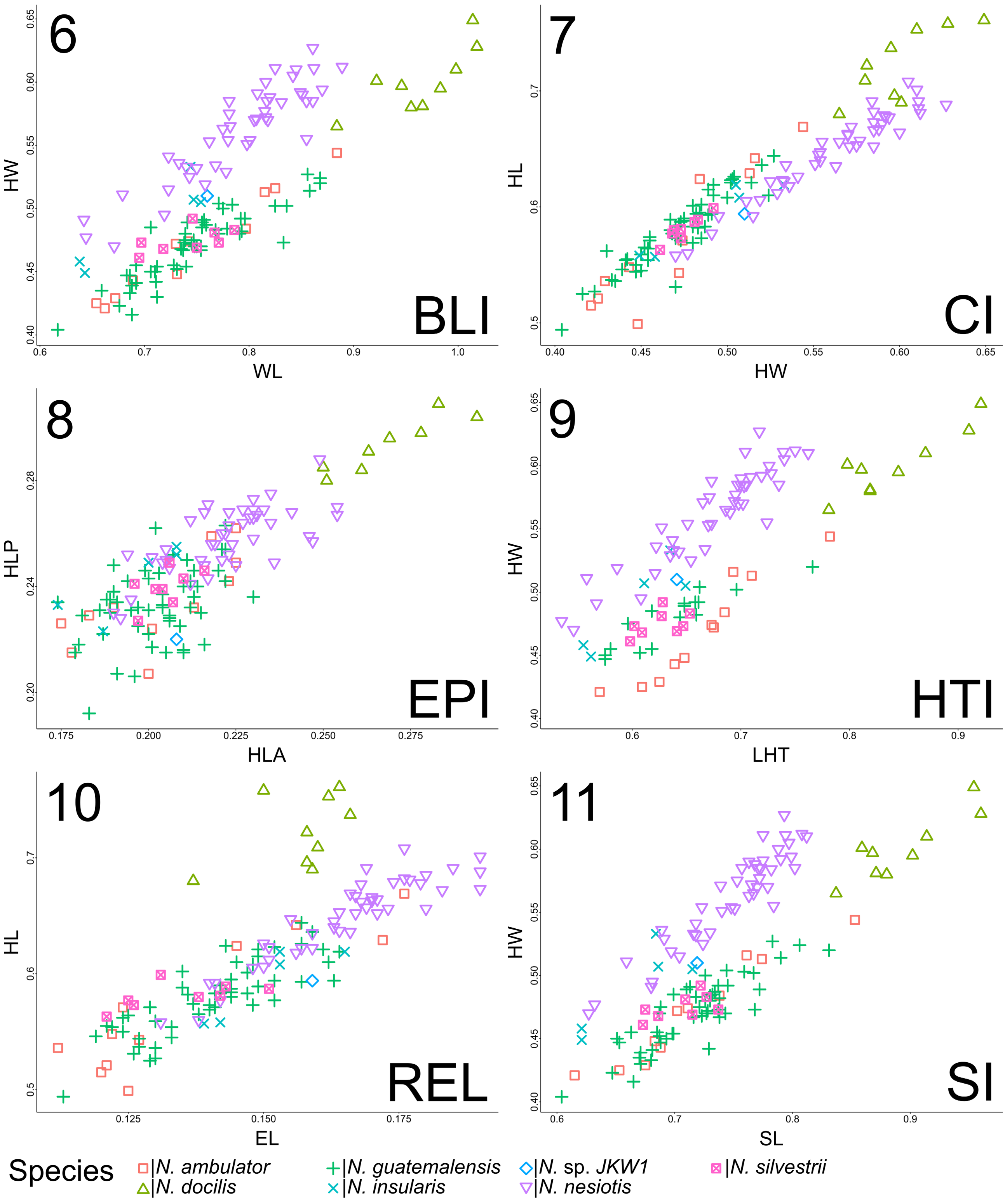



**FIGURE 5.** *Nylanderia* mesosoma shapes in lateral view: (A) mesonotum flat and not sloping into and discontinuous with the metanotal groove, and (B) mesonotum sloping into and continuous with the metanotal groove, forming a deep impression anterior to the propodeum. Shape A is characteristic of all *N. guatemalensis* complex species.




**FIGURES 6–11.** Bivariate plots of measurements: (6) Body Length Index (BLI: WL/HW), (7) Cephalic Index (CI: HW/HL), (8) Eye Position Index (EPI: HLA/HLP), (9) Hind Tibia Index (HTI: LHT/HW), (10) Relative Eye Length (REL: EL/HL), and (11) Scape Index (SI: SL/HW).

## Worker-based key to *N. guatemalensis* complex species

**1.** Body pale yellow to yellow, with concolorous yellow scape, and with dark macrosetae across body strongly contrasting with surrounding cuticle; protrochanter, mesocoxa, and metacoxa concolorous with or lighter yellow than mesosoma. . . **2**

- Body light to dark brown, with lighter yellow to brown scape, and with color of macrosetae variable; protrochanter, mesocoxa, and metacoxa whitish to pale yellow, strongly contrasting with mesosoma . . . . . . . . . . . . . . . . . . . . . . . . . . . . **3**

**2.** Dense cephalic pubescence; body pale yellow, with protrochanter, mesocoxa, and metacoxa concolorous with mesosoma (Grenada) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***N. coveri***

- Sparse cephalic pubescence, mostly concentrated lateral to antennal sockets; body yellow, with protrochanter, mesocoxa, and metacoxa lighter yellow than mesosoma . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***N. docilis***

**3.** Overall cuticle with fine cuticular microsculpture, resulting in light blue cuticular iridescence, usually most apparent on pronotum or toward posterior margin of head . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***N. ambulator***

- Overall cuticle smooth, lacking microsculpture and iridescence. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **4**

**4.** More gracile in proportions, with relatively long mesosoma (BLI > 145; Fig. 6) metatibia long (HTI > 124; Fig. 9); scape long, surpassing posterior margin of head by nearly half its length (SI > 142; Fig 11); body usually dark brown, sometimes light to medium brown; mesopleuron glabrous . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **5**

- More robust in proportions, with relatively short mesosoma (BLI < 155; Fig. 6); metatibia short (HTI < 131; Fig. 9); scape short, surpassing posterior margin of head by less than half its length (SI < 143; Fig. 11); body light to medium brown; mesopleuron ranging from glabrous to densely pubescent . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **6**

**5.** Dense cephalic pubescence; gaster with moderate to dense pubescence across entire surface . . . . . . . . . . ***N. guatemalensis***

- Sparse cephalic pubescence, mostly concentrated lateral to antennal sockets; gaster mostly glabrous, at most with patch of pubescence concentrated anterodorsally on abdominal segment III . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***N. silvestrii***

**6.** Mesopleuron moderately to densely pubescent; overall size variable, but usually larger (TL = 1.9–3.2; HW = 0.47–0.63; WL = 0.64–0.89; Figs. 6–11) (Galápagos). . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***N. nesiotis***

- Mesopleuron glabrous, lacking pubescence; overall size usually smaller (TL = 1.8–2.4; HW = 0.45–0.53; WL = 0.64–0.75; Figs. 6–11) (Lesser Antilles, northern coast of South America) . . . . . . . . . . . . . . . . . . . . . . . ***N. insularis* or *N.* sp. JKW1***

*Workers of these two species are morphologically indistinguishable based on currently available material. Reliable identification may require additional specimens, particularly males. Queens and males are currently unknown for both species, and *N.* sp. JKW1 is known from just a single worker specimen.

## Species Accounts

### *Nylanderia ambulator* Williams *et al.,* 2025

Figs. 12–14 (worker); Figs. 36–37 (queen); Figs. 42–43, 50–51, 58 (male)

*Nylanderia ambulator* Williams *et al.,* 2025: 11 (w.q.m.). Holotype worker, **COSTA RICA:** Limón, Res. Biol. Hitoy Cerere, 9.66644 -83.02266 ±10m, elev. 200m, mix of primary and secondary rainforest, ex sifted leaf litter (miniWinkler), 10.vi.2015, J. T. Longino *et al.*, ADMAC#Wa-E-02-1-14 (USNM: USNMENT01131112). 6 paratype workers and 1 paratype queen with same locality information as holotype (USNM: USNMENT01131284, USNMENT01131286, USNMENT01131287, USNMENT01131285; MNCR: USNMENT01131288, USNMENT01131289, USNMENT01131290). 2 paratype males, **COSTA RICA:** Limón, Res. Biol. Hitoy-Cerere, 9.6653 −83.02346 ±10m, elev. 240m, mix of primary and secondary rainforest, ex sifted leaf litter (miniWinkler), 10.vi.2015, J. T. Longino *et al.*, ADMAC#Wa-E-02-2-49 (USNM: USNMENT01132147; MNCR: USNMENT01131283).

### *Nylanderia coveri* LaPolla & Kallal, 2019

Figs. 15–17 (worker)

*Nylanderia coveri* LaPolla & Kallal, 2019: 412 (w.m.). Holotype worker, **GRENADA:** Saint Andrew Parish, 1.0 mi. WNW of Lower Capital on road to Gouave (measured to junction of north-south road), 19-VI-1995, S.P. Cover, SPC G-148 (MCZC). 7 paratype workers and 2 paratype males with same locality information as holotype (MCZC, USNM).

### *Nylanderia docilis* (Forel, 1908)

Fig. 18–20 (worker)

*Prenolepis vividula* subsp. *docilis* Forel, 1908a: 402 (w.). Lectotype worker (designated here), **BRAZIL:** São Paulo, H. von Ihering, ANTC33328 (MHNG: USNMENT00753567).

**Worker diagnosis:** Relatively gracile; mesosoma long (BLI = 153–166), metatibia long (HTI = 133–145), scape long, surpassing posterior margin of head by nearly half its length (SI = 143–153); body color yellow, with macrosetal bases distinctly thick and dark against light-colored cuticle; protrochanter, mesocoxa, and metacoxa whitish to yellow; relatively sparse pubescence across head and mesosoma, except for dorsal face of propodeum; mesopleuron sparsely pubescent or entirely glabrous; gaster mostly glabrous, at most with patch of pubescence concentrated anterodorsally on abdominal segment III.

**Compare with:** *N. cf. docilis* (*sensu* Williams *et al.* 2025b)*, N. silvestrii.*

WORKER. *Measurements (n=9)*: TL: 2.4–2.9 (HL+WL=1.6–1.8); EL: 0.14–0.17; EW: 0.11–0.12; IOD: 0.37–0.42; HE: 0.01; HL: 0.68–0.76; HW: 0.57–0.65; HLA: 0.25–0.29; HLP: 0.28–0.31; SL: 0.84–0.96; PW: 0.43–0.50; MW: 0.23–0.27; PrW: 0.31–0.37; PDH: 0.23–0.27; PTW: 0.15–0.19; LHT: 0.78–0.92; WL: 0.88–1.01; GL: 0.86–1.02; SMC: 26–36; PMC: 6–9; MMC: 4–6. *Indices*: BLI: 153–166; CI: 80–87; EPI: 88–97; HTI: 133–145; REL: 20–23; SI: 143–153.

*Color:* yellow, with macrosetal bases distinctly thick and dark against light-colored cuticle; concolorous yellow antennae, mandibles, and tarsi; protrochanter, mesocoxa, and metacoxa whitish to pale yellow, strongly contrasting with mesosoma; overall cuticle smooth and shining, with no cuticular microsculpture and no iridescence. *Pilosity:* abundant suberect to erect setae on scape (SMC = 26–36) contrasting in length from fine, appressed hairs; sparse cephalic pubescence, mostly concentrated lateral to antennal sockets; sparse pubescence across most of mesosoma, except for some dorsally on pronotum and anterior fringe on dorsal face of propodeum; gaster pubescence mostly concentrated anterodorsally on abdominal segment III, but otherwise sparse to absent; no mesopleural setae; 1-2 small setae may be found posterolateral to propodeal spiracle; no erect setae on apex of petiole. *Head:* in full-face view, head longer than broad (CI = 80–87) and quadrate with rounded posterolateral corners and flattened posterior margin, with slight medial emargination (HE = 0.01); scape relatively long and surpasses posterior margin of head by nearly half its length (SI = 143–153); compound eye moderately sized (REL = 20–23); compound eye positioned anterior to midline of head (EPI = 88–97); all three ocelli apparent, small, and evenly sized. *Mesosoma:* relatively elongate (BLI = 153–166); in profile view, anterior margin of mesonotum rising above posterior margin of pronotum; mesonotum flat and not declining posteriorly into metanotal groove; metanotal groove shallow, with posterior margin of mesonotum discontinuous with metanotal area; propodeum low, rounded, and at lower height than promesonotum; dorsal face of propodeum about half as long as posterior face.

**Other material examined: BRAZIL:** Amazonas, Faz. Esteio, 80km ENE Manaus, -2.416667 -59.766667, elev. 80m, 15-Sep-1987, rainforest, sifted litter (leaf mold, rotten wood), P.S. Ward, PSW9159-34 (USNM: USNMENT01129199, USNMENT01886909, USNMENT01886911); Minas Gerais, Viçosa, Mata do Cristais, -20.766666 -42.833332, 20-Apr-2013, semideciduous seasonal forest, J. Chaul, R. Jesus, tc-299834353 (CELC: UFV-LABECOL-003305); **COLOMBIA:** Magdalena, Canaveral, 11.316667 -73.933333, elev. 200m, 11-Aug-1985, tropical dry forest, sifted litter (leaf mold, rotten wood), P.S. Ward, PSW7858-34 (USNM: USNMENT01129227, USNMENT01886907, USNMENT01886910); Meta, Villavicencio, La Vanguardia, 4.173056 -73.623333, 19-Mar-2015, F. Fernández (USNM: USNMENT01886926); Putumayo, Orito, El Líbano, RN La Isla Escondida, 0.65547 -77.07302, elev. 800m, 21-Aug-2004, M. Leponce *et al.*, LOT03-12405/BX1 (USNM: USNMENT01886924, USNMENT01886925); **FRENCH GUIANA:** Régina, PK9 helipad, 22-Aug-2018, ~10m in forest, rotten log, P. Hoenle (USNM: USNMENT01129209); **PARAGUAY:** Canindeyú, Reserva Natural del Bosque Mbaracayú, Jejuimi, -24.1244 -55.4341, elev. 170m, 17-Nov-2002, humid subtropical tall forest, ground forager(s), A.L. Wild, AW1707 (ALWC: CASENT0173490); **PERU:** Cusco, Est. Biol. Villa Carmen, -12.90032 -71.41132, elev. 650m, 6-Aug-2013, second-growth rainforest, sifted litter (leaf mold, rotten wood), P.S. Ward, PSW16964-66 (USNM: USNMENT01129220, USNMENT01886912, USNMENT01886913, USNMENT01886914, USNMENT01886915).

**Notes:** This species is most superficially similar to but distinct from an undescribed species in clade AC1 referred to as *N. cf. docilis* (Williams *et al.* 2025b) and instead belongs to clade AC2. Though both species are typically yellow with distinctly dark macrosetae that contrast strongly with the surrounding cuticle, and both species are relatively sparsely pubescent overall, *N. cf. docilis* has far fewer erect setae on the scape (SMC = 6–9) and light microsculpture that results in a subtle blue iridescence of the cuticle; in contrast, true *N. docilis* has far more erect scape setae (SMC = 26–36) and completely lacks any microsculpture or iridescence. Within the *N. guatemalensis* complex, *N. docilis* is most like *N. silvestrii* in its overall sparse pubescence patterns across the head, mesosoma, and gaster, but is readily distinguished by its yellow color and overall larger size (TL = 2.4–2.9; Figs. 6–11).

***Nylanderia guatemalensis* (Forel, 1893)**
Figs. 21–23 (worker); Figs. 38–39 (queen); Figs. 44–45, 52–53, 58 (male)

*Prenolepis vividula* var. *guatemalensis* Forel, 1885: 348 (w.q.). Lectotype worker (designated by Trager, 1984: 141), **GUATEMALA:** Retaluleu, O. Stoll (MCZC) (examined). 6 paralectotype workers and 2 paralectotype queens with same locality data as lectotype (MHNG).

*Prenolepis guatemalensis* r. *antillana* Forel, 1893: 340 (w.q.m.). Junior synonym of *Nylanderia guatemalensis* (Kallal & LaPolla 2012). Lectotype worker (designated here), **ST. VINCENT AND THE GRENADINES:** Richmond Valley, 13.23888 -61.25, elev. 335m, thick forest, on decaying leaves, H.H. Smith, ANTC22713 (NHMUK: CASENT0903131). Paralectotype workers, queens, males, **ST. VINCENT AND THE GRENADINES:** St. Vincent, Morne à Garou, elev. 457m, H.H. Smith (MHNG); St. Vincent, Wallilobo Valley, H.H. Smith (MHNG); St Vincent I., Bowwood Valley, near Kingstown, elev. 244m, H.H. Smith (MHNG); St. Vincent, H.H. Smith (MHNG); St. Vincent, mountain forest, elev. 914m, H.H. Smith (MHNG); St. Vincent, Richmond Valley, elev. 244m, H.H. Smith (MHNG); St Vincent I., Upper Richmond Valley, 457m, H.H. Smith (MHNG); St. Vincent, Hermitage Estate, Cumberland Valley, elev. 305m, H.H. Smith (MHNG); St. Vincent, leeward side at various points near the coast, H.H. Smith (MHNG).

