Molecular Phylogenetics, Phylogenomics, and Phylogeography

Phylogenomic Species Delimitation, Taxonomy, and 'Bird Guide' Identification for the Neotropical Ant Genus Rasopone (Hymenoptera: Formicidae)

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Abstract

Rasopone Schmidt and Shattuck is a poorly known lineage of ants that live in Neotropical forests. Informed by phylogenetic results from thousands of ultraconserved elements (UCEs) and mitochondrial DNA barcodes, we revise the genus, providing a new morphological diagnosis and a species-level treatment. Analysis of UCE data from many Rasopone samples and select outgroups revealed non-monophyly of the genus. Monophyly of Rasopone was restored by transferring several species to the unrelated genus Mayaponera Schmidt and Shattuck. Within Rasopone, species are morphologically very similar, and we provide a ‘bird guide’ approach to identification rather than the traditional dichotomous key. Species are arranged by size in a table, along with geographic range and standard images. Additional diagnostic information is then provided in individual species accounts. We recognize a total of 15 named species, of which the following are described as new species: R. costaricensis, R. cryptergates, R. cubitalis, R. guatemalensis, R. mesoamericana, R. pluviselva, R. politognatha, R. subcultibalis, and R. tianis. An additional 12 morphospecies are described but not formally named due to insufficient material. Rasopone panamensis (Forel, 1899) is removed from synonymy and elevated to species. The following species are removed from Rasopone and made new combinations in Mayaponera: M. arhuaca (Forel, 1901), M. becculata (Mackay and Mackay, 2010), M. cerna (Mackay and Mackay, 2010), M. conicula (Mackay and Mackay, 2010), M. longidentata (Mackay and Mackay, 2010), and M. pergandei (Forel, 1909).

Key words: Neotropics, ultraconserved elements, DNA barcoding, new species, molecular systematics

Two major challenges to solving the taxonomic impediment for hyperdiverse insect groups are specimen rarity and morphological complexity, with the latter often coming in the form of continuous subtle variation among and within species. In ants, those genera that predominately occupy the leaf-litter microenvironment tend to suffer from both of these problems. Leaf-litter ants nest and forage in the ground, leaf-litter, and rotting wood and rarely expose themselves above cover where they can be readily detected by visual collectors. Consequently, routinely collecting these ants requires the use of bulk sampling techniques, such as leaf-litter sifting (Winkler and Berlese methods) and pitfall traps. Ants that are predominately subterranean or have small colonies tend to be especially rare (Wong and Guénard 2017). Many leaf-litter ant genera also tend to exhibit very subtle morphological differences among species, with many of the most obvious differences, e.g., size, varying continuously or tracking environmental variables like elevation. The Neotropical ant genus Rasopone exhibits both of these impeding characteristics (rarity and morphological complexity), making taxonomic revision and species identification very challenging in this group. Here, we aim to greatly improve Rasopone taxonomy and address these challenges. We do this by 1) examining new specimens collected during several large-scale sampling projects in Middle America, 2) integrating molecular phylogenomic and barcode data into our assessments of species boundaries, and 3) using a ‘bird guide’ approach to species identification.

The genus Rasopone was established by Schmidt and Shattuck (2014) to contain a small set of Neotropical species of the ant subfamily Ponerinae. The genus was diagnosed by a suite of morphological characters, none of which was definitively autapomorphic. The phylogenetic placement of the genus was not treated in Schmidt’s (2013) phylogeny and affinities were uncertain. Prior to Schmidt and Shattuck the species were placed in a very broadly defined genus Pachycondyla. Mackay and Mackay (2010) revised the New World species of Pachycondyla, and the species that were later segregated in Rasopone were placed in two species complexes. The arhuaca complex contained six species (R. arhuaca,
R. becculata, R. cernua, R. conicula, R. longidentata, and R. pergandei) and the ferruginea complex contained five (R. breviscapa, R. ferruginea, R. lunaris, R. minuta, and R. rupinicola).

Prior to routine use of mass sampling methods (Berlese and Winkler) very few collections of Rasopone were known. Over the last 25 yr, quantitative inventory projects in Middle America have greatly increased the number of specimens from this region, allowing for a much finer examination of species diversity and morphological variability. For Middle American taxa, the biodiversity landscape is one of many extremely similar species, each exhibiting its own geographic range and elevational specialization, and occurring in communities of locally sympatric species. The morphological similarity of species and the frequent convergence in species-level characters make purely morphological approaches to species delimitation and identification difficult, particularly among geographically separated populations.

To improve Rasopone taxonomy we rely on both morphological and molecular evidence, and take an iterative approach to resolving species boundaries, involving morphological species assignments, sequencing of multiple populations of putative species, and subsequent refinement of species concepts using tree-based results. Such an approach is commonplace in the era of mitochondrial (mt) DNA barcoding (Hebert et al. 2003), but instead of using single or only a few genetic markers, we employ a phylogenomic method: the targeted enrichment of ultraconserved elements (UCEs; Faircloth et al. 2012, Branstetter et al. 2017). The UCE method generates thousands of nuclear loci for samples at relatively low cost, and unlike DNA barcoding, which uses a single fast-evolving marker, can provide definitive information to resolve both very deep and very shallow phylogenetic relationships (Faircloth et al. 2015, Branstetter et al. 2017, Branstetter and Longino 2019). Resolving relationships above the species level, even in taxonomic studies, has value, because it makes it possible to confidently gauge phylogenetic distance among species or populations, which might have convergent morphologies. Another positive feature of the UCE method is that mitochondrial DNA, including the animal barcode gene cytochrome oxidase I (COI), can often be extracted as bycatch in the sequencing process (Pierce et al. 2017, Branstetter and Longino 2019), making it possible to generate complementary nuclear and mitochondrial datasets for testing species boundaries and to include additional samples from the Barcode of Life Database (Ratnasingham and Hebert 2007). The combination of detailed imagery, comprehensive sampling across the Middle American region, and molecular evidence of underlying genetic structure allows a major advance in our understanding of this group of ants and the ability of researchers to identify new material.

Identification with traditional dichotomous keys becomes more difficult with the increasing number and ever-finer resolution of cryptic species. Species exhibit very subtle differences in continuous characters, which stymies efforts to organize them in a hierarchical decision tree. An alternative approach is the ‘bird guide’ style: species are organized by one or few variables, with a page or figure for each species that encapsulates information and provides identification tips (e.g., Longino 2019). Non-specialists have always relied on this style and it continues to be favored in the digital age (Stevenson et al. 2003). For insect genera with large numbers of very similar species, the bird guide approach might be more useful for specialists and non-specialists alike. In this revision of Rasopone, we apply the bird guide style in lieu of the traditional dichotomous key.

The ‘bird guide’ approach includes range maps to facilitate identification. A traditional goal of taxonomy is to be geography-free. Species should be defined such that they can be identified regardless of where they are found. Such global definitions can be achieved using genetic sequence data and may also be achievable with morphological data that are sufficiently detailed (e.g., extensive morphometrics as in Seifert 2003). But UCE phylogenomics show that in most cases, especially among litter ants, species have relatively restricted ranges. At the same time, the most easily observed or measured morphological characteristics show strong convergence in geographically separate clades. Easily observable characters may readily differentiate locally sympatric species but fail to separate geographically distant species. Thus, geography becomes an important identification aid when sequence or detailed morphometric data are not available.

The sampling of Rasopone species is still a long way from complete. Even with the intensive sampling in Middle America, we were able to examine a total of only 549 species occurrences (i.e., not counting duplicate occurrences of the same species within individual collection events). Among these, we recognized 29 species, but eight of these, nearly 30%, are still known from single occurrences. Panama and South America in particular are terra incognita, where a combination of greater sampling and DNA sequencing would undoubtedly reveal many additional species.

Our primary objective in this work is to provide foundational descriptive taxonomy that will facilitate research on the biogeography, ecology, and evolutionary history of ants in the Middle American corridor, while also demonstrating the value of integrating phylogenomic data into species delimitation. We hope that this improved taxonomy will contribute to the general ‘biodiversity map’ of Middle America, revealing zones of endemism and contributing to conservation efforts in the region.

**Materials and Methods**

**Material Examined**

This study was based on 549 separate species occurrence records. Most of the examined material was from the Middle American corridor (Veracruz, Mexico to Nicaragua). Almost all the specimens were from Winkler or Berlese samples of sifted leaf litter and rotten wood from wet forest habitats. Most material was from large-scale biodiversity inventory projects in Central America and southern Mexico, spanning 25 yr (Projects ALAS, LLAMA, and ADMAC). All holotypes and paratypes associated with the new species described here have unique specimen-level identifiers (‘specimen codes’) affixed to each pin, and most dry-mounted 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. 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. Material examined is not listed in the species accounts, but instead is available as digital supplementary material to this article (Supp Table 1 [online only]), at the journal’s website. Images of holotypes, distribution maps, and all specimen data on which this paper is based are available on AntWeb (www.antweb.org), where they are subject to future modification (data corrections and reidentifications).

**Specimen Repositories**

| Code | Repository |
|------|------------|
| ALWC | Alex Wild, personal collection, The University of Texas, Austin, TX. |
| BEBC | Brendon E. Boudinot, personal collection, University of California, Davis, CA. |
| BMNH | British Museum of Natural History, London, United Kingdom. |
lowed a standard UCE enrichment protocol (version 1.5; available Biosciences (Ann Arbor, MI) myBaits v4 protocol, and day 2 fol-

For a few samples, we followed a modified en-
deriment, qPCR quantification, final pooling (100–104 total samples per sequencing pool), and sequencing. All sequencing was
singly performed on an Illumina HiSeq 2500 instrument (2x125 bp v4)

terrating 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 re-
solve 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).

**UCE Matrix Assembly**

After sequencing, the University of Utah bioinformatics core demultiplexed the data using bcftools 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 environ-
ment, 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 statics, including sequencing coverage, we used scripts from the PHYLUCE package (phyluce_assembly_get_trinity_coverage and phyluce_as-
semble_get_trinity_coverage_for_uce_loci) that use the programs

**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 1,252 data subsets and had a significantly better log likelihood than alternative partitioning schemes (SWSC-EN: −11,959,697.15; By Locus: −12,331,121.88; Unpartitioned: −12,481,042.22).

**DNA Sequence Generation**

We selected 75 specimens for DNA sequencing (Table 1): 62 Rasopone, 1 Mayaponera constricta (the type species of this genus), 8 additional Mayaponera (formerly in Rasopone, transferred here), and single outgroup specimens from the genera Dinoponera, Neoponera, Pachycondyla, and Simopelta. All data were newly gen-
erated for this study, except for five samples, in which data were
taken from http://ultraconserved.org). 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 re-
solve 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).

