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Research

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. subcubitalis*, and *R. titanis*. 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. cernua* (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

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.

CAS	California Academy of Sciences, San Francisco, CA.
DZUP	Coleção Entomológica Padre Jesus Santiago Moure of Universidade Federal do Paraná (UFPR), Curitiba, Paraná, Brazil.
EcoFoG	Ecology of Guianan Forests Research Unit, Kourou, French Guiana.
INECOL	Instituto de Ecología, Xalapa, Veracruz, Mexico.
JTLC	John T. Longino, personal collection, University of Utah, Salt Lake City, UT.
MASC	M. Alex Smith, personal collection, University of Guelph, Guelph, Ontario, Canada.
MCZC	Museum of Comparative Zoology, Cambridge, MA.
MGBPC	Michael G. Branstetter, personal collection, USDA/Utah State University, Logan, UT.
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland.
MPEG	Museu Paraense Emilio Goeldi, Belem, Pará, Brazil.
MSNG	Museo Civico de Storia Naturale 'Giacomo Doria', Genoa, Italy.
UCD	University of California, Davis, CA.
UCR	Universidad de Costa Rica, San Pedro, Costa Rica.
UNAM	Universidad Nacional Autonoma de Mexico, Mexico D. F., Mexico.
USNM	National Museum of Natural History, Washington, DC.
UVGC	Colección de Artrópodos, Universidad del Valle de Guatemala, Guatemala City, Guatemala.

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 generated for this study, except for five samples, in which data were taken from Branstetter et al. (2017) (Table 1).

To examine species boundaries and phylogenetic relationships among species and populations, we employed the UCE approach to phylogenomics (Faircloth et al. 2012, Faircloth et al. 2015, Branstetter et al. 2017), a method that combines target enrichment of UCEs with multiplexed, next-generation sequencing. All UCE molecular work was performed following the UCE methodology described in Branstetter et al. (2017). Briefly, the process involves DNA extraction, sample QC, DNA fragmentation (400–600 bp), library preparation, library pooling (equimolar pools of 10 samples), UCE enrichment, qPCR quantification, final pooling (100–104 total samples per sequencing pool), and sequencing. All sequencing was performed on an Illumina HiSeq 2500 instrument (2x125 bp v4 chemistry; Illumina Inc., San Diego, CA) by the University of Utah genomics core facility. For a few samples, we followed a modified enrichment protocol, in which the day 1 procedure followed the Arbor Biosciences (Ann Arbor, MI) myBaits v4 protocol, and day 2 followed a standard UCE enrichment protocol (version 1.5; available 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 resolve relationships in ants has been demonstrated in several studies (Branstetter et al. 2017, Pierce et al. 2017, Ward and Branstetter 2017, Blaimer et al. 2018, Branstetter and Longino 2019).

UCE Matrix Assembly

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

After extracting UCE contigs, we aligned each UCE locus using a stand-alone version of the program MAFFT v7.130b (Katoh and Standley 2013) and the L-INS-I algorithm. We then used a PHYLUCE script to trim flanking regions and poorly aligned internal regions using the program GBLOCKS (Talavera and Castresana 2007). The program was run with reduced stringency parameters (b1:0.5, b2:0.5, b3:12, b4:7). We then used another PHYLUCE script to filter the initial set of alignments so that each alignment was required to include data for ≥90% of taxa. This resulted in a final set of 1,802 alignments and 1,542,220 bp of sequence data for analysis. To calculate summary statistics for the final data matrix, we used a script from the PHYLUCE package (*phyluce_align_get_align_summary_data*). Information related to UCE sequencing and assembly results can be found in Supp Table S2 (online only). All steps, including the phylogenetic analyses described below, were performed on a multicore Linux workstation (40 CPUs and 512 Gb of memory) housed in the Branstetter lab.

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).

Table 1. Voucher list of specimens used for DNA extraction and sequencing

Taxon	ExtractionID	Country	Admin1	Latitude	Longitude	VoucherID
Dinoponera longipes[a]	EX1643	Peru	Loreto	−2.24897	−72.09111	CASENT0004663
Mayaponera arhuaca	EX1435	Costa Rica	Heredia	10.42864	−84.01866	INBIOCRI001241794
Mayaponera arhuaca	EX1676	Guyana	Potaro-Siparuni	5.30479	−59.83746	CASENT0636916
Mayaponera becculata	EX1429	Costa Rica	Alajuela	10.29644	−84.77132	CASENT0635158
Mayaponera becculata	EX1434	Costa Rica	Heredia	10.26863	−84.08287	CASENT0633229
Mayaponera constricta[a]	EX1649	Costa Rica	Puntarenas	8.40811	−83.32745	CASENT0636005
Mayaponera pergandei	EX1424	Guatemala	Petén	16.44198	−89.53494	CASENT0614317
Mayaponera pergandei	EX1431	Panama	Darién	8.79151	−78.45309	CASENT0633514
Mayaponera pergandei	EX1436	Costa Rica	Heredia	10.41924	−84.02062	INB0003695621
Mayaponera pergandei	EX1463	Honduras	Comayagua	14.86613	−87.89820	CASENT0617265
Neoponera unidentata[a]	EX1650	Costa Rica	Puntarenas	8.40820	−83.32766	CASENT0636011
Pachycondyla harpax[a]	EX838	Costa Rica	Puntarenas	8.40667	−83.32833	CASENT0636063
Rasopone costaricensis	EX1427	Costa Rica	Puntarenas	10.30892	−84.78498	CASENT0635809
Rasopone costaricensis	EX1964	Costa Rica	San Jose	9.57553	−83.95181	CASENT0644237
Rasopone costaricensis	EX1966	Costa Rica	Cartago	9.74917	−83.77649	CASENT0644253
Rasopone costaricensis Form a	EX1443	Costa Rica	Heredia	10.23617	−84.11767	INB0003659344
Rasopone costaricensis Form b	EX1447	Costa Rica	Heredia	10.23617	−84.11767	INB0003664817
Rasopone costaricensis Form c	EX1462	Costa Rica	Heredia	10.23617	−84.11767	INB0003659307
Rasopone cryptergates	EX1450	Costa Rica	Heredia	10.41745	−84.01627	INB0003660648
Rasopone cubitalis	EX1428	Costa Rica	Alajuela	10.30677	−84.71650	CASENT0633211
Rasopone cubitalis	EX1437	Costa Rica	Heredia	10.40677	−84.03982	CASENT0633282
Rasopone cubitalis	EX1451	Nicaragua	Boaco	12.58180	−85.46661	CASENT0619842
Rasopone ferruginea	EX1426	Nicaragua	Matagalpa	12.96817	−85.23301	CASENT0624181
Rasopone ferruginea	EX1439	Honduras	Atlántida	15.69714	−87.47451	CASENT0618624
Rasopone ferruginea	EX1444	Honduras	Atlántida	15.69843	−87.47256	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	JTLC000014402
Rasopone ferruginea	EX1967	Mexico	Oaxaca	18.04793	−96.69065	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	18.58693	−95.07648	CASENT0640257
Rasopone ferruginea	EX1974	Mexico	Veracruz	19.51211	−96.93914	CASENT0641093
Rasopone guatemalensis	EX1411	Mexico	Chiapas	15.72096	−92.95020	JTLC000014265
Rasopone guatemalensis	EX1412	Mexico	Chiapas	15.71549	−92.93816	CASENT0633224
Rasopone guatemalensis	EX1433	Guatemala	Suchitepéquez	14.55483	−91.19299	CASENT0611754
Rasopone JTL027	EX1430	Panama	Darién	8.79151	−78.45309	CASENT0633216
Rasopone JTL029	EX1452	Panama	Darién	8.79805	−78.46250	CASENT0633053
Rasopone JTL030	EX1453	Panama	Darién	8.79487	−78.46095	CASENT0633075
Rasopone JTL034	EX1441	Honduras	Olancho	14.79972	−86.01415	CASENT0610796
Rasopone JTL034	EX1969	Mexico	Puebla	19.97807	−97.42486	CASENT0640987
Rasopone JTL034	EX1972	Mexico	Veracruz	18.58038	−95.08110	CASENT0640282
Rasopone JTL035	EX1973	Mexico	Veracruz	18.52290	−95.15441	CASENT0640453
Rasopone JTL047	EX2214	Brazil	Amapá	1.24514	−52.40543	CASENT0646302
Rasopone JTL049	EX2215	Colombia	Amazonas	−4.04667	−70.00567	CASENT0644557
Rasopone lunaris	EX2216	Brazil	Minas Gerais	−20.80303	−42.85786	CASENT0644556
Rasopone mesoamericana	EX1415	Guatemala	Zacapa	14.94654	−89.27600	CASENT0614532
Rasopone mesoamericana	EX1417	Guatemala	Suchitepéquez	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	14.93693	−85.90535	CASENT0616284
Rasopone mesoamericana	EX1454	Mexico	Chiapas	15.72099	−92.95054	JTLC000015360
Rasopone mesoamericana	EX1455	Costa Rica	Heredia	10.26900	−84.08646	INB0003213391
Rasopone minuta	EX1413	Mexico	Chiapas	17.12681	−91.63022	JTLC000014374
Rasopone minuta	EX1458	Honduras	Atlántida	15.76570	−87.45567	CASENT0618570
Rasopone minuta	EX1459	Honduras	Comayagua	14.87314	−87.90297	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	JTLC000014019
Rasopone panamensis	EX1963	Costa Rica	Limón	9.66530	−83.02300	CASENT0644251
Rasopone panamensis	EX1965	Costa Rica	San Jose	9.48059	−83.96402	CASENT0644252

