

A new ant genus from southern Argentina and southern Chile, *Patagonomyrmex* (Hymenoptera: Formicidae)

ROBERT A. JOHNSON^{1,3} & CORRIE S. MOREAU²

¹School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501, USA

²Field Museum of Natural History, Department of Science and Education, 1400 South Lake Shore Drive, Chicago, IL 60605, USA

³Corresponding author. E-mail: Robert.Johnson4@asu.edu

Abstract

The ant genus *Pogonomyrmex* (Hymenoptera: Formicidae: Myrmicinae) comprises 71 described species that occur in North America, South America, and Hispaniola, and it is the nominal genus in the recently established tribe Pogonomyrmecini. A molecular phylogeny using 3,647 base pairs from fragments of one mitochondrial gene (*cytochrome oxidase I*) and five nuclear genes (*long-wavelength rhodopsin*, *elongation factor 1α F1*, *elongation factor 1α F2*, *wingless*, *rudimentary*) inferred that *Pogonomyrmex* was not monophyletic. The vast majority of species belonged to a monophyletic clade (*Pogonomyrmex* sensu stricto), whereas species in the *Po. angustus*-group formed a second lineage outside of *Pogonomyrmex* and *Hylomyrma*, the latter being the only other genus in the tribe. To maintain monophyly of *Pogonomyrmex*, we create the genus *Patagonomyrmex* gen. n., which consists of the three *angustus*-group species (*Patagonomyrmex angustus* comb. n., *Patagonomyrmex laevigatus* comb. n., and *Patagonomyrmex odoratus* comb. n.) that are sister to all other pogonomyrmecines. The genus is restricted to southern Argentina and southern and southcentral Chile. Workers are characterized by: (1) poorly-developed psammophore that consists of short to medium-length hairs scattered over the ventral surface of the head, (2) anterior clypeal margin strongly convex in full-face view, (3) clypeus strongly convex in profile, (4) superior and inferior propodeal spines long, (5) dorsal surface of promesonotum smooth and shiny, lacking rugae or if rugae present, then interrugae strongly granulate-punctate, (6) anteroventral margin of peduncle of the petiole with a small, acuminate spine, and (7) palp formula 5,4. We also provide information on biology, distribution maps, and a key to workers, queens, and males in English and Spanish.

Key words: key to species, myrmicinae, new ant genus, Patagonia, *Patagonomyrmex*, Pogonomyrmecini, *Pogonomyrmex*, South America

Resumen

El género de hormigas *Pogonomyrmex* (Hymenoptera: Formicidae: Myrmicinae) comprende en 71 especies descritas las cuales se encuentran en Norteamérica, Suramérica e Hispaniola, y es el género nominal de la tribu recientemente establecida Pogonomyrmecini. Con el uso de 3,647 pares de bases de fragmentos de un gen mitocondrial (*citocromo oxidasa I*) y cinco genes nucleares (*rodopsina de longitud de onda larga*, *factor de alargamiento 1aF1*, *factor de alargamiento 1aF2*, *wingless*, *rudimentario*) se obtuvo una filogenia molecular la cual señala que *Pogonomyrmex* no es monofilético. La gran mayoría de especies pertenecen al clado monofilético *Pogonomyrmex* (sensu stricto) mientras que las especies del grupo *Po. angustus* forman un segundo linaje diferente a *Pogonomyrmex* e *Hylomyrma*, este último constituyendo el único otro género de la tribu. Para mantener la monofilia de *Pogonomyrmex* creamos el género *Patagonomyrmex* gen. n., el cual consiste en las tres especies del grupo de *angustus* (*Patagonomyrmex angustus* comb. n., *Patagonomyrmex laevigatus* comb. n. y *Patagonomyrmex odoratus* comb. n.) las cuales son hermanas de todas las demás pogonomirmecinas. El género está restringido al sur de la Argentina, además del sur y surcentro de Chile. Las obreras se caracterizan por: (1) un psamóforo de poco desarrollo el cual consiste en pelos de longitudes cortas a medianas dispersos sobre la superficie ventral cefálica, (2) el margen anterior del clípeo es fuertemente convexo en vista frontal cefálica, (3) el clípeo es fuertemente convexo de perfil, (4) tanto las espinas propodeales superiores como las inferiores son largas, (5) la superficie dorsal del promesonoto es liso y brillante, sin arrugas pero sí las hay entonces los espacios entre las arrugas son fuertemente granulados – punteadas –

dos, (6) el margen anteroventral de pedúnculo peciolar presenta una pequeña espina acuminada, y (7) fórmula palpo 5,4. También suministramos información sobre la biología, mapas de distribución, y una clave para las obreras, reinas, y machos tanto en inglés y español.

Palabras Claves: claves a especies, mirmicinae, nuevo género de hormiga, Patagonia, *Patagonomyrmex*, Pogonomyrmecini, *Pogonomyrmex*, Sudamérica

Introduction

The myrmicine ant genus *Pogonomyrmex* comprises 71 described species that occur throughout most of North and South America, and also on the island of Hispaniola (Bolton, 2014; Johnson, 2015; Johnson & Cover, 2015). Species of *Pogonomyrmex* have been the focus of numerous studies that have facilitated our understanding of ant biology (Anderson *et al.*, 2006; Cole & Wiernasz, 1999; Gordon & Kulig, 1996; Hölldobler, 1971, 1976; Johnson, 2001, 2002, 2006; Wiernasz & Cole, 2003), and they are ecologically important because of their direct and indirect effects on community structure and function (MacMahon, Mull, & Crist, 2000). Despite the ecological importance of *Pogonomyrmex*, molecular phylogenetic tools have been used only to describe new species (Johnson & Overson, 2009; Johnson, Overson, & Moreau, 2013) or to examine relationships among small groups of species such as the two social parasite species (Parker & Rissing, 2002). Several phylogenies that included numerous ant species have shown some genera to be polyphyletic (LaPolla, Kallal, & Brady, 2012; Moreau & Bell, 2013; Schmidt & Shattuck, 2014; Ward, 2011; Ward, Brady, Fisher, & Schultz, 2015). Consequently, a molecular phylogeny that includes numerous species of *Pogonomyrmex* would prove valuable for understanding the origin and relationships among the three faunal groups and to test if the genus is monophyletic.

Ward *et al.* (2015) reconstructed a phylogeny for myrmicine ants, and therein erected the tribe Pogonomyrmecini, which consisted of two genera, *Pogonomyrmex* and *Hylomyrma*, and the *Po. angustus*-group, with the latter group shown to be a monophyletic clade that was sister to all other pogonomyrmecines. However, Ward *et al.* (2015) refrained from assigning the *Po. angustus*-group to a new genus given the more detailed phylogeny that was reconstructed herein using samples from all species groups in North America, South America, and Hispaniola. Our phylogeny also supported erecting a new genus for species in the *Po. angustus*-group. We redescribe workers of all three species (they were initially described in German, French, and Spanish) in order to provide a homogenous treatment in one language, along with distribution maps, keys for all castes, and information on their biology.

Methods

Molecular analyses and phylogenetic inferences. Historically, the ant genus *Pogonomyrmex* has been separated into two subgenera, *Pogonomyrmex* and *Ephebomyrmex*, with the primary differences between these groups being that species in the latter group are smaller, have an incomplete or poorly-developed psammophore, and their mesosomal rugae are usually more rugoreticulate. All three *Po. angustus*-group species were described as *Ephebomyrmex* or were placed within *Ephebomyrmex* soon after their description (Emery, 1921; Kusnezov, 1949; Santschi, 1921).