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| Taxon                          | Voucher list of specimens used for DNA extraction and sequencing                                                                 |
|-------------------------------|-----------------------------------------------------------------------------------------------------------------------------------|
| Dinoponera longipes\*         | EX1643 Peru Loreto -2.24897 -72.09111 CASENT0004663                                                                          |
| Mayaponea arbuaca             | EX1435 Costa Rica Heredia 10.42864 -84.01866 INBOICR001241794                                                                |
| Mayaponea arbuaca             | EX1676 Guaya Potaro-Siparuni 5.30479 -89.83746 CASENT0636916                                                                   |
| Mayaponea becculata           | EX1429 Costa Rica Alajuela 10.29644 -84.77132 CASENT0635158                                                                   |
| Mayaponea becculata           | EX1434 Costa Rica Heredia 10.26863 -84.08227 CASENT06363229                                                                   |
| Mayaponea constricta\*        | EX1649 Costa Rica Puntarenas 8.40811 -83.32547 CASENT0636005                                                                   |
| Mayaponea pergandei           | EX1424 Guatemala Petén 15.44198 -89.53494 CASENT0614317                                                                     |
| Mayaponea pergandei           | EX1431 Panama Darién 8.79511 -78.45309 CASENT0633514                                                                         |
| Neoponea rufipesa\*           | EX1436 Costa Rica Heredia 10.41924 -84.02062 INBO003695621                                                                  |
| Pachycondyla harpax\*         | EX838 Costa Rica Puntarenas 8.40667 -83.32837 CASENT0636063                                                                   |
| Rasopone costaricensis        | EX1427 Costa Rica Heredia 10.23617 -84.11767 INBO003659344                                                                   |
| Rasopone costaricensis Form a | EX1443 Guatemala Petén 16.44198 -89.78892 CASENT0617265                                                                     |
| Rasopone costaricensis Form b | EX1447 Costa Rica Heredia 10.23617 -84.11767 INBO00366817                                                                   |
| Rasopone costaricensis Form c | EX1462 Costa Rica Heredia 10.23617 -84.11767 INBO003659307                                                                   |
| Rasopone cryptogena           | EX1450 Costa Rica Puntarenas 10.30892 -84.78498 CASENT0635809                                                               |
| Rasopone costulata            | EX1451 Nicaragua Boaco 12.58180 -85.46661 CASENT0619842                                                                       |
| Rasopone ferruginea           | EX1426 Nicaragua Matagalpa 12.96187 -85.23301 CASENT062418                                                                       |
| Rasopone ferruginea           | EX1439 Honduras Atlántida 15.69714 -84.74751 CASENT0618624                                                                      |
| Rasopone ferruginea           | EX1444 Honduras Atlántida 15.69843 -84.74256 CASENT0618637                                                                     |
| Rasopone ferruginea           | EX1445 Mexico Chiapas 16.98023 -91.58610 CASENT0609807                                                                        |
| Rasopone ferruginea           | EX1446 Mexico Chiapas 16.15687 -93.59878 CASENT0609710                                                                        |
| Rasopone ferruginea           | EX1456 Mexico Chiapas 17.12373 -91.63699 JTL000014402                                                                         |
| Rasopone ferruginea           | EX1967 Mexico Oaxaca 18.04793 -96.69063 CASENT0644238                                                                        |
| Rasopone ferruginea           | EX1968 Mexico Oaxaca 18.04860 -96.69080 CASENT0644239                                                                        |
| Rasopone ferruginea           | EX1970 Mexico Puebla 20.03307 -97.45143 CASENT0640997                                                                        |
| Rasopone ferruginea           | EX1971 Mexico Veracruz 18.58695 -95.07648 CASENT0640257                                                                       |
| Rasopone ferruginea           | EX1974 Mexico Veracruz 19.51211 -96.59314 CASENT0641093                                                                        |
| Rasopone guatemalensis        | EX1411 Mexico Chiapas 15.72096 -92.95020 JTL000014265                                                                         |
| Rasopone guatemalensis        | EX1412 Mexico Chiapas 15.71549 -92.93816 CASENT0633224                                                                        |
| Rasopone guatemalensis        | EX1433 Guatemala Suchitpéquez 14.55483 -91.19299 CASENT0611754                                                                |
| Rasopone JTL027               | EX1430 Panama Darién 8.79151 -78.45309 CASENT0633216                                                                         |
| Rasopone JTL029               | EX1452 Panama Darién 8.79805 -78.46250 CASENT063305                                                                           |
| Rasopone JTL030               | EX1453 Panama Darién 8.79478 -78.46095 CASENT063307                                                                           |
| Rasopone JTL034               | EX1441 Honduras Olancho 14.79972 -86.01415 CASENT061079                                                                         |
| Rasopone JTL034               | EX1969 Mexico Puebla 19.97807 -97.42486 CASENT0640987                                                                        |
| Rasopone JTL034               | EX1972 Mexico Veracruz 18.58038 -95.08110 CASENT064028                                                                         |
| Rasopone JTL035               | EX1973 Mexico Veracruz 18.52290 -95.04039 CASENT0640453                                                                        |
| Rasopone JTL047               | EX2214 Brazil Amapá 12.4514 -52.40543 CASENT0646305                                                                          |
| Rasopone JTL049               | EX2215 Colombia Amazonas 4.04667 -70.05676 CASENT064557                                                                         |
| Rasopone lunaris              | EX2216 Brazil Minas Gerais 20.80303 -42.85786 CASENT064556                                                                         |
| Rasopone mesoamericana        | EX1415 Guatemala Zacapa 14.94634 -89.27600 CASENT061453                                                                         |
| Rasopone mesoamericana        | EX1417 Guatemala Suchitpéquez 14.54870 -91.19086 CASENT0612910                                                                  |
| Rasopone mesoamericana        | EX1418 Honduras Olancho 15.09547 -86.73872 CASENT0615014                                                                        |
| Rasopone mesoamericana        | EX1420 Honduras Cortés 15.48695 -88.23452 CASENT0617624                                                                       |
| Rasopone mesoamericana        | EX1421 Nicaragua Matagalpa 12.96024 -85.22486 CASENT0624089                                                                     |
| Rasopone mesoamericana        | EX1422 Nicaragua Jinotega 13.77174 -85.01290 CASENT0633871                                                                       |
| Rasopone mesoamericana        | EX1423 Nicaragua Jinotega 13.56754 -85.69690 CASENT0629241                                                                       |
| Rasopone mesoamericana        | EX1432 Honduras Olancho 14.93690 -85.90353 CASENT0616284                                                                       |
| Rasopone mesoamericana        | EX1454 Mexico Chiapas 15.72099 -92.95054 JTLCC00001536                                                                          |
| Rasopone mesoamericana        | EX1455 Costa Rica Heredia 10.26900 -84.08646 INBO00321393                                                                         |
| Rasopone minuta               | EX1413 Mexico Chiapas 17.12681 -91.63022 JTLCC00001437                                                                         |
| Rasopone minuta               | EX1458 Honduras Atlántida 15.76570 -87.45567 CASENT0618570                                                                       |
| Rasopone minuta               | EX1459 Honduras Comayagua 14.87314 -89.92997 CASENT0617277                                                                       |
| Rasopone minuta               | EX1460 Guatemala Petén 17.13202 -89.68206 CASENT0610667                                                                         |
| Rasopone minuta               | EX1461 Guatemala Izabal 15.41186 -88.71071 CASENT0611483                                                                        |
| Rasopone panamensis           | EX1410 Costa Rica Puntarenas 8.40667 -83.32833 JTLCC00001409                                                                       |
| Rasopone panamensis           | EX1963 Costa Rica Limón 9.66330 -83.02300 CASENT0644251                                                                        |
| Rasopone panamensis           | EX1965 Costa Rica San José 9.48059 -83.96402 CASENT0644251                                                                       |
Using the SWSC-EN partitioning scheme, we inferred phylogenetic relationships of *Rasopone* with the likelihood-based program IQ-TREE v1.6.8 (Nguyen et al. 2015). For the analysis we selected the ‘-app’ option for partitioning and the GTR+G model of sequence evolution. To assess branch support, we performed 1,000 replicates of the ultrafast bootstrap approximation (UFBoot) (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 (Ströher et al. 2016) 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 *Rasopone* COI sequences downloaded from the BOLD database (Ratnasingham and Hebert 2007) (Accessed 13 May 2019). To extract COI from UCE data, we downloaded a complete 658 bp barcode sequence of *Rasopone* JTL-014 from BOLD (Acc.#ASNEI075-09) and used this as the bait input sequence (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 ‘Rasopone’. 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 filtered for quality. Because some of the 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 or other anomalies using MESQUITE v3.2 (Maddison and Maddison 2018). The final matrix was partitioned by codon position and analyzed with IQ-TREE using GTR+G, 1,000 ultrafast bootstrap replicates, and 1,000 SH-like replicates. Following a preliminary analysis of all samples, we pruned out many samples that we viewed as extraneous, and then repeated the analysis. In Supp Table S3 (online only), the full set of specimens is reported, with a column indicating which specimens were pruned. The full COI tree with all specimens is also presented in Supp. Fig. S1 (online only).

**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. In species accounts, measurements are presented as mean (minimum–maximum, sample size) for each variable when more than one specimen was measured for the variable. Otherwise the single measured value is shown. The following measurements and indices are reported:

- **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 anterior most projection of clypeus to posterior most projection of vertex.
- **SL**: Scape length, maximum length of scape not including basal condyle and neck.
- **PTH**: Petiole height, in lateral view, perpendicular distance from posteroverentral lobe of petiolar tergite to dorsal margin of petiolar node (Fig. 1B). In lateral view, the posteroverental lobe and the dorsal margin of the node are in different focal planes, requiring refocusing during measurement.
- **PTL**: Petiole length, in lateral view, perpendicular distance from anterior face of petiolar node to posterior margin of node (Fig. 1B). In lateral view, the two faces are in different focal planes, requiring refocusing during measurement.
- **CI**: Cephalic index, 100*HW/HL.
- **SI**: Scape index, 100*SL/HW.
- **PTI**: Petiolar index, 100*PTH/PTL.

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, United States). Distribution maps were plotted with SimpleMappr (Shorthouse 2010).

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**Table 1. Continued**

| Taxon                     | ExtractionID | Country    | Admin1 | Latitude  | Longitude | VoucherID |
|--------------------------|--------------|------------|--------|-----------|-----------|-----------|
| *Rasopone politognatha*  | EX1448       | Nicaragua  | RAAN   | 13.7216   | -84.99613 | CASENT0628853 |
| *Rasopone politognatha*  | EX1449       | Costa Rica | Heredia | 10.41930  | -84.01832 | INB0004099727 |
| *Rasopone politognatha*  | EX1416       | Guatemala  | Zacapa  | 14.95442  | -89.27697 | CASENT0612523 |
| *Rasopone politognatha*  | EX1425       | Honduras   | Cortés  | 15.48965  | -88.23833 | CASENT0617668 |
| *Rasopone politognatha*  | EX1438       | Nicaragua  | Matagalpa | 12.97725 | -85.23212 | CASENT0623897 |
| *Rasopone politognatha*  | EX1440       | Honduras   | Comayagua | 14.53448 | -87.55155 | CASENT0611720 |
| *Rasopone politognatha*  | EX1442       | Mexico     | Chiapas | 16.15947  | -93.60512 | CASENT0603323 |
| *Rasopone politognatha*  | EX1414       | Mexico     | Chiapas | 16.96408  | -91.59236 | JTL000014483 |
| *Rasopone politognatha*  | EX1419       | Honduras   | Comayagua | 14.87120 | -87.90011 | CASENT0615252 |
| *Rasopone politognatha*  | EX1457       | Guatemala  | Petén   | 16.44167  | -89.53496 | CASENT0614335 |
| *Simopelta andersonii*   | EX1375       | Costa Rica | Alajuela | 10.30926  | -84.72941 | CASENT0635057 |

Vouchers may be the same specimen (non-destructive DNA extraction) or with varying degrees of subjectivity (destructive extraction of specimen from same nest, same series, or same population); Full voucher specimen details are in Supp Table S1 (online only).

*Sequence data extracted from Branstetter et al. (2017).*
Species Delimitation and Identification

In most cases, species were delimited by identifying sets of specimens that 1) were morphologically very similar, 2) formed monophyletic or paraphyletic groups (mtDNA only) based on sequence data, and 3) showed no evidence of having separate morphological or genotypic clusters within communities (separate clusters indicated the presence of multiple species). In one case a species was named for which the third criterion was not satisfied, and this particular case is discussed in the species account. New species were formally named when there were enough specimens from a local population for an adequate type series, such that specimens with high probability of conspecificity could be distributed to at least two institutions. Otherwise they were given informal, and unavailable, morphospecies codes, pending additional collections and better knowledge 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.

Identification should be carried out using diagnoses in individual species accounts, Figs. 6–13, and Table 2. These figures are standard images and a distribution map of each species, with species in order of mean HW. Specimen identification can be done by measuring the HW, going to that HW in the figures, and working up and down from there to locate potentially matching species. Table 2 provides a list of species in order of size, with key characteristics and geographic ranges.

Phylogenetic Results

UCE Sequencing and Matrix Assembly

After sequencing, assembly, and the extraction of contigs representing UCE loci from our set of 75 specimens (70 new to this study),
we recovered an average per contig coverage of 41.0x (range: 10.1–78.2x) and a mean contig length of 872 bp (range: 367–1,108 bp). Following alignment trimming, and filtering of the UCE contigs, our UCE matrix consisted of 1,802 loci and 1,542,220 bp of sequence data, of which 339,246 bp were informative. The mean alignment length post-trimming was 853.8 bp (range: 223–2,268 bp). The final matrix included 12.3% missing data (including gaps). For additional sequencing assembly information see Supp Table S2 (online only).

**COI Extraction and Matrix Assembly**

We successfully extracted COI mtDNA sequence for 73 out of 75 UCE samples, but removed one sequence from the dataset (Dinoponera longipes) for being short and unnecessary for species delimitation. Except for two sequences, all were above 650 bp in length and most were 657 or 658 bp. No sequences had any obvious indications of being pseudogenes. From BOLD, we down-loaded an initial set of 313 samples (Supp Table S3 [online only]) and pruned this set down to 22 key samples for the final analysis. The final aligned matrix included 94 COI sequences and was 658 bp in length.

**Phylogenetics and Species Delimitation**

Analysis of the UCE data recovered a robust phylogenetic hypothesis with most nodes receiving maximum support (Fig. 2). Rasopone was found to be non-monophyletic due to species in the arhuaca complex (R. arhuaca, R. becculata, R. pergandei) being
recovered as sister to the genus *Mayaponera* and phylogenetically very distinct from true *Rasopone*. Using our criteria for species delimitation, we identified 19 putative *Rasopone* species based on morphospecies codes as terminal labels in Fig. 2. To demonstrate the challenge of separating species by morphology-alone, we left previous morphospecies codes generally failed. To make connections among widely separated populations was typically straightforward and correct, but attempts to make connections among widely separated populations generally failed. To demonstrate the challenge of separating species by morphology-alone, we left previous morphospecies codes as terminal labels in Fig. 2.

Although we save analysis of biogeographic patterns for later investigation, we note the existence of a core *Rasopone* clade that includes most species from Panama to Mexico and two more divergent clades, one consisting of a set of species related to the South American taxon *R. minuta* and one consisting of only the new species *R. cubitalis* from Costa Rica and Nicaragua. The latter clade was found to be sister to all other *Rasopone* species.

COI results were mostly concordant with UCE results at the species level (Fig. 3). One striking exception was *R. minuta*, which was found to be sister to all other species. *R. minuta* was monophyletic and phylogenetically distant from *R. panamensis* in the COI tree. The COI data also included a couple of COI-only samples that might belong to additional new species.
species since they did not cluster closely with any of our UCE samples. The relationships among species within *Rasopone* were largely discordant, although the deep split between *R. cubitalis* and the remaining *Rasopone* species was supported in both trees. At deeper levels, relationships were again congruent, although lacking strong node support in the COI tree.

**Taxonomic Results**

**Redeinition of *Rasopone* and *Mayaponera***

Schmidt and Shattuck (2014) provided the following diagnosis for *Rasopone*, based on workers: eyes present, mandibles relatively long, mandibular pit or groove absent, mesosomal profile nearly continuous, the metanotal groove shallow or absent, metapleural gland orifice without a posterior U-shaped cuticular lip, propodeal spiracle round or ovoid, mesotibiae dorsally without abundant stout traction setae, ventral apex of the metatibia with both a large pectinate spur and a smaller simple spur, fenestra absent from the petiolar process, prora present on anterior margin of first gastric sternite, and stridulatory organ absent from A4 pretergite. This should be emended to 'prora absent'. There is no true prora in any caste of *Rasopone* or *Mayaponera* as defined here. In some cases there is a denticle on the sternite of the helcium that can be misinterpreted as a prora.