*Prenolepis guatemalensis* var. *cocoensis* Forel, 1902: 178 (w.) Lectotype worker (designated here), **COSTA RICA:** Puntarenas, Cocos Island, 5.533333 -87.05, P. Biolley, ANTC35776 (NHMB: CASENT0912303). Paralectotype workers with same locality data as lectotype (MHNG). **SYN. NOV.**

*Prenolepis guatemalensis* var. *itinerans* Forel, 1901: 81 (w.). Lectotype worker (designated here; top specimen on pin, marked with a red dot), **BRAZIL:** on orchids intercepted in quarantine at Hamburg, Germany (MHNG: USNMENT01886865). 5 paralectotype workers with same locality data as lectotype (MHNG: USNMENT01886865, USNMENT01886866, USNMENT01886867) **SYN. NOV.**

*Prenolepis* (*Nylanderia*) *lietzi* Forel, 1908b: 66 (w.q.). Lectotype worker (designated here), **COSTA RICA:** Surubrès, nr. San Mateo, 9.936347 -84.522, elev. 250m, P. Biolley, ANTC33304 (MHNG: CASENT0911035). 1 paralectotype queen, same locality data as lectotype (MHNG). **SYN. NOV.**

*Prenolepis vividula* var. *kuenzleri* Forel, 1909: 269 (w.q.m.). Lectotype worker (designated here), **ARGENTINA:** Island delta at Buenos Aires, 23.iii.1908, J. Richter, ANTC33305 (MHNG: CASENT0911037). Paralectotype workers, queens, and males with same locality as lectotype (MHNG). **SYN. NOV.**

*Prenolepis steinheili* Forel, 1893: 342 (w.). Lectotype worker (designated by LaPolla & Kallal, 2019: 437, who cited an unpublished designation by Trager, 1984; bottom specimen on pin), **US VIRGIN ISLANDS (ST. THOMAS):** 13.X.1878, A. Forel (MHNG: CASENT0101936) (examined). 2 paralectotype workers with same locality data as lectotype (MHNG: CASENT0101936, CASENT0101839). **SYN. NOV.**

*Prenolepis steinheili* var. *minuta* Forel, 1893: 343 (w.q.m.). Junior synonym of *Nylanderia steinheili* (LaPolla & Kallal 2019). Lectotype worker (designated by LaPolla & Kallal, 2019: 437; specimen on pin marked with a red dot) **ST. VINCENT AND THE GRENADINES:** St. Vincent (MHNG: USNMENT00754828) (examined). 1 paralectotype queen and 1 paralectotype male with same locality data as lectotype (MHNG: USNMENT00754828) (examined). 4 paralectotype workers, 2 paralectotype queens, and 1 paralectotype male, **ST. VINCENT AND THE GRENADINES:** St. Vincent, Richmond Estate, 31.x., H.H. Smith, 19a; St. Vincent, southern end of island, 14.x., H.H. Smith, 19b; St. Vincent, Cumberland Valley, 500 ft, 10.x., H.H. Smith, 19c and 19e; St Vincent, nr. Kingstown, 250 ft, 15.x., H.H. Smith, 19d; St Vincent, Golden Grove Estate, 300 ft, H.H. Smith, 19f; St Vincent, Fitz-Hugh Valley, 500 ft, 3.xi., H.H. Smith, 19g and 19h; St Vincent, Wallilobo Valley, 500 ft, 8.xi., H.H. Smith, 19i; St Vincent, Villa Estate, H.H. Smith, 19j; St Vincent, Camden Park Estate, 20.xi., H.H. Smith, 19k; St Vincent, Petit Bordelle Valley, 1200 ft, 13.xi., H.H. Smith, 19l; St Vincent, Old Botanical Garden, nr. Kingstown, 500 ft, 22.x., H.H. Smith, 19m; St Vincent, nr. Dry River, 1.i., H.H. Smith, 19n; St Vincent, Robocca, 2.i., H.H. Smith, 19o; St Vincent, Grand Sable, 3.i., H.H. Smith, 19p (MHNG).

**Worker diagnosis:** Relatively gracile; mesosoma long (BLI = 146–176), metatibia long (HTI = 125–147), scape long, surpassing posterior margin of head by nearly half its length (SI = 144–165); body color light to dark brown; protrochanter, mesocoxa, and metacoxa whitish to yellow; abundant pubescence concentrated dorsally and absent laterally on mesosoma; mesopleuron sparsely pubescent or entirely glabrous; gaster densely pubescent.

**Compare with:** *N. ambulator*, *N. insularis*, *N. nesiotis, N. silvestrii*

WORKER. *Measurements (n=51)*: TL: 1.8–2.6 (HL+WL=1.1–1.5); EL: 0.11–0.16; EW: 0.10–0.12; IOD: 0.27–0.34; HE: 0.00–0.02; HL: 0.49–0.64; HW: 0.40–0.53; HLA: 0.17–0.23; HLP: 0.19–0.26; SL: 0.60–0.83; PW: 0.32–0.42; MW: 0.17–0.26; PrW: 0.22–0.32; PDH: 0.17–0.27; PTW: 0.09–0.15; LHT: 0.58–0.77; WL: 0.62–0.87; GL: 0.56–1.15; SMC: 15–25; PMC: 2–4; MMC: 2–3. *Indices*: BLI: 146–176; CI: 77–89; EPI: 74–99; HTI: 125–147; REL: 22–27; SI: 144–165.

*Color:* medium to dark brown; lighter brown antennae, mandibles, and tarsi; protrochanter, mesocoxa, and metacoxa whitish to pale yellow, strongly contrasting with mesosoma; overall cuticle smooth and shining, with no cuticular microsculpture and no iridescence. *Pilosity:* moderate to abundant suberect to erect setae on scape (SMC

= 15–25), contrasting in length from fine, appressed hairs; dense cephalic pubescence covering all surfaces of head; pubescence on mesosoma concentrated dorsally and absent laterally on the pronotum and propodeum; mesopleuron glabrous or sparsely pubescent, with pubescence limited to fringe between mesonotum and propodeum; pubescence on propodeum primarily limited to dorsal face; gaster densely pubescent; no mesopleural setae; 1-2 small setae may be found posterolateral to propodeal spiracle; no erect setae on apex of petiole. *Head:* in full-face view, head longer than broad (CI = 77–89) and quadrate with rounded posterolateral corners and flattened posterior margin, with slight to moderate medial emargination (HE = 0.00–0.02); scape relatively long and surpasses posterior margin of head by nearly half its length (SI = 144–165); compound eye moderately sized to relatively large (REL = 22–27); compound eye positioned anterior to midline of head (EPI = 74–99); all three ocelli apparent, small, and evenly sized. *Mesosoma:* relatively elongate (BLI = 146–176); in profile view, anterior margin of mesonotum rising above posterior margin of pronotum; mesonotum flat and not declining posteriorly into metanotal groove; metanotal groove shallow, with posterior margin of mesonotum discontinuous with metanotal area; propodeum low, rounded, and at lower height than promesonotum; dorsal face of propodeum about half as long as posterior face.

QUEEN. *Measurements (n=4)*: TL: 3.4–4.2 (HL+WL=1.9–2.2); EL: 0.19–0.27; HL: 0.69–0.79; HW: 0.69–0.74; SL: 0.80–0.90; LHT: 0.85–0.92; WL: 1.23–1.44; GL: 1.44–1.94. *Indices*: BLI: 178–203; CI: 95–100; HTI: 118–124; REL: 26–34; SI: 116–123.

*Color:* medium to dark brown; mesocoxa and metacoxa whitish to yellow. *Pilosity:* most of body covered in moderate to dense pubescence. *Head:* about as broad as long (CI = 95–100) and subtriangular, with distinct posterolateral corners and flattened posterior margin.

MALE. *Measurements (n=7)*: TL: 1.8–2.4 (HL+WL=1.1–1.5); EL: 0.16–0.21; HL: 0.47–0.56; HW: 0.36–0.50; SL: 0.54–0.78; LHT: 0.57–0.78; WL: 0.67–0.92; GL: 0.70–1.04. *Indices*: BLI: 178–196; CI: 76–89; HTI: 150–160; REL: 33–38; SI: 151–167.

*Color:* medium to dark brown; mesocoxa and metacoxa whitish to yellow. *Pilosity:* dense pubescence on head, pronotum, mesonotum, propodeum, and gaster; pubescence on mesosoma concentrated dorsally and absent laterally on propodeum; mesopleuron glabrous or sparsely pubescent, with pubescence limited at most to patch on ventral portion of katepisternum; macrosetae across head, body, and legs dark and strongly contrasting with surrounding cuticle; macrosetae on scape and genitalia not dark and not strongly contrasting with surrounding cuticle. *Head:* longer than broad (CI = 76–89) and oval, with rounded posterolateral corners and convex posterior margin; compound eyes surpass lateral margins of head in full-face view; scapes long, surpassing posterior margin of head by about half their length. (SI = 151–167). *Mesosoma:* in profile view, propodeum gently rounded with dorsal face about twice as long as posterior face. *Genitalia:* in ectal view, harpe broadly triangular, with large, prominent, roughly quadrate dorsal lobe and weakly convex ventral margin (Fig. 58); in ventral view, ventromedial edge of basivolsella rounded, slightly sinuous posteriorly, and flattened near base of gonossiculus (Fig. 53).

