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Taxonomy

# Integrating UCE Phylogenomics With Traditional Taxonomy Reveals a Trove of New World *Syscia* Species (Formicidae: Dorylinae)

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## Abstract

The ant genus *Syscia* Roger, 1861 is part of the cryptic ant fauna inhabiting leaf litter and rotten wood in the Asian and American tropics. It is a distinct clade within the Dorylinae, the subfamily from which army ants arose. Prior to this work, the genus comprised seven species, each known from a single or very few collections. Extensive collecting in Middle America revealed an unexpected and challenging diversity of morphological forms. Locally distinct forms could be identified at many sites, but assignment of specimens to species spanning multiple sites was problematic. To improve species delimitation, Ultra-Conserved Element (UCE) phylogenomic data were sequenced for all forms, both within and among sites, and a phylogeny was inferred. Informed by phylogeny, species delimitation was based on monophyly, absence of within-clade sympatry, and a subjective degree of morphological uniformity. UCE phylogenomic results for 130 specimens were complemented by analysis of mitochondrial COI (DNA barcode) data for an expanded taxon set. The resulting taxonomy augments the number of known species in the New World from 3 to 57. We describe and name 31 new species, and 23 species are assigned morphospecies codes pending improved specimen coverage. Queens may be fully alate or brachypterous, and there is a wide variety of intercaste female forms. Identification based on morphology alone is very difficult due to continuous character variation and high similarity of phylogenetically distant species. An identification aid is provided in the form of a set of distribution maps and standard views, with species ordered by size.

**Key words:** taxonomy, new species, species diversity, ultra-conserved element, phylogenetics

The Dorylinae is a subfamily of ants that contains the conspicuous army ants and driver ants that are found in tropical regions of the world. The conspicuous and morphologically distinct army ants and driver ants emerge from a paraphyletic grade of generally rare and inconspicuous ants, many of which were formerly in the genus *Cerapachys* Smith, 1857. Borowiec (2016) revised the subfamily, defining and diagnosing the constituent genera and providing a new phylogenetic classification. The former *Cerapachys* is now divided into numerous monophyletic genera, one of which is *Syscia*.

*Syscia* has a disjunct distribution, occurring in the Asian and American tropics and subtropics. The Asian and American species are estimated to have diverged ~20 million years ago (Ma) (Borowiec 2019). The published taxonomy of the genus is very sparse, with just seven named species, four Asian and three American. The four known Asian species are based on isolated species descriptions from Sri Lanka, Thailand, and Japan (Jaitrong et al. 2020). The three American species were described in the 19th and early 20th centuries, based on single collections each from United States (Texas), Guatemala, and Honduras. But recent collecting efforts have shown that there are radiations of species and unrecognized pools of diversity in Southeast Asia (Borowiec, pers. com.), west of Wallace's line, and in the Americas from the southern United States to Panama. The genus also occurs in the Caribbean and in South America, but there are very few records from these regions.

*Syscia* workers are eyeless and live in the leaf litter and soil. They are very rarely encountered by hand collecting, and the great majority of records are from Winkler or Berlese samples of forest litter. In large-scale litter sampling projects in Central America (Projects ALAS, LLAMA, and ADMAC), 100 m$^2$ plots were sampled (miniWinkler samples) at each of 55 sites, and *Syscia* were in at most 13% of samples, and typically <5%. When they do occur in samples, series are small, from 1 to 20 individuals. *Syscia* are thus part of the cryptobiotic fauna, with small low-density colonies scattered in the litter and soil, and almost unknown prior to the advent of mass litter sampling methods in recent decades.



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These intensive sampling efforts in Central America and southern Mexico yielded close to 1,000 occurrence records. This specimen set allowed, for the first time, an assessment of character variation and an attempt at species delimitation across a large region. Here we provide a first revision of the American *Syscia* based on a combination of morphology and DNA sequence data. We were unable to find easily observed morphological correlates of the DNA-based phylogeny, which was a challenge to traditional taxonomic practices. The historical development of the project illustrates these challenges and our approach to combining molecular systematics and 'practical' taxonomy, building a species framework to advance taxonomy in this lineage.

## History, Rationale, and Strategy for Species Delimitation

The study's origins were a quantitative biodiversity inventory in Costa Rica, at La Selva Biological Station and the adjacent elevational transect (the Barva transect). We collected over 100 specimens of the rare genus *Syscia*. They could be sorted, using morphology alone, into 10 morphospecies. Differences among species were subtle but consistent, and it would have been a simple matter to provide a dichotomous key to the species. There were only two previously described species for all of Central America, and thus it was clear that there was a pool of unrecognized diversity in this genus.

Subsequent biodiversity inventories of litter ant diversity from southern Mexico to Costa Rica resulted in nearly 1,000 specimens. These were focused inventories at a limited number of sites. At each site (or groups of sites within a region) the specimens could be sorted into local morphospecies. For example, the eastern part of the state of Chiapas, Mexico, also had 10 morphospecies. Some of these were similar to the Barva Transect morphospecies, and some were quite different. We used morphology to sort all of our *Syscia* specimens into local morphospecies.

The characters we focused on were size, surface sculpture, the shape of the subpetiolar process, the shape of abdominal segments III and IV, and pilosity. These were characters easily seen on dry-mounted specimens, without dissection. Few other surface characters were discovered that revealed morphological clusters. As specimens accumulated, and after repeated examination, all characters showed considerable variation, but discrete sympatric morphological clusters were still discernable, which we interpreted as local reproductively isolated species. However, when comparing across sites, many distinctions dissolved and it became increasingly difficult to discern species boundaries that transcended local definitions.

At this stage, we turned to DNA sequencing, using a combination of genome-scale Ultra-Conserved Element (UCE) loci (Branstetter et al. 2017) and the mitochondrial COI 'barcode' region (BOLD Systems, Ratnasingham and Hebert 2007). We selected individuals of our locally-defined morphospecies from the intensively surveyed sites, typically a single specimen from each local morphospecies, and added additional specimens, in an ad hoc manner, from sites outside of our intensively sampled sites for which we had some recently collected material. We obtained UCE sequence data for a set of these specimens and examined the resulting tree. We found pronounced phylogenetic structure, with local morphospecies being broadly distributed across the phylogeny and typically clustering most closely with individuals from other sites. We also obtained COI sequences from our specimens and combined them with BOLD sequences. This was done to expand the taxon set, test the UCE phylogeny, and provide a potential molecular identification tool for future work.

Focusing on the UCE phylogeny, because it produced the best resolution among samples, we identified clades for which all sequenced specimens were allopatric (i.e., geographically separate). These were our initial definitions of species. Thus our locally defined morphospecies were always treated as separate species. 'Geographically separate' was loosely defined, such that localities had to be more than a few hundred km from each other and/or in different mountain ranges to be considered separate. In most clades so defined, with geographically separate terminals, morphology was relatively uniform within the clade. In some cases, however, there was large morphological divergence within such a clade. In these cases, we further recognized separate species based on morphology. What constituted 'large' versus 'small' variation was not precisely defined, but nevertheless was informed by expected variation as seen in other clades. In all such cases, the further subdivision was consistent with the within-clade phylogeny, representing monophyletic lineages with some molecular distinction from clades with differing morphology. Our locally-defined morphospecies were always molecularly distant from each other. In other words, the species in community assemblages, recognized as morphological clusters, were scattered across the phylogeny. There were no cases in which our local morphospecies were close enough genetically to suggest intraspecific variation. We were also alert to the possibility of paraphyletic assemblages of morphologically uniform specimens, which might reflect paraphyletic species (Wheeler and Meier 2000), but none were found.

For clades with multiple samples across sites, we examined DNA vouchers and additional specimens from the matching morphospecies clusters from the respective populations to further assess intra- and inter-population variability. This defined the morphological and geographic envelopes for our putative species. However, many of our species were single or very few collections from single sites, limiting our understanding of variability and range for these rare species. We also found that many of our morphological envelopes for species were overlapping somewhat with other species, and thus are not fully diagnostic.

We then examined material that was neither sequenced nor from one of our intensively sampled sites. This was mostly material borrowed from museums, much of it very old and problematic for DNA extraction. We attempted identifications based on geographic proximity to delimited species from our sequencing work and morphological differences among them. This was often quite tentative, because many of our species from sequencing work had deep genetic divergences with very little morphological divergence, and there were many species known from single localities. It was clear that identifying a specimen from beyond the geographic scope of the sequencing work often could not be done with confidence.

In two cases, *S. borowieci* and *S. quisquilis*, new species were described without DNA sequence data. These were cases in which morphological divergence alone was sufficient to differentiate them from other species.

Lastly, using the UCE phylogeny, we re-examined specimens in a search for morphological synapomorphies for higher clades. We were not successful.

What is the best approach to taxonomy for a group that is rare, with low morphological variability, yet with deep genetic divergences and high uncertainty in the biological reality of morphologically defined species across sites? Biological reality can be clades, clusters recognized by a multispecies coalescent method, or reproductively isolated genetic clusters in sympatry, but these entities are not always congruent (Campillo et al. 2020) and they are not always morphologically distinct (Fišer et al. 2018). Taxonomy is also a communication tool, providing a shorthand for some biological entity that requires many words to adequately describe (Winston 1999, Christenhusz 2020). Due to uncertainty in assigning specimens from across a large geographic area to species, one approach for New World *Syscia* would be to identify everything as a single species, *S. augustae*, which would be shorthand for a well-supported clade. But this approach would neglect the fact that multiple molecularly and morphologically distinct forms can occur in sympatry. If you were working on the Barva transect in Costa Rica, you would probably want to identify the 10 reproductively isolated clusters and develop a way to refer to them. Most likely you would not refer to each one with a full-text description of the diagnostic characters. You would probably develop your own shorthand, *S. augustae* Barva form 1, etc. But this is creating a parallel naming system, which is the kind of idiosyncrasy that binomial nomenclature was designed to obviate. While trying to identify biologically real species is a worthy goal, it is not something that can be easily achieved for lineages harboring large numbers of morphologically cryptic and uncertain species such as this. We believe our approach of naming species (defined as clades or paraphyletic assemblages, which may be composed of multiple populations that show any level of genetic isolation and divergence, but which display a subjective degree of morphological uniformity) is conservative in this case. It better reflects biological reality than the one species approach but does not overinflate species diversity, and provides a template for further exploration of species in the future. By providing some morphological correlates with our species, we also tried to create a practical taxonomy that does not necessarily require all specimens to be sequenced in order to be identified.

Having taxonomy be 'practical' can refer to which entities are being named, as above, or it can refer to ease of identification. In the past, morphology was the only tool in the toolbox. Taxonomy was a search for morphological clusters and gaps. Specimens were searched at ever finer levels of morphological detail to discover gaps. Specimens were disarticulated and dissected to see minute and hidden characters. Dozens of metric characters were painstakingly measured with high accuracy to allow the search for gaps in morphospace. The understanding was that we were searching for morphological clues to underlying genetic structure. Currently, we are able to directly observe the genetic structure through sequencing. This has allowed a practice similar to what we outline here, in which specimens are first sorted based on easily observed characters, sequencing is carried out, and phylogenetic and phylogeographic relationships are revealed with sequence data. Commonly, there is then a search for morphological correlates of that phylogeny that would allow identification based on morphology alone (and ideally the construction of a dichotomous key). But that requires delving into the minutia of dissections and measurements, requiring equipment, training, and experience. Ultimately it is a fishing exercise, with no guarantee of success. We are rapidly approaching (or have already arrived at) the point where DNA sequencing is easier and more efficient than the dissections or measurements needed for identification (Tautz et al. 2002), even if the morphological correlates of genetic structure are known. Fišer et al. (2018) argue that finding these morphological correlates should not be a requirement for recognizing and naming species. We are not arguing that morphology is unimportant. Morphology is the form and function that has evolved in lineages, interacting with the environment and being shaped by selection and drift. But we take the approach here that genetic structure is the primary evidence for species, onto which we map easily observable characters, acknowledging a frequent lack of morphological diagnosis. Importantly, we are not arguing that a single locus (e.g., the COI barcode region) or a few loci will always reveal species boundaries better than morphology. Incomplete lineage sorting and introgression can blur the relationship between DNA sequence history and the history of the organisms that carry and transmit the DNA (Mallet et al. 2016). But in many cases, broad patterns in the genome correlate with morphology, when extremely thorough morphological data are available. We expect that detailed morphological examination, including morphometrics, might eventually provide a morphological diagnosis for our species of *Syscia*. The species we define in this work provide a framework for more thorough morphological examination to refine this taxonomy in the future.

## Materials and Methods

### Material Examined

This study relied on a database of 996 individual specimen records (Supp Table 2 [online only]). All holotypes and paratypes associated with the new species described here have unique specimen-level identifiers ('specimen codes') affixed to each pin, and most non-type specimens do as well. Specimen codes should not be confused with collection codes, which are associated with particular collection events. When reported, collection codes follow the collector. Specimen collection data are derived from a specimen database and are not direct transcriptions of labels. Latitudes and longitudes, when present, are reported in decimal degrees, as a precise point (five decimal places) followed by an error term in meters. Images of holotypes, distribution maps, and all specimen data on which this paper is based are available on AntWeb (AntWeb.org), where they are subject to future modification (data corrections and reidentifications). Material examined is not listed in the species accounts, but instead is available as a parsed data file in Supp Table S2 (online only).

### Specimen Repositories

- CASC: California Academy of Sciences, San Francisco, CA, USA.
- DZUP: Coleção Entomológica Padre Jesus Santiago Moure of Universidade Federal do Paraná (UFPR), Curitiba, Paraná, Brazil.
- EPN: Museo de Colecciones Biologicas Gustavo Orcés, Escuela Politécnica Nacional, Quito, Ecuador.
- FMNH: Field Museum of Natural History, Chicago, IL, USA.
- ICN: Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá D.C., Colombia.
- INBio: Instituto Nacional de Biodiversidad, Costa Rica.
- INPA: Instituto Nacional de Pesquisas da Amazônia, Manaus, AM, Brazil.
- JDMC: Jonathan D. Majer Collection, Curtin University of Technology, Perth, Western Australia.
- JTLC: John T. Longino, personal collection, University of Utah, Salt Lake City, UT, USA.
- LACM: Los Angeles County Museum of Natural History, Los Angeles, CA, USA.
- MCZC: Museum of Comparative Zoology, Cambridge, MA, USA.
- MGBC: Michael G. Branstetter, personal collection, USDA-ARS, Utah State University, Logan, UT, USA.
- MHNG: Muséum d'Histoire Naturelle, Geneva, Switzerland.
- MIZA: Museo del Instituto de Zoologia Agricola, Universidad Central de Venezuela, Maracay, Venezuela.
- MLBC: Marek L. Borowiec, personal collection, University of Idaho, Moscow, ID, USA.
- PSWC: P.S. Ward Collection, University of California at Davis, CA, U.S.A.

SHSUE: Sam Houston State University Entomology Collection, Huntsville, TX, USA.
UCD: University of California, Davis, CA, USA.
UCR: Universidad de Costa Rica, San Pedro, Costa Rica.
UNAM: Universidad Nacional Autonoma de Mexico, Mexico D. F., Mexico.
USNM: National Museum of Natural History, Washington, DC, USA.
UTIC: University of Texas Insect Collection, Austin, TX, USA.
UVGC: Colección de Artrópodos, Universidad del Valle de Guatemala, Guatemala City, Guatemala.

## DNA Sequence Generation

We selected 130 specimens for inclusion in molecular phylogenomic analysis (Supp Table S1 [online only]): 128 *Syscia* and two outgroup specimens from the genus *Ooceraea* Roger, 1862. All sequence data were newly generated for this study, except for 5 samples, for which data were extracted from Oxley et al. (2014; Genome), Branstetter et al. (2017), and Borowiec (2019) (Supp Table S1 [online only]). Vouchers were designated for each extraction and may be the same specimen (non-destructive DNA extraction) or with varying degrees of subjectivity from the same nest, collection series, or rarely, population. Full voucher specimen details are in Supp Table S2 (online only).

To examine species boundaries and phylogenetic relationships among species and populations, we employed the UCE approach to phylogenomics (Faircloth et al. 2012, Faircloth et al. 2015, Branstetter et al. 2017), a method that combines targeted enrichment of UCEs with multiplexed, next-generation sequencing. All UCE molecular work was performed following the UCE methodology described in Branstetter et al. (2017). Briefly, the process involves DNA extraction, sample QC, DNA fragmentation (400–600 bp), library preparation, library pooling (equimolar pools of 10 or 11 samples), UCE enrichment, qPCR quantification, final pooling (up to 102 samples per sequencing pool), and sequencing. All sequencing was performed on an Illumina HiSeq 2500 instrument (2x125 bp v4 chemistry; Illumina Inc., San Diego, CA) by the University of Utah genomics core facility. To enrich UCE loci, we used an ant-customized bait set ('ant-specific hym-v2') that includes 9,898 baits (120 mer) targeting 2,524 UCE loci shared across Hymenoptera and a set of legacy markers (data not used) (Branstetter et al. 2017). The ability of this bait set to successfully enrich UCE loci and resolve relationships in ants has been demonstrated in several studies (Branstetter et al. 2017, Pierce et al. 2017, Ward and Branstetter 2017, Blaimer et al. 2018, Branstetter and Longino 2019, Longino and Branstetter 2020).

## UCE Matrix Assembly

After sequencing, the University of Utah bioinformatics core demultiplexed the data using bcl2fastq v1.8 (Illumina 2013) and made the data available for download. Once received, the sequence data were cleaned, assembled and aligned using PHYLUCE v1.6 (Faircloth 2016), which includes a set of wrapper scripts that facilitates batch processing of large numbers of samples. Within the PHYLUCE environment, we used the programs ILLUMIPROCESSOR v2.0 (Faircloth 2013), which incorporates TRIMMOMATIC (Bolger et al. 2014), for quality trimming raw reads, TRINITY v2013-02-25 (Grabherr et al. 2011) for *de novo* assembly of reads into contigs, and LASTZ v1.0 (Harris 2007) for identifying UCE contigs from all contigs. All optional PHYLUCE settings were left at default values for these steps. For the bait sequences file needed to identify and extract UCE contigs, we used the ant-specific hym-v2 bait file. To calculate assembly statistics, including sequencing coverage, we used scripts from the PHYLUCE package (*phyluce_assembly_get_trinity_coverage* and *phyluce_assembly_get_trinity_coverage_for_uce_loci*) that call the programs BWA v 0.7.7 (Li and Durbin 2010) and GATK v3.8 (McKenna et al. 2010).

After extracting UCE contigs, we aligned each UCE locus using a stand-alone version of the program MAFFT v7.130b (Katoh and Standley 2013) and the L-INS-i algorithm. We then used a PHYLUCE wrapper to trim flanking regions and poorly aligned internal regions using the program GBLOCKS (Talavera and Castresana 2007). The program was run with reduced stringency parameters (b1:0.5, b2:0.5, b3:12, b4:7). We then used another PHYLUCE script to filter the initial set of alignments so that each alignment was required to include data for ≥ 90% of taxa. This resulted in a final set of 1,388 alignments and 1,035,633 bp of sequence data for analysis. To calculate summary statistics for the final data matrix, we used a script from the PHYLUCE package (*phyluce_align_get_align_summary_data*). Information related to UCE sequencing and assembly results can be found in Supp Table S3 (online only). All steps, including the phylogenetic analyses described below, were performed on a multicore Linux workstation (40 CPUs and 512 Gb of memory).

## Phylogenomic Analysis

To partition the UCE data for phylogenetic analysis, we used the Sliding-Window Site Characteristics based on entropy method (SWSC-EN; Tagliacollo and Lanfear 2018), which breaks UCE loci into three regions, corresponding to the right flank, core, and left flank. The theoretical underpinning of the approach comes from the observation that UCE core regions are conserved, while the flanking regions become increasingly more variable (Faircloth et al. 2012). After running the SWSC-EN algorithm, the resulting data subsets were analyzed using PARTITIONFINDER2 (Lanfear et al. 2012, Lanfear et al. 2017). For this analysis, we used the rclusterf algorithm, AICc model selection criterion, and the GTR+G model of sequence evolution. The resulting best-fit partitioning scheme included 1,126 data subsets and had a significantly better log likelihood than alternative partitioning schemes (SWSC-EN: −5,608,249.502; By Locus: −5,639,169.680; Unpartitioned: −5,731,679.666).

Using the SWSC-EN partitioning scheme, we inferred phylogenetic relationships of *Syscia* with the likelihood-based program IQ-TREE v1.5.5 (Nguyen et al. 2015). For the analysis, we selected the '-spp' option for partitioning (linked branch lengths but allowing each partition to have its own evolutionary rate) and the GTR+F+G4 model of sequence evolution. To assess branch support, we performed 1,000 replicates of the ultrafast bootstrap approximation (UFB) (Minh et al. 2013, Hoang et al. 2018) and 1,000 replicates of the branch-based, SH-like approximate likelihood ratio test (Guindon et al. 2010). For these support measures, values ≥ 95% and ≥ 80%, respectively, signal that a clade is supported.

## COI Barcode Analysis

Due to the high abundance of mitochondrial DNA in samples and the less-than-perfect efficiency of target enrichment methods, *Cytochrome Oxidase I* (COI) sequence data, and sometimes entire mitochondrial genomes (see Ströher et al. 2017) are often generated as a byproduct of the UCE sequencing process. To provide a separate assessment of species identities, possibly with more samples included, we extracted COI sequences from our UCE enriched samples and combined them with *Syscia* COI sequences downloaded from the BOLD database (Ratnasingham and Hebert 2007) (Accessed 16 May 2019). To extract COI from UCE data, we downloaded

**Table 1.** *Syscia* species in order of mean HW of worker

| Species | HW | Range | Habitat | Figures |
|---|---|---|---|---|
| Syscia minuta | 0.33–0.40 | Nicaragua to Brazil (Rondonia) | Lowland | 8,S34–36 |
| Syscia parva | 0.34–0.42 | Mexico (Chiapas) to Nicaragua | Lowland | 8,S42–43 |
| Syscia JTL067 | 0.38–0.46 | Mexico (Tamaulipas) | Montane | 8 |
| Syscia pollula | 0.38–0.47 | Nicaragua to Panama | Lowland | 8,S53–55 |
| Syscia JTL069 | 0.40–0.49 | Mexico (Tamaulipas, Oaxaca) | Montane | 8 |
| Syscia JTL068[a] | 0.41–0.51 | Honduras | Lowland | 8,S75 |
| Syscia austrella | 0.42–0.52 | Panama, Ecuador | Montane | 8,S7–8 |
| Syscia JTL037 | 0.43–0.53 | Costa Rica | Lowland | 8 |
| Syscia boudinoti | 0.46–0.56 | Honduras (Guatemala?) | Lowland | 8,S12–13 |
| Syscia pervagata | 0.46–0.56 | Mexico (Chiapas) to Costa Rica | Lowland | 9,S47–50 |
| Syscia peten | 0.46–0.56 | Guatemala | Lowland | 9,S51–52 |
| Syscia JTL074 | 0.46–0.56 | Panama | Lowland | 9 |
| Syscia brachyptera | 0.47–0.57 | Honduras | Montane | 9,S14–15 |
| Syscia valenzuelai | 0.47–0.57 | Mexico (Veracruz) to Honduras | Lowland | 9,S69–71 |
| Syscia JTL071 | 0.46–0.57 | Mexico (San Luis Potosi) | Lowland | 9 |
| Syscia quisquillis | 0.47–0.57 | United States (California, Arizona) | Temperate | 8,9,S56–57 |
| Syscia sumnichti | 0.48–0.59 | Guatemala to Nicaragua | Montane | 9,S62 |
| Syscia JTL060 | 0.48–0.59 | Mexico (Veracruz) | Montane | 9 |
| Syscia JTL085 | 0.48–0.59 | Mexico (Chiapas) | Montane | 9 |
| Syscia jennierussae | 0.48–0.59 | Mexico (Chiapas), Guatemala | Lowland | 10,S24–25 |
| Syscia persimilis | 0.49–0.59 | Mexico (Chiapas) to Nicaragua | Montane | 10,S44–46 |
| Syscia JTL018 | 0.49–0.60 | Costa Rica | Lowland | 10 |
| Syscia machaquila | 0.50–0.61 | Mexico (Chiapas), Guatemala | Lowland | 10,S31–32 |
| Syscia murillocruzae | 0.50–0.61 | Costa Rica, Panama | Lowland | 10,S37–38 |
| Syscia truncata | 0.50–0.61 | Guatemala, Honduras | Lowland | 10,S68 |
| Syscia JTL084 | 0.50–0.61 | Mexico (Tamaulipas) | Montane | 10 |
| Syscia JTL050 | 0.50–0.61 | Cuba, Dominican Republic | Lowland | 10 |
| Syscia JTL082 | 0.50–0.62 | Honduras | Montane | 10 |
| Syscia honduriana | 0.51–0.62 | Honduras | Lowland | 10,S22–23 |
| Syscia madrensis | 0.51–0.62 | USA (Arizona, New Mexico) | Temperate | 11,S33 |
| Syscia JTL066 | 0.52–0.64 | Mexico (Chiapas), Guatemala | Lowland | 11 |
| Syscia benevidesae | 0.53–0.64 | Costa Rica to Ecuador, Venezuela | Lowland | 11,S9–10 |
| Syscia chiapaneca | 0.53–0.65 | Mexico (Chiapas) | Montane | 11,S16–17 |
| Syscia parietalis | 0.53–0.64 | Guatemala, Honduras | Montane | 11,S39–41 |
| Syscia setosa | 0.53–0.65 | Mexico (Tamaulipas to Chiapas) | Lowland | 11,S58–61 |
| Syscia JTL073 | 0.54–0.66 | Mexico (Chiapas) | Montane | 11,S76 |
| Syscia JTL075 | 0.54–0.66 | Mexico (Oaxaca) | Montane | 11 |
| Syscia disjuncta | 0.54–0.67 | Mexico (Tamaulipas to Oaxaca), Costa Rica | Montane | 11,S18–20 |
| Syscia augustae | 0.56–0.68 | United States (TX, AR), Mexico (NL) | Temperate | 11,S4–6 |
| Syscia tolteca | 0.55–0.68 | Guatemala, Honduras | Lowland | 12,S64–65 |
| Syscia atitlana | 0.57–0.70 | Mexico (Chiapas) to Guatemala | Montane | 12,S3 |
| Syscia lacandona | 0.57–0.69 | Mexico (Chiapas) | Lowland | 12,S2–28 |
| Syscia JTL049 | 0.57–0.69 | Mexico (Veracruz, Oaxaca) | Montane | 12 |
| Syscia JTL065 | 0.58–0.71 | Mexico (Chiapas) | Montane | 12 |
| Syscia amblyogyna | 0.60–0.73 | Guatemala | Montane | 12,S1–2 |
| Syscia ticomontana | 0.60–0.73 | Costa Rica | Montane | 12,S63 |
| Syscia JTL017 | 0.60–0.74 | Costa Rica | Lowland | 12 |
| Syscia JTL079 | 0.61–0.74 | Guatemala | Lowland | 12 |
| Syscia transisthmica | 0.61–0.75 | Mexico (Puebla) to Guatemala | Lowland | 12,S66–67 |
| Syscia latapuncta | 0.62–0.76 | Costa Rica | Lowland | 13,S29–30 |
| Syscia borowieci | 0.62–0.75 | Honduras | Montane | 13,S11 |
| Syscia volucris | 0.63–0.77 | Honduras to Costa Rica | Lowland | 13,S72–74 |
| Syscia JTL076[a] | 0.64–0.78 | Guatemala | Lowland | 13,S77 |
| Syscia JTL064 | 0.68–0.83 | Costa Rica | Montane | 13 |
| Syscia JTL033 | 0.69–0.85 | Guatemala | Montane | 13 |
| Syscia grandis | 0.70–0.86 | Guatemala | Montane | 13,S21 |
| Syscia JTL003 | 0.77–0.94 | Costa Rica | Montane | 13 |

HW is shown as ± 10% of mean (an approximate 95% confidence interval).
[a]Morphospecies known from queens only.

a complete 658 bp barcode sequence of a Costa Rican *Syscia* specimen from BOLD (Process ID ACGAE095-10, identified by us as *S. benevidesae*, one of the new species in this work) and used this as the bait input sequence for a PHYLUCE program (*phyluce_assembly_match_contigs_to_barcodes*) that extracts COI sequence from bulk sets of contigs.

After extracting COI sequence from UCE sample data, we downloaded accessible barcode sequences from BOLD following a series of steps. First, using the BOLD workbench interface, we searched for all records matching the taxonomy search term '*Syscia*' or '*Cerapachys*'. We then copied all of the resulting Barcode Index Numbers (BINs) and performed a second search using these numbers in the identifiers field. This approach recovers taxonomically mislabeled samples because BINs group sequences into units by sequence similarity, not name (Ratnasingham and Hebert 2013). All returned sequences were downloaded, examined, and subsequently filtered to remove Old World specimens and entries with no sequence data. We also removed a misidentified sample from Madagascar and a sequence mined from GenBank that had no accompanying specimen data. Because some of the remaining sequences included private, unpublished data, we contacted data owners for permission to use the private sequences in our analyses.

We combined the final set of BOLD sequences with the successfully extracted COI sequences from UCE samples and aligned the data using MAFFT. We visually inspected the resulting alignment for signs of pseudogenes/numts (e.g., presence of stop codons, indels, or highly divergent sequence) or other anomalies using MESQUITE v3.51 (Maddison and Maddison 2018). The final matrix was partitioned by codon position and analyzed with IQ-TREE using GTR+F+G4, 1,000 ultrafast bootstrap replicates, and 1,000 SH-like replicates. Following a preliminary analysis of all samples, we discovered that a set of 79 putative '*Cerapachys*' samples actually belonged to the phylogenetically distinct genus *Neocerapachys*. Consequently, we removed these samples from our data set and updated determinations in BOLD. Sample information for the final set of 86 BOLD specimens included in our analysis is available in Supp Table S4 (online only).

To facilitate identification using COI barcodes, we calculated uncorrected pairwise p-distances among all our samples using PAUP* v4.0 build 168 (Swofford 2020). Species accounts provide references to GenBank and BOLD sequences, ranges of intraspecific distances, and smallest interspecific distance.

## Morphological Characters

Borowiec (2016) fully characterized the genus *Syscia* and described the general features common to all species. Here we summarize characters that vary among species and can aid species-level identification. We do not examine characters that require dissection (e.g., mouthparts). All characters are continuous, with species more or less evenly filling the range of variation. Terminology follows Borowiec (2016).

The occipital carina varies from small and shifted ventrally, such that it is hardly visible in face view (Fig. 1A), to large and shifted dorsally, and easily visible in face view (Fig. 1B). This is difficult to quantify, because slight shifts in the tilt of the head in face view cause large differences in the visibility of the carina, altering the appearance of the posterior profile of the head.

A subpetiolar process is invariably present but varies in shape. The terms 'shallow' and 'deep' are used for the relative size vertically, 'narrow' and 'wide' for relative size horizontally. The process in lateral view is composed of a short, convex anterior margin and a longer posterior margin extending along the ventral surface of the petiole. The posterior margin may be flat or slightly concave, such that the process forms an asymmetrical triangle (Fig. 2A), or slightly convex (Fig. 2B), or with a small tooth (Fig. 2C), or angulate such that the process is subquadrate (Fig. 2D), or with a large acute tooth (Fig. 2E), or with a fenestra or notch (Fig. 2F). These states are points on a continuum, and there can be considerable intraspecific variation, especially among geographically separated populations.

The third and fourth abdominal segments are referred to as AIII and AIV, respectively. In dorsal view, AIII varies from weakly to strongly trapezoidal, and with sides convex to flat (Fig. 3A–C). The dorsal profiles of AIII and AIV vary from convex to flat (Fig. 3G–L).

The dorsal surface of AIII is always punctate. The puncta vary from small to large and with variable density (Fig. 3). Spacing varies from confluent to having interspaces as broad as the puncta diameters. The interspaces, when present, are smooth and shining. The puncta may be 'distinct', which means being a defined circular pit. Alternatively, they can be faintly impressed and with less defined edges. Puncta are often 'lunate', which means being in the form of semicircles, with a defined anterior border but indistinct posterior border. The posttergite of AIV is always at least partially punctate. Puncta can be small to large, confluent to widely spaced, distinct or lunate, as described for AIII. There is always a gradation, with strongest sculpture anteriorly, and puncta gradually becoming smaller and sparser posteriorly (referred to as 'fading'). There is a gradation from species that have the puncta restricted to a small anterior strip (with the rest of the tergite smooth and shiny) (e.g., Fig. 3E), to species with puncta covering the entire posttergite (although puncta always become smaller posteriorly) (Fig. 3D). Although a continuum, species are characterized as having the puncta notably fade on the anterior third, at about midlength, or covering the entire posttergite.

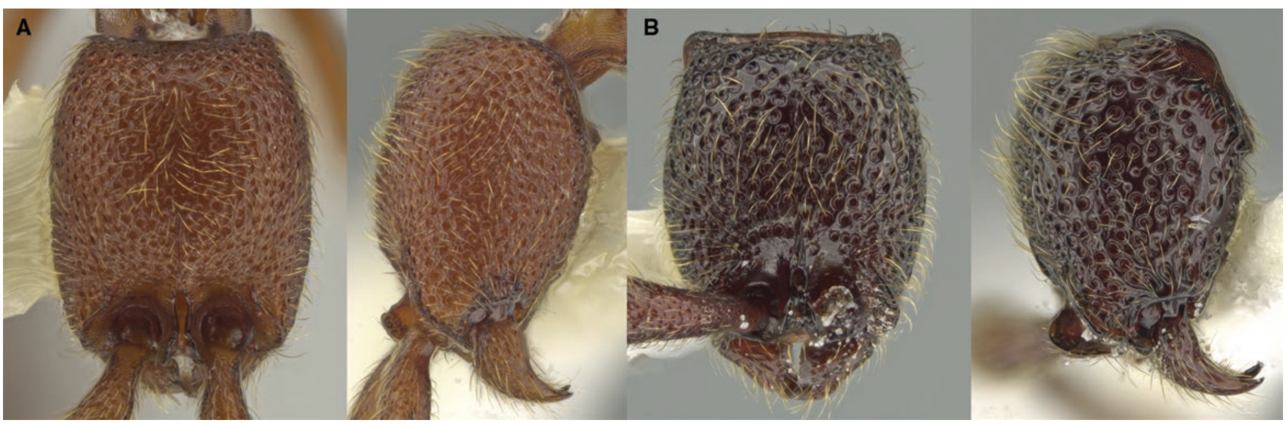


**Fig. 1.** Variation in *Syscia* occipital carina. (A) Flange weakly developed, less visible in face view. (B) Flange strongly developed, easily visible in face view.

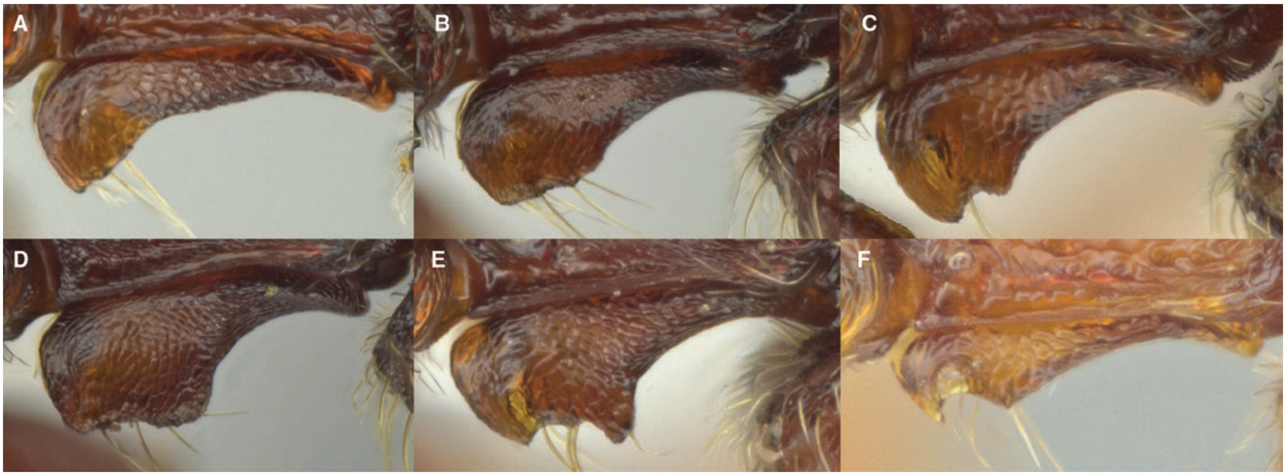


**Fig. 2.** Variation in *Syscia* subpetiolar process. (A) Subtriangular with flat to concave posterior margin. (B) Subtriangular with convex posterior margin. (C) Subtriangular with small tooth on posterior margin. (D) Subquadrate. (E) Subtriangular with large acute tooth on posterior margin. F. With fenestra and notch on posterior margin.