Table 1. Continued

Taxon	ExtractionID	Country	Admin1	Latitude	Longitude	VoucherID
Rasopone pluviselva	EX1448	Nicaragua	RAAN	13.77216	−84.99613	CASENT0628853
Rasopone pluviselva	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	−88.23383	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 subcubitalis	EX1414	Mexico	Chiapas	16.96408	−91.59236	JTLC000014483
Rasopone subcubitalis	EX1419	Honduras	Comayagua	14.87120	−87.90011	CASENT0615252
Rasopone subcubitalis	EX1457	Guatemala	Petén	16.44167	−89.53496	CASENT0614335
Simopelta andersoni[a]	EX1575	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).

[a]Sequence data extracted from Branstetter et al. (2017).

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 '-spp' 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 for a PHYLUCE program (*phyluce_assembly_match_contigs_to_barcodes*) that extracts COI sequence from bulk sets of contigs.

After extracting COI sequence from UCE sample data, we downloaded accessible barcode sequences from BOLD following a series of steps. First, using the BOLD workbench interface, we searched for all records matching the taxonomy search term '*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 anteriormost projection of clypeus to posteriormost 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 posteroventral lobe of petiolar tergite to dorsal margin of petiolar node (Fig. 1B). In lateral view, the posteroventral 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).

Fig. 1. Characteristics of *Rasopone* species. (A) Habitus. (B) Scale-like petiole, showing definitions of petiole height (PTH) and petiole length (PTL), and the distinctive shape of the sternite. (C) Petiolar node intermediate between scale-like and cuboidal. (D) Cuboidal petiolar node. (E) Anterior clypeal margin truncate, with angulate lateral lobes. (F) Anterior clypeal margin sinuous, with rounded lateral lobes.

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),

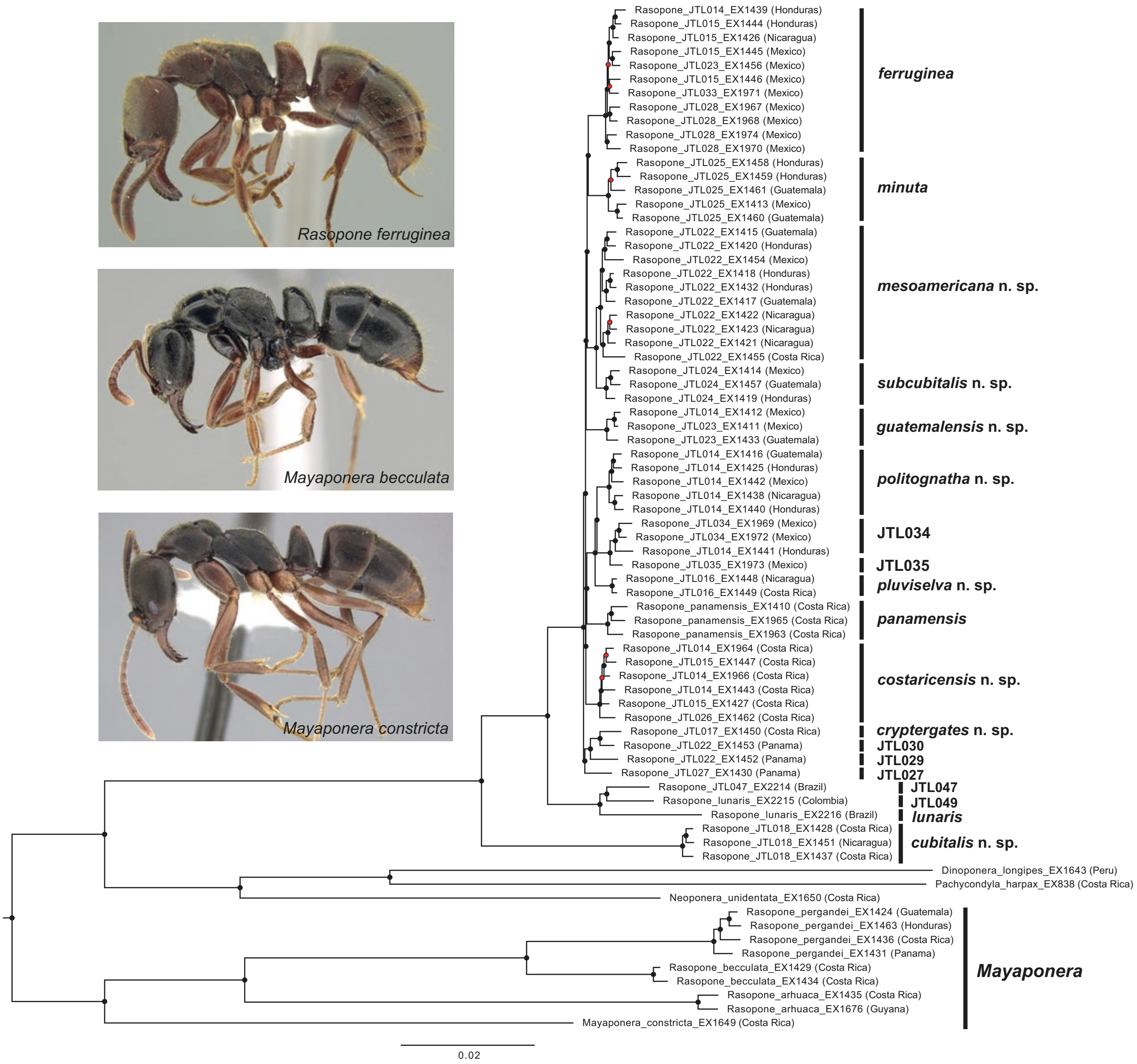

Fig. 2. Phylogeny of *Rasopone*, *Mayaponera*, and selected outgroup taxa, inferred using the program IQ-TREE and 1,802 UCE loci. Node support values (ultrafast bootstrap/SH-like) <100/100 are depicted with red dots. Terminal names show original, morphology-based species assignments and depict morphological convergence across clades. The 'EX#' code in terminal names indicate unique extraction codes that link specimens to specimen data in provided tables. *Simopelta andersoni*, a distant outgroup, is not shown in the figure. Images depict workers of *Rasopone ferruginea* (Nicaragua, CASENT0644264), *Mayponera becculata* (Peru, CASENT0374638, modified from AntWeb, credit Michele Esposito), and *Mayaponera constricta* (Bolivia, CASENT0249137, modified from AntWeb, credit Ryan Perry).