We sequenced 54 specimens to test the monophyly of the putative new genus, focusing on species formerly placed in the subgenus *Ephebomyrmex*. These samples included available species from the three geographic faunas (five sequences from two *Po. angustus*-group species, 15 sequences from six North American species, five sequences from two South American species, and six sequences from two Hispaniolan species) (Table 1). We also included broad coverage from the former subgenus *Pogonomyrmex* by sequencing one to two species from each species-group for a total of seven North American species and 11 South American species. We also sampled one species of *Hylomyrma*, a genus nested within *Pogonomyrmex* sensu lato (Ward *et al.*, 2015) and, as outgroups, one sample of *Veromessor pergandei*, one sample of *Novomessor cockerelli*, and one sample from each of two species of *Myrmica* (all subfamily Myrmicinae) (Table 1). Sequences for three samples (RAJ 4128, RAJ 4217, RAJ 4256) were included in a previous study (see Johnson *et al.*, 2013 for GenBank accession numbers). All other sequences are deposited in Genbank: KU318715—KU318943.

Field collections were made in 95% EtOH and kept in the laboratory until DNA extraction. Total genomic DNA was isolated for one worker per series in lysis buffer with a Teflon grinding tool, followed by purification using the DNeasy® Tissue Kit (Qiagen Inc., Valencia, CA) following the protocol of the manufacturer.

TABLE 1. Locale data for specimens used to reconstruct the DNA phylogeny for pogonomyrmecine ants (**Figure 1**). Locales are given as COUNTRY: *first administrative division (department, province, state)*, county (USA only), locale. Specimens used in the phylogeny are from Hispaniola, North America, and South America; species within each area are listed alphabetically by species group. Voucher specimens are deposited at FMNH, MCZ, RAJC, and/or UCDC (see below).

TAXON AND LOCALITY	Latitude	Longitude	ELEVATION (m)	COLLECTOR, ACCESSION NUMBER, AND LOCATION OF VOUCHERS ⁺
<i>Patagonomyrmex</i>*				
<i>Pa. angustus</i> (Mayr)				
ARGENTINA Neuquén: Brazo Huemul Nahual Huapi Lago	40° 58'S	71° 21'W	860	RA Johnson #4643 ^(2,3) , 4645 ^(2,3)
ARGENTINA Neuquén: San Martín de los Andes	40° 10'S	71° 22'W	800	PS Ward #12719 ⁽⁴⁾
ARGENTINA Río Negro: Cerro Lopez	41° 05'S	71° 33'W	1005	RA Johnson #4155 ^(2,3)
<i>Pa. odoratus</i> (Kusnezov)				
ARGENTINA Neuquén: Lago Tromen	39° 34'S	71° 26'W	1050	PS Ward #12731 ⁽⁴⁾
ARGENTINA Neuquén: Brazo Huemul Nahual Huapi Lago	40° 58'S	71° 21'W	860	RA Johnson #4644 ^(2,3)
<i>Pogonomyrmex</i>				
HISPANIOLA				
<i>Po. schmitti</i>-group*				
<i>Po. saucius</i> Wheeler & Mann				
DOMINICAN REPUBLIC Pedernales: Cabo Rojo	17° 54'N	71° 40'W	5	PS Ward #11730 ^(2,4)
DOMINICAN REPUBLIC Pedernales: Pedernales	18° 02'N	71° 44'W	20	A Clark #007 ^(2,3)
<i>Po. schmitti</i> Forel				
DOMINICAN REPUBLIC La Altagracia: Punta Cana, Indigenous Eyes Nature Preserve	18° 31'N	68° 23'W	5	SP Cover #DR08 ^(2,3)
DOMINICAN REPUBLIC La Altagracia: Parque Nacional del Este at Caseta de Guaraguao	18° 20'N	68° 48'W	10	SP Cover #DR144 ^(2,3)
DOMINICAN REPUBLIC Valverde: Parque Nacional Monte Cristi	18° 54'N	71° 40'W	20	SP Cover #DR101 ^(2,3)
DOMINICAN REPUBLIC Valverde: Rt 1 at 1.6 mi N Villa Elisa	19° 44'N	71° 15'W	150	G Alpert #site 13 ^(2,3)
NORTH AMERICA				
<i>Po. barbatus</i>-group				
<i>Po. barbatus</i> (F. Smith)				
USA TX: Oldham, Hwy 214 at 1.5 mi S Adrian	35° 15'N	102° 39'W	1240	RA Johnson #2161 ^(2,3)
<i>Po. desertorum</i> Wheeler				
USA AZ: Cochise, 2.3 mi N Jct Portal & Foothills Rd	31° 57'N	109° 08'W	1380	RA Johnson #4269 ^(2,3)
<i>Po. californicus</i>-group				
<i>Po. badius</i>				
USA FL: Gulf, Wewahitchka at Steele Rd & Brannon Ln	30° 10'N	85° 15'W	42	CS Moreau #0257 ⁽¹⁾
<i>Po. californicus</i> Buckley				
USA CA: Inyo, Alabama Hills at 4.7 mi W Lone Pine	36° 36'N	118° 09'W	1540	RA Johnson #4128 ^(2,3)
<i>Po. hoelldobleri</i> Johnson, Moreau & Overson				
USA NV: Nye, Hwy 95 at 4.0 mi NW Lathrop Wells (=Amargosa Valley)	36° 40'N	116° 28'W	790	RA Johnson #4217 ^(2,3)

... continued on the next page

TABLE 1. (Continued)

Taxon and locality	Latitude	Longitude	Elevation (m)	Collector, accession number, and location of vouchers ⁺
<i>Po. guatemaltecus</i>-group*				
<i>Po. guatemaltecus</i> Wheeler				
GUATEMALA <i>El Progreso</i> : San Augustín Acasaguastlán Tulumaje	14° 56'N	89° 58'W	285	JG Polo #539, 540 ^(2,3)
<i>Po. humerotumidus</i> Vásquez-Bolaños & MacKay				
MEXICO <i>Michoacán</i> : La Huacana, km 189 on Carretera Nueva Italia-Infiernillo	18° 44'N	102° 01'W	195	L Escalante & M Vásquez-Bolaños #1-3 ^(2,3)
<i>Po. huachucanus</i>-group*				
<i>Po. huachucanus</i> Wheeler				
MEXICO <i>Sonora</i> : Sierra Mazatán	29° 06'N	110° 09'W	1240	RA Johnson #3397 ^(2,3)
USA AZ: Cochise, 1.8 mi NW Southwest Research Station	31° 54'N	109° 14'W	1795	RA Johnson #4288 ^(2,3)
USA AZ: Yavapai, Hwy 89 at 7.1 mi NE Paulden	34° 58'N	112° 24'W	1425	RA Johnson #3426 ^(2,3)
<i>Po. imberbiculus</i>-group*				
<i>Po. imberbiculus</i> Wheeler				
MEXICO <i>Sonora</i> : Lavender Canyon at 4.0 mi E Esqueda	30° 42'N	109° 31'W	1280	RA Johnson #3354 ^(2,3)
USA AZ: Cochise, 1.4 mi NW Portal	31° 55'N	109° 10'W	1510	RA Johnson #4271 ^(2,3)
USA AZ: Cochise, Chiricahua Mtns at 5.7 km 356°N Portal	31° 58'N	109° 09'W	1400	CS Moreau #1128 ⁽¹⁾
USA AZ: Maricopa, Mazatzal Mtns at 1.5 mi S Mesquite Wash	33° 42'N	111° 27'W	955	RA Johnson #4247 ^(2,3)
USA AZ: Mohave, I-40 at 7.5 mi E Kingman	35° 12'N	113° 54'W	1240	RA Johnson #4227 ^(2,3)
<i>Po. laevinodis</i> Snelling				
MEXICO <i>Baja California Sur</i> : 1.6 mi S Las Pocitas	24° 22'N	111° 07'W	55	RA Johnson #2679 ^(2,3)
<i>Po. pima</i> Wheeler				
USA AZ: McCartney Rd at 2 mi E Jct I-10	32° 56'N	111° 40'W	435	RA Johnson #4197 ^(2,3)
<i>Po. occidentalis</i>-group				
<i>Po. occidentalis</i> (Cresson)				
USA NV: Mineral, Montgomery Pass	37° 58'N	118° 20'W	2150	RA Johnson #4256 ^(2,3)
<i>Po. subnitidus</i> Emery				
USA CA: San Diego, Kitchen Creek at 7 mi N I-8	32° 47'N	116° 27'W	1370	RA Johnson #3428 ^(2,3)
SOUTH AMERICA				
<i>Po. brevibarbis</i>-group				
<i>Po. brevibarbis</i> Emery				
ARGENTINA <i>Santa Cruz</i> : Rt 3 at 37.2 km N Piedrabuena	49° 46'S	68° 35'W	15	RA Johnson #4686 ^(2,3)
<i>Po. coarctatus</i>-group				
<i>Po. coarctatus</i> Mayr				
ARGENTINA <i>Entre Ríos</i> : Rt 18 at 3.3 mi NW Villaguay	31° 49'S	59° 03'W	65	RA Johnson #3859 ^(2,3)