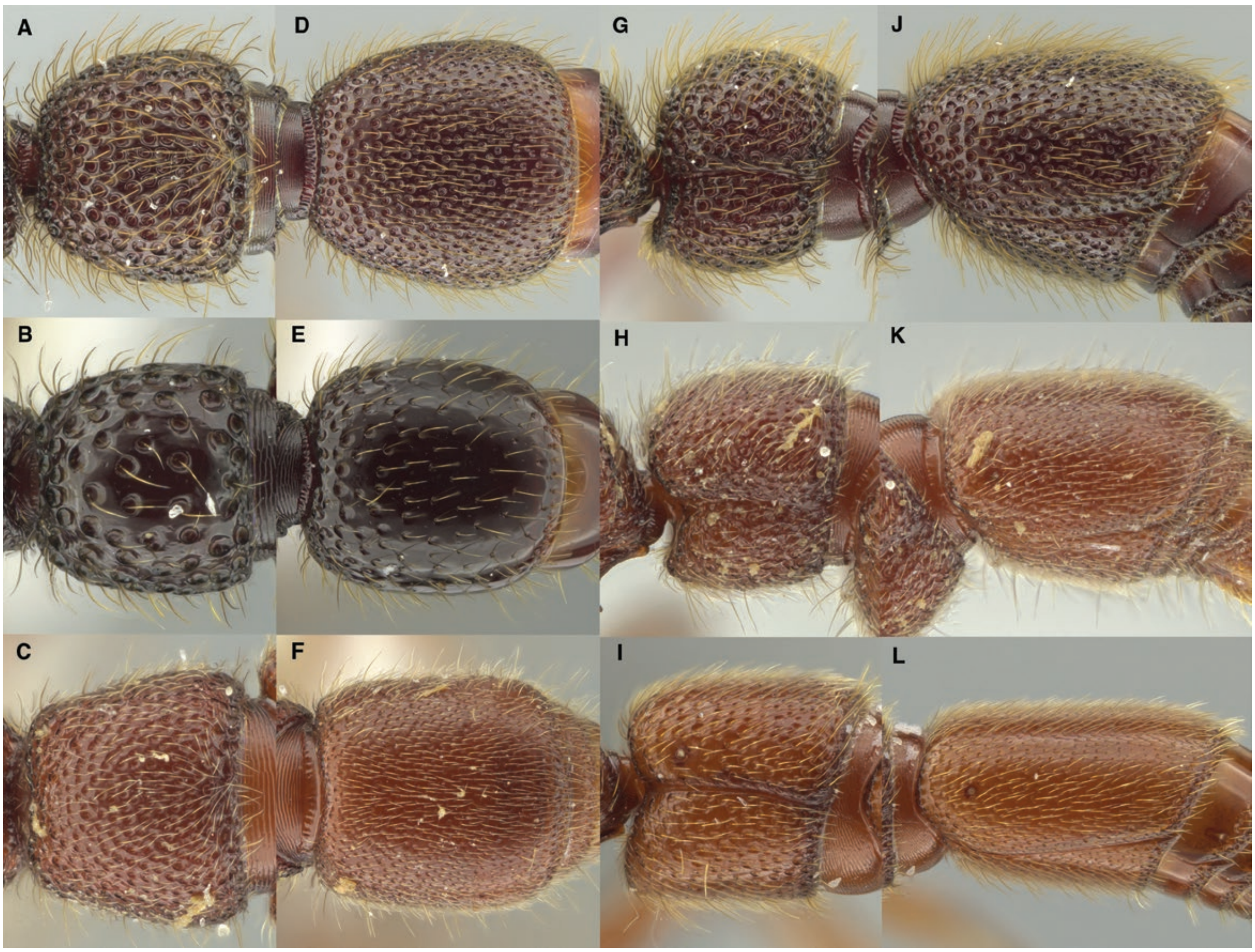


**Fig. 3.** Variation in *Syscia* profiles and pilosity. (A) AIII in dorsal view trapezoidal, with convex sides. (B) AIII in dorsal view weakly trapezoidal, with convex sides. (C) AIII in dorsal view trapezoidal, with flat sides. (D) AIV in dorsal view, with convex sides, anterior margin not truncate. (E) AIV in dorsal view, with convex sides, anterior margin moderately truncate. (F) AIV in dorsal view, with nearly flat sides, anterior margin strongly truncate. (G) AIII dorsal profile strongly convex. (H) AIII dorsal profile weakly convex. (I) AIII dorsal profile flat. (J) AIV dorsal profile convex. (K) AIV dorsal profile weakly convex. (L) AIV dorsal profile flat. (A, B, G, J) Standing pilosity long, coarse. (C, H, K) Standing pilosity of medium length and thickness. (I, L) Standing pilosity short, fine.

Pilosity is differentiated into standing pilosity and underlying pubescence. Standing pilosity is longer erect setae, often of irregular length. Standing pilosity varies in abundance, length, and thickness (Fig. 3). Underlying pubescence, which may be present or absent, is a layer of uniformly short, decumbent or appressed setae.

## Morphological Measurements

Measurements were made with a dual-axis micrometer stage with output in increments of 0.001 mm. However, variation in specimen orientation, alignment of crosshairs with edges of structures, and interpretation of structure boundaries resulted in measurement accuracy to the nearest 0.01 mm. All measurements are presented in mm.

The following measurements and indices are reported (Fig. 4):

HW, Head width: maximum width of head capsule in full-face view (not including eyes).
HL, Head length: maximum length of head capsule in full-face view, from anteriormost projection of anterolateral genal teeth or extensions of antennal fossae, to posteriormost projections of vertex.
SL, Scape length: maximum length of scape not including basal condyle and neck.
MSL, Mesosoma length: in lateral view, distance from base of convex portion of pronotum (not including anteriormost projection that inserts into the occipital cavity) to posteriormost projection of propodeal lobes.
AIIIW, Width of third abdominal tergite: maximum width in dorsal view.
AIIIL, Length of third abdominal posttergite: maximum length in dorsal view.
AIVW, Width of fourth abdominal tergite: maximum width in dorsal view.
AIVL, Length of fourth abdominal posttergite: maximum length in dorsal view.
SI, Scape index: 100*SL/HW.
AIII-I, Third abdominal tergite index: 100*AIIIW/AIIIL.
AIV-I, Fourth abdominal tergite index: 100*AIVW/AIVL.

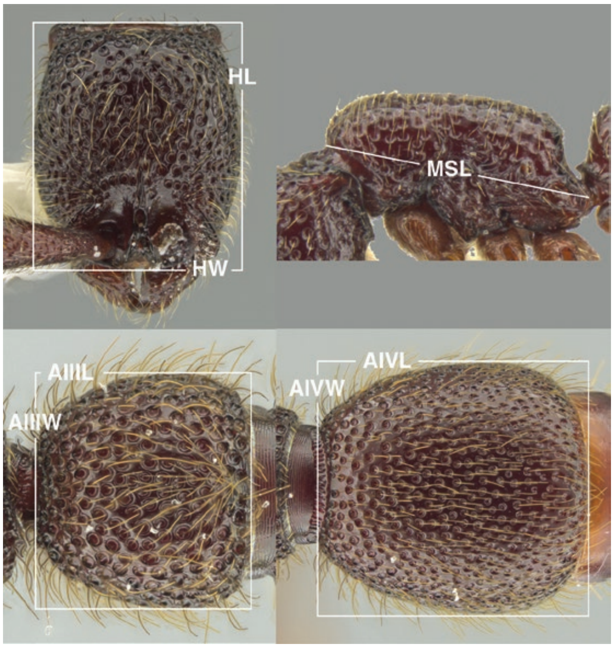


**Fig. 4.** Illustrations of *Syscia* measurements. HL: head length, HW: head width, MSL: mesosoma length, AIIIL: abdominal tergite III length, AIIIW: abdominal tergite III width, AIVL: abdominal tergite IV length, AIIVW: abdominal tergite IV width.

Measurements were typically made on specimens from one or more different collections from each population, avoiding measurements of multiple specimens from the same collection. In species accounts, mean, minimum, and maximum values are shown, followed by sample size. *Syscia pervagata* had the largest sample size, with 27 measured workers. For this species, the coefficient of variation (C.V., ratio of standard deviation/mean, as a percent) was 6% for HW, 7% for HL, 9% for SL, 9% for MSL, 9% for AIIIW, 9% for AIIIL, 9% for AIVW, 11% for AIVL, 3% for SI, 3% for AIII-I, 4% for AIV-I. Using the C.V. values from *S. pervagata*, one can estimate an expected range of variation. An approximate 95% confidence interval is mean ± (2*C.V.*mean).

Stacked images were created using Leica Application Suite V3.7 from source images captured using a Leica Z16 APO stereomicroscope coupled with a Leica DCF450 camera. All images were edited in Adobe Photoshop CS6 (Adobe Systems Inc., California, USA). Distribution maps were plotted with SimpleMappr (Shorthouse 2010).

## Castes

Borowiec (2016) summarized the occurrence of reproductive castes in *Syscia*, and we abundantly confirm here that multiple queen forms are common. Very few fully alate queens (i.e., with fully developed, functional wings still attached) are known. These have been captured in Malaise traps, yellow pan traps, or in one case associated with workers in a Winkler sample. These queens have three ocelli, fully formed compound eyes, typical queen-like mesosomal sclerites, and the mesosoma broadened medially (in dorsal view). In addition, the mesoscutum extends forward dorsally, at the expense of the pronotum, such that the anteromedian pronotum is longitudinally compressed, and the mesoscutum is proportionately longer (Fig. 5A). There are also occasional collections of brachypterous queens, which have very small, linear wings that are shorter than the length of the mesosoma. These brachypterous queens have ocelli, compound eyes, and mesosomal sclerites the same as fully alate queens, but the mesosoma is narrower in dorsal view, the mesoscutum is shorter, and the anteromedian pronotum is more elongate (Fig. 5B). Workers in samples are often accompanied by dealate queens (sometimes several). In many cases, the form of the mesosoma suggests whether the queens were fully alate or brachypterous before becoming dealate, but in some cases it is uncertain. A continuous range of intercaste females occurs, showing a great variety of intergradations between worker and fully alate queen. Intercaste females have one or three ocelli and compound eyes, but the mesosoma is worker-like. In *S. amblyogyna* the form of the queen is highly unusual: the mesosoma has the form of a brachypterous queen, but the compound eye is nearly absent, comprising a few small fused ommatidia. Males occur in Malaise trap samples, again as low-density elements. In our study, we were able to associate males with workers in a few cases, using COI sequence data. Figures of these males are provided but no attempt is made to investigate male morphology or differentiate species based on males.

## Species Description and Naming

Many of the species recognized here are based on single or very few specimens. We formally name species only if there are multiple specimens from a single locality, allowing an adequate type series that

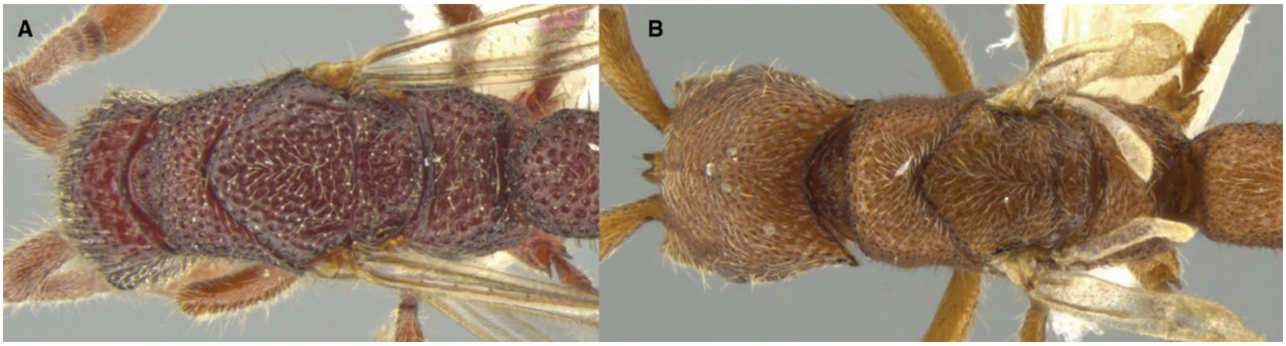


**Fig. 5.** Mesosomal structure of fully alate (A) vs. brachypterous (B) queen.

can be distributed to multiple institutions. Species with low representation are left with an informal morphospecies code, pending the acquisition of additional specimens and an improved understanding of the species. Diagnoses in species descriptions provide separatory characters for all species that are within the same geographic area and morphological size range. Detailed text descriptions are omitted, relying instead on detailed imagery. Images of face, dorsal, and profile views of all holotypes are provided in Supp Material (online only).

### Identification

We found during the course of this work that the phylogeny was geographically structured, with related species often occurring in the same region, but morphology was at most weakly coupled with phylogeny. Two processes, convergence and morphological stasis, confound identification based on morphology alone. We found many cases in which phylogenetically distant species were hardly or not at all identifiable by simply looking at specimens of workers or queens. We were frustrated in attempts to create a dichotomous key. Here we use an alternative approach to aid identification. Species are listed in order of size in Table 1, accompanied by geographic range, habitat, and references to figures. An identification tool is provided in Figs. 8–13, in which each species is represented as a row of standard views of the worker: distribution map, face view, petiole profile, AIII profile, AIV profile, AIII dorsal view, AIII dorsal view. Species are arranged in order of mean HW, which is shown in the lower left of the distribution map for each species. To attempt identification, one can measure HW of an unknown specimen, find the species that is both closest to that HW and within geographic range, and examine both the species account and the figures for that species. If the specimen does not sufficiently match, species can be examined with progressively more distant mean HW.

The species accounts contain information on how to differentiate the focal species from other species that are within size and geographic range. Species within size range are those with mean HW that falls within ±10% of the mean HW of the focal species. Species within geographic range are selected somewhat subjectively, either species with known sites of sympatry with the focal species, or occurring within ~100km of a known site of occurrence. The morphological separation criteria are often relative, such as structures being more or less convex, with the expectation that the figures will be compared. Separation criteria are meant to increase the likelihood of a correct identification, without being strictly diagnostic. Thus a 'lowland' species may occasionally occur in a cloud forest, and differences in mean values of measurements and indices may not indicate that the range of values does not overlap.

A major caveat is that the taxonomy and identification tools presented here will be most useful for areas that we have intensively sampled. Any identifications of specimens from areas that have not been previously sampled should be viewed as very tentative unless confirmed with DNA sequence data. This includes some of the identifications reported here, for museum specimens with no sequence data, and from isolated localities that we did not sample as part of our quantitative inventory projects.

### Nomenclature

This paper and the nomenclatural act(s) it contains have been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: urn:lsid:zoobank.org:pub:FF189A51-5F62-429B-9076-509310C79117

## Phylogenetic Results

### UCE Sequencing and Matrix Assembly

For newly sequenced samples (125 out of 130 total samples), we recovered a mean UCE contig coverage of 48.5x (range: 3.9–91.1x) and a mean UCE contig length of 775 bp (range: 253–1,037 bp). Following alignment, alignment trimming, and filtering of the UCE contigs, our UCE matrix consisted of 1,388 loci and 1,035,633 bp of sequence data, of which 193,176 bp were informative. The mean alignment length post-trimming was 746 bp (range: 244–1,558 bp) and the final matrix included 15.1% missing data (including gaps). For additional sequencing assembly information see Supp Table S3 (online only).

### COI Extraction and Matrix Assembly

We successfully extracted COI mtDNA sequence for all 129 UCE samples (the one genome sample was not included). Except for nine sequences, all were above 650 bp in length and most were 656 to 658 bp. No sequences had any obvious indications of being pseudogenes. From BOLD, we downloaded an initial set of 164 sequences, but pruned this set down to 86 sequences as described above (Supp Table S4 [online only]). The final aligned matrix included 215 COI sequences and was 658 bp in length. Four of the BOLD sequences were generated from the same specimens as UCE-derived sequences. In all cases, the paired sequences were identical.

### Phylogenetics and Species Delimitation

Analysis of the UCE data recovered a robust phylogenetic hypothesis with most nodes receiving maximum support (Fig. 6). With the tree rooted on *Ooceraea*, the two Old World *Syscia* formed a clade sister to, and very distinct from, an exclusively New World clade. The New World clade was composed of a diverse radiation of species split

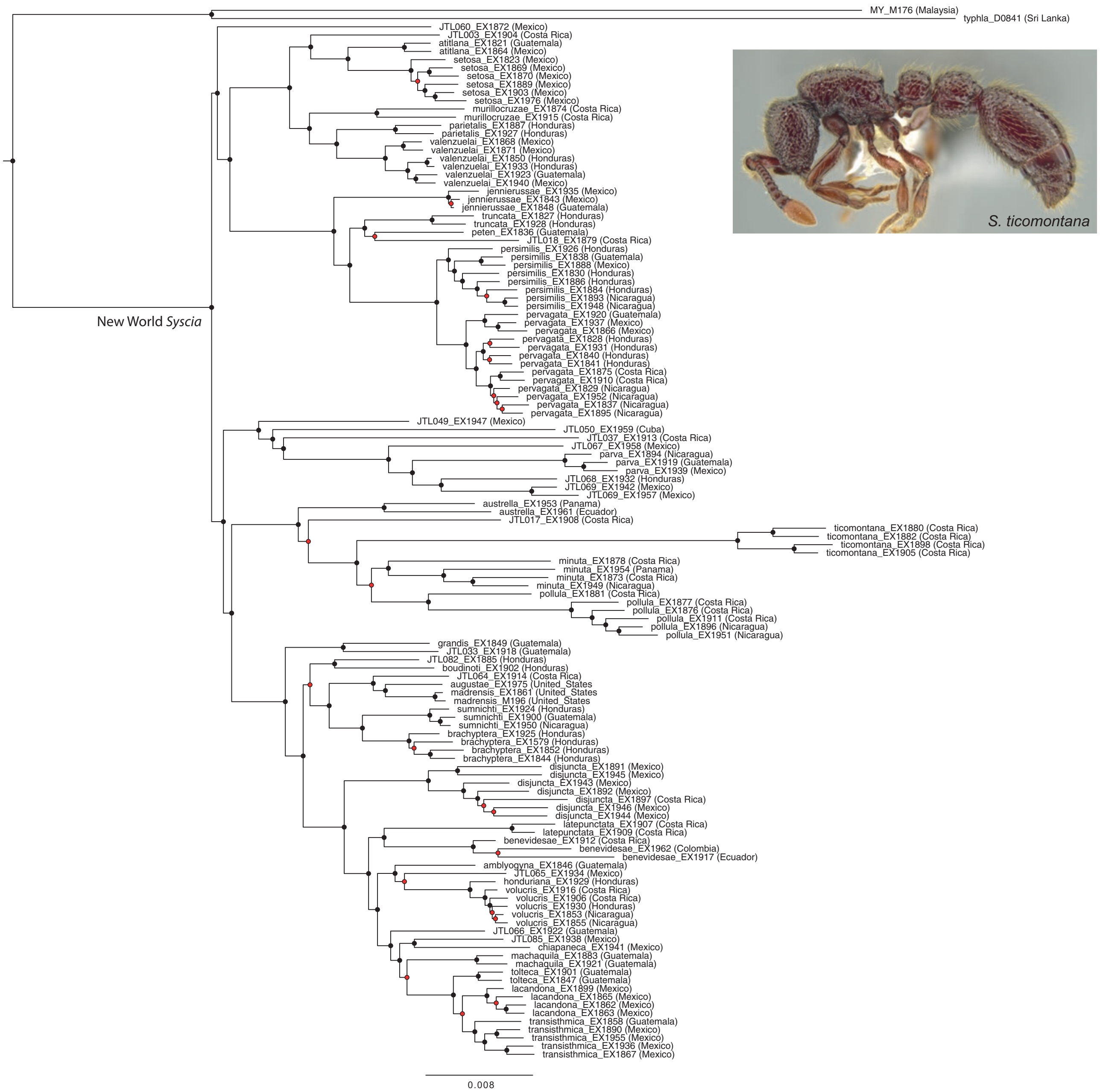


**Fig. 6.** Phylogeny of New World *Syscia*, inferred using the program IQ-TREE and 1,388 UCE loci. Two outgroup taxa (two species of *Ooceraea*) are not shown. Node support values (ultrafast bootstrap/SH-like) < 100/100 are depicted with red dots. The imaged specimen is *S. ticomontana* (CASENT0644376).

among several well-separated and well-supported clades. Several of these clades had broad distributions and included species that occur in sympatry with species from other clades. With respect to the sequenced specimens and the UCE phylogeny (see mtDNA below), our delimited species were all monophyletic. Branch lengths among intraspecific populations were similar to branch lengths among species, suggesting a more or less continuous process of dispersal, geographic isolation, and genetic divergence of allopatric populations. All but one species had geographically cohesive ranges. The exception was the new species *S. disjuncta*, with a paraphyletic assemblage of populations north of the Isthmus of Tehuantepec and a disjunct population in Costa Rica. We save detailed analysis of biogeographic patterns for later investigation, but note that the New World *Syscia* clade appears to have originated and diversified in the Middle American corridor, with perhaps two incursions into South America and one into the Caribbean.

COI results partially correspond to UCE results and are often useful for placing specimens that have not been sequenced for UCEs (Fig. 7). Strongly supported nodes are in the minority and mostly near the tips. In most cases, COI and UCE results are congruent at the species level, but they are often incongruent above species. Species-level incongruencies are 1) *S. pervagata* is paraphyletic with respect to *S. persimilis*, 2) *S. minuta* is paraphyletic with respect to *S. ticomontana* and *S. pollula*, and 3) *S. transisthmica* is paraphyletic with respect to *S. lacandona*. In all of these cases, inter-populational relationships received low support. Considering all species, minimum interspecific distances varied from 1 to 15% (median 9%, $n = 49$). Among the 31 species for which more than one COI sequence was available, maximum intraspecific p-distance varied from 0 to 16% (median 4.73%), and 13 of the 31 species had at least one intraspecific p-distance higher than the minimum

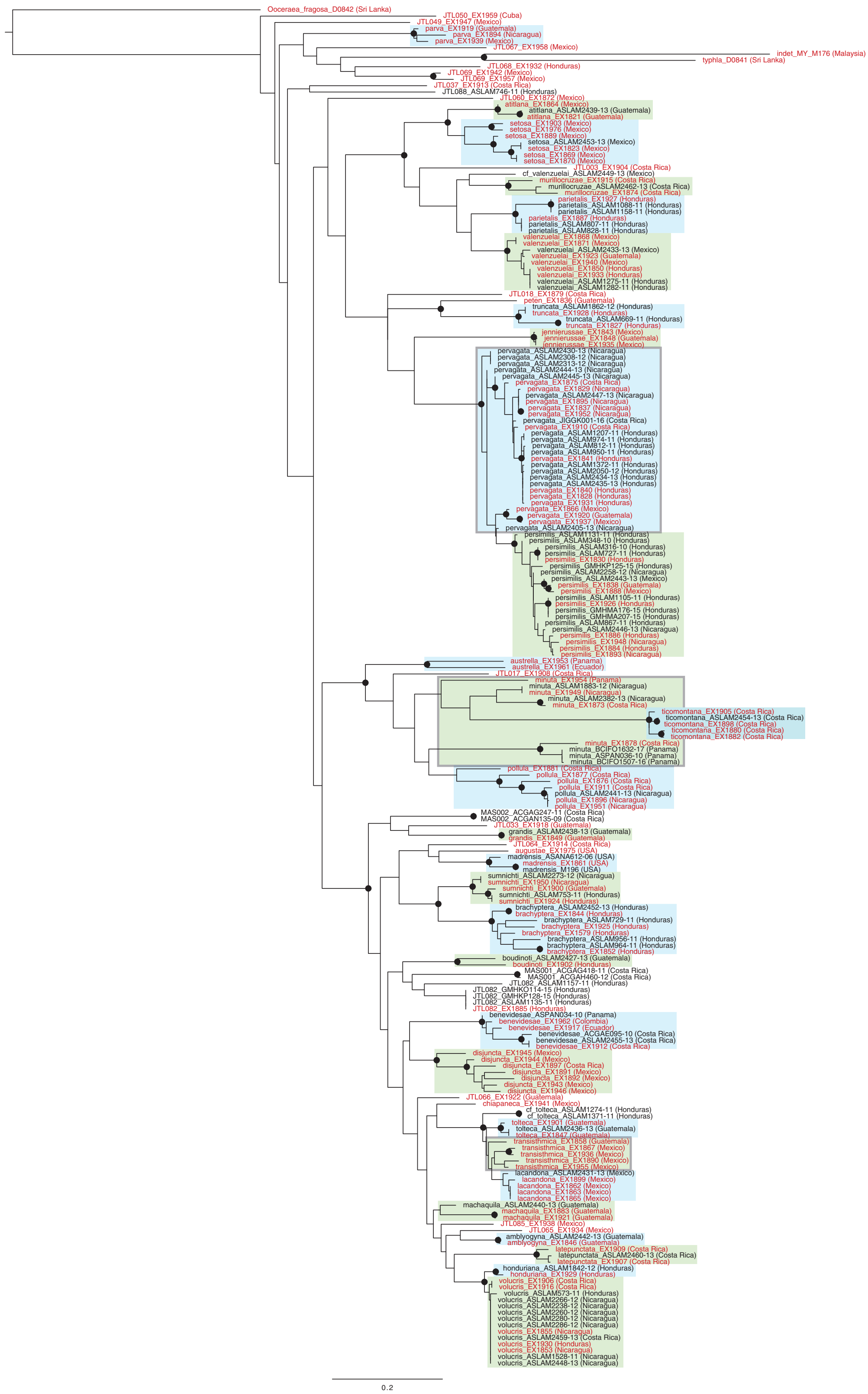

**Fig. 7.** Phylogenetic relationships among COI barcode sequences for *Syscia*. Red samples were sequenced for UCEs. Black samples were downloaded from the BOLD database. The tree was inferred using IQ-TREE with the data partitioned by codon position. Black circles on nodes indicate high support, which we define as ≥95% ultrafast bootstrap support and ≥95% SH-like branch support. Clades of named species are shaded as a visual aid, with gray outlines indicating non-monophyly of species.

interspecific distance. There was no evidence of a 'barcode gap' (around 3%), probably due to high levels of population differentiation and the likelihood of multiple cryptic species within many of our species.

COI results include three isolated specimens or clusters of specimens that are not treated separately in the species accounts. One is an isolated male, labeled JTL088 in Fig. 7, from Sierra de Agalta, Honduras. One is a worker and male from Guanacaste, Costa Rica, labeled MAS001 in Fig. 7, that are near *S. boudinoti* and *S.* JTL082. One is two males, also from Guanacaste, labeled MAS002 in Fig. 7, that cluster near *S. grandis* and *S.* JTL033. The latter two are large species from Volcán Atitlán, Guatemala.

## Taxonomic Results

### List of Named New World species

*Syscia amblyogyna* **new species**
*Syscia atitlana* **new species**
*Syscia augustae* (Wheeler 1902)
*Syscia austrella* **new species**
*Syscia benevidesae* **new species**
*Syscia borowieci* **new species**
*Syscia boudinoti* **new species**
*Syscia brachyptera* **new species**
*Syscia chiapaneca* **new species**
*Syscia disjuncta* **new species**
*Syscia grandis* **new species**
*Syscia honduriana* (Mann, 1922)
*Syscia jennierussae* **new species**
*Syscia lacandona* **new species**
*Syscia latepunctata* **new species**
*Syscia machaquila* **new species**
*Syscia madrensis* **new species**
*Syscia minuta* **new species**
*Syscia murillocruzae* **new species**
*Syscia parietalis* **new species**
*Syscia parva* **new species**
*Syscia persimilis* **new species**
*Syscia pervagata* **new species**
*Syscia peten* **new species**
*Syscia pollula* **new species**
*Syscia quisquilis* **new species**
*Syscia setosa* **new species**
*Syscia sumnichti* **new species**
*Syscia ticomontana* **new species**
*Syscia tolteca* (Forel, 1909)
*Syscia transisthmica* **new species**
*Syscia truncata* **new species**
*Syscia valenzuelai* **new species**
*Syscia volucris* **new species**

### List of Unnamed Morphospecies

*Syscia* JTL003
*Syscia* JTL017
*Syscia* JTL018
*Syscia* JTL033
*Syscia* JTL037
*Syscia* JTL049
*Syscia* JTL050
*Syscia* JTL060
*Syscia* JTL064
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*Syscia* JTL069
*Syscia* JTL071
*Syscia* JTL073
*Syscia* JTL074
*Syscia* JTL075
*Syscia* JTL076
*Syscia* JTL079
*Syscia* JTL082
*Syscia* JTL084
*Syscia* JTL085

## Species Accounts

### *Syscia amblyogyna*, New Species

Figure 12 (map, worker), S1 (holotype worker), S2 (brachypterous queen)

***Holotype.*** 1 worker, GUATEMALA, *Zacapa*: 2km SE La Unión, 14.94714 –89.27679 ±50m, 1550m, 12-May-2009, cloud forest, ex sifted leaf litter (LLAMA, Wa-B-03-1-37) [CASC, unique specimen identifier CASENT0644402]. PARATYPES: same data as holotype [brachypterous queen: CASC, USNM; worker: CASC, DZUP, JTLC, MCZC, UCD, UNAM, USNM, UVGC].

***Geographic Range.*** Guatemala.

***Diagnosis.*** Montane; subpetiolar process a shallow lobe with weakly convex posterior margin; AIII in dorsal view with strongly convex sides; AIV in dorsal view with convex sides, anterior margin not truncate; AIII and AIV dorsal profile convex; puncta on AIII large, separate; puncta on AIV large, separate, fading at midlength; standing pilosity long, coarse; color dark brown. Pairwise distance between two COI barcodes (GenBank accession MT267540 and BOLD Process ID ASLAM2442-13) was 0.15%. The smallest interspecific distance was 6.08%.

Four species are within size and geographic range of *S. amblyogyna*: *S. borowieci*, *S. tolteca*, *S.* JTL076, and *S.* JTL079.

*S. borowieci (*Fig. 13*):* allopatric; AIII in dorsal view more trapezoidal, with flatter sides; subpetiolar process with angulate posterior margin; standing pilosity longer.

*S. tolteca (*Fig. 12*):* lowland; no known site of local sympatry, but occurs in nearby lowland forest; sides of AIII and AIV in dorsal view less convex; AIII narrower on average (mean AIII-I 100 vs. 111).

*S. JTL076 (*Fig. 13*):* lowland; allopatric; AIII in dorsal view more trapezoidal, with flatter sides; AIV in dorsal view with less convex sides, anterior margin more truncate.

*S. JTL079 (*Fig. 12*):* lowland; allopatric; puncta on AIII more closely spaced; puncta on AIV more closely spaced, covering entire tergite.

***Measurements, Worker.*** HW 0.66 (0.65–0.67), HL 0.81 (0.80–0.83), SL 0.52 (0.51–0.55), MSL 1.11 (1.07–1.15), AIIIW 0.56 (0.54–0.59), AIIIL 0.51 (0.49–0.55), AIVW 0.83 (0.79–0.86), AIVL 0.96

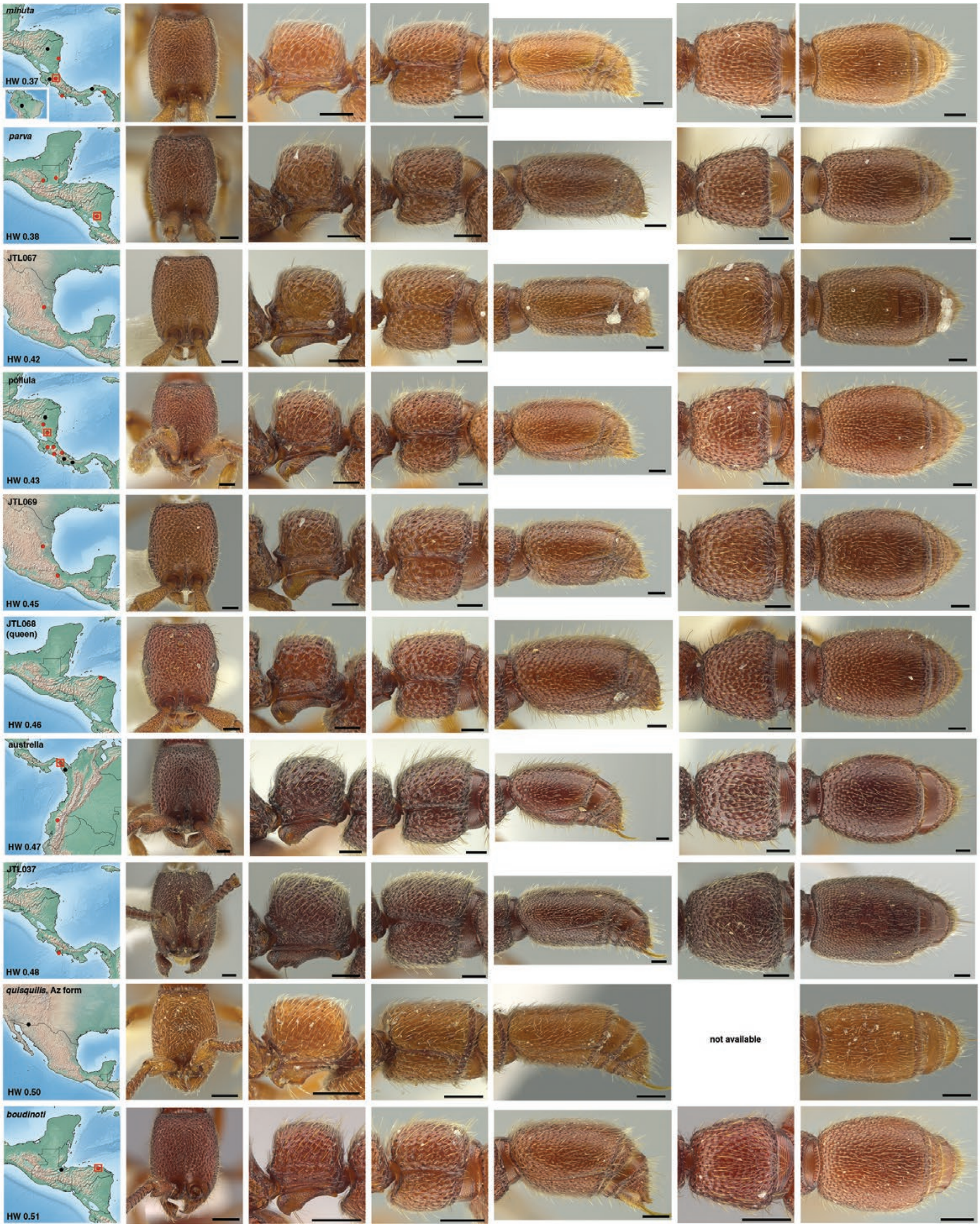


**Fig. 8.** Distribution map, face view, lateral view of petiole-AIV, and dorsal view of AIII-AIV of *Syscia minuta* (holotype worker), *S. parva* (holotype worker), *S.* JTL067 (worker, CASENT0644012), *S. pollula* (holotype worker), *S.* JTL069 (worker, CASENT0644008), *S.* JTL068 (queen, CASENT0613276), *S. austrella* (holotype worker), *S.* JTL037 (worker, CASENT0635747), *S. quisquillis* Arizona form (worker, FMNHINS0000095772), and *S. boudinoti* (holotype worker). Species are in order of mean HW, which is shown in the lower left of the distribution map. Scale bars 0.1 mm for *S. minuta* to *S.* JTL037, 0.2 mm for *S. quisquillis* Arizona form and *S. boudinoti*. On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality.