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 855.8 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 downloaded 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

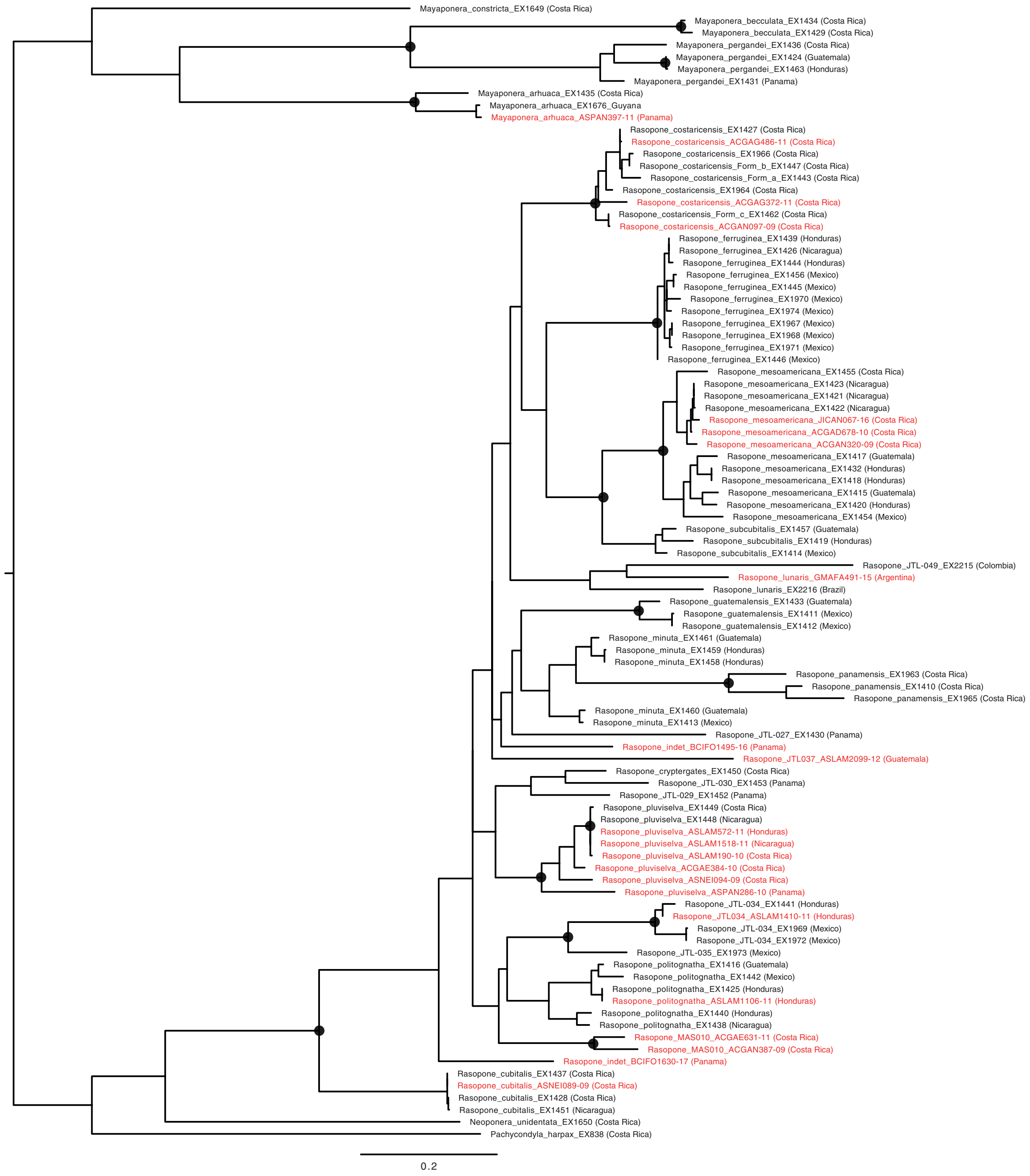

Fig. 3. Phylogenetic relationships among a curated set of COI barcode sequences for *Rasopone*. Black samples were sequenced for UCEs. Red samples were downloaded from the BOLD database. The tree was inferred using IQ-TREE with the data partitioned by codon position. Black circles on nodes indicate high support, which we define as ≥95% ultrafast bootstrap support and ≥95% SH-like branch support. Terminal names match taxonomic changes proposed in paper and provide useful sample identifiers (e.g., extraction codes [EX#] or BOLD process IDs). A complete, unpruned COI tree is available in Supp Fig. S1 (online only).

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 the phylogenetic results. Morphological separation of locally sympatric species 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. lunaris* 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*. *Rasopone minuta* was monophyletic and phylogenetically distant from *R. panamensis* in the UCE tree, but paraphyletic with respect to *R. panamensis* in the COI tree. The COI data also included a couple of COI-only samples that might belong to additional new 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

Redefinition 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 gastral 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 *arhuaca* complex. The *arhuaca* 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 *arhuaca* 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 *arhuaca* complex is that the former has an impressed metanotal groove and the species of the *arhuaca* 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 Honduras to southern Brazil. In contrast, species of the *arhuaca* complex are found only in shaded rainforest habitats, and the species have smaller geographic ranges. In spite of these differences, we place the *arhuaca* 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 *sinuous* 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. mesoamericana* **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 mesoamericana **new species**. Mexico (Chiapas) to Costa Rica.
Rasopone minuta (Mackay and Mackay, 2010). Mexico (Chiapas) to Honduras.
Rasopone panamensis (Forel, 1899) (**new status, revived status**). Costa Rica, Panama.
Rasopone pluviselva **new species**. Honduras to Panama.

Fig. 4. Dealate queen of *Rasopone ferruginea* (Nicaragua, CASENT0624181). Scale bars are 0.5 mm for face view, 1.0 mm for dorsal and lateral views.

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,

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.

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 scapes (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