**Other material examined: ANGUILLA:** Katouche Valley, 18.217 -63.075, 26-May-2006, lower forest, J.K. Wetterer, JKW219 (USNM: USNMENT01129188); **BELIZE:** Belize, La Democracia, Belize Zoo, 17.35 -88.56 ±500, elev. 37m, 22-Jun-2019, R.S. Anderson, RSA2019-004 (USNM: USNMENT01130995); Belize, La Democracia, Trop. Educ. Cent., 17.36 -88.537 ±500, elev. 26m, 22-Jun-2019, dry scrub, ex sifted litter, Winkler, R.S. Anderson, RSA2019-002 (USNM: USNMENT01130996, USNMENT01132161); Stann Creek, Bocawina, ca. 15km W. Dangriga, 16.927 -88.397 ±500, elev. 86m, 3-Jul-2019, rainforest, ex sifted litter, Winkler, R.S. Anderson, RSA2019-011 (USNM: USNMENT01131006); **COLOMBIA:** Cundinamarca, Quipile, Arabia, Fca San Antonio, 4.691944 -74.589722, elev. 1830m, 15-Jun-2022, forest, Winkler, J. Cepeda *et al.* (ICN: ICN088944); Cundinamarca, Quipile, El Tiber, Fca La Aldea, 4.521111 -74.558056, elev. 1663m, 17-Sep-2011, coffee plantation, Winkler, J. Cepeda (ICN: ICN088936); Putumayo, Orito, El Líbano, RN La Isla Escondida, 0.65547 -77.07302, elev. 800m, 21-Aug-2004, M. Leponce *et al.* (USNM: USNMENT01886927, USNMENT01886928, USNMENT01886929); **COSTA RICA:** 14-Jun-1951, A.S. Mills, 51-6187 (USNM: USNMENT00753716, USNMENT01130936); Cartago, Turrialba (Catie), 10-Jun-1981, in rotting wood, J.C. Trager (FSCA: USNMENT01223748, USNMENT01223877); Puntarenas, 15km SSW Pto. Jimenez, 8.407665 -83.327745 ±30, elev. 170m, 7-Mar-2010, mature wet forest, ex sifted leaf litter, MiniWinkler, J.T. Longino, JTL6901.42 (USNM: USNMENT01130949); Puntarenas, Esterillos Este, 9.51667 -84.45 ±2, elev. 5m, 29-Jul-1985, mangrove estuary, nest in base of bulbous-base Tillandsia, J.T. Longino, JTL0668 (USNM: USNMENT01130929); Puntarenas, Isla del Coco, Sendero a Cerro Iglesias, 5.53999 -87.0546 ±50, elev. 24m, 19-Apr-2013, ex sifted leaf litter, Winkler, C. Viquez, A. Azofeifa, CVApr13_1/10 (USNM: USNMENT01130923); Puntarenas, Monteverde, 10.2993 -84.81227 ±50, elev. 1380m, 5-Jun-2014, road edge, 2nd growth forest, nest under stone, search, J.T. Longino, JTL8719.1 (USNM: CASENT0635198, CASENT0635199, CASENT0635200, USNMENT01130952); Puntarenas, Monteverde, 10.30537 -84.82241 ±20, elev. 1140m, 6-May-2021, moist forest, in dead stick on ground, hand, J.T. Longino, JTL11584 (USNM: USNMENT01130941); Puntarenas, Piro Station, 8.4062 -83.32835 ±100, elev. 175m, 6-May-2014, rainforest, ex sifted leaf litter, MiniWinkler, J.T. Longino, JTL8624.58 (USNM: USNMENT01130935); Puntarenas, Piro Station, 8.407 -83.32815 ±100, elev. 175m, 6-May-2014, rainforest, ex sifted leaf litter, MiniWinkler, J.T. Longino, JTL8624.40 (USNM: USNMENT01130944, USNMENT01131855); **CUBA:** Holguín, La Melba, P.N. Alexander v. Humboldt, 20.44403 -74.80699, 23-Aug-2001, elev. 248m, 20-Sep-2014, rainforest, ex sifted litter, R. Anderson, F. Cala Riquelme, A. Deler Hernandez, RSA2014-001 (;CASENT0655986) Santiago de Cuba, Parque Nacional Gran Piedra, nr. Museo Isabelica, 20.007 -75.619 ±150, elev. 1115m, 26.i.2012, R.S. Anderson, RSA2012-003 (FSCA: CASENT0629923); Santiago de Cuba, Siboney-Jutici Ecol. Reserve, 19.955 -75.747 ±150, elev. 20m, 26-Jan-2012, dry scrub, ex sifted leaf litter, R.S. Anderson, RSA2012-002 (FSCA: CASENT0630093); **DOMINICAN REPUBLIC:** Santo Domingo Botanical Garden, 6-Dec-2003, M. Deyrup (USNM: USNMENT01129184); Samaná, Las Terrenas, 21-Jul-1978, R.O. Schuster (FSCA: USNMENT01886859); **ECUADOR:** Galápagos, San Cristóbal, J. Gavilanez-Slone, EC-GA-SC-C13 (USNM: USNMENT01132080); Galápagos, San Cristóbal, El Progreso, cerca de CBD INIAP, -0.921922 -89.554839, elev. 226m, 29-Nov-2022, J. Gavilanez-Slone, R. Gazis, J.L. Guerra, SC2022-s26-C127-129 (USNM: USNMENT01132084); Galápagos, San Cristóbal, El Progreso, cerca de la Finca Agroturística Voluntad de Dios, -0.904028 -89.441581, elev. 223m, 29-Nov-2022, J. Gavilanez-Slone, R. Gazis, J.L. Guerra, SC2022-s24-C116/118/120 (USNM: USNMENT01132083); Galápagos, San Cristóbal, El Progreso, vía a la Reserva Biológica de San Cristóbal, -0.899958 -89.524628, elev. 509m, 29-Nov-2022, J. Gavilanez-Slone, R. Gazis, J.L. Guerra, SC2022-s14-C66/67 (USNM: USNMENT01132082); Galápagos, Santa Cruz, Bellavista, -0.638444 -90.429056, elev. 180m, 15-Jul-2006, nest in leaf litter, aspirator, H. Herrera (CDRS: ICCDRS0003319, ICCDRS0003323); Galápagos, Santa Cruz, Bellavista, -0.638444 -90.429056, elev. 180m, 7-Jan-2007, aspirator, H. Herrera, HWH179 (CDRS: ICCDRS0003318, ICCDRS0003325, CASENT0173235); Galápagos, Santa Cruz, Bellavista, -0.69389 -90.32139, elev. 180m, 15-Jul-2006, nest in leaf litter, aspirator, H. Herrera, ANTC8217 (CDRS: CASENT0173233); Galápagos, Santa Cruz, Bellavista, -0.69389 -90.32139, elev. 180m, 15-Jul-2006, nest in leaf litter, aspirator, H. Herrera, ANTC8218 (CDRS: CASENT0173234); Galápagos, Santa Cruz, Bellavista, -0.693917 -90.321333, elev. 180m, 15-Jul-2005, transition zone, aspirator, H. Herrera (CDRS: ICCDRS0003320); Galápagos, Santa Cruz, Bellavista, -0.693917 -90.321333, elev. 180m, 21-Oct-2007, H. Herrera, HWH208 (CDRS: ICCDRS0002634, ICCDRS0002633); Galápagos, Santa Cruz, Bellavista, -0.693917 -90.321333, 20-Aug-2008, hand, H. Herrera, HWH228 (CDRS: ICCDRS0012942, ICCDRS0012943, ICCDRS0012944, ICCDRS0012945, ICCDRS0012946, ICCDRS0012947, ICCDRS0012948, ICCDRS0012949, ICCDRS0012950, ICCDRS0012951, ICCDRS0012952, ICCDRS0012953, ICCDRS0012954, ICCDRS0012955, ICCDRS0012956, ICCDRS0012957, ICCDRS0012959, ICCDRS0012960, ICCDRS0012961, ICCDRS0012962, ICCDRS0012963, ICCDRS0012964, ICCDRS0012965, ICCDRS0012966, ICCDRS0012967, ICCDRS0012968, ICCDRS0012969, ICCDRS0012970); Galápagos, Santa Cruz, Bellavista, -0.693917 -90.321333, 21-Sep-2008, aspirator, H. Herrera, HWH229 (CDRS: ICCDRS0012971, ICCDRS0012972, ICCDRS0012973, ICCDRS0012974); Galápagos, Santa Cruz, Bellavista, -0.693917 -90.321333, Jun-2008, aspirator, H. Herrera, HWH226 (CDRS: ICCDRS0011089, ICCDRS0011090, ICCDRS0011091); Galápagos, Santa Cruz, Bellavista, Cerro Mesa, -0.64615 -90.287475, elev. 425m, 5-Aug-2021, Y.M. Campaña, R. Gazis, EC2021-GA-SZ5-T7 (USNM: USNMENT01132085); Galápagos, Santa Cruz, Bellavista, Cerro Mesa, -0.64615 -90.287475, elev. 425m, 5-Aug-2021, Y.M. Campaña, R. Gazis, GA-SZ-T07 (USNM: USNMENT01132081); Galápagos, Santa Cruz, Bellavista, vía a El Puntudo/Garrapatero, -0.680272 -90.323791, elev. 283m, 27-Nov-2019, Y.M. Campaña, R. Gazis, EC2019-GA-SZ-S1-T06 (USNM: USNMENT01132086); Galápagos, Santa Cruz, Bellavista, -0.702696 -90.335677, 176m, 22-Nov-2025, wet zone near human habitation, on vegetation on side of dirt road, J.L. Williams, H. Herrera, JLW206 (USNM: USNMENT01886878); Galápagos, Santa Cruz, Bellavista, -0.704889 -90.335523, 172m, 22-Nov-2025, wet zone near human habitation, soil under dead wood, J.L. Williams, H. Herrera, JLW205 (USNM: USNMENT01886877); Galápagos, Santa Cruz, Bellavista, Cerro Mesa, -0.637323 -90.291516, 429m, 11-Nov-2025, rainforest, nest under rotten log, J.L. Williams, H. Herrera, JLW164 (USNM: USNMENT01886872); Galápagos, Santa Cruz, Bellavista, Cerro Mesa, -0.637323 -90.291516, 429m, 11-Nov-2025, rainforest, nest under rotten log, J.L. Williams, H. Herrera, JLW165 (USNM: USNMENT01886873); Galápagos, Santa Cruz, Bellavista, Cerro Mesa, -0.637712 -90.291843, 429m, 11-Nov-2025, rainforest, nest in rotten log, J.L. Williams, H. Herrera, JLW161 (USNM: USNMENT01886869); Galápagos, Santa Cruz, Bellavista, Cerro Mesa, -0.637712 -90.291843, 429m, 11-Nov-2025, rainforest, nest under stone, J.L. Williams, H. Herrera, JLW160 (USNM: USNMENT01886868); Galápagos, Santa Cruz, Bellavista, Cerro Mesa, -0.637818 -90.291948, 429m, 11-Nov-2025, rainforest, in soil under leaf litter, J.L. Williams, H. Herrera, JLW163 (USNM: USNMENT01886871); Galápagos, Santa Cruz, Bellavista, Cerro Mesa, -0.637818 -90.291948, 429m, 11-Nov-2025, rainforest, under stone, J.L. Williams, H. Herrera, JLW162 (USNM: USNMENT01886870); Galápagos, Santa Cruz, Bellavista, Cerro Mesa, -0.642175 -90.286082, 488m, 11-Nov-2025, rainforest on peak, nest under volcanic rock, J.L. Williams, H. Herrera, JLW166 (USNM: USNMENT01886874); Galápagos, Santa Cruz, Cueva Cañon, 10-Mar-2014, 10 ft. into cave, dry bedrock ceiling, S. Taylor, J. Jacoby, M. Sutton, S. Hagen (DBBC: CASENT0751624, CASENT0751626, CASENT0751627); Galápagos, Santa Cruz, Cueva Carlon, 10-Mar-2014, cave entrance, leaf litter w/ moss, S. Taylor, J. Jacoby, M. Sutton, S. Hagen (DBBC: CASENT0751641, CASENT0751642, CASENT0751643); Galápagos, Santa Cruz, Cueva Cascajo, 9-Mar-2014, cave skylight entrance, leaf litter, S. Taylor, J. Jacoby, M. Sutton (DBBC: CASENT0751586, CASENT0751587, CASENT0751589, CASENT0751590, CASENT0751592, CASENT0751594, CASENT0751631); Galápagos, Santa Cruz, Cueva Gallardo (=Bellevista), 8-Mar-2014, cave entrance, on decaying organic debris, S. Taylor, J. Jacoby (DBBC: CASENT0751547,CASENT0751580,CASENT0751610,CASENT0751611,CASENT0751612,CASENT0751613, CASENT0751652, CASENT0751653, CASENT0751654); Galápagos, Santa Cruz, ECCD, -0.742194 -90.303611, elev. 10m, 27-Jul-2006, littoral zone, hand, H. Herrera (CDRS: ICCDRS0003324); Galápagos, Santa Cruz, Los Gemelos, -0.619974 -90.367192, 612m, 22-Nov-2025, dry scrub, mixed foragers in leaf litter, J.L. Williams, H. Herrera, JLW199 (USNM: USNMENT01886875); Galápagos, Santa Cruz, Los Gemelos, -0.621683 -90.364706, 616m, 22-Nov-2025, wet forest, nest around roots in leaf litter, J.L. Williams, H. Herrera, JLW201 (USNM: USNMENT01886876); Galápagos, Santa Cruz, Puerto Ayora, Hwy/E5, cerca del Royal Palm, -0.661911 -90.397462, elev. 398m, 27-Nov-2019, J. Gavilanez-Slone, Y.M. Campaña, EC2019-GA-SZ-S1-T03 (USNM: USNMENT01132087); Galápagos, Santa Cruz, Reserva de Tortugas, El Chato, -0.671606 -90.437997, elev. 225m, 10-Jan-2001, humid zone, pitfall, G. Estévez, G6-F2-T3 (USNM: USNMENT01132075, USNMENT01886822); Galápagos, Santa Cruz, Santa Rosa, -0.631219 -90.425203, elev. 414m, 4-Aug-2021, Y.M. Campaña, R. Gazis, GA-SZ-S1-T03 (USNM: USNMENT01132088); Galápagos, Santa Cruz, Zona de Parque, Nov-2007, pitfall, R. Boada (CDRS: ICCDRS0002838); Guayas, Guayaquil, Tarqui, Jardin Botanico de Guayaquil, 6° Pasaje 1A NE, -2.079725 -79.909806, elev. 71m, 5-Dec-2019, J. Gavilanez-Slone, 2019-EC-GY-C72 (USNM: USNMENT01886521, USNMENT01886856); Guayas, Guayaquil, Tarqui, Mobil, Pedro Menéndez Gilbert, -2.164192 -79.880286, elev. 6m, 2-Dec-2019, J. Gavilanez-Slone, 2019-B-EC-GY-C6 (USNM: USNMENT01886535); Napo, Jatun Sacha, 7km ESE Pto. Misahuallí, -1.066667 -77.6166667, elev. 400m, 5-Aug-1991, rainforest, sifted litter (leaf mold, rotten wood), P.S. Ward, PSW11364-74 (USNM: USNMENT01132032); Napo, Jatun Sacha, 7km ESE Pto. Misahuallí, -1.066667 -77.616667, elev. 400m, 5-Aug-1991, rainforest, sifted litter (leaf mold, rotten wood), P.S. Ward, PSW11364-75 (USNM: USNMENT01132031); **FRENCH GUIANA:** Nouragues, Grand Plateau, 22-Aug-2018, leaf litter, Winkler, M. Wong, MW00015 (USNM: USNMENT01132035); Nouragues, helipad at Inselberg Camp, 25-Aug-2018, leaf litter, Winkler, P. Hoenle (USNM: USNMENT01132034); Nouragues, trail to Petit Plateau, 4.08441 -52.68413 ±10, 28-Aug-2018, forest, leaf litter, Winkler, J.L. Williams, JLW036 (USNM: USNMENT01132033); Régina, Route De Belizon, 4.328725 -52.357307 ±5, 22-Aug-2018, forest edge, rotting plywood pile, hand, J.L. Williams, JLW180822-02 (USNM: USNMENT01131807); **HONDURAS:** Atlántida, 2km SSE Tela, 15.76502 -87.45693 ±20, elev. 30m, 15-Jun-2010, 2º tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-08-1-01 (USNM: USNMENT01131046); Atlántida, 2km SSW Tela, 15.763573 -87.456324 ±20, elev. 30m, 15-Jun-2010, 2º tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-08-1-36 (USNM: USNMENT01131065); Atlántida, 2km SSW Tela, 15.763741 -87.456393 ±20, elev. 30m, 15-Jun-2010, 2º tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-08-1-32 (USNM: USNMENT01131056); Atlántida, 2km SSW Tela, 15.763824 -87.456428 ±20, elev. 30m, 15-Jun-2010, 2º tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-08-1-30 (USNM: USNMENT01131052, USNMENT01132171); Atlántida, 2km SSW Tela, 15.763908 -87.456462 ±20, elev. 30m, 15-Jun-2010, 2º tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-08-1-28 (USNM: USNMENT01131051); Atlántida, 2km SSW Tela, 15.76394 -87.45647 ±300, elev. 30m, 15-Jun-2010, 2º tropical rainforest, ex sifted leaf litter, MaxiWinkler, LLAMA, Wm-C-08-1-01 (USNM: USNMENT01131248); Atlántida, 2km SSW Tela, 15.764034 -87.456514 ±20, elev. 30m, 15-Jun-2010, 2º tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-08-1-25 (USNM: USNMENT01131053); Atlántida, 2km SSW Tela, 15.764118 -87.456549 ±20, elev. 30m, 15-Jun-2010, 2º tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-08-1-23 (USNM: USNMENT01131054); Atlántida, 2km SSW Tela, 15.764244 -87.456601 ±20, elev. 30m, 15-Jun-2010, 2º tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-08-1-20 (USNM: USNMENT01131044); Atlántida, 2km SSW Tela, 15.764369 -87.456653 ±20, elev. 30m, 15-Jun-2010, 2º tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-08-1-17 (USNM: USNMENT01131049); Atlántida, 2km SSW Tela, 15.764411 -87.45667 ±20, elev. 30m, 15-Jun-2010, 2º tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-08-1-16 (USNM: USNMENT01131048); Atlántida, 2km SSW Tela, 15.764956 -87.456895 ±20, elev. 30m, 15-Jun-2010, 2º tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-08-1-03 (USNM: USNMENT01131043, USNMENT01132169); Atlántida, 2km SSW Tela, 15.7657 -87.45567 ±30, elev. 20m, 16-Jun-2010, old cacao plantation, ex sifted leaf litter, MaxiWinkler, LLAMA, Wm-C-08-1-07 (USNM: USNMENT01131889); Atlántida, 7km SSW Tela, 15.723141 -87.451745 ±20, elev. 190m, 15-Jun-2010, tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-08-2-48 (USNM: USNMENT01131059); Atlántida, 7km SSW Tela, 15.723231 -87.451756 ±20, elev. 190m, 15-Jun-2010, tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-08-2-46 (USNM: USNMENT01131060); Atlántida, 7km SSW Tela, 15.723712 -87.451942 ±20, elev. 190m, 15-Jun-2010, tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-08-2-13 (USNM: USNMENT01131064); Atlántida, 7km SSW Tela, 15.72429 -87.45188 ±300, elev. 190m, 15-Jun-2010, tropical rainforest, ex sifted leaf litter, MaxiWinkler, LLAMA, Wm-C-08-1-02 (USNM: USNMENT01131249); Atlántida, 7km SSW Tela, 15.724397 -87.451903 ±20, elev. 190m, 15-Jun-2010, tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-08-2-20 (USNM: USNMENT01131062); Atlántida, 7km SSW Tela, 15.724442 -87.451909 ±20, elev. 190m, 15-Jun-2010, tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-08-2-19 (USNM: USNMENT01131063); Atlántida, 7km SSW Tela, 15.724801 -87.451954 ±20, elev. 190m, 15-Jun-2010, tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-08-2-11 (USNM: USNMENT01131066); Atlántida, 7km SSW Tela, 15.724891 -87.451965 ±20, elev. 190m, 15-Jun-2010, tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-08-2-09 (USNM: USNMENT01131068); Atlántida, 7km SSW Tela, 15.725205 -87.452004 ±20, elev. 190m, 15-Jun-2010, tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-08-2-02 (USNM: USNMENT01131069); Atlántida, 7km SSW Tela, 15.72792 -87.4497 ±20, elev. 120m, 16-Jun-2010, tropical rainforest, ex sifted leaf litter, MaxiWinkler, LLAMA, Wm-C-08-1-05 (USNM: USNMENT01131252); Atlántida, 8km SSW Tela, 15.70914 -87.46623 ±20, elev. 330m, 17-Jun-2010, ex sifted leaf litter, MaxiWinkler, LLAMA, Wm-C-08-2-08 (USNM: USNMENT01136841); Atlántida, 8km SSW Tela, 15.70932 -87.46296 ±20, elev. 260m, 17-Jun-2010, tropical rainforest, ex sifted leaf litter, MaxiWinkler, LLAMA, Wm-C-08-2-09 (USNM: USNMENT01131265); Atlántida, 8km SSW Tela, 15.71083 -87.4612 ±20, elev. 210m, 17-Jun-2010, tropical rainforest, ex sifted leaf litter, MaxiWinkler, LLAMA, Wm-C-08-2-10 (USNM: USNMENT01136267); Atlántida, 8km SSW Tela, 15.71251 -87.46005± 20, elev. 170m, 17-Jun-2010, tropical rainforest, ex sifted leaf litter, MaxiWinkler, LLAMA, Wm-C-08-2-11 (USNM: USNMENT01131267); Atlántida, 9km SSW Tela, 15.70207 -87.47304 ±20, elev. 450m, 17-Jun-2010, tropical rainforest, ex sifted leaf litter, MaxiWinkler, LLAMA, Wm-C-08-2-05 (USNM: USNMENT01131262); Gracias a Dios, Las Marias, 15.664018 -84.857633 ±20, elev. 60m, 8-Jun-2010, tropical rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-C-07-1-16 (USNM: USNMENT01131041); Gracias a Dios, Las Marias, 15.67303 -84.82487 ±100, elev. 60m, 11-Jun-2010, tropical rainforest, vegetation, beating, LLAMA, Go-C-07-2-03 (USNM: USNMENT01130930); Gracias a Dios, Las Marias, 15.70856 -84.862 ±10, elev. 60m, 9-Jun-2010, tropical rainforest, ex sifted leaf litter, MaxiWinkler, LLAMA, Wm-C-07-2-01 (USNM: USNMENT01131244); Gracias a Dios, Las Marias, 15.71314 -84.86517 ±100, elev. 110m, 11-Jun-2010, tropical rainforest, ex sifted leaf litter, MaxiWinkler, LLAMA, Wm-C-07-2-05 (USNM: USNMENT01131246); Islas de la Bahía, 1.5km NNW East Harbor, Utila, 16.1 -86.90167, 29-Dec-2007, sifted litter (leaf mold, rotten wood), P.S. Ward, PSW15998.26 (FSCA: CASENT0625096); Islas de la Bahía, 1.5km NNW East Harbor, Utila, 16.1 -86.90167, 29-Dec-2007, sifted litter (leaf mold, rotten wood), P.S. Ward, PSW15998.27 (FSCA: CASENT0625094); **JAMAICA:** Saint James, Great River, 18.43333 -77.98333, elev. 5m, 17-Mar-1984 riparian wet forest, nest in soil under leaf litter, search, J.T. Longino, JTL17Mar84/1630 (JTLC: JTLC000005977); Trelawny, 5km S Sawyers - Rt 5, 18.3298 -77.51313, elev. 440m, 10-Sep-2001, A.L. Wild, ALW1373, (UTIC: UTIC00214860, UTIC00214861); Trelawny, 5km N Quick Step, 18.2691 -77.7115, 11-Sep-2001, A.L. Wild (UTIC: UTIC00214866, UTIC00214867, UTIC00214868, UTIC00214869), Westmoreland, Holly Hill, 18.2 -78, elev. 600m, second growth forest edge, in dead wood on ground, search, J.T. Longino, JTL13Mar84/1357 (JTLC: JTLC000005978); **MEXICO:** Quintana Roo, Puerto Morelos, 7-Apr-1986, A. Dejean (FSCA: USNMENT01223957); **NICARAGUA:** Matagalpa, RN Cerro Musún, 12.96013 -85.23271 10, elev. 750m, 1-May-2011, tropical wet forest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-D-01-1-43 (USNM: USNMENT01131075); Región Autónoma del Atlántico Sur, RN Kahka Creek, 12.672147 -83.716258 ±10, elev. 30m, 6-Jun-2011, 2º lowland rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-D-07-1-15 (USNM: USNMENT01131119); Región Autónoma del Atlántico Sur, RN Kahka Creek, 12.672302 -83.716043 ±10, elev. 30m, 6-Jun-2011, 2º lowland rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-D-07-1-21 (USNM: USNMENT01131086); Región Autónoma del Atlántico Sur, RN Kahka Creek, 12.672437 -83.715802 ±10, elev. 30m, 6-Jun-2011, 2º lowland rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-D-07-1-27 (USNM: USNMENT01131085); Región Autónoma del Atlántico Sur, RN Kahka Creek, 12.67246 -83.715762 ±10, elev. 30m, 6-Jun-2011, 2º lowland rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-D-07-1-28 (USNM: USNMENT01131089); Región Autónoma del Atlántico Sur, RN Kahka Creek, 12.672641 -83.715502 ±10, elev. 30m, 6-Jun-2011, 2º lowland rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-D-07-1-35 (USNM: USNMENT01131091); Región Autónoma del Atlántico Sur, RN Kahka Creek, 12.672674 -83.715471 ±10, elev. 30m, 6-Jun-2011, 2º lowland rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-D-07-1-36 (USNM: USNMENT01131097); Región Autónoma del Atlántico Sur, RN Kahka Creek, 12.672941 -83.715278 ±10, elev. 30m, 6-Jun-2011, 2º lowland rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-D-07-1-44 (USNM: USNMENT01131095); Región Autónoma del Atlántico Sur, RN Kahka Creek, 12.677274 -83.715193 ±10, elev. 30m, 7-Jun-2011, 2º lowland rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-D-07-2-32 (USNM: USNMENT01131102); Región Autónoma del Atlántico Sur, RN Kahka Creek, 12.677365 -83.715193 ±10, elev. 30m, 7-Jun-2011, 2º lowland rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-D-07-2-30 (USNM: USNMENT01131096); Región Autónoma del Atlántico Sur, RN Kahka Creek, 12.67741 -83.715193 ±10, elev. 30m, 7-Jun-2011, 2º lowland rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-D-07-2-29 (USNM: USNMENT01131099); Región Autónoma del Atlántico Sur, RN Kahka Creek, 12.6775 -83.715193 10, elev. 30m, 7-Jun-2011, 2º lowland rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-D-07-2-27 (USNM: USNMENT01131100); Región Autónoma del Atlántico Sur, RN Kahka Creek, 12.67763 -83.715161 ±10, elev. 30m, 7-Jun-2011, 2º lowland rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-D-07-2-24 (USNM: USNMENT01131101); Región Autónoma del Atlántico Sur, RN Kahka Creek, 12.677811 -83.715161 ±10, elev. 30m, 7-Jun-2011, 2º lowland rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-D-07-2-20 (USNM: USNMENT01131088); Región Autónoma del Atlántico Sur, RN Kahka Creek, 12.67811564 -83.71520744 10, elev. 30m, 7-Jun-2011, 2º lowland rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-D-07-2-13 (USNM: USNMENT01131092); Región Autónoma del Atlántico Sur, RN Kahka Creek, 12.678206 -83.715207 ±10, elev. 30m, 7-Jun-2011, 2º lowland rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-D-07-2-11 (USNM: USNMENT01131093); Región Autónoma del Atlántico Sur, RN Kahka Creek, 12.678342 -83.715207 ±10, elev. 30m, 7-Jun-2011, 2º lowland rainforest, ex sifted leaf litter, MiniWinkler, LLAMA, Wa-D-07-2-08 (USNM: USNMENT01131094); **PANAMA:** Coclé, 6km NNW El Copé, PN Omar Torrijos, 8.66946 -80.59316 ±50, elev. 765m, 22-Jan-2015, cloud forest, sifted litter (leaf mold, rotten wood), P.S. Ward, PSW17335-30 (USNM: USNMENT01886853); Colón, Gigante Peninsula, 9.11363 -79.8543 ±1000, elev. 90m, Jun-2010, wet forest, ex leaf litter, T.P. Sumnicht (FSCA: CASENT0643738, CASENT0643739, CASENT0643740, CASENT0643741); Darién, 5km S Platanilla, 8.78105 -78.41251 ±50, elev. 160m, 20-Jan-2015, ex sifted leaf litter, Winkler, J.T. Longino, JTL9081-s (USNM: USNMENT01130954); Darién, Reserva Chucantí, 8.78803 -78.45035 ±50, elev. 720m, 20-Jan-2015, moist forest, ex sifted leaf litter, Winkler, J.T. Longino, JTL9071-s (USNM: USNMENT01130953); Darién, Reserva Chucantí, 8.78964 -78.45347 ±6, elev. 810m, 19-Jan-2015, rainforest, on tree trunk, P.S. Ward, PSW17306 (USNM: USNMENT01886854); **PERU:** Rio Tambopata, Explorer's Inn, Rio Tower, -12.8368 -69.29338, 2-Aug-2005, J.T. Osborne (USNM: USNMENT01131894, USNMENT01886700); **PUERTO RICO:** Vieques, SE of airport, 18.135 -65.487, 8-Jun-2006, forest, J.K. Wetterer, JKW331 (USNM: USNMENT01229180); **ST. LUCIA:** Mamiku Garden, 13.864 -60.902, 8-Jul-2006, garden, J.K. Wetterer, JKW771 (USNM: USNMENT01886855); **ST. MARTIN:** Little Bay Pond, east side, 18.024 -63.065, 26-May-2006, J.K. Wetterer, JKW170 (USNM: USNMENT01129183); **ST. VINCENT AND THE GRENADINES:** St. Vincent, Vermont Nature Trail, 13.21632 -61.21416 ±25, elev. 365m, 14-May-2015, rainforest, ex soil, hand, B.L. Fisher, BLF37242 (CASC: CASENT0767550, CASENT0767551, CASENT0767552); **USA:** Florida, Dade Co., Homestead Exp. Sta., 31-Oct-1974, nesting 6 ft. from ground, E. Nickerson (FSCA: USNMENT01223750, USNMENT01223850, USNMENT01223919); Florida, Dade Co., Shark Valley, 25.66667 -80.76667, 2-Sep-1990, tropical hammock, at observation tower, M. Deyrup, ANTC5021 (ABS: CASENT0104221); Florida, Dade Co., Shark Valley, 25.66667 -80.76667, 2-Sep-1990, tropical hammock, at observation tower, M. Deyrup, ANTC5022 (ABS: CASENT0104222);