To Schmidt and Shattuck’s diagnosis we add the following characters: 1) petiolar sternite with deep transverse posterior groove such that posterior portion of sternite forms a shovel-like extension separate from tergite (Fig. 1B) (this character applies to all castes); 2) anterior margin of clypeus truncate to emarginate, never entirely convex (Fig. 1E and F); and 3) color light to dark red brown, never entirely black. These additional characters exclude the *arhaca* complex. The *arhaca* complex has a variously shaped anteroventral petiolar process, but the posterior portion of the sternite is closely appressed to the tergite. The anterior margin of the clypeus is convex, and the color is black.

Members of the *arhaca* complex share many characters with *Mayaponera constricta* (currently the sole member of the genus), and the molecular data place them near each other (and distant from *Rasopone*). The main morphological difference between *Mayaponera constricta* and the *arhaca* complex is that the former has an impressed metanotal groove and the species of the *arhaca* complex do not. *Mayaponera constricta* is a surface forager found in a wide variety of habitats, from mature forest to open or disturbed areas, and from wet to seasonally dry areas. It also has a very large geographic range, from Hondurus to southern Brazil. In contrast, species of the *arhaca* complex are found only in shaded rainforest habitats, and the species have smaller geographic ranges. In spite of these differences, we place the *arhaca* complex in *Mayaponera*, and we consider the impressed metanotal groove of *M. constricta* to be a species-level trait and not a diagnostic feature of the genus. A full diagnosis of *Mayaponera* is not attempted here and should await a true revision of the genus.

**Rasopone Species-Level Characters**

The species of *Rasopone* have a uniform habitus (Fig. 1A). Worker HW varies from 0.80 to 1.70. The coefficient of variation for metric characters is typically ~5%. The medial projection of the anterior clypeal margin varies from strongly square-cut, flat medially and with sharp lateral corners (Fig. 1E), to medially emarginate with rounded lateral lobes (Fig. 1F). These two states are referred to as truncate or simious in species accounts. The mandibles vary from striate to smooth and shining. The sides of the head show variable levels of pilosity, from bare to having numerous short setae uniformly distributed. Face sculpture is usually a uniform surface of dense minute puncta, but in some species these are overlain with larger, more widely spaced puncta. When present, the larger puncta are usually faint and only visible under particular orientation and lighting. The degree of expression of these larger puncta is a continuum across species, and their presence is only noted for species with relatively strong expression. The petiole in lateral view varies from scale-like to cuboidal. The anterior margin is always flat to slightly concave. In species with strongly cuboidal nodes the posterior margin is also flat, parallel to the anterior margin, and there is a differentiated dorsal face (Fig. 1D). In species with a scale-like node, the dorsal and posterior faces are not differentiated and form a single convex curve (Fig. 1B). Among species there is a continuum from cuboidal to scale-like nodes (Fig. 1B–D). Petiolar nodes also vary in height to length ratio, some being relatively tall and thin, others shorter and longer.

Queens are very similar to workers except for larger compound eyes, presence of ocelli, and queen-typical mesosomal sclerites (Fig. 4). The ocelli are always very small. In species for which queens and workers are known, HW is approximately the same for the two castes. *Rasopone cubitalis* may be an exception, with queens ~1.17× larger than workers.

Males are known for a few species. The type series of *R. rupinicola* was collected with one or more males. Males occur in Malaise samples and a few have been associated with workers using COI sequence data. A figure is provided of the associated male of *R. mesoamerica* sp. nov. (Fig. 5), and several males are figured in Supp Figs. S18, S21, and S31 (online only), but otherwise males are not examined in this study.

**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:0DE2398D-199F-40A7-8207-91148630CD76.

**RASOPONE Schmidt and Shattuck**

*Rasopone* Schmidt and Shattuck, 2014: 208. Type-species: *Rasopone ferruginea* (F. Smith, 1858: 100).

**Geographic Range**

Southern Mexico to Bolivia, Paraguay, and southern Brazil. There are no records from the Caribbean.

**List of Species**

*Rasopone breviscapa* (Mackay and Mackay, 2010). Bolivia.

*Rasopone costaricensis* new species. Costa Rica, Panama.

*Rasopone cryptergates* new species. Costa Rica.

*Rasopone cubitalis* new species. Nicaragua, Costa Rica.

*Rasopone ferruginea* (F. Smith, 1858). Mexico to Nicaragua.

*Rasopone guatemalensis* new species. Mexico (Chiapas) to Guatemala.

*Rasopone lunaris* (Emery, 1896). South America.

*Rasopone mesoamerica* new species. Mexico (Chiapas) to Costa Rica.

*Rasopone munita* (Mackay and Mackay, 2010). Mexico (Chiapas) to Honduras.

*Rasopone panamensis* (Forel, 1899) (new status, revised status). Costa Rica, Panama.

*Rasopone pluriselva* new species. Honduras to Panama.
**Rasopone politognatha** new species. Mexico to Nicaragua.

**Rasopone rupinicola** (Mackay and Mackay, 2010). Panama, Colombia.

**Rasopone subcubitalis** new species. Mexico (Chiapas) to Honduras.

**Rasopone titanis** new species. Mexico (Chiapas).

**Unnamed Morphospecies**

- **Rasopone JTL027.** Panama (Darien).
- **Rasopone JTL029.** Panama (Darien).
- **Rasopone JTL030.** Panama (Darien).
- **Rasopone JTL034.** Mexico (Puebla, Veracruz), Honduras.
- **Rasopone JTL035.** Mexico (Veracruz).
- **Rasopone JTL037.** Guatemala, El Salvador.
- **Rasopone JTL040.** Colombia.
- **Rasopone JTL041.** Colombia.
- **Rasopone JTL042.** Colombia, Brazil (Pará).
- **Rasopone JTL043.** Ecuador.
- **Rasopone JTL047.** French Guiana.
- **Rasopone JTL048.** French Guiana.
- **Rasopone JTL049.** Colombia.
- **Rasopone MAS010.** Costa Rica.

### Species Transferred to **Mayaponera**

- **Mayaponera arhuaca** (Forel, 1901) (comb. nov.)
- **Mayaponera becculata** (Mackay and Mackay, 2010) (comb. nov.)
- **Mayaponera cernua** (Mackay and Mackay, 2010) (comb. nov.)
- **Mayaponera conicula** (Mackay and Mackay, 2010) (comb. nov.)
- **Mayaponera longidentata** (Mackay and Mackay, 2010) (comb. nov.)
- **Mayaponera pergandei** (Forel, 1909) (comb. nov.)

### Species Accounts

**Rasopone breviscapa** (MacKay and MacKay)

(Fig. 13; Supp Fig. S2 [online only])

Pachycondyla breviscapa MacKay and MacKay, 2010: 220, figs. 347, 349. HOLOTYPE: 1 queen, Bolivia, La Paz: Tumupasa,
XII 1921, W. M. Mann, Mulford Expedition [USNM, AntWeb images examined].

*Rasopone breviscapa*: Schmidt and Shattuck, 2014: 210.

Measurements, queen: HW 1.7, HL 1.7, SL 1.35, CI 100, SI 79 (n = 1) (from MacKay and MacKay, 2010).

Comments
This species is known only from the type queen. *Rasopone breviscapa*, *R. rupinicola*, and *R. titanis* are the largest species in the genus, with HW ~1.7. *Rasopone breviscapa* has the anterior clypeal margin truncate, mandibles striate, and petiole intermediate between cuboidal and scale-like. It is differentiated from *R. rupinicola* (Fig. 13; Supp Figs. S30 and S31 [online only]) by the shorter scape (SI 79 vs 106), and from *R. titanis* (Fig. 13; Supp Fig. S33 [online only]) by the truncate clypeal margin and striate mandibles.

*Rasopone costaricensis* New Species
(Figs. 8–11; Supp Figs. S3–S7 [online only])
(Zoobank LSID: urn:lsid:zoobank.org:act:3B2E87D5-CD8A-4CBE-B6B9-BDC604DC9500)

HOLOTYPE: 1 worker, Costa Rica, Puntarenas: Monteverde, 10.30892 –84.78498 ±50 m, 1,617 m, 13-v-2014, cloud forest, ex sifted leaf litter, J. Longino, JTL8628-s [UCR, unique specimen identifier CASENT0635809]. PARATYPES: same data as holotype [1 worker, CAS, CASENT0644841]; same data except 10.29905 –84.78292 ±200 m, 1,570 m, 30-iv-1989, JTL2486-s [1 worker, MCZC, INBIOCRI001281356; 1 worker, UCD, INBIOCRI001281355]; 10.3 –84.8 ±2 km, 1,500 m, 26-vi-1984, JTL26Jun84/grou [1 worker, DZUP, INBIOCRI002278996]; 10.30649 –84.81756 ±100 m, 1,290 m, 21-xii-2013, evergreen forest, in clay bank soil, JTL8467 [1 worker, CAS, CASENT0635758]; 10.30719 –84.78627 ±50 m, 1,670 m, 13-v-2014, JTL8627-s [1

Fig. 5. Male of *Rasopone mesoamericana* sp. nov. (Nicaragua, CASENT0627722). Scale bars are 0.5 mm for face view, 1.0 mm for dorsal and lateral views.
Fig. 6. Distribution map, face view, and lateral view of petiole of Rasopone pluviselva (holotype worker), R. minuta (worker, Mexico, Chiapas, CASENT0609834), R. JTL043 (worker, Ecuador, MCZ-ENT00716620), and R. JTL048 (worker, French Guiana, CASENT0645961). On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality.
Fig. 7. Distribution map, face view, and lateral view of Rasopone MAS010 (worker, Costa Rica, 08COSTA-1723), R. cryptergates (worker, Costa Rica, INB0003660648), R. JTL042 (worker, Colombia, MCZ-ENT00716611), and R. JTL034 (worker, Mexico, CASENT0640282). On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality.
Fig. 8. Distribution map, face view, and lateral view of petiole of *Rasopone lunaris* (worker, Brazil, Minas Gerais CASENT0644556), *R. guatemalensis* (holotype worker), *R. costaricensis* form c (worker, Costa Rica, INB0003659307), and *R. JTL027* (worker, Panama, CASENT0633216). On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality.
Fig. 9. Distribution map, face view, and lateral view of petiole of *Rasopone costaricensis* (holotype worker), *R. politognatha* (holotype worker), *R. JTL035* (worker, Mexico, CASENT0640453), and *Rasopone JTL049* (worker, Colombia, CASENT0644557). On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality.
Fig. 10. Distribution map, face view, and lateral view of petiole of Rasopone costaricensis form b (worker, Costa Rica, INB0003223929), R. JTL047 (worker, French Guiana, CASENT0645960), R. panamensis (worker, Costa Rica, CASENT0644252), and R. subcubitalis (holotype worker). On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality.
Fig. 11. Distribution map, face view, and lateral view of Rasopone ferruginea (worker, Nicaragua, CASENT0644264), R. JTL040 (worker, Colombia, MCZ-ENT00716609), R. JTL041 (worker, Colombia, MCZ-ENT00716614), and R. costaricensis form a (worker, Costa Rica, INB0003659312). On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality (type locality for R. ferruginea is ‘Mexico’).
Fig. 12. Distribution map, face view, and lateral view of petiole of Rasopone JTL030 (worker, Panama, CASENT0633075), R. JTL037 (worker, Guatemala, CASENT0625283), R. mesoamericana (holotype worker), and R. JTL029 (worker, Panama, CASENT0633053). On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality.
Fig. 13. Distribution map, face view, and lateral view of petiole of *Rasopone cubitalis* (holotype worker), *R. titanis* (worker, Mexico, Chiapas, MCZ-ENT00716640), *R. breviscapa* (holotype queen), and *R. rupinicola* (worker, Colombia, face view MCZ-ENT00716589, petiole CASENT0217567). On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality.
Table 2. *Rasopone* species in order of mean HW of worker (queen values substituted for *R. breviscapa*)