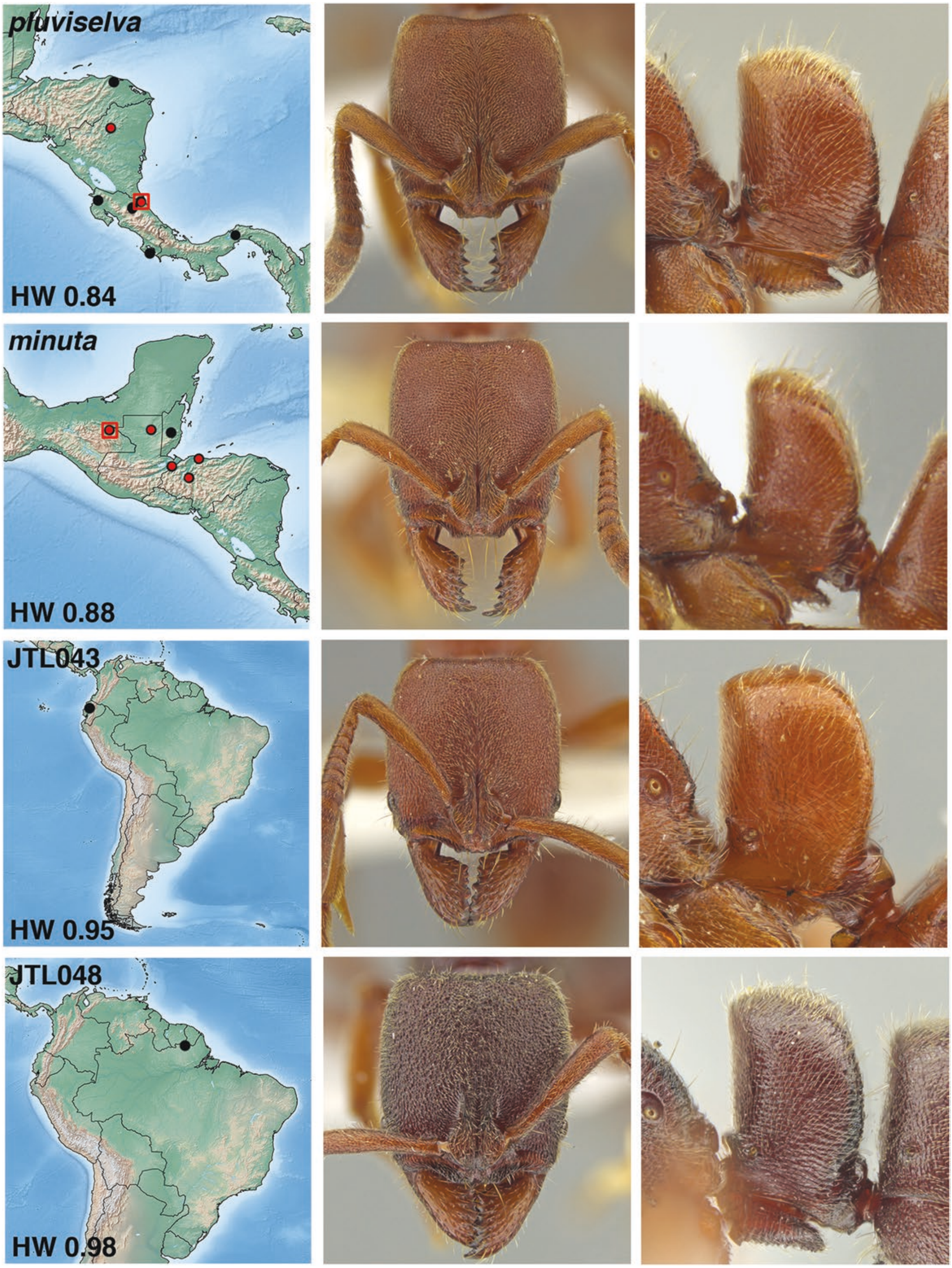

Fig. 6. Distribution map, face view, and lateral view of petiole of *Rasopone pluviselva* (holotype worker), *R. minuta* (worker, Mexico, Chiapas, CASENT0609834), *R.* JTL043 (worker, Ecuador, MCZ-ENT00716620), and *R.* JTL048 (worker, French Guiana, CASENT0645961). On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality.

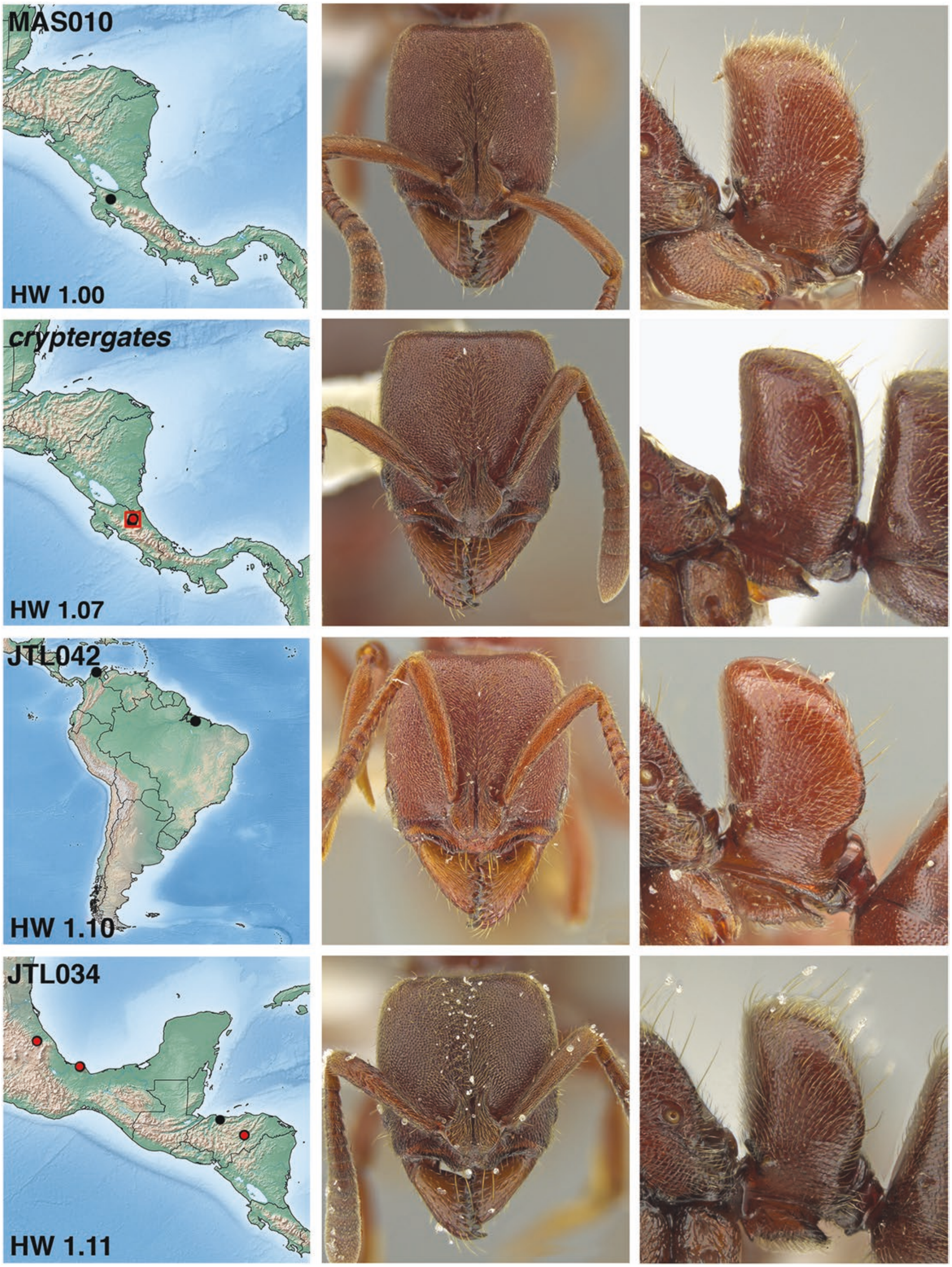

Fig. 7. Distribution map, face view, and lateral view of petiole of *Rasopone* MAS010 (worker, Costa Rica, 08COSTA-1723), *R. cryptergates* (worker, Costa Rica, INB0003660648), *R.* JTL042 (worker, Colombia, MCZ-ENT00716611), and *R.* JTL034 (worker, Mexico, CASENT0640282). On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality.