Florida, Hillsborough Co., Lutz, 28.103997 -82.450105, elev. 16m, 5-May-2018, mixed forest, sandy soil, hand, J.L. Williams, JLW180505-01 (USNM: USNMENT01129155); Florida, Monroe Co., Big Pine Key, 17th St., 0.1mi to Wilder St., 24.67917 -81.35317 ±10, 21-Aug-2009, C.S. Moreau, CSM1153e (FSCA: USNMENT01223848); Florida, Monroe Co., Key West, 29-Dec-1954, on *Flaveria linearis*, H.V. Weems Jr. (FSCA: USNMENT01223852); **VENEZUELA:** Barinas, Ciudad Bolivia (17km SW), 8.066667 -70.8, elev. 240m, 26-Aug-1987, second-growth rainforest, foraging on ground, P.S. Ward, PSW8988-15 (USNM: CASENT0281001).

**Notes:** New synonymies are established based on original descriptions, along with inspection of and morphometric comparisons with type material. The original *N. guatemalensis* types from Guatemala are difficult to examine due to age-related damage and yellowing, but their measurement indices (i.e., BLI, HTI, and SI) are more consistent with material previously identified as *N. steinheili*, including the original *N. steinheili* types from the US Virgin Islands. Since *N. guatemalensis* is the senior name, all specimens formerly assigned to *N. steinheili* are here treated as *N. guatemalensis* (*sensu stricto*). Importantly, this clarification updates previous work: In (Williams *et al.* 2020, 2022, 2024), samples labeled as *N. steinheili* are actually *N. guatemalensis*, whereas samples labeled as *N. guatemalensis* correspond to *N. insularis*.

### *Nylanderia insularis* Williams sp. nov.

urn:lsid:zoobank.org:act:8C0CFDBE-7476-46EC-A8CA-8E23B64CD0AD
Figs. 24–26 (worker)

Holotype worker, **ST. LUCIA:** Chassin, 13.992917 -60.929133, elev. 70m, 17-Nov-2003, secondary forest, J.K. Wetterer, JKW58 (USNM: USNMENT01129187). 1 paratype worker with same locality data as holotype (CDRS: USNMENT01886861). 2 paratype workers, **GRENADA:** Coral Cove, 11.992693 -61.754913, elev. 8m, 11-Nov-2003, J.K. Wetterer, JKW30 (USNM: USNMENT01129186, USNMENT01886862).

**Worker diagnosis:** Relatively small to moderately-sized (TL = 1.8–2.4) and relatively compact; mesosoma short (BLI = 139–149), metatibia short (HTI = 119–129), scape short, surpassing posterior margin of head by less than half its length (SI = 128–142); body color light to medium brown; protrochanter, mesocoxa, and metacoxa yellow to yellow-brown; mesopleuron lacking pubescence.

**Compare with:** *N. ambulator, N. guatemalensis*, *N. silvestrii*

WORKER. *Measurements (n=10)*: TL: 1.8–2.4 (HL+WL=1.2–1.4); EL: 0.14–0.17; EW: 0.11–0.13; IOD: 0.27–0.34; HE: 0.00–0.01; HL: 0.56–0.62; HW: 0.45–0.53; HLA: 0.17–0.21; HLP: 0.22–0.26; SL: 0.62–0.72; PW: 0.33–0.40; MW: 0.19–0.23; PrW: 0.25–0.29; PDH: 0.19–0.22; PTW: 0.10–0.13; LHT: 0.56–0.65; WL: 0.64–0.75; GL: 0.58–1.06; SMC: 16; PMC: 2–3; MMC: 2–3. *Indices*: BLI: 139–149; CI: 80–86; EPI: 75–84; HTI: 119–129; REL: 25–27; SI: 128–142.

*Color:* light to medium brown; lighter yellow to yellow-brown antennae, mandibles, and tarsi; protrochanter, mesocoxa, and metacoxa whitish to pale yellow, strongly contrasting with mesosoma; overall cuticle smooth and shining, with no cuticular microsculpture and no iridescence. *Pilosity:* moderate to abundant suberect to erect setae on scape (SMC = ~16), contrasting in length from fine, appressed hairs; dense cephalic pubescence covering all surfaces of head; pubescence on mesosoma concentrated dorsally and absent laterally on the pronotum and propodeum; mesopleuron glabrous or sparsely pubescent, with pubescence limited to fringe between mesonotum and propodeum; pubescence on propodeum primarily limited to dorsal face; gaster densely pubescent; no mesopleural setae; 1-2 small setae may be found posterolateral to propodeal spiracle; no erect setae on apex of petiole. *Head:* in full-face view, head longer than broad (CI = 80–86) and quadrate with rounded posterolateral corners and flattened posterior margin, with little to no medial emargination (HE = 0.00–0.01); scape relatively short and surpasses posterior margin of head by less than half its length (SI = 128–142); compound eye relatively large (REL = 25–27); compound eye positioned anterior to midline of head (EPI = 75–84); all three ocelli apparent, small, and evenly sized. *Mesosoma:* relatively stout (BLI = 139–149); in profile view, anterior margin of mesonotum rising above posterior margin of pronotum; mesonotum flat and not declining posteriorly into metanotal groove; metanotal groove shallow, with posterior margin of mesonotum discontinuous with metanotal area; propodeum low, rounded, and at lower height than promesonotum; dorsal face of propodeum about half as long as posterior face.

**Other material examined: BARBADOS WI:** Turner's Hall Woods, 13.23444 -59.58784, elev. 100m, 18-Mar-1998, E.O. Wilson, S.P. Cover, JKWB-29 (USNM); **DOMINICA WI:** Melville Hall, 15.5469 -61.30114, elev. 16m, 14-Jun-2004, 1km N airport, J.K. Wetterer, JKW212 (USNM); **FRENCH GUIANA:** Régina, Nouragues, 28-Aug-2018, forest, bait (honey), J.L. Williams, F-JLW-HT-01 (USNM: USNMENT01129213, USNMENT01886899, USNMENT01886916); Cayenne, Botanical Gardens, 4.9401363 -52.3205913 ±10, 21-Aug-2018, gardens, hand, J.L. Williams, JLW180821-01 (USNM: USNMENT) USNMENT01129208; **GUADALOUPE:** Petit Bourg, 9-Apr-1977, W.H. Whitcomb, (FSCA: USNMENT01223889, USNMENT01223921); **NEVIS:** Prison Farm, 17.168 -62.571, elev. 264m, 15-May-2007, 26 min. up trail, J.K. Wetterer, JKW188 (USNM: USNMENT01129182); **ST. KITTS:** Old Road Bay, 17.318 -62.797, elev. 53m, 5-May-2007, roadside forest, J.K. Wetterer, JKW23 (USNM: USNMENT01129181); **ST. LUCIA:** Mamiku Garden, 13.864 -60.902, elev. 50m, 8-Jul-2006, J.K. Wetterer, JKW770 (USNM); **ST. VINCENT AND THE GRENADINES:** St. Vincent, Kingstown waterfront, 13.157 -61.231, elev. 5m, 9-Jun-004, J.K. Wetterer, JKW142 (USNM: USNMENT01129179); **TRINIDAD:** 10.597 -61.37, elev. 8m, 15-Sep-2003, 9km E bird sanctuary, La Solita Rd., J.K. Wetterer, JKW45 (USNM: USNMENT01129178).

**Etymology:** The species epithet *insularis* is derived from the Latin for "of islands," referring both to the species' native distribution in the Lesser Antilles and its apparent adaptation to primarily insular and coastal habitats.

**Notes:** This species is comprised of more compact specimens previously identified as *N. guatemalensis*. Compared with true *N. guatemalensis* (*sensu stricto*), *N. insularis* has a proportionately shorter mesosoma, scapes, and legs. Combined phylogenetic and morphometric evidence supports recognition of *N. insularis* as a distinct species, with a distribution restricted to the Lesser Antilles and the northern coast of South America (Trinidad and French Guiana).

### *Nylanderia nesiotis* (Wheeler 1919) stat. nov.

Figs. 27–29 (worker); Figs. 40–41 (queen); Figs. 46–47, 54–55, 58 (male)

*Prenolepis* (*Nylanderia*) *fulva* subsp. *nesiotis* Wheeler, 1919: 277 (w.q.m.). Lectotype worker (designated here; top specimen on pin), **ECUADOR:** Galápagos Islands, Santiago, F.X. Williams (CASC: CASTYPE00449) (examined). 3 paralectotype workers and 2 paralectotype males with same locality data as lectotype (CASC: CASTYPE00449; MCZC: MCZ-ENT21672) (examined).

*Paratrechina* (*Nylanderia*) *vividula* subsp. *edenensis* Linsley & Usinger, 1966: 175 (w.q.). Lectotype worker (designated here), **ECUADOR:** Galápagos, Eden Rock, W.M. Wheeler (MCZC: MCZ-ENT21674). 7 paralectotype workers, 1 paralectotype queen, same locality data as lectotype (MCZC). **SYN. NOV.**

**Worker diagnosis:** Body relatively robust; mesosoma short (BLI = 131–154), metatibia short (HTI = 109–130), scape short, surpassing posterior margin of head by less than half its length (SI = 126–141); body color light to medium brown; protrochanter, mesocoxa, and metacoxa yellow to yellow-brown; mesopleuron moderately to densely pubescent.

**Compare with:** *N. fulva, N. guatemalensis, N. pubens*

WORKER. *Measurements (n=44)*: TL: 1.9–3.2 (HL+WL=1.2–1.6); EL: 0.13–0.19; EW: 0.10–0.15; IOD: 0.28–0.38; HE: 0.00–0.02; HL: 0.56–0.71; HW: 0.47–0.63; HLA: 0.19–0.25; HLP: 0.23–0.29; SL: 0.63–0.81; PW: 0.33–0.50; MW: 0.21–0.31; PrW: 0.23–0.37; PDH: 0.15–0.26; PTW: 0.11–0.17; LHT: 0.54–0.76; WL: 0.64–0.89; GL: 0.67–1.77; SMC: 12–22; PMC: 2–5; MMC: 2–4. *Indices*: BLI: 131–154; CI: 84–91; EPI: 77–96; HTI: 109–130; REL: 23–28; SI: 126–141.

*Color:* light to medium brown; lighter yellow to yellow-brown antennae, mandibles, and tarsi; protrochanter, mesocoxa, and metacoxa whitish to pale yellow, strongly contrasting with mesosoma; overall cuticle smooth and shining, with no cuticular microsculpture and no iridescence. *Pilosity:* moderate to abundant suberect to erect setae on scape (SMC = 12–22), contrasting in length from fine, appressed hairs; dense cephalic pubescence covering all surfaces of head; pubescence on mesosoma primarily concentrated dorsally and often more sparsely distributed laterally on the pronotum and propodeum; mesopleuron moderately to densely pubescent across entire surface; gaster densely pubescent; no mesopleural setae; 2-3 small setae may be found posterolateral to propodeal spiracle; 1-3 pairs of small, erect setae on apex of petiole. *Head:* in full-face view, head longer than broad (CI = 84–91) and quadrate with rounded posterolateral corners and flattened posterior margin, with little to no medial emargination (HE = 0.00–0.01); scape relatively short and surpasses posterior margin of head by less than half its length (SI = 126–141); compound eye moderately sized to relatively large (REL = 22–27); compound eye positioned anterior to midline of head (EPI = 77–96); all three ocelli apparent, small, and evenly sized. *Mesosoma:* relatively stout

(BLI = 131–154); in profile view, anterior margin of mesonotum rising above posterior margin of pronotum; mesonotum flat to weakly rounded and not declining posteriorly into metanotal groove; metanotal groove shallow, with posterior margin of mesonotum discontinuous with metanotal area; propodeum low, rounded, and at lower height than promesonotum; dorsal face of propodeum about half as long as posterior face.

QUEEN. *Measurements (n=2)*: TL: 4.2–4.5 (HL+WL=2.3); EL: 0.27–0.28; HL: 0.85–0.87; HW: 0.84–0.85; SL: 0.93–0.94; LHT: 0.99–1.00; WL: 1.41–1.42; GL: 1.94–2.27. *Indices*: BLI: 167; CI: 97–100; HTI: 117–119; REL: 31–33; SI: 109–111.

*Color:* light to medium brown; mesocoxa and metacoxa yellow-brown to brown. *Pilosity*: most of body covered in moderate to dense pubescence. *Head:* about as broad as long (CI = 97–100) and quadrate, with distinct posterolateral corners and flattened posterior margin.

MALE. *Measurements (n=5)*: TL: 2.2–2.8 (HL+WL=1.3–1.6); EL: 0.20–0.24; HL: 0.54–0.61; HW: 0.48–0.58; SL: 0.71–0.81; LHT: 0.65–0.77; WL: 0.78–1.00; GL: 0.84–1.18. *Indices*: BLI: 161–179; CI: 88–94; HTI: 134–141; REL: 37–41; SI: 134–151.

*Color:* light to medium brown; mesocoxa and metacoxa yellow-brown to brown. *Pilosity:* dense pubescence on head, pronotum, mesonotum, propodeum, and gaster; pubescence on mesosoma concentrated dorsally and absent laterally on propodeum; mesopleuron sparsely pubescent, with pubescence limited at most to patch on ventral portion of katepisternum; macrosetae across entire body, including scape and genitalia, brownish and not dark and not strongly contrasting with surrounding cuticle. *Head:* slightly longer than broad (CI = 88–94) and quadrate, with distinct posterolateral corners and lightly convex to flattened posterior margin; compound eyes surpass lateral margins of head in full-face view; scapes surpass posterior margin of head by about a third of their length (SI = 134–151). *Mesosoma:* in profile view, propodeum angled with dorsal face about as long as posterior face. *Genitalia:* in ectal view, harpe broadly triangular, with large, evenly convex dorsal lobe and straight ventral margin (Fig. 58); in ventral view, ventromedial edge of basivolsella nearly straight anteriorly, gently and evenly curving posteriorly, and evenly rounded near base of gonossiculus (Fig. 55).