| Species         | HW        | CI        | SI        | PTI       | Clypeus     | Petiole     | Mandible   | Range          | Figures          |
|-----------------|-----------|-----------|-----------|-----------|-------------|-------------|------------|----------------|-----------------|
| *Pluviselva*    | 0.76–0.93 | 79–97     | 66–81     | 57–70     | Truncate    | Intermediate| Striate    | Honduras-Panama | Fig. 6; Supp Figs. S26 and S27 (online only) |
| *minuta*       | 0.79–0.96 | 78–96     | 70–85     | 51–63     | Truncate    | Tapered     | Smooth     | Chiapas-Honduras | Fig. 6; Supp Figs. S22 and S23 (online only) |
| JTL043         | 0.85–1.04 | 81–98     | 72–87     | 54–65     | Truncate    | Cuboidal    | Smooth     | Ecuador         | Fig. 6; Supp Fig. S43 (online only) |
| JTL048         | 0.88–1.08 | 80–98     | 73–89     | 49–59     | Truncate    | Intermediate| Smooth     | French Guiana   | Fig. 6; Supp Fig. S45 (online only) |
| MAS010         | 0.90–1.10 | 79–97     | 72–87     | 53–64     | Truncate    | Tapered     | Striate    | Costa Rica      | Fig. 7; Supp Fig. S47 (online only) |
| cryptergates   | 0.96–1.18 | 77–95     | 71–87     | 51–63     | Truncate    | Cuboidal    | Striate    | Costa Rica      | Fig. 7; Supp Figs. S8 and S9 (online only) |
| JTL042         | 0.99–1.21 | 81–99     | 71–87     | 49–60     | Truncate    | Intermediate| Striate    | Colombia-Brazil | Fig. 7; Supp Fig. S42 (online only) |
| JTL034         | 0.99–1.22 | 83–102    | 69–85     | 52–64     | Truncate    | Intermediate| Smooth     | Puebla-Honduras | Fig. 7; Supp Fig. S37 (online only) |
| lunaris        | 1.00–1.22 | 82–100    | 70–85     | 54–66     | Truncate    | Intermediate| Smooth     | South America   | Fig. 8; Supp Figs. S16–S18 (online only) |
| guatemalensis  | 1.00–1.22 | 77–94     | 77–95     | 51–62     | Truncate    | Tapered     | Smooth     | Chiapas-Guatemala | Fig. 8; Supp Figs. S14 and S15 (online only) |
| costaricensis, Form c | 1.00–1.23 | 79–96     | 80–97     | 48–58     | Truncate    | Tapered     | Striate    | Costa Rica      | Fig. 8; Supp Fig. S7 (online only) |
| JTL027         | 1.00–1.23 | 75–91     | 86–106    | 58–70     | Truncate    | Cuboidal    | Striate    | Panama          | Fig. 8; Supp Fig. S34 (online only) |
| costaricensis  | 1.03–1.26 | 78–95     | 76–93     | 48–59     | Truncate    | Tapered     | Striate    | Costa Rica      | Fig. 9; Supp Figs. S3 and S4 (online only) |
| politognatha   | 1.05–1.28 | 83–101    | 74–90     | 50–62     | Truncate    | Intermediate| Smooth     | Chiapas-Nicaragua | Fig. 9; Supp Figs. S28 and S29 (online only) |
| JTL035         | 1.05–1.28 | 87–107    | 69–85     | 48–58     | Truncate    | Intermediate| Smooth     | Veracruz        | Fig. 9; Supp Fig. S38 (online only) |
| JTL049         | 1.07–1.31 | 82–100    | 69–85     | 55–67     | Truncate    | Intermediate| Smooth     | Colombia        | Fig. 9; Supp Fig. S46 (online only) |
| costaricensis, Form b | 1.07–1.31 | 77–94     | 82–100    | 49–60     | Truncate    | Tapered     | Striate    | Costa Rica      | Fig. 10; Supp Fig. S6 (online only) |
| JTL047         | 1.09–1.33 | 86–105    | 66–81     | 53–65     | Truncate    | Intermediate| Smooth     | French Guiana   | Fig. 10; Supp Fig. S44 (online only) |
| panamensis     | 1.11–1.35 | 79–97     | 75–92     | 52–63     | Truncate    | Cuboidal    | Striate    | Costa Rica-Panama | Fig. 10; Supp Figs. S24 and S25 (online only) |
| subcubitalis    | 1.13–1.38 | 80–98     | 76–93     | 50–61     | Truncate    | Intermediate| Striate    | Chiapas-Honduras | Fig. 10; Supp Fig. S32 (online only) |
| ferruginea     | 1.14–1.39 | 82–101    | 74–90     | 48–59     | Sinuous     | Tapered     | Striate    | Mexico-Nicaragua | Figs. 4 and 11; Supp Figs. S12 and S13 (online only) |
| JTL040         | 1.16–1.42 | 82–100    | 66–80     | 53–65     | Truncate    | Cuboidal    | Smooth     | Colombia        | Fig. 11; Supp Fig. S40 (online only) |
| JTL041         | 1.19–1.45 | 83–101    | 74–91     | 50–61     | Truncate    | Tapered     | Smooth     | Colombia        | Fig. 11; Supp Fig. S41 (online only) |
| costaricensis, Form a | 1.19–1.46 | 76–93     | 79–97     | 50–61     | Truncate    | Intermediate| Smooth     | Costa Rica      | Fig. 11; Supp Fig. S5 (online only) |
| JTL030         | 1.26–1.54 | 79–97     | 74–90     | 51–63     | Truncate    | Tapered     | Striate    | Panama          | Fig. 12; Supp Fig. S36 (online only) |
| JTL037         | 1.27–1.55 | 80–98     | 83–101    | 46–56     | Truncate    | Intermediate| Striate    | Guatemala        | Fig. 12; Supp Fig. S39 (online only) |
| mesoamericana  | 1.33–1.62 | 80–98     | 76–93     | 50–61     | Truncate    | Tapered     | Striate    | Chiapas-Costa Rica | Figs. 5 and 12; Supp Figs. S19–S21 (online only) |
Montane. Three unrelated species are within geographic and size vary in size, mandibular sculpture, and petiole shape. They are all petiole scale-like. The species forms a clade of cryptic species that cate; side of head bare or with a few inconspicuous short setae; Costa Rica, Panama.

Geographic range. USNM, CASENT0632484. 1,480 m, 31-xii-2015, cloud forest, under stone, JTL9474 [1 worker, worker, USNM, CASENT0635807]; 10.31156 –84.80459 ±50 m, 1,480 m, 31-xii-2015, cloud forest, under stone, JTL9474 [1 worker, USNM, CASENT0632484].

Diagnosis Montane; mandibular broad or smooth; anterior clypeal margin truncate; side of head bare or with a few inconspicuous short setae; petiole scale-like. The species forms a clade of cryptic species that vary in size, mandibular sculpture, and petiole shape. They are all montane. Three unrelated species are within geographic and size range of the clade:

Rasopone cryptergates (Fig. 7; Supp Figs. S8 and S9 [online only]): lowland; petiolar node more cuboidal; posterolateral margins of head more angular.

Rasopone panamensis (Fig. 10; Supp Figs. S24 and S25 [online only]): lowland; petiolar node cuboidal. Rasopone MAS010 (Fig. 7; Supp Fig. S47 [online only]): smaller, HW 1.00 for both of the measured specimens of R. MAS010 versus 1.09 for the smallest measured specimen of R. costaricen; petiole somewhat thicker (average PTI 59 vs 53).

Measurements, Barva Form a, worker: HW 1.32 (1.25–1.41, 6); HL 1.56 (1.51–1.65, 6); SL 1.20 (1.19–1.21, 3); PTH 0.90 (0.83–0.94, 5); PTL 0.50 (0.48–0.53, 5); CI 85 (83–86, 6); SI 88 (85–93, 3); PTI 56 (54–58, 5).

Measurements, Barva Form b, worker: HW 1.19 (1.14–1.25, 10); HL 1.39 (1.33–1.47, 10); SL 1.08 (1.04–1.11, 3); PTH 0.85 (0.78–0.93, 7); PTL 0.46 (0.42–0.51, 7); CI 86 (84–89, 10); SI 91 (87–93, 3); PTI 54 (52–61, 7).

Measurements, Barva Form c, worker: HW 1.11 (1.09–1.14, 2); HL 1.28 (1.26–1.29, 2); SL 0.99 (0.98–1.00, 2); PTH 0.78 (0.77–0.78, 2); PTL 0.41 (0.41–0.41, 2); CI 88 (86–89, 2); SI 89 (87–90, 2); PTI 53 (53–53, 2).

Measurements, other populations, worker: HW 1.15 (1.09–1.21, 12); HL 1.33 (1.26–1.43, 12); SL 0.98 (0.91–1.09, 7); PTH 0.85 (0.72–0.95, 9); PTL 0.45 (0.39–0.53, 9); CI 86 (83–92, 12); SI 83 (76–91, 7); PTI 54 (50–58, 5).

Measurements, other populations, queen: HW 1.18 (1.08–1.27, 2); HL 1.32 (1.26–1.38, 2); SL 0.91; PTH 0.75; PTL 0.42; CI 89 (86–92, 2); SI 84; PTI 55.

Table 2. Continued

| Species                      | HW     | CI | SI | PTI | Clypeus  | Petiole         | Mandible     | Range             | Figures   |
|------------------------------|--------|----|----|-----|----------|-----------------|--------------|-------------------|-----------|
| JTL029                       | 1.37–1.67 | 84–102 | 67–81 | 50–61 | Intermediate | Striate        | Panama        | Fig. 12; Supp Fig. S35 (online only) |
| cubitalis                    | 1.40–1.71 | 82–100 | 82–100 | 50–61 | Sinuous   | Cuboidal        | Smooth        | Nicaragua-Costa Rica Fig. 13; Supp Figs. S10 and S11 (online only) |
| titanis                      | 1.51–1.84 | 84–102 | 78–96 | 52–64 | Sinuous   | Tapered         | Smooth        | Chiapas Fig. 13; Supp Fig. S33 (online only) |
| breviscapa                   | 1.53–1.87 | 90–110 | 71–87 |        | Truncate  | Intermediate    | Striate       | Bolivia Fig. 13, Supp Fig. S2 (online only) |
| rupinicola                   | 1.53–1.87 | 78–96 | 95–117 |        | Sinuous   | Intermediate    | Smooth        | Panama-Colombia Fig. 13; Supp Figs. S30 and S31 (online only) |

Metric characters are ±10% of mean.

Biology
This species complex occurs in cloud forest habitats, from 1,000 to 2,000 m elevation (although one enigmatic collection is from 250 m elevation on the Osa Peninsula). Workers, and in one case a dealate queen, are collected in Winkler samples of forest floor leaf litter and rotten wood. Workers have been collected beneath epiphytes in trees and beneath rotten wood on the ground. Workers have been found both in closed-canopy cloud forest and in open pastures near cloud forest edges (beneath wood on the ground). In Monteverde, in addition to specimens from multiple Winkler samples, a worker was found in soil of a clay bank in a steep-sided ravine, and a worker was found beneath a stone. At Estación Pittier in the Talamanca range, a dealate queen was found beneath a stone. It is likely that the most common forms (of the various cryptic species) nest in the soil, with workers foraging in the litter. One nest beneath epiphytes. Males can be common in Malaise traps (associated with COI results). An alate queen was collected by an INBio Parataxonomist, at Tapanti National Park, on 30 October 1991. Cryptic species in the complex may specialize on particular microhabitats (e.g., beneath epiphytes; see Comments).

Comments
DNA sequence data, both COI and UCE, support a clade endemic to Costa Rican and adjacent Panamanian cloud forest. Within the clade, genetic evidence also supports the occurrence of multiple sympatric species at two intensively sampled sites. But the genetic data are fragmentary and the relationships among species across sites is unclear. We take the approach of referring to the entire clade as R. costaricensis, with the acknowledgment that further study will almost certainly result in the further splitting of the clade into component species. We describe here what we currently know of the sympatric forms at particular sites.

There is evidence that three sympatric species occur on the Barva transect, on Costa Rica’s Caribbean slope. The three species differ in morphology, microhabitat, and COI sequence.

Form a (Fig. 11; Supp Fig. S5 [online only]): This is the largest of the three. The mandibles are smooth and shiny; the other two forms have striate mandibles. It is known from five separate collections: 1) 2 workers under epiphytes in an old treefall; 2) a worker and some brood in a rotten knot in a treefall; 3) a worker under epiphytes on dead wood at the edge between pasture and forest; 4) a Berlese sample of epiphytic material; and 5) a worker in a collection of mixed ants collected by hand. The first four collections were from a 1,500 m site and the last collection from an 1,100 m site. It is notable that no specimens were collected in the 350 miniWinkler samples of forest floor litter that were taken at the two sites.
Form b (Fig. 10; Supp Fig. S6 [online only]): This and Form c have striate mandibles. Form b is very similar to Form c, but the petiolar node is somewhat more tapering and scale-like. It occurred at the 1,500 m and 2,000 m sites on the Barva transect, where it was moderately abundant in miniWinkler samples. Parataxonomist Ronald Vargas collected a worker by hand at the 2,000 m site.

Form c (Fig. 8; Supp Fig. S7 [online only]): This form has a relatively less scale-like node than Form b. It occurred at the 1,500 m site, from two collections. One worker was collected by hand from under rotten wood. Two workers were collected by student Andy Boring in an open pasture area, beneath rotten wood. These two collections were united by DNA sequence data (see below), which also supported their distinctness from Form b. However, a few specimens from miniWinklers from the 1,500 m and 2,000 m sites lacked sequence data and were intermediate in petiolar shape, and thus could not be assigned to one form or the other.

There is evidence for at least three sympatric species, based on COI clusters in the BOLD database, on the peak of Volcán Cacao, a cloud forest site in Guanacaste, Costa Rica. The evidence comes mostly or entirely from males in Malaise traps, sampled by Alex Smith and others. Barva Form a and Form b cluster with one of the Cacao clusters. Form a and Form b differ from each other by about 5%, while each differs from the Cacao specimens by about 3%. Barva Form c clusters with the largest Cacao cluster, which contains over 120 specimens, with much less than 0.5% sequence divergence among them. A third Cacao cluster is small, and currently unassociated with any other specimens (Fig. 3; Supp Fig. S1 [online only]).

Other populations are known from Monteverde (the type locality) in the Cordillera de Tilarán, multiple cloud forest sites in the Cordillera de Talamanca and mountains of western Panama, and one lowland site near the Osa Peninsula (Fig. 9; Supp Figs. S3 and S4 [online only]).