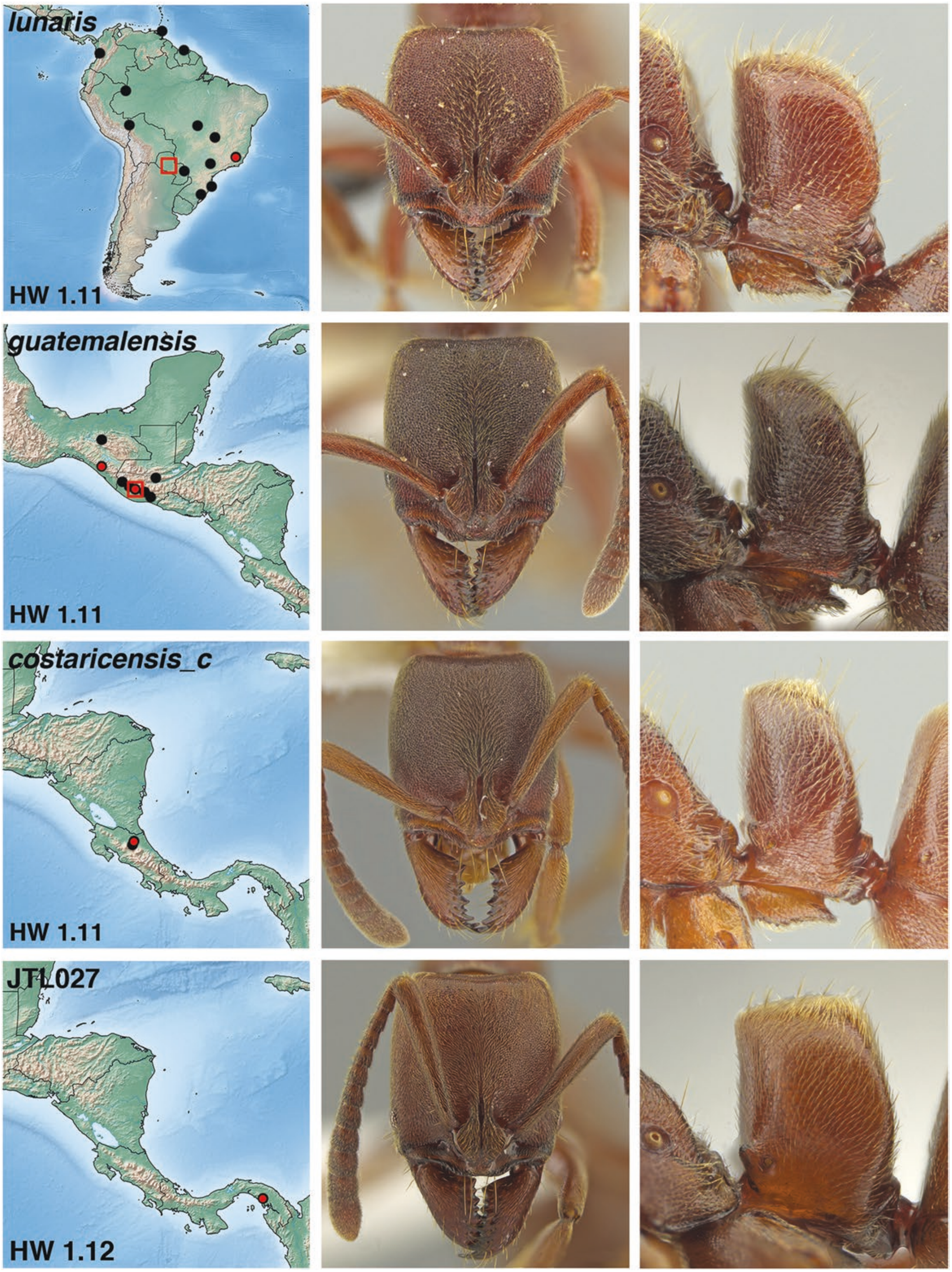

Fig. 8. Distribution map, face view, and lateral view of petiole of *Rasopone lunaris* (worker, Brazil, Minas Gerais CASENT0644556), *R. guatemalensis* (holotype worker), *R. costaricensis* form *c* (worker, Costa Rica, INB0003659307), and *R.* JTL027 (worker, Panama, CASENT0633216). On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality.

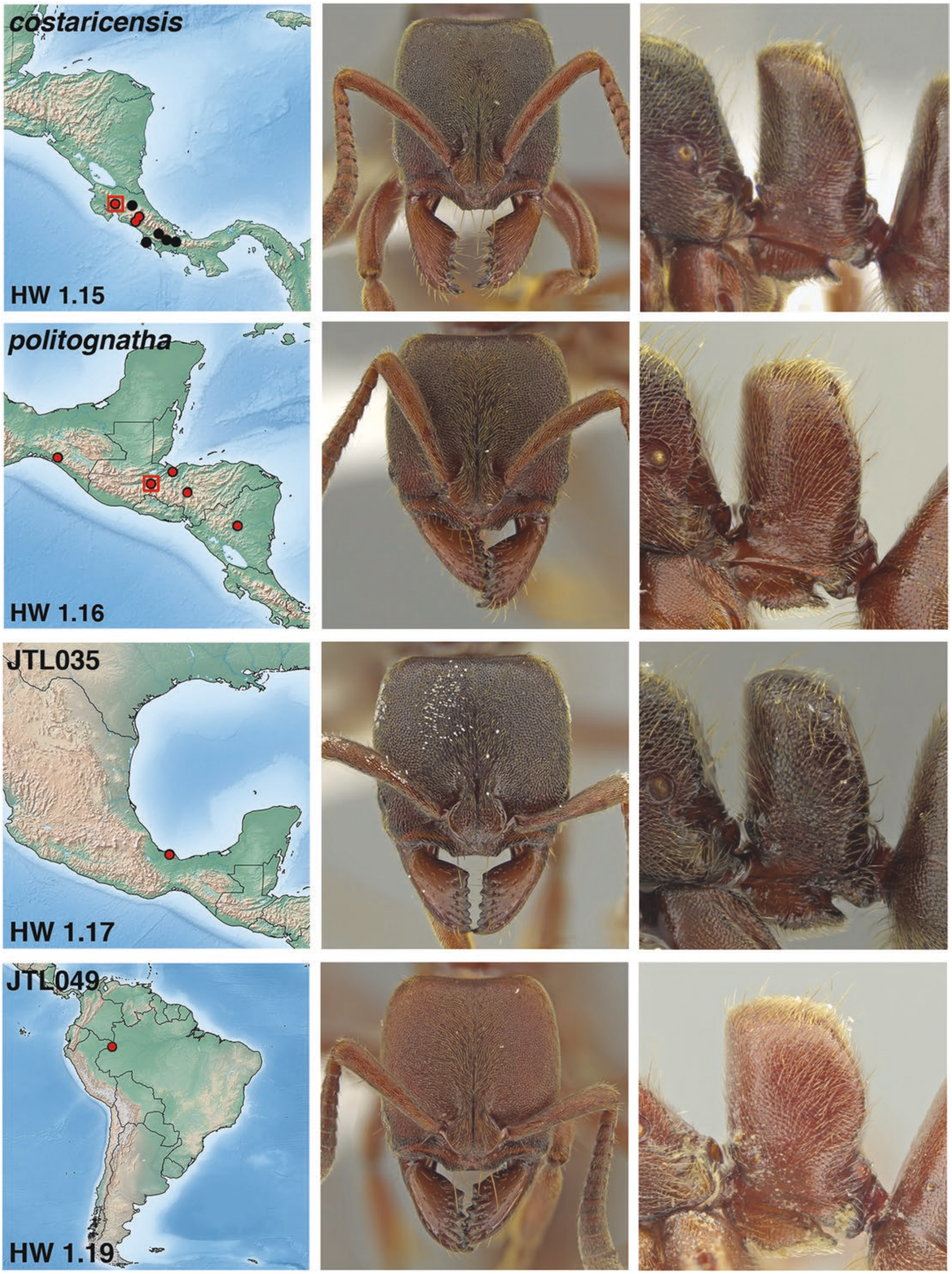

Fig. 9. Distribution map, face view, and lateral view of petiole of *Rasopone costaricensis* (holotype worker), *R. politognatha* (holotype worker), *R.* JTL035 (worker, Mexico, CASENT0640453), and *Rasopone* JTL049 (worker, Colombia, CASENT0644557). On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality.