**Other material examined: ECUADOR:** Galápagos, Champion, -1.238217 -90.386247, elev. 20m, 19-May-2008, bait, R. Jimenez (CDRS: ICCDRS0010975, ICCDRS0010976, ICCDRS0010977, ICCDRS0010978, ICCDRS0010979); Galápagos, Eden, -0.561444 -90.5365, 11m, 18-Nov-2025, littoral, under rocky outcrop on shore, J.L. Williams, H. Herrera, JLW195 (USNM: USNMENT01886889); Galápagos, Fernandina, Punta Espinosa, -0.284028 -91.520361, 24-Jul-1992, dry zone, S. Abedrabbo, G5-F9-T10 (USNM: USNMENT01886713, USNMENT01886830); Galápagos, Fernandina, Punta Mangle Camp, De Laguna, -0.4495 -91.392306, 16-Jun-1998, pitfall, L. Roque, C. Causton (CDRS: ICCDRS0001085, ICCDRS0001086, ICCDRS0001087, ICCDRS0001088, ICCDRS0001098, ICCDRS0001099, ICCDRS0001100, ICCDRS0001103, ICCDRS0001104, ICCDRS0001105, ICCDRS0001106, ICCDRS0001107, ICCDRS0001108, ICCDRS0001109, ICCDRS0001110); Galápagos, Fernandina, Punta Mangle, -0.445361 -91.393917, 14-Jun-1998, *Conocarpus erectus*, sweep, L. Roque, C. Causton (CDRS: ICCDRS0001089, ICCDRS0001090, ICCDRS0001091, ICCDRS0001092, ICCDRS0001093); Galápagos, Fernandina, Punta Mangle, -0.4495 -91.392306, 14-Jun-1998, sticky trap, L. Roque, C. Causton (CDRS: ICCDRS0001101, ICCDRS0001102); Galápagos, Fernandina, Punta Mangle, Copiano, -0.353 -91.3912, 16-Jun-1998, *Conocarpus erectus*, pitfall, L. Roque, C. Causton (CDRS: ICCDRS0001094, ICCDRS0001095); Galápagos, Floreana, -1.277625 -90.478089, elev. 50m, 9-Jun-1992, low arid zone, bait, M.T. Lasso, G5-F14-T14 (USNM: USNMENT01886734); Galápagos, Floreana, C. Laguna, -1.269983 -90.388103, 17-Jan-2011, inside crater, pitfall, H. Herrera (CDRS: ICCDRS0040216); Galápagos, Floreana, G5-F14-T17 (USNM: USNMENT01132070, USNMENT01132094, USNMENT01886524, USNMENT01886810, USNMENT01886825); Galápagos, Floreana, Islote Gardner, -1.198056 -90.176111, 4-Jul-2006, hand, H. Herrera *et al.*, HWH173 (CDRS: ICCDRS0003321, ICCDRS0003377); Galápagos, Floreana, Islote Gardner, -1.332806 -90.299556, elev. 25m, 19-May-2008, aspirator, H. Herrera, HWH224 (CDRS: ICCDRS0011007, ICCDRS0011008, ICCDRS0011009, ICCDRS0011010, ICCDRS0011011, ICCDRS0011012, ICCDRS0011013, ICCDRS0011014, ICCDRS0011015, ICCDRS0011016, ICCDRS0010956, ICCDRS0010957, ICCDRS0010958, ICCDRS0010959, ICCDRS0010960, ICCDRS0010961, ICCDRS0010962, ICCDRS0010963, ICCDRS0010964, ICCDRS0010965); Galápagos, Floreana, Loberia, 5-Aug-1992, S. Abedrabbo, G5-F9-T12 (USNM: USNMENT01886771); Galápagos, Floreana, Loberia, 8-May-1992, S. Abedrabbo, G5-F9-T22 (USNM: USNMENT01886728, USNMENT01886795); Galápagos, Floreana, Pampa Larga, -1.327439 -90.4532, 12-Jan-2011, aspirator, H. Herrera, HWH295 (CDRS: ICCDRS00040217); Galápagos, isabela, -0.91528 -91.07944, 20-Feb-1996, on *Scalesia cordata* flower, P. Delgado, ANTC8219 (CDRS:

CASENT0173236); Galápagos, Isabela, 8-Sep-1988, pitfall, S. Abedrabbo, G5-F17-T68 (USNM: USNMENT01132069, USNMENT01886714, USNMENT01886754, USNMENT01886777); Galápagos, Isabela, G5-F17-T45 (USNM: USNMENT01886750, USNMENT01886783); Galápagos, Isabela, Playa Tortuga Negra, 8-Feb-1997, mangrove, pitfall, L. Roque (CDRS: ICCDRS0000124, ICCDRS0000125, ICCDRS0000149); Galápagos, Isabela, Playa Tortuga Negra, 7-Feb-1997, mangrove, pitfall, L. Roque (CDRS: ICCDRS0003355, ICCDRS0003356, ICCDRS0003367); Galápagos, Isabela, Punta Estrado, 3-Aug-2002, bait, R. Boada, G5-F19-T7 (USNM: USNMENT01132062); Galápagos, Isabela, Punta Garcia, -0.300752 -91.10726, elev. 0m, 3-Aug-2002, bait, R. Boada, G5-F19-T34 (USNM: USNMENT01132060, USNMENT01886540, USNMENT01886826); Galápagos, Isabela, Punta Garcia, -0.30472222 -91.1044444, elev. 0m, 3-Aug-2002, pitfall, R. Boada, G5-F19-T16 (USNM: USNMENT01132102); Galápagos, Isabela, Punta Garcia, 14-Jul-2002, bait, R. Boada, G5-F19-T40 (USNM: USNMENT01132067, USNMENT01886781); Galápagos, Isabela, Punta Garcia, 3-Aug-2002, bait, R. Boada (USNM: USNMENT01886787, USNMENT01886788, USNMENT01886789); Galápagos, Isabela, Punta Garcia, 3-Aug-2002, bait, R. Boada, G5-F19-T2 (USNM: USNMENT01886539, USNMENT01886715, USNMENT01886792); Galápagos, Isabela, Punta Garcia, 3-Aug-2002, bait, R. Boada, G5-F19-T31 (USNM: USNMENT01132063, USNMENT01132079); Galápagos, Isabela, Punta Garcia, 3-Aug-2002, pitfall, R. Boada, G5-F19-T15 (USNM: USNMENT01132050, USNMENT01886544, USNMENT01886804); Galápagos, Isabela, Punta Garcia, 3-Aug-2002, pitfall, R. Boada, G5-F19-T20 (USNM: USNMENT01886739); Galápagos, Isabela, Punta Garcia, 3-Aug-2002, R. Boada (CDRS: ICCDRS0003337, ICCDRS0003383); Galápagos, Isabela, Punta Garcia, 3-Aug-2002, R. Boada, G5-F19-T25 (USNM: USNMENT01132076); Galápagos, Isabela, Punta Garcia, 3-Jul-2002, bait, R. Boada, G5-F19-T37 (USNM: USNMENT01886807); Galápagos, Isabela, Punta Garcia, Volcán Alcedo, -0.298611111 -91.10555556, elev. 0m, Aug-2002, littoral zone, bait, R. Boada, G5-F19-T13 (USNM: USNMENT01132047, USNMENT01886720); Galápagos, Isabela, S. Negra/Pampa, -0.847833 -91.048689, elev. 700m, 13-Jun-1987, pitfall, S. Abedrabbo, G5-F9-T2 (USNM: USNMENT01886812, USNMENT01666912); Galápagos, Isabela, S. Negra/Pampa, 8-Sep-1988, pitfall, S. Abedrabbo, G5-F17-T68 (USNM: USNMENT01886799); Galápagos, Isabela, S. Negra/Pampa, 9-Mar-1988, S. Abedrabbo, G5-F5-T17 (USNM: USNMENT01886746); Galápagos, Isabela, Sierra Negra, -0.821111 -90.142778, Jun-1987, pitfall, S. Abedrabbo (CDRS: ICCDRS0002571); Galápagos, Isabela, V. Alcedo, 18-Apr-1998, low arid zone, pitfall, L. Roque, #98.17 (CDRS: ICCDRS0003372); Galápagos, Isabela, V. Alcedo, elev. 850m, 21-Apr-1998, low arid zone, Winkler, L. Roque, #98.15 (CDRS: ICCDRS0003395); Galápagos, Isabela, V. Alcedo, elev. 850m, 22-Nov-1997, yellow trap, L. Roque (CDRS: ICCDRS0003336); Galápagos, Isabela, V. Alcedo, elev. 850m, 22-Nov-1999, yellow trap, L. Roque, P. Viteri (CDRS: ICCDRS0003335); Galápagos, Isabela, V. Alcedo, Guayabillo, pitfall, L. Roque, X98 (CDRS: ICCDRS0003371); Galápagos, Isabela, V. Sierra Negra, Bosque de los Niños, Jan-1996, on flowers of S. cordata, P. Delgado, F#14 (CDRS: ICCDRS0000111); Galápagos, Isabela, Volcán Alcedo, 200, 4-Apr-1996, L. Baert, #96/102 (CDRS: ICCDRS0003352); Galápagos, Isabela, Volcán Alcedo, -0.360290075705 -91.0616560955, elev. 200m, 11-May-2000, dry zone, hand, L. Roque, G5-F8-T8 (USNM: USNMENT01886711, USNMENT01886779); Galápagos, Isabela, Volcán Alcedo, -0.416047 -91.076775, elev. 900m, 13-May-2000, fern-sedge zone, leaf litter, L. Roque, G5-F8-T3 (USNM: USNMENT01886727, USNMENT01886833); Galápagos, Isabela, Volcán Alcedo, 14-May-2000, L. Roque (CDRS: ICCDRS0003347); Galápagos, Isabela, Volcán Alcedo, Arida Alta, -0.390333 -90.996083, 13-Oct-1999, high arid, pitfall, L. Roque (CDRS: ICCDRS0036858); Galápagos, Isabela, Volcán Alcedo, elev. 1025m, 7-Feb-1991, pitfall, S. Abedrabbo, G5-F9-T15 (USNM: USNMENT01132099); Galápagos, Isabela, Volcán Alcedo, elev. 800m, 2-Apr-1996, pitfall, L. Baert, #96/92 (CDRS: ICCDRS0003349); Galápagos, Isabela, Volcán Alcedo, elev. 900m, 13-May-2000, litter, L. Roque (CDRS: ICCDRS0003370); Galápagos, Isabela, Volcán Alcedo, Guayavillos, -0.416047 -91.076775, elev. 200m, 10-May-2000, humid zone, leaf litter, leaf litter, L. Roque, G5-F8-T2 (USNM: USNMENT01886732); Galápagos, Isabela, Volcán Alcedo, Guayavillos, -0.416047 -91.076775, elev. 900m, 10-May-2000, humid zone, leaf litter, L. Roque, G5-F8-T1 (USNM: USNMENT01886532, USNMENT01886828); Galápagos, Isabela, Volcán Alcedo, Guayavillos, -0.416047 -91.076775, elev. 900m, 10-May-2000, leaf litter, L. Roque, G5-F8-T1 (USNM: USNMENT01886712, USNMENT01886784); Galápagos, Isabela, Volcán Sierra Negra, -0.847833 -91.048689, elev. 700m, 16-Sep-1990, pitfall, S. Abedrabbo, G5-F5-T36 (USNM: USNMENT01886735, USNMENT01886786); Galápagos, Isabela, Volcán Sierra Negra, -0.847833 -91.048689, elev. 700m, 8-Sep-1988, S. Abedrabbo, G5-F5-T27 (USNM: USNMENT01886753); Galápagos, Isabela, Volcán Sierra Negra, -0.847833 -91.048689, elev. 700m, fern-sedge zone, pitfall, S. Abedrabbo, G5-F9-T2 (USNM: USNMENT01886534); Galápagos, Islote Cousin, 18-Aug-2000, pitfall, A. Mieles (CDRS:

ICCDRS0003381); Galápagos, Marchena, Playa Negra, 0.300037 -90.50689, 25-May-2003, pitfall, A. Mieles, N. Chasiliquin, J. Key (CDRS: ICCDRS0039563); Galápagos, Marchena, Playa Negra, 0.300037 -90.50689, 6-Mar-2007, pitfall, A. Mieles, N. Chasiliquin, J. Key (CDRS: ICCDRS00059564); Galápagos, Marchena, Playa Negra, 0.300123 -90.504523, 25-May-2003, pitfall, A. Mieles, N. Chasiliquin, J. Key (CDRS: ICCDRS0039562); Galápagos, Marchena, Playa Negra, 0.300798 -90.505633, 7-Apr-2004, pitfall, A. Mieles, H. Herrera, N. Chasiliquin (CDRS: ICCDRS0039559); Galápagos, Marchena, Playa Negra, 0.302017 90.505717, 27-Oct-2002, pitfall, L. Roque, A. Mieles, R. Boada (CDRS: ICCDRS0039553); Galápagos, Marchena, Playa Negra, 0.30207 90.507865, 25-May-2003, pitfall, A. Mieles, N. Chasiliquin, J. Key (CDRS: ICCDRS0039557, ICCDRS0039558); Galápagos, Marchena, Playa Negra, 0.30225 -90.50355, 28-Oct-2002, pitfall, L. Roque, A. Mieles, R. Boada (CDRS: ICCDRS0039549); Galápagos, Marchena, Playa Negra, 0.303743 -90.507983, 28-May-2003, pitfall, A. Mieles, N. Chasiliquin, J. Key (CDRS: ICCDRS0039554); Galápagos, Marchena, Playa Negra, 0.30427 90.509732, 28-May-2003, pitfall, A. Mieles, N. Chasiliquin, J. Key (CDRS: ICCDRS0039551); Galápagos, Marchena, Playa Negra, 0.305097 -90.503923, 10-Apr-2004, pitfall, A. Mieles, H. Herrera, N. Chasiliquin (CDRS: ICCDRS0039561); Galápagos, Marchena, Playa Negra, 0.305097 -90.503923, 9-Mar-2007, berlese, A. Mieles, A. Ulloa (CDRS: ICCDRS0039546); Galápagos, Marchena, Playa Negra, 0.305467 -90.505532, 14-Apr-2006, pitfall, R. Azuero, A Mieles (CDRS: ICCDRS0039555); Galápagos, Marchena, Playa Negra, 0.305467 -90.505532, 8-Apr-2002, pitfall, G. Estevez, A. Mieles, R. Boada (CDRS: ICCDRS0039547); Galápagos, Marchena, Playa Negra, 0.305955 -90.510055, 14-Apr-2006, pitfall, R. Azuero, A Mieles (CDRS: ICCDRS0039556); Galápagos, Marchena, Playa Negra, 0.305955 -90.510055, 28-May-2003, pitfall, A. Mieles, N. Chasiliquin, J. Key (CDRS: ICCDRS0039552); Galápagos, Marchena, Playa Negra, 0.305955 -90.510055, 8-Apr-2002, pitfall, G. Estevez, A. Mieles, R. Boada (CDRS: ICCDRS0039548, ICCDRS0039550); Galápagos, Pinta, 200, 21-Mar-1986, littoral zone, pitfall, L. Baert (CDRS: ICCDRS0003331); Galápagos, Pinzón, -0.598832 -90.65458, 8m, 18-Nov-2025, littoral, nest entrances in stony ground under leaf litter in shade of rock wall, J.L. Williams, H. Herrera, JLW193 (USNM: USNMENT01886888); Galápagos, Pinzón, -0.603139 -90.666944, 250m, 17-Nov-2025, arid, on trunk and inside rotten cactus fruit of *Opuntia*, J.L. Williams, H. Herrera, JLW186 (USNM: USNMENT01886884); Galápagos, Pinzón, -0.603833 -90.667944, 250m, 17-Nov-2025, arid, on *Opuntia*, J.L. Williams, H. Herrera, JLW187 (USNM: USNMENT01886885); Galápagos, Pinzón, -0.604111 -90.668444, 250m, 17-Nov-2025, arid, under stones at base of *Opuntia*, J.L. Williams, H. Herrera, JLW191 (USNM: USNMENT01886887); Galápagos, Pinzón, -0.605667 -90.669528, 250m, 17-Nov-2025, arid, under stones near roots, J.L. Williams, H. Herrera, JLW189 (USNM: USNMENT01886886); Galápagos, Rábida, -0.399527 -90.709833, 12-May-1981, dry zone, Y. Lubin, G5-F15-T8 (USNM: USNMENT01886764, USNMENT01886765, USNMENT01886766); Galápagos, Rábida, -0.399527 -90.709833, 12-May-1981, dry zone, Y. Lubin, G5-F15-T9 (USNM: USNMENT01886545, USNMENT01886741, USNMENT01886780); Galápagos, Rábida, -0.407833 -90.707889, 214m, 15-Nov-2025, arid, in soil at base of arrayancillo, J.L. Williams, H. Herrera, JLW169 (USNM: USNMENT01886880); Galápagos, Rábida, nr. flamingo lagoon, -0.399667 -90.708639, 10m, 16-Nov-2025, mangrove, forager in damp soil, J.L. Williams, H. Herrera, JLW175 (USNM: USNMENT01886881); Galápagos, Rábida, nr. flamingo lagoon, -0.399667 -90.708639, 10m, 16-Nov-2025, mangrove, foragers in mangrove leaf litter, J.L. Williams, H. Herrera, JLW176 (USNM: USNMENT01886882); Galápagos, Rábida, nr. flamingo lagoon, -0.399667 -90.708639, 10m, 16-Nov-2025, mangrove, nest under rotten log; excavated from mangrove root system, J.L. Williams, H. Herrera, JLW177 (USNM: USNMENT01886883); Galápagos, Rábida, nr. flamingo lagoon, -0.399917 -90.708611, 10m, 15-Nov-2025, mangrove, nest in moist soil under dry log, J.L. Williams, H. Herrera, JLW167 (USNM: USNMENT01886879); Galápagos, San Cristóbal, El Junco, 650, 21-Feb-1992, humid zone, pitfall, S. Abedrabbo, S. Gavilanes (CDRS: ICCDRS0003332, ICCDRS0003345, ICCDRS0003360, ICCDRS0003365); Galápagos, San Cristóbal, El Junco, -0.894611 -89.482583, elev. 630m, 21-Feb-1992, humid zone, pitfall, S. Abedrabbo, S. Gavilanes, G5-F14-T30 (USNM: USNMENT01886736, USNMENT01886801); Galápagos, San Cristóbal, El Junco, 21-Feb-1992, pitfall, S. Abedrabbo, S. Gavilanes (CDRS: ICCDRS0003334, ICCDRS0003391); Galápagos, San Cristóbal, elev. 540m, 3-Mar-1988, pitfall, B. Novak, #437/'88 (CDRS: ICCDRS0003362); Galápagos, San Cristóbal, La Toma, 530, 20-Feb-1992, humid zone, pitfall, S. Abedrabbo, S. Gavilanes (CDRS: ICCDRS0003330); Galápagos, San Cristóbal, La Toma, -0.910111 -89.507305, elev. 530m, 20-Feb-1992, humid zone, pitfall, S. Abedrabbo, S. Gavilanes, G5-F15-T2 (USNM: USNMENT01886743, USNMENT01886821); Galápagos, San Cristóbal, Loberia, 23-Feb-1992, pitfall, S. Abedrabbo, S. Gavilanes (CDRS: ICCDRS0000283); Galápagos, San Cristóbal, Sendera a loberia, -0.922528 -89.615406, 14-Jul-2008, aspirator, J. Loaiza (CDRS: ICCDRS0011035); Galápagos, San Cristóbal, Zona Humeda, 21-Feb-1992, humid zone, pitfall, S. Abedrabbo, S. Gavilanes (CDRS: ICCDRS0003339, ICCDRS0003340, ICCDRS0003361, ICCDRS0003364); Galápagos, San Cristóbal, Zona Humeda, Feb-1992, humid zone, pitfall, S. Abedrabbo, S. Gavilanes (CDRS: ICCDRS0003338, ICCDRS0003354); Galápagos, Santa Cruz, 17-Apr-2007, A. Mieles (CDRS: ICCDRS0003322); Galápagos, Santa Cruz, 25-Mar-1986, sphagnum, G5-F15-T13 (USNM: USNMENT01886726, USNMENT01886778); Galápagos, Santa Cruz, 8-Oct-1993, pitfall, G5-F17-T29 (USNM: USNMENT01132046, USNMENT01186805); Galápagos, Santa Cruz, Barranco, 2-Jun-2024, A. Mieles, TBN4 (CDRS: ICCDRS0038743); Galápagos, Santa Cruz, Cerro Crocker Cumbre, 15-Sep-1994, pitfall, J. Olmedo, N. Criollo (CDRS: ICCDRS0001315); Galápagos, Santa Cruz, Cerro Crocker, -0.642472222222222 -90.3260277777778, elev. 864m, 24-Nov-2012, humid zone, H.W. Herrera, HWH348 (USNM: USNMENT01132068, USNMENT01132077, USNMENT01886759, USNMENT01886760, USNMENT01886813); Galápagos, Santa Cruz, Cerro Crocker, -0.642561111 -90.32576111, elev. 881m, 9-Jan-2001, humid zone, pitfall, G. Estévez, G6-F1-T3 (USNM: USNMENT01132048, USNMENT01886814); Galápagos, Santa Cruz, Cerro Crocker, -0.642561111111111 -90.3257611111111, elev. 881m, 9-Jan-2001, pitfall, G. Estévez, G6-F1-T18 (USNM: USNMENT01886547, USNMENT01886816); Galápagos, Santa Cruz, Cerro Crocker, -1.07378 -91.085, elev. 881m, 9-Jan-2001, pitfall, G. Estévez, G6-F2-T11 (USNM: USNMENT01132078, USNMENT01886744, USNMENT01886827); Galápagos, Santa Cruz, Cerro Crocker, 15-Aug-1992, sphagnum, pitfall, S. Abedrabbo, J. Soriano (CDRS: ICCDRS0003373); Galápagos, Santa Cruz, Cerro Crocker, 16-Sep-1992, pitfall, S. Abedrabbo, S. Gavilanes, G5-F15-T11 (USNM: USNMENT01132064, USNMENT01886541, USNMENT01886798); Galápagos, Santa Cruz, ECCD, -0.742194 -90.303611 10, 9-Dec-2005, H. Herrera (CDRS: ICCDRS0003333, ICCDRS0003351); Galápagos, Santa Cruz, ECCD, -0.74222 -90.30361, elev. 10m, 19-Jun-2005, hand, H. Herrera, ANTC8221 (CDRS: CASENT0173238); Galápagos, Santa Cruz, El Garrapatero, -0.693822222222222 -90.2210777777778, elev. 0m, 10-Oct-2001, littoral zone, pitfall, G. Estévez, G6-F1-T11 (USNM: USNMENT01886809); Galápagos, Santa Cruz, km 27 vía Baltra, -0.584 -90.3551388888889, 17-Oct-2001, dry zone, pitfall, G. Estévez, G6-F1-T28 (USNM: USNMENT01132066); Galápagos, Santa Cruz, Los Gemelos, 630, 13-Feb-1988, pitfall, L. Baert, #307/'88 (CDRS: ICCDRS0003346); Galápagos, Santa Cruz, Los Gemelos, -0.624269444 -90.38573889, elev. 580m, 17-Sep-2001, G. Estévez, G6-F1-T17 (USNM: USNMENT01886549); Galápagos, Santa Cruz, Los Gemelos, -0.624269444444444 -90.3857388888889, 17-Jan-2003, G. Estévez, G6-F1-T30 (USNM: USNMENT01886751, USNMENT01886806, USNMENT01886724, USNMENT01886817, USNMENT01886818); Galápagos, Santa Cruz, Los Gemelos, -0.624269444444444 -90.3857388888889, elev. 580m, 17-May-2001, G. Estévez, G6-F1-T37 (USNM: USNMENT01132071, USNMENT01886815); Galápagos, Santa Cruz, Los Gemelos, -0.625913888888889 -90.3850388888889, 11-Apr-2015, humid zone, P. Schmidt, F213T778 (USNM: USNMENT01132093, USNMENT01132097, USNMENT01886523, USNMENT01886530, USNMENT01886537, USNMENT01886733, USNMENT01886774); Galápagos, Santa Cruz, Los Gemelos, -0.625913888888889 -90.3850388888889, 19-Mar-2015, humid zone, P. Schmidt, F213T747 (USNM: USNMENT01132101, USNMENT01886528, USNMENT01886772, USNMENT01886773); Galápagos, Santa Cruz, Los Gemelos, -0.625913888888889 -90.3850388888889, 19-Mar-2015, humid zone, P. Schmidt, F213T750 (USNM: USNMENT01132091, USNMENT01886527, USNMENT01886775); Galápagos, Santa Cruz, Los Gemelos, -0.625913888888889 -90.3850388888889, 20-Mar-2015, humid zone, P. Schmidt, F213T856 (USNM: USNMENT01886767, USNMENT01886768, USNMENT01886769); Galápagos, Santa Cruz, Los Gemelos, -0.625913888888889 -90.3850388888889, 21-Mar-2015, humid zone, P. Schmidt, F213T775 (USNM: USNMENT01132095, USNMENT01886529); Galápagos, Santa Cruz, Los Gemelos, -0.625913888888889 -90.3850388888889, 23-Mar-2015, humid zone, P. Schmidt, F213T765 (USNM: USNMENT01886770); Galápagos, Santa Cruz, Los Gemelos, -0.625913888888889 -90.3850388888889, 23-Mar-2015, humid zone, P. Schmidt, F213T816 (USNM: USNMENT01886525, USNMENT01886526, USNMENT01886538, USNMENT01886776); Galápagos, Santa Cruz, Los Gemelos, 17-Jan-2001, pitfall, G. Estévez (CDRS: ICCDRS0003369); Galápagos, Santa Cruz, Los Gemelos, 27-Aug-1997, peanut butter bait, L. Roque (CDRS: ICCDRS0001070); Galápagos, Santa Cruz, Marchena, Playa de los Muertos, 16-Aug-1998, aspirator, L. Roque (CDRS: ICCDRS0003375); Galápagos, Santa Cruz, Media Luna, elev. 630m, Dec-1992, pitfall, J. Palacios (CDRS: ICCDRS0003342); Galápagos, Santa Cruz, Mirador, -0.662402778 -90.32736944, elev. 490m, Dec-1992, humid zone, pitfall, J. Palacios, G5-F17-T10 (USNM: USNMENT01886731); Galápagos, Santa Cruz, Mirador, -0.662402778 -90.32736944, elev. 490m, Dec-1992, humid zone, pitfall, J. Palacios, G5-F17-T16 (USNM: USNMENT01132072, USNMENT01886823); Galápagos, Santa Cruz, Mirador, elev. 490m, Dec-1992, pitfall, J. Palacios, G5-F17-T17 (USNM: USNMENT01132096, USNMENT01886790); Galápagos, Santa Cruz, Muelle cana del Itabaca, -0.487222 -90.279722, elev. 2m, 5-Mar-2010, littoral zone, aspirator, H.W. Herrera, HWH282 (USNM: USNMENT01132073, USNMENT01886543, USNMENT01886782); Galápagos, Santa Cruz, Parque Nacional Galápagos, Los Gemelos, Cerro Maternidad, -0.623654 -90.38396, elev. 611m, 27-Nov-2019, J. Gavilanez-Slone, Y.M. Campaña, 2019 B EC-GA-CZ C75 (USNM: USNMENT01886536); Galápagos, Santa Cruz, Parque Nacional Galápagos, Santa Cruz Hwy/E5, entrada zona de caceria, -0.575769 -90.34355, elev. 284m, 27-Nov-2019, J. Gavilanez-Slone, Y.M. Campaña, 2019 B EC-GA-CZ-C65 (USNM: USNMENT01132043); Galápagos, Santa Cruz, Parque Nacional Galápagos, vía Playa Garrapatero/E5, por parqueadero, -0.689607 -90.223323, elev. 13m, 28-Nov-2019, J. Gavilanez-Slone, Y.M. Campaña, EC-GA-CZ-C93 (USNM: USNMENT01886520, USNMENT01132030); Galápagos, Santa Cruz, Picachos, -0.60278 -91.35333, elev. 670m, 1-Jun-1992, pitfall, J. Palacios, ANTC8220 (CDRS: CASENT0173237); Galápagos, Santa Cruz, Picachos, -0.64544444 -90.31477778, elev. 630m, 8-Sep-1988, humid zone, pitfall, J. Palacios, G5-F17-T4 (USNM: USNMENT01886748, USNMENT01886749, USNMENT01886832, USNMENT01886834, USNMENT01886840); Galápagos, Santa Cruz, Picachos, -0.64544444 -90.31477778, elev. 630m, Dec-1992, humid zone, pitfall, J. Palacios, G5-F17-T5 (USNM: USNMENT01886522); Galápagos, Santa Cruz, Picachos, -0.648694 -90.3113, elev. 630m, Dec-1992, humid zone, pitfall, J. Palacios, G5-F17-T11 (USNM: USNMENT01132065, USNMENT01886824); Galápagos, Santa Cruz, Picachos, -0.648694444 -90.3113, elev. 630m, Dec-1992, humid zone, pitfall, S. Paludos, G5-F17-T7 (USNM: USNMENT01886737); Galápagos, Santa Cruz, Picachos, -0.648694444444444 -90.3113, elev. 630m, Dec-1992, humid zone, pitfall, J. Palacios, FF-5.70 (USNM: USNMENT01132098, USNMENT01886829); Galápagos, Santa Cruz, Picachos, elev. 630m, Dec-1992, pitfall, J. Palacios (CDRS: ICCDRS0003376, ICCDRS0003378, ICCDRS0003379, ICCDRS0003393, ICCDRS0003350, ICCDRS0003328, ICCDRS0003382, ICCDRS0003392, ICCDRS0003394); Galápagos, Santa Cruz, Picachos, elev. 670m, Jun-1992, pitfall, J. Palacios (CDRS: ICCDRS0003386, ICCDRS0003326, ICCDRS0003357, ICCDRS0003384); Galápagos, Santa Cruz, Puerto Ayora, 13-Jan-1991, S. Abedrabbo (CDRS: ICCDRS0003358); Galápagos, Santa Cruz, Puerto Ayora, ECCD, -0.7381111 -90.30170556, elev. 15m, 10-Oct-1992, dry zone, pitfall, S. Abedrabbo, S. Gavilanes, G5-F17-T21 (USNM: USNMENT01886721, USNMENT01886808); Galápagos, Santa Cruz, Puerto Ayora, Hotel Fernandina, 9-Jul-1992, pitfall, S. Abedrabbo, S. Gavilanes, G5-F17-T71 (USNM: USNMENT01886716, USNMENT01886797); Galápagos, Santa Cruz, Puntudo, -0.645152778 -90.33688888, 17-Nov-1991, J. Soriano, G5-F9-T16 (USNM: USNMENT01886548); Galápagos, Santa Cruz, Reserva de Tortugas, El Chato, -0.671605556 -90.43799722, elev. 225m, 10-Jan-2001, pitfall, G. Estévez, G6-F2-T5 (USNM: USNMENT01886546); Galápagos, Santa Cruz, Tortuga Bay, -0.760216667 -90.33260556, elev. 2m, 7-Dec-1994, pitfall, N. Criollo, G5-F13-T11 (USNM: USNMENT01886755); Galápagos, Santa Cruz, Tortuga Bay, 13-Oct-1991, G5-F13-T2 (USNM: USNMENT01132049); Galápagos, Santa Cruz, Tortuga Bay, 16-Jun-1993, pitfall, S. Abedrabbo, J. Soriano (CDRS: ICCDRS0003327, ICCDRS0003329, ICCDRS0003344); Galápagos, Santa Cruz, Tortuga Bay, 20-Feb-1992, pitfall, S. Abedrabbo, S. Gavilanes (CDRS: ICCDRS0000251, ICCDRS0000253); Galápagos, Santa Cruz, Tortuga Bay, 22-Nov-1991, S. Abedrabbo, G5-F9-T13 (USNM: USNMENT01132092, USNMENT01886802, USNMENT01886803); Galápagos, Santa Cruz, Tortuga Bay, 23-May-2024, A. Mieles, TTN1 (CDRS: ICCDRS0038737); Galápagos, Santa Cruz, Tortuga Bay, 25-Jul-1991, pitfall, S. Abedrabbo, J. Soriano (CDRS: ICCDRS0003374); Galápagos, Santa Cruz, Tortuga Bay, 25-Nov-1989, R. Meier, G5-F9-T4 (USNM: USNMENT01886740, USNMENT01886747); Galápagos, Santa Cruz, Tortuga Bay, 26-Apr-1992, pitfall, S. Abedrabbo, S. Caullauae, G5-F17-T62 (USNM: USNMENT01886742, USNMENT01886800); Galápagos, Santa Cruz, Tortuga Bay, 3-Jun-1992, C. Ponce, G5-F9-T5 (USNM: USNMENT01886730, USNMENT01886831); Galápagos, Santa Cruz, Tortuga Bay, 7-Jan-1995, N. Criollo, G5-F13-T12 (USNM: USNMENT01886531); Galápagos, Santa Cruz, Tortuga Bay, pitfall, G5-F13-T5 (USNM: USNMENT01886761); Galápagos, Santa Fe, -0.800607 -90.044317, 11-Dec-1986, G5-F16-T44 (USNM: USNMENT01132061, USNMENT01886762, USNMENT01886763); Galápagos, Santa Fe, 10-Dec-1986, M.A. Prieto, G5-F16-T38 (USNM: USNMENT01886722, USNMENT01886819); Galápagos, Santa Fe, 11-Dec-1986, M.A. Prieto, G5-F16-T10 (USNM: USNMENT01886719, USNMENT01886796); Galápagos, Santa Fe, 11-Dec-1986, M.A. Prieto, G5-F16-T20 (USNM: USNMENT01886723); Galápagos, Santa Fe, 11-Dec-1986, M.A. Prieto, G5-F16-T35 (USNM: USNMENT01886752, USNMENT01886811); Galápagos, Santa Fe, 1986, M.A. Prieto, G5-F16-T46 (USNM: USNMENT01886718, USNMENT01886785); Galápagos, Santa Fe, 1986, M.A. Prieto, G5-F16-T56 (USNM: USNMENT01886725); Galápagos, Santa Fe, 19-Dec-1986, M.A. Prieto, G5-F21-T1 (USNM: USNMENT01886756); Galápagos, Santa Fe, Noreste, -0.81247782493 -90.0467871717, elev. 100m, 25-Mar-1986, dry zone, L. Baert, G5-F7-T14 (USNM: USNMENT01886717); Galápagos, Santa Fe, Noreste, 25-Mar-1986, M. Prieto (CDRS: ICCDRS0003388, ICCDRS0003385); Galápagos, Santa Fe, Noreste, Mar-1986, G5-F7-T26 (USNM: USNMENT01886533, USNMENT01886794); Galápagos, Santa Fe, Sector Turistico, 1-Apr-1992, S. Abedrabbo, G5-F9-T8 (USNM: USNMENT01886542); Galápagos, Santiago, Causin, -0.23555 -90.5746, 22-Aug-2000, pitfall, A. Mieles, G1-F1-T5 (USNM: USNMENT01132045); Galápagos, Santiago, Causin, -0.235638888888889 -90.57475, 18-Aug-2000, A. Mieles, G1-F1-T4 (USNM: USNMENT01886745, USNMENT01886791); Galápagos, Santiago, Causin, -0.235638888888889 -90.57475, 18-Aug-2000, A. Mieles, G1-F1-T6 (USNM: USNMENT01886729); Galápagos, Santiago, Causin, -0.235638888888889 -90.57475, 22-Aug-2000, dry zone, pitfall, A. Mieles, G1-F1-T1 (USNM: USNMENT01886738, USNMENT01886793); Galápagos, Santiago, Causin, -0.235833 -90.5746, 22-Aug-2000, pitfall, A. Mieles, G1-F1-T2 (USNM: USNMENT01132103, USNMENT01886820); Galápagos, Santiago, Playa Espumilla, elev. 5m, 4-Apr-1992, edge young lava flow, blue cheese bottle traps, S. Peck, #92-99 (USNM: USNMENT01132036); Galápagos, Saymour Norte, 24-Feb-1998, Winkler, L. Roque (CDRS: ICCDRS0003366, ICCDRS0003343, ICCDRS0000749); Galápagos, Sombrero Chino, 27-Jun-1999, M.L. Johnson (CDRS: ICCDRS0001312); Galápagos, Zona Arida Baja, 12-Dec-1999 (CDRS: ICCDRS0003380); Galápagos, Zona Arida Baja, 12-Oct-1999, pitfall (CDRS: ICCDRS0003389).

**Notes:** The overall size of *N. nesiotis* is variable (TL = 1.9–3.2), and although it is typically somewhat larger, its body proportions are like those of *N. insularis* and not like those of *N. guatemalensis* (Figs. 6–11). Notably, like *N. insularis*, *N. nesiotis* is distinctly less gracile than *N. guatemalensis*. The mesosoma of *N. nesiotis* also bears moderate to dense pubescence across its entire surface, including the mesopleuron, whereas other *N. guatemalensis* complex species lack mesopleural pubescence. In a *N. nesiotis* colony from James (Santiago) Island, F. X. Williams observed six myrmecophilous bethylid wasps (Wheeler 1919), which were subsequently described as a new species (Brues 1919), currently recognized as *Sclerodermus galapagensis* Brues. *Nylanderia nesiotis* exhibits a preference for wet habitats across the archipelago, occurring most abundantly in mangrove systems, where foragers are common in the leaf litter and colonies excavate nests along mangrove root networks in damp soil. During fieldwork, when a root was pulled from the ground, workers erupted rapidly from the disturbed nest. Although primarily associated with moist environments, the species also occurs in arid zones, where it nests at the bases of endemic plants such as the leatherleaf (*Maytenus octogona* (L'Hér.) DC) and the Galápagos prickly pear cactus (*Opuntia galapageia* Henslow). Workers have been observed foraging actively on cactus pads, and in one instance numerous foragers burst from a decaying cactus fruit when it was broken open. Colonies appear to comprise no more than a few hundred workers, and the workers themselves move with notable speed and erratic motion reminiscent of *N. fulva*.