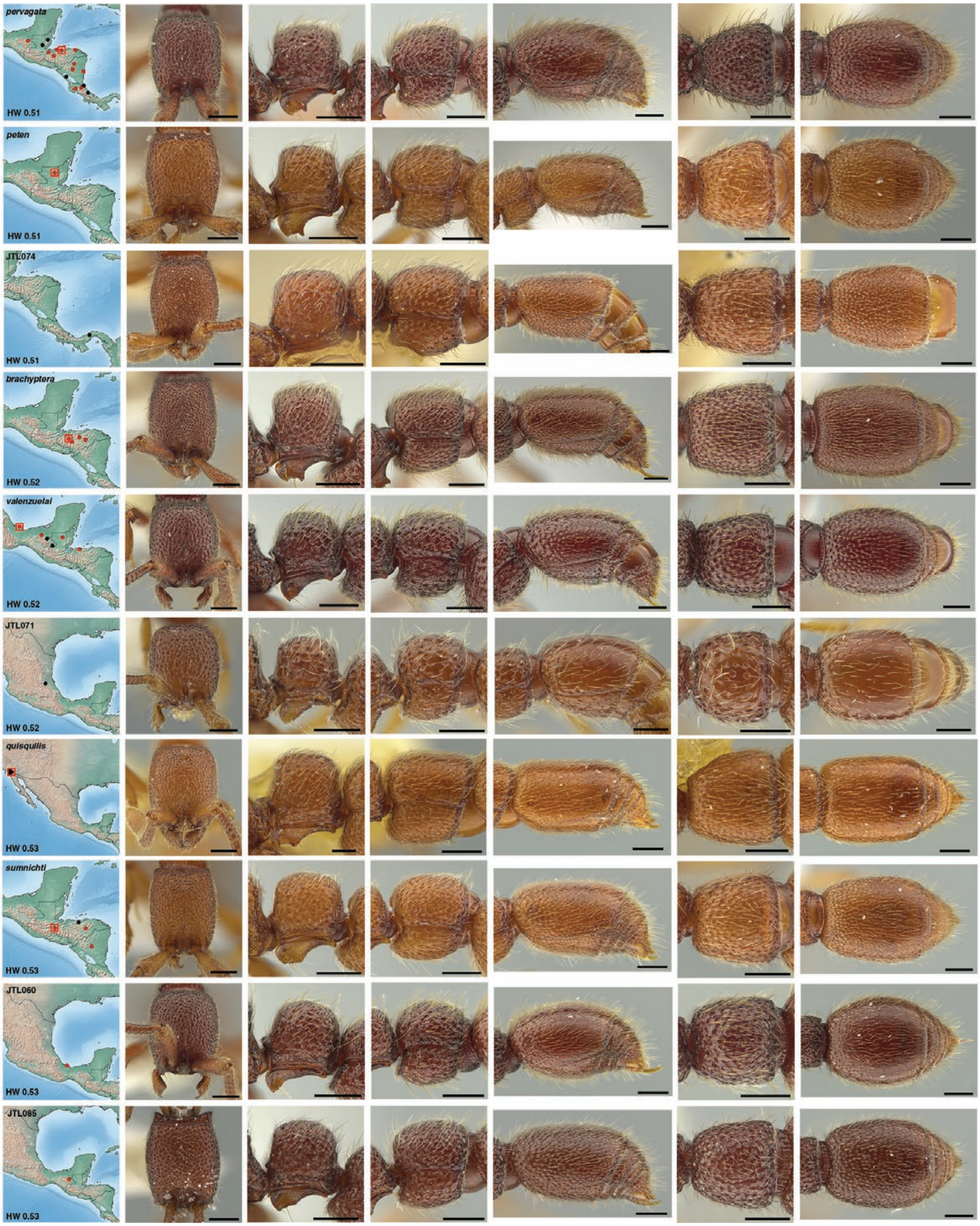


**Fig. 9.** Distribution map, face view, lateral view of petiole-AIV, and dorsal view of AIII-AIV of *Syscia pervagata* (holotype worker), *S. peten* (holotype worker), *S.* JTL074 (worker, MCZ-ENT00511564), *S. brachyptera* (holotype worker), *S. valenzuelai* (holotype worker), *S.* JTL071 (worker, FMNHINS0000095759), *S. quisquillis* (holotype worker), *S. sumnichti* (holotype worker), *S.* JTL060 (worker, CASENT0644220), and *S.* JTL085 (worker, CASENT0602939). Scale bars 0.2 mm. Species are in order of mean HW, which is shown in the lower left of the distribution map. On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality.

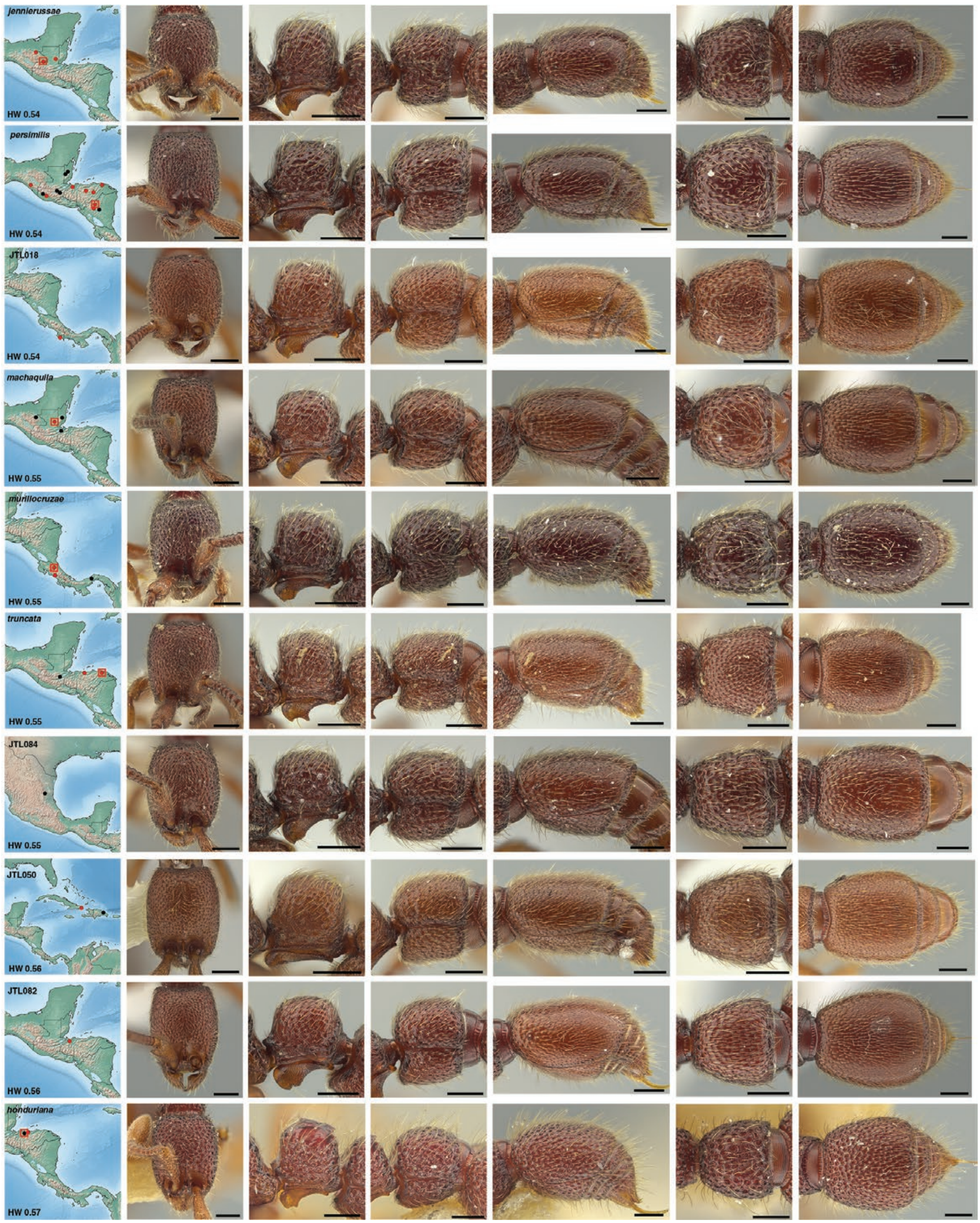


**Fig. 10.** Distribution map, face view, lateral view of petiole-AIV, and dorsal view of AIII-AIV of *Syscia jennierussae* (holotype worker), *S. persimilis* (holotype worker), *S.* JTL018 (worker, JTLC000013995), *S. machaquila* (holotype worker), *S. murillocruzae* (holotype worker), *S. truncata* (holotype worker), *S.* JTL084 (worker, FMNHINS0000095760), *S.* JTL050 (worker, CASENT0249320), *S.* JTL082 (worker, CASENT0617700), and *S. honduriana* (lectotype worker). Species are in order of mean HW, which is shown in the lower left of the distribution map. Scale bars 0.2 mm. On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality.

(0.93–1.00), SI 79 (77–81), AIII-I 111 (108–115), AIV-I 87 (85–89) (*n* = 4).

***Measurements, Queen.*** HW 0.69 (0.69-0.69), HL 0.82 (0.81–0.82), SL 0.52 (0.51–0.52), MSL 1.28 (1.26–1.31), AIIIW 0.63 (0.63–0.64), AIIIL 0.57 (0.57–0.58), AIVW 0.92 (0.92–0.93), AIVL 1.12 (1.10–1.13), SI 76 (75–76), AIII-I 111 (111-111), AIV-I 83 (82–83) (*n* = 2).

***Biology.*** This species is known from one montane wet forest site, with multiple collections ranging from 1,325 to 1,550 m elevation. All specimens are from Winkler samples of forest floor leaf litter and rotten wood.

This species has brachypterous queens that show variation in eye development. One series from a miniWinkler sample, and thus likely a single colony, contained 14 workers and 9 brachypterous queens. All of the queens had a single median ocellus and no discernable lateral ocelli. Six of the queens had no discernable compound eye, and three had minute compound eyes of a few small, fused ommatidia, the eye little larger than a punctum of the surrounding coarse sculpture (Supp Fig. S1D [online only]). Another series, from another miniWinkler sample 5 m distant, contained 13 workers and 2 brachypterous queens, both with the single median ocellus, one with no detectable compound eye, and one with a barely detectable eye, of 3 fused ommatidia, and smaller than a punctum. The proximity of the two collections raises the possibility that they were part of one larger colony. A series from a maxiWinkler sample contained multiple workers and a brachypterous queen that had larger compound eyes, of about 10 fused ommatidia, and slightly larger than the surrounding puncta (Supp Fig. S1E [online only]).

***Comments.*** The occurrence of queens with the fully formed mesosoma of winged queens but lacking or nearly lacking compound eyes is unusual. Trible and Kronauer (2017) show that there is typically a hierarchical continuum of phenotypes between worker and queen, with queen-like compound eyes generally occurring at smaller sizes than the occurrence of queen-like mesosomal structure associated with wings. Intercastes with queen-like compound eyes but worker-like mesosoma are common, but the reverse is unusual.

### *Syscia atitlana*, New Species

Figure 12 (map, worker), S3 (holotype worker)

***Holotype:*** 1 worker, GUATEMALA, *Suchitepéquez*: Refugio El Quetzal, 14.55483 –91.19299 ±50m, 1838m, 15-Jun-2009, oak forest, ex sifted leaf litter (R. S. Anderson, RSA2009-102) [CASC, unique specimen identifier CASENT0611764]. PARATYPES: same data as holotype [worker: CASC, MCZC, USNM, UVGC].

***Geographic Range.*** Mexico (Chiapas) to Guatemala.

***Diagnosis.*** Montane; subpetiolar process an asymmetrical lobe with slightly convex posterior margin; AIII in dorsal view trapezoidal, sides moderately convex; AIV in dorsal view with sides convex, anterior margin not truncate; dorsal profile of AIII and AIV convex; puncta on AIII large, widely separated; puncta on AIV large, widely separated, fading at midlength; standing pilosity long, coarse; color dark brown. Pairwise distances among three COI barcodes (GenBank accessions MT267541 and MT267542, BOLD process ID ASLAM2439-13) varied from 0.19 to 2.34%. The smallest interspecific distance was 7.48%.

Eight species are within size and geographic range of *S. atitlana*: *S. chiapaneca*, *S. lacandona*, *S. setosa*, *S. transisthmica*, *S.* JTL065, *S.* JTL066, JTL073, and *S.* JTL079.

*S. chiapaneca* (Fig. 11)*:* allopatric, but ranges adjacent; puncta on AIII and AIV much smaller; anterior margin of AIV more truncate; subpetiolar process shallower; standing pilosity shorter.

*S. lacandona* (Fig. 12)*:* possibly locally sympatric in Sierra de Chiapas, but no sympatric workers to directly compare; very similar; dorsal profile of petiole somewhat more rounded; AIII in dorsal view with sides slightly more convex; subpetiolar process shallower, with less convex posterior margin.

*S. setosa* (Fig. 11)*:* allopatric; AIII in dorsal view less trapezoidal; AIV in dorsal view with sides less converging anteriorly.

*S. transisthmica* (Fig. 12)*:* locally sympatric; very similar; puncta on AIII more closely spaced; subpetiolar process shallower.

*S. JTL065* (Fig. 12)*:* allopatric, but adjacent ranges; AIII and AIV in dorsal view with sides more convex; puncta on AIII more closely spaced.

*S. JTL066* (Fig. 11)*:* lowland; allopatric; puncta on AIII and AIV smaller; posterior margin of subpetiolar process with a small tooth.

*S. JTL073* (Fig. 11): allopatric, but adjacent ranges; very similar; AIII and AIV in dorsal view with sides more convex; AIV wider on average (mean AIV-I 101 vs. 86).

*S. JTL079* (Fig. 12)*:* sympatric; puncta on AIV closely spaced, covering entire tergite; posterior margin of subpetiolar process with a tooth.

***Measurements, Worker.*** HW 0.63 (0.60–0.67), HL 0.75 (0.69–0.79), SL 0.49 (0.46–0.51), MSL 0.98 (0.86–1.06), AIIIW 0.46 (0.41–0.48), AIIIL 0.42 (0.39–0.44), AIVW 0.76 (0.67–0.81), AIVL 0.88 (0.79–0.94), SI 78 (73–83), AIII-I 108 (103–115), AIV-I 86 (82–89) (*n* = 9).

***Biology.*** This species occurs in montane wet forest, from 1475 to 1850 m elevation. Only workers are known, and all are from Winkler or Berlese samples of forest floor leaf litter and rotten wood.

### *Syscia augustae* (Wheeler, 1902)

Figure 11 (map, worker), S4 (worker), S5 (brachypterous queen), S6 (male)

*Cerapachys* (*Parasyscia*) *augustae* Wheeler, W. M., 1902: 182, fig. 1, 2. Syntype worker, apterous queen: USA, Texas, Austin, 11 May 1902 (Rucker) [USNM, not examined]. Wheeler, W. M., 1903: 206 (description of immature larva). Wheeler, G. C., 1950: 106 (review of larvae of Cerapachyinae; no new material, W. M. Wheeler's 1903 observations repeated).

*Syscia augustae:* Borowiec, 2016: 224.

Smith (1942) described the putative male of *S. augustae*, but Borowiec (2016) reidentified Smith's male as *Acanthostichus*.

***Geographic Range.*** United States (Texas, Arkansas), Mexico (Nuevo Leon).

***Diagnosis.*** Occipital carina strongly developed, visible in face view; subpetiolar process subtriangular with small convexity on

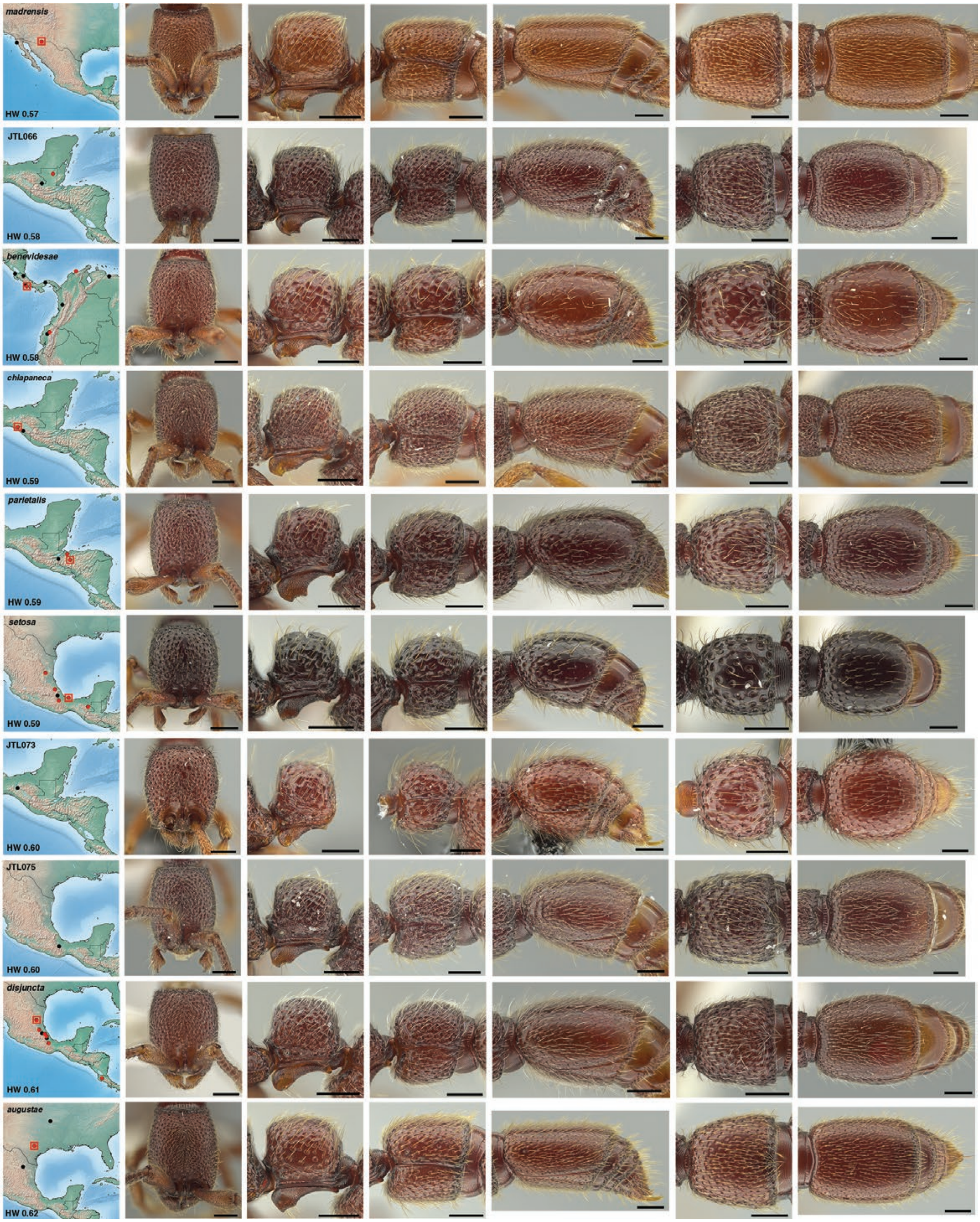


**Fig. 11.** Distribution map, face view, lateral view of petiole-AIV, and dorsal view of AIII-AIV of *Syscia madrensis* (holotype worker), *S.* JTL066 (worker, CASENT0610648), *S. benevidesae* (holotype worker), *S. chiapaneca* (holotype worker), *S. parietalis* (holotype worker), *S. setosa* (holotype worker), *S.* JTL073 (worker, MCZ-ENT00511569), *S.* JTL075 (worker, CASENT0601445), *S. disjuncta* (holotype worker), and *S. augustae* (worker, CASENT0644275). Species are in order of mean HW, which is shown in the lower left of the distribution map. Scale bars 0.2 mm. On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality.

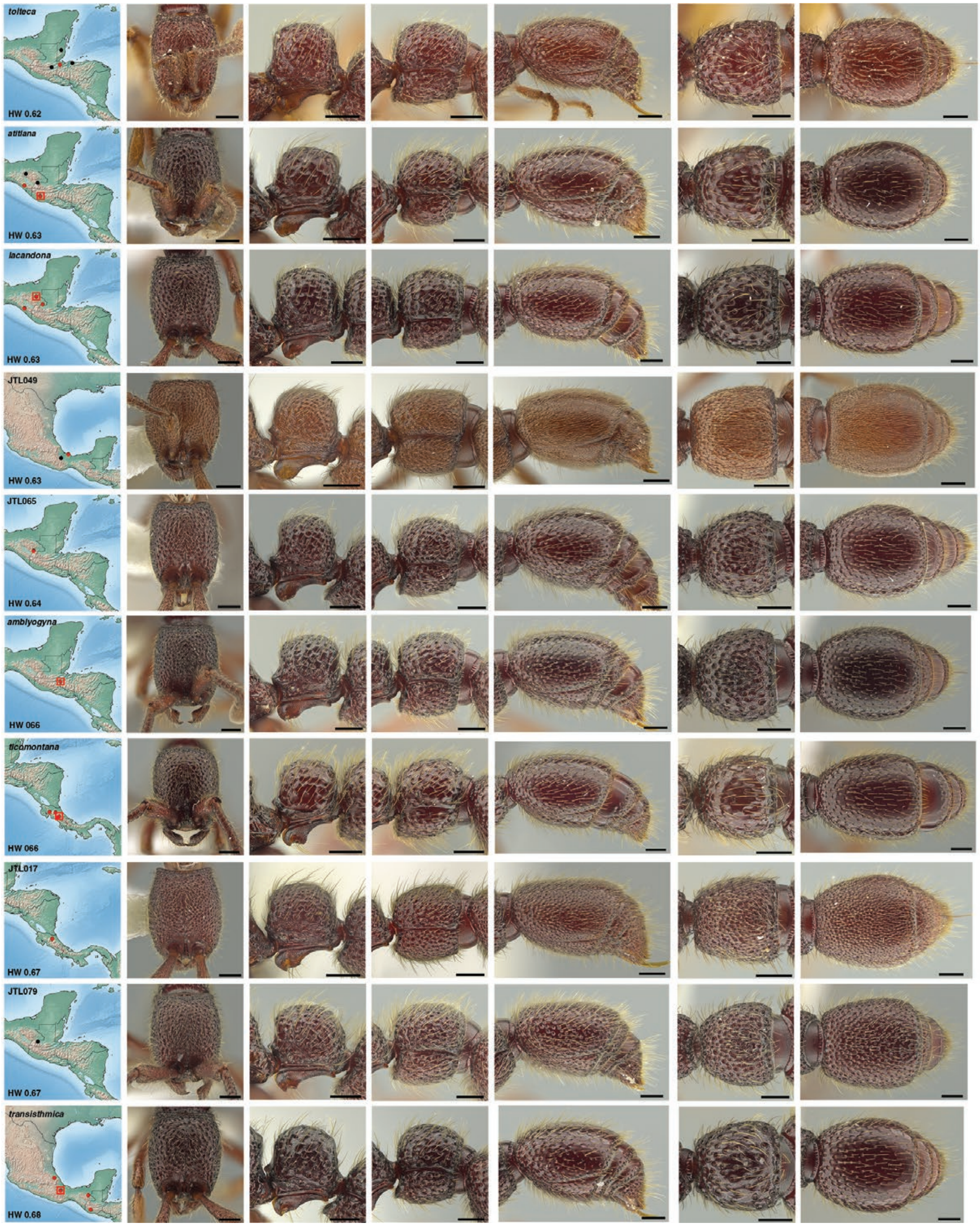


**Fig. 12.** Distribution map, face view, lateral view of petiole-AIV, and dorsal view of AIII-AIV of *Syscia tolteca* (lectotype worker), *S. atitlana* (holotype worker), *S. lacandona* (holotype worker), *S.* JTL049 (worker, CASENT0644222), *S.* JTL065 (worker, CASENT0602939), *S. amblyogyna* (holotype worker), *S. ticomontana* (holotype worker), *S.* JTL017 (worker, INB0003693097), *S.* JTL079 (worker, CASENT0642985), and *S. transisthmica* (holotype worker). Species are in order of mean HW, which is shown in the lower left of the distribution map. Scale bars 0.2 mm. On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality (not shown for *S. tolteca*, with type locality 'Guatemala').

posterior margin; AIII in dorsal view trapezoidal, with nearly flat sides; AIV in dorsal view with sides flat to weakly convex, subparallel, anterior margin somewhat truncate; dorsal profile of AIII and AIV flat; standing pilosity of medium length and thickness; puncta on AIII small, widely spaced; puncta on AIV small, widely spaced, fading at midlength; color red brown. Based on the COI barcode of the sequenced specimen (GenBank accession MT267543), the smallest pairwise interspecific distance was 9.16%.

Three species are within size and geographic range of *S. augustae*: *S. disjuncta*, *S. madrensis*, and *S. setosa*.

*S. disjuncta* (Fig. 11): allopatric; AIV in dorsal view with sides more convex; dorsal profile of AIII and AIV more convex; standing pilosity longer; smaller on average (mean HW 0.56 vs. 0.62).

*S. madrensis* (Fig. 11): allopatric; subpetiolar process less triangular, more quadrate; sides of AIII in dorsal view less convex; standing pilosity less evident; smaller on average (mean HW 0.56 vs. 0.62); AIII narrower on average (mean AIII-I 96 vs. 107).

*S. setosa* (Fig. 11): allopatric; AIII in dorsal view with more convex sides; puncta on AIII large, widely spaced; standing pilosity long, coarse.

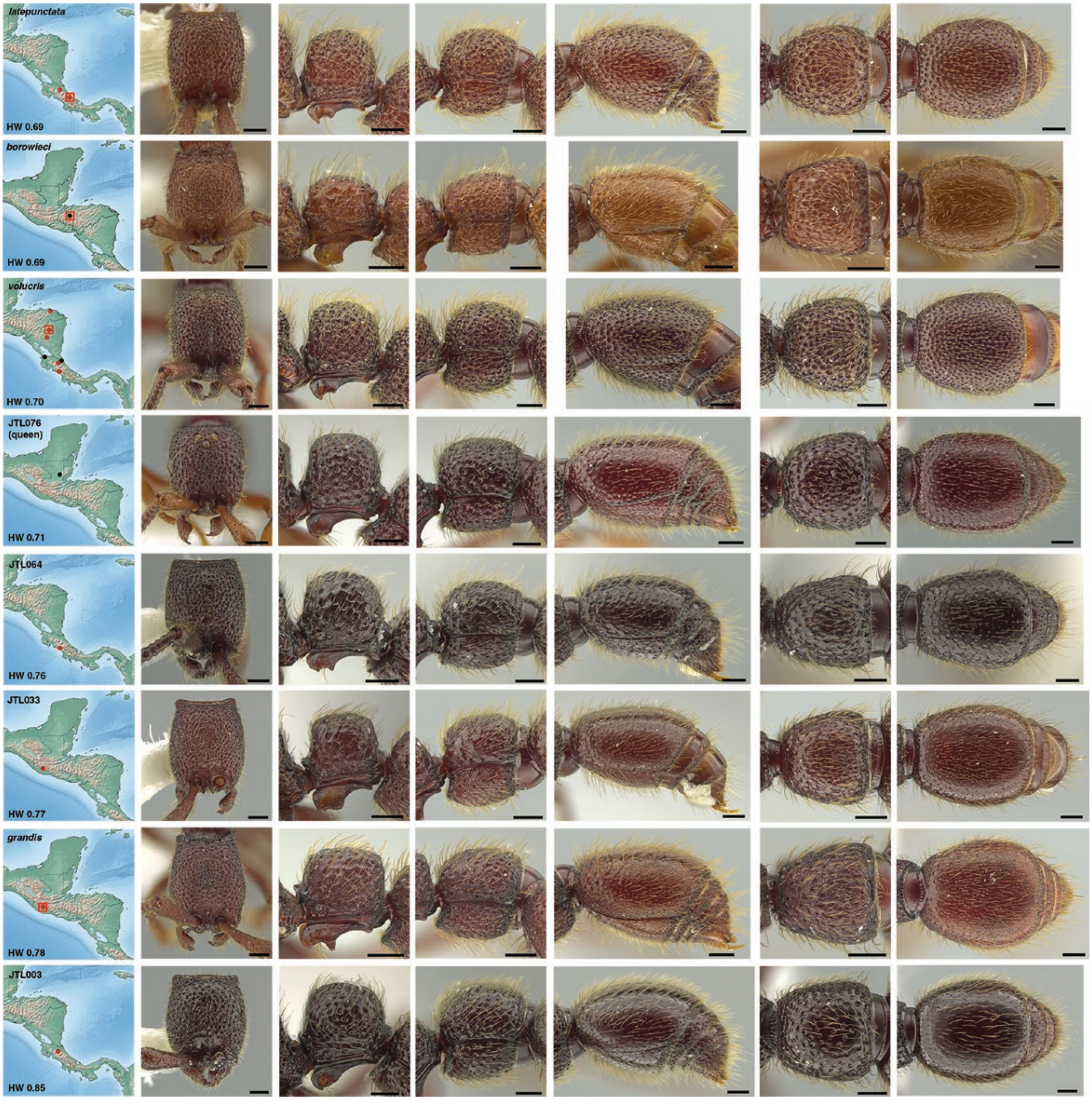


**Fig. 13.** Distribution map, face view, lateral view of petiole-AIV, and dorsal view of AIII-AIV of *Syscia latepunctata* (holotype worker), *S. borowieci* (holotype worker), *S. volucris* (holotype worker), *S.* JTL076 (queen, CASENT0614221), *S.* JTL064 (worker, CASENT0631661), *S.* JTL033 (worker, CASENT0611831), *S. grandis* (holotype worker), and *S.* JTL003 (worker, INB0003213589). Species are in order of mean HW, which is shown in the lower left of the distribution map. Scale bars 0.2 mm. On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality.

***Measurements, Worker.*** HW 0.62 (0.62–0.63), HL 0.79 (0.75–0.83), SL 0.45 (0.44–0.45), MSL 1.02 (0.99–1.05), AIIIW 0.54 (0.53–0.55), AIIIL 0.50 (0.49–0.53), AIVW 0.70 (0.67–0.71), AIVL 0.88 (0.86–0.89), SI 72 (70–73), AIII-I 107 (105–108), AIV-I 79 (76–82) ($n$ = 4).

***Measurements, Queen.*** HW 0.67, HL 0.84, SL 0.46, MSL 1.23, AIIIW 0.66, AIIIL 0.61, AIVW 0.81, AIVL 1.09, SI 69, AIII-I 109, AIV-I 75 ($n$ = 1).

***Biology.*** The first American species of *Syscia* to be described was named for Miss Augusta Rucker, who found the type series on the outskirts of Austin, Texas. Wheeler had not found this species previously, in spite of 3 yr of careful collecting in the vicinity of Austin. Wheeler (1903) discovered a second colony the next year. He kept them alive for a while, recording his observations as follows:

> 'The colony of *C. augustae*, on which the following observations were made, was discovered May 6th, 1903, near high water mark in the bottom of Shoal Creek at Austin, Texas. It was inhabiting a simple, straight gallery about 5 cm. long by 7 mm. in diameter, under the very center of a large block of limestone. At one end the gallery dipped down into the soil to a depth of 4 cm. The ants, 29 in number, were all congregated in the surface gallery with their long bodies wrapped about a large packet of eggs. Only workers were found, though careful search was made for the peculiar wingless female described in my former paper. The whole colony, with the possible exception of a few ants that may have been out foraging, was captured and placed in a small Petri dish, the bottom of which had been provided with a thin layer of damp soil partly covered with a glass microscope slide. The ants soon took up their abode under the slide after collecting their scattered eggs. Nymphs of two common Texan termites (*Amitermes tubiformans* and *Eutermes cinereus*) were cut into a few pieces and given them as food. Even when these were placed only a few millimeters from the ants, the latter showed no signs of noticing them till they were actually touched with the antennae. And even then the ants often hesitated before attacking the still struggling heads and thoraces. Eventually the termites were dispatched by the ants curling about them and using both mandibles and sting. The latter produced sudden paralysis. Then the ants eagerly lapped up the juices excuding from the cut ends of the termite fragments, while remaining very quiet as if absorbed in the delight of feeding. The mandibles seemed to be too feeble to cut or puncture even so thin a chitinous investment as that of the termites'.

Wheeler (1902) described the queen of *S. augustae*. The specimen had fully developed compound eyes, ocelli, and an enlarged mesosoma with all the typical sclerites of winged queens, but he wrote 'There is nothing to show that the thorax has ever borne wings'. We examined a similar queen in a series collected in Arkansas. One side of the mesosoma bears minute wing remnants, suggesting brachyptery. The wings are mere linear stubs and could not function in flight.

The first male of the species was discovered by Alex Wild in the University of Texas Insect Collection. It was from a Malaise trap, from the Brackenridge Field Lab in Austin, Texas. It is assumed to be conspecific, since it is from the type locality and there are unlikely to be multiple species of *Syscia* in the vicinity.

MacGown et al. (2017) report the species from USA, Arkansas.

***Comments.*** This species is at the far northern range limit of the genus in the Americas. Within its geographic range it is not known to be sympatric with any other *Syscia* species. However, the southernmost record of the species, from Nuevo Leon, Mexico, is less than 300 km north of the Rancho Cielo site in Tamaulipas, where four species occur.

Material from southern New Mexico and Arizona has been identified as *S. augustae* (e.g., Mackay 2002, AntWeb), but here we describe these populations as a distinct species, *S. madrensis*. UCE sequence data are available for two specimens of *S. madrensis* from Arizona and one specimen of *S. augustae* from Texas. The three specimens form a clade, but the genetic distance between the Texas specimen and the two Arizona specimens is relatively large. We examined five collections of *S. madrensis*: four from Arizona and one from Baja California. We examined three widely-dispersed collections of *S. augustae*: from Arkansas, Texas, and the Mexican state of Nuevo Leon. The two groups of specimens were morphologically distinct, with differences greater than many examples of sympatric species elsewhere in the range of *Syscia*. Variation within the groups was low, with the Arkansas, Texas, and Nuevo Leon specimens being very similar to each other, regardless of the large geographic distances among them, and the Arizona and Baja California specimens of *S. madrensis* being very similar to each other.

The *S. augustae* clade shows a sister taxon relationship with a single specimen from Costa Rica (*S.* JTL064). The Costa Rican specimen is morphologically completely different from the *S. augustae* clade. COI data show *S. augustae*, *S. madrensis*, and JTL064 in a single cluster, but as three separate groups with deep divergences.

## *Syscia austrella*, New Species

Figure 8 (map, worker), S7 (holotype worker), S8 (queen)

***Holotype:*** 1 worker, PANAMA, *Darién*: Reserva Chucantí, 8.79924 −78.46148 ±20m, 1335m, 18-Jan-2015, cloud forest, ex sifted leaf litter (M. G. Branstetter, MGB2483) [CASC, unique specimen identifier CASENT0633043]. PARATYPES: same data as holotype [dealate queen: CASC]; same data except 8.79805 −78.4625, 1305m (MGB2484) [dealate queen: USNM].

***Geographic Range.*** Panama, Ecuador.

***Diagnosis.*** Cloud forest; subpetiolar process a moderately deep rounded lobe with minute apical tooth; AIII in dorsal view trapezoidal with weakly convex sides; AIV in dorsal view with convex sides sloping to non-truncate anterior margin; dorsal of AIII and AIV convex in lateral view; puncta on AIII discrete, large, nearly confluent; puncta on AIV discrete, large, separated, fading at midlength; standing pilosity long and coarse; color red brown. Pairwise distance between two COI barcodes (GenBank accessions MT267544 and MT267545) was 11.43%. The smallest interspecific distance was 12.02%.

Two species are within size and geographic range of *S. austrella*: *S. pollula* and *S.* JTL037.

*S. pollula* (Fig. 8)*:* parapatric, with adjacent ranges in Panama; smaller on average (HW 0.43 vs. 0.47); puncta on anterior AIV smaller and more closely spaced.

*S. JTL037* (Fig. 8)*:* parapatric, known from one worker from Osa Peninsula, Costa Rica; sides of AIV less convex.

***Measurements, Worker.*** HW 0.47 (0.45–0.50), HL 0.61 (0.59–0.64), SL 0.32 (0.30–0.35), MSL 0.77 (0.73–0.84), AIIIW 0.36 (0.33–0.40), AIIIL 0.34 (0.32–0.37), AIVW 0.58 (0.54–0.64), AIVL 0.69 (0.63–0.77), SI 69 (65–72), AIII-I 104 (96–109), AIV-I 84 (81–87) ($n$ = 3).

***Measurements, Queen.*** HW 0.49, HL 0.61, SL 0.33, MSL 1.02, AIIIW 0.41, AIIIL 0.40, AIVW 0.67, AIVL 0.85, SI 68, AIII-I 100, AIV-I 78 ($n$ = 1).

***Biology.*** This species occurs in montane wet forest from 500 to 1,350 m elevation. Workers and dealate queens are known, all from Winkler or Berlese samples of forest floor litter and rotten wood.

***Comments.*** Sequence data place Panama and Ecuador material together in a clade, but with deep divergences (Figs. 6 and 7).

## *Syscia benevidesae*, New Species

Figure 11 (map, worker), S9 (holotype worker), S10 (queen)

***Holotype:*** 1 worker, COSTA RICA, *Puntarenas*: 10km SW Pto. Jimenez, 8.46553 −83.36928 ±30m, 240m, 12-Mar-2008, wet forest, ex sifted leaf litter (J. Longino, JTL6197-s) [UCR, unique specimen identifier CASENT0601652]. PARATYPE: 13km SSW Pto. Jimenez, 8.40667 −83.32833 ±200m, 130m, 10-Mar-2008, tropical rainforest, ex sifted leaf litter (J. Longino, JTL6209-21) [dealate queen: CASC].