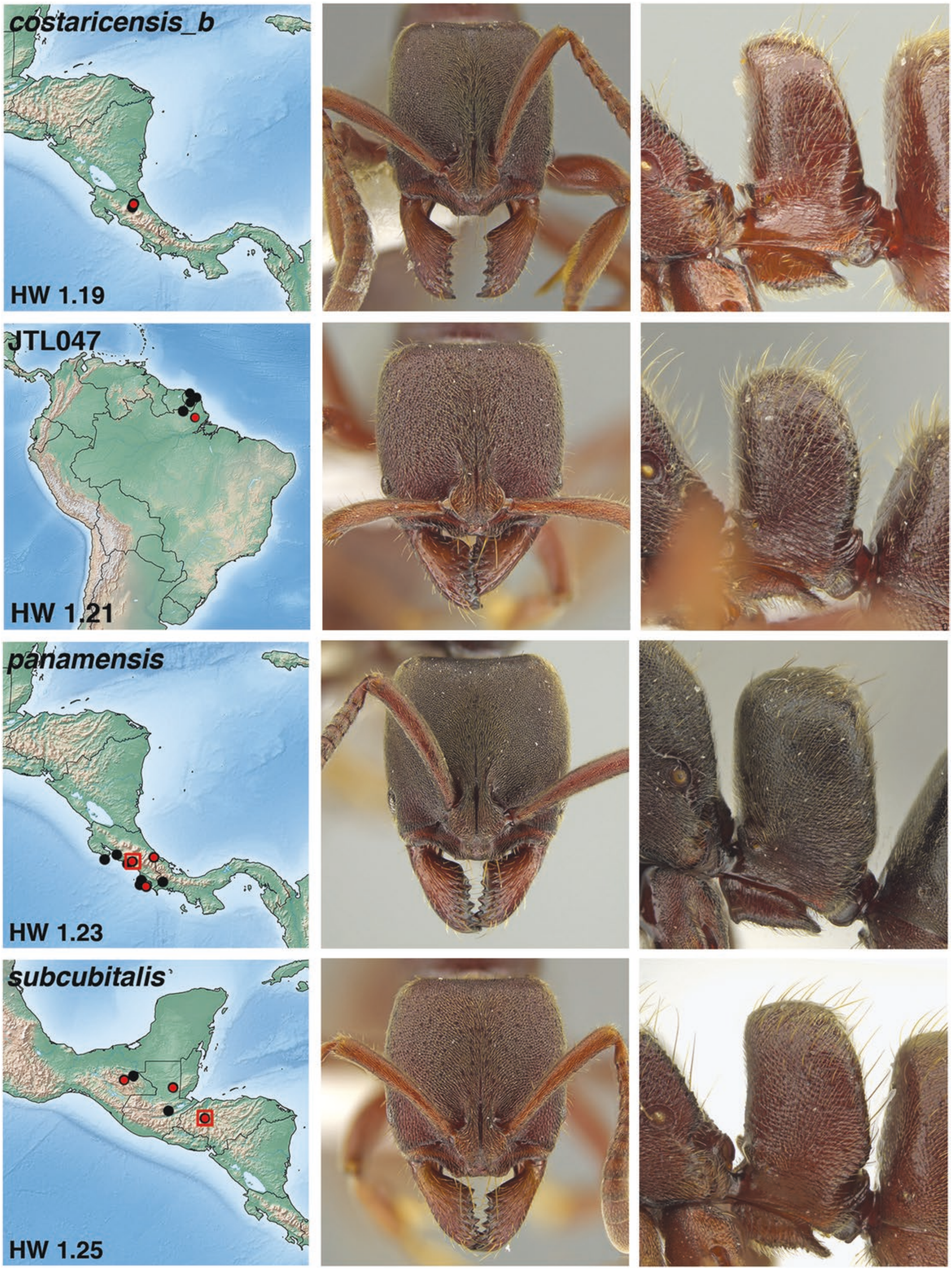

Fig. 10. Distribution map, face view, and lateral view of petiole of *Rasopone costaricensis* form *b* (worker, Costa Rica, INB0003223929), *R.* JTL047 (worker, French Guiana, CASENT0645960), *R. panamensis* (worker, Costa Rica, CASENT0644252), and *R. subcubitalis* (holotype worker). On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality.

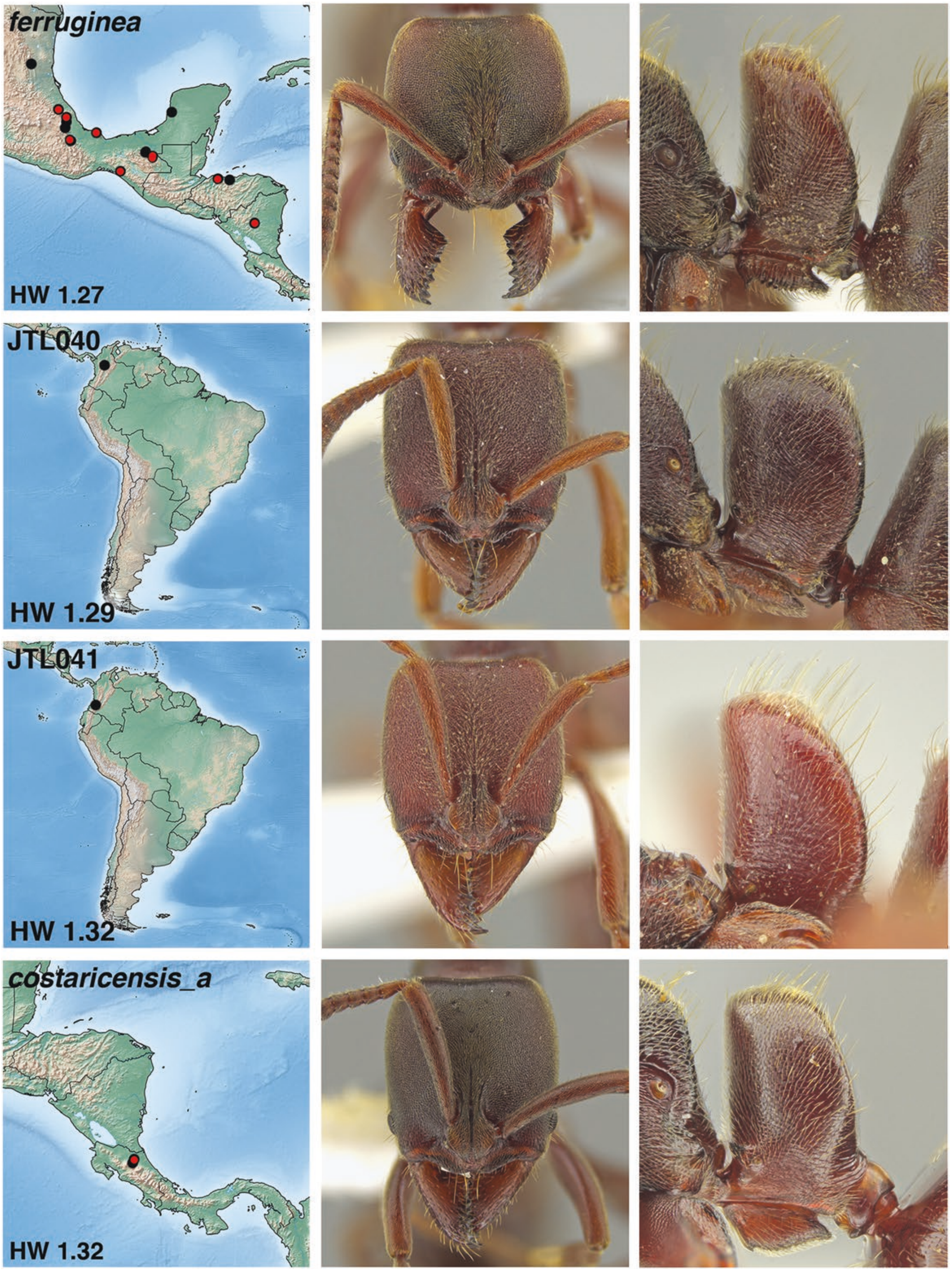

Fig. 11. Distribution map, face view, and lateral view of petiole of *Rasopone ferruginea* (worker, Nicaragua, CASENT0644264), *R.* JTL040 (worker, Colombia, MCZ-ENT00716609), *R.* JTL041 (worker, Colombia, MCZ-ENT00716614), and *R. costaricensis* form *a* (worker, Costa Rica, INB0003659312). On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality (type locality for *R. ferruginea* is 'Mexico').