**Rasopone cryptergates New Species**

(Fig. 7; Supp Figs. S8 and S9 [online only])

(Zoobank LSID: urn:lsid:zoobank.org:act:FFE0F396-AC3E-46B5-A78F-B0786C8E44DE)

**HOLOTYPE:** 1 alate queen, Costa Rica, Heredia: La Selva Biological Station, 10.43748 -84.01381 ±20 m, 50 m, 9-iii-2004, lowland rainforest, ALAS, M25787 [UCR, unique specimen identifier JTLC000008527]. **PARATYPE:** same data as holotype except 10.41745 -84.01627 ±20 m, 50 m, 2-ii-2005, mature wet forest, ex sifted leaf litter, TEAM, AMI-1-W-022-06 [1 worker, CAS, INBio003660648]; 10.42519 -84.00399 ±20 m, 50 m, 18-v-1999, light trap, ALAS, L002038 [1 alate queen, MCZC, INBioCRIO1001276531; 1 alate queen, UCD, INBioCRIO1001276532]; 10.43333 -84.01667 ±2 km, 50 m, 1-ix-2003, wet forest, H. A. Hespenheide [1 alate queen, USNM, JTLC000005546].

**Geographic range.** Costa Rica.

**Diagnosis**

Lowland; mandible striate; anterior clypeal margin truncate; side of head with a few inconspicuous short setae; posterior margin of head in face view flat, posterolateral margins subangulate; petiolar node nearly cuboidal. Two species are within size and geographic range of **R. cryptergates**.

**Rasopone costaricensis** (Fig. 9; Supp Figs. S3 and S4 [online only]): montane; petiolar node more scale-like; posterolateral margins of head more rounded.

**Rasopone MAS010** (Fig. 7; Supp Fig. S47 [online only]): montane; side of head bare; posterolateral margins of vertex somewhat more rounded.

**Measurements, worker:** HW 1.07, HL 1.25, SL 0.84, PTL 0.47, PTH 0.82, CI 86, SI 79, PTI 57 (n = 1).

**Measurements, queen:** HW 1.16 (1.10–1.23, 9); HL 1.37 (1.28–1.46, 9); SL 1.10 (1.06–1.13, 2); PTH 0.81 (0.76–0.92, 9); PTL 0.48 (0.44–0.55, 5); CI 85 (81–87, 9); SI 93 (92–94, 2); PTI 59 (57–60, 5).

**Biology**

This species occurs in lowland rainforest, from sea level to about 500 m elevation. Only one worker is known, from a Winkler sample of forest floor litter and rotten wood. Multiple alate queens are known, from Malaise traps, flight intercept traps, and light traps. One alate queen is from a Berlese sample of litter and soil; it is possible the queen was a contaminant, attracted to the light bulb of the Berlese funnel. The queen records are from the months of January, February, March, May, and September.

**Comments**

There has been intensive Winkler sampling at La Selva Biological Station, and workers of the smaller species **R. pluviselva** occur moderately frequently in these samples, yet only one worker of **R. cryptergates** has been discovered. The alate queens are the reverse, with moderately abundant queens of **R. cryptergates**, and a single alate queen of **R. pluviselva**. Dealate queens of **R. pluviselva** occur occasionally in Winkler samples. It is possible that **R. cryptergates** is more subterranean than **R. pluviselva**, and workers hardly ever forage in the litter. Alternatively, **R. cryptergates** may prefer open habitats such as pastures and lawns, and thus be more abundant in the agricultural landscape adjoining La Selva. **Rasopone cryptergates** may produce more abundant alate queens, or queens that fly greater distances or higher above the ground. In contrast, **R. pluviselva** may rely on fewer or less vagile queens that fly close to the ground, rarely being captured by Malaise or light traps.

UCE and COI data are available for the single worker specimen, placing it in a clade with three other species known only from Panama. However, the worker was associated with the queens based on morphology alone: the cuboidal shape of the petiolar node and matching size. There are currently no genetic data definitively associating the sequenced worker with the holotype queen, so future confirmation is warranted.

**Rasopone cubitalis New Species**

(Fig. 13; Supp Figs. S10 and S11 [online only])

(urn:lsid:zoobank.org:act:71BE7581-29AF-40A5-5797-1ECFA88160EC)

**HOLOTYPE:** 1 worker, Costa Rica, Alajuela, 10 km E Monteverde, 10.30677 -84.7165 ±50 m, 880 m, 17-v-2014, wet forest, nest in clay bank, J. Longino, JTL8670 [UCR, unique specimen identifier CASENT0635091]. **PARATYPE:** same data as holotype [1 worker, CASENT0633211].

**Geographic range.** Southern Nicaragua to Costa Rica.

**Diagnosis**

Lowland; mandible smooth and shiny; anterior clypeal margin short, sinuous; side of head with abundant erect setae; face with abundant short erect setae; face sculpture of dense, minute puncta overlain...
with larger, more widely spaced puncta visible in particular orientation and lighting; petiole cuboidal.

**Measurements, worker:** HW 1.56 (1.50–1.65, 4); HL 1.70 (1.65–1.76, 4); SL 1.41 (1.34–1.50, 4); PTH 1.06 (1.00–1.13, 4); PTL 0.58 (0.54–0.64, 4); CI 91 (89–93, 4); SI 91 (90–92, 4); PTI 55 (51–58, 4).

**Measurements, queen:** HW 1.82, HL 1.93, SL 1.61, PTL 0.66, PTH 1.26, CI 94, SI 88, PTI 52 (n = 1).

**Biology**
This species occurs in lowland rainforest, with records from 160 to 880 m elevation. Workers have twice been collected in Winkler samples of forest floor litter and rotten wood. An alate queen was collected in a Malaise trap in October. Two workers and a larva were collected in a small chamber in a clay bank, in mature rainforest.

**Comments**
This species is known from three localities, one in southern Nicaragua and two in northern Costa Rica. UCE and COI data show a single cluster with little sequence divergence among the three populations.

**Rasopone ferruginea** *(Smith)*
*(Figs. 4 [queen] and 11; Supp Figs. S12 and S13 [online only])*

*Ponera ferruginea* *Smith,* 1858: 100. Holotype queen: Mexico [BMNH, AntWeb image examined].

*Euponera* *(Mesoponera)* *ferruginea* : *Emery,* 1901: 47.

*Trachymesopus ferrugineus:* *Brown,* 1963: 7.

*Pachycondyla ferruginea* : Brown, in *Bolton,* 1995: 305; *MacKay,* 2010: 319 (description of worker).

*Rasopone ferruginea* : *Schmidt* and *Shattuck,* 2014: 210.

**Geographic range.** Mexico (Tamaulipas) to Nicaragua.

**Measurements, worker:** HW 1.27 (1.19–1.33, 4); HL 1.38 (1.33–1.45, 4); SL 1.04 (0.99–1.10, 4); PTH 0.86 (0.80–0.92, 4); PTL 0.46 (0.42–0.47, 4); CI 92 (88–94, 4); SI 82 (81–84, 4); PTI 53 (50–60, 4).

**Measurements, queen:** HW 1.33 (1.23–1.43, 2); HL 1.42 (1.31–1.54, 2); SL 1.15; PTH 0.93; PTL 0.50; CI 94 (93–94, 2); SI 81; PTI 53.

**Diagnosis**
Mandible striate; anterior clypeal margin sinuous; side of head lacking erect setae; petiolar node tapering, scale-like. Three species are within geographic and size range of *R. ferruginea:*

*Rasopone politognatha* *(Fig. 9; Supp Figs. S28 and S29 [online only]):* mandible smooth; anterior clypeal margin truncate; petiole less scale-like.

*Rasopone subcubitalis* *(Fig. 10; Supp Fig. S32 [online only]):* anterior clypeal margin truncate; petiole nearly cuboidal.

*Rasopone JTL035* *(Fig. 9; Supp Fig. S38 [online only]):* mandible smooth; anterior clypeal margin truncate; petiole less scale-like.

**Biology**
This species occurs in a variety of wet forest habitats, across an elevational range of 180–1,340 m. Habitats include mature and second growth forests, from lowland rainforest to cloud forest. Cloud forest habitats include *Liquidambar* dominated forests in Mexico to mesophyll cloud forest in Nicaragua. Most specimens are workers from Winkler samples of forest floor litter and rotten wood. Student D. J. Cox collected a dealate queen and a worker while hand collecting at night. A worker was collected on a clay bank at a stream edge, and another one was collected at a cookie bait.

**Comments**
The image of the holotype queen on AntWeb shows the distinctive clypeal shape, with a sinuous, non-trapezoidal anterior margin. The size (measured on image), lack of setae on the side of the head, and the asymmetrical, scale-like node also match material identified here as *R. ferruginea.* North of the Isthmus of Tehuantepec, *R. ferruginea* is sympatric with *R. JTL034* and *R. JTL035.* In the northern lowlands of Chiapas, it is sympatric with *R. minuta* and *R. subcubitalis.* In the Cordillera de Chiapas it is sympatric with *R. politognatha.* There are no records from Guatemala. In Honduras, it is known from the hills above Tela, where it is sympatric with *R. minuta.* In Nicaragua, it is known from Cerro Musin, where it is sympatric with *R. mesoamericana* and *R. politognatha.*

**Rasopone guatemalensis** *(New Species)*
*(Fig. 8; Supp Figs. S14 and S15 [online only])*

(Zoobank LSID: urn:lsid:zoobank.org:act:8ADF3C2C-761B-4BD8-B44A-E74B563BF801)

**Holotype:** Guatemala, Suchitepéquez: Refugio El Quetzal, 14.55483 −91.19299 ±50 m, 1.388 m, 15-vi-2009, oak forest, ex sifted leaf litter, R. S. Anderson, RSA2009-102 [CAS, unique specimen identifier CASENT0611754].

**Paratypes:** same data as holotype [1 worker, DZUP, CASENT0644547; 1 worker, JTLC, CASENT0644546; 1 worker, MCZC, CASENT0644544; 1 worker, UCE, CASENT0644545; 1 worker, UNAM, CASENT0644548]; same data except 14.54967 −91.19357 ±50 m, 1.641 m, mixed hardwood forest, RSA2009-103 [1 worker, UVGC, CASENT0611773]; 4 km S Vol. Atitlán, 14.54992 −91.18999 ±50 m, 1.625 m, 15-vi-2009, cloud forest, ex sifted leaf litter, LLAMA, Wa-B-09-1-46 [1 dealate queen, CAS, CASENT0612926]; 14.55103 −91.1935 ±306 m, 1.750 m, 15-vi-2009, Wm-B-09-2-01 [1 worker, USNM, CASENT0611836].

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

**Diagnosis.** Montane; mandible smooth and shining or very faintly striate; anterior clypeal margin truncate; side of head bare or with few, inconspicuous setae; petiolar node tapering, scale-like. One species is within geographic and size range of *R. guatemalensis:*

*Rasopone politognatha* *(Fig. 9; Supp Figs. S28 and S29 [online only]):* petiole less scale-like; head broader (mean CI 92 vs 86).

**Measurements, worker:** HW 1.11 (1.05–1.23, 9); HL 1.29 (1.20–1.43, 9); SL 0.97 (0.94–1.00, 3); PTH 0.75 (0.72–0.79, 9); PTL 0.43 (0.39–0.46, 9); CI 86 (82–89, 9); SI 86 (85–87, 3); PTI 56 (52–61, 9).

**Measurements, queen:** HW 1.11 (1.06–1.16, 2); HL 1.25 (1.22–1.28, 2); SL 0.95 (0.91–0.99, 2); PTH 0.75 (0.71–0.79, 2); PTL 0.42 (0.42–0.43, 2); CI 89 (87–90, 2); SI 86 (85–86, 2); PTI 57 (54–59, 2).

**Biology**
This species occurs in cloud forest habitats, with a known elevational range of 1,270–1,850 m. Habitats include pine and oak forests, and diverse mesophyll forests. All known specimens are from Winkler and Berlese samples of forest floor litter and rotten wood. Most specimens are workers, but two dealate queens are known.

**Comments**
UCE and COI results support this species delimitation.

**Rasopone lunaris** *(Emery)*
*(Fig. 8; Supp Figs. S16–S18 [online only])*

With larger, more widely spaced puncta visible in particular orientation and lighting; petiole cuboidal.

**Measurements, worker:** HW 1.56 (1.50–1.65, 4); HL 1.70 (1.65–1.76, 4); SL 1.41 (1.34–1.50, 4); PTH 1.06 (1.00–1.13, 4); PTL 0.58 (0.54–0.64, 4); CI 91 (89–93, 4); SI 91 (90–92, 4); PTI 55 (51–58, 4).

**Measurements, queen:** HW 1.82, HL 1.93, SL 1.61, PTL 0.66, PTH 1.26, CI 94, SI 88, PTI 52 (n = 1).
**Ponera lunaris** Emery, 1896: 55, pl. 1, fig. 12. Holotype worker: Paraguay (Balzan) [MSNG, AntWeb image examined].

_Pachycondyla lunaris:_ Emery, 1901: 45; Brown, in Bolton, 1995: 307. [Queen described by MacKay and MacKay, 2010: 44 is _R. panamensis._]

_Euponea (Trachymesopus) lunaris:_ Emery, 1911: 85.

*Trachymesopus lunaris* Kempf, 1960: 424.

*Rasopone lunaris* Schmidt and Shattuck, 2014: 210.

**Geographic range.** Widespread in tropical South America.

**Diagnosis**

Mandible smooth and shining or very faintly striate; anterior clypeal margin truncate; side of head with short erect setae; petiolar node relatively long, posterior margin forming a continuous curve, without differentiated dorsal face. This is the only known species from Paraguay and southern Brazil.

**Measurements, worker:** HW 1.11 (0.98–1.23, 12); HL 1.22 (1.07–1.34, 12); SL 0.86 (0.77–0.98, 12); PTH 0.78 (0.70–0.85, 11); PTL 0.47 (0.41–0.52, 11); CI 91 (88–96, 12); SI 78 (70–81, 12); PTI 60 (51–65, 11).