... continued on the next page

TABLE 1. (Continued)

Taxon and locality	Latitude	Longitude	Elevation (m)	Collector, accession number, and location of vouchers ⁺
<i>Po. cunicularius</i>-group				
<i>Po. cunicularius</i> Mayr				
ARGENTINA <i>Entre Ríos</i> : Pueblo Liebig	32° 09'S	58° 12'W	20	RA Johnson #3628 ^(2,3)
<i>Po. bispinosus</i>-group				
<i>Po. uruguayensis</i> Mayr				
ARGENTINA <i>San Luis</i> : Rt 20 at 1 km NE Luján	32° 21'S	65° 56'W	590	RA Johnson #3680 ^(2,3)
<i>Po. laticeps</i>-group				
<i>Po. mendozanus</i> Claver & Cuezzo				
ARGENTINA <i>Mendoza</i> : 22.1 km S Jct Rts 7 & 153	33° 27'S	68° 06'W	575	RA Johnson #4077 ^(2,3)
<i>Po. mayri</i>-group				
<i>Po. mayri</i>				
COLOMBIA <i>Magdalena</i> : Santa Marta, Vereda Mosquito, Finca El Reposo	11° 10'N	74° 11'W	95	R Guerrero #1038 ⁽¹⁾
<i>Po. naegelii</i>-group*				
<i>Po. abdominalis</i> Santschi				
ARGENTINA <i>Entre Ríos</i> : Victoria	32° 38'S	60° 10'W	25	RA Johnson #4600 ^(2,3)
<i>Po. naegelii</i> Forel				
BRAZIL <i>Rio Grande do Sul</i> : Tramandai	30° 00'S	50° 08'W	0	C Rabeling #081220-03 ^(2,3)
PARAGUAY <i>Boquerón</i> : Mister Long	20° 36'S	60° 03'W	140	T Delsinne #4272 ⁽³⁾
PERU <i>Madre de Dios</i> : Puerto Maldonado	12° 36'S	69° 11'W	200	F Azorsa #4826 ⁽³⁾
VENEZUELA <i>Aragua</i> : Maracay, Corte Fuego de Mata Seca (Sendero de Mata Seca)	10° 18'S	67° 39'W	515	D Kronauer #4199 ⁽³⁾
<i>Po. rastratus</i>-group				
<i>Po. andinus</i> Kusnezov				
ARGENTINA <i>Salta</i> : Rt 51 at 3.8 km E San Antonio de los Cobres	24° 13'S	66° 18'W	3885	RA Johnson #3792 ^(2,3)
<i>Po. pronotalis</i> Santschi				
ARGENTINA <i>Mendoza</i> : Rt 145 at 42.2 km W Bardas Blancas	35° 50'S	70° 11'W	1630	RA Johnson #4107 ^(2,3)
<i>Po. rastratus</i> Mayr				
ARGENTINA <i>Mendoza</i> : 19.7 km W Villavincencio	32° 29'S	69° 04'W	2685	RA Johnson #4041 ^(2,3)
<i>Po. vermiculatus</i> Emery				
ARGENTINA <i>Santa Cruz</i> : Rt 11 at 19.3 km W El Calafete	50° 21'S	72° 31'W	220	RA Johnson #4681 ^(2,3)
<i>Po. sylvestris</i>-group				
<i>Po. striatinodus</i> Fernández & Palacio				
ECUADOR <i>Pichincha</i> : Choco Valley at 3 km S Mindo	04° 13'S	78° 46'W	1320	CS Moreau #0389 ⁽¹⁾

... continued on the next page

TABLE 1. (Continued)

Taxon and locality	Latitude	Longitude	Elevation (m)	Collector, accession number, and location of vouchers ⁺
OUTGROUP SAMPLES				
Subfamily Myrmicinae				
<i>Hylomyrma dentiloba</i> (Santschi)				
COSTA RICA Heredia: La Selva Biological Station	10° 26'N	84° 01'W	50	MM Olson WF/MO/1/ 03 ^(1,3)
<i>Myrmica</i>				
<i>Myrmica</i> n.sp. 02				
USA AZ: Gila, Pinal Mtns at Russell Gulch	33° 18'N	110° 52'W	1805	RA Johnson #4202 ^(2,3)
<i>Myrmica</i> sp.				
USA AZ: Cochise, Chiricahua Mtns at 11.7 km 270°W Portal	31° 56'N	109° 16'W	2365	CS Moreau #1134 ⁽¹⁾
<i>Novomessor cockerelli</i> (André)				
USA AZ: Cochise, Chiricahua Mtns at 5.7 km 356°N Portal	31° 58'N	109° 09'W	1400	CS Moreau #1131 ⁽¹⁾
<i>Veromessor pergandei</i> (Mayr)				
USA CA: San Bernardino, Hwy 15 at Basin Rd exit ramp	35° 05'N	116° 16'W	350	CS Moreau #0122 ⁽¹⁾

*denotes species that have been placed in or have morphological characters that could place them in the former subgenus *Ephebomyrmex*.

⁺Location of voucher specimens: 1=FMNH, 2=MCZ, 3=RAJC, 4=UCDC.