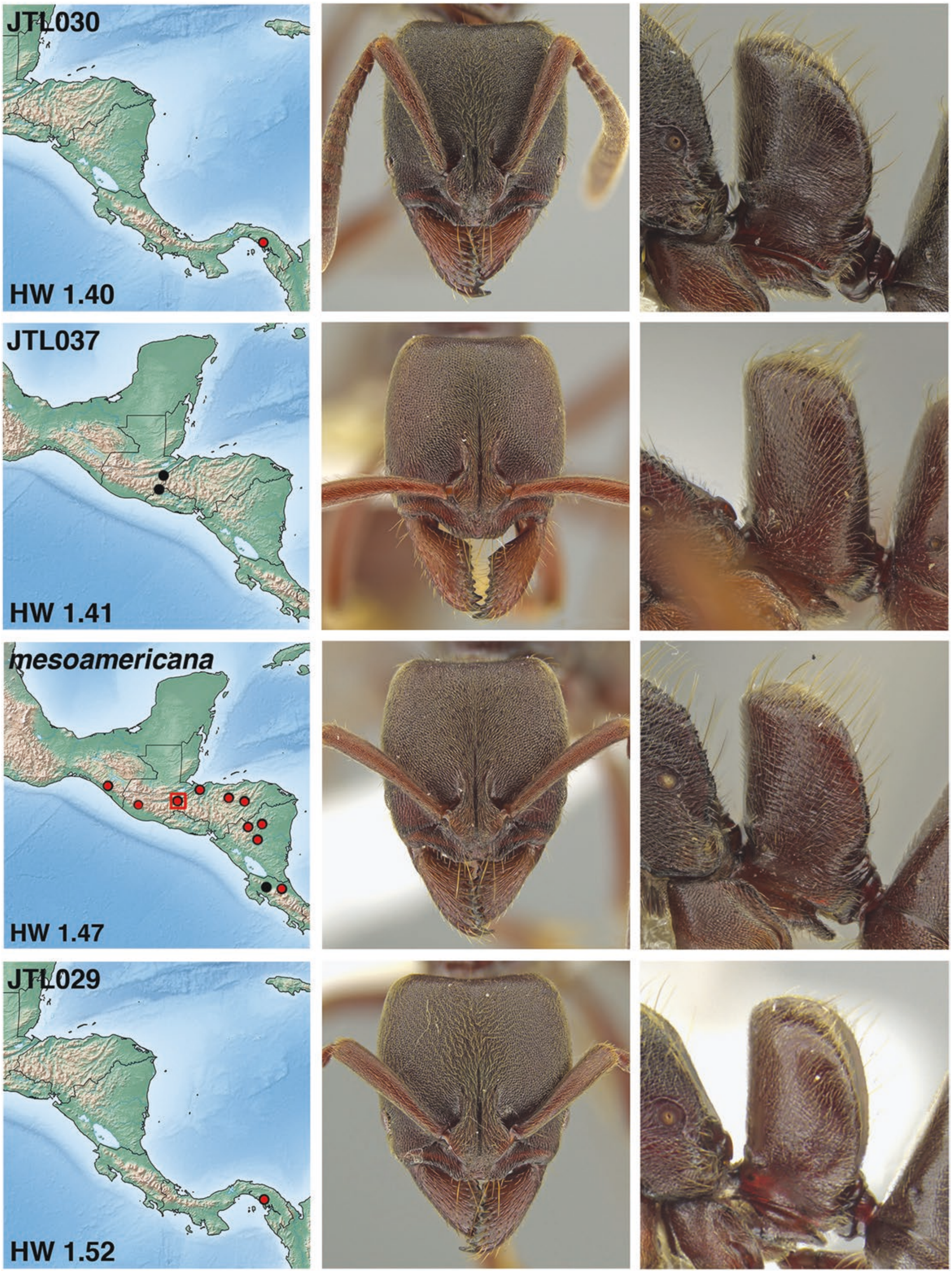

Fig. 12. Distribution map, face view, and lateral view of petiole of *Rasopone* JTL030 (worker, Panama, CASENT0633075), *R.* JTL037 (worker, Guatemala, CASENT0625283), *R. mesoamericana* (holotype worker), and *R.* JTL029 (worker, Panama, CASENT0633053). On distribution maps, red dots are sites with UCE sequence data. Red boxes are type locality.

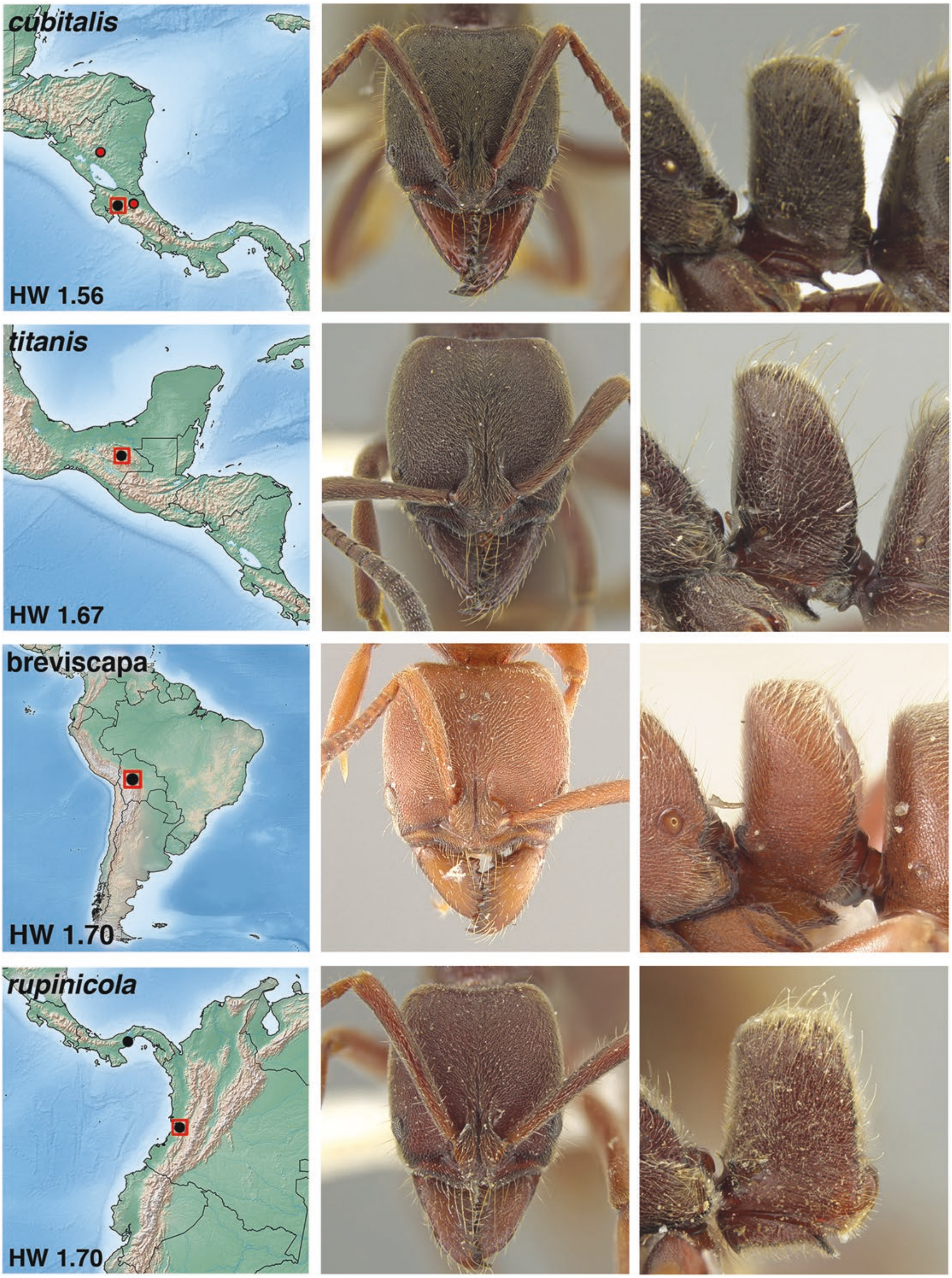

Fig. 13. Distribution map, face view, and lateral view of petiole of *Rasopone cubitalis* (holotype worker), *R. titanis* (worker, Mexico, Chiapas, MCZ-ENT00716640), *R. breviscapa* (holotype queen), and *R. rupinicola* (worker, Colombia, face view MCZ-ENT00716589, petiole CASENT0217567). On distribution 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)

Table 2. Continued

Species	HW	CI	SI	PTI	Clypeus	Petiole	Mandible	Range	Figures
JTL029	1.37–1.67	84–102	67–81	50–61	Truncate	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.