***Geographic Range.*** Costa Rica to Ecuador, Venezuela.

***Diagnosis.*** Subpetiolar process shallow, broad, with obtuse posterior angle; AIII in dorsal view trapezoidal with moderately convex sides; AIV in dorsal view with convex sides, anterior margin not truncate; dorsal profile of AIII and AIV convex; puncta on AIII large, widely spaced; puncta on AIV large, widely spaced, somewhat lunate, restricted to anterior third; standing pilosity long, abundant, coarse, no underlying pubescence; color red brown. Pairwise distances among six COI barcodes (GenBank accessions MT267546 - MT267548, BOLD Process IDs ASLAM2455-13, ASPAN034-10, ACGAE095-10) varied from 0 to 5.32%. The smallest interspecific distance was 10.05%.

Four species are within size and geographic range of *S. benevidesae*: *S. murillocruzae*, *S. pervagata*, *S.* JTL018, and *S.* JTL074.

*S. murillocruzae (*Fig. 10*):* locally sympatric; subpetiolar process deeper and narrower; puncta on AIII and AIV smaller and more closely spaced.

*S. pervagata (*Fig. 9*):* Overlapping ranges, but no known areas of local sympatry; subpetiolar process acute posterior tooth; smaller on average (mean HW 0.51 vs. 0.57).

*S. JTL018 (*Fig. 10*):* locally sympatric; puncta on AIII small and nearly confluent; puncta on AIV small, fading at midlength; standing pilosity short, fine.

*S. JTL074 (*Fig. 9*):* locally sympatric; smaller on average (HW 0.51 vs. 0.57); puncta on AIV fade at midlength; standing pilosity short, fine.

***Measurements, Worker.*** HW 0.58 (0.56–0.62), HL 0.73 (0.71–0.78), SL 0.45 (0.41–0.50), MSL 0.97 (0.90–1.05), AIIIW 0.46 (0.43–0.50), AIIIL 0.44 (0.41–0.51), AIVW 0.71 (0.68–0.77), AIVL 0.83 (0.78–0.94), SI 77 (74–81), AIII-I 104 (99–107), AIV-I 85 (82–88) ($n$ = 5).

***Measurements, Queen.*** HW 0.64, HL 0.76, SL 0.47, MSL 1.23, AIIIW 0.54, AIIIL 0.50, AIVW 0.81, AIVL 0.99, SI 74, AIII-I 107, AIV-I 82 ($n$ = 1).

***Biology.*** This species occurs in wet to dry forest habitat. Most records are from the lowlands, from sea level to around 800 m, but one record from Venezuela is from 1100 m. Most records are from Winkler or Berlese samples of forest floor leaf litter and rotten wood. A collection from Tayrona park in Colombia was in a 'rotten termite log'. Dealate queens are known.

***Comments.*** UCE and COI data cluster specimens that occur from Costa Rica to Ecuador (Figs. 6 and 7). Sequence divergence is relatively large among specimens, suggesting long-term reproductive isolation and the potential for cryptic species.

## *Syscia borowieci*, New Species

Figure 13 (map, worker), S11 (holotype worker)

***Holotype:*** 1 worker, Honduras, Santa Barbara, 4km SW Mina El Mochito, 14.84034 −88.06096 ±?, 1040m, 14-Mar-1979, forest ravine, rotten wood (W. L. Brown) [MCZC, unique specimen identifier MCZ-ENT00511558]. PARATYPES: same data as holotype [worker: CASC, MCZC, USNM].

***Geographic Range.*** Honduras.

***Diagnosis.*** Lower montane; subpetiolar process subquadrate, with angular posterior margin; AIII in dorsal view trapezoidal, with nearly flat sides; AIV in dorsal view with moderately convex sides that narrow to a weakly truncate anterior margin; dorsal profile of AIII convex, of AIV weakly convex; puncta on AIII of medium size, nearly confluent; puncta on AIV small, separated, restricted to anterior margin, most of tergite smooth and shining; standing pilosity abundant, long, coarse; color red brown.
One other species is within size and geographic range of *S. borowieci*: *S. volucris (*Fig. 13*):* lowland; allopatric; puncta on AIV covering entire tergite.

***Measurements, Worker.*** HW 0.69, HL 0.82, SL 0.64, MSL 1.13, AIIIW 0.55, AIIIL 0.50, AIVW 0.83, AIIIL 0.80, SI 93, AIII-I 110, AIV-I 104 ($n$ = 1).

## *Syscia boudinoti*, New Species

Figure 8 (map, worker), S12 (holotype worker), S13 (male)

***Holotype:*** 1 worker, HONDURAS, *Gracias a Dios*: Las Marias, 15.71011 −84.86304 ±20m, 100m, 9-Jun-2010, tropical rainforest, ex sifted leaf litter (LLAMA, Wm-C-07-1-03) [CASC, unique specimen identifier CASENT0628997]. PARATYPES: same data as holotype [worker: MCZC, USNM].

***Geographic Range.*** Honduras, Guatemala.

***Diagnosis.*** Lowland; occipital carina short, hardly visible in face view; subpetiolar process triangular, with slightly convex posterior margin; AIII trapezoidal with flat sides; sides of AIV moderately convex; puncta on AIV distinct, slightly separated, fading at about midlength; AIV dorsum relatively flat in profile; standing pilosity of moderate length and abundance; color orange brown. Pairwise distance between two COI barcodes (GenBank accession MT267549 and BOLD Process ID ASLAM2427-13) was 7.31%. The smallest interspecific distance was 9.29%.

Eleven species are within size and geographic range of *S. boudinoti*: *S. brachyptera, S. honduriana, S. jennierussae, S. machaquila, S. persimilis, S. pervagata, S. peten, S. sumnichti, S. truncata, S. valenzuelai*, and *S. JTL082*.

*S. brachyptera, S. persimilis, S. pervagata, S. peten, S. truncata*: subpetiolar process with strong posterior tooth.

*S. honduriana (*Fig. 10*):* AIV with large confluent puncta over entire surface.

*S. jennierussae (*Fig. 10*):* allopatric; scapes shorter on average (mean SI 67 vs. 75); anterior margin of AIV more truncate.

*S. machaquila (*Fig. 10*):* locally sympatric; puncta larger on AIII and AIV; AIII in profile relatively more rounded (*S. boudinoti* relatively more quadrate); standing pilosity coarser.

*S. sumnichti (*Fig. 9*):* cloud forest; no known site of local sympatry; subpetiolar process with more convex posterior margin; erect pilosity shorter and finer; puncta on AIV fade at about third length.

*S. valenzuelai (*Fig. 9*):* broadly sympatric but no known site of local sympatry; puncta larger on AIII and AIV; AIV dorsum more convex in profile; standing pilosity coarser.

*S. JTL082 (*Fig. 10*):* cloud forest; no known site of local sympatry; larger on average (mean HW 0.56 vs. 0.52); sides of AIV more convex.

***Measurements, Worker.*** HW 0.51 (0.51–0.52), HL 0.63 (0.62–0.63), SL 0.38 (0.37–0.39), MSL 0.79 (0.79–0.80), AIIIW 0.39 (0.38–0.41), AIIIL 0.37 (0.36–0.38), AIVW 0.60 (0.57–0.61), AIVL 0.72 (0.69–0.74), SI 74 (73–74), AIII-I 106 (103–108), AIV-I 83 (82–84) ($n$ = 3).

***Biology.*** This species occurs in lowland moist to wet forest. The three workers are from a miniWinkler sample of forest floor litter and rotten wood. The male is from a Malaise trap.

***Comments.*** The UCE tree shows a clade with two specimens, one specimen of *S. boudinoti* from a lowland Honduras site (Las Marias) and one specimen of *S.* JTL082 from a highland Honduras site (Cusuco) (Fig. 6). This clade has greater representation in the COI tree, with nine sequences that form three clusters (Fig. 7). One cluster is the worker of *S. boudinoti* from Las Marias and a male from a moist forest site in Guatemala (Montaña Chiclera). The male is provisionally identified as *S. boudinoti* based on COI evidence, even though the pairwise distance between the two specimens is 7%. One cluster is a worker and a male from Guanacaste, Costa Rica, identified by Alex Smith as MAS001. One cluster is two workers and three males from Cusuco National Park Honduras, identified as *S.* JTL082. Four of these specimens have identical haplotypes. One male is 9% distant from the others, probably due to poor sequence quality (only 266 bp).

### *Syscia brachyptera*, New Species

Figure 9 (map, worker), S14 (holotype worker), S15 (brachypterous queen)

***Holotype:*** 1 worker, HONDURAS, *Comayagua*: PN Cerro Azul Meambar, 14.87045 –87.90567 ±70m, 750m, 21-May-2010, montane rainforest, ex sifted leaf litter (LLAMA, Wm-C-04-2-02) [CASC, unique specimen identifier CASENT0644389]. PARATYPES: same data as holotype [worker: CASC, DZUP, JTLC, MCZC, UCD, UNAM, USNM].

***Geographic Range.*** Honduras.

***Diagnosis.*** Lower montane forest; subpetiolar process with acute posterior tooth; AIII in dorsal view trapezoidal, sides nearly flat, weakly diverging posteriorly; AIV in dorsal view with weakly convex, subparallel sides and truncate anterior margin; dorsal profile of AIII and AIV nearly flat; puncta on AIV small, distinct, relatively dense to about midlength; standing pilosity short, fine; color red brown. Pairwise distances among eight COI barcodes (GenBank accessions MT267550 - MT267553, BOLD Process IDs not listed here) varied from 0 to 8.23%. The smallest interspecific distance was 8.99%.

Eleven species are within size and geographic range of *S. brachyptera: S. boudinoti, S. honduriana, S. jennierussae, S. machaquila, S. persimilis, S. pervagata, S. peten, S. sumnichti, S. truncata, S. valenzuelai*, and *S.* JTL082.

*S. boudinoti (*Fig. 8*), S. machaquila* (Fig. 10), *S. valenzuelai* (Fig. 9), *S.* JTL082 (Fig. 10): subpetiolar process subtriangular, posterior tooth weak to absent.

*S. honduriana (*Fig. 10*):* AIV entirely covered with large puncta; standing pilosity coarser.

*S. jennierussae (*Fig. 10*):* standing pilosity coarser; puncta on anterior AIV larger and more lunate.

*S. persimilis (*Fig. 10*), S. pervagata* (Fig. 9): standing pilosity longer, coarser.

*S. peten (*Fig. 9*):* broader AIII on average (AIII-I 119 vs. 103).

*S. sumnichti (*Fig. 9*):* AIV in dorsal view slightly less rectangular, sides more convergent anteriorly, anterior margin less truncate; subpetiolar process with less developed posterior tooth. A specimen (not sequenced) from near La Ceiba, Honduras, is intermediate, with AIV like *S. sumnichti* but with a sharp posterior angle on the subpetiolar process.

*S. truncata (*Fig. 10*):* AIV in dorsal view with anterior border more truncate; scapes shorter on average (mean SI 70 vs. 77); AIII wider on average (mean AIII-I 111 vs. 103).

***Measurements, Worker.*** HW 0.52 (0.48–0.54), HL 0.67 (0.62–0.70), SL 0.40 (0.37–0.44), MSL 0.84 (0.74–0.89), AIIIW 0.42 (0.36–0.46), AIIIL 0.41 (0.36–0.45), AIVW 0.61 (0.54–0.65), AIVL 0.75 (0.67–0.80), SI 77 (76–82), AIII-I 103 (100–107), AIV-I 82 (80–84) ($n$ = 6).

***Measurements, Queen.*** HW 0.56 (0.55–0.57), HL 0.70 (0.68–0.71), SL 0.41 (0.39–0.44), MSL 0.98 (0.91–1.02), AIIIW 0.51 (0.48–0.54), AIIIL 0.47 (0.43–0.49), AIVW 0.73 (0.71–0.76), AIVL 0.93

(0.89–1.01), SI 74 (69–77), AIII-I 109 (105–113), AIV-I 78 (75–80) (*n* = 3).

***Measurements, Intercaste Female.*** HW 0.54, HL 0.66, SL 0.39, MSL 0.89, AIIIW 0.49, AIIIL 0.48, AIVW 0.72, AIVL 0.90), SI 72, AIII-I 102, AIV-I 79 (*n* = 1).

***Biology.*** This species occurs in moist forest and cloud forest habitats, from 600 to 1650 m elevation. MGB observed a small cluster of brachypterous queens in leaf litter near a bait card; it was not clear if they were foraging. Other specimens have been collected from Winkler samples of forest floor litter and rotten wood. No alate or dealate queens are known, but brachypterous queens have been collected on three occasions. A series from one Winkler sample (R.S.Anderson, RSA2010-009) contained two workers and five brachypterous queens. Some of the queens had short, stubby wings (Supp Fig. S7 [online only]). One collection contained two intercaste females, intermediate in structure between workers and brachypterous queens (with compound eyes, ocelli, and queen-like mesosomal sclerites, but no wing scars).

### *Syscia chiapaneca*, New Species

Figure 11 (map, worker), S16 (holotype worker), S17 (queen)

***Holotype:*** 1 worker, MEXICO, *Chiapas*: 19km ENE Tonalá, 16.14775 −93.60918 ±50m, 1450m, 15-Jul-2007, mixed cloud forest, ex sifted leaf litter (R. S. Anderson, RSA2007-014A) [UNAM, unique specimen identifier CASENT0601738]. PARATYPES: same data as holotype [dealate queen, worker: CASC]; 17km ENE Tonalá, 16.14153 −93.60958 ±50m, 1650m, 16-Jul-2007, montaine wet forest, ex sifted leaf litter (M. G. Branstetter, MGB668) [worker: MCZC, USNM].

***Geographic Range.*** Mexico (Chiapas).

***Diagnosis.*** Cloud forest; subpetiolar process shallow, asymmetrically triangular, posterior margin weakly or not convex; AIII in dorsal view weakly trapezoidal, with moderately convex sides; AIV in dorsal view with moderately convex sides, anterior margin moderately truncate; dorsal profile of AIII convex, of AIV weakly convex; puncta on AIII nearly confluent; puncta on AIV small, separated, fading at midlength; standing pilosity of medium length and coarseness; color red brown. Based on the COI barcode of the sequenced specimen (GenBank accession MT267554), the smallest pairwise interspecific distance was 5.39%.

Eleven species are within size and geographic range of *S. chiapaneca*: *S. atitlana*, *S. jennierussae*, *S. lacandona*, *S. machaquila*, *S. persimilis*, *S. setosa*, *S. valenzuelai*, *S.* JTL065, *S.* JTL066, *S.* JTL073, and *S.* JTL085.

*S. atitlana (*Fig. 12*):* allopatric, but ranges adjacent; puncta on AIII and AIV larger; anterior margin of AIV less truncate; subpetiolar process more convex; standing pilosity longer.

*S. jennierussae (*Fig. 10*):* lowland; allopatric; smaller on average (mean HW 0.53 vs. 0.58); scapes shorter on average (mean SI 67 vs. 79); AIII broader on average (mean AIII-I 110 vs. 100).

*S. lacandona (*Fig. 12*):* locally sympatric; AIII in dorsal view with more convex sides, puncta larger and more widely spaced; occipital carina more developed and visible in face view.

*S. machaquila (*Fig. 10*):* allopatric; subpetiolar process deeper; puncta on AIII larger; AIII wider on average (mean AIII-I 107 vs. 100).

*S. persimilis (*Fig. 10*):* locally sympatric; subpetiolar process with acute posterior tooth.

*S. setosa (*Fig. 11*):* allopatric; AIII in dorsal view with more convex sides, puncta larger and more widely spaced; standing pilosity long, coarse; lacking underlying pubescence.

*S. valenzuelai (*Fig. 9*):* lowland; allopatric; smaller on average (mean HW 0.52 vs. 0.58); AIII in dorsal view with flatter sides; puncta on AIII and AIV larger and more widely separated; subpetiolar process deeper; standing pilosity coarser.

*S. JTL065 (*Fig. 12*):* allopatric; AIII and AIV in dorsal view with sides more convex; puncta on AIII larger; subpetiolar process deeper; color darker brown.

*S. JTL066 (*Fig. 11*):* lowland; allopatric; subpetiolar process deeper, with posterior tooth; occipital carina more visible in face view.

*S. JTL073 (*Fig. 11*):* allopatric, but with adjacent ranges; AIII and AIV in dorsal view with sides more convex; puncta on AIII larger; puncta on AIV fading at anterior third; standing pilosity longer, coarser.

*S. JTL085 (*Fig. 9*):* allopatric; smaller on average (mean HW 0.53 vs. 0.58); scapes shorter (mean SI 73 vs. 79).

***Measurements, Worker.*** HW 0.59 (0.57–0.63), HL 0.75 (0.73–0.78), SL 0.48 (0.47–0.49), MSL 0.95 (0.91–1.01), AIIIW 0.46 (0.43–0.49), AIIIL 0.46 (0.43–0.50), AIVW 0.71 (0.66–0.75), AIVL 0.88 (0.82–0.96), SI 81 (79–82), AIII-I 99 (97–102), AIV-I 81 (79–84) (*n* = 6).

***Measurements, Queen.*** HW 0.63, HL 0.76, SL 0.47, MSL 1.14, AIIIW 0.52, AIIIL 0.51, AIVW 0.80, AIVL 1.05, SI 75, AIII-I 102, AIV-I 77 (*n* = 1).

***Biology.*** This species occurs in cloud forest. All specimens are from Winkler samples of forest floor leaf litter and rotten wood. One queen is known; it has the mesosomal structure of a brachypterous queen.

### *Syscia disjuncta*, New Species

Figure 11 (map, worker), S18 (holotype worker), S19 (queen), S20 (intercaste female)

***Holotype:*** 1 worker, MEXICO, *Tamaulipas*: Rancho del Cielo, nr cabins, 23.10105 −99.19233 ±50m, 1200m, 17-Jul-2006, mixed oak, ex forest litter (R. S. Anderson, RSA2006-0005) [UNAM, unique specimen identifier CASENT0644247]. PARATYPES: same data as holotype [worker: CASC, USNM]; Rancho del Cielo, along road, 23.09428 −99.20318 ±50m, 1100m, 18-Jul-2006, mixed hardwood, ex forest litter (R. S. Anderson, RSA2006-0006) [worker: MCZC].

***Geographic Range.*** Mexico (Tamaulipas to Oaxaca), Costa Rica.

***Diagnosis.*** Montane; subpetiolar process asymmetrically triangular; AIII in dorsal view weakly trapezoidal, sides weakly convex; AIV in dorsal view with convex sides, anterior margin not truncate; AIII dorsal profile convex; AIV dorsal profile weakly convex; puncta on AIII of medium size, with narrow interspaces; puncta on AIV small, separated, fading at anterior third; standing pilosity of medium length and thickness; color red brown. Pairwise distances among seven COI barcodes (GenBank accessions MT267555 - MT267561) varied from 2.74 to 9.41%. The smallest interspecific distance was 7.1%.

In the Mexican portion of the range, nine species are within size range of *S. disjuncta*: *S. augustae*, *S. setosa*, *S. transisthmica*, *S. valenzuelai*, *S.* JTL049, *S.* JTL060, *S.* JTL071, *S.* JTL075, and *S.* JTL084.

In the Costa Rican portion of the range, four species are within size range of *S. disjuncta*: *S. latepunctata*, *S. ticomontana*, *S. volucris*, and *S.* JTL017.

*S. augustae (*Fig. 11*):* Allopatric, but populations in close proximity; AIII more broadly trapezoidal in dorsal view; sides of AIV in dorsal view flatter; AIV dorsal profile flatter.

*S. latepunctata, S. volucris (*Fig. 13*):* lowland; allopatric; puncta on AIV covering entire tergite.

*S. setosa (*Fig. 11*):* locally sympatric; puncta on AIII and AIV much larger and more widely separated; color darker brown; standing pilosity longer.

*S. ticomontana (*Fig. 12*):* locally sympatric; posterior margin of subpetiolar process angulate; AIII in dorsal view with more convex sides, less trapezoidal; puncta on AIV larger and more widely spaced.

*S. transisthmica (*Fig. 12*):* lowland to lower montane; overlapping ranges but no known site of local sympatry, and collections of the two species are within 10 km of each other; puncta on AIII more widely spaced; puncta on AIV larger and extending further posteriorly; scapes longer on average (mean SI 87 vs. 73).

*S. valenzuelai (*Fig. 9*):* allopatric; puncta on AIV larger, fading at midlength.

*S. JTL017 (*Fig. 12*):* lowland; allopatric; puncta on AIII and AIV smaller, more closely spaced; puncta on AIV small, confluent, covering most of tergite.

*S. JTL049 (*Fig. 12*):* with adjacent ranges but no known site of local sympatry; no discovered means of differentiating.

*S. JTL060 (*Fig. 9*):* Allopatric; sides of AIV in dorsal view more convex, more strongly converging anteriorly; dorsal profile of AIV more convex; subpetiolar process more sharply triangular.

*S. JTL071 (*Fig. 9*):* Allopatric; puncta on AIII and AIV much larger and more widely spaced.

*S. JTL075 (*Fig. 11*):* Allopatric; sides of AIV in dorsal view more convex, more strongly converging anteriorly; dorsal profile of AIV more convex; scapes longer on average (mean SI 82 vs. 73).

*S. JTL084 (*Fig. 10*):* locally sympatric; much larger puncta on AIV, fading at midlength.

***Measurements, Worker.*** HW 0.61 (0.54–0.69), HL 0.73 (0.65–0.82), SL 0.44 (0.39–0.54), MSL 0.91 (0.00–1.12), AIIIW 0.47 (0.38–0.55), AIIIL 0.43 (0.34–0.50), AIVW 0.73 (0.62–0.86), AIVL 0.84 (0.68–0.97), SI 74 (67–85), AIII-I 108 (103–120), AIV-I 87 (83–99) (*n* = 16).

***Measurements, Queen.*** HW 0.64 (0.59–0.67), HL 0.74 (0.73–0.76), SL 0.45 (0.44–0.46), MSL 1.24 (1.14–1.34), AIIIW 0.56 (0.53–0.58), AIIIL 0.50 (0.45–0.53), AIVW 0.83 (0.80–0.86), AIVL 1.00 (0.98–1.04), SI 71 (68–76), AIII-I 112 (109–119), AIV-I 83 (81–84) (*n* = 3).

***Measurements, Intercaste Female.*** HW 0.70, HL 0.87, SL 0.58, MSL 1.25, AIIIW 0.60, AIIIL 0.52, AIVW 0.99, AIVL 1.11), SI 83, AIII-I 114, AIV-I 89 (*n* = 1).

***Biology.*** This species occurs in montane wet forest, from 930 to 1730 m elevation. All specimens are from Winkler or Berlese samples of forest floor leaf litter and rotten wood. Dealate queens and intercaste females are known. It is uncertain whether dealate queens were fully alate or brachypterous.

***Comments.*** This is the only known species with a strongly disjunct distribution. Multiple collections are known from north of the Isthmus of Tehuantepec, and one collection is known from Monteverde, Costa Rica. Molecular data unambiguously place the Monteverde population within the species. A second Monteverde specimen was sequenced independently, to test for repeatability of the result, and it verified the placement of the Monteverde collection. One might expect a sister relationship between the northern populations and the Monteverde population, with a greater genetic distance between the two ranges than among populations within the northern range, but even this is not supported. UCE results support the northern populations being paraphyletic with respect to the Monteverde collection.

The Monteverde collection was made in 1989, a series of workers and queens from a single maxiWinkler sample. In spite of intensive additional collecting in Monteverde and elsewhere in Costa Rica, no other Costa Rican records are known.

### *Syscia grandis*, New Species

Figure 13 (map, worker), S21 (holotype worker)

***Holotype:*** 1 worker, GUATEMALA, *Suchitepéquez*: 4km S Vol. Atitlán, 14.54863 −91.19092 ±50m, 1625m, 15-Jun-2009, cloud forest, ex sifted leaf litter (LLAMA, Wa-B-09-1-11) [CASC, unique specimen identifier CASENT0644380]. PARATYPES: same data as holotype [worker: CASC, DZUP, JTLC, MCZC, UCD, UNAM, USNM, UVGC].

***Geographic Range.*** Guatemala.

***Diagnosis.*** Montane; occipital carina strongly developed, visible in face view; subpetiolar process a shallow lobe with a large, acute posterior tooth that is larger than the anterior tooth; AIII trapezoidal in dorsal view, with weakly convex sides; AIV in dorsal view with convex sides and non-truncate anterior margin; dorsum of AIII and AIV weakly convex in lateral view; puncta on AIII distinct, of medium size and spacing; puncta on AIV small, widely spaced, fading at anterior third; standing pilosity long, coarse; color dark brown. Two COI barcodes (GenBank accession MT267568 and BOLD Process ID ASLAM2438-13) were the same, and the smallest pairwise interspecific distance was 11.48%.

Only the locally sympatric *S.* JTL033 is within size and geographic range of *S. grandis*. *Syscia* JTL033 has a subquadrate subpetiolar process, without an acute posterior tooth, and AIII is wider on average (mean AIII-I 107 vs. 98).

***Measurements, Worker.*** HW 0.78 (0.77–0.79), HL 0.93 (0.92–0.95), SL 0.68 (0.67–0.69), MSL 1.25 (1.22–1.28), AIIIW 0.56 (0.55–0.57), AIIIL 0.57 (0.55–0.59), AIVW 0.96 (0.95–0.97), AIVL 1.13 (1.09–1.18), SI 87 (86–89), AIII-I 98 (96–100), AIV-I 85 (82–88) (*n* = 3).

***Biology.*** This species occurs in montane wet forest, from 1070 to 1625 m elevation. All specimens are from Winkler samples of forest floor leaf litter and rotten wood. Only workers are known.

***Comments.*** *Syscia grandis* and *S.* JTL033 form a clade, known from one site on the north slope of Volcán Atitlán. They are genetically and morphologically divergent. COI data show a related species in Guanacaste, Costa Rica (Fig. 7).

## Syscia honduriana (Mann, 1922)

Figure 10 (map, worker), S22 (lectotype worker), S23 (queen)

*Cerapachys* (*Parasyscia*) *hondurianus* Mann, 1922: 1. Syntype worker, queen: Honduras, Lombardia (W. M. Mann) [USNM, examined]. One worker here designated LECTOTYPE (specimen identifier USNMENT01126300) to ensure nomenclatural stability.

***Geographic Range.*** Honduras.

***Diagnosis.*** Lowland; subpetiolar process with small posterior tooth; AIII in dorsal view with convex sides, converging anteriorly; AIV in dorsal view with convex sides, converging anteriorly, anterior margin not truncate; AIII and AIV dorsal profile convex; puncta on AIII large, near confluent; puncta on AIV large, nearly confluent, and covering entire tergite; standing pilosity long, abundant, coarse; color red brown. Pairwise distance between two COI barcodes (GenBank accession MT267563 and BOLD Process ID ASLAM1842-12) was 0.76%. The smallest interspecific distance was 1.09%.

Multiple species are within size and geographic range of *S. honduriana*, but only *S. truncata* has AIV punctate over the entire surface. *Syscia truncata* has much smaller dorsal puncta, shorter standing pilosity, and a larger and more distinctly acute posterior tooth on the subpetiolar process.

***Measurements, Worker.*** HW 0.57 (0.55–0.58), HL 0.69 (0.66–0.73), SL 0.41 (0.40–0.43), MSL 0.88 (0.84–0.93), AIIIW 0.41 (0.39–0.44), AIIIL 0.40 (0.37–0.43), AIVW 0.67 (0.63–0.71), AIVL 0.74 (0.71–0.76), SI 73 (72–74), AIII-I 104 (102–105), AIV-I 91 (89–93) (*n* = 2).

***Measurements, Queen.*** HW 0.64, HL 0.81, SL 0.48, MSL 1.27, AIIIW 0.56, AIIIL 0.48, AIVW 0.85, AIVL 0.95, SI 74, AIII-I 115, AIV-I 90 (*n* = 1).

***Biology.*** Mann described the species from a small colony he found beneath a stone. The species is known from two collections: the types and two workers from near La Ceiba, a site about 50 km from the type locality. The latter specimens were from a miniWinkler sample from lowland rainforest. Mann's type series contains a fully formed queen with large compound eyes and ocelli. It has no wings but has the mesosomal structure of a typical alate queen.

***Comments.*** UCE data were available for one specimen from near La Ceiba, Honduras. It is sister to the parapatric *S. volucris*, which occurs from the La Mosquitia region of Honduras south to Costa Rica. COI data are congruent with the UCE results. The two species share shape characters, but *S. honduriana* is lighter colored, smaller on average (mean HW 0.57 vs. 0.70), and the scapes are shorter on average (SI 72–74 vs. 80–87). The puncta on AIV are closely spaced, more or less confluent. In *S. volucris* these puncta are most often more widely spaced, with interspaces between puncta similar in width to puncta diameters. However, there is variation in this trait, and one series from Saslaya National Park in Nicaragua has puncta nearly confluent, like *S. honduriana*. *Syscia* JTL079, based on one unsequenced specimen from Guatemala, is similar to *S. volucris* in size and SI. AIII is broader than either *S. honduriana* or *S. volucris* (AIII-I 118 vs. < 106), and the puncta on AIV are confluent.

## Syscia jennierussae, New Species

Figure 10 (map, worker), S24 (holotype worker), S25 (queen)

***Holotype:*** 1 worker, MEXICO, *Chiapas*: Playón de la Gloria, 16.16118 –90.90127 ±50m, 160m, 24-Jun-2008, mature wet forest, ex sifted leaf litter (LLAMA, Wa-A-09-1-45) [UNAM, unique specimen identifier CASENT0609668]. PARATYPES: same data as holotype except 16.16021 –90.90145 (Wa-A-09-1-22) [worker: CASC, MCZC]; same data except 16.16133 –90.90116 ±50m (LLAMA, Wa-A-09-1-49) [USNM, unique specimen identifier CASENT0609670]; same data except 16.15929 –90.90155 ±200m, 26-Jun-2008 (LLAMA, Wm-A-09-1-all) [JTLC, unique specimen identifier CASENT0610036].

***Geographic Range.*** Mexico (Chiapas), Guatemala.

***Diagnosis.*** Lowland; subpetiolar process triangular with a small posterior tooth; AIII in dorsal view trapezoidal, with weakly convex sides; AIV in dorsal view with moderately convex sides, somewhat truncate anterior margin; dorsal profile of AIII convex; dorsal profile of AIV weakly convex; puncta on AIV discrete, nearly confluent, fading at about midlength; standing pilosity abundant, coarse; color red brown. Pairwise distances among three COI barcodes (GenBank accessions MT267564 - MT267566) were < 1%. The smallest interspecific distance was 10.85%.

Twelve species are within size and geographic range of *S. jennierussae: S. boudinoti, S. chiapaneca, S. machaquila, S. parietalis, S. persimilis, S. pervagata, S. peten, S. sumnichti, S. truncata, S. valenzuelai, S.* JTL066, and *S.* JTL085.

*S. boudinoti (*Fig. 8*):* allopatric; scapes longer on average (mean SI 75 vs. 67); anterior margin of AIV less truncate.

*S. chiapaneca (*Fig. 11*):* cloud forest; allopatric; larger on average (mean HW 0.58 vs. 0.53); scapes longer on average (mean SI 79 vs. 67); AIII narrower on average (mean AIII-I 100 vs. 110).

*S. machaquila (*Fig. 10*):* scapes longer on average (mean SI 74 vs. 67); otherwise very similar.

*S. parietalis (*Fig. 11*):* subpetiolar process relatively more quadrate, with larger posterior angle or tooth; larger on average (mean HW

0.58 vs. 0.53); scapes longer on average (mean SI 76 vs. 67); AIV narrower on average (mean AIV-I 80 vs. 87).

*S. persimilis* (Fig. 10), *S. pervagata* (Fig. 9), *S. peten* (Fig. 9), *S. truncata* (Fig. 10): subpetiolar process subquadrate with acute posterior tooth *S. sumnichti* (Fig. 9): cloud forest; no known site of local sympatry; scapes longer on average (mean SI 79 vs. 67); AIII narrower on average (mean AIII-I 101 vs. 110); anterior margin of AIV less truncate; AIV narrower on average (mean AIV-I 79 vs. 87); color lighter brown.

*S. valenzuelai* (Fig. 9): not always distinguishable; sympatric in eastern Chiapas lowlands; scapes longer on average (mean SI 72 vs. 67); AIII narrower on average (mean AIII-I 107 vs. 110); in face view occipital carina more visible; sides of AIV slightly more convex and anterior margin less truncate.

*S. JTL066* (Fig. 11): locally sympatric; occipital carina larger, more visible in face view; subpetiolar process relatively more quadrate, with larger posterior angle or tooth; larger on average (mean HW 0.58 vs. 0.53); scapes longer on average (mean SI 75 vs. 67).

*S. JTL085* (Fig. 9): occurs nearby at higher elevation; occipital carina more visible in face view; subpetiolar process smaller, shallower; scapes longer on average (mean SI 73 vs. 67); AIII narrower on average (mean AIII-I 104 vs. 110); AIV narrower on average (mean AIV-I 80 vs. 87).

***Measurements, Worker.*** HW 0.54 (0.52–0.55), HL 0.64 (0.61–0.67), SL 0.35 (0.34–0.37), MSL 0.78 (0.74–0.82), AIIIW 0.46 (0.43–0.48), AIIIL 0.41 (0.37–0.44), AIVW 0.63 (0.60–0.66), AIVL 0.72 (0.68–0.77), SI 66 (63–68), AIII-I 113 (111–116), AIV-I 88 (86–90) ($n$ = 6).

***Measurements, Queen.*** HW 0.55, HL 0.67, SL 0.42, MSL 0.99, AIIIW 0.44, AIIIL 0.42, AIVW 0.69, AIVL 0.84, SI 76, AIII-I 106, AIV-I 82 ($n$ = 1).

***Measurements, Intercaste Female.*** HW 0.53, HL 0.64, SL 0.35, MSL 0.79, AIIIW 0.48, AIIIL 0.41, AIVW 0.65, AIVL 0.76), SI 65, AIII-I 115, AIV-I 85 ($n$ = 1).

***Biology.*** This species occurs in lowland moist to wet forest. Workers, a dealate queen, and an intercaste female are known. All specimens are from Winkler samples of forest floor litter and rotten wood.

## *Syscia lacandona*, New Species

Figure 12 (map, worker), S26 (holotype worker), S27 (queen), S28 (male)

***Holotype:*** 1 worker, MEXICO, *Chiapas*: Nahá, 16.97417 –91.58592 ±50m, 950m, 14-Jul-2007, montane wet forest, ex sifted leaf litter (J. Longino, JTL6047-s) [UNAM, unique specimen identifier CASENT0644513]. PARATYPES: same data as holotype [queen: CASC; worker: CASC, DZUP, JTLC, MCZC, UCD, UNAM, USNM].

***Geographic Range.*** Mexico (Chiapas).

***Diagnosis.*** Lowland to lower montane; subpetiolar process subtriangular, posterior border flat; AIII in dorsal view moderately trapezoidal, with convex sides; AIV in dorsal view with moderately convex sides, anterior margin not truncate; dorsal profile of AIII and AIV convex; puncta on AIII large, widely separated; puncta on AIV distinct, somewhat lunate, widely spaced, fading at anterior third; standing pilosity long, coarse; color dark brown. Pairwise distances among five COI barcodes (GenBank accessions MT267584 - MT267587, BOLD Process ID ASLAM2431-13) were < 1%. The smallest interspecific distance was 1.97%.

Seven species are within size and geographic range of *S. lacandona*: *S. atitlana*, *S. chiapaneca*, *S. setosa*, *S. transisthmica*, *S.* JTL065, *S.* JTL066, and *S.* JTL073.

*S. atitlana* (Fig. 12): possibly locally sympatric in Sierra de Chiapas, but no sympatric workers to directly compare; very similar; dorsal profile of petiole somewhat more quadrate, less rounded; AIII in dorsal view with sides slightly less convex; subpetiolar process with more convex posterior margin.

*S. chiapaneca* (Fig. 11): allopatric or possible sympatric (see Comments); AIII in dorsal view with less convex sides, puncta smaller and more closely spaced; occipital carina less developed, less visible in face view.

*S. setosa* (Fig. 11): locally sympatric; occipital carina less visible in face view; AIV more quadrate, sides less converging anteriorly; standing pilosity longer.

*S. transisthmica* (Fig. 12): The two species are sympatric at Naha and Metzabok in eastern Chiapas. In this zone, *S. transisthmica* has more widely spaced puncta and is distinguishable from *S. lacandona*. All other specimens, including *S. transisthmica* north of the Isthmus of Tehuantepec, have more closely spaced puncta and are indistinguishable from *S. lacandona*.

*S. JTL065* (Fig. 12): montane; overlapping ranges but no known site of local sympatry; AIII in dorsal view with more convex sides; AIV in dorsal view with more convex sides, sides more convergent anteriorly.

*S. JTL066* (Fig. 11): locally sympatric; subpetiolar process relatively more quadrate, with posterior angle or tooth; puncta on AIII smaller, more closely spaced; scapes shorter on average (mean SI 75 vs. 81); AIII wider on average (mean AIII-I 87 vs. 81).