Six gene fragments were amplified via PCR (Mullis *et al.* 1987; Saiki *et al.* 1988) using specific primers for each gene region following the protocols of Moreau, Bell, Vila, Archibald, and Pierce (2006), Moreau (2008), Ward, Brady, Fisher, and Schultz (2010) and Moreau (2014). These six gene fragments included: (1) *cytochrome oxidase I* (COI) protein encoding mitochondrial marker (1019 base pairs [bp]), (2) *long-wavelength rhodopsin* (LR) protein encoding nuclear marker (549 bp), (3) *elongation factor 1α F1* (EF1α-F1) protein encoding nuclear marker (357 bp), (4) *elongation factor 1α F2* (EF1α-F2) protein encoding nuclear marker (517 bp), (5) *wingless* (Wg) protein encoding nuclear marker (409 bp), and (6) *rudimentary* (CAD) protein encoding nuclear marker (796 bp) for a total of 3,647 bp of aligned sequence. Specimens were sequenced for all six genes with the following exceptions: COI missing for nine taxa (CSM1131, GA_site13, PSW12719, PSW12731, RAJ2679, RAJ4600, RAJ4643, SPC_DR144, TD4272); CAD missing for 15 taxa (AC007, CSM0389, CSM1134, GA_site13, MMO_WF_MO_1_03, PSW11730, PSW12719, PSW12731, RAJ3354, RAJ4271, RAJ4600, RAJ4643, RAJ4645, SPC_DR08, SPC_DR144); EF1α-F1 missing for 10 taxa (CR_081220_03, DK4199, FA4826, GA_site13, PSW11730, RAJ2679, RAJ4600, SPC_DR08, SPC_DR144, TD4272); LR missing for two taxa (PSW12719, RAJ4645); Wg missing for 10 taxa (LE_MVB2, PSW11730_3, RAJ2679, RAJ4202, RAJ4227, RAJ4643, RAJ4644, RAJ4645, SPC_DR08, SPC_DR144).

All sequencing used dye terminator cycle sequencing following the protocol specified by the ABI PRISM™ Dye Terminator Cycle Sequencing Ready Reaction Kit (Revision B, August 1995, Perkin-Elmer, Norwalk, CT). Primers used for amplification served as sequencing primers. Additional internal primers were used for the COI mitochondrial gene to provide overlapping sequence coverage for the entire region, as per Moreau *et al.* (2006). Samples were sequenced in both directions following the protocol of Moreau *et al.* (2006). The homology of introns can be difficult to assign, so they were excluded from the CAD and LR alignment before phylogenetic analyses. Sequences were then analyzed and initially aligned using the computer programs Sequencing Analysis 3.7 (ABI Prism™ 2001) and Geneious v5.6 (Drummond *et al.*, 2012). Inferred amino acid sequences were used for all genes, allowing for comparatively uncomplicated alignment using Mesquite v2.75 (Maddison & Maddison, 2011).

To infer relationships among species, several model based phylogenetic analyses were performed on the CIPRES Science Gateway (Miller, Pfeiffer, & Schwartz, 2010) using RAxML v7.3.2 (Stamatakis, Ludwig, & Meier, 2005) and MrBayes v3.1.2 (Huelsnbeck & Ronquist, 2001). Modeltest 3.06 (Posada & Crandall, 2001)

was used to determine the most appropriate nucleotide substitution model for all analyses and partitions (GTR+Γ+I). The maximum likelihood search implemented in RAxML allowed each region to have a separate GTR+Γ+I model with parameters unlinked (partitioned) with 500 bootstrap pseudoreplicates.

Bayesian inference analyses were performed using MrBayes, with model parameters estimated during the run, and using the default value of four Markov chains. A “temperature” parameter of 0.2 was implemented to produce incremental heating of each chain. The Markov chain Monte Carlo length was 25,000,000 generations, with the chain sampled every 1000 generations. Bayesian posterior probabilities (BPP) were estimated as the proportion of trees sampled after 10% burn-in that contained each of the observed bipartitions (Larget & Simon, 1999; Rannala & Yang, 1996). Again, this analysis allowed each gene region to have a separate GTR+Γ+I model with parameters unlinked (partitioned). Independence of runs was ensured by accepting only analyses in which the average standard deviation of split frequencies was below 0.01. The database (nexus file) on which the molecular analyses are based is available on TreeBASE (TreeBASE ID: 19049).

Measurements and indices. Morphological characters were photographed using a Spot Insight QE camera attached to a Leica MZ 125 microscope. Images were then projected onto a video monitor, and characters were measured using ImageJ (available at <http://rsb.info.nih.gov/nih-image/>). Measurements were calibrated using photographs of an ocular micrometer scaled in 0.01 mm increments. All measurements are given in mm; those in parentheses represent minimum and maximum values. The following standard measurements are used:

- HL** **Head Length:** length of the head capsule excluding mandibles, in full-face view, from the midpoint of the anterior clypeal margin to the midpoint of the posterior margin.
HW **Head Width:** maximum width of the head immediately behind the eyes, measured in full-face view.
CI **Cephalic Index:** $(\text{HW}/\text{HL}) \times 100$.
MOD **Maximum Ocular Diameter:** maximum diameter of the eye measured with the head in full lateral aspect.
OI **Ocular Index:** $(\text{MOD}/\text{HW}) \times 100$.
OMD **Oculo-Mandibular Distance:** minimum distance from the anterior eye margin to the nearest point of the malar area (base of mandible).
SL **Scape Length:** maximum straight line length of the antennal scape from apex to base.
SI **Scape Index:** $(\text{SL}/\text{HW}) \times 100$.
PNW **Pronotal Width:** maximum width of the pronotum, as seen from above, measured at a right angle to the longitudinal axis of the mesosoma.
HFL **Hind Femur Length:** hind femur measured along the dorsal margin from the articulation with the trochanter to most distal tip of the femur.
HFI **Hind Femur Index:** $(\text{HFL}/\text{HW}) \times 100$.
ML **Mesosoma Length:** diagonal length of the mesosoma in profile from the point at which the pronotum meets the cervical shield to the posterior base of the metapleural lobe.
PW **Petiole Width:** maximum width of petiolar node, as seen from above, at a right angle to the longitudinal axis of the mesosoma.
PPW **Postpetiole Width:** maximum width of postpetiole, as seen from above, at a right angle to the longitudinal axis of the mesosoma.

Collections are referred to by the following acronyms:

CASC	California Academy of Sciences, San Francisco, California, USA
FML	Instituto Miguel Lillo, Tucumán, Tucumán Province, Argentina
LACM	Los Angeles County Museum of Natural History, Los Angeles, California, USA
MACN	Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
MHNG	Museum of Natural History, Geneva, Switzerland
MLPA	Museo de La Plata, La Plata, Buenos Aires Province, Argentina
MZUSP	Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil
NMW	Naturhistorisches Museum, Vienna, Austria
PSWC	Phillip S. Ward collection, Davis, California, USA
RAJC	Robert A. Johnson collection, Tempe, Arizona, USA
UCDC	University of California, Davis, Davis, California, USA
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
ZSM	Zoologische Staatssammlung, München, Germany