**Measurements, queen:** HW 1.16 (1.04–1.31, 4); HL 1.27 (1.15–1.41, 4); SL 0.89 (0.82–0.98, 4); PTH 0.82 (0.74–0.90, 4); PTL 0.48 (0.41–0.53, 4); CI 92 (90–93, 4); SI 77 (74–79, 4); PTI 58 (55–62, 4).

**Biology**

This species occurs in lowland habitats, with records from sea level to 1,050 m elevation. Sampling methods, when indicated on specimen labels, are Winkler and ‘hypogaeic Winkler’.

**Comments**

UCE results reveal that most _Rasopone_ species are in a clade of relatively smaller species that is sister to the large species _R. cubitalis._ These smaller species occur throughout Middle and South America. Within this clade of smaller species, three South American specimens were sequenced for UCEs, and these form a clade sister to all the Middle American specimens (Panama northward). One of the sequenced South American specimens is from southern Brazil (Minas Gerais). The morphology closely matches the type of _R. lunaris_, and the locality is not too distant from the type locality. Thus, this specimen can be identified as _R. lunaris_ with confidence. This species is sister to the two other sequenced specimens from South America. One of the latter is from Amazonian Colombia and was initially identified as _R. lunaris_, differing only in the lack of erect setae on the side of the head, and somewhat larger size. The other one is from French Guiana and has distinctive puncta on the face. The former is placed in the morphospecies JTL049, and the latter in JTL047. Given the sparse sampling from South America, we can expect continued discovery of cryptic species and geographic structuring there. The examined specimens of _R. lunaris_ from southern South America are quite uniform and suggest a single widespread species at the southern range limit of the genus. However, the scattered records from northern South America are more variable and future sequencing work may identify them as multiple cryptic species, perhaps more related to the nearby morphospecies JTL047, JTL048, and JTL049.

MacKay and MacKay had a broad view of _R. lunaris_, identifying material from Guatemala to Paraguay as _Pachycondyla lunaris_. Our definition is narrower and more geographically limited.

**Rasopone mesoamericana** New Species

(Figs. 5 [male] and 12; Supp Figs. S19–S21 [online only])

(urn:lsid:zoobank.org:act:11404229-093E-4FFE-B5B9-3750F2572DC2)

**HOLOTYPE:** 1 worker, Guatemala, Zacapa: 3.5 km SE La Union, 14.95 – 89.27 ±?, 1,500 m, 6-vi-1991, cloud forest, forest litter, R. S. Anderson, RSA91-053 [CAS, unique specimen identifier CASENT0603245]. **PARATYPES:** same data as holotype except 4-vi-1991, RSA91-050 [1 worker, MCZC, CASENT0603696; 1 worker, UCD, CASENT0603728; 1 worker, USNM, CASENT0603690; 1 worker, UVCJ, CASENT0603565].

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

**Diagnosis**

Mandible striate; anterior clypeal margin truncate; side of head with variable pilosity, nearly bare to evenly distributed short erect setae; face sculpture of dense, minute puncta overlain with larger, more widely spaced puncta visible in particular orientation and lighting (very faint in some specimens); petiolar node tapering, scale-like. Two species are within geographic and size range of _R. mesoamericana:_

*Rasopone subcubitalis* (Fig. 10; Supp Fig. S32 [online only]): petiole less scale-like.

*Rasopone JTL037* (Fig. 12; Supp Fig. S39 [online only]): petiole less scale-like.

**Measurements, worker:** HW 1.47 (1.38–1.59, 8); HL 1.65 (1.53–1.81, 8); SL 1.23 (1.08–1.33, 6); PTH 1.07 (0.99–1.22, 8); PTL 0.60 (0.55–0.67, 8); CI 89 (86–92, 8); SI 85 (78–88, 6); PTI 56 (53–58, 8).

**Measurements, queen:** HW 1.40 (1.32–1.48, 2); HL 1.51 (1.44–1.58, 2); SL 1.15 (1.05–1.25, 2); PTH 1.02 (0.97–1.07, 2); PTL 0.56 (0.56–0.56, 2); CI 93 (92–94, 2); SI 82 (79–85, 2); PTI 55 (53–57, 2).

**Biology**

This species occurs across a range of wet forest habitats, from 310 to 1,750 m elevation. Most records are from cloud forest, but often at the lower edge, at the transition to lowland habitat. For example, on the Barva transect in Costa Rica, _R. mesoamericana_ is known from an 1,100 m site, while _R. costaricensis_ occurs at 1,300 and 2,000 m sites. BOLD specimens from Guanacaste, Costa Rica are males from Malaise traps at 1,080 m and 1,185 m, and workers from a litter sample and a bait at 1,000 m and 972 m, respectively. In contrast, none are known from the nearby higher elevation peak, where _R. costaricensis_ is common. In some sites workers can be moderately abundant in Winkler samples of forest floor litter and rotten wood. Dead queens occasionally occur in Winkler samples. Workers are occasionally collected at baits. Males occur in Malaise traps.

**Comments**

Molecular data indicate that _Rasopone mesoamericana_ and _R. subcubitalis_ are sister species and the two are quite similar. _Rasopone mesoamericana_ has a more asymmetrical, scale-like petiolar node and is larger on average (but the size ranges overlap). The two have no known cases of sympatry in a local assemblage, but the geographic ranges broadly overlap. It may be somewhat arbitrary to treat them as two species at this stage, but they do form two separate clades, and the petiolar shape differences are consistent. BOLD COI sequences are available for many specimens in this clade, and the BOLD results are fully congruent with the UCE results. BOLD...
sequences segregate into five allopatric BINs, raising the potential for multiple cryptic species.

**Rasopone minuta** (MacKay and MacKay)

*(Fig. 6; Supp Figs. S22 and S23 [online only])*

*Rasopone minuta* MacKay and MacKay, 2010: 463, figs. 181, 585. Holotype queen: Mexico, Chiapas, 10 km W Palenque [label indicates 10 km S], 30 May 1988 (W. Mackay #10600) [MCZC, examined].

*Rasopone minuta*: Schmidt and Shattuck, 2014: 210.

**Geographic range.** Mexico (Chiapas) to Honduras.

**Diagnosis**

Lowland; mandible smooth and shiny; anterior clypeal margin truncate; side of head bare or with a few inconspicuous erect setae; petiolar node moderately tapering, scale-like; color orange. The most similar species is *R. pluviselva* (Fig. 6; Supp Figs. S26 and S27 [online only]), which has shorter scapes on average (mean SI 73 vs 77).

**Measurements, worker:** HW 0.88 (0.83–0.93, 7); HL 1.01 (0.95–1.08, 7); SL 0.68 (0.64–0.72, 7); PTH 0.59 (0.58–0.61, 7); PTL 0.34 (0.31–0.37, 7); CI 87 (85–90, 7); SI 77 (76–80, 7); PTI 57 (52–60, 7).

**Measurements, queen:** HW 0.88 (0.85–0.90, 2); HL 1.02 (0.99–1.05, 2); SL 0.66 (0.63–0.69, 2); PTH 0.59 (0.58–0.60, 2); PTL 0.36 (0.34–0.39, 2); CI 86 (86-86, 2); SI 76 (75–76, 2); PTI 61 (58–64, 2).

**Biology**

This species occurs in lowland wet to seasonal moist forest, with records from sea level to 890 m elevation. The holotype queen was collected in a pitfall trap. Other specimens are from Winkler samples of forest floor litter and rotten wood. A dealate queen was collected in a Winkler sample.

**Comments**

This is one of the two smallest species, the other being the allopatric *R. pluviselva*, which occurs further south. These two species are very similar but differ in relative scape length: *R. minuta*, SI 76–80 (n = 7); *R. pluviselva*, SI 72–74 (n = 7). *Rasopone minuta* is a lowland species, typically without sympatric forms at low elevation, but overlapping with cloud forest species (such as *P. ferruginea* panamensis) at the upper end of its elevational range. UCE and COI data support the delimitation of this species.

MacKay and MacKay included in the description a worker from Guatemala, but expressed doubts of its conspecificity. They indicated that the worker petiolar node was rectangular, rather than narrowed dorsally as in the holotype queen. Petiole shape shows little intraspecific variation, and the worker is undoubtedly not conspecific. They also identified a worker from Venezuela as *R. minuta*, but this is also unlikely to be conspecific.

**Rasopone panamensis** (Forel) New Status

*(Fig. 10; Supp Figs. S24 and S25 [online only])*

*Ponera ferruginea var. panamensis* Forel, 1899: 15. Neotype worker: Costa Rica, San José: Cerro Plano, 9.48059 –83.96402 ±10 m, 1,060 m, 4-vii-2015, ridgetop cloud forest, isolated peak with oak trees, ex sifted leaf litter, ADMAC, Wa-E-06-1-45 [CAS, unique specimen identifier CASENT0644252].

*Eunympa* (Mesoponera) *ferruginea var. panamensis*: Emery, 1911: 82.

*Trachymesopus ferrugineus var. panamensis*: Kempf, 1972: 251.

**Pachycondyla ferruginea panamensis**: Brown, in Bolton, 1995: 308.

**Pachycondyla ferruginea**: MacKay and MacKay, 2010: 319 (incorrect synonymy).

**Pachycondyla lunaris**: MacKay and MacKay, 2010: 445 (description of queen, misidentification).

**Geographic range.** Costa Rica, Panama.

**Diagnosis**

Lowland; mandible striate; anterior clypeal margin truncate; side of head bare; petiolar node cuboidal. One species is within geographic and size range of *R. panamensis*:

*Rasopone costaricensis* (Fig. 9; Supp Figs. S3 and S4 [online only]): montane; petiole more scale-like.

**Measurements, worker:** HW 1.23 (1.12–1.36, 6); HL 1.40 (1.31–1.54, 6); SL 1.05 (0.94–1.15, 5); PTH 0.95 (0.87–1.06, 6); PTI 0.54 (0.48–0.61, 6), CI 88 (86–89, 6); SI 84 (82–85, 5); PTI 58 (55–60, 6).

**Measurements, queen:** HW 1.16 (1.13–1.18, 2); HL 1.32 (1.30–1.34, 2); SL 0.97 (0.94–1.01, 2); PTH 0.88; PTI 0.46; CI 88 (87–88, 2); SI 84 (83–85, 2); PTI 52.

**Biology**

This species occurs in lowland wet to seasonal dry forest habitat, with records from sea level to 1,070 m elevation. Nearly all specimens are workers and occasional dealate queens from Winkler samples of forest floor litter and rotten wood.

**Comments**

This is a lowland species known from both coasts of Costa Rica. On the Pacific coast, it occurs from Cabo Blanco on the Nicoya Peninsula to the Osa, where it is the common species in litter samples. On the Caribbean side, it is the common species in litter at Hitoy Cerere, south of Limón, but is unknown north of there, in spite of intensive sampling at La Selva Biological Station and the Barva transect.

The original type of *R. panamensis* is missing. Longino searched for it during a visit to MHNG in 1990, Mackay and Mackay (2010) reported it missing, and Fisher did not find it when imaging MHNG types in 2013. The queen is described as being 6.5 mm long, the mandible with an oblique sulcus, and the petiolar node concave posteriorly but as thick at the top as at the base (‘mais aussi épaisse en haut qu’en bas’). These characters match the relatively common lowland species found in the southern Pacific lowlands of Costa Rica, near the originally published type locality (Bugaba, Panama).

**Rasopone pluviselva** New Species

*(Fig. 6; Supp Figs. S26 and S27 [online only])*

(urn:lsid:zoobank.org:act:F2F28C33-1DA6-44E1-A2AF-A1A147C3D033)

*Mesoponera ferruginea*: Wheeler and Wheeler, 1976: 54 (description of larva) [based on a specimen from Turrialba, Costa Rica, January 1973, received from W. L. Brown].

**HOLOTYPE:** 1 worker, Costa Rica, Heredia: La Selva Biological Station, 10.4171 –84.02216 ±20 m, 50 m, 13-vi-2005, mature wet forest, ex sifted leaf litter, TEAM, AMI-1-W-036-06 [UCR, unique specimen identifier INB0003677242]. PARATYPES: same data as holotype except 10.41561 –84.02097 ±20 m, 50 m, 3-iii-2005, AMI-1-W-023-02 [1 worker, UCD, INB0003660695]; 7 km SW Pro. Viejo, 10.40132 –84.03892 ±20 m, 160 m,
3-iii-2005, AMI-2-W-031-01 [1 worker, MCZC, INB0003667438]; 10.40395 −84.04011 ±20 m, 160 m, 16-vi-2005, AMI-2-W-042-10 [1 worker, DZUP, INB0003678004]; 10.40601 −84.04189 ±20 m, 160 m, 2-ii-2007, AMI-2-W-116-08 [1 worker, USNM, INB0003698324]; 11 km ESE La Virgen, 10.35 −84.05 ± 2 km, 300 m, 15-ii-2004, montane wet forest, hojarasca, ALAS, 03/WF/01/13 [1 worker, CAS, INB0003620958]; 03/WF/01/20 [1 worker, UNAM, INB0003621052].

**Geographic range.** Honduras (La Moskitia) to Panama.

**Diagnosis**

Lowland; mandible smooth and shiny to faintly striate; anterior clypeal margin truncate; side of head bare or with a few inconspicuous erect setae; petiolar node moderately tapering, scale-like; color orange. The most similar species is *R. minuta* (Fig. 6; Supp Figs. S22 and S23 [online only]), which has longer scapes on average (mean SI 77 vs 73).

**Measurements, worker:** HW 0.84 (0.80–0.91, 26); HL 0.96 (0.93–1.02, 26); SL 0.64 (0.60–0.66, 7); PTH 0.57 (0.55–0.62, 23); PTL 0.36 (0.34–0.40, 23); CI 88 (72–74, 7); PTI 63 (60–68, 23).