*S. JTL073* (Fig. 11): occurs in nearby lowlands, but no known site of local sympatry; occipital carina less visible in face view; AIII broader on average (mean AIII-I 113 vs. 105); AIV broader on average (mean AIV-I 101 vs. 85).

***Measurements, Worker.*** HW 0.63 (0.60–0.67), HL 0.77 (0.74–0.81), SL 0.51 (0.48–0.54), MSL 1.00 (0.94–1.06), AIIIW 0.49 (0.46–0.53), AIIIL 0.47 (0.44–0.51), AIVW 0.75 (0.70–0.81), AIVL 0.88 (0.82–0.95), SI 81 (80–82), AIII-I 105 (102–108), AIV-I 85 (83–86) ($n$ = 6).

***Measurements, Queen.*** HW 0.71, HL 0.83, SL 0.53, MSL 1.22, AIIIW 0.61, AIIIL 0.54, AIVW 0.94, AIVL 1.10, SI 75, AIII-I 113, AIV-I 85 ($n$ = 1).

***Biology.*** This species occurs in lowland to lower montane wet forest, up to 950 m elevation in the eastern part of Chiapas (see Comments on potential occurrence at a higher elevation in western Chiapas). All female specimens are from Winkler samples of forest floor leaf litter and rotten wood. One queen is known, and from the structure of the mesosoma is probably brachypterous. One male is known, from a Malaise trap, and associated with workers using COI sequence data.

***Comments.*** The UCE tree shows a monophyletic *S. lacandona* sister to *S. transisthmica* (Fig. 6). The COI tree is congruent (Fig. 7). A difficulty arose when a destructively sampled worker from Custepec in the Sierra de Chiapas in western Chiapas fell within *S. lacandona* specimens from eastern Chiapas. The destructively sampled worker was in a maxiWinkler sample with one other worker that was presumed conspecific. However, that remaining worker was later identified as *S. chiapaneca*. The DNA extraction immediately preceding this one was a destructively sampled worker of *S. lacandona* from Nahá in eastern Chiapas. Two alternative scenarios are 1) contamination of the Custepec specimen with DNA from the previous Nahá specimen, or 2) *S. lacandona* occurs in the Sierra de Chiapas, at considerably higher elevation (1,520 m), and we destructively sampled the single known specimen from this region. To try and differentiate these two scenarios we examined the extracted DNA barcode sequences for this sample and only found a single copy. If the sample was contaminated, there would likely be two different COI sequences. Thus, scenario (2) seems more plausible. The specimen data for the problematic destroyed specimen are: 2km SE Custepec, 15.72099 –92.95054 ±200m, 1520m, 17-May-2008, mesophil forest, ex sifted leaf litter (LLAMA, Wm-A-02-1).

## *Syscia latepunctata*, New Species

Figure 13 (map, worker), S29 (holotype worker), S30 (queen)

***Holotype:*** 1 worker, COSTA RICA, *Limón*: Res. Biol. Hitoy-Cerere, 9.66655 –83.02283 ±10m, 200m, 10-Jun-2015, tropical rainforest, with some big trees, probably a mix of primary and secondary forest, near a small stream, ex sifted leaf litter (ADMAC, Wa-E-02-1-19) [UCR, unique specimen identifier CASENT0637043]. PARATYPES: same data as holotype [queen: CASC]; Res. Biol. Hitoy-Cerere, 9.65238 –83.02206 ±25m, 670m, 11-Jun-2015, tropical rainforest, with big trees, probably primary, ex sifted leaf litter (ADMAC, Wm-E-02-1-06) [worker: CASC].

***Geographic Range.*** Costa Rica.

***Diagnosis.*** Lowland; subpetiolar process a shallow lobe with sharp, recurved anterior tooth and smaller posterior tooth; AIII in dorsal view trapezoidal with convex sides; AIV in dorsal view with convex sides, anterior margin not truncate; dorsal profile of AIII and AIV convex; puncta on AIII large, confluent; puncta on AIV large, closely spaced, covering entire tergite; standing pilosity long, coarse; color red brown. Pairwise distances among three COI barcodes (GenBank accessions MT267588 - MT267589, BOLD Process ID ASLAM2460-13) varied from 0.61 to 2.90%. The smallest interspecific distance was 8.47%.

Five species are within size and geographic range of *S. latepunctata*: *S. disjuncta*, *S. ticomontana*, *S. volucris*, *S.* JTL017, and *S.* JTL064.

*S. disjuncta (*Fig. 11*)*, *S. ticomontana* (Fig. 12): montane; allopatric; puncta on AIV fading at anterior third to midlength.

*S. volucris (*Fig. 13*):* locally sympatric; extremely similar; subpetiolar process slightly deeper; AIV narrower on average (mean AIV-I 88 vs. 98).

*S. JTL017 (*Fig. 12): locally sympatric; puncta on AIII and AIV smaller, more closely spaced; subpetiolar process deeper and with less distinct posterior tooth; AIV dorsal profile flat.

*S. JTL064 (*Fig. 13*):* lower montane; allopatric; puncta on AIV faint, lunate, fading at midlength.

***Measurements, Worker.*** HW 0.69, HL 0.83, SL 0.57, MSL 1.10, AIIIW 0.56, AIIIL 0.54, AIVW 0.91, AIIIL 0.94, SI 83, AIII-I 104, AIV-I 98 ($n$ = 1).

***Measurements, Queen.*** HW 0.77, HL 0.93, SL 0.64, MSL 1.60, AIIIW 0.71, AIIIL 0.64, AIVW 1.07, AIVL 1.20, SI 83, AIII-I 111, AIV-I 89 ($n$ = 1).

***Biology.*** This species occurs in lowland rainforest. It is known from two Winkler samples from the type locality and two Winkler samples from La Selva Biological Station, Costa Rica.

## *Syscia machaquila*, New Species

Figure 10 (map, worker), S31 (holotype worker), S32 (queen)

***Holotype:*** 1 worker, GUATEMALA, *Petén*: 13km NW Machaquilá, 16.4404 –89.53447 ±37m, 390m, 28-May-2009, tropical moist forest, ex sifted leaf litter (LLAMA, Wm-B-06-1-03) [CASC, unique specimen identifier CASENT0644493]. PARATYPES: same data as holotype [worker: MCZC, USNM, UVGC]; same data except 16.44167 –89.53496 (Wm-B-06-1-04) [JTLC, UCD].

***Geographic Range.*** Mexico (Chiapas), Guatemala.

***Diagnosis.*** Lowland; subpetiolar process triangular; AIII in dorsal view weakly trapezoidal, sides moderately convex; AIV in dorsal view with sides moderately convex, anterior margin not truncate; dorsal profile of AIII and AIV convex; puncta on AIV large, separated, somewhat lunate, fading at midlength; standing pilosity long, coarse; color red brown. Pairwise distances among three COI barcodes (GenBank accessions MT267590 - MT267591, BOLD Process ID ASLAM2440-13) varied from 0.15–6.27%. The smallest interspecific distance was 5.21%.

Fourteen species are within size and geographic range of *S. machaquila*: *S. boudinoti*, *S. chiapaneca*, *S. jennierussae*, *S. parietalis*, *S. persimilis*, *S. pervagata*, *S. peten*, *S. setosa*, *S. tolteca*, *S. truncata*, *S. valenzuelai*, *S.* JTL066, *S.* JTL073, and *S.* JTL085.

*S. boudinoti (*Fig. 8*):* locally sympatric; puncta smaller on AIII and AIV; AIII in profile relatively more quadrate (*S. machaquila* relatively more rounded); standing pilosity finer.

*S. chiapaneca (*Fig. 11*):* allopatric; subpetiolar process shallower; puncta on AIII smaller; AIII narrower on average (mean AIII-I 100 vs. 107).

*S. jennierussae (*Fig. 10*):* locally sympatric; scapes shorter on average (mean SI 67 vs. 74); otherwise very similar.

*S. parietalis (*Fig. 11*):* cloud forest; allopatric but in close proximity; subpetiolar process broader, with distinct posterior tooth.

*S. persimilis (*Fig. 10), *S. pervagata* (Fig. 9), *S. peten* (Fig. 9), *S. truncata* (Fig. 10): subpetiolar process with strong posterior tooth.

*S. setosa* (Fig. 11)*:* locally sympatric in Mexico (Chiapas); puncta on AIII and AIV larger and more widely separated; color darker brown.

*S. tolteca* (Fig. 12)*:* locally sympatric; larger on average (mean HW 0.61 vs. 0.56); scapes longer on average (mean SI 84 vs. 74).

*S. valenzuelai* (Fig. 9)*:* not readily distinguishable, even though phylogenetically distant; sympatric in eastern Chiapas lowlands.

*S. JTL066* (Fig. 11)*:* overlapping ranges but no known site of local sympatry; subpetiolar process broader, with distinct posterior tooth; puncta on AIII smaller and more closely spaced; occipital carina more pronounced in face view.

*S. JTL073* (Fig. 11)*:* overlapping ranges but no known site of local sympatry; puncta on AIII larger and more widely spaced; sides of AIII and AIV more convex on average (mean AIV-I 101 vs. 86).

*S. JTL085* (Fig. 9)*:* locally sympatric; occipital carina more visible in face view; subpetiolar process smaller, shallower; AIV narrower on average (mean AIV-I 80 vs. 86).

***Measurements, Worker.*** HW 0.55 (0.52–0.59), HL 0.68 (0.63–0.71), SL 0.40 (0.34–0.44), MSL 0.85 (0.76–0.93), AIIIW 0.42 (0.40–0.48), AIIIL 0.39 (0.36–0.43), AIVW 0.66 (0.59–0.72), AIVL 0.75 (0.62–0.85), SI 73 (67–78), AIII-I 109 (102–116), AIV-I 88 (84–94) (*n* = 12).

***Measurements, Queen.*** HW 0.59 (0.58–0.60), HL 0.72 (0.69–0.75), SL 0.43 (0.42–0.45), MSL 1.11 (1.05–1.18), AIIIW 0.48 (0.46–0.50), AIIIL 0.43 (0.42–0.44), AIVW 0.75 (0.73–0.78), AIVL 0.91 (0.88–0.94), SI 73 (72–74), AIII-I 112 (110–114), AIV-I 83 (83-83) (*n* = 2).

***Biology.*** This species occurs in lowland moist to wet forest, with records from 186 to 985 m elevation. Most records are from Winkler samples of forest floor leaf litter and rotten wood. Dealate queens are known from Winkler samples, and two alate queens were collected by yellow pan trap in Belize.

***Comments.*** Collection Wa-B-06-2-26 from Machaquilá contained two workers and one dealate queen. One of the workers was initially dry-mounted, and legs used for COI sequencing at BOLD. Later, the second worker was pulled from alcohol for destructive DNA extraction and UCE sequencing. The UCE data and the COI sequence from the destructively sampled worker matched material from another site (Montaña Chiclera). However, the COI sequence from the BOLD worker was divergent, with distance between the two workers of 6.1%. The workers from multiple collections from Machaquilá look relatively uniform, and the measurements are similar. At this point, the discrepancy in COI sequences is unexplained.

## *Syscia madrensis*, New Species

Figure 11 (map, worker), S33 (holotype worker)

***Holotype:*** 1 worker, UNITED STATES, *Arizona*: Vista Pt., 3.5 km SSW Portal, 31.88506 −109.17339 ± 1 km, 1560m, 13-Aug-2003, nest under stone (J.L. Smith & E.M. Sarnat) [CASC, unique specimen identifier CASENT0638281]. PARATYPES: same data as holotype [worker: CASC, FMNH, DZUP, JTLC, LACM, MCZC, UCD, UNAM, USNM].

***Geographic Range.*** United States (Arizona, New Mexico), Mexico (Baja California).

***Diagnosis.*** Occipital carina well developed and visible in face view; subpetiolar process subquadrate with erose ventral margin; AIII in dorsal view trapezoidal, with flat sides; AIV in dorsal view with nearly flat, subparallel sides, moderately truncate anterior margin; dorsal profile of AIII and AIV flat; puncta on AIV small, faint, dispersed, fading at midlength; standing pilosity nearly absent; color light red brown. Pairwise distances among three COI barcodes (GenBank accession MT267592 and MT267642, BOLD Process ID ASANA612-06) varied from 0 to 3.37%. The smallest interspecific distance was 9.16%. One species is within size and geographic range: *S. quisquillis* (Fig. 8,9)*:* no known site of local sympatry but ranges overlap; smaller on average (mean HW 0.53 vs. 0.57); subpetiolar process shallower, with anterior hook and notch.

***Measurements, Worker.*** HW 0.57 (0.55–0.58), HL 0.71 (0.69–0.73), SL 0.43 (0.42–0.43), MSL 0.94 (0.91–0.99), AIIIW 0.50 (0.48–0.53), AIIIL 0.52 (0.51–0.55), AIVW 0.64 (0.62–0.65), AIVL 0.86 (0.85–0.87), SI 75 (74–76), AIII-I 96 (95–97), AIV-I 75 (73–76) (*n* = 4).

***Biology.*** This species occurs in the 'sky islands' of southern Arizona, in mixed oak pine woodlands. Relatively large colonies have been observed as columns of workers moving under stones. The species appears to be completely subterranean. No sexuals are known.

***Comments.*** The population of this species that occurs in the Chiricahua Mountains, Arizona, has previously been identified as *S. augustae* (Fig. 11). True *S. augustae* occurs in Texas, Arkansas, and northeastern Mexico. *Syscia augustae* differs from *S. madrensis* in a more triangular subpetiolar process; more convex sides of AIII in dorsal view; and more pronounced standing pilosity. See further notes under *S. augustae*.

## *Syscia minuta*, New Species

Figure 8 (map, worker), S34 (holotype worker), S35 (queen), S36 (male)

***Holotype:*** 1 worker, COSTA RICA, *Heredia*: La Selva Biological Station, 10.43360 −84.01249 ±20m, 50m, 2-May-1993, Bosque Primario, Suelo (ALAS, B/10/074) [UCR, unique specimen identifier CASENT0644367]. PARATYPES: same data as holotype [queen: CASC; worker: CASC, DZUP, JTLC, MCZC, UCD, UNAM, USNM].

***Geographic Range.*** Nicaragua to Brazil (Rondonia).

***Diagnosis.*** Lowland; smallest of all known species; in northern part of the range (Nicaragua and most of Costa Rica), subpetiolar process shallow, with anterior hook-like portion, fenestra, and posterior convexity; further south the process is deeper, without fenestra; petiole subquadrate in profile; AIII trapezoidal in dorsal view, with straight sides, and with nearly flat dorsum in lateral view; sides of AIV nearly flat and the anterior margin somewhat truncate in dorsal view; puncta on AIII distinct, nearly confluent; puncta on AIV distinct, small, fading at midlength; standing pilosity short and fine; color light brown. Pairwise distances among 6 COI barcodes (GenBank accessions MT267593 - MT267596, 3 BOLD Process IDs not listed here) varied from 0 to 16.30%. The smallest interspecific distance was 8.96%.

Three species are within size and geographic range of *S. minuta*: *S. austrella*, *S. parva*, and *S. pollula*.

*S. austrella (*Fig. 8*)*: sympatric in Panama; sides of AIV more convex and the anterior border less truncate in dorsal view; larger on average (mean HW 0.45 vs. 0.37).

*S. parva (*Fig. 8*)*, *S. pollula* (Fig. 8): broadly sympatric in the northern part of the range; subpetiolar process lacking notch-like fenestra (where sympatric, *S. minuta* has a notch-like fenestra).

***Measurements, Worker.*** HW 0.37 (0.35–0.38), HL 0.48 (0.45–0.52), SL 0.24 (0.22–0.26), MSL 0.59 (0.55–0.65), AIIIW 0.29 (0.27–0.34), AIIIL 0.30 (0.29–0.33), AIVW 0.42 (0.38–0.47), AIVL 0.50 (0.46–0.54), SI 66 (62–70), AIII-I 98 (93–105), AIV-I 83 (75–90) (*n* = 12).

***Measurements, Queen.*** HW 0.36 (0.35–0.36), HL 0.46 (0.45–0.48), SL 0.23 (0.22–0.23), MSL 0.67 (0.65–0.70), AIIIW 0.30 (0.29–0.31), AIIIL 0.30 (0.29–0.30), AIVW 0.44 (0.42–0.46), AIVL 0.56 (0.54–0.58), SI 64 (64-64), AIII-I 100 (98–101), AIV-I 78 (78-78) (*n* = 2).

***Biology.*** All collections have been from wet forest habitats. This is a lowland species, with most collections from sea level to about 800 m elevation. Two collections are from somewhat higher: a nest series from a moist forest habitat at 1170 m elevation, on the Pacific slope below Monteverde, Costa Rica; and a single worker from a cloud forest site at 1,305 m elevation in Darien, Panama. The type series was from a Berlese sample of litter and soil, taken in primary rainforest at La Selva Biological Station. The sample was a single litter/soil core 14.5 cm diameter and 10 cm deep, and so the series is almost certainly a single colony. The series is 29 workers and one fully formed dealate queen. An alate queen occurred in a canopy fogging sample from La Selva. Most other collections are workers from Winkler and Berlese samples. No intercaste females are known.

The collection from 1,170 m, below Monteverde, was a colony discovered in loose soil beneath a stone. As many specimens as possible were recovered from the soil and kept alive for several days. About 30 adult workers, a single dealate queen, and about a dozen larvae were recovered. These quickly formed a tight cluster, with the larvae in a central mound, covered by the workers and queen. Workers carried the larvae longitudinally beneath the body, grasping them in the head region. Workers persistently clung to larvae, even when poked or picked up with forceps. The larvae writhed vigorously when touched. The larvae all appeared to be in the same developmental stage, somewhat smaller than the adult workers, and varying slightly in size. There were no pupae. Some workers left the cluster and explored the enclosure; the queen never left the brood pile. During the first day of captivity about half of the workers escaped from the enclosure and were lost. Over a period of days the remainder of the colony was offered a wide variety of live or freshly killed prey: late-stage larva of *Solenopsis* (one of the small, thief ant species), a pupa and an adult worker of *Cyphomyrmex salvini*, an adult worker of *Stenamma felixi*, a late-stage larva and an adult worker of *Gnamptogenys strigata*, a late-stage larva and an adult worker of *Strumigenys biolleyi*, a termite, a scarab larva, a cerambycid larva, an earwig egg, a silverfish, an earthworm fragment, an oribatid mite, and a centipede. All items were small, the same order of magnitude as the workers. The workers seemed to completely ignore these objects, walking over or around them with no notable response or change in behavior. The one exception was when a live *S. biolleyi* worker was held with forceps near the colony. One worker hesitantly antenna-tapped the *Strumigenys*, then made a sharp, brief recoil with mandibles open.

***Comments.*** This is almost certainly multiple cryptic species, albeit with no currently known cases of sympatry. UCE data support this species as a clade of morphologically similar specimens, but with relatively deep genetic divergences among all populations (Fig. 6). The COI phylogeny shows *S. minuta* paraphytletic with respect to *S. ticomontana* and *S. pollula* (Fig 7). Given the deep divergences among populations, the discordance is likely due to lack of signal in the COI gene as evidenced by the low support values. The distances are 4–16% for almost every inter-populational comparison. The one exception is a distance of <1% between a worker from La Selva Biological Station and a male from Saslaya, a park in north-central Nicaragua. Specimens from northern Costa Rica and Nicaragua have a distinctively-shaped subpetiolar process, shallow with a central notch (Fig. 2F). Material from Costa Rica's Osa Peninsula southward has a more produced process, without a central notch.

## *Syscia murillocruzae*, New Species

Figure 10 (map, worker), S37 (holotype worker), S38 (intercaste female)

***Holotype:*** 1 worker, COSTA RICA, *Heredia*: La Selva Biological Station, 10.43333 −84.01667 ± 2km, 50m, 15-Jul-1986, wet forest, ex sifted leaf litter (J. Longino, JTL1386-s) [UCR, unique specimen identifier CASENT0628992]. PARATYPES: same data as holotype [worker: CASC]; [all following La Selva Biological Station] 10.41442 −84.01619 ±20m, 50m, 14-Jun-2004, mature wet forest, ex sifted leaf litter (TEAM, AMI-1-W-009-03) [worker: MCZC]; La Selva Biological Station, 10.41657 −84.01916 ±20m, 50m, 1-Mar-2005, mature wet forest, ex sifted leaf litter (TEAM, AMI-1-W-028-02) [worker: INBio]; La Selva Biological Station, 10.41287 −84.01956 ±20m, 50m, 5-Sep-2006, mature wet forest, ex sifted leaf litter (TEAM, AMI-1-W-093-08) [worker: MCZC]; La Selva Biological Station, 10.41184 −84.02030 ±20m, 50m, 24-Nov-2006, mature wet forest, ex sifted leaf litter (TEAM, AMI-1-W-108-02) [worker: INBio]; La Selva Biological Station, 10.41891 −84.02142 ±20m, 50m, 4-Sep-2007, mature wet forest, ex sifted leaf litter (TEAM, AMI-1-W-150-05) [intercaste female: DZUP]; La Selva Biological Station, 10.41080 −84.01880 ±20m, 50m, 5-Sep-2007, mature wet forest, ex sifted leaf litter (TEAM, AMI-1-W-151-02) [worker: DZUP]; La Selva Biological Station, 10.41343 −84.03579 ±20m, 50m, 16-Apr-1993 (ALAS, B/16/064) [worker: USNM]; La Selva, 8km SW Pto. Viejo, 10.4 −84.05 ±2km, 150m, 17-Jul-1986, mature wet forest, ex sifted leaf litter (J. Longino, JTL1391-s) [intercaste female: CASC]; La Selva Biological Station, 10.43333 −84.01667 ±2km, 50m, 4-May-1993, sifted litter sample (J. Longino, JTL3483-s) [intercaste female: JTLC; worker: INBio]; La Selva Biological Station, 10.42576 −84.01383 ±20m, 50m, 25-Jun-1999, Hojarasca (D. Brenes, W/07/014) [intercaste female: USNM].

***Geographic Range.*** Costa Rica.

***Diagnosis.*** Lowland; subpetiolar process with posterior margin convex but not sharply angulate or acute; AIII in dorsal view trapezoidal with moderately convex sides; AIV with convex sides, non-truncate anterior margin; dorsal profiles of AIII and AIV convex; puncta on AIII large, closely spaced; puncta on AIV large, somewhat lunate, fading at midlength; standing pilosity long, coarse; color dark red brown. Pairwise distances among three COI barcodes (GenBank accessions MT267597 and MT267598, BOLD Process ID ASLAM2462-13) varied from 1.61 to 6.00%. The smallest interspecific distance was 5.38%.

Five species are within size and geographic range of *S. murillocruzae*: *S. benevidesae*, *S. pervagata*, *S. sumnichti*, *S.* JTL018, *S.* JTL074.

*S. benevidesae (*Fig. 11*):* locally sympatric; subpetiolar process shallower and longer; puncta on AIII and AIV larger and more widely spaced; all meso- and metasomal surfaces look glassier, with broader shiny interspaces.

*S. pervagata (*Fig. 9*):* Locally sympatric; subpetiolar process with acute posterior tooth; smaller on average (mean HW 0.51 vs. 0.56); profile of the promesonotum and the dorsal face of the propodeum form a single shallow convexity (vs. dorsal face of propodeum differentiated from promesonotum and sloping downward).

*S. sumnichti (*Fig. 9*):* Cloud forest; allopatric; AIV narrower on average (mean AIV-I 79 vs. 87); lighter colored; standing pilosity shorter.

*S. JTL018 (*Fig. 10*):* Allopatric; dorsal AIV punctate throughout.

*S. JTL074 (*Fig. 9*):* Locally sympatric; lighter colored; standing pilosity shorter, finer; dorsal profile of AIV flatter; sides of AIV in dorsal view more divergent posteriorly.

***Measurements, Worker.*** HW 0.55 (0.51–0.60), HL 0.67 (0.63–0.71), SL 0.40 (0.36–0.43), MSL 0.82 (0.76–0.89), AIIIW 0.43 (0.39–0.48), AIIIL 0.41 (0.36–0.45), AIVW 0.68 (0.62–0.74), AIVL 0.79 (0.68–0.88), SI 71 (69–74), AIII-I 106 (100–113), AIV-I 87 (81–93) ($n$ = 10).

***Measurements, Queen.*** HW 0.63 (0.63–0.64), HL 0.77 (0.77-0.77), SL 0.47 (0.45–0.48), MSL 1.23 (1.23-1.23), AIIIW 0.53 (0.51–0.55), AIIIL 0.50 (0.50–0.51), AIVW 0.81 (0.77–0.85), AIVL 1.02 (0.95–1.09), SI 74 (72–76), AIII-I 106 (101–110), AIV-I 79 (77–81) ($n$ = 2).

***Measurements, Intercaste Female.*** HW 0.59 (0.55–0.63), HL 0.70 (0.67–0.75), SL 0.42 (0.39–0.45), MSL 0.90 (0.83–0.99), AIIIW 0.49 (0.44–0.54), AIIIL 0.46 (0.42–0.51), AIVW 0.74 (0.69–0.80), AIVL 0.88 (0.80–0.98), SI 71 (68–73), AIII-I 105 (101–110), AIV-I 84 (81–88) ($n$ = 8).

***Biology.*** This species occurs in lowland rainforest, and all material is from Winkler or Berlese samples of forest floor leaf litter and rotten wood. Most material is from the lower portion of the Barva Transect in Costa Rica, to 500 m elevation. In this area, in spite of abundant collecting, no fully formed queens are known. Instead, intercaste females occur which are worker-like, lacking ocelli and queen-like mesosomal sclerites, but with small compound eyes of one to about seven partially-fused ommatidia. These intercaste females are relatively abundant, being found in Winkler samples with similar frequency to eyeless workers. A single fully formed queen (lacking wings) was collected on the Pacific slope of Costa Rica.

***Comments.*** UCE and COI sequence data place the isolated queen from the Pacific slope of Costa Rica as sister to material from the Caribbean slope (Barva transect), with a relatively high genetic divergence between the two. The queen is similar to Caribbean slope specimens in size and general metrics, but the subpetiolar process has a more prominent posterior tooth.

### *Syscia parietalis*, New Species

Figure 11 (map, worker), S39 (holotype worker), S40 (queen), S41 (male)

***Holotype:*** 1 worker, HONDURAS, *Comayagua*: PN Cerro Azul Meambar, 14.86944 −87.89619 ±20m, 1140m, 20-May-2010, ridgetop cloud forest, ex sifted leaf litter (LLAMA, Wa-C-04-2-40) [CASC, unique specimen identifier CASENT0617110]. PARATYPES: same data as holotype but 14.87034 −87.89894 ±20m, 1120m, 20-May-2010, ridgetop cloud forest, ex sifted leaf litter (LLAMA, Wa-C-04-1-36) [queen: CASC]; 14.86951 −87.89828 ±20m, 1140m, 20-May-2010, ridgetop cloud forest, ex sifted leaf litter (LLAMA, Wa-C-04-2-12) [worker: USNM]; 14.86943 −87.89615 ±20m, 1140m, 20-May-2010, ridgetop cloud forest, ex sifted leaf litter (LLAMA, Wa-C-04-2-41) [worker: MCZC].

***Geographic Range.*** Guatemala, Honduras.

***Diagnosis.*** Cloud forest; subpetiolar process broad and deep, posterior margin with a small tooth; propodeum with continuous carina that completely encircles and delimits the posterior face; AIII in dorsal view trapezoidal, with nearly flat sides; AIV in dorsal view with moderately convex sides, anterior margin weakly truncate; dorsal profile of AIII and AIV convex; puncta on AIII large, with narrow interspaces; puncta on AIV distinct, separate, fading at midlength; standing pilosity long, coarse; color red brown. COI barcodes are available for three specimens from Cerro Azul Meambar in Honduras (the type locality) (GenBank accession MT267600 and BOLD Process IDs ASLAM828-11 and ASLAM807-11) and three specimens from Cusuco National Park, Honduras (GenBank accession MT267601 and BOLD Process IDs ASLAM1158-11 and ASLAM1088-11). Within-population pairwise distances were 0%, while between-population distances were 3.51–3.65%. The smallest interspecific distance was 6.70%.

Twelve species are within size and geographic range of *S. parietalis*: *S. boudinoti*, *S. brachyptera*, *S. honduriana*, *S. jennierussae*, *S. machaquila*, *S. persimilis, S. sumnichti, S. tolteca, S. truncata, S. valenzuelai, S.* JTL066, and *S.* JTL082. In general the propodeal carina will help distinguish *S. parietalis* from other species, but other characters are provided below.

*S. boudinoti (*Fig. 8*):* lowland; no known site of local sympatry; smaller on average (mean HW 0.52 vs. 0.58); puncta on AIII and AIV smaller; standing pilosity shorter, finer.

*S. brachyptera (*Fig. 9*):* locally sympatric; posterior margin of subpetiolar process with acute tooth; smaller on average (mean HW 0.52 vs. 0.58); standing pilosity shorter and finer; puncta on AIII and AIV smaller.

*S. honduriana (*Fig. 10*):* lowland; no known site of local sympatry; puncta on AIV large, confluent, covering entire tergite.

*S. jennierussae (*Fig. 10*):* subpetiolar process relatively more triangular, with small tooth on posterior margin; smaller on average (mean HW 0.53 vs. 0.58); scapes shorter on average (mean SI 67 vs. 76); AIV wider on average (mean AIV-I 87 vs. 80).

*S. machaquila* (Fig. 10)*:* lowland; allopatric but in close proximity; subpetiolar process narrower, more triangular; otherwise very similar.

*S. persimilis* (Fig. 10)*:* locally sympatric; tooth on posterior margin of subpetiolar process larger, acute.

*S. sumnichti* (Fig. 9)*:* sympatric at one site in Guatemala; smaller on average (mean HW 0.53 vs. 0.58); erect pilosity shorter and finer; color lighter brown.

*S. tolteca* (Fig. 12)*:* lowland; no known site of local sympatry; scapes longer on average (mean SI 84 vs. 76).

*S. truncata* (Fig. 10)*:* lowland; no known site of local sympatry; tooth on posterior margin of subpetiolar process larger, acute; anterior margin of AIV strongly truncate.

*S. valenzuelai* (Fig. 9)*:* lowland; no known site of local sympatry; smaller on average (mean HW 0.52 vs. 0.58); subpetiolar process more triangular.

*S. JTL066* (Fig. 11)*:* allopatric, lowland; occipital carina more visible in face view; puncta on AIV smaller.

*S. JTL082* (Fig. 10)*:* locally sympatric; subpetiolar process lacking tooth on posterior margin, at most a small convexity; puncta on face, AIII, AIV smaller; dorsal profile AIII less convex; AIII wider on average (mean AIII-I 110 vs. 103); AIV wider on average (mean AIV-I 87 vs. 80).

***Measurements, Worker.*** HW 0.59 (0.56–0.61), HL 0.72 (0.70–0.74), SL 0.45 (0.41–0.48), MSL 0.92 (0.85–0.99), AIIIW 0.44 (0.42–0.48), AIIIL 0.43 (0.41–0.47), AIVW 0.71 (0.68–0.75), AIVL 0.89 (0.82–0.96), SI 76 (74–78), AIII-I 104 (101–108), AIV-I 80 (78–83) ($n$ = 4).

***Measurements, Queen.*** HW 0.60, HL 0.73, SL 0.44, MSL 0.98, AIIIW 0.46, AIIIL 0.43, AIVW 0.74, AIVL 0.92, SI 74, AIII-I 106, AIV-I 81 ($n$ = 1).

***Biology.*** This species occurs in mesophyl cloud forest and pine-*Liquidambar* forest. All workers and the one known queen were in Winkler samples of forest floor leaf litter and rotten wood. The structure of the mesosoma of the queen suggests it is brachypterous. One male is known, from a Malaise trap, and associated with workers using COI data.

### *Syscia parva* New Species

Figure 8 (map, worker), S42 (holotype worker), S43 (queen)

***Holotype:*** 1 worker, NICARAGUA, *Chontales*: 2.5km NE Santo Domingo, 12.27641 −85.0635 ±100m, 730m, 21-Apr-2011, wet forest, ex sifted leaf litter (J.Longino, JTL7365-s) [CASC, unique specimen identifier CASENT0644363]. PARATYPES: same data as holotype [worker: DZUP, JTLC, MCZC, UCD, UNAM, USNM].

***Geographic Range.*** Mexico (Chiapas) to Nicaragua.

***Diagnosis.*** Lowland; subpetiolar process moderately deep, forming a rounded lobe; petiole subquadrate in profile; AIII trapezoidal in dorsal view, with straight sides, and with nearly flat dorsum in lateral view; sides of AIV nearly flat and the anterior margin somewhat truncate in dorsal view; puncta on AIII distinct, nearly confluent; puncta on AIV distinct, small, fading at midlength; standing pilosity short and fine; color light brown. Pairwise distances among three COI barcodes (GenBank accessions MT267602 - MT267604) varied from 2.44 to 4.73%. The smallest interspecific distance was 14.50%.

Three species are within size and geographic range of *S. parva*: *S. minuta*, *S. pollula*, and *S.* JTL068.

*S. minuta* (Fig. 8)*:* in the part of the range where sympatric with *S. parva*, subpetiolar process with an anterior hook-like portion, a fenestra, and a posterior convexity (an even rounded lobe in *S. parva*).

*S. pollula* (Fig. 8)*:* sympatric in Nicaragua; larger on average (mean HW 0.42 vs. 0.38); AIII in profile more globular; posterior margin of subpetiolar process weakly convex or forming a slight notch near apex (posterior margin straight or concave in *S. parva*).

*S. JTL068* (Fig. 8)*:* known from a single queen from the La Mosquitia region of Honduras; larger (HW 0.46); darker red brown; subpetiolar process shaped more like *S. pollula*.

***Measurements, Worker.*** HW 0.38 (0.37–0.39), HL 0.50 (0.48–0.51), SL 0.25 (0.24–0.26), MSL 0.58 (0.56–0.61), AIIIW 0.30 (0.28–0.32), AIIIL 0.29 (0.27–0.30), AIVW 0.41 (0.38–0.42), AIVL 0.55 (0.53–0.58), SI 67 (65–68), AIII-I 105 (104–106), AIV-I 74 (73–76) ($n$ = 3).

***Measurements, Queen.*** HW 0.41, HL 0.54, SL 0.28, MSL 0.77, AIIIW 0.35, AIIIL 0.35, AIVW 0.47, AIVL 0.72), SI 68, AIII-I 99, AIV-I 66 ($n$ = 1).

***Biology.*** This species is known from lowland wet to moist forest habitats, from near sea level to just over 700 m elevation. All collections are from Winkler samples of sifted leaf litter and rotten wood.

***Comments.*** This species is known from three widely spaced populations that form a clade based on molecular evidence.

### *Syscia persimilis*, New Species

Figure 10 (map, worker), S44 (holotype worker), S45 (queen), S46 (intercaste female)

***Holotype:*** 1 worker, NICARAGUA, *Jinotega*: RN Cerro Kilambé, 13.57028 −85.69737 ±20m, 1500m, 23-May-2011, cloud forest, ex sifted leaf litter (LLAMA, Wa-D-05-1-26) [CASC, unique specimen identifier CASENT0630852]. PARATYPES: same data as holotype [worker: MCZC]; same data except 13.56924 −85.69746 ±10m, 1500m, 23-May-2011, cloud forest, ex sifted leaf litter (LLAMA, Wa-D-05-1-03) [intercaste female: CASC; worker: USNM]; same data except 13.56726 −85.69782 ±15m, 1400m, 23-May-2011, cloud forest, ex sifted leaf litter (LLAMA, Wa-D-05-2-27) [worker: UCD].

***Geographic Range.*** Mexico (Chiapas) to Nicaragua.

***Diagnosis.*** Mainly cloud forest, occasionally lowland; subpetiolar process with acute posterior tooth; AIII in dorsal view trapezoidal, with moderately convex sides; AIV in dorsal view with weakly convex sides and moderately truncate anterior border; dorsum of AIII convex in lateral view; dorsum of AIV moderately convex in lateral view; puncta on AIV distinct, separated, fading at about midlength; standing pilosity abundant, long, coarse; color red brown. Pairwise distances among 17 COI barcodes (GenBank accessions MT267605 - MT267612, 9 BOLD Process IDs not listed here) varied from 0 to 4.12%. The smallest interspecific distance was 1.83%.

Fourteen species are within size and geographic range of *S. persimilis: S. boudinoti, S. brachyptera, S. chiapaneca, S. honduriana, S. jennierussae, S. machaquila, S. murillocruzae, S. parietalis, S. pervagata, S. peten, S. sumnichti, S. truncata, S. valenzuelai,* and *S.* JTL066.

*S. boudinoti (*Fig. 8*):* locally sympatric; more closely spaced puncta on AIV; weaker standing pilosity; subpetiolar process with reduced posterior tooth.

*S. brachyptera (*Fig. 9*):* locally sympatric; standing pilosity much weaker.