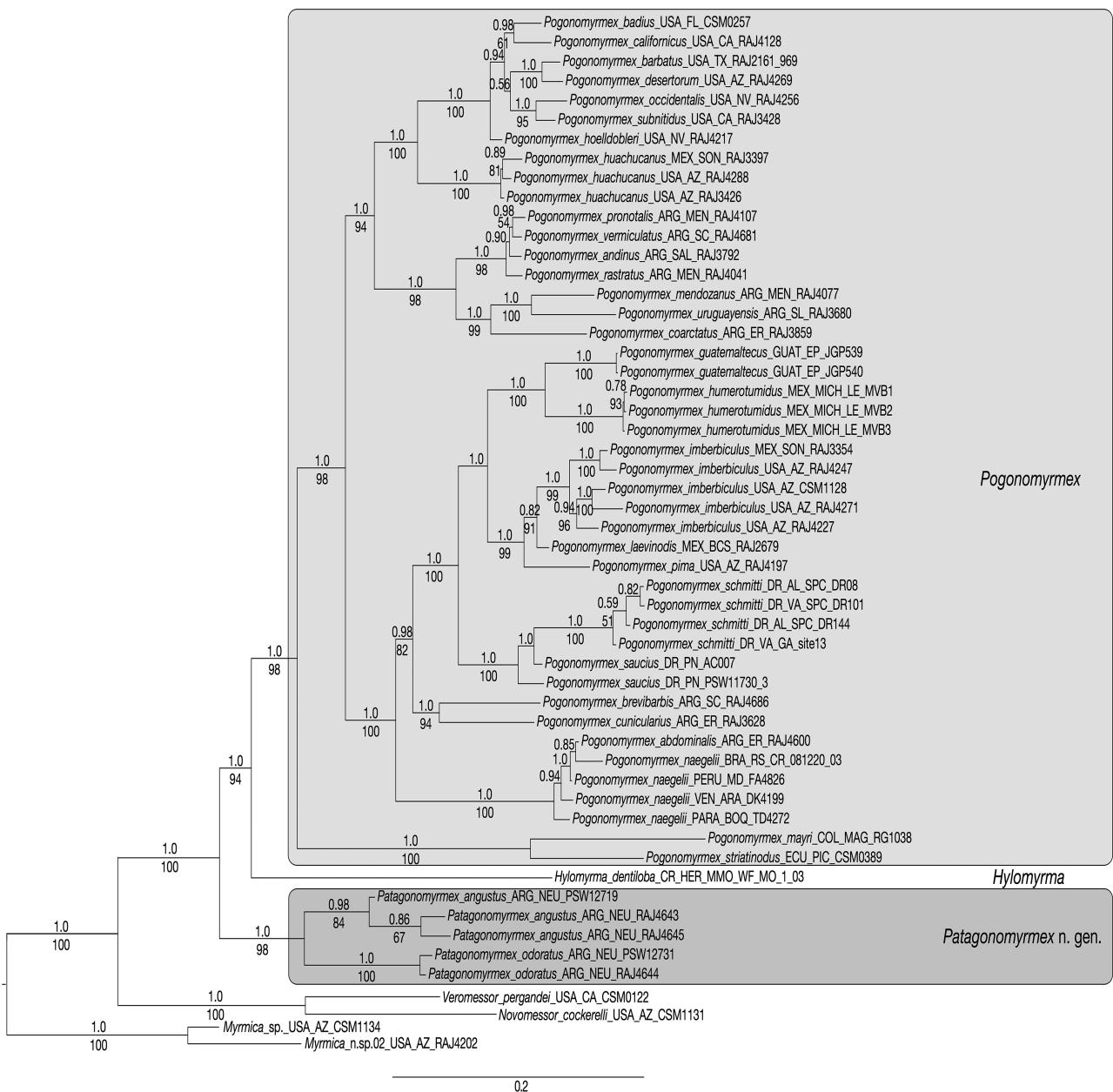


FIGURE 1. Phylogram for ants in the genera *Patagonomyrmex*, *Hylomyrma*, and *Pogonomyrmex* as inferred through Bayesian analysis for the partitioned dataset. Specimens of the two *Patagonomyrmex* species are in the darker grey box and those of *Pogonomyrmex* in the lighter grey box. Branch lengths are proportional to substitution/site as indicated by the bottom legend. Clade support greater than 50% is denoted on branches: values above and below branches represent Bayesian posterior probabilities (BPP) and maximum likelihood bootstrap (ML BS), respectively. Missing ML BS values denote clades with less than 50% support. Locality data (country and state/province) and accession number of the series from which the individual was taken follow species names (see also Table 1).

Results

Phylogenetic data. The aligned matrix of 3,647 bp contained 2,319 constant sites (64%), 305 variable non-parsimoniously informative sites (8%) and 1,023 parsimoniously informative sites (28%). The Bayesian inference topology for the partitioned analysis is presented in **Figure 1** with support values for the Bayesian posterior probabilities (BPP) and maximum likelihood bootstrap (ML BS). The Bayesian inference and maximum likelihood analyses resulted in nearly identical topologies with weakly supported clades (i.e., those below 50%) represented on **Figure 1** by missing ML BS values. All Bayesian inference and maximum likelihood tree topologies showed strong support for the monophyly of the new genus *Patagonomyrmex* (1.0 BPP partitioned; 98% ML BS

partitioned; **Figure 1**). We restore monophyly of *Pogonomyrmex* by creating the genus *Patagonomyrmex gen. n.*, which consists of the three *angustus*-group species, *Patagonomyrmex angustus*, *Patagonomyrmex laevigatus*, and *Patagonomyrmex odoratus*; this new genus is sister to all other pogonomyrmecines (**Figure 1**).

Worker key to genera in the ant tribe Pogonomyrmecini

Patagonomyrmex is one of three genera within the recently erected tribe Pogonomyrmecini (Ward *et al.*, 2015). Pogonomyrmecine workers can be separated from other neotropical myrmecine ants by: (1) antennal scrobes lacking, (2) antenna with 12 segments, apical and preapical segments never terminating in a conspicuously differentiated 2-segmented club, (3) frontal lobes present, horizontal and somewhat elevated; in full-face view, frontal lobes partly to completely cover antennal sockets, (4) petiole pedunculate, and (5) tibial spurs of hind legs finely pectinate (see also Bolton, 1994). The following key separates the three pogonomyrmecine genera.

- 1 Psammophore well-developed, consisting of numerous, long, curved hairs along basolateral margin of head *Pogonomyrmex (part)*
- Psammophore poorly-developed, consisting of numerous, short to long hairs scattered over ventral surface of head 2
- 2 Inferior propodeal spines biaculeate, upper and lower portions both acuminate; apical (masticatory) margin of mandible markedly oblique in full-face view *Hylomyrma*
- Inferior propodeal spines rounded, triangular, or spiniform; when prominent they are always with a single point, never biaculeate; apical (masticatory) margin of mandible perpendicular or nearly so in full-face 3
- 3 In full-face view, anterior margin of clypeus flat or concave, entire or rarely with small medial tooth; clypeus flat to weakly convex in profile; anteroventral margin of peduncle of petiole with or without a small, acuminate spine; posterior surface of petiolar node usually with transverse to oblique rugae or rugoreticulate; dorsum of postpetiole with longitudinal to oblique rugae to rugoreticulate *or* strongly granulate-punctate, dull; promesonotum rugose to rugoreticulate, interrugae smooth and shining to moderately coriarious, weakly shining; palp formula 4,3 *Pogonomyrmex (part)*
- In full-face view, anterior margin of clypeus convex, entire; clypeus strongly convex in profile; anteroventral margin of peduncle of petiole with a small, acuminate spine; posterior surface of petiolar node and dorsum of postpetiole smooth and shining to moderately coriarious, weakly shining; promesonotum smooth and shining *or* if rugose to rugoreticulate, then promesonotal interrugae strongly granulate, dull; palp formula 5,4 *Patagonomyrmex*

Clave a los géneros de la tribu de hormigas Pogonomyrmecini basada en las obreras

Patagonomyrmex es uno de los géneros de la recien creada tribu Pogonomyrmecini (Ward *et al.*, 2015). Obreras pogonomirmecinas se pueden diferenciar de otras mirmicinas neotropicales por: (1) la carencia de escrobo antenales, (2) antenas de 12 segmentos con los artejos apicales y preapicales jamás formando un mazo conspicuo de 2 segmentos, (3) lóbulos frontales horizontales y algo elevados, cubriendo las inserciones antenales de manera parcial a total en vista frontal, (4) pecíolo pedunculado, y (5) las metatibias con espolones finamente pectinados (ver también Bolton, 1994). La siguiente clave permite separar los tres géneros pogonomirmecinos.