**Measurements, queen:** HW 0.87 (0.84–0.91, 4); HL 0.98 (0.97–0.99, 4); SL 0.65 (0.64–0.67, 2); PTH 0.59 (0.59–0.60, 3); PTL 0.37 (0.36–0.38, 3); CI 89 (86–92, 4); SI 73 (72–74, 2); PTI 62 (61–63, 3).

**Biology**

This species occurs in lowland wet to seasonal dry forest habitats, with records from 50 to 1100 m elevation. BOLD data associate a male from a Malaise trap in Santa Rosa National Park, a dry forest site in Costa Rica. Most specimens are workers and the occasional dealate queen in Winkler or Berlese samples of forest floor litter and rotten wood. One worker was hand collected beneath a stone. An inexplicable record is a worker in a vegetation beating sample from an 1,100 m site on the Barva transect in Costa Rica. An alate queen was collected in February in a Malaise trap.

**Comments**

This is one of the two smallest species, the other being *R. minuta*. These two species have mean HW < 0.9, while all other species have mean HW > 0.9. Both are lowland species. They are allopatic, *R. pluviselva* occurring east and south of the Sierra de Agalta in Honduras, and *R. minuta* occurring north and west of this range. They are extremely similar, but differ in relative scape length: *R. minuta*, SI 76–80 (n = 7); *R. pluviselva*, SI 72–74 (n = 7).

BOLD COI data unite specimens from Honduras (Las Marias), Nicaragua (Saslaya), Costa Rica (Barva transect, Santa Rosa National Park, Osa), and Panama (Barro Colorado Island). UCE data likewise unite two specimens, one from Saslaya and one from the Barva transect, and the COI sequence from these specimens is consistent with the BOLD results. We have not examined Panama specimens directly, but BOLD images of a dealate queen from the Barro Colorado Island match our concept of *R. pluviselva*. The COI data form four geographically structured BINs with Panama sister to Costa Rica northward, and Pacific slope Costa Rica sister to an Atlantic slope region that extends from Costa Rica to Honduras. Pacific slope Costa Rica further separates into two BINs, based on one specimen from Santa Rosa National Park and one specimen from the Osa Peninsula.

**Rasopone politognatha** New Species

(Fig. 9; Supp Figs. S28 and S29 [online only])

(Zoobank LSID: urn:lsid:zoobank.org:act:C0B95FEC-48C6-468C-8E08-46D429972551)

HOLOTYPE: 1 worker, Guatemala, Zacapa: 2 km SE La Unión, 14.95442 −89.27697 ±50 m, 1,430 m, 12-v-2009, cloud forest, ex sifted leaf litter, LLAMA, Wa-B-03-2-08 [CAS, unique specimen identifier CASENT0612523]. PARATYPES: same data as holotype except 14.95448 −89.27704 ±50 m, 1,430 m, Wa-B-03-2-06 [1 worker, UNAM, CASENT0612522]; 14.95454 −89.27711 ±50 m, 1,430 m, Wa-B-03-2-04 [1 dealate queen, CASENT0612518]; 14.9546 −89.27718 ±50 m, 1,430 m, Wa-B-03-2-02 [1 worker, MCZC, CASENT0612516; 1 worker, UCD, CASENT0612517]; 3.5 km SE La Unión, 14.95 −89.26667 ±20 m, 1,500 m, 4-v-1991, cloud forest, forest litter, R. S. Anderson, RSA91-050 [1 worker, UVGC, CASENT0603718]; 6-v-1991, RSA91-053 [1 worker, USNM, CASENT0603251].

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

**Diagnosis**

Montane; mandible smooth and shiny; anterior clypeal margin truncate; side of head bare; petiolar node weakly tapering, subcuboidal. Three species are within geographic and size range of *R. politognatha*:

- **Rasopone ferruginea** (Fig. 11; Supp Figs. S12 and S13 [online only]): mandible striate; anterior clypeal margin sinusous; petiole more scale-like.
- **Rasopone guatemalensis** (Fig. 8; Supp Figs. S14 and S15 [online only]): petiole more scale-like; head narrower (mean CI 86 vs 92).
- **Rasopone subcubitalis** (Fig. 10; Supp Fig. S32 [online only]): mandible striate.

**Measurements, worker:** HW 1.16 (1.10–1.24, 12); HL 1.27 (1.20–1.36, 12); SL 0.95 (0.87–0.99, 11); PTH 0.78 (0.71–0.82, 10); PTL 0.43 (0.40–0.47, 10); CI 92 (88–96, 12); SI 82 (79–86, 11); PTI 56 (52–60, 10).

**Measurements, queen:** HW 1.17, HL 1.28, SL 0.98, PTL 0.45, PTH 0.81, CI 91, SI 83, PTI 55 (n = 1).

**Biology**

This species occurs in cloud forest habitats, with records from 1,200 to 1,550 m elevation. All collections are workers and, in one case, a dealate queen in Winkler or Berlese samples of forest floor litter and rotten wood.

**Comments**

UCE and COI data support the delimitation of this species.

**Rasopone rupinicola** (MacKay and MacKay)

(Fig. 13; Supp Figs. S30 and S31 [online only])

*Pachycondyla rupinicola* MacKay and MacKay, 2010: 504, figs. 94, 96, 205, 309, 627–631. Holotype worker, paratype queen, male: Colombia, Valle: Mun. Buenaventura, 4.5 km above R. Aguacalera on old rd. to Cali, 17–19 June 1971 (W. L. Brown, S. Chaplin, R. B. Root, C. Pearson) [MCZC] (examined).

**Rasopone rupinicola:** Schmidt and Shattuck, 2014: 210.

**Geographic range.** Panama, Colombia.

**Measurements, worker:** HW 1.70, HL 1.95, SL 1.80, CI 87, SI 106 (n = 1).
Comments
This species is much larger than all but one Central American species (R. titanis from Chiapas, Mexico), with larger eyes and longer scape. W. L. Brown and colleagues made multiple collections from a lowland wet forest area in southwestern Colombia, ~300 m elevation. One label says ‘rocky wet quebrada’. A disjunct collection is from Cerro Campana, a cloud forest site in Panama, 975 m elevation.

*Rasopone subcubitalis* New Species
(Fig. 10; Supp Figs. S32 [online only])
(urn:lsid:zoobank.org:act:DAC52866-DD20-4B90-84EF-DC01811C98A3)

**HOLOTYPE:** 1 worker, Honduras, Comayagua: PN Cerro Azul Meambar, 14.87137−87.90032 ±20 m, 1,120 m, 20-v-2010, ridgetop cloud forest, ex sifted leaf litter, LLAMA, Wa-C-04-1-02 [CAS; unique specimen identifier CASENT0615367]. **PARATYPES:** same data as holotype 1 worker, JTLC, CASENT0644540; 1 worker, UNAM, CASENT0644539; same data except 14.87112−87.99938 ±300 m, 1,100 m, Wm-C-04-1-01 [1 worker, DZUP, CASENT0644538; 1 worker, UCD, CASENT0644537]; 14.8712−87.90011 ±20 m, 1,120 m, Wa-C-04-1-08 [1 worker, MCZC, CASENT0615252; 1 worker, USNM, CASENT0617285].

**Geographic range.** Mexico (Chiapas) to Honduras.

**Diagnosis.** Mandible striate; anterior clypeal margin truncate; side of head with evenly distributed short erect setae; face sculpture of dense, minute puncta overlain with larger, more widely spaced puncta visible in particular orientation and lighting; petiolar node subcuboidal. Among the three species in Darien, *R. cryptergates* (JTL027 and JTL030) and other species: two morphospecies from the same site in Darien (UCE phylogenetic results place this specimen together with three species: two morphospecies from the same site in Darien (JT029 and JT030) and *R. cryptergates* from Costa Rica.

**Measurements, worker:** HW 1.42, HL 1.56, SL 1.07, PTL 0.51, PTH 0.80, CI 93, SI 87, PTI 58 (n = 1).

**Comments**
This is the species known from a single worker, from a moist forest site at 810 m elevation. The worker was collected in a ravine, in excavated soil of a clay bank.

**Rasopone JTL027**
(Fig. 8; Supp Figs. S34 [online only])
**Geographic range.** Panama (Darien).

**Diagnosis**
Mandible striate; anterior clypeal margin truncate; side of head bare; petiolar node cuboidal. The other two species from Darien are much larger, with HW ≥ 1.4. It is similar to *R. cryptergates* (Fig. 7; Supp Figs. S8 and S9 [online only]), but with relatively longer petiole (mean PTI 64 vs 57).

**Measurements, worker:** HW 1.12, HL 1.34, SL 1.07, PTL 0.51, PTH 0.80, CI 83, SI 96, PTI 64 (n = 1).

**Biology**
The species is known from a single worker, from a moist forest site at 810 m elevation. The worker was collected in a ravine, in excavated soil of a clay bank.

**Comments**
UCE phylogenetic results place this specimen together with three other species: two morphospecies from the same site in Darien (JT029 and JT030) and *R. cryptergates* from Costa Rica.

**Rasopone JTL029**
(Fig. 12; Supp Figs. S35 [online only])
**Geographic range.** Panama (Darien).

**Diagnosis**
Mandible striate; anterior clypeal margin truncate; side of head bare; petiolar node weakly tapering, subcuboidal. Among the three species in Darien, *R. JTL027* is much smaller and *R. JTL030* (Fig. 12; Supp Fig. S36 [online only]) has a more tapering, scale-like petiolar node.

**Measurements, worker:** HW 1.52, HL 1.64, SL 1.12, PTL 0.64, PTH 1.16, CI 93, SI 74, PTI 55 (n = 1).

**Biology**
This species is known from one worker, from a cloud forest site at 1,305 m elevation. It was collected in a Winkler sample of forest floor litter and rotten wood.

**Comments**
See *Rasopone* JTL027.
Rasopone JTL030
(Fig. 12; Supp Fig. S36 [online only])
Geographic range. Panama (Darien).

Diagnosis
Mandible striate; anterior clypeal margin truncate; side of head with short erect setae; petiolar node tapering, scale-like. Among the three species in Darien, R. JTL027 is much smaller and R. JTL029 (Fig. 12; Supp Fig. S35 [online only]) has a more cuboidal petiolar node.

Measurements, worker: HW 1.40, HL 1.58, SL 1.15, PTL 0.61, PTH 1.08, CI 88, SI 82, PTI 57 (n = 1).

Biology
This species is known from one worker, from a montane wet forest site at 1,190 m elevation. It was collected in a Winkler sample of forest floor litter and rotten wood.

Comments
See Rasopone JTL027.

Rasopone JTL034
(Fig. 7; Supp Fig. S37 [online only])
Geographic range. Mexico (Puebla, Veracruz), Honduras.

Diagnosis
Mandible smooth and shining or very faintly striate; anterior clypeal margin truncate; side of head with short erect setae; petiolar node moderately tapering, intermediate between cuboidal and scale-like. Among the three species in Darien, R. JTL027 forms a clade with specimens from Puebla (Mexico) and Honduras. COI data unite a male from Tela, Honduras, with the three worker specimens (Fig. 3).

Rasopone JTL035
(Fig. 9; Supp Fig. S38 [online only])
Geographic range. Mexico (Veracruz).

Diagnosis
Mandible smooth and shining; anterior clypeal margin truncate; side of head bare; petiolar node moderately tapering, intermediate between cuboidal and scale-like. Two species are within geographic and size range of R. JTL035:

- Rasopone guatemalensis (Fig. 8; Supp Figs. S14 and S15 [online only]): no known local sympatry, but ranges overlap; petiolar node slightly more tapering, scale-like; scape longer (mean SI 86 vs 76); head narrower (mean CI 86 vs 93).
- Rasopone politognatha (Fig. 9; Supp Figs. S28 and S29 [online only]): no known local sympatry, but ranges overlap; side of head bare; scape slightly longer (mean SI 82 vs 76).

Measurements, worker: HW 1.17, HL 1.20, SL 0.89, PTL 0.41, PTH 0.76, CI 97, SI 77, PTI 53 (n = 1).

Biology
This species is known from one specimen from mixed hardwood cloud forest at 1,114 m elevation. The specimen is from a Winkler sample of forest floor litter and rotten wood.

Comments
See Rasopone JTL034.

Rasopone JTL037
(Fig. 12; Supp Fig. S39 [online only])
Geographic range. Guatemala, El Salvador.

Diagnosis
Mandible striate; anterior clypeal margin truncate; side of head mostly bare, with a few erect setae posterior to eye; petiolar node subcuboidal. Three species are within geographic and size range of R. JTL037:

- Rasopone ferruginea (Fig. 11; Supp Figs. S12 and S13 [online only]): mandible striate; anterior clypeal margin sinuose; petiole more scale-like.
- Rasopone mesoamericana (Fig. 12; Supp Figs. S19–S21 [online only]): petiolar node more scale-like.
- Rasopone subcubitalis (Fig. 10; Supp Fig. S32 [online only]): scape shorter (mean SI 84 vs 92).

Measurements, worker: HW 1.41 (1.39–1.43, 2); HL 1.59 (1.58–1.59, 2); SL 1.30 (1.28–1.32, 2); PTH 1.06 (1.04–1.08, 2); PTL 0.54 (0.53–0.55, 2); CI 89 (88–90, 2); SI 92 (92–92, 2); PTI 51 (51-51, 2).

Biology
This species is known from two specimens, one from a 1,550 m elevation cloud forest in Guatemala, and one from a 1,760 m cloud forest in El Salvador. The specimens are from Winkler and Berlese samples of forest floor litter and rotten wood.

Comments
There are no UCE data for this morphospecies. COI data from the Guatemala specimen place it on an isolated branch in Rasopone.
Rasopone JTL040
(Fig. 11; Supp Fig. S40 [online only])
Geographic range. Colombia.