*S. chiapaneca (*Fig. 11*):* locally sympatric; more extensive punctation on AIV, covering the entire tergite; subpetiolar process triangular, without a posterior tooth.

*S. honduriana (*Fig. 10*):* lowland; no zone of local sympatry; AIV covered with coarse, nearly confluent puncta; subpetiolar process lacks posterior tooth.

*S. jennierussae (*Fig. 10*)*, *S. machaquila* (Fig. 10), *S. valenzuelai* (Fig. 9): lowland; ranges overlap with *S. persimilis* but no known zones of local sympatry; subpetiolar process quadrate to convex with reduced posterior tooth.

*S. murillocruzae (*Fig. 10*):* Costa Rican allopatric but adjacent to *S. persimilis*; subpetiolar process triangular, without posterior tooth.

*S. parietalis (*Fig. 11*):* locally sympatric with *S. persimilis* in Cusuco National Park, Honduras; with a more continuous carina that completely encircles and delimits the posterior face of the propodeum (in *S. persimilis* and in *Syscia* generally the carina fades dorsally).

*S. pervagata (*Fig. 9*):* mostly lowland; broadly sympatric with *S. persimilis*; in zone of sympatry, AIV with confluent, somewhat irregular puncta (distinct and separate in *S. persimilis*).

*S. peten (*Fig. 9*):* embedded within range of *S. persimilis* but lowland, not locally sympatric; puncta on anterior AIV more dense and closely spaced; AIII in profile slightly less convex.

*S. sumnichti (*Fig. 9*):* locally sympatric; weaker standing pilosity; subpetiolar process quadrate, without acute posterior tooth.

*S. truncata (*Fig. 10*):* AIV with very straight sides and strongly truncate anterior border.

*S. JTL066 (*Fig. 11*):* lowland; no known site of local sympatry; puncta on AIV smaller, more closely spaced, extend further posteriorly.

***Measurements, Worker.*** HW 0.54 (0.53–0.57), HL 0.67 (0.66–0.70), SL 0.40 (0.38–0.43), MSL 0.85 (0.82–0.89), AIIIW 0.45 (0.44–0.47), AIIIL 0.42 (0.40–0.44), AIVW 0.64 (0.62–0.66), AIVL 0.77 (0.76–0.82), SI 74 (72–76), AIII-I 107 (104–110), AIV-I 82 (80–86) ($n$ = 7).

***Measurements, Queen.*** HW 0.60, HL 0.72, SL 0.44, MSL 1.13, AIIIW 0.54, AIIIL 0.49, AIVW 0.77, AIVL 0.97, SI 74, AIII-I 110, AIV-I 79 ($n$ = 1).

***Biology.*** This species is known mainly from cloud forest habitat, typically from 1000 to 1600 m, but populations can occur in lowland rainforest (e.g., La Moskitia, Honduras). All records are from Winkler or Berlese samples of forest floor leaf litter and rotten wood. Relatively small, lighter colored alate queens and more robust, darker dealate queens are known, paralleling the phenomenon in *S. pervagata* (see further discussion under *S. pervagata*). One intercaste female is known, with compound eyes, ocelli, and mesosoma slightly elongated with weakly impressed promesonotal suture.

***Comments.*** *Syscia persimilis* is sister to *S. pervagata* (Fig. 6), and additional discussion of the two species is under *S. pervagata*. Within *S. persimilis*, specimens from Cusuco National Park, Honduras, are relatively shinier, with sparser punctation, than all other material, and UCE sequence data place the Cusuco population as sister to all other sequenced populations. The COI tree also showed a monophyletic *S. persimilis*, but relationships within the species were not congruent with the UCE tree (Fig. 7).

### *Syscia pervagata*, New Species

Figure 9 (map, worker), S47 (holotype worker), S48 (alate queen), S49 (dealate queen), S50 (male)

***Holotype:*** 1 worker, HONDURAS, *Atlántida*: 12km SW La Ceiba, 15.69449 −86.86307 ±20m, 200m, 19-Jun-2010, tropical rainforest, ex sifted leaf litter (LLAMA, Wa-C-09-1-32) [CASC, unique specimen identifier CASENT0644356]. PARATYPES: same data as holotype [male: CASC; worker: CASC, DZUP, JTLC, MCZC, UCD, UNAM, USNM].

***Geographic Range.*** Mexico (Chiapas) to Costa Rica.

***Diagnosis.*** Mostly lowland but extends into lower cloud forest; subpetiolar process with acute posterior tooth; AIII in dorsal view trapezoidal, with moderately convex sides; AIV in dorsal view with weakly convex sides and moderately truncate anterior border; dorsum of AIII convex in lateral view; dorsum of AIV moderately convex in lateral view; puncta on AIV geographically variable, confluent to separated, fading at about midlength; standing pilosity abundant, long, coarse; color red brown. Pairwise distances among 29 COI barcodes (GenBank accessions MT267613 - MT267625, 16 BOLD Process IDs not listed here) varied from 0 to 6.45%. The smallest interspecific distance was 1.83%.

Sixteen species are within size and geographic range of *S. pervagata: S. boudinoti, S. brachyptera, S. jennierussae, S. machaquila, S. murillocruzae, S. persimilis, S. peten, S. sumnichti, S. truncata, S. valenzuelai, S.* JTL018, *S.* JTL037*, S.* JTL068, JTL074, JTL082, and *S.* JTL085.

*S. boudinoti (*Fig. 8*):* locally sympatric; weaker dorsal pilosity; subpetiolar process with reduced posterior tooth.

*S. brachyptera (*Fig. 9*):* locally sympatric; dorsal pilosity much weaker; punctation on anterior AIV fine, somewhat regularly spaced, and with narrow shiny interspaces (in zone of sympatry, *S. pervagata* has confluent, somewhat irregular puncta).

*S. jennierussae* (Fig. 10), *S. machaquila* (Fig. 10), *S. valenzuelai* (Fig. 9): locally sympatric; subpetiolar process quadrate to convex, with reduced posterior tooth.

*S. murillocruzae* (Fig. 10)*:* locally sympatric; subpetiolar process triangular, without posterior tooth.

*S. persimilis* (Fig. 10)*:* difficult to distinguish from *S. pervagata* (see Comments); AIV with separate puncta (in zone of sympatry, *S. pervagata* has confluent, somewhat irregular puncta).

*S. peten* (Fig. 9)*:* overlapping ranges, but no known site of local sympatry; not readily distinguishable from *S. pervagata*, although perhaps with slightly less convex AIII in profile.

*S. sumnichti* (Fig. 9)*:* cloud forest; locally sympatric; weaker dorsal pilosity; subpetiolar process quadrate, without acute posterior tooth.

*S. truncata* (Fig. 10)*:* AIV in dorsal view with very straight sides and strongly truncate anterior border.

*S. JTL018* (Fig. 10)*:* Osa Peninsula, Costa Rica; no known site of local sympatry; dorsal pilosity short; AIV punctate throughout.

*S. JTL037* (Fig. 8)*:* Osa Peninsula, Costa Rica; no known site of local sympatry; AIV with strongly trunctate anterior border.

*S. JTL068* (Fig. 8)*:* locally sympatric; known from one queen from La Moskitia region, Honduras; smaller on average (mean HW 0.46 vs. 0.51); subpetiolar process with reduced posterior tooth.

*S. JTL074* (Fig. 9)*:* allopatric, occurs in Panama; finer dorsal pilosity; smaller puncta on AIV; less convex dorsal profile of AIV.

*S. JTL082* (Fig. 10)*:* allopatric; known from one cloud forest site in Honduras; subpetiolar process lacking acute posterior tooth.

*S. JTL085* (Fig. 9)*:* locally sympatric; known from one specimen from eastern Chiapas; subpetiolar process lacking acute posterior tooth.

***Measurements, Worker.*** HW 0.51 (0.46–0.56), HL 0.63 (0.56–0.70), SL 0.36 (0.32–0.42), MSL 0.78 (0.65–0.92), AIIIW 0.41 (0.36–0.50), AIIIL 0.38 (0.33–0.45), AIVW 0.58 (0.50–0.69), AIVL 0.68 (0.58–0.84), SI 70 (68–76), AIII-I 109 (102–117), AIV-I 86 (80–95) ($n$ = 27).

***Measurements, Queen.*** HW 0.56 (0.54–0.59), HL 0.66 (0.65–0.69), SL 0.37 (0.36–0.39), MSL 1.01 (0.96–1.05), AIIIW 0.49 (0.45–0.54), AIIIL 0.43 (0.39–0.46), AIVW 0.68 (0.65–0.71), AIVL 0.80 (0.75–0.84), SI 67 (66–69), AIII-I 114 (111–117), AIV-I 85 (83–86) ($n$ = 3).

***Measurements, Intercaste Female.*** HW 0.55 (0.55-0.55), HL 0.66 (0.64–0.69), SL 0.38 (0.36–0.39), MSL 0.88 (0.82–0.94), AIIIW 0.49 (0.47–0.52), AIIIL 0.43 (0.41–0.45), AIVW 0.68 (0.66–0.70), AIVL 0.82 (0.76–0.87), SI 69 (66–71), AIII-I 116 (116-116), AIV-I 84 (80–87) ($n$ = 2).

***Biology.*** This species is known mainly from lowland rainforest, with records up to 1300 m elevation. Almost all collections are from Winkler or Berlese samples of forest floor leaf litter and rotten wood.

Queens, intercaste females, and males are known. A series from Chiapas contains 11 workers and 6 alate queens. The queens are slightly smaller than the workers and lighter colored. A dealate queen from a nearby site is larger and more robust, with relatively larger eyes, and is slightly larger than workers from the site. Two series from Cerro Azul Meambar, Honduras, have intercaste females with slightly elongated mesosoma and fully developed compound eyes and ocelli. Similar intercaste females occur at a site near La Ceiba, Honduras. Collections from Cerro Musún, Nicaragua, include a robust dealate queen and an intercaste female. The intercaste is similar to those from Chiapas and Honduras, but with the promesonotal suture present. Collections from Kahka Creek, Nicaragua, include a robust dealate queen, an alate queen that is very like the alate queens from the Chiapas series (smaller than workers, lighter colored), and a dealate queen that is intermediate in size and color. There is also a 'slightly' intercaste female, with a tiny compound eye of a few fused ommatidia, a slightly elongated mesosoma, but otherwise worker-like. Specimens from La Selva Biological Station and vicinity in Costa Rica include an alate queen that was collected in a Malaise trap (Feb-Apr 2004) and a robust dealate queen. The alate queen is small and lighter colored. A male, associated using COI data, was collected in a Malaise trap in Kahka Creek, Nicaragua in June 2011. Two other collections of males were with worker series in single Winkler samples, and are assumed to come from the same colony as the workers.

There appear to be two queen forms, both widespread. Small queens are lighter colored, and have been collected as both alate and dealate individuals. Robust queens are darker, and are only known as dealate individuals. The large queens have the typical size relationship to workers. None of the small queens have been sequenced, and they are identified as *S. pervagata* because of co-occurrence with workers (some of which have been sequenced) and general morphological congruence. But it remains to be seen whether this is intraspecific variation in queens, or some other phenomenon such as social parasitism.

***Comments.*** This is the most abundant and widespread species of New World *Syscia*. There is geographic variation in sculpture, which complicates identification. *Syscia pervagata* occurs as two allopatric sister clades, occurring on opposite sides of the Motagua fault zone in Guatemala (Fig. 6). The populations in the clade south of the Motagua fault divide into two subclades, one in Honduras and the other in Nicaragua and Costa Rica. The northern clades, north of the Motagua fault and in Honduras, have dense confluent puncta on the dorsal mesosoma and on anterior AIV (Fig. 9). The Nicaraguan-Costa Rican clade has sparser, more widely spaced puncta.

UCE results show a reciprocally monophyletic pair of sister species, *S. pervagata* and *S. persimilis* (Fig. 6). The COI tree shows *S. pervagata* being paraphyletic with respect to *S. persimilis* (Fig. 7), but the branches showing paraphyly have low support. The two species are broadly sympatric and bear the hallmarks of a very recent and perhaps only partial speciation, segregating by elevation. *Syscia persimilis* occurs from Mexico (Chiapas) to Nicaragua, and has relatively sparser punctation like the southern clade of *S. pervagata*. Currently there is no known morphological feature to distinguish *S. persimilis* and the southernmost clade of *S. pervagata*.

Local zones of sympatry are known for two sites. In the La Moskitia region of Honduras, both species occur and they are distinguishable there because the Honduras clade of *S. pervagata* has confluent puncta on AIV. The COI sequences of the two species at this site differ by 6.9%. The other site of sympatry is Cerro Musún in central Nicaragua, where the two species are indistinguishable. The COI sequences differ by 5–6%.

The two species differ in habitat preference, with *S. pervagata* being mostly from lowland rainforest and *S. persimilis* being mostly from cloud forest. An example of this division is possibly seen at Cerro Musún, where sampling was carried out along an elevational gradient from 700 to 1,300 m. The two specimens determined to be *S. pervagata* by sequence data were from 700 to 1,200 m forest. The one specimen determined to be *S. persimilis* by sequence data was from 1300 m, near the local peak of the gradient, and a distinctly wet, mossy habitat. However, *S. persimilis* can occur in lowland sites (e.g., La Moskitia).

## *Syscia peten*, New Species

Figure 9 (map, worker), S51 (holotype worker), S52 (queen)

***Holotype:*** 1 worker, GUATEMALA, *Petén*: Parq. Nac. Tikal, 17.23506 −89.63623 ±26m, 270m, 22-May-2009, tropical moist forest, ex sifted leaf litter (LLAMA, Wm-B-05-2-03) [CASC, unique specimen identifier CASENT0610652]. PARATYPES: same data as holotype [queen: CASC, JTLC, MCZC, USNM; worker: DZUP, MCZC, UNAM, USNM, UVGC].

***Geographic Range.*** Guatemala.

***Diagnosis.*** Lowland; subpetiolar process with acute posterior tooth; AIII in dorsal view trapezoidal with flat sides; AIV in dorsal view with convex sides, non-truncate anterior margin; AIII dorsal profile convex; AIV dorsal profile weakly convex to flat; puncta on AIV distinct, separated, fading at midlength; standing pilosity long, moderately abundant, fine; color red brown. Based on the COI barcode of the sequenced specimen (GenBank accession MT267626), the smallest pairwise interspecific distance was 10.82%.

Nine species are within size and geographic range of *S. peten*: *S. boudinoti*, *S. brachyptera*, *S. jennierussae*, *S. machaquila*, *S. persimilis*, *S. pervagata*, *S. sumnichti*, *S. truncata*, and *S. valenzuelai*. The combination of a strongly developed posterior tooth on the subpetiolar process and a broad AIII (AIII-I 119) will separate it from all of these species.

***Measurements, Worker.*** HW 0.51, HL 0.61, SL 0.35, MSL 0.79, AIIIW 0.42, AIIIL 0.35, AIVW 0.60, AIIIL 0.66, SI 69, AIII-I 119, AIV-I 90 ($n$ = 1).

***Measurements, Queen.*** HW 0.53, HL 0.62, SL 0.35, MSL 0.95, AIIIW 0.45, AIIIL 0.39, AIVW 0.65, AIVL 0.74, SI 66, AIII-I 116, AIV-I 88 ($n$ = 1).

***Biology.*** This species is known from one series collected in lowland moist forest, in a Winkler sample of forest floor leaf litter and rotten wood. Multiple dealate queens, an alate queen, and multiple workers occurred in the sample.

## *Syscia pollula*, New Species

Figure 8 (map, worker), S53 (holotype worker), S54 (queen), S55 (brachypterous queen)

***Holotype:*** 1 worker, NICARAGUA, *Matagalpa*: RN Cerro Musún, 12.96817 −85.23301 ±20m, 1060m, 2-May-2011, montane wet forest, ex sifted leaf litter (LLAMA, Wm-D-01-1-07) [CASC, unique specimen identifier CASENT0624110]. PARATYPES: NICARAGUA, *Matagalpa*: RN Cerro Musún, 12.96087 −85.2329 ±10m, 750m, 1-May-2011, tropical wet forest, ex sifted leaf litter (LLAMA, Wa-D-01-1-10) [worker: MCZC, USNM]; RN Cerro Musún, 12.95884 −85.22486 ±10m, 700m, 1-May-2011, tropical wet forest, ex sifted leaf litter (LLAMA, Wa-D-01-2-14) [worker: CASC].

***Geographic Range.*** Nicaragua to Panama.

***Diagnosis.*** *Syscia pollula* occurs in lowland and lower montane forests. The subpetiolar process is asymmetrically triangular, with a sharp anterior point and a convex posterior margin; AIII in dorsal view is trapezoidal with weakly convex sides; AIV in dorsal view has convex sides that slope to a non-truncate anterior margin; the dorsal of AIII and AIV are nearly flat in lateral view; puncta on AIII are discrete and nearly confluent; puncta on AIV are distinct, small, fading at midlength; standing pilosity is short and sparse; color is red brown. Pairwise distances among seven COI barcodes (GenBank accessions MT267627 - MT267632, BOLD Process ID ASLAM2441-13) varied from 0 to 10.52%. The smallest interspecific distance was 8.96%.

Five species are within size and geographic range of *S. pollula*: *S. austrella*, *S. minuta*, *S. parva*, *S.* JTL037, and *S.* JTL068.

*S. austrella (*Fig. 8*)*: parapatric, with adjacent ranges in Panama; larger on average (HW 0.47 vs. 0.43); puncta on anterior AIV larger and more widely spaced.

*S. minuta (*Fig. 8*)*: in the part of the range where sympatric with *S. pollula*, subpetiolar process shallow, with an anterior hook-like portion, a fenestra, and a posterior convexity (deeper and lacking the fenestra in *S. pollula*).

*S. parva (*Fig. 8*):* locally sympatric; sides of AIV less convex; AIV narrower on average (mean AIV-I 74 vs. 79).

*S. JTL037 (*Fig. 8*):* parapatric in Costa Rica, known from one worker from Osa Peninsula; sides of AIV less convex.

*S. JTL068 (*Fig. 8*)*: parapatric, known from one queen from the La Moskitia region of Honduras; sides of AIV less convex and anterior border more truncate.

***Measurements, Worker.*** HW 0.43 (0.41–0.44), HL 0.54 (0.51–0.56), SL 0.29 (0.27–0.30), MSL 0.67 (0.63–0.70), AIIIW 0.33 (0.32–0.35), AIIIL 0.31 (0.30–0.33), AIVW 0.51 (0.49–0.53), AIVL 0.65 (0.63–0.68), SI 67 (65–69), AIII-I 106 (104–108), AIV-I 79 (77–84) ($n$ = 6).

***Measurements, Queen.*** HW 0.45 (0.43–0.47), HL 0.57 (0.54–0.61), SL 0.30 (0.28–0.32), MSL 0.85 (0.78–0.95), AIIIW 0.36 (0.35–0.38), AIIIL 0.35 (0.33–0.38), AIVW 0.55 (0.52–0.58), AIVL 0.74 (0.71–0.79), SI 66 (62–68), AIII-I 104 (100–106), AIV-I 73 (70–77) ($n$ = 4).

***Biology.*** This species occurs in wet forest habitats from near sea level to cloud forest. Most records are between 50 and 1100 m elevation, but the alate queen is from a 1500 m elevation site. All records except the alate queen are from Winkler or Berlese samples of litter and rotten wood. There are no additional collection data with the alate queen, but it was probably from a Malaise trap or net sample.

***Comments.*** Queens occur in two forms, alate and (probably) brachypterous. Alate queens have the mesoscutum wider and with more acute anterior border in dorsal view, the pronotum relatively shorter medially, and the eyes relatively larger (Supp Fig. S29 [online only]). One specimen with this morphology is fully alate, with wings present. Other queens with this morphology are presumed dealate. Putative brachypterous queens have all of the standard sclerites of alate queens, but the mesoscutum is narrower and with less acute anterior border, the pronotum is more elongate medially, and the eyes are relatively smaller (Supp Fig. S30 [online only]). No specimens with brachypterous wings are known, but tiny wings have been found on brachypterous queens of other *Syscia* species.

There is potential for this species to contain up to four cryptic species (or at least strong isolation-by-distance effects). Three cloud forest populations have COI distances < 1.5%: the two Nicaraguan sites Saslaya and Cerro Musún, and the Costa Rican site Monteverde. These show progressively greater distances, all > 5%, to specimens from La Selva Biological Station, Hitoy Cerere (both lowland Caribbean slope sites), and Cerro Plano (montane forest site on the Pacific slope of Costa Rica). Specimens from the latter three sites differ from each other by > 7%.

### *Syscia quisquilis*, New Species

Figures 8 and 9 (map, worker), S56 (holotype worker), S57 (Arizona form worker)

***Holotype:*** 1 worker, USA, California, San Diego Co.: ca. 3mi N Warner Springs, Cleveland National Forest, 33.32285 –116.6328 ±?, 1000m, 19-v-1974, south facing chaparral slope, with *Neivamyrmex californicus* (R. Berkelhamer) [LACM, unique specimen identifier LACM ENT 365113]. PARATYPES: same data as holotype [1 worker, USNM, LACM ENT 365115; 2 workers, CASC, LACM ENT 365114].

***Geographic Range.*** Unites States (California, Arizona).

***Diagnosis.*** Subtropical/temperate chaparral and riparian woodland; occipital carina small and shifted ventrally (typical form) or larger and more visible in face view (Arizona form); subpetiolar process shallow, with anterior hook-like portion, notch, and posterior convexity; AIII in dorsal view trapezoidal with flat sides; AIV in dorsal view with flat sides, weakly truncate anterior margin; AIII dorsal profile weakly convex; AIV dorsal profile flat; puncta on AIV distinct, separated, fading at midlength; standing pilosity short, moderately abundant, fine; color light brown. One species is within size and geographic range:

*S. madrensis (*Fig. 11*):* no known site of local sympatry but ranges overlap; larger on average (mean HW 0.57 vs. 0.53); subpetiolar process deeper, without anterior hook and notch.

***Measurements, Worker.*** HW 0.52 (0.50–0.53), HL 0.67 (0.66–0.69), SL 0.38 (0.38–0.39), MSL 0.85 (0.84–0.85), AIIIW 0.46 (0.45–0.46), AIIIL 0.47 (0.47-0.47), AIVW 0.58 (0.57–0.59), AIVL 0.76 (0.74–0.78), SI 73 (71–77), AIII-I 97 (95–99), AIV-I 77 (73–80) ($n$ = 3).

***Biology.*** This species has been collected mainly in chaparral habitats and is presumably subterranean. The type series was referenced in Snelling and George (1979), with workers 'taken from a column of *Neivamyrmex californicus* in a chaparral habitat'. Fragments have twice been collected in middens of *Forelius*, at two chaparral sites in southern California. One collection is a head, mesosoma, and petiole. A second collection is a mesosoma and petiole. An Arizona collection, here identified as a geographic variant of *S. quisquilis*, was presumably in a riparian woodland (based on locality), under a stone.

***Comments.*** This is an infrequently encountered species, and there are no sequence data yet so its phylogenetic position is unknown. The three California collections are relatively uniform in size and shape. The Arizona collection differs in some characters, and is referred to as the Arizona form. It is similar in size and in the shape of the subpetiolar process, but the occipital carina is more visible in face view and the scape is longer (SI 77 vs. 71–72). These two latter characters are thus more like *S. madrensis*.

### *Syscia setosa*, New Species

Figure 11 (map, worker), S58 (holotype worker), S59 (queen), S60 (intercaste female), S61 (male)

***Holotype:*** 1 worker, MEXICO, *Veracruz*: Est. Biol. Los Tuxtlas, 18.58584 –95.07665 ±20m, 180m, 29-May-2016, tropical rainforest, ex sifted leaf litter (ADMAC, Wa-F-01-2-27) [UNAM, unique specimen identifier CASENT0644336]. PARATYPES: same data as holotype [queen: CASC, USNM; worker: CASC, DZUP, JTLC, MCZC, UCD, USNM].

***Geographic Range.*** Mexico (Tamaulipas to Chiapas).

***Diagnosis.*** Lowland to lower montane; subpetiolar process deep, posterior margin convex but not forming a tooth; AIII in dorsal view subquadrate, sides convex; AIV in dorsal view subquadrate, with weakly convex, nearly parallel sides; dorsal profile of AIII and AIV convex; puncta on AIII large, widely separated; puncta on AIV large, widely separated, fading at anterior third; standing pilosity long, coarse, lacking underlying pubescence; color dark brown. Pairwise distances among seven COI barcodes (GenBank accessions MT267633-MT267638, BOLD Process ID ASLAM2453-13) varied from 0 to 8.16%. The smallest interspecific distance was 7.48%.

Fifteen species are within size and geographic range of *S. setosa*: *S. atitlana*, *S. chiapaneca*, *S. disjuncta*, *S. jennierussae*, *S. lacandona*, *S. machaquila*, *S. persimilis*, *S.* JTL049, *S.* JTL060, *S.* JTL065, *S.* JTL066, *S.* JTL073, *S.* JTL075, *S.* JTL084, and *S.* JTL085. Most species differ by having AIII in dorsal view distinctly trapezoidal, with smaller and more closely spaced puncta. Four species have AIII similar to *S. setosa*: *S. atitlana*, *S. lacandona*, *S.* JTL065, and *S.* JTL073.

*S. atitlana (*Fig. 12*):* allopatric; AIII in dorsal view more trapezoidal; AIV in dorsal view with sides more converging anteriorly.

*S. lacandona (*Fig. 12*):* locally sympatric; occipital carina more visible in face view; AIV less quadrate, sides converging anteriorly; standing pilosity shorter.

*S. JTL065 (*Fig. 12*):* cloud forest; allopatric but adjacent ranges; AIII in dorsal view with similarly convex sides, but puncta more dense, more closely spaced; AIV in dorsal view with sides very convex, strongly converging anteriorly; standing pilosity shorter.

*S. JTL073 (*Fig. 11*):* cloud forest; allopatric but adjacent ranges; very similar; AIV in dorsal view with sides more convex, more converging anteriorly; scapes longer on average (mean SI 78 vs. 70); AIV broader on average (mean AIV-I 101 vs. 89).

***Measurements, Worker.*** HW 0.59 (0.55–0.62), HL 0.70 (0.67–0.73), SL 0.41 (0.39–0.44), MSL 0.87 (0.81–0.92), AIIIW 0.45 (0.40–0.49), AIIIL 0.41 (0.38–0.44), AIVW 0.70 (0.64–0.76), AIVL 0.78 (0.74–0.83), SI 70 (68–71), AIII-I 110 (106–116), AIV-I 89 (85–91) (*n* = 4).

***Measurements, Queen.*** HW 0.56, HL 0.65, SL 0.38, MSL 1.02, AIIIW 0.43, AIIIL 0.40, AIVW 0.70, AIVL 0.78, SI 68, AIII-I 108, AIV-I 90 (*n* = 1).

***Biology.*** This species occurs in wet forest habitats, from near sea level to 1400 m elevation. All collections are Winkler or Berlese samples of forest floor leaf litter and rotten wood. Alate queens and intercaste females have been collected. Adult males were collected together with workers in one miniWinkler sample, and are assumed to be conspecific.

***Comments.*** Multiple populations have been sequenced, and together they form a well-separated clade (Figs. 6 and 7). Within the species there is a broad range of COI distances, with some intraspecific distances greater than interspecific distances. Distances greater than 3% separate 1) specimens from the states of Tamaulipas and Puebla, Mexico; 2) a specimen from the Sierra Mazateca in Oaxaca, Mexico; and 3) specimens from the Los Tuxtlas region in Veracruz and a specimen from northeastern Chiapas, Mexico. UCE results more sharply differentiate the species, with all intraspecific distances much smaller than any interspecific distance (Fig. 6). The sister species is *S. atitlana*, with which it has a parapatric distribution. The contact zone is in central Chiapas, Mexico. Sequenced specimens of *S. atitlana* are from the Sierra de Chiapas and Volcán Atitlán. Collections of *S. atitlana* from Huehuetenango and the north central highlands of Chiapas have not been sequenced but share morphology with *S. atitlana*. Morphologically, all specimens of *S. setosa* are relatively uniform and differ from *S. atitlana* as described above.

## *Syscia sumnichti*, New Species

Figure 9 (map, worker), S62 (holotype worker)

***Holotype:*** 1 worker, GUATEMALA, *Zacapa*: 2km SE La Unión, 14.94981 –89.27807 ±16m, 1475m, 12-May-2009, cloud forest, ex sifted leaf litter (LLAMA, Wm-B-03-1-03) [CASC, unique specimen identifier CASENT0612556]. PARATYPES: three workers from same site, slightly different coordinates and elevation, each from a different miniWinkler sample [worker: MCZC, USNM, UVGC].

***Geographic Range.*** Guatemala to Nicaragua.

***Diagnosis.*** Cloud forest; subpetiolar process trapezoidal, with the posterior border rounded or forming a sharp right angle; sides of AIII relatively flat; sides of AIV weakly convex; puncta on AIV small, faint, fading at the anterior third; standing pilosity fine, short; color orange brown. Pairwise distances among five COI barcodes (GenBank accessions MT267639 - MT267641, BOLD Process IDs ASLAM2273-12 and ASLAM753-11) varied from 0 to 3.05%. The smallest interspecific distance was 8.99%.

Fourteen species are within size and geographic range of *S. sumnichti*: *S. boudinoti*, *S. brachyptera*, *S. honduriana*, *S. jennierussae*, *S. machaquila*, *S. murillocruzae*, *S. parietalis*, *S. persimilis*, *S. pervagata*, *S. peten*, *S. truncata*, *S. valenzuelai*, *S.* JTL066, and *S.* JTL082.

*S. boudinoti* (Fig. 8)*:* lowland; no known site of local sympatry; subpetiolar process more triangular; AIII wider on average (mean AIII-I 107 vs. 101); puncta on AIV fading at about midlength; AIV broader on average (mean AIV-I 84 vs. 79).

*S. brachyptera*, *S. persimilis*, *S. pervagata*, *S. peten*, *S. truncata*: subpetiolar process with acute posterior tooth.

*S. honduriana* (Fig. 10)*:* AIV with large confluent puncta over entire surface.

*S. jennierussae* (Fig. 10)*:* lowland; no known site of local sympatry; scapes shorter on average (mean SI 67 vs. 79); AIII broader on average (mean AIII-I 110 vs. 101); anterior margin of AIV more truncate; AIV broader on average (mean AIV-I 87 vs. 79); color darker brown.

*S. machaquila* (Fig. 10)*:* lowland; no known site of local sympatry; AIII wider on average (mean AIII-I 107 vs. 101); AIV broader on average (mean AIV-I 86 vs. 79); standing pilosity longer, coarser; color darker brown.

*S. murillocruzae* (Fig. 10)*:* lowland; no known site of local sympatry; scapes shorter on average (mean SI 72 vs. 79); AIV broader on average (mean AIV-I 87 vs. 79); erect pilosity longer and coarser; color darker brown.

*S. parietalis* (Fig. 11)*:* sympatric at one site in Guatemala; larger on average (mean HW 0.58 vs. 0.53); erect pilosity longer and coarser; color darker brown.

*S. valenzuelai* (Fig. 9)*:* lowland; no known site of local sympatry; scapes shorter on average (mean SI 72 vs. 79); AIII wider on average (mean AIII-I 107 vs. 101); erect pilosity longer and coarser; color darker brown.

*S. JTL066* (Fig. 11)*:* lowland; no known site of local sympatry; larger on average (mean HW 0.58 vs. 0.53); AIV broader on average (mean AIV-I 86 vs. 79); color darker brown.

*S. JTL082* (Fig. 10)*:* no known site of local sympatry; AIII wider on average (mean AIII-I 110 vs. 101); AIV broader on average (mean AIV-I 87 vs. 79); color darker brown.

***Measurements, Worker.*** HW 0.53 (0.52–0.55), HL 0.68 (0.65–0.70), SL 0.42 (0.41–0.44), MSL 0.88 (0.85–0.91), AIIIW 0.41 (0.38–0.43), AIIIL 0.41 (0.38–0.44), AIVW 0.65 (0.63–0.68), AIVL 0.83 (0.79–0.89), SI 79 (77–82), AIII-I 100 (99–102), AIV-I 79 (76–84) (*n* = 9).

***Biology.*** This species occurs in cloud forest from 1370 to 1650 m. All collections are from Winkler samples of forest floor litter and rotten wood. No sexuals are known.

***Comments.*** Specimens from three sites were sequenced for UCEs and COI (Figs. 6 and 7). UCE and COI results were incongruent for relationships among populations, with UCE data showing (Honduras (Guatemala Nicaragua)) and COI data showing (Nicaragua (Honduras Guatemala)).

## *Syscia ticomontana*, New Species

Figure 12 (map, worker), S63 (holotype worker)

***Holotype:*** 1 worker, COSTA RICA, *Cartago*: PN Tapantí, 9.73307 −83.78258 ±20m, 1360m, 6-Jun-2015, cloud forest, old second growth, riparian, ex sifted leaf litter (ADMAC, Wm-E-01-1-04) [UCR, unique specimen identifier CASENT0644376]. PARATYPES: same data as holotype [worker: MCZC, UCD, USNM]; same data except 9.73473 −83.78187, 1340m, (Wm-E-01-1-03) [CASC, DZUP].

***Geographic Range.*** Costa Rica.

***Diagnosis.*** Montane; subpetiolar process subquadrate, with angulate posterior margin; AIII in dorsal view weakly trapezoidal, with convex sides; AIV in dorsal view with convex sides, strongly tapering to non-truncate anterior margin; AIII and AIV dorsal profile convex; puncta on AIII large, widely separated; puncta on AIV medium size, widely separated, fading at midlength; standing pilosity long, coarse; color dark brown. Pairwise distances among 5 COI barcodes (GenBank accessions MT267645 - MT267648, BOLD Process ID ASLAM2454-13) varied from 0.22–3.09%. The smallest interspecific distance was 11.11%.

Three species are within size and geographic range of *S. ticomontana*: *S. disjuncta*, *S. latepunctata*, and *S.* JTL017.
*S. disjuncta (*Fig. 11*):* locally sympatric; posterior margin of subpetiolar process shallowly convex but not angulate; AIII in dorsal view with less convex sides, more trapezoidal; puncta on AIII smaller and more closely spaced; AIII narrower on average (mean AIII-I 67 vs. 77).

*S. latepunctata (*Fig. 13*):* lowland; no known site of local sympatry but together on upper and lower parts of Barva transect in Costa Rica; puncta on AIII more closely spaced; puncta on AIV more closely spaced and covering entire tergite.

*S. JTL017 (*Fig. 12*):* lowland; no known site of local sympatry but together on upper and lower parts of Barva transect in Costa Rica; occipital carina more developed, visible in face view; puncta on AIII smaller and nearly confluent; puncta on AIV smaller and more closely spaced; AIII narrower on average (mean AIII-I 97 vs. 109).

***Measurements, Worker.*** HW 0.66 (0.62–0.70), HL 0.83 (0.78–0.86), SL 0.51 (0.47–0.55), MSL 1.05 (0.98–1.09), AIIIW 0.51 (0.47–0.57), AIIIL 0.47 (0.42–0.50), AIVW 0.88 (0.79–0.96), AIVL 1.05 (0.93–1.13), SI 77 (74–81), AIII-I 109 (105–116), AIV-I 83 (80–85) (*n* = 6).

***Biology.*** This species occurs in montane wet forests in Costa Rica, from 1340 to 1590 m elevation. All collections, where known, are from Winkler samples of forest floor leaf litter and rotten wood. Only workers are known.

***Comments.*** *Syscia ticomontana* is on a very long branch in both UCE and COI trees (Figs. 6 and 7), suggesting strong heterochrony in this species. It is a morphologically distinctive cloud forest species that is much larger and darker than its relatives *S. minuta* and *S. pollula*. It is endemic to the mountains of Costa Rica, probably derived from an ancestor that was small and lowland, like *S. minuta* and *S. pollula*.

## *Syscia tolteca* (Forel, 1909)

Figure 12 (map, worker), S64 (lectotype worker), S65 (queen)

*Cerapachys toltecus* Forel, 1909: 247. Syntype workers: Guatemala ('received from Pergande') [MHNG, examined]. One worker here designated LECTOTYPE (specimen identifier CASENT0644430) to ensure nomenclatural stability. A pin at MCZC is labeled as cotype, with label 'Guatemala, Pergande coll'., and is presumably part of original syntype series.

*Syscia tolteca* Forel: Borowiec, 2016: 224.

***Geographic Range.*** Guatemala, Honduras.

***Diagnosis.*** Usually lowland; subpetiolar process triangular; AIII in dorsal view weakly trapezoidal, sides moderately convex and converging anteriorly; AIV in dorsal view with moderately convex sides, anterior margin not truncate; dorsal profile of AIII convex, of AIV weakly convex; puncta on AIII large, widely separated; puncta on AIV large, distinct, fading at midlength; standing pilosity of medium length and thickness; color red brown. Pairwise distances among five COI barcodes (GenBank accessions MT267649 - MT267650, BOLD Process IDs ASLAM2436-13, ASLAM1274-11, ASLAM1371-11) varied from 0 to 5.84%. The smallest interspecific distance was 1.97%.