### *Nylanderia silvestrii* (Emery, 1906)

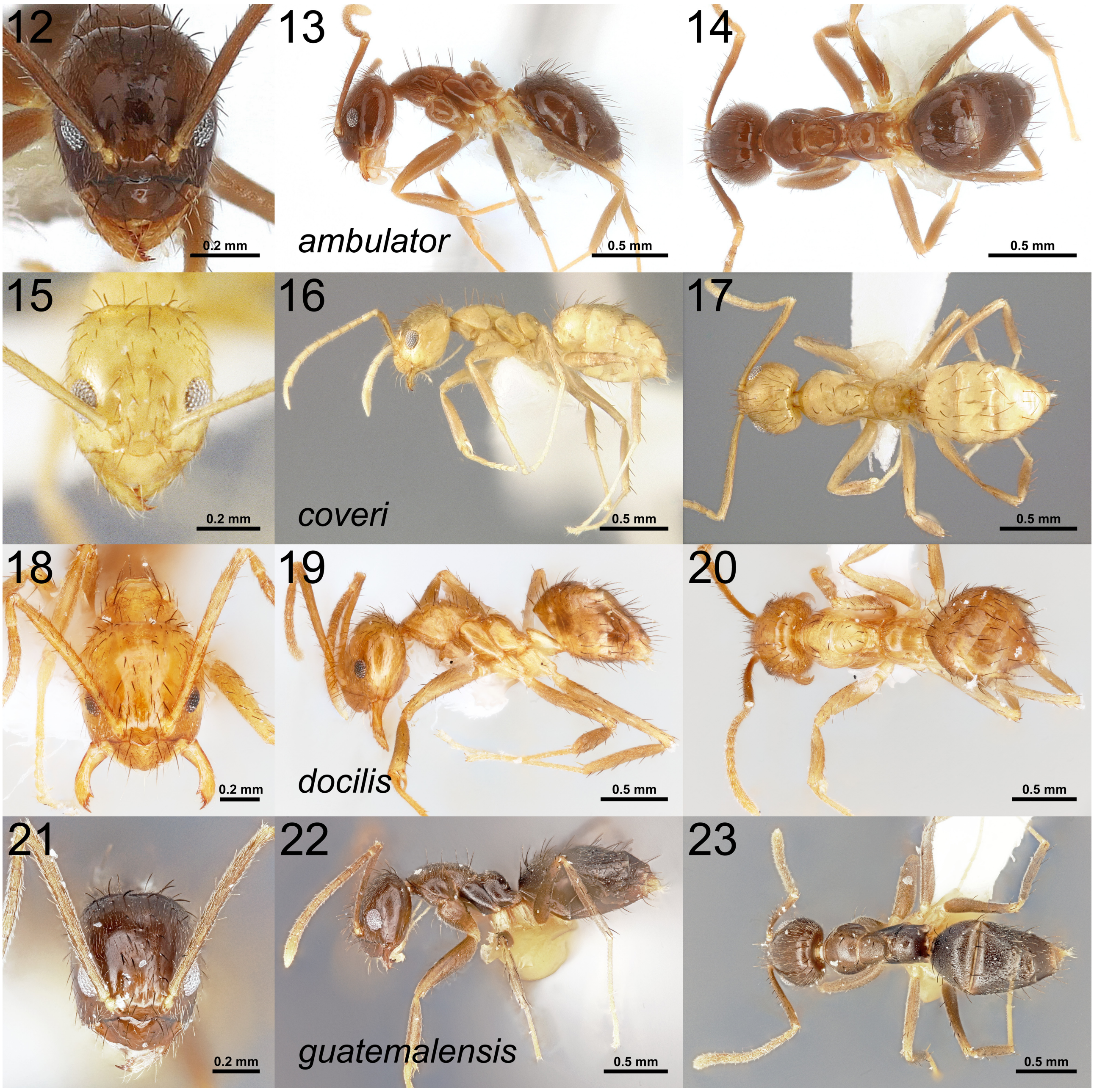
Figs. 30–32 (worker); Figs. 48–49, 56–58 (male)

*Prenolepis silvestrii* Emery, 1906: 186 (w.q.m.). Lectotype worker (designated here), **ARGENTINA:** Buenos Aires, San Isidro, 24-Jul-1898, F. Silvestri, ANTC26683 (MSNG: CASENT0905659). Paralectotype workers, queens, males, **ARGENTINA:** Buenos Aires, San Isidro, Santa Catalina, and La Plata, F. Silvestri (MSNG); Tucumán, Tafi Viejo, F. Silvestri (MSNG).

**Worker diagnosis:** Relatively gracile; mesosoma long (BLI = 147–163), metatibia long (HTI = 127–137), scape long, surpassing posterior margin of head by nearly half its length (SI = 143–156); body color medium to dark brown; protrochanter, mesocoxa, and metacoxa whitish to yellow; relatively sparse pubescence across head and mesosoma, except for dorsal face of propodeum; mesopleuron sparsely pubescent or entirely glabrous; gaster mostly glabrous, at most with patch of pubescence concentrated anterodorsally on abdominal segment III.

**Compare with:** *N. ambulator, N. guatemalensis, N. insularis*

WORKER. *Measurements (n=8)*: TL: 2.0–2.2 (HL+WL=1.3–1.4); EL: 0.12–0.15; EW: 0.09–0.11; IOD: 0.29–0.32; HE: 0.00–0.01; HL: 0.56–0.60; HW: 0.46–0.49; HLA: 0.20–0.22; HLP: 0.23–0.25; SL: 0.67–0.74; PW: 0.34–0.36; MW: 0.18–0.21; PrW: 0.25–0.28; PDH: 0.19–0.22; PTW: 0.12–0.13; LHT: 0.60–0.65; WL: 0.70–0.79; GL: 0.70–0.92; SMC: 22–27; PMC: 2–4; MMC: 2–3. *Indices*: BLI: 147–163; CI: 81–83; EPI: 81–88; HTI: 127–137; REL: 21–26; SI: 143–156.




**FIGURES 12–23.** *Nylanderia* workers in head, lateral, and dorsal views: *N. ambulator* (12–14; USNM: USNMENT01131112), *N. coveri* (15–17; MCZC: MCZENT00525580), *N. docilis* (18–20; USNM: USNMENT01129209), and *N. guatemalensis* (21–23; USNM: USNMENT01886856).

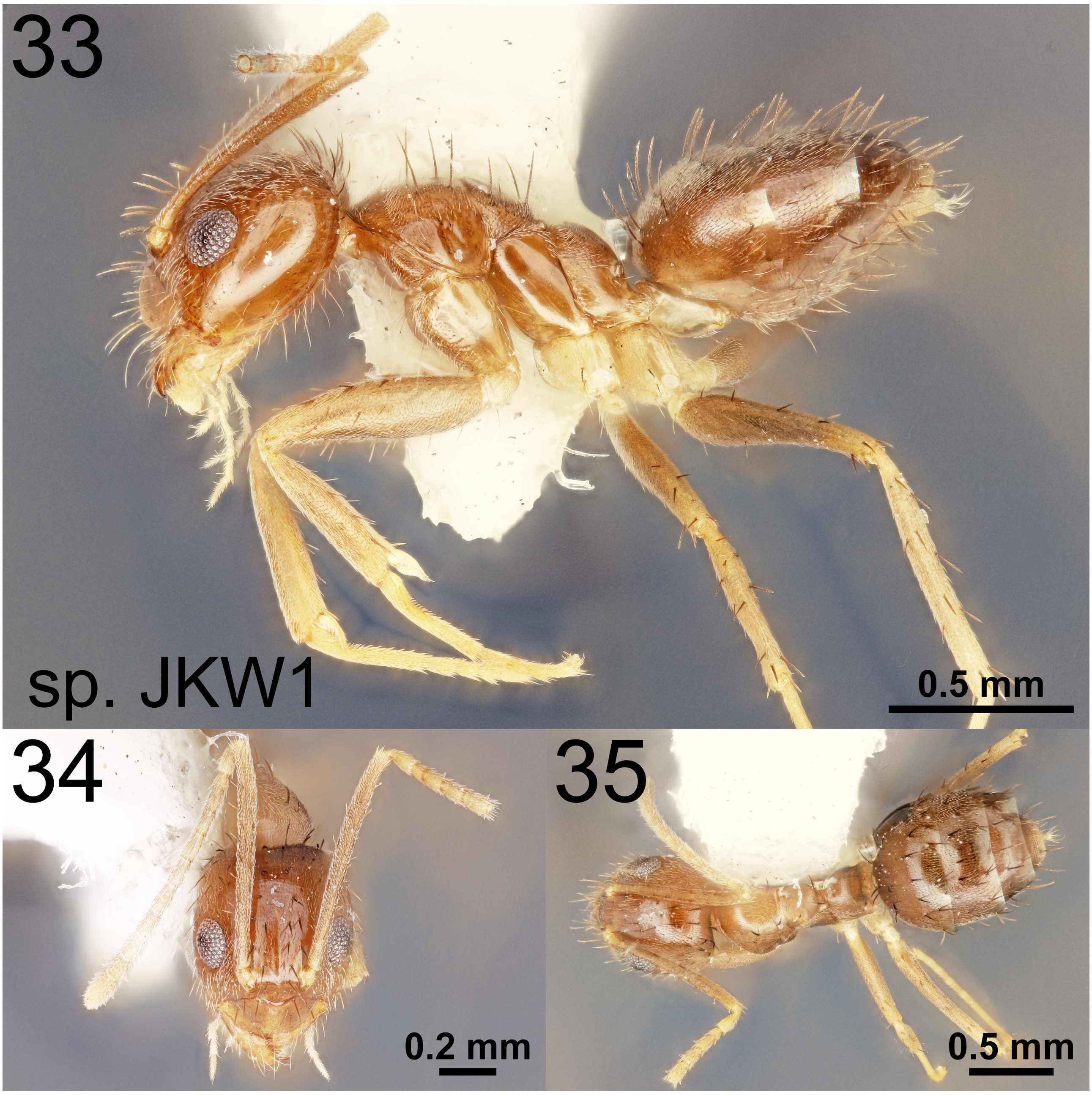
*Color:* medium to dark brown; lighter brown antennae and mandibles and yellow tarsi; protrochanter, mesocoxa, and metacoxa whitish to pale yellow, strongly contrasting with mesosoma; overall cuticle smooth and shining, with no cuticular microsculpture and no iridescence. *Pilosity:* abundant suberect to erect setae on scape (SMC = 22–27), contrasting in length from fine, appressed hairs; sparse cephalic pubescence, mostly concentrated lateral to antennal sockets; sparse pubescence across most of mesosoma, except for dorsal face of propodeum; gaster pubescence mostly concentrated anterodorsally on abdominal segment III, but otherwise sparse to absent; no mesopleural setae; 1-2 small setae may be found posterolateral to propodeal spiracle; no erect setae on apex of petiole. *Head:* in full-face view, head longer than broad (CI = 81–83) and quadrate with rounded posterolateral corners and flattened posterior margin, with little to no medial emargination (HE = 0.00–0.01); scape relatively long and surpasses posterior margin of head by nearly half its length (SI = 143–156); compound eye moderately sized (REL = 21–26); compound eye positioned anterior to midline of head (EPI = 81–88); all three ocelli apparent, small, and evenly sized. *Mesosoma:* relatively elongate (BLI = 147–163); in profile view, anterior margin of mesonotum rising above posterior margin of pronotum; mesonotum flat and not declining posteriorly into metanotal groove; metanotal groove shallow, with posterior margin of mesonotum discontinuous with metanotal area; propodeum low, rounded, and at lower height than promesonotum; dorsal face of propodeum about half as long as posterior face.


**FIGURES 24–32.** *Nylanderia* workers in head, lateral, and dorsal views: *N. insularis* (24–26; USNM: USNMENT01129187), *N. nesiotis* (27–29; USNM: USNMENT01886840), and *N. silvestrii* (30–32; USNM: USNMENT01886908).

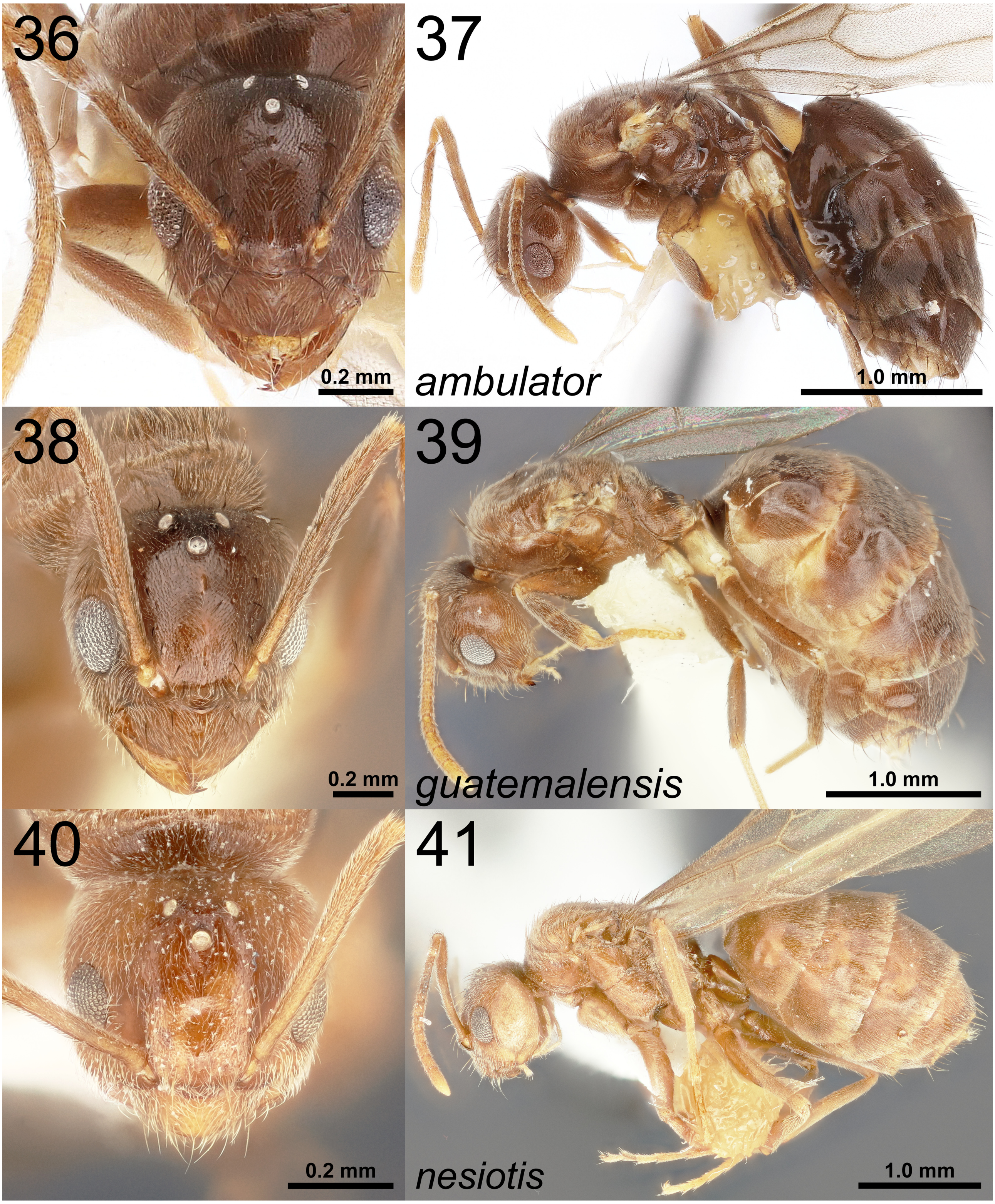
MALE. *Measurements (n=3)*: TL: 2.0–2.2 (HL+WL=1.2–1.3); EL: 0.20–0.21; HL: 0.48–0.50; HW: 0.38; SL: 0.67–0.70; LHT: 0.62–0.65; WL: 0.73–0.81; GL: 0.83–0.87. *Indices*: BLI: 190–212; CI: 80; HTI: 161–169; REL: 42–43; SI: 174–182.

*Color:* medium to dark brown; mesocoxa and metacoxal whitish to yellow. *Pilosity:* dense pubescence on head, pronotum, mesonotum, propodeum, and gaster; mesopleuron mostly to entirely pubescent, with at most a small dorsal portion of katepisternum glabrous; macrosetae across entire body, including scape and genitalia, dark and strongly contrasting with surrounding cuticle. *Head:* longer than broad (CI = ~80) and oval, with rounded posterolateral corners and convex posterior margin; compound eyes surpass lateral margins of head in full-face view; scapes long (SI = 174–182), surpassing posterior margin of head by about half their length. *Mesosoma:* in profile view, propodeum gently rounded with dorsal face about twice as long as posterior face. *Genitalia:* in ectal view, harpe broadly triangular, with large, prominent, roughly quadrate dorsal lobe and weakly convex ventral margin (Fig. 58); in ventral view, ventromedial edge of basivolsella rounded, slightly sinuous posteriorly, and flattened near base of gonossiculus (Fig. 57).