Diagnosis
Mandible smooth; anterior clypeal margin truncate, medial lobe concave; side of head with erect setae; petiolar node cuboidal. Two species are within geographic and size range of R. JTL040:

Rasopone JTL041 (Fig. 11; Supp Fig. S41 [online only]): petiolar node more scale-like.

Rasopone JTL042 (Fig. 7; Supp Fig. S42 [online only]): mandible striate.

Measurements, worker: HW 1.29, HL 1.42, SL 0.95, PTL 0.63, PTH 1.07, CI 91, SI 73, PTI 59 (n = 1).

Biology
This species is known from one specimen, from a Berlese sample taken at 830 m elevation.

Rasopone JTL041
(Fig. 11; Supp Fig. S41 [online only])
Geographic range. Colombia.

Diagnosis
Mandible smooth; anterior clypeal margin truncate, medial lobe concave; side of head with erect setae; petiolar node scale-like. Two species are within geographic and size range of R. JTL041:

Rasopone JTL040 (Fig. 11; Supp Fig. S40 [online only]): petiolar node cuboidal.

Rasopone JTL042 (Fig. 7; Supp Fig. S42 [online only]): mandible striate.

Measurements, worker: HW 1.32 (1.29–1.35, 3); HL 1.43 (1.40–1.48, 3); SL 1.09 (1.07–1.12, 3); PTH 0.98 (0.98–0.98, 2); PTL 0.54 (0.52–0.55, 3); CI 92 (91–92, 2); SI 83 (82–83, 3); PTI 56 (55–56, 2).

Biology
This species is known from three sites in the Cauca region of Colombia, from montane forest habitat, 1,550–1,800 m elevation.

Rasopone JTL042
(Fig. 7; Supp Fig. S42 [online only])
Geographic range. Colombia, Brazil (Pará).

Diagnosis
Mandible striate; otherwise very similar to R. lunaris (Fig. 8; Supp Figs. S16–S18 [online only]).

Measurements, worker: HW 1.10 (0.94–1.23, 3); HL 1.22 (1.06–1.35, 3); SL 0.87 (0.71–1.01, 3); PTH 0.80 (0.69–0.89, 3); PTL 0.43 (0.38–0.48, 3); CI 90 (89–91, 3); SI 79 (75–82, 3); PTI 54 (54–55, 3).

Biology
Two specimens are from the Santa Marta region of Colombia, one from seasonal forest at 260 m and one from montane forest at 1,300 m elevation. Both are from forest floor litter samples.

Comments
This species is a version of R. lunaris with striate mandibles. An old collection at MCZC is a pin with two workers labeled ‘Para, Brazil, Beebe’. These specimens are a close match to the Colombian specimens, but given the geographic distance the similarity may be superficial and not reflect conspecificity.

Rasopone JTL043
(Fig. 6; Supp Fig. S43 [online only])
Geographic range. Ecuador.

Diagnosis
Very similar to R. lunaris (Fig. 8; Supp Figs. S16–S18 [online only]), differing in less rounded posterior face of petiole in lateral view; smaller size (mean HW 0.95 vs 1.11).

Measurements, worker: HW 0.95 (0.90–1.00, 2); HL 1.06 (1.00–1.12, 2); SL 0.76 (0.70–0.81, 2); PTH 0.69 (0.69–0.69, 2); PTL 0.41 (0.39–0.44, 2); CI 90 (89–90, 2); SI 80 (78–81, 2); PTI 60 (56–63, 2).

Biology
This species is from wet forest habitat on the Pacific slope of Ecuador, 250–1,300 m elevation, in Berlese samples of forest floor litter.

Rasopone JTL047
(Fig. 10; Supp Fig. S44 [online only])
Geographic range. French Guiana.

Diagnosis
Mandible smooth and shining; anterior clypeal margin truncate; side of head with short erect setae; petiolar node subcuboidal; face sculpture of dense, minute puncta overlain with larger, more widely spaced puncta visible in particular orientation and lighting. Two species are within geographic and size range of R. JTL047:

Rasopone JTL048 (Fig. 6, Supp Fig. S45 [online only]): smaller (HW 0.98 vs 1.21).

Measurements, worker: HW 1.21 (1.21–1.21, 2); HL 1.26 (1.26–1.27, 2); SL 0.89 (0.88–0.89, 2); PTH 0.84 (0.81–0.87, 2); PTL 0.50 (0.48–0.51, 2); CI 96 (95–96, 2); SI 74 (73–74, 2); PTI 59 (55–63, 2).

Biology
This species is known from lowland rainforest sites, <800 m elevation, from Winkler samples of sifted litter and rotten wood.

Comments
See under R. lunaris.

Rasopone JTL048
(Fig. 6, Supp Fig. S45 [online only])
Geographic range. French Guiana.

Diagnosis
Mandible smooth and shining; anterior clypeal margin truncate; side of head with short erect setae; petiolar node subcuboidal; face sculpture of dense, minute puncta overlain with larger, more widely spaced puncta visible in particular orientation and lighting. Two species are within geographic and size range of R. JTL048:
Rasopone lunaris (Fig. 8, Supp Figs. S16–S18 [online only]): posterior face of petiolar node more rounded; face with uniform small puncta, not overlain with larger puncta.

Rasopone JTL047 (Fig. 10, Supp Fig. S44 [online only]): larger (HW 1.21 vs 0.98).

Measurements, worker: HW 0.98, HL 1.10, SL 0.79, PTL 0.39, PTH 0.72, CI 89, SI 81, PTI 54 (n = 1).

Biology
This species is known from one specimen from a lowland rainforest site, 380 m elevation, from a pitfall trap.

Comments
See under R. lunaris.

Rasopone JTL049
(Fig. 9; Supp Fig. S46 [online only])
Geographic range. Colombia.

Diagnosis
Similar to R. lunaris (Fig. 8; Supp Figs. S16–S18 [online only]) in most respects, differing in lack of erect setae on sides of head.

Measurements, worker: HW 1.19, HL 1.30, SL 0.92, PTL 0.52, PTH 0.85, CI 91, SI 77, PTI 61 (n = 1).

Biology
This species is known from one collection from a lowland rainforest site in Amazonian Colombia, from a litter/soil core collected by D. Castro. One worker and one alate queen were examined.

Comments
See under R. lunaris.

Rasopone MAS010
(Fig. 7; Supp Fig. S47 [online only])
Geographic range. Costa Rica.

Diagnosis
Montane; mandible striate; anterior clypeal margin truncate; side of head bare or with a few inconspicuous short setae; petiole scale-like. Two species are within geographic and size range of R. MAS010:

Rasopone cryptergates (Fig. 7; Supp Figs. S8 and S9 [online only]): lowland; side of head with a few short erect setae; posterolateral margins of vertex somewhat more angular.

Rasopone costaricensis (Fig. 9; Supp Figs. S3 and S4 [online only]): larger, HW of the smallest measured specimen 1.09, versus 1.00 for both of the measured specimens of R. MAS010; petiole somewhat narrower (average PTI 53 vs 59).

Measurements, worker: HW 1.00 (1.00–1.00, 2); HL 1.13 (1.13–1.13, 2); SL 0.79 (0.78–0.81, 2); PTH 0.70 (0.70–0.71, 2); PTL 0.41 (0.41–0.41, 2); CI 88 (88–88, 2); SI 80 (78–81, 2); PTI 59 (58–59, 2).

Biology
This species occurs in lower cloud forest.

Comments
This species is known from three specimens that form a DNA barcode cluster. One specimen is a male from Volcán Cacao, a cloud forest site (1,080 m) in the Cordillera de Guanacaste in northwestern Costa Rica. The other two specimens are workers from Las Pailas, a cloud forest site in Rincon de la Vieja National Park, about 20 km SE of the first site. One of the workers from Las Pailas was collected in a pitfall trap. We were able to examine the two workers.

The COI results place this species near three species from northern Central America and southern Mexico: R. politognatha, R. JTL034, and R. JTL035 (Fig. 3).

Molecular Data Availability
Raw Illumina reads and contigs representing UCE loci have been deposited at the NCBI Sequence Read Archive and GenBank, respectively (BioProject# PRJNA563172 for new data and PRJNA360290 for previously sequenced samples). All newly generated COI sequences have been deposited at GenBank (MN928390-MN928461). A complete list of relevant NCBI accession numbers are available in Supp Table S4 (online only). The concatenated UCE matrix, the COI matrix, all Trinity contigs, all tree files, and additional data analysis files have been deposited at Dryad (doi:10.5061/dryad.br15dv5). The Phylose package and associated programs can be downloaded from github (github.com/faircloth-lab/phylose). 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 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. Material examined for taxonomic revision of the ant genus Rasopone.

Table S2. Sequencing and assembly statistics for UCE samples used in the revision of the ant genus Rasopone.

Table S3. Data for the COI samples used in the revision of the ant genus Rasopone.

Table S4. NCBI accession numbers for sequence data used in the revision of the ant genus Rasopone.

Fig. S1. Phylogenetic relationships among COI barcode sequences for Rasopone. Red samples were sequenced for UCEs. Other samples were downloaded from the BOLD database. The tree was inferred using IQ-TREE with the data partitioned by codon position.

Fig. S2. Rasopone breviscapa. Holotype queen. Scale bars 1 mm for face view, 2 mm for dorsal and lateral views. Modified from AntWeb images by E. Okonski.

Fig. S3. Rasopone costaricensis. Holotype worker. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S4. Rasopone costaricensis. Queen, Costa Rica, INBIOCRI001280801. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S5. Rasopone costaricensis (form a). Worker, Costa Rica, specimen code INB0003659312. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S6. Rasopone costaricensis (form b). Worker, Costa Rica, specimen code INB0003223929. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S7. Rasopone costaricensis (form c). Worker, Costa Rica, specimen code INB0003659307. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.
Fig. S8. *Rasopone cryptergates*. Holotype queen. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S9. *Rasopone cryptergates*. Worker, Costa Rica, specimen code INB0003660648. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S10. *Rasopone cubitalis*. Holotype worker. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S11. *Rasopone cubitalis*. Queen, Costa Rica, specimen code INB0003662382. Scale bars 1 mm for face view, 2 mm for dorsal and lateral views.

Fig. S12. *Rasopone ferruginea*. Worker, Nicaragua, specimen code CASENT0644264. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S13. *Rasopone ferruginea*. Queen, Nicaragua, specimen code CASENT0624181. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S14. *Rasopone guatemalensis*. Holotype worker. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S15. *Rasopone guatemalensis*. Queen, Guatemala, specimen code CASENT0612926. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S16. *Rasopone lunaris*. Worker, Brazil (MG), specimen code CASENT0644556. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S17. *Rasopone lunaris*. Queen, Brazil (MG), specimen code UFV-LABEBCOL-000359. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S18. *Rasopone lunaris*. Male, Brazil (MG), specimen code UFV-LABEBCOL-007332. Scale bars 0.2 mm for face view, 0.5 mm for dorsal and lateral views. Modified from AntWeb images by Gabriela de Figueiredo.

Fig. S19. *Rasopone mesoamericanica*. Holotype worker. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S20. *Rasopone mesoamericanica*. Queen, Honduras, specimen code CASENT0617675. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S21. *Rasopone mesoamericanica*. Male, Nicaragua, specimen code CASENT0627722. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S22. *Rasopone minuta*. Worker, Mexico (Chiapas), specimen code CASENT0609834. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S23. *Rasopone minuta*. Holotype queen. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S24. *Rasopone panamensis*. Neotype worker. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S25. *Rasopone panamensis*. Queen, Costa Rica, specimen code CASENT0644543. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S26. *Rasopone pluriselia*. Holotype worker. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S27. *Rasopone pluriselia*. Queen, Nicaragua, specimen code CASENT0628788. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S28. *Rasopone politognatha*. Holotype worker. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S29. *Rasopone politognatha*. Queen, Guatemala, specimen code CASENT0612518. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S30. *Rasopone rupinicola*. Worker, Colombia, specimen code MCZ-ENT00716589. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S31. *Rasopone rupinicola*. Male, Colombia, specimen code CASENT0645958. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S32. *Rasopone subcubitalis*. Holotype worker. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S33. *Rasopone titanis*. Holotype worker. Scale bars 1 mm for face view, 2 mm for dorsal and lateral views.

Fig. S34. *Rasopone JTL027*. Worker, Panama, specimen code CASENT0633216. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S35. *Rasopone JTL029*. Worker, Panama, specimen code CASENT0633053. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S36. *Rasopone JTL030*. Worker, Panama, specimen code CASENT0633075. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S37. *Rasopone JTL034*. Worker, Mexico (Veracruz), specimen code CASENT0640282. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S38. *Rasopone JTL035*. Worker, Mexico (Veracruz), specimen code CASENT0640453. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S39. *Rasopone JTL037*. Worker, Guatemala, specimen code CASENT0625283. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S40. *Rasopone JTL040*. Worker, Colombia, specimen code MCZ-ENT00716609. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S41. *Rasopone JTL041*. Worker, Colombia, specimen code MCZ-ENT00716615. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S42. *Rasopone JTL042*. Worker, Colombia, specimen code MCZ-ENT00716611. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S43. *Rasopone JTL043*. Worker, Ecuador, specimen code MCZ-ENT00716620. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S44. *Rasopone JTL047*. Worker, French Guiana, specimen code CASENT0645960. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S45. *Rasopone JTL048*. Worker, French Guiana, specimen code CASENT0645961. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S46. *Rasopone JTL049*. Worker, Colombia, specimen code CASENT0644557. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S47. *Rasopone MAS010*. Worker, Costa Rica, specimen code 08COSTA-1723. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

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