- 1 Psamóforo bien desarrollado, con numerosos pelos largos y arqueados dispuestos sobre el margen laterobasal de la cabeza *Pogonomyrmex (parte)*
- Psamóforo poco desarrollado, con numerosos pelos, cortos hasta largos, dispersos sobre la superficie ventral céfálica 2
- 2 Espinas propodeales inferiores biaculeadas, tanto las porciones superior como inferior acuminadas; margen apical (masticador) mandibular bastante oblicuo en vista frontal *Hylomyrma*
- Espinas propodeales inferiores redondeadas, triangulares o espiniformes; si son prominentes siempre tienen un solo ápice, jamás son biaculeadas; margen apical (masticador) mandibular es totalmente o casi perpendicular en vista frontal 3
- 3 En vista dorsal céfálica, el margen anterior del clípeo es totalmente recto o cóncavo, rara vez con un dentículo mediano; el clípeo es recto o débilmente convexo en perfil; el margen anteroventral del pedúnculo petiolar puede o no presentar una pequeña espina acuminada; superficie posterior del nódulo petiolar usualmente tiene arrugas o arrugas reticuladas desde transversas hasta oblicuas; superficie dorsal pospetiolar puede tener arrugas o arrugas reticuladas desde longitudinales hasta oblicuas como también ser punteado con granulosidad y opaco; promesonoto puede ser arrugado o arrugado reticulado, espacio entre las arrugas puede ser desde liso y brillante hasta con líneas reticuladas y poco brillo; fórmula palpo 4,3 *Pogonomyrmex (parte)*
- En vista dorsal céfálica, todo el margen anterior del clípeo es convexo; en perfil el clípeo es bastante convexo; margen anteroventral del pedúnculo petiolar con un espina acuminada; superficie posterior del nodo petiolar y el dorso del pospetiolo liso y brillante como también moderadamente con líneas reticuladas, débilmente brillante; promesonoto liso y brillante pero si tiene arrugas o arrugas reticuladas los espacios entre las arrugas son muy granulosos y opacos; fórmula palpo 5,4 *Patagonomyrmex*

Description of *Patagonomyrmex*, gen. n.

Type species of the genus: *Patagonomyrmex angustus* (Mayr, 1870).

Etymology. The genus name, *Patagonomyrmex*, alludes to the distribution of these species, which are mostly restricted to the Patagonia region of Argentina and Chile.

Diagnosis of worker. Monomorphic, small (HW = 0.81–1.16 mm), soil-nesting, myrmicine ants with the following combination of characters:

- (1) Head weakly elongate to elongate (CI = 78.86–95.50).
- (2) Mandible with six teeth.
- (3) Psammophore poorly-developed, consisting of short to medium-length hairs scattered over ventral surface of head.
- (4) Superior propodeal spines long; inferior propodeal spines moderately long to long.
- (5) Dorsal surface of promesonotum smooth and shiny, lacking rugae *or* if rugae present, then interrugae strongly granulate-punctate, dull.
- (6) Anteroventral margin of peduncle of petiole with a small, acuminate spine.
- (7) In full-face view, anterior margin of clypeus convex and entire.
- (8) In profile, clypeus strongly convex.
- (9) Petiolar node triangular in profile, anterior surface slightly shorter than posterior surface, node subangulate to rounded.
- (10) Palp formula = 5,4.

Diagnosis of queen—as in worker except:

- (1) Small (HW < 1.25 mm and ML < 2.00 mm).
- (2) Mandible with 5–6 teeth.
- (3) Mesosoma with full complement of sclerites associated with presence of wings; head with well-developed ocelli.
- (4) Forewing lacking Rsf2–3, with submarginal cell 1+2.

Diagnosis of male.

- (1) Small (HW < 1.15 mm and ML < 2.00 mm).
- (2) Anteroventral margin of peduncle of petiole with a small, acuminate spine.
- (3) Funicular segments with very dense, short, suberect to erect pubescence.
- (4) Forewing lacking Rsf2–3, with submarginal cell 1+2.
- (5) In full-face view, strongly produced anterior margin of clypeus, nearly angulate medially.
- (6) In profile, clypeus strongly convex.

Synopsis of *Patagonomyrmex* species

Patagonomyrmex angustus (Mayr, 1870). NEW COMBINATION

Patagonomyrmex laevigatus (Santschi, 1921). NEW COMBINATION

Patagonomyrmex odoratus (Kusnezov, 1949). NEW COMBINATION

Key to species of *Patagonomyrmex*

Workers

- 1 Dorsum of promesonotum with subparallel rugae to rugoreticulate, interrugae strongly granulate-punctate, dull; rugae on cephalic dorsum continue to posterior margin of head (**Figure 2**) *angustus*
- Dorsum of promesonotum smooth and shining, lacking rugae; rugae on cephalic dorsum rarely continue to posterior margin of head (**Figures 6, 9**) 2

- 2 Body mostly concolorous blackish to black (**Figure 6**) *laevigatus*
 - Head and mesosoma light orangish-red, gaster slightly darker to brownish (**Figure 9**) *odoratus*

Queens

- 1 Mesoscutum and mesoscutellum with weak to moderately coarse longitudinal rugae, interrugae weakly to strongly granulate-punctate; inferior propodeal spines elongate, length similar to that of superior propodeal spines (**Figure 3**) *angustus*
 - Mesoscutum and mesoscutellum smooth and shiny; inferior propodeal spines triangular, much shorter than superior propodeal spines (**Figures 7, 10**) 2
 2 Body concolorous black (**Figure 7**) *laevigatus*
 - Body orangish to orangish-brown (**Figure 10**) *odoratus*

Males

- 1 Mesopleura, metapleura, pronotal sides, and dorsum of propodeum strongly granulate, dull, with a beaded appearance; at least several hairs on ventral surface of head and those protruding from mandibles approach to exceed MOD; scapes usually long, reaching to near posterior margin of eye (**Figure 4**) *angustus*
 - Mesopleura, metapleura, pronotal sides, and/or dorsum of propodeum with weak to strong rugae; no hairs on ventral surface of head or those protruding from mandibles approach MOD; scapes short, reaching only slightly beyond anterior margin of eye (**Figures 8, 11**) 2
 2 In profile, juncture between cephalic dorsum and posterior declivity (near posterior margin of ocelli) weakly angulate to rounded; posterior declivity weakly convex to weakly concave (**Figure 8**) *laevigatus*
 - In profile, juncture between cephalic dorsum and posterior declivity strongly angulate; posterior declivity strongly concave (**Figure 11**) *odoratus*

Clave a especies de *Patagonomyrmex*

Obreras

- 1 Dorso del promesonoto con arrugas desde semiparalelas hasta reticuladas, espacio entre las arrugas fuertemente granulado y punteado, opaco; arrugas del dorso cefálico continúan hasta el margen posterior de la cabeza (**Figura 2**) *angustus*
 - Dorso del promesonoto liso y brillante, sin arrugas; arrugas del dorso cefálico rara vez continúan hasta el margen posterior de la cabeza (**Figuras 6, 9**) 2
 2 La mayor parte del cuerpo negro a negruzco (**Figura 6**) *laevigatus*
 - Cabeza y mesosoma rojo anaranjado leve, el gaster ligeramente más oscuro, hasta marrón (**Figura 9**) *odoratus*