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

Geographic range. Costa Rica, Panama.

Diagnosis

Montane; mandible striate 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. costaricensis*; 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 85 (76–91, 7); PTI 54 (50–58, 9).

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.

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 treefalls 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 nests beneath epiphytes. Males can be common in Malaise traps (associated with COI results). An alate queen was collected by an INBio Parataxonomist, at Tapantí 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 petiole 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 petiole 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-B0786CBE44DE)

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, M/25/787 [UCR, unique specimen identifier JTLC000008527]. PARATYPES: 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, INB0003660648]; 10.42519 −84.00399 ±20 m, 50 m, 18-v-1993, light trap, ALAS, L/02/038 [1 alate queen, MCZC, INBIOCRI001276551; 1 alate queen, UCD, INBIOCRI001276552]; 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; petiole 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, 5); 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-A579-1ECFA88160EC)

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, CAS, 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 and 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 Musún, 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-BC4A-E74B563BF801)

HOLOTYPE: Guatemala, Suchitepéquez: Refugio El Quetzal, 14.55483 −91.19299 ±50 m, 1,838 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, UCD, 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])

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: 445 is *R. panamensis*.]

Euponera (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 specimen 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, UVGC, 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 1,500 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. Dealate 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])

Pachycondyla 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 *R. subcubitalis*) 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].

Euponera (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); PTL 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; PTL 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-ii-2005, AMI-1-W-023-02 [1 worker, UCD, INB0003660695]; 7 km SW Pto. 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 Mosquitia) 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 (86–91, 26); SI 73 (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 74 (73–74, 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 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 allopatric, *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, CAS, 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 Union, 14.95 −89.26667 ±?, 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 sinuous; 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. Aguaclara 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 scapes. 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 Fig. S32 [online only])
(urn:lsid:zoobank.org:act:DAC52866-DD20-4B90-84EF-DC01811CB9A3)

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 −87.89938 ±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. Three species are within geographic and size range of *R. subcubitalis*:

Rasopone ferruginea (Fig. 11; Supp Figs. S12 and S13 [online only]): anterior clypeal margin sinuous; petiole more scale-like.

Rasopone guatemalensis (Fig. 8; Supp Figs. S14 and S15 [online only]): mandible smooth; petiole more scale-like.

Rasopone politognatha (Fig. 9; Supp Figs. S28 and S29 [online only]): mandible smooth and shining.

Measurements, worker: HW 1.25 (1.21–1.30, 9); HL 1.40 (1.36–1.44, 9); SL 1.06 (1.03–1.09, 3); PTH 0.94 (0.90–1.00, 8); PTL 0.52 (0.50–0.55, 8); CI 89 (88–90, 9); SI 84 (84–85, 3); PTI 55 (53–60, 8).

Biology

This species occurs in a range of wet to moist forest habitats, with records from 390 to 1400 m elevation. Only workers are known, all from Winkler or Berlese samples of forest floor litter and rotten wood.

Comments

UCE and COI data support this species delimitation.

Rasopone titanis New Species

(Fig. 13; Supp Fig. S33 [online only])

HOLOTYPE: 1 worker, Mexico, Chiapas, Ocosingo, 16.906 −92.099 ±?, 2-vi-1969, around waterfall, ex sifted leaf litter, J. M. Campbell [MCZC, unique specimen identifier MCZ-ENT00716640]. PARATYPES: same data as holotype [1 worker, UNAM, MCZ-ENT00716641; 1 worker, USNM, MCZ-ENT00716642; 1 worker, MCZC, MCZ-ENT00716659].
Geographic range. Mexico (Chiapas).

Diagnosis

Mandible smooth; anterior clypeal margin sinuous; side of head lacking erect setae; petiolar node tapering. Differing from *R. rupinicola* (Fig. 13; Supp Figs. S30 and S31 [online only]) in more robust mesosoma and more tapering petiolar node.

Measurements, worker: HW 1.67, HL 1.80, SL 1.45, PTL 0.64, PTH 1.09, CI 93, SI 87, PTI 58 ($n = 1$).

Comments

This species is known from one series of four workers. The locality is simply 'Ocosingo' and there is no habitat or microhabitat information. It is one of the largest species in the genus.

Rasopone JTL027

(Fig. 8; Supp Fig. 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 (JTL029 and JTL030) and *R. cryptergates* from Costa Rica.

Rasopone JTL029

(Fig. 12; Supp Fig. 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. Three species are within geographic and size range of *R.* JTL034:

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).

Rasopone JTL035 (Fig. 9; Supp Fig. S38 [online only]): no known local sympatry but in close proximity in Sierra de Los Tuxtlas, possibly segregating by elevation; somewhat larger and darker red brown; side of head bare.

Measurements, worker: HW 1.11 (1.04–1.15, 3); HL 1.19 (1.12–1.23, 3); SL 0.85 (0.79–0.91, 3); PTH 0.73 (0.68–0.77, 3); PTL 0.42 (0.39–0.45, 3); CI 93 (92–93, 3); SI 77 (75–79, 3); PTI 58 (56–61, 3).

Biology

This species occurs in wet to moist forest, with records from 170 to 980 m elevation. It is known from four widely separated localities. The three known worker specimens are from Winkler samples of forest floor litter and rotten wood. A male was collected 14 June 2010 in a Malaise trap.

Comments

UCE results unite three workers from widely separated localities. The sister taxon is the single specimen of *R.* JTL035, which appears to be a more montane version of *R.* JTL034 that is slightly larger and darker. The specimen of *R.* JTL035 is from a cloud forest site in Sierra de Los Tuxtlas, while one of the specimens of *R.* JTL034 is from just a few kilometers away, in the lowland rainforest of Los Tuxtlas Biological Station. However, the Los Tuxtlas specimen of *R.* JTL034 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 ferruginea (Fig. 11; Supp Figs. S12 and S13 [online only]): mandible striate; anterior clypeal margin sinuous; petiole more scale-like.

Rasopone JTL034 (Fig. 7; Supp Fig. S37 [online only]): no known local sympatry but in close proximity in Sierra de Los Tuxtlas, possibly segregating by elevation; somewhat smaller and lighter brown; side of head with inconspicuous, short erect setae.

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]): anterior clypeal margin sinuous; 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, 3); 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 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 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.brv15dv5v). The Phyluce package and associated programs can be downloaded from github (github.com/faircloth-lab/phyluce). The ant-specific baits used to enrich UCE loci can be purchased from Arbor Biosciences (arborbiosci.com/genomics/targeted-sequencing/mybaits/mybaits-expert/mybaits-expert-uce/) and the 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-LABECOL-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-LABECOL-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 mesoamericana*. Holotype worker. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

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

Fig. S21. *Rasopone mesoamericana*. 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 pluviselva*. Holotype worker. Scale bars 0.5 mm for face view, 1 mm for dorsal and lateral views.

Fig. S27. *Rasopone pluviselva*. 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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