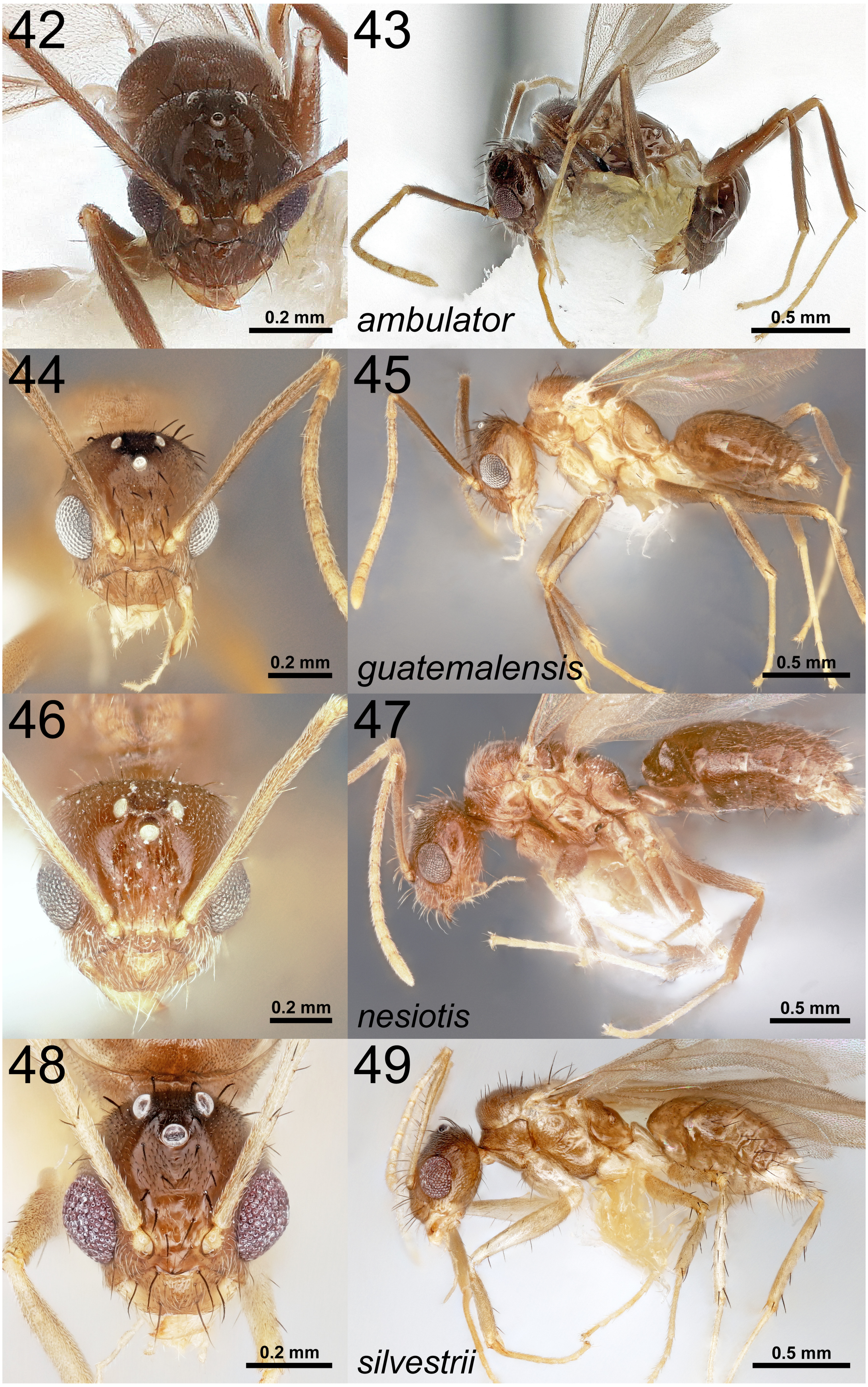
**Other material examined: ARGENTINA:** Tucumán, Tafí Viejo, 11km N Tafi Viejo, -26.63333 -65.23333, elev. 820m, 1-Feb-1995, tropical moist forest, sifted litter (leaf mold, rotten wood), P.S. Ward, PSW12826-24 (PSWC: CASENT0280577); **BOLIVIA:** Cuchabamba, route 7 between Cuchabamba and Villa Tunari, 8-Jan-2004, Svenson, Cameron, Bybee (USNM: USNMENT01132044); **BRAZIL:** Amazonas, Manaus, Finca Lucia, -3.131389 -59.9825, 3-Apr-2014, F. Fernández (USNM: USNMENT01886920); **COLOMBIA:** Amazonas, vas Leticia km4, 30-Oct-2005, F. Fernández (USNM: USNMENT01886919); Meta, Reserva El Caduceo, 3.665361 -73.657828, elev. 400m, 1-May-2006, Winkler, F. Fernández (USNM: USNMENT01886917); Meta, Rio Camoa, 3.696944 -73.698611, elev. 400m, 1-May-2000, Winkler, F. Fernández (USNM: USNMENT01886918); Putumayo, Orito, El Líbano, RN La Isla Escondida, 0.65547 -77.07302, elev. 800m, 21-Aug-2004, M. Leponce *et al.*, LOT03-22108/y-d3 (USNM: USNMENT01886922); Putumayo, Orito, El Líbano, RN La Isla Escondida, 0.65547 -77.07302, elev. 800m, 21-Aug-2004, M. Leponce *et al.*, LOT03-18409/BX2 (USNM: USNMENT01886923); **ECUADOR:** Pichincha, elev. 900m, 5-Sep-2003, H. Vieira (USNM: USNMENT01886921); **FRENCH GUIANA:** Roura, Camp Patawa, 4.54465 -52.15258, elev. 177m, May-2006, B. Noonan (USNM: USNMENT01886701, USNMENT01886702, USNMENT01886703, USNMENT01886704, USNMENT01886705); Régina, Nouragues, 4.08799 -52.67978, 25-Aug-2018, forest edge, nest in rotting twig, J.L. Williams, JLW022 (USNM: USNMENT01129206, USNMENT01886706, USNMENT01886900, USNMENT01886901, USNMENT01886902, USNMENT01886903, USNMENT01886904, USNMENT01886905, USNMENT01886906, USNMENT01886908).




**FIGURES 33–35.** *Nylanderia* sp. JKW1 (undescribed) worker in lateral, head, and dorsal views (USNM: USNMENT01129185).




**FIGURES 36–41.** *Nylanderia* queens in head and lateral views: *N. ambulator* (36–37; USNM: USNMENT01132133), *N. guatemalensis* (38–39; USNM: USNMENT01132181), and *N. nesiotis* (40–41; USNM: USNMENT01886749).

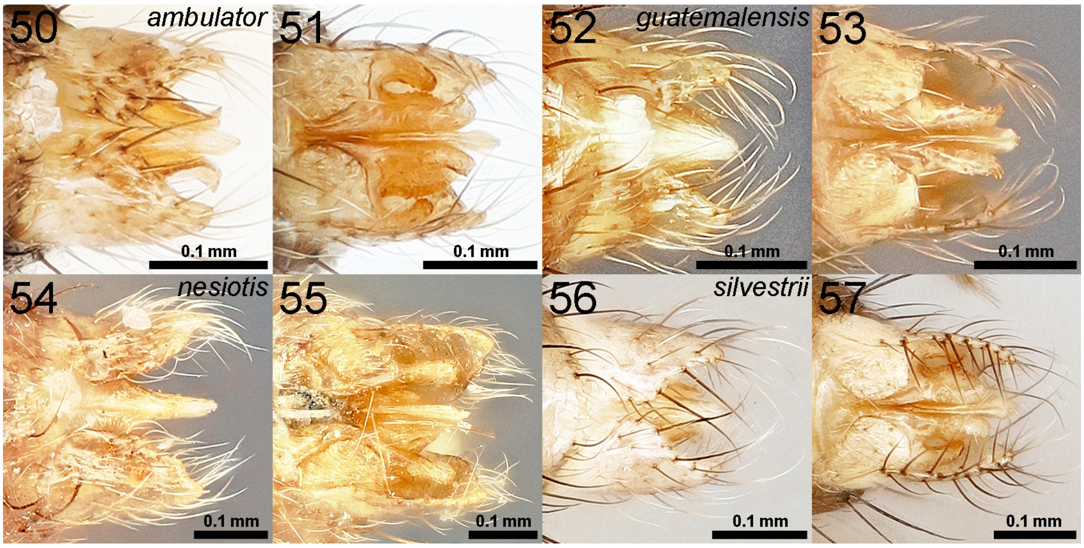



**FIGURES 42–49.** *Nylanderia* males in head and lateral views: *N. ambulator* (42–43; USNM: USNMENT01132147), *N. guatemalensis* (44–45; USNM: USNMENT01886841), *N. nesiotis* (46–47; USNM: USNMENT01886834), and *N. silvestrii* (48–49; USNM: USNMENT01886905).

**Notes:** This species most closely resembles *N. ambulator* and *N. guatemalensis* but is markedly more glabrous. In the original description, Emery (1906) emphasized its much sparser pubescence, reduced pilosity, and smaller size relative to *N. fulva*. *Nylanderia silvestrii kuenzleri* was also described from Buenos Aires, but we synonymize it with *N. guatemalensis* based on its relatively abundant pubescence across the head, dorsal mesosoma, and entire gaster. Given that *N. guatemalensis* is primarily known from more northern regions (Mesoamerica, the West Indies, and northern South America), its occurrence in Buenos Aires may not have been recognized at the time, leading to the description of *N. guatemalensis* specimens in Buenos Aires instead as a subspecies of the more locally familiar *N. silvestrii*.

***Nylanderia* sp. JKW1, undescribed**

Figs. 33–35 (worker)




**FIGURES 50–57.** *Nylanderia* male genital capsules in dorsal and ventral views: *N. ambulator* (50–51; USNM: USNMENT01132147), *N. guatemalensis* (52–53; USNM: USNMENT01886841), *N. nesiotis* (54–55; USNM: USNMENT01886834), and *N. silvestrii* (56–57; USNM: USNMENT01886905).

## Discussion

In this study, we revise the *N. guatemalensis* complex by integrating morphological, molecular, and distributional data from Neotropical taxa to evaluate species boundaries and evolutionary relationships among the eight recognized species: *N. ambulator, N. coveri, N. docilis, N. guatemalensis, N. insularis, N. nesiotis, N. silvestrii,* and *N.* sp. JKW1 (undescribed). To determine species limits, we consider *N. guatemalensis* complex specimens sampled from across their known ranges. We also formally describe one new species from the Lesser Antilles, propose one new status change, establish six new synonymies, and update historical identifications for all known species in the *N. guatemalensis* complex. These taxonomic changes are necessary to support monitoring and management of invasive ants, especially in sensitive island systems such as the Galápagos and the Caribbean. Phylogenetic analysis using maximum likelihood weakly supported monophyly of the *N. guatemalensis* complex (Fig. 3), while the multispecies coalescent recovered it with relatively high, though not maximal, support (LPP = 0.92; Fig. S1). These results suggest minor underlying gene tree discordance. Previous maximum likelihood analyses inconsistently resolved this lineage, recovering it with varying support as either monophyletic (Williams *et al.* 2024) or non-monophyletic (Williams *et al.* 2020, 2022) with respect to the *N. fulva* complex. In contrast, multispecies coalescent approaches, particularly those using allele-phased data, consistently recovered the *N. guatemalensis* complex as monophyletic with strong support (Williams *et al.* 2022, 2024).

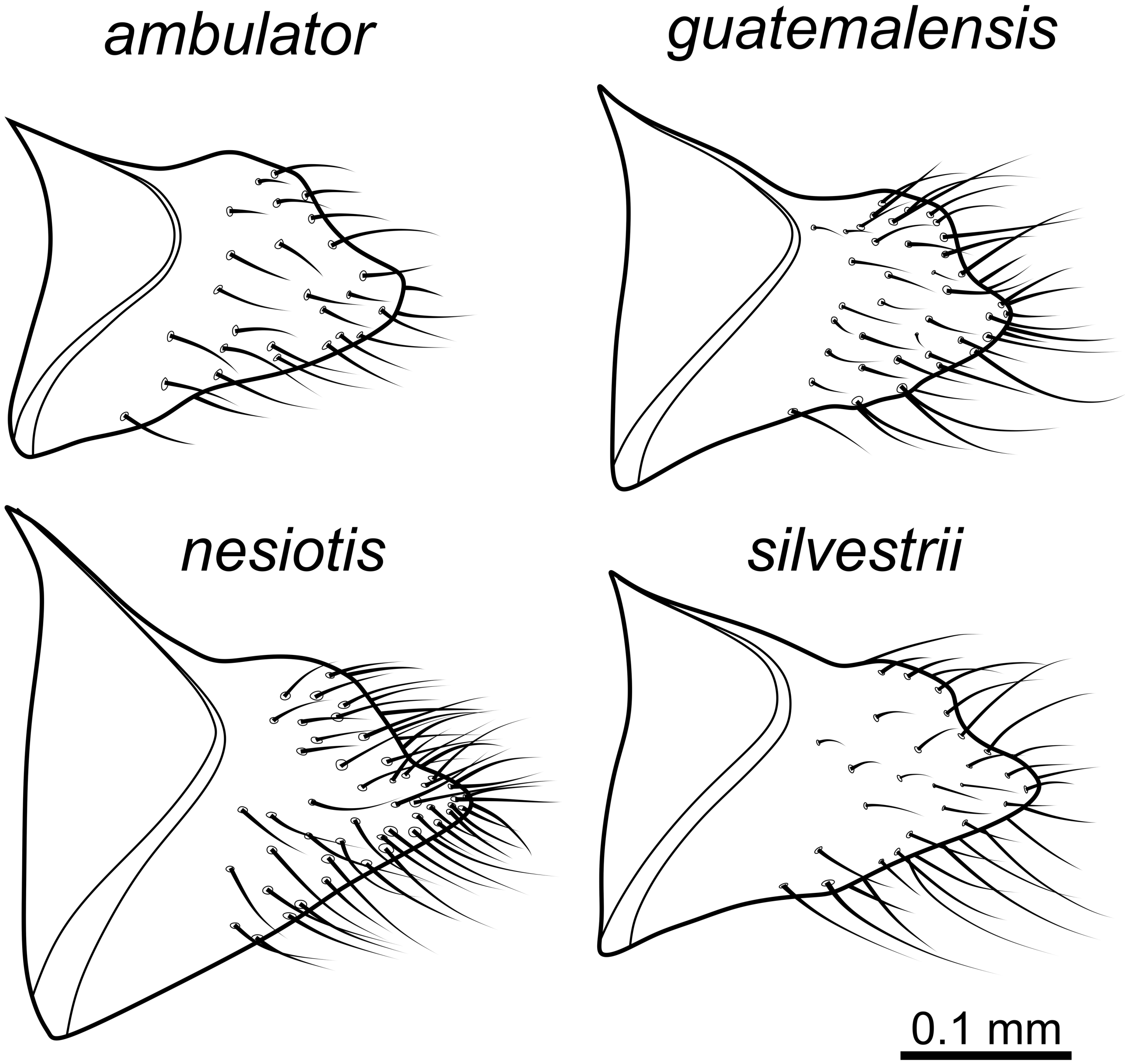



**FIGURE 58.** Illustrations of the gonopods (in ectal view) of *N. ambulator, N. guatemalensis, N. nesiotis,* and *N. silvestrii*.

This variation in phylogenetic support can be explained by discordance and instability in difficult nodes, which are increasingly recognized as expected features of rapidly radiating lineages (Borowiec *et al.* 2025; Kandziora *et al.* 2022; Myers *et al.* 2024). Short internodes tend to reduce phylogenetic signal and make incomplete lineage sorting more likely, which can lead to widespread gene tree conflict and multiple, similarly supported topologies. Introgression, reticulation, and methodological sensitivities further contribute to variation across datasets and analyses. Complex histories along short branches can constrain even genome-scale datasets, sometimes yielding inherently intractable nodes. In essence, strictly bifurcating trees may not fully capture evolutionary history amid extensive gene tree discordance (Borowiec *et al.* 2025; Edelman *et al.* 2019; Pease *et al.* 2016; Suh 2016). Because our molecular sampling focused primarily on specimens collected from Mesoamerica, the Caribbean, and northern South America, additional sequences from across the entire South American continent—especially those of species such as *N. docilis* and *N. silvestrii* sampled across their full geographic range—will be essential to more completely understand species limits in this historically intractable complex.

Historical misclassifications characterize broader challenges in *Nylanderia* taxonomy: morphological similarity often leads to misidentification, with researchers either assigning names based on the most similar-looking species (which may be distantly related) or retreating from attempts at species-level identification altogether because diagnostic tools are not available or reliable. Issues are especially pronounced in biodiversity hotspots such the West Indies, wherein sympatry of many morphologically similar native and introduced *Nylanderia* can complicate ecological and biosecurity assessments (LaPolla & Kallal 2019; Williams & Lucky 2020). Difficulties with conservation and invasive species management are compounded when widespread "globetrotting" species, such as *N. guatemalensis*, occur alongside endemic species. Because cryptic morphology complicates early detection of newly established non-native and invasive species and can increase the risk of misidentification, combining accurate taxonomy with distribution mapping is essential for situating taxa within broader patterns of native and introduced *Nylanderia* and for identifying both historical dispersal and human-mediated introductions.

We apply this revised framework for the *N. guatemalensis* complex to the Galápagos fauna to clarify the taxonomy of *Nylanderia* in the archipelago and recognize the presence of two species: *N. guatemalensis* and *N. nesiotis*. The elevation of *N. nesiotis* to full species status is significant because it definitively separates this species from widespread and potentially invasive close relatives such as *N. fulva* and *N. guatemalensis*. Here, *Nylanderia nesiotis* is formally recognized as a probable endemic to the Galápagos and is no longer classified as a subspecies of an economically and ecologically destructive species (*N. fulva*). This is the first demonstration of ant endemism in the Galápagos, achieved through a combination of morphological, phylogenomic, and distributional evidence. This conclusion is supported by high abundance of the species across the archipelago (especially in areas uninhabited by humans), its specific interactions with endemic plants such as leatherleaf (*M. octogona*) and Galápagos prickly pear cactus (*O. galapageia*), and the absence of any records outside the islands. In contrast, *N. guatemalensis* is recognized on the islands as a non-native species restricted to areas of high human disturbance.

This revision provides a comprehensive assessment of species boundaries and diversity within the *N. guatemalensis* complex and clarifies the identity and status of Galápagos *Nylanderia*. It also supplies diagnostic tools and images for morphologically difficult species and demonstrates how this integrative framework can be applied to cryptic taxa in other groups. Together, these results demonstrate the value of combining morphological, phylogenomic, and distributional evidence to inform biodiversity research, conservation management, and biosecurity, particularly in sensitive island systems and other at-risk regions.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**Supplementary Materials.** The following supporting information can be downloaded at the DOI landing page of this paper.

**Figure S1.** Multispecies coalescent (MSC) phylogeny of the *N. fulva* and *N. guatemalensis* complexes, reconstructed with ASTRAL-III using gene trees from the 80% complete SWSC-partitioned matrix. Support values on nodes are local posterior probabilities (LPP), with LPP ≥ 95% considered strongly supported.

**File S1.** Alignment file (.phylip) for the 80% complete SWSC-partitioned UCE data matrix.

**File S2.** Partition information file (.charsets) corresponding to the SWSC-partitioned 80% complete UCE data matrix.

**File S3.** Newick tree file for the maximum likelihood phylogeny of the *N. fulva* and *N. guatemalensis* complexes reconstructed using the 80% complete SWSC partitioned matrix.

**File S4.** Newick tree file for the multispecies coalescent (MSC) phylogeny of the *N. fulva* and *N. guatemalensis* complexes, reconstructed with ASTRAL-III using gene trees from the 80% complete SWSC partitioned matrix.

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

**Table S2.** Locality information for all UCE sequence data used in this study.

**Table S3.** Sample quality data for all specimens used for UCE sequencing.

**Table S4.** All specimen measurements used in this study.