Seven species are within size and geographic range of *S. tolteca*: *S. amblyogyna, S. honduriana*, *S. machaquila*, *S. parietalis*, *S. truncata*, *S.* JTL079, and *S.* JTL082.

*S. amblyogyna (*Fig. 12*):* montane; no known site of local sympatry, but occurs in nearby montane forest; sides of AIII and AIV in dorsal view more convex; AIII wider on average (mean AIII-I 111 vs. 100).

*S. honduriana (*Fig. 10*):* no known site of local sympatry, but adjacent ranges; puncta on AIV large, confluent, covering entire tergite; subpetiolar process with acute posterior tooth.

*S. machaquila (*Fig. 10*):* locally sympatric; smaller on average (mean HW 0.56 vs. 0.61); scapes shorter on average (mean SI 74 vs. 84).

*S. parietalis (*Fig. 11*):* montane; no known site of local sympatry; scapes shorter on average (mean SI 76 vs. 84).

*S. truncata (*Fig. 10*):* overlapping ranges, but no known site of local sympatry; subpetiolar process with acute posterior tooth; anterior margin of AIV strongly truncate; puncta on AIV small, dispersed, covering entire tergite.

*S. JTL079 (*Fig. 12*):* allopatric; puncta on AIV large, nearly confluent, covering entire tergite; AIII wider on average (mean AIII-I 118 vs. 100).

*S. JTL082 (*Fig. 10*):* montane; overlapping ranges but no known site of local sympatry; puncta on AIII and AIV smaller, less separated; AIII in dorsal view more trapezoidal, sides more converging anteriorly; smaller on average (mean HW 0.56 vs. 0.61); AIII wider on average (mean AIII-I 110 vs. 100).

***Measurements, Worker.*** HW 0.62 (0.58–0.65), HL 0.77 (0.72–0.82), SL 0.51 (0.49–0.54), MSL 1.00 (0.94–1.06), AIIIW 0.47 (0.44–0.53), AIIIL 0.47 (0.43–0.53), AIVW 0.74 (0.69–0.83), AIVL 0.87 (0.78–0.96), SI 83 (78–89), AIII-I 101 (97–109), AIV-I 85 (81–90) (*n* = 14).

***Measurements, Queen.*** HW 0.65, HL 0.80, SL 0.52, MSL 1.17, AIIIW 0.59, AIIIL 0.54, AIVW 0.89, AIVL 1.04, SI 80, AIII-I 110, AIV-I 86 (*n* = 1).

***Biology.*** This species occurs mostly in lowland moist to wet forest, but one collection is from 1550 m cloud forest. All material is from Winkler or Berlese samples of forest floor leaf litter and rotten wood. Dealate queens are known.

***Comments.*** The UCE tree shows *S. tolteca* sister to and well-separated from *S. lacandona* and *S. transisthmica* (Fig. 6), based on two specimens from one site in Guatemala. The COI tree shows the same relationship for three specimens from the same site (Fig. 7). Material from lowland Honduras is provisionally identified as *S. tolteca* but may be a separate species. COI data place Honduras specimens in a separate cluster (Fig. 7), and the puncta on AIV are denser compared to Guatemalan specimens. This material has not been sequenced for UCEs. An unsequenced series from a montane site in Honduras (Cusuco) is also placed in *S. tolteca*, based on morphological similarity, but the dorsal puncta on the mesosoma are somewhat smaller and more widely spaced. It is likely that this will ultimately prove to be a separate species, elevationally segregating from the lowland *S. tolteca*.

### *Syscia transisthmica*, New Species

Figure 12 (map, worker), S66 (holotype worker), S67 (queen)

***Holotype:*** 1 worker, MEXICO, *Oaxaca*: Mirador Grande, 17.89844 –96.36253 ±503m, 990m, 14-Aug-2009, montane tropical rainforest, ex sifted leaf litter (M. G. Branstetter, MGB1405) [UNAM, unique specimen identifier CASENT0644006]. PARATYPES: same data as holotype [queen, worker: CASC].

***Geographic Range.*** Mexico (Puebla) to Guatemala.

***Diagnosis.*** Lowland to lower montane; subpetiolar process subtriangular, posterior border flat to weakly convex; AIII in dorsal view moderately trapezoidal, with convex sides; AIV in dorsal view with moderately convex sides, anterior margin not truncate; dorsal profile of AIII and AIV convex; puncta on AIII large, widely separated; puncta on AIV distinct, somewhat lunate, widely spaced, fading at anterior third; standing pilosity long, coarse; color dark brown. Pairwise distances among five COI barcodes (GenBank accessions MT267651 - MT267655) varied from 1.16 to 4.45%. The smallest interspecific distance was 1.97%.

Six species are within size and geographic range of *S. transisthmica*: *S. atitlana*, *S. disjuncta*, *S. lacandona*, *S.* JTL049, *S.* JTL065, and *S.* JTL079.

*S. atitlana (*Fig. 12*):* locally sympatric; very similar; puncta on AIII more widely spaced; subpetiolar process deeper.

*S. disjuncta (*Fig. 11*):* montane; overlapping ranges but no known site of local sympatry, and collections of the two species are within 10 km of each other; puncta on AIII more closely spaced; puncta on AIV smaller and more restricted to anterior margin; scapes shorter on average (mean SI 67 vs. 87).

*S. lacandona (*Fig. 12*):* The two species are sympatric at Naha and Metzabok in eastern Chiapas. In this zone, *S. transisthmica* has more widely spaced puncta and is distinguishable from *S. lacandona*. All other specimens, including *S. transisthmica* north of the Isthmus of Tehuantepec, have more closely spaced puncta and are indistinguishable from *S. lacandona*.

*S. JTL049 (*Fig. 12*):* locally sympatric; puncta on AIII and AIV smaller, more closely spaced; AIV in dorsal view with anterior margin more truncate.

*S. JTL065 (*Fig. 12*):* overlapping ranges but no known site of local sympatry; very similar; subpetiolar process deeper; AIII wider on average (mean AIII-I 111 vs. 98).

*S. JTL079 (*Fig. 12*):* lowland; allopatric; puncta on AIII more closely spaced; puncta on AIV more closely spaced, covering entire tergite.

***Measurements, Worker.*** HW 0.68 (0.68-0.68), HL 0.83 (0.82–0.85), SL 0.59 (0.59-0.59), MSL 1.13 (1.12–1.14), AIIIW 0.53 (0.53–0.54), AIIIL 0.55 (0.54–0.55), AIVW 0.83 (0.82–0.84), AIVL 0.98 (0.97–0.99), SI 87 (86–87), AIII-I 98 (97–98), AIV-I 85 (84–86) ($n$ = 2).

***Measurements, Queen.*** HW 0.67, HL 0.81, SL 0.56, MSL 1.30, AIIIW 0.63, AIIIL 0.55, AIVW 1.02, AIVL 1.04, SI 84, AIII-I 116, AIV-I 98 ($n$ = 1).

***Biology.*** This species occurs in lowland to lower montane wet forest. All specimens are from Winkler samples of forest floor leaf litter and rotten wood. One dealate queen is known; the structure of the mesosoma suggests brachyptery.

***Comments.***The UCE tree shows a monophyletic *S. transisthmica*, sister to *S. lacandona* (Fig. 6). The COI tree shows a paraphyletic *S. transisthmica*, but the branches showing paraphyly are not well supported (Fig. 7).

### *Syscia truncata*, New Species

Figure 10 (map, worker), S68 (holotype worker)

***Holotype:*** 1 worker, HONDURAS, *Gracias a Dios*: Las Marias, 15.70854 –84.86252 ±20m, 80m, 9-Jun-2010, tropical rainforest, ex sifted leaf litter (LLAMA, Wa-C-07-2-34) [CASC, unique specimen identifier CASENT0644352]. PARATYPES: same data as holotype [worker: DZUP, JTLC, MCZC, UCD, USNM].

***Geographic Range.*** Guatemala, Honduras.

***Diagnosis.*** Lowland; subpetiolar process with acute posterior tooth; AIII trapezoidal, with straight sides; AIV with weakly convex, subparallel sides, anterior margin strongly truncate; dorsal profile of AIII and AIV weakly convex to flat; puncta on AIII small, closely spaced; puncta on AIV small, dispersed, covering entire tergite; standing pilosity of medium length and coarseness; color red brown. Pairwise distances among four COI barcodes from three specimens (GenBank accessions MT267656 and MT267657, BOLD Process IDs ASLAM1862-12 and ASLAM669-11) varied from 0 to 5.20%. The 5.1% distance was between two specimens from different sites in Honduras. The smallest interspecific distance was 10.82%.

Fifteen species are within size and geographic range of *S. truncata*, but the combination of (1) acute posterior tooth on the subpetiolar process, (2) strongly truncate anterior margin of AIV, and (3) uniformly punctate AIV eliminates most of them. Only the following species might be confused with *S. truncata*:

*S. brachyptera (*Fig. 9*):* sides of AIV more convex; generally more gracile, with longer scapes on average (mean SI 77 vs. 70), narrower AIII on average (mean AIII-I 103 vs. 111), and narrower AIV on average (mean AIV-I 82 vs. 88).

***Measurements, Worker.*** HW 0.55 (0.53–0.56), HL 0.65 (0.62–0.66), SL 0.38 (0.37–0.40), MSL 0.80 (0.75–0.83), AIIIW 0.50 (0.46–0.53), AIIIL 0.45 (0.42–0.47), AIVW 0.63 (0.61–0.65), AIVL 0.72 (0.65–0.76), SI 70 (68–71), AIII-I 111 (110–112), AIV-I 89 (86–93) ($n$ = 3).

***Biology.*** This species inhabits lowland moist to wet forest. All specimens are from Winkler samples of forest floor leaf litter and rotten wood. No sexuals are known.

### *Syscia valenzuelai*, New Species

Figure 9 (map, worker), S69 (holotype worker), S70 (queen), S71 (male)

***Holotype:*** 1 worker, MEXICO, *Veracruz*: Ruiz Cortínez, 12 km NE San Andrés Tuxtla, 18.53276 –95.14302 ±20m, 1120m, 3-Jun-2016, montane wet forest, ex sifted leaf litter (ADMAC, Wa-F-02-2-13) [UNAM, unique specimen identifier CASENT0644345]. PARATYPES: same data as holotype [queen: CASC; worker: CASC, DZUP, JTLC, MCZC, UCD, USNM].

***Geographic Range.*** Mexico (Veracruz) to Honduras.

***Diagnosis.*** Lowland; subpetiolar process variably shaped, in northernmost population, in the Sierra de Los Tuxtlas, nearly triangular, with the posterior tooth weak to absent, in other populations more trapezoidal, with a distinct posterior angle, but never developed as a tooth; sides of AIV relatively convex; puncta on AIV relatively large and well defined, fading at about midlength; color red brown. Pairwise distances among nine COI barcodes (GenBank accessions MT267658 - MT267663, BOLD Process IDs ASLAM1275-11, ASLAM1282-11, ASLAM2433-13) varied from 0 to 3.20%. One outlier sequence (BOLD Process ID ASLAM2449-13), discussed below, was 7–8% distant from the others. The smallest interspecific distance was 5.38%.

Fourteen species are within size and geographic range of *S. valenzuelai*: *S. boudinoti*, *S. brachyptera*, *S. disjuncta*, *S. honduriana*, *S. jennierussae*, *S. machaquila*, *S. persimilis*, *S. pervagata*, *S. peten*, *S. sumnichti*, *S. truncata*, *S.* JTL060, *S.* JTL071, and *S.* JTL082.

*S. boudinoti (*Fig. 8*):* no known site of local sympatry; dorsum of AIV flatter in profile; puncta on AIII and AIV smaller; erect pilosity shorter and finer.

*S. brachyptera (*Fig. 9*):* cloud forest; no known site of local sympatry; subpetiolar process with strong posterior tooth; dorsum of AIV flatter in profile; puncta on AIII and AIV smaller; side of AIV less convex, anterior margin more truncate; erect pilosity shorter and finer.

*S. disjuncta (*Fig. 11*):* allopatric; no known site of local sympatry; puncta on AIV smaller and fainter, fading at anterior third.

*S. honduriana (*Fig. 10*):* AIV with large confluent puncta over entire surface.

*S. jennierussae (*Fig. 10*):* not always distinguishable; sympatric in eastern Chiapas lowlands; scapes shorter on average (mean SI 67 vs. 72); AIII broader on average (mean AIII-I 110 vs. 107); in face view occipital carina less visible; sides of AIV slightly less convex and anterior margin more truncate.

*S. machaquila (*Fig. 10*):* not readily distinguishable, even though phylogenetically distant; sympatric in eastern Chiapas lowlands.

*S. persimilis (*Fig. 10*):* mostly cloud forest; no known site of local sympatry; subpetiolar process with strong posterior tooth; puncta on AIV fainter, fading at anterior third.

*S. pervagata (*Fig. 9*):* frequently sympatric; subpetiolar process with strong posterior tooth; in zones of sympatry, puncta on AIV more closely spaced, side of AIV less convex.

*S. peten (*Fig. 9*):* sympatric at Tikal National Park; subpetiolar process with strong posterior tooth; AIII broader on average (mean AIII-I 119 vs. 107).

*S. sumnichti (*Fig. 9*):* cloud forest; no known site of local sympatry; scapes longer on average (mean SI 79 vs. 72); AIII longer on average (AIII-I 101 vs. 107); erect pilosity shorter and finer; color lighter brown.

*S. truncata (*Fig. 10*):* no known site of local sympatry, but broadly overlapping ranges; anterior margin of AIV strongly truncate; puncta on AIV smaller.

*S. JTL060 (*Fig. 9*):* sympatric in Sierra de Los Tuxtlas, Veracruz, Mexico; AIII narrower on average, less distinctly trapezoidal (mean AIII-I 103 vs. 107); puncta on AIV fainter, fading at anterior third.

*S. JTL071 (*Fig. 9*):* allopatric; scapes shorter on average (mean SI 64 vs. 72); AIII broader on average (mean AIII-I 124 vs. 107); puncta on AIII larger and more widely spaced; puncta on AIV larger, more widely spaced, and restricted to anterior third.

*S. JTL082 (*Fig. 10*):* cloud forest; no known site of local sympatry; AIII in dorsal view with sides more strongly converging anteriorly; puncta on AIII and AIV smaller; dorsal profile of AIII and AIV flatter; scapes longer on average (mean SI 78 vs. 72).

***Measurements, Worker.*** HW 0.52 (0.51–0.54), HL 0.64 (0.61–0.66), SL 0.37 (0.36–0.38), MSL 0.78 (0.74–0.82), AIIIW 0.40 (0.38–0.41), AIIIL 0.37 (0.35–0.39), AIVW 0.62 (0.59–0.64), AIVL 0.72 (0.70–0.76), SI 72 (70–74), AIII-I 107 (102–111), AIV-I 86 (84–87) ($n$ = 6).

***Measurements, Queen.*** HW 0.53, HL 0.64, SL 0.36, MSL 0.90, AIIIW 0.40, AIIIL 0.38, AIVW 0.64, AIVL 0.80, SI 67, AIII-I 105, AIV-I 81 ($n$ = 1).

***Biology.*** This species occurs in lowland moist to wet forest, up to 1100 m in low cloud forest. All collections are from Winkler samples of forest floor litter and rotten wood. Dealate queens are known, and from the broad mesosoma and short pronotum, it is likely they were fully winged and not brachypterous. Two males were collected in one miniWinkler sample (see Comments); No other *Syscia* were in the sample.

***Comments.*** UCE and COI sequence data unite specimens from most of the known collection sites. Specimens north and south of the Isthmus of Tehuantepec form two clades, with about 3% COI distance between them.

COI data reveal the potential for a second species at Salto de Agua, a site in Chiapas, Mexico. One dealate queen was sequenced for UCEs and COI. This queen clusters with other material of *S. valenzuelai*. A second dealate queen was sequenced only for COI. This COI sequence does not cluster with other *S. valenzuelai*, and instead occurs as an isolated sequence in the clade that contains

*S. murillocruzae*, *S. parietalis*, and *S. valenzuelai* (Fig. 7). This second queen is more robust than the first one (HW 0.58 vs. 053). But in Veracruz, Mexico, in the Sierra de Los Tuxtlas, similar variation in queen size occurs, but they have similar COI haplotypes. Thus it is uncertain whether this Salto de Agua queen represents a separate species or is the result of a misleading COI sequence.

Two males were collected in a miniWinkler sample from Naha, Chiapas, Mexico, one of which was sequenced for COI. The sequence placed it in *S. valenzuelai*, even though no other specimens of *S. valenzuelai* were collected at the site. However, *S. valenzuelai* workers were collected at the nearby site of Metzabok, so its occurrence at Naha is expected.

## *Syscia volucris*, New Species

Figure 13 (map, worker), S72 (holotype worker), S73 (queen), S74 (brachypterous queen)

***Holotype***: 1 worker, NICARAGUA, *Región Autónoma del Atlántico Norte*: PN Cerro Saslaya, 13.76939 −84.98383 ±10m, 360m, 7-May-2011, mature wet forest, ex sifted leaf litter (LLAMA, Wa-D-02-1-02) [CASC, unique specimen identifier CASENT0644413]. PARATYPES: same data as holotype [worker: MCZC, UCD, USNM]; same data except 13.76943 −84.98382 (Wa-D-02-1-01) [worker: DZUP].

***Geographic Range.*** Honduras to Costa Rica.

***Diagnosis.*** Lowland; subpetiolar process a shallow lobe with sharp, recurved anterior tooth and smaller posterior tooth; AIII in dorsal view weakly trapezoidal with convex sides; AIV in dorsal view with convex sides, anterior margin not truncate; dorsal profile of AIII and AIV convex; puncta on AIII large, confluent; puncta on AIV large, closely spaced, covering entire tergite; standing pilosity long, coarse; color red brown. Pairwise distances among 14 COI barcodes (GenBank accessions MT267664 - MT267668, BOLD Process IDs not listed here) varied from 0 to 1.09%. The smallest interspecific distance was 1.09%.

Five species are within size and geographic range of *S. volucris*: *S. disjuncta*, *S. latepunctata*, *S. ticomontana*, *S.* JTL017, and *S.* JTL064.

*S. disjuncta (*Fig. 11), *S. ticomontana* (Fig. 12): montane; allopatric; puncta on AIV fading at anterior third to midlength.

*S. latepunctata (*Fig. 13*):* locally sympatric; extremely similar; subpetiolar process slightly shallower; AIV wider on average (mean AIII-I 98 vs. 88).

*S. JTL017 (*Fig. 12*):* locally sympatric; puncta on AIII and AIV smaller, more closely spaced; subpetiolar process deeper and with less distinct posterior tooth; AIV dorsal profile flat.

*S. JTL064 (*Fig. 13*):* lower montane; allopatric; puncta on AIV faint, lunate, fading at midlength.

***Measurements, Worker.*** HW 0.70 (0.62–0.76), HL 0.86 (0.78–0.91), SL 0.58 (0.50–0.64), MSL 1.18 (1.00–1.28), AIIIW 0.58 (0.47–0.63), AIIIL 0.56 (0.46–0.61), AIVW 0.90 (0.76–1.01), AIVL 1.02 (0.81–1.14), SI 83 (80–87), AIII-I 103 (99–106), AIV-I 88 (85–94) (*n* = 7).

***Measurements, Queen.*** HW 0.69 (0.64–0.75), HL 0.86 (0.79–0.93), SL 0.56 (0.52–0.60), MSL 1.35 (1.19–1.51), AIIIW 0.60 (0.55–0.65), AIIIL 0.58 (0.55–0.61), AIVW 0.92 (0.85–0.99), AIVL 1.08 (0.99–1.16), SI 82 (81–82), AIII-I 104 (100–108), AIV-I 85 (85-85) (*n* = 2).

***Biology.*** This is one of the more abundant species in lower Central America. It occurs in lowland to lower montane wet forest, from near sea level to 1180 m elevation. Most collections are from Winkler samples of forest floor leaf litter and rotten wood. It is one of the few species for which alate queens are known. Two alate queens are from Malaise trap samples. A series in the INBio collection has both workers and alate queens, all with the same label data, including a Parataxonomist collection code. Thus the collection may have been a colony. Two brachypterous queens are known, from two different sites. They are smaller and lighter colored than the alate queens. One of the brachypterous queens has minute wing remnants that are shorter than the width of the mesosoma.

At Saslaya National Park, Longino observed three workers on the forest floor, walking in a line, and one of the workers was carrying an ant larva. The larva had dorsal capitate tubercles like those seen on some Ponerinae (e.g., *Cryptopone*) and was presumably prey.

***Comments.*** Five specimens from five different sites were sequenced for UCE loci (Fig. 6). They form a clade with small genetic distances among them. The phylogeny of these five specimens is pectinate and geographically structured from south to north: Pacific slope of Talamanca range, Costa Rica (Barva transect, Costa Rica (Cerro Musun, Nicaragua (Cerro Saslaya, Nicaragua - La Mosquitia, Honduras))). COI sequence from these specimens and nine additional BOLD specimens are very tightly clustered and do not show geographic structure (Fig. 7).

## *Syscia* JTL003, Unnamed Morphospecies

Figure 13 (map, worker)

***Geographic Range.*** Costa Rica.

***Diagnosis.*** Montane; occipital carina strongly developed, visible in face view; subpetiolar process an asymmetrical triangular lobe; AIII in dorsal view trapezoidal, with weakly convex sides; AIV in dorsal view with convex sides, converging anteriorly, anterior margin not truncate; AIII and AIV dorsal profile convex; puncta on AIII large, widely spaced; puncta on AIV very small, widely spaced, fading at anterior third; standing pilosity abundant, long, coarse; color dark brown. Based on the COI barcode of the sequenced specimen (GenBank accession MT267567), the smallest pairwise interspecific distance was 13.39%.

No other species is within size and geographic range of *S.* JTL003.

***Measurements, Worker.*** HW 0.85, HL 0.98, SL 0.68, MSL 1.45, AIIIW 0.73, AIIIL 0.67, AIVW 1.07, AIIIL 1.48, SI 80, AIII-I 108, AIV-I 72 (*n* = 1).

***Comments.*** This species is known from one specimen from mature cloud forest habitat on the Caribbean slope of Costa Rica. The single specimen was in a Winkler sample from 1100 m elevation on the Barva transect, above La Selva Biological Station. In spite of intensive sampling of the Barva transect over multiple years, this remains the only known specimen. It is the largest of the known New World species. Phylogenetically, it is sister to *S. atitlana* and *S. setosa*, a pair of species that occur from Guatemala northward.

### *Syscia* JTL017, Unnamed Morphospecies

Figure 12 (map, worker)

***Geographic Range.*** Costa Rica.

***Diagnosis.*** Lowland; occipital carina strongly developed, easily visible in face view; subpetiolar process a shallow lobe with convex posterior margin; AIII in dorsal view weakly trapezoidal with weakly convex sides; AIV in dorsal view with convex sides, anterior margin not truncate; dorsal profile of AIII weakly convex, of AIV flat; puncta on AIII small, confluent; puncta on AIV small, confluent, covering most of tergite; standing pilosity long, coarse; color red brown. Based on the COI barcode of the sequenced specimen (GenBank accession MT267568), the smallest pairwise interspecific distance was 11.44%.

Four species are within size and geographic range of *S.* JTL017: *S. disjuncta*, *S. latepunctata*, *S. ticomontana*, and *S. volucris*.
*S. disjuncta (*Fig. 11*):* montane; allopatric; puncta on AIII and AIV larger, more widely separated; puncta on AIV fading at anterior third.
*S. latepunctata, S. volucris (*Fig. 13*):* locally sympatric; puncta on AIII and AIV larger, more widely separated; subpetiolar process shallower and with more distinct posterior tooth; AIV dorsal profile convex.

*S. ticomontana (*Fig. 12*):* montane; no known site of local sympatry but together on upper and lower parts of Barva transect in Costa Rica; puncta on AIII more widely spaced; puncta on AIV more widely spaced and fading at midlength.

***Measurements, Worker.*** HW 0.67 (0.66–0.68), HL 0.80 (0.80–0.81), SL 0.55 (0.53–0.56), MSL 1.02 (1.02–1.03), AIIIW 0.51 (0.50–0.51), AIIIL 0.52 (0.52–0.53), AIVW 0.77 (0.76–0.78), AIVL 0.91 (0.89–0.93), SI 82 (78–85), AIII-I 98 (95–100), AIV-I 84 (81–87) ($n$ = 2).

***Biology.*** The two known workers are from lowland rainforest, from Winkler samples of forest floor leaf litter and rotten wood.

### *Syscia* JTL018, Unnamed Morphospecies

Figure 10 (map, worker)

***Geographic Range.*** Costa Rica (Osa).

***Diagnosis.*** Lowland; subpetiolar process with convex posterior margin but no sharp angle or tooth; AIII in dorsal view trapezoidal with weakly convex sides; AIV in dorsal view with moderately convex sides and weakly truncate anterior margin; dorsal profiles of AIII and AIV weakly convex; puncta on AIV small, separated, fading at midlength; standing pilosity short, fine; color medium red brown. Based on the COI barcode of the sequenced specimen (GenBank accession MT267569), the smallest pairwise interspecific distance was 12.35%.

Four species are within size and geographic range of *S.* JTL018: *S. benevidesae*, *S. murillocruzae*, *S. pervagata*, and *S.* JTL074.
*S. benevidesae (*Fig. 11*):* Locally sympatric; puncta on AIII large, widely separated; AIV with large, somewhat lunate puncta restricted to anterior third; standing pilosity long, coarse.
*S. murillocruzae (*Fig. 10*):* Allopatric; scapes longer on average (mean SI 72 vs. 63); standing pilosity long, coarse; color darker red brown.
*S. pervagata (*Fig. 9*):* Allopatric; subpetiolar process with acute posterior tooth; standing pilosity long, coarse.*S.* JTL074 (Fig. 9): Allopatric; scapes longer on average (mean SI 77 vs. 63); AIII narrower on average (mean AIII-I 99 vs. 108).

***Measurements, Worker.*** HW 0.54, HL 0.63, SL 0.34, MSL 0.81, AIIIW 0.46, AIIIL 0.43, AIVW 0.64, AIIIL 0.74, SI 63, AIII-I 108, AIV-I 87 ($n$ = 1).

***Biology.*** The single series of this species was from lowland rainforest, from a Winkler sample of forest floor leaf litter and rotten wood.

### *Syscia* JTL033, Unnamed Morphospecies

Figure 13 (map, worker)

***Geographic Range.*** Guatemala.

***Diagnosis.*** Montane; occipital carina strongly developed, visible in face view; subpetiolar process a deep quadrate lobe; AIII trapezoidal in dorsal view, with weakly convex sides; AIV in dorsal view with convex sides and non-truncate anterior margin; dorsum of AIII and AIV weakly convex in lateral view; puncta on AIII shallow, of medium size and spacing; puncta on AIV small, widely spaced, fading at anterior third; standing pilosity long, coarse; color dark brown. Based on the COI barcode of the sequenced specimen (GenBank accession MT267570), the smallest pairwise interspecific distance was 8.20%.

Only the locally sympatric *S. grandis* is within size and geographic range of *S.* JTL033. *Syscia grandis* has a large, acute posterior tooth on the subpetiolar process, and AIII is narrower on average (mean AIII-I 98 vs. 107).

***Measurements, Worker.*** HW 0.77, HL 0.92, SL 0.65, MSL 1.28, AIIIW 0.60, AIIIL 0.56, AIVW 0.96, AIIIL 1.14, SI 85, AIII-I 107, AIV-I 84 ($n$ = 1).

### *Syscia* JTL037, Unnamed Morphospecies

Figure 8 (map, worker)

***Geographic Range.*** Costa Rica.

***Diagnosis.*** Lowland; subpetiolar process shallow, trapezoidal, with small anterior and posterior teeth; AIII trapezoidal in dorsal view, with flat sides; AIV in dorsal view with flat, nearly parallel sides and strongly truncate anterior margin; dorsum of AIII weakly convex in lateral view; dorsum of AIV flat in lateral view; puncta on AIII small, dense, confluent; puncta on AIV similarly small, dense, and cover the entire tergite; standing pilosity very short, sparse; color red brown. Based on the COI barcode of the sequenced specimen (GenBank accession MT267571), the smallest pairwise interspecific distance was 11.55%.

Three species are within size and geographic range of *S.* JTL037: *S. austrella* (Fig. 8), *S. pervagata* (Fig. 9), and *S.* JTL074 (Fig. 9). All of these species have more developed dorsal pilosity, variable punctation, sides of AIV more convex, anterior border of AIV less truncate, and subpetiolar process larger.

***Measurements, Worker.*** HW 0.48, HL 0.61, SL 0.31, MSL 0.77, AIIIW 0.39, AIIIL 0.39, AIVW 0.57, AIIIL 0.73, SI 65, AIII-I 99, AIV-I 79 ($n$ = 1).

***Biology.*** The one specimen is from lowland rainforest, from a Winkler sample of sifted litter and rotten wood.

## *Syscia* JTL049, Unnamed Morphospecies

Figure 12 (map, worker)

***Geographic Range.*** Mexico (Oaxaca, Veracruz).

***Diagnosis.*** Montane; subpetiolar process a deep lobe, posterior margin convex; AIII in dorsal view trapezoidal, sides convex; AIV in dorsal view with sides convex, anterior margin moderately truncate; dorsal profile of AIII weakly convex, of AIV moderately convex; puncta on AIII small, faint, closely spaced; puncta on AIV small, closely spaced, fading at midlength; standing pilosity of medium length and thickness; color red brown. Based on the COI barcode of the sequenced specimen (GenBank accession MT267572), the smallest pairwise interspecific distance was 13.32%.

Four species are within size and geographic range of *S.* JTL049: *S. disjuncta*, *S. setosa*, *S. transisthmica*, and *S.* JTL075.

*S. disjuncta (*Fig. 11*):* with adjacent ranges but no known site of local sympatry; puncta on AIII larger and more widely spaced; AIV with anterior margin less truncate; larger on average (mean HW 0.68 vs. 0.63).

*S. setosa (*Fig. 11*):* locally sympatric; AIII in dorsal view less trapezoidal; puncta on AIII larger and more widely spaced.

*S. transisthmica (*Fig. 12*):* locally sympatric; puncta on AIII and AIV larger, more widely spaced; AIV in dorsal view with anterior margin not truncate.

*S. JTL075 (*Fig. 11*):* puncta on AIII and AIV much larger; underlying pubescence weaker; scapes longer on average (mean SI 82 vs. 65). The one collection of *S.* JTL075 is from a site about 30 km from a collection of *S.* JTL049, and from similar habitat and elevation, so the species are potentially locally sympatric.

***Measurements, Worker.*** HW 0.63, HL 0.74, SL 0.41, MSL 1.02, AIIIW 0.55, AIIIL 0.49, AIVW 0.79, AIIIL 0.88, SI 65, AIII-I 111, AIV-I 90 ($n$ = 1).

## *Syscia* JTL050, Unnamed Morphospecies

Figure 10 (map, worker)

***Geographic Range.*** Cuba, Dominican Republic.

***Diagnosis.*** Subpetiolar process very shallow, posterior margin flat to concave; AIII in dorsal view trapezoidal, sides weakly convex; AIV in dorsal view with sides weakly convex, anterior margin weakly truncate; dorsal profile of AIII weakly convex, of AIV nearly flat; puncta on AIII small, faint; puncta on AIV small, separated, fading at midlength; standing pilosity of medium length and thickness; color red brown. Based on the COI barcode of the sequenced specimen (GenBank accession MT267573), the smallest pairwise interspecific distance was 13.82%.

***Measurements, Worker.*** HW 0.56 (0.55–0.56), HL 0.66 (0.65–0.67), SL 0.36 (0.36-0.36), MSL 0.83 (0.80–0.86), AIIIW 0.45 (0.43–0.46), AIIIL 0.41 (0.38–0.44), AIVW 0.63 (0.60–0.67), AIVL 0.72 (0.71–0.73), SI 65 (64–65), AIII-I 109 (105–113), AIV-I 88 (84–91) ($n$ = 2).

***Comments.*** So far just two specimens, both workers, are known from the Caribbean. One is a worker collected by P. S. Ward in Cuba. That specimen was non-destructively sequenced and has been placed in the phylogeny. One was collected by G. Alpert in the Dominican Republic, and images are available at www.antwiki.org/wiki/Dominican_Republic_species_and_images#Syscia. Based on the images, the specimen is superficially similar to the Cuban specimen, but has less standing pilosity. It is placed here based on geographic proximity and approximate similarity, but its placement in the phylogeny and genetic distance from other populations remains unknown.

## *Syscia* JTL060, Unnamed Morphospecies

Figure 9 (map, worker)

***Geographic Range.*** Mexico (Veracruz: Sierra de Los Tuxtlas).

***Diagnosis.*** Cloud forest; subpetiolar process triangular; AIII weakly trapezoidal; sides of AIV convex; puncta on AIV faint, lunate, fading at anterior third; standing pilosity long, coarse; color red brown. Based on the COI barcode of the sequenced specimen (GenBank accession MT267574), the smallest pairwise interspecific distance was 11.81%.

Four species are within size and geographic range of *S.* JTL060: *S. disjuncta*, *S. valenzuelai*, *S.* JTL071, *S.* JTL084.

*S. disjuncta (*Fig. 11*):* allopatric; no known site of local sympatry; subpetiolar process more rounded, not sharply triangular; sides of AIV less convex.

*S. valenzuelai (*Fig. 9*):* locally sympatric; AIII more trapezoidal, with flatter, more posteriorly divergent sides; sides of AIV less convex; puncta on AIV more distinct, extending to midlength.

*S. JTL071 (*Fig. 9*):* allopatric; scapes shorter on average (mean SI 64 vs. 74); AIII broader on average (mean AIII-I 124 vs. 103).

*S. JTL084 (*Fig. 10*):* allopatric; AIII more trapezoidal, with flatter, more posteriorly divergent sides; sides of AIV less convex; puncta on AIV more distinct, extending to midlength.

***Measurements, Worker.*** HW 0.53 (0.53–0.54), HL 0.63 (0.62–0.65), SL 0.39 (0.39–0.40), MSL 0.80 (0.78–0.82), AIIIW 0.36 (0.34–0.37), AIIIL 0.35 (0.33–0.36), AIVW 0.62 (0.60–0.64), AIVL 0.70 (0.66–0.74), SI 74 (74-74), AIII-I 103 (102–103), AIV-I 89 (87–91) ($n$ = 2).

***Comments.*** This species is known from two specimens, from separate miniWinkler samples at a cloud forest site in Mexico, Veracruz, Sierra de Los Tuxtlas. It is phylogenetically somewhat isolated, being the monotypic sister taxon to a widespread clade of 12 species (Fig. 6).

## *Syscia* JTL064, Unnamed Morphospecies

Figure 13 (map, worker)

***Geographic Range.*** Costa Rica.

***Diagnosis.*** Occipital carina developed, visible in face view; subpetiolar process a broad shallow lobe with anterior and posterior teeth; AIII in dorsal view trapezoidal, with weakly convex sides; AIV in dorsal view with sides weakly convex, anterior margin not truncate; puncta on AIII somewhat lunate, of medium size and spacing; puncta on AIV separate, lunate, fading at midlength;

standing pilosity long, coarse, underlying pubescence absent; color dark brown. Based on the COI barcode of the sequenced specimen (GenBank accession MT267575), the smallest pairwise interspecific distance was 9.93%.

Three species are within size and geographic range of *S.* JTL064: *S. disjuncta*, *S. latepunctata*, and *S. volucris*.

*S. disjuncta (*Fig. 11*):* allopatric, subpetiolar process more triangular, lacking posterior tooth; scapes shorter on average (mean SI 67 vs. 89); AIII wider on average (mean AIII-I 109 vs. 99).

*S. latepunctata, S. volucris (*Fig. 13*):* allopatric; puncta on AIV distinct, closely spaced, covering entire tergite.

***Measurements, Worker.*** HW 0.76, HL 0.93, SL 0.68, MSL 1.22, AIIIW 0.58, AIIIL 0.58, AIVW 0.89, AIIIL 1.03, SI 89, AIII-I 99, AIV-I 86 ($n$ = 1).

***Comments.*** This species is known from one specimen from a 1,070 m elevation site on the Pacific slope of Costa Rica. It was collected in wet forest habitat, in a Winkler sample.