Reinas

- 1 Mesoscelo y mesoescelo con arrugas longitudinales débil a moderadamente toscas, espacios entre las arrugas débil a moderadamente granulado-punteado; espinas propodeales inferiores alargadas, su longitud similar al de las espinas superiores (**Figura 3**) *angustus*
 - Mesoscelo y mesoescelo liso y brillante; espinas propodeales inferiores triangulares, mucho más cortas que las espinas superiores (**Figuras 7, 10**) 2
 2 Cuerpo uniformemente negro (**Figura 7**) *laevigatus*
 - Cuerpo anaranjado a marrón anaranjado (**Figura 10**) *odoratus*

Machos

- 1 Lados del pronoto, mesometapleura y dorso del propodeo fuertemente granulado, opaco, de aspecto grumoso; por lo menos algunos pelos del lado ventral cefálico y de la mandíbula se aproximan o superan el diámetro máximo ocular; escapos usualmente largos, aproximándose al margen posterior del ojo (**Figura 4**) *angustus*
 - Lados del pronoto, mesometapleura y como también el dorso del propodeo con arrugas débiles a fuertes; ningún pelo del lado ventral cefálico ni los de la mandíbula se aproximan a el diámetro máximo ocular; escapos cortos, apenas superando al margen anterior del ojo (**Figuras 8, 11**) 2
 2 Visto en perfil, la unión entre el dorso cefálico y la hendidura posterior (cerca del margen posterior de los ocelos) es débilmente angular a redondeado; la hendidura posterior es débilmente convexa a cóncava (**Figura 8**) *laevigatus*
 - Visto de perfil, la unión entre el dorso cefálico y la hendidura posterior es fuertemente angular; la hendidura posterior es fuertemente cóncava (**Figura 11**) *odoratus*

Species accounts

Patagonomyrmex angustus NEW COMBINATION

(Figures 2–4)

Pogonomyrmex angustus Mayr, 1870: 970 (worker, in key). Syntypes examined: 2 workers [MHNG], 1 worker [NMW], CHILE, Valdivia (Edm. Reitter); Mayr, 1887: 612 (queen, male). See also Gallardo, 1932: 103; Kusnezov, 1949: 294. NMW worker here designated LECTOTYPE [CASENT0173374].

Pogonomyrmex (Ephebomyrmex) angustus Mayr; Emery, 1921: 48, first combination in *Pogonomyrmex (Ephebomyrmex)*. *Ephebomyrmex angustus* (Mayr); Kusnezov, 1960: 353, first combination in *Ephebomyrmex*.

Pogonomyrmex angustus Mayr; Snelling & Hunt, 1975: 72, fig. 23, revived combination in *Pogonomyrmex*.

Worker. Diagnosis. This species is uniquely characterized by the following combination of features: (1) strongly granulate-punctate interrugae on cephalic dorsum and dorsum of mesosoma, (2) posterior surface of petiolar node and dorsum of postpetiole moderately to strongly granulate-punctate, weakly shining to dull, (3) rugae on cephalic dorsum continue to posterior margin, (4) inferior propodeal spines long, length similar to that of superior spines, and (5) body concolorous dark brownish-black to black, usually with dark brown legs (**Figure 2**).

Measurements. Lectotype ($n = 15$). HL 1.25 (0.97–1.32); HW 1.12 (0.81–1.16); MOD 0.27 (0.21–0.29); OMD 0.27 (0.18–0.26); SL 0.93 (0.78–1.00); PNW 0.79 (0.59–0.82); HFL 1.21 (0.89–1.25); ML 1.59 (1.21–1.58); PW 0.31 (0.23–0.34); PPW 0.44 (0.36–0.51). Indices: SI 83.01 (83.04–104.94); CI 89.60 (80.58–91.74); OI 24.11 (21.55–29.63); HFI 108.04 (103.60–118.52).

Redescription. Longitudinal rugae on cephalic dorsum coarse, weakly wavy, running from frontal lobes to posterior margin; posterior margin flat in full-face view. Rugae on lateral surfaces more irregular, usually weaker than those on cephalic dorsum. Interrugae on cephalic dorsum strongly granulate-punctate, dull; vertex rugose. Dorsum of clypeus with several moderately coarse, subparallel, longitudinal rugae. Mandible with six teeth; mandibular dorsum strongly rugose. MOD ranging from 0.19–0.24x HL. In profile, eyes situated anterior to middle of head, OMD = 0.73–1.05x MOD. In full-face view, eyes protruding slightly beyond lateral margins of head. Antennal scapes long (SI = 83.01–104.94), reaching vertex; scapes moderately to strongly granulate-punctate, often with faint striae, dull; basal flange moderately well-developed with carinate margin.

Mesosomal profile weakly convex; dorsum of promesonotum with moderately coarse, irregular rugae; longitudinal rugae on mesospleura and metapleura wavy to irregular. Interrugae on promesonotum strongly granulate-punctate, dull; promesonotal suture usually faintly to weakly impressed. Superior propodeal spines long, acuminate, length rarely >0.7 –0.8x the distance between their bases; inferior propodeal spines well-developed, longer than wide, acuminate, length similar to that of superior spines. Propodeal spiracles weakly ovate to circular facing posterad. Legs smooth and shining to weakly granulate, weakly shining.

Peduncle of petiole about 0.7x as long as petiolar node, anteroventral margin of peduncle of petiole with a small, acuminate spine. In profile, posterior surface of petiolar node weakly convex; petiolar node asymmetrical with anterior surface shorter than posterior surface, apex bluntly subangulate to rounded. In dorsal view, petiolar node longer than wide, sides subparallel, narrowing to a rounded to subangulate anterior margin; all surfaces of petiolar node strongly granulate-punctate, dull, occasionally with few weak rugae. Dorsum of postpetiole convex in profile; in dorsal view, widest near posterior margin, narrowing to anterior margin, maximum width and length similar; dorsum and sides moderately granulate-punctate, weakly shining. First gastral tergum smooth and shining.

Erect to suberect, medium-length, white to cream colored hairs moderately abundant on head, few hairs >0.5 x MOD. Moderately abundant subdecumbent to decumbent hairs on antennal scapes; abundant decumbent to appressed hairs on funicular segments. Legs with moderately abundant subdecumbent to decumbent setae. Mesosoma with moderate number of medium-length erect to suberect setae, but few present on propodeum, longest hairs usually about 0.7–0.8x MOD; petiolar node, postpetiole, gastral terga with sparse medium-length setae, longest notably shorter than MOD. Body mostly concolorous dark brownish-black to black; antennae, legs dark brown (**Figure 2**).

Queen. Diagnosis. This caste is diagnosed by: (1) caste-specific morphology of the mesosoma related to wing-bearing and presence of ocelli on head, (2) mesoscutum and mesoscutellum with weak to moderately strong longitudinal rugae, interrugae weakly to strongly granulate-punctate, (3) inferior propodeal spines elongate, length similar to that of superior propodeal spines, and (4) body concolorous brownish-black to black (**Figure 3**).