### *Syscia* JTL065, Unnamed Morphospecies

Figure 12 (map, worker)

***Geographic Range.*** Mexico (Chiapas).

***Diagnosis.*** Montane; subpetiolar process triangular with convex posterior margin; AIII in dorsal view trapezoidal, with convex sides; AIV in dorsal view with sides convex, anterior margin not truncate; puncta on AIII large, separate; puncta on AIV separate, somewhat lunate, fading at midlength; standing pilosity long, coarse, underlying pubescence absent; color dark brown. Based on the COI barcode of the sequenced specimen (GenBank accession MT267576), the smallest pairwise interspecific distance was 7.10%.

Eight species are within size and geographic range of *S.* JTL065: *S. atitlana*, *S. chiapaneca*, *S. lacandona*, *S. setosa*, *S. transisthmica*, *S.* JTL066, *S.* JTL073, and *S.* JTL079.

*S. atitlana (*Fig. 12*):* allopatric, but adjacent ranges; AIII and AIV in dorsal view with sides less convex; puncta on AIII more widely spaced.

*S. chiapaneca (*Fig. 11*):* allopatric; AIII and AIV in dorsal view with sides less convex; puncta on AIII smaller; subpetiolar process shallower; color lighter brown.

*S. lacandona (*Fig. 12*):* lowland; overlapping ranges but no known site of local sympatry; AIII in dorsal view with less convex sides; AIV in dorsal view with less convex sides, sides less convergent anteriorly.

*S. setosa (*Fig. 11*):* lowland; allopatric but adjacent ranges; AIII in dorsal view with similarly convex sides, but puncta less dense, more widely spaced; AIV in dorsal view with sides less convex, less converging anteriorly; standing pilosity longer.

*S. transisthmica (*Fig. 12*):* Overlapping ranges but no known site of local sympatry; very similar; subpetiolar process shallower; AIII narrower on average (mean AIII-I 98 vs. 111).

*S. JTL066 (*Fig. 11*):* lowland; allopatric, but adjacent ranges; sides of AIII and AIV in dorsal view less convex; puncta on AIII smaller, more closely spaced; smaller on average (mean HW 0.58 vs. 0.64).

*S. JTL073 (*Fig. 11*):* adjacent ranges; very similar; smaller on average (mean HW 0.60 vs. 0.64); AIV wider on average (mean AIV-I 101 vs. 89); color lighter brown.

*S. JTL079 (*Fig. 12*):* no known site of local sympatry, but collection sites within 50 km of each other; subpetiolar process with posterior angle; puncta on AIV large, nearly confluent, covering entire tergite.

***Measurements, Worker.*** HW 0.64, HL 0.79, SL 0.52, MSL 1.06, AIIIW 0.54, AIIIL 0.49, AIVW 0.83, AIIIL 0.93, SI 81, AIII-I 111, AIV-I 89 ($n$ = 1).

***Comments.*** This species is known from one specimen from Lagos de Montebello, Chiapas, a montane wet forest site. It was collected in a litter sample.

### *Syscia* JTL066, unnamed morphospecies

Figure 11 (map, worker)

***Geographic Range.*** Mexico (Chiapas), Guatemala.

***Diagnosis.*** Lowland; subpetiolar process broad, posterior margin with small tooth; AIII in dorsal view trapezoidal, with weakly convex sides; AIV in dorsal view moderately convex; dorsal profile of AIII and AIV moderately convex; puncta on AIV small, separated, fading midlength; occipital carina visible in face view; standing pilosity of medium length, coarseness; color red brown. Based on the COI barcode of the sequenced specimen (GenBank accession MT267577), the smallest pairwise interspecific distance was 6.61%.

Sixteen species are within size and geographic range of *S.* JTL066*: S. atitlana, S. boudinoti, S. chiapaneca, S. jennierussae, S. lacandona, S. machaquila, S. parietalis, S. persimilis, S. setosa, S. sumnichti, S. tolteca, S. truncata, S. valenzuelai, S.* JTL065*, S.* JTL073*, and S.* JTL085.

*S. atitlana (*Fig. 12*):* lowland; allopatric; puncta on AIII and AIV larger; posterior margin of subpetiolar process weakly convex, without a small tooth.

*S. boudinoti (*Fig. 8*):* allopatric; occipital carina short, hardly visible in face view; subpetiolar process triangular, with slightly convex posterior margin.

*S. chiapaneca (*Fig. 11*):* cloud forest; allopatric; subpetiolar process shallower, lacking posterior tooth; occipital carina less visible in face view.

*S. jennierussae (*Fig. 10*):* locally sympatric; occipital carina smaller, less visible in face view; subpetiolar process relatively more triangular, with reduced posterior angle or tooth; smaller on average (mean HW 0.53 vs. 0.58); scapes shorter on average (mean SI 67 vs. 75).

*S. lacandona (*Fig. 12*):* locally sympatric; subpetiolar process relatively more triangular, with reduced posterior angle or tooth; puncta on AIII larger, with wider interspaces; scapes longer on average (mean SI 81 vs. 75).

*S. machaquila (*Fig. 10*):* overlapping ranges but no known site of local sympatry; subpetiolar process narrower, tooth on posterior margin reduced or absent; puncta on AIII larger and more widely spaced; occipital carina less pronounced in face view.

*S. parietalis* (Fig. 11)*:* allopatric, cloud forest; occipital carina less visible in face view; puncta on AIV larger.

*S. persimilis* (Fig. 10)*:* cloud forest; no known site of local sympatry; puncta on AIV larger, more widely spaced; tooth on posterior margin of subpetiolar process larger, acute.

*S. setosa* (Fig. 11)*:* allopatric, but adjacent ranges; AIII in dorsal view with more convex sides; puncta on AIII larger, more widely spaced; puncta on AIV larger, fading at anterior third; dorsal surfaces lacking underlying pubescence; occipital carina less visible in face view.

*S. sumnichti* (Fig. 9)*:* cloud forest; no known site of local sympatry; smaller on average (mean HW 0.53 vs. 0.58); AIV narrower on average (mean AIV-I 79 vs. 86); color lighter brown.

*S. tolteca* (Fig. 12)*:* allopatric, but adjacent ranges; puncta on AIV larger; posterior margin of subpetiolar process lacking tooth; scapes longer on average (mean SI 84 vs. 75).

*S. truncata* (Fig. 10)*:* allopatric; puncta cover entire surface of AIV; tooth on posterior margin of subpetiolar process larger, acute.

*S. valenzuelai* (Fig. 9)*:* locally sympatric; occipital carina less visible in face view; sides of AIII in dorsal view flatter; puncta on AIV larger; smaller on average (mean HW 0.52 vs. 0.58).

*S. JTL065* (Fig. 12)*:* cloud forest; allopatric, but adjacent ranges; sides of AIII and AIV in dorsal view more convex; puncta on AIII larger, more widely separated; larger on average (mean HW 0.64 vs. 0.58).

*S. JTL073* (Fig. 11)*:* cloud forest; allopatric, but adjacent ranges; sides of AIII and AIV in dorsal view more convex; puncta on AIII larger, more widely separated; occipital carina less visible in face view; standing pilosity longer, coarser.

*S. JTL085* (Fig. 9)*:* cloud forest; no known sites of local sympatry, but found nearby at higher elevation; subpetiolar process with less developed posterior tooth; smaller on average (mean HW 0.53 vs. 0.58).

***Measurements, Worker.*** HW 0.58 (0.58-0.58), HL 0.74 (0.74-0.74), SL 0.44 (0.43–0.45), MSL 0.94 (0.94-0.94), AIIIW 0.48 (0.47–0.49), AIIIL 0.46 (0.45–0.47), AIVW 0.72 (0.71–0.72), AIVL 0.84 (0.84-0.84), SI 76 (75–77), AIII-I 106 (105–106), AIV-I 86 (85–86) ($n$ = 2).

***Biology.*** The two known workers are from lowland moist to wet forest, in Winkler samples of forest floor leaf litter and rotten wood.

## *Syscia* JTL067, Unnamed Morphospecies

Figure 8 (map, worker)

***Geographic Range.*** Mexico (Tamaulipas).

***Diagnosis.*** Cloud forest; subpetiolar process shallow, with short anterior point and convex posterior margin; AIII trapezoidal in dorsal view with slightly convex sides; AIV in dorsal view with straight sides and truncate anterior margin; dorsa of AIII and AIV flat in lateral view; standing pilosity short, sparse; color light brown. Based on the COI barcode of the sequenced specimen (GenBank accession MT267578), the smallest pairwise interspecific distance was 14.21%.

One species, *S.* JTL069, is within the size and geographic range of *S.* JTL067. These two are sympatric at a cloud forest site in Tamaulipas state, Mexico. *Syscia* JTL069 is a slightly more robust version of *S.* JTL067, with broader AIII (AIII-I 114 vs. 101) and AIV on average (AIV-I 79 vs. 71). On *S.* JTL069 the puncta on dorsal AIV are coarser anteriorly and more rapidly fade posteriorly.

***Measurements, Worker.*** HW 0.42, HL 0.56, SL 0.28, MSL 0.70, AIIIW 0.35, AIIIL 0.35, AIVW 0.45, AIIIL 0.64, SI 68, AIII-I 101, AIV-I 71 ($n$ = 1).

## *Syscia* JTL068, Unnamed Morphospecies

Figure 8, S75 (queen)

***Geographic Range.*** Honduras.

***Diagnosis.*** One species, *S. pollula* (Fig. 8), is within size and geographic range of *S.* JTL068. *Syscia* JTL068 is known from one queen from the La Moskitia area of Honduras, and *S. pollula* is known from Nicaragua to Panama. *Syscia* JTL068 has the sides of AIV less convex and the anterior border more truncate than in *S. pollula*. Based on the COI barcode of the sequenced specimen (GenBank accession MT267579), the smallest pairwise interspecific distance was 13.59%.

***Measurements, Queen.*** HW 0.46, HL 0.56, SL 0.29, MSL 0.84, AIIIW 0.40, AIIIL 0.33, AIVW 0.54, AIVL 0.69, SI 64, AIII-I 121, AIV-I 78 ($n$ = 1).

***Biology.*** The single specimen was from a Winkler sample from lowland rainforest.

## *Syscia* JTL069, Unnamed Morphospecies

Figure 8 (map, worker)

***Geographic Range.*** Mexico (Tamaulipas, Oaxaca).

***Diagnosis.*** Cloud forest; subpetiolar process deep, triangular; AIII in dorsal view trapezoidal, with weakly convex sides; sides of AIV in dorsal view weakly convex and the anterior margin somewhat truncate; dorsa of AIII and AIV in lateral view nearly flat; puncta on AIV discrete, large, separated, fading at midlength; standing pilosity short, sparse; color red brown. Pairwise distance between two COI barcodes (GenBank accessions MT267580 and MT267581) was 2.90%. The smallest interspecific distance was 13.36%.

One species, *S.* JTL067, is within size and geographic range of *S.* JTL069. These two are sympatric at a cloud forest site in Tamaulipas state, Mexico. *Syscia* JTL069 is a slightly more robust version of *S.* JTL067, with broader AIII (AIII-I 114 vs. 101) and AIV on average (AIV-I 79 vs. 71). On *S.* JTL069 the puncta on dorsal AIV are coarser anteriorly and more rapidly fade posteriorly.

***Measurements, Worker.*** HW 0.45, HL 0.57, SL 0.30, MSL 0.71, AIIIW 0.38, AIIIL 0.33, AIVW 0.51, AIIIL 0.65, SI 68, AIII-I 114, AIV-I 79 ($n$ = 1).

## *Syscia* JTL071, Unnamed Morphospecies

Figure 9 (map, worker)

***Geographic Range.*** Mexico (San Luis Potosí).

***Diagnosis.*** Subpetiolar process asymmetrically triangular; AIII in dorsal view subquadrate, weakly diverging posteriorly, with moderately convex sides; AIV in dorsal view with weakly convex, subparallel sides; puncta on AIII large and widely spaced; puncta on AIV large, lunate, restricted to strip on anterior third; dorsal profiles of AIII and AIV convex; standing pilosity long, abundant, coarse; color red brown.

Three species are within size and geographic range of *Syscia* JTL071: *S. disjuncta*, *S. valenzuelai*, and *S.* JTL060.

*S. disjuncta (*Fig. 11*):* smaller, more closely spaced puncta on AIII and AIV.

*S. valenzuelai (*Fig. 9*):* more extensive puncta on AIV, extending to midlength; sides of AIII flat, less convex.

*S. JTL060 (*Fig. 9*):* puncta on anterior AIV much smaller.

***Measurements, Worker.*** HW 0.52, HL 0.61, SL 0.33, MSL 0.75, AIIIW 0.39, AIIIL 0.31, AIVW 0.55, AIIIL 0.63, SI 64, AIII-I 124, AIV-I 88 (*n* = 1).

***Biology.*** The single specimen was from 'coffee plantation, ex log litter'.

## *Syscia* JTL073, Unnamed Morphospecies

Figure 11 (map, worker), S76 (queen)

***Geographic Range.*** Mexico (Chiapas).

***Diagnosis.*** montane; subpetiolar process a rounded asymmetrical lobe; AIII in dorsal view weakly trapezoidal with convex sides; AIV in dorsal view with strongly convex sides that narrow to a non-truncate anterior margin; dorsal profiles of AIII and AIV convex; puncta on AIII large and widely separated; puncta on AIV large, widely spaced, lunate, fading at anterior third; standing pilosity abundant, long, coarse; color red brown.

Eight other species are within size and geographic range of *S.* JTL073: *S. atitlana*, *S. chiapaneca*, *S. lacandona*, *S. machaquila*, *S. persimilis*, *S. setosa*, *S.* JTL065, and *S.* JTL066. The following species have AIII in dorsal view distinctly trapezoidal, with flatter sides, and with smaller and more closely spaced puncta: *S. chiapaneca*, *S. machaquila*, *S. persimilis*, and *S.* JTL066. Four species have AIII similar to *S.* JTL073: *S. atitlana*, *S. lacandona*, *S. setosa*, and *S.* JTL065.

*S. atitlana (*Fig. 12*):* allopatric, but adjacent ranges; very similar; AIII and AIV in dorsal view with sides less convex; AIV narrower on average (mean AIV-I 86 vs. 101).

*S. lacandona (*Fig. 12*):* occurs in nearby lowlands, but no known site of local sympatry; occipital carina more visible in face view; AIII narrower on average (mean AIII-I 105 vs. 113); AIV narrower on average (mean AIV-I 85 vs. 101).

*S. setosa (*Fig. 11*):* lowland; allopatric but adjacent ranges; very similar; AIV in dorsal view with sides less convex, less converging anteriorly; scapes shorter on average (mean SI 70 vs. 78); AIV narrower on average (mean AIV-I 89 vs. 101).

*S. JTL065 (*Fig. 12*):* adjacent ranges; very similar; larger on average (mean HW 0.64 vs. 0.60); AIV narrower on average (mean AIV-I 89 vs. 101); color darker brown.

***Measurements, Worker.*** HW 0.60, HL 0.71, SL 0.47, MSL 0.90, AIIIW 0.44, AIIIL 0.39, AIVW 0.73, AIIIL 0.73, SI 78, AIII-I 113, AIV-I 101 (*n* = 1).

***Measurements, Queen.*** HW 0.62, HL 0.73, SL 0.47, MSL 1.18, AIIIW 0.51, AIIIL 0.45, AIVW 0.84, AIVL 0.87, SI 76, AIII-I 112, AIV-I 96 (*n* = 1).

***Biology.*** This species is known from one series of workers and dealate queens, from forest floor leaf litter.

## *Syscia* JTL074, Unnamed Morphospecies

(Figure 9)

***Geographic Range.*** Panama.

***Diagnosis.*** Lowland; known from one collection from Barro Colorado Island, Panama; subpetiolar process not visible on available specimens; AIII in dorsal view weakly trapezoidal with weakly convex sides; AIV in dorsal view with weakly convex sides that narrow to a non-truncate anterior margin; dorsum of AIII convex in lateral view; dorsum of AIV nearly flat in lateral view; puncta on AIV discrete, large, separated, fading at midlength; standing pilosity short, fine; color red brown.

Four other species are within size and geographic range of *S.* JTL071: *S. austrella*, *S. murillocruzae*, *S. pervagata*, and *S.* JTL018.

*S. austrella* (Fig. 8): parapatric, with adjacent ranges in Panama; coarser dorsal pilosity; more convex sides of AIV; more convex dorsal profile of the petiole and AIV.

*S. murillocruzae (*Fig. 10*):* known mainly from Costa Rica, but a dealate queen from Barro Colorado Island is tentatively identified as *S. murillocruzae*; broader AIII on average (mean AIII-I 109 vs. 99); larger puncta on AIV; sides of AIV less converging anteriorly.

*S. pervagata (*Fig. 9*):* parapatric, Costa Rica northward; coarser dorsal pilosity; larger puncta on AIV; more convex dorsal profile of AIV.

*S. JTL018 (*Fig. 10*):* broader AIII on average (AIII-I 108 vs. 99); AIV with less tapering sides; anterior border of AIV relatively broader, more truncate.

***Measurements, Worker.*** HW 0.51, HL 0.66, SL 0.39, MSL 0.85, AIIIW 0.38, AIIIL 0.38, AIVW 0.61, AIIIL 0.72, SI 77, AIII-I 99, AIV-I 84 (*n* = 1).

***Biology.*** This species is known from lowland wet forest.

## *Syscia* JTL075, Unnamed Morphospecies

Figure 11 (map, worker)

***Geographic Range.*** Mexico (Oaxaca).

***Diagnosis.*** montane; subpetiolar process asymmetrically triangular, with weak notch on posterior margin; AIII in dorsal view subquadrate, with weakly convex sides that slightly converge anteriorly; AIV in dorsal view with convex sides that narrow to a non-truncate anterior margin; dorsum of AIII and AIV convex in lateral view; puncta on AIII large, nearly confluent; puncta on AIV discrete, separated, fading at anterior third; standing pilosity of medium length, thickness; color red brown.

Two other species are within size and geographic range of *S.* JTL075: *S. setosa* and *S.* JTL049.

*S. setosa (*Fig. 11*):* allopatric; lowland; puncta on AIII large and widely separated; standing pilosity long, coarse, no underlying pubescence.

*S. JTL049 (*Fig. 12*):* puncta on AIII and AIV much smaller; underlying pubescence denser; scapes shorter on average (mean SI 65 vs. 82). The one collection of *S.* JTL075 is from a site about 30 km from a collection of *S.* JTL049, and from similar habitat and elevation, so the species are potentially locally sympatric.

***Measurements, Worker.*** HW 0.60, HL 0.79, SL 0.49, MSL 1.04, AIIIW 0.47, AIIIL 0.45, AIVW 0.80, AIIIL 0.86, SI 82, AIII-I 103, AIV-I 93 (*n* = 1).

***Biology.*** This species is known from one cloud forest site, from a Berlese sample of forest floor leaf litter and rotten wood.

## *Syscia* JTL076, Unnamed Morphospecies

Figure 13, S77 (queen)

***Geographic Range.*** Guatemala.

***Diagnosis.*** Lowland; subpetiolar process subquadrate; AIII in dorsal view trapezoidal with moderately convex sides; AIV in dorsal view with shallowly convex sides that narrow to a weakly truncate anterior margin; dorsum of AIII weakly convex in lateral view; dorsum of AIV nearly flat in lateral view; puncta on AIII of medium size with narrow interspaces; puncta on AIV of medium size, widely separated, fading at midlength; standing pilosity of medium length and coarseness; color dark brown.

Two species are within size and geographic range of *S.* JTL076: *S. amblyogyna* and *S.* JTL079.

*S. amblyogyna (*Fig. 12*):* montane; allopatric; AIII in dorsal view less trapezoidal, with more convex sides; AIV in dorsal view with more convex sides, anterior margin less truncate.

*S. JTL079 (*Fig. 12*)*: allopatric; AIII in dorsal view with sides more convergent anteriorly; puncta on AIII more closely spaced; puncta on AIV more closely spaced, covering entire tergite.

***Measurements, Queen.*** HW 0.71, HL 0.84, SL 0.57, MSL 1.31, AIIIW 0.67, AIIIL 0.60, AIVW 0.96, AIVL 1.10, SI 80, AIII-I 111, AIV-I 87 (*n* = 1).

***Biology.*** The single specimen is from tropical moist forest, from a Winkler sample of sifted leaf litter.

## *Syscia* JTL079, Unnamed Morphospecies

Figure 12 (map, worker)

***Geographic Range.*** Guatemala.

***Diagnosis.*** Lowland; subpetiolar process asymmetrically triangular with small, obtuse tooth on posterior margin; AIII trapezoidal with convex sides; sides of AIV moderately convex, converging anteriorly, anterior margin weakly truncate; dorsal profile of AIII convex; dorsal profile of AIV flat in center; puncta on AIII and AIV large, nearly confluent, those on AIV covering entire tergite; standing pilosity long, coarse; color dark brown.

Five species are within size and geographic range of *S.* JTL079: *S. amblyogyna*, *S. atitlana*, *S. tolteca*, *S. transisthmica*, and *S.* JTL076.

*S. amblyogyna, S. transisthmica (*Fig. 12*):* montane; allopatric; puncta on AIII more widely spaced; puncta on AIV more widely spaced, fading at midlength.

*S. atitlana (*Fig. 12*):* sympatric; puncta on AIV widely spaced, fading at midlength; posterior margin of subpetiolar process weakly convex, without a tooth.

*S. tolteca (*Fig. 12*):* allopatric; puncta on AIV smaller, more widely spaced, fading at midlength; AIII narrower on average (mean AIII-I 100 vs. 118).

*S. JTL076 (*Fig. 13*):* allopatric; AIII in dorsal view with sides less convergent anteriorly; puncta on AIII more widely spaced; puncta on AIV more widely spaced, fading at midlength.

***Measurements, Worker.*** HW 0.67, HL 0.86, SL 0.57, MSL 1.14, AIIIW 0.62, AIIIL 0.53, AIVW 0.86, AIIIL 1.00, SI 85, AIII-I 118, AIV-I 86 (*n* = 1).

***Comments.*** This species is based on a single specimen from Guatemala, from a litter sample. It is very similar to *S. volucris*, a species from eastern Honduras south to Costa Rica. The single specimen has the sides of AIV less convex and the anterior margin more truncate than *S. volucris*. The specimen has not been sequenced, so its placement in the phylogeny is unknown.

## *Syscia* JTL082, Unnamed Morphospecies

Figure 10 (map, worker)

***Geographic Range.*** Honduras.

***Diagnosis.*** Cloud forest; subpetiolar process large, subtriangular, with weak convexity on posterior margin; AIII strongly trapezoidal; sides of AIV nearly flat, strongly converging anteriorly; puncta on AIV small, separate, fading at anterior third; standing pilosity short, fine; color red brown. Four COI barcodes (GenBank accession MT267582, BOLD Process IDs GMHKO114-15, GMHKP128-15, ASLAM1135-11) were identical to each other. One sequence (BOLD Process ID ASLAM1157-11) was 9.40–11.38% distant, probably due to poor sequence quality (only 266 bp). The smallest interspecific distance was 8.20%.

Ten species are within size and geographic range of *S.* JTL082: *S. boudinoti, S. brachyptera, S. honduriana, S. persimilis, S. parietalis, S. pervagata, S. sumnichti, S. tolteca, S. truncata*, and *S. valenzuelai.*

*S. boudinoti (*Fig. 8*):* lowland; no known site of local sympatry; smaller on average (mean HW 0.52 vs. 0.56); sides of AIV less convex.

*S. brachyptera (*Fig. 9*)*, *S. honduriana* (Fig. 10), *S. persimilis* (Fig. 10), *S. pervagata* (Fig. 9), *S. truncata* (Fig. 10): subpetiolar process with acute posterior tooth.

*S. parietalis (*Fig. 11*):* locally sympatric; subpetiolar process with small tooth on posterior margin; puncta on face, AIII, AIV larger; dorsal profile AIII more convex; AIII narrower on average (mean AIII-I 103 vs. 110); AIV narrower on average (mean AIV-I 80 vs. 87).

*S. sumnichti (*Fig. 9*):* no known site of local sympatry; AIII narrower on average (mean AIII-I 101 vs. 110); AIV narrower on average (mean AIV-I 79 vs. 87); color lighter brown.

*S. tolteca (*Fig. 12*):* lowland; overlapping ranges but no known site of local sympatry; puncta on AIII and AIV larger, more separated; AIII in dorsal view less trapezoidal, sides less converging anteriorly; larger on average (mean HW 0.61 vs. 0.56); AIII narrower on average (mean AIII-I 100 vs. 110).

*S. valenzuelai (*Fig. 9*):* lowland; no known site of local sympatry; AIII in dorsal view with sides less strongly converging anteriorly; puncta on AIII and AIV larger; dorsal profile of AIII and AIV more convex; scapes shorter on average (mean SI 72 vs. 78).

***Measurements, Worker.*** HW 0.56, HL 0.70, SL 0.44, MSL 0.91, AIIIW 0.45, AIIIL 0.41, AIVW 0.72, AIIIL 0.83, SI 78, AIII-I 110, AIV-I 87 (*n* = 1).

***Biology.*** This species is known from five specimens, all from montane wet forest in Cusuco National Park, Honduras. Two workers were collected in Winkler samples and three males were from Malaise traps. One worker was from 1260 m elevation and one from 2030 m elevation.

***Comments.*** The males were associated with the workers with COI barcode data. See further discussion under *S. boudinoti*.

### *Syscia* JTL084, Unnamed Morphospecies

Figure 10 (map, worker)

***Geographic Range.*** Mexico (Tamaulipas).

***Diagnosis.*** Based on a single specimen from a cloud forest site; subpetiolar process triangular, with weakly convex posterior margin; AIII in dorsal view trapezoidal, with weakly convex sides; AIV in dorsal view moderately convex, anterior margin not truncate; dorsal profile of AIII convex; dorsal profile of AIV weakly convex; puncta on AIV large, somewhat lunate, fading at midlength; standing pilosity of medium length and stoutness; color red brown.

Three species are within size and geographic range of *S.* JTL084: *S. disjuncta*, *S. setosa*, and *S.* JTL071.

*S. disjuncta (*Fig. 11*):* locally sympatric; much smaller puncta on AIV.

*S. setosa (*Fig. 11*) and S. JTL071 (*Fig. 9*):* Allopatric; AIII less trapezoidal; puncta on AIII larger and more widely spaced; standing pilosity longer and coarser.

***Measurements, Worker.*** HW 0.55, HL 0.68, SL 0.38, MSL 0.85, AIIIW 0.42, AIIIL 0.39, AIVW 0.62, AIIIL 0.72, SI 69, AIII-I 108, AIV-I 86 (*n* = 1).

***Comments.*** This specimen has not been sequenced.

### *Syscia* JTL085, Unnamed Morphospecies

Figure 9 (map, worker)

***Geographic Range.*** Mexico (Chiapas).

***Diagnosis.*** Based on a single specimen from a cloud forest site; small version of *S. chiapaneca*; occipital carina strongly developed and visible in face view; subpetiolar process shallowly triangular; AIII trapezoidal; sides of AIV moderately convex; puncta on AIV distinct, separate from each other, fading at about midlength; standing pilosity of moderate abundance and length; color red brown. Based on the COI barcode of the sequenced specimen (GenBank accession MT267583), the smallest pairwise interspecific distance was 6.44%.

Eight species are within size and geographic range of *S.* JTL085: *S. chiapaneca*, *S. jennierussae*, *S. machaquila*, *S. persimilis*, *S. pervagata*, *S. peten*, *S. valenzuelai*, and *S.* JTL066.

*S. chiapaneca (*Fig. 11*):* allopatric; larger on average (mean HW 0.58 vs. 0.53); scapes longer on average (mean SI 79 vs. 73).

*S. jennierussae (*Fig. 10*):* occurs nearby at lower elevation; occipital carina less visible in face view; subpetiolar process larger, deeper; scapes shorter on average (mean SI 67 vs. 73); AIII wider on average (mean AIII-I 110 vs. 104); AIV wider on average (mean AIV-I 87 vs. 80).

*S. machaquila (*Fig. 10*):* locally sympatric; occipital carina less visible in face view; subpetiolar process larger, deeper; AIV wider on average (mean AIV-I 86 vs. 80).

*S. persimilis (*Fig. 10*), S. pervagata* (Fig. 9), *S. peten* (Fig. 9): subpetiolar process with acute posterior tooth.

*S. valenzuelai (*Fig. 9*):* locally sympatric; occipital carina less visible in face view; subpetiolar process larger, deeper; AIV wider on average (mean AIV-I 85 vs. 80).

*S. JTL066 (*Fig. 11*):* lowland; no known sites of local sympatry, but found nearby at lower elevation; subpetiolar process with more developed posterior tooth; larger on average (mean HW 0.58 vs. 0.53).

***Measurements, Worker.*** HW 0.53, HL 0.66, SL 0.39, MSL 0.84, AIIIW 0.41, AIIIL 0.40, AIVW 0.64, AIIIL 0.80, SI 73, AIII-I 104, AIV-I 80 (*n* = 1).

***Comments.*** The UCE tree places this single specimen as sister to *S. chiapaneca*, which occurs on the opposite side of Chiapas. The two species differ in size, and the COI distance between them is 8.4%.

## Molecular Data Availability

Raw Illumina reads and contigs representing UCE loci have been deposited at the NCBI Sequence Read Archive and GenBank, respectively (BioProject# PRJNA615631). All newly generated COI sequences have been deposited at GenBank (MT267540-MT267668). A complete list of relevant NCBI accession numbers are available in Supp Table S5 (online only). The concatenated UCE matrix, the COI matrix, all Trinity contigs, all tree files, unfiltered UCE alignments, and additional data analysis files (partitioning schemes, log files) have been deposited at Dryad (https://doi.org/10.5061/dryad.08kprr50s). The Phyluce package and associated programs can be downloaded from github (github.com/faircloth-lab/phyluce). The ant-specific baits used to enrich UCE loci can be purchased from Arbor Biosciences (arborbiosci.com/genomics/targeted-sequencing/mybaits/mybaits-expert/mybaits-expert-uce/) and the UCE bait sequence file is available at figshare (figshare.com/authors/brant-faircloth/97201/).

## Supplementary Data

Supplementary data are available at *Insect Systematics and Diversity* online.

Table S1. Voucher specimens for UCE samples used in taxonomic revision of New World *Syscia*.

Table S2. Material examined for taxonomic revision of New World *Syscia*.

Table S3. Sequencing and assembly statistics for UCE samples used in the revision of New World *Syscia*.

Table S4. Data for the COI samples used in the revision of New World *Syscia*.

Table S5. NCBI accession numbers for sequence data used in the revision of New World *Syscia*.

Figure S1. *Syscia amblyogyna* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.5 mm for face view, 1.0 mm for profile and dorsal views.

Figure S2. *Syscia amblyogyna* brachypterous queen. Guatemala (CASENT0644403). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.5 mm for face view, 1.0 mm for profile and dorsal views. Variation in eye size of brachypterous queens: A. CASENT0644403. B. CASENT0612570.

Figure S3. *Syscia atitlana* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S4. *Syscia augustae* worker. United States, Texas (CASENT0644275). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.5 mm for face view, 1.0 mm for profile and dorsal views.

Figure S5. *Syscia augustae* brachypterous queen. United States, Arkansas (MCZ-ENT00511555). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S6. *Syscia augustae* male. USA, Texas (CASENT0644536). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S7. *Syscia austrella* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S8. *Syscia austrella* queen. Panama (CASENT0633045). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 0.5 mm for profile and dorsal views.

Figure S9. *Syscia benevidesae* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S10. *Syscia benevidesae* queen. Costa Rica (JTLC000014009). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S11. *Syscia borowieci* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S12. *Syscia boudinoti* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.3 mm for face view, 1.0 mm for profile and dorsal views.

Figure S13. *Syscia boudinoti* male. Guatemala (CASENT0630833). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S14. *Syscia brachyptera* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S15. *Syscia brachyptera* brachypterous queen. Honduras (CASENT0614143). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 0.5 mm for profile and dorsal views.

Figure S16. *Syscia chiapaneca* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S17. *Syscia chiapaneca* queen. Mexico, Chiapas (CASENT0601746). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S18. *Syscia disjuncta* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S19. *Syscia disjuncta* queen. Mexico, Tamaulipas (CASENT0644503). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S20. *Syscia disjuncta* intercaste female. Mexico, Puebla (CASENT0640943). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S21. *Syscia grandis* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.5 mm for face view, 1.0 mm for profile and dorsal views.

Figure S22. *Syscia honduriana* lectotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S23. *Syscia honduriana* queen. Honduras (USNMENT00921971). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S24. *Syscia jennierussae* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S25. *Syscia jennierussae* queen. Guatemala (CASENT0644019). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S26. *Syscia lacandona* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S27. *Syscia lacandona* queen. Mexico, Chiapas (JTLC000009793). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S28. *Syscia lacandona* male. Mexico, Chiapas (CASENT0630837). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S29. *Syscia latepunctata* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S30. *Syscia latepunctata* queen. Costa Rica (CASENT0637042). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S31. *Syscia machaquila* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S32. *Syscia machaquila* queen. Guatemala (CASENT0644491). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S33. *Syscia madrensis* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S34. *Syscia minuta* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S35. *Syscia minuta* queen. Costa Rica (CASENT0644439). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 0.5 mm for profile and dorsal views.

Figure S36. *Syscia minuta* male. Nicaragua (CASENT0628949). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.1 mm for face view, 0.5 mm for profile and dorsal views.

Figure S37. *Syscia murillocruzae* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S38. *Syscia murillocruzae* intercaste female. Costa Rica (CASENT0644501). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S39. *Syscia parietalis* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S40. *Syscia parietalis* queen. Honduras (CASENT0617089). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S41. *Syscia parietalis* male. Honduras (CASENT0617722). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S42. *Syscia parva* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 0.5 mm for profile and dorsal views.

Figure S43. *Syscia parva* queen. Guatemala (CASENT0614340). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 0.5 mm for profile and dorsal views.

Figure S44. *Syscia persimilis* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S45. *Syscia persimilis* dealate queen. Honduras (CASENT0615012). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S46. *Syscia persimilis* intercaste female. Nicaragua (CASENT0629228). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S47. *Syscia pervagata* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S48. *Syscia pervagata* alate queen. Mexico, Chiapas (CASENT0644017). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 0.5 mm for profile and dorsal views.

Figure S49. *Syscia pervagata* dealate queen. Mexico, Chiapas (CASENT0644423). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 0.5 mm for profile and dorsal views.

Figure S50. *Syscia pervagata* male. Honduras (CASENT0630840). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 0.5 mm for profile and dorsal views.

Figure S51. *Syscia peten* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S52. *Syscia peten* queen. Guatemala (CASENT0644482). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 0.5 mm for profile and dorsal views.

Figure S53. *Syscia pollula* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S54. *Syscia pollula* queen. Costa Rica (CASENT0637057). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 0.5 mm for profile and dorsal views.

Figure S55. *Syscia pollula* brachypterous queen. Costa Rica (CASENT0644478). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 0.5 mm for profile and dorsal views.

Figure S56. *Syscia quisquillis* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S57. *Syscia quisquillis* (Arizona form) worker. United States, Arizona (FMNHINS0000095772). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S58. *Syscia setosa* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S59. *Syscia setosa* queen. Mexico, Veracruz (CASENT0644334). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S60. *Syscia setosa* intercaste female. Mexico, Veracruz (CASENT0640468). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S61. *Syscia setosa* male. Mexico, Oaxaca (CASENT0640810). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S62. *Syscia sumnichti* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S63. *Syscia ticomontana* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S64. *Syscia tolteca* lectotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S65. *Syscia tolteca* queen. Guatemala (CASENT0644415). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S66. *Syscia transisthmica* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S67. *Syscia transisthmica* queen. Mexico, Oaxaca (CASENT0644007). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.5 mm for face view, 1.0 mm for profile and dorsal views.

Figure S68. *Syscia truncata* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S69. *Syscia valenzuelai* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S70. *Syscia valenzuelai* queen. Mexico, Veracruz (CASENT0644344). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S71. *Syscia valenzuelai* male. Mexico, Veracruz (CASENT0630839). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.5 mm for face view, 1.0 mm for profile and dorsal views.

Figure S72. *Syscia volucris* holotype worker. A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S73. *Syscia volucris* queen. Costa Rica (INB0003237379). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.5 mm for face view, 1.0 mm for profile and dorsal views.

Figure S74. *Syscia volucris* brachypterous queen. Costa Rica (INBIOCRI000522290). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.5 mm for face view, 1.0 mm for profile and dorsal views.

Figure S75. *Syscia* JTL068 queen. Honduras (CASENT0613276). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 0.5 mm for profile and dorsal views.

Figure S76. *Syscia* JTL073 queen. Mexico, Chiapas (MCZENT00511568). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.2 mm for face view, 1.0 mm for profile and dorsal views.

Figure S77. *Syscia* JTL076, queen. Guatemala (CASENT0614221). A. Face view. B. Dorsal view. C. Profile view. Scale bars are 0.5 mm for face view, 1.0 mm for profile and dorsal views.

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## Author Contributions

JTL and MGB contributed equally to all aspects of the project.

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