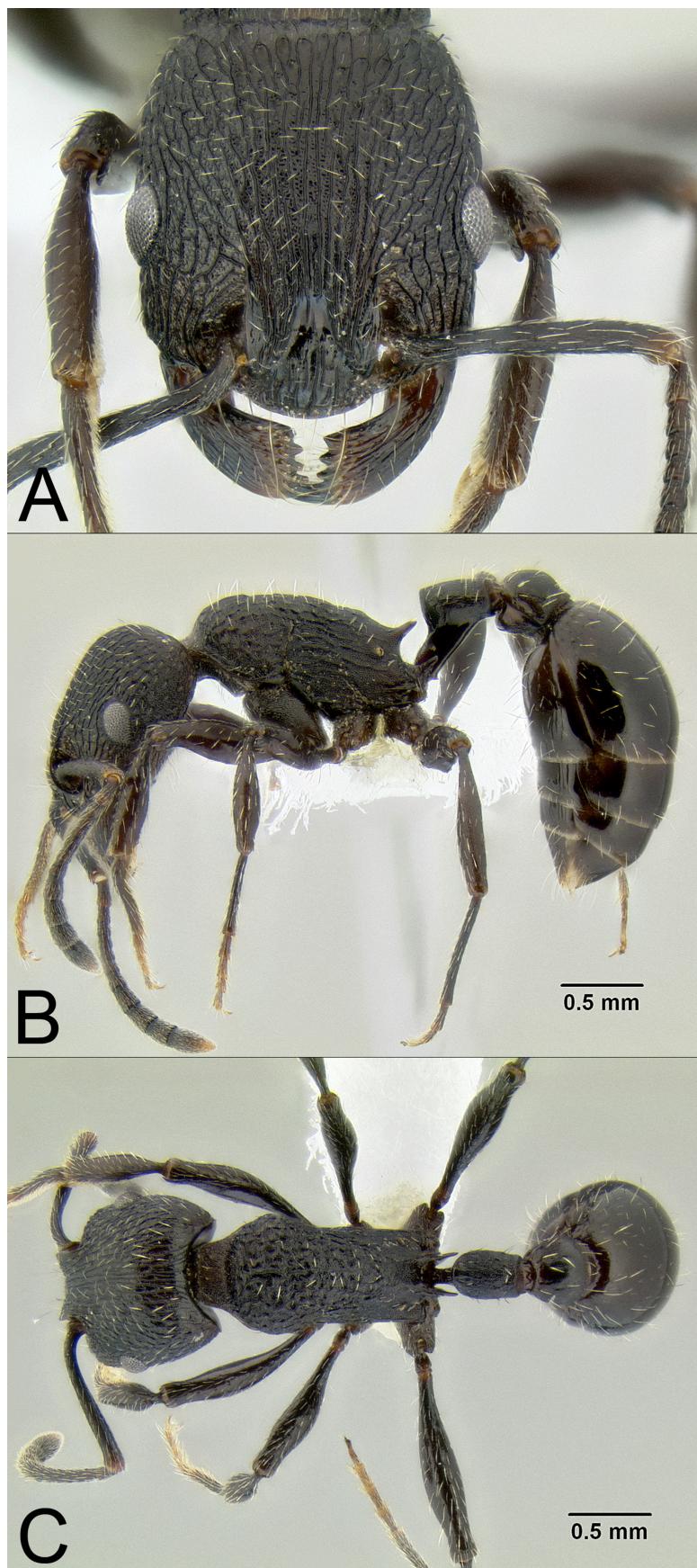


FIGURE 2. Photograph of *Patagonomyrmex angustus* (Mayr) worker: (A) frontal view of head, (B) lateral view of body, (C) dorsal view of body (CASENT0106125). Photos taken by Michael Branstetter and www.antweb.com.

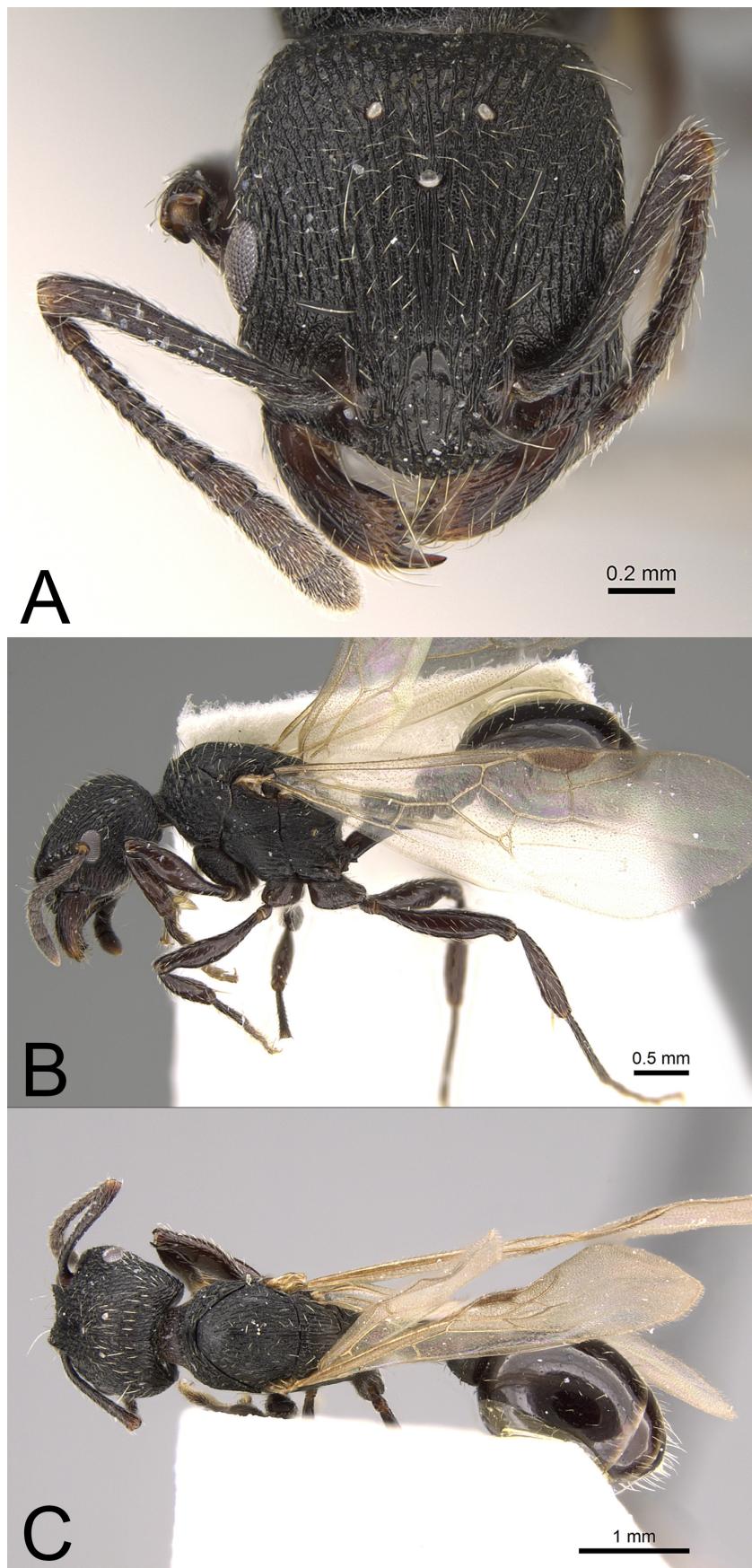


FIGURE 3. Photograph of *Patagonomyrmex angustus* (Mayr) alate queen: (A) frontal view of head, (B) lateral view of body, (C) dorsal view of body (CASENT0914808). Photos taken by Michele Esposito and www.antweb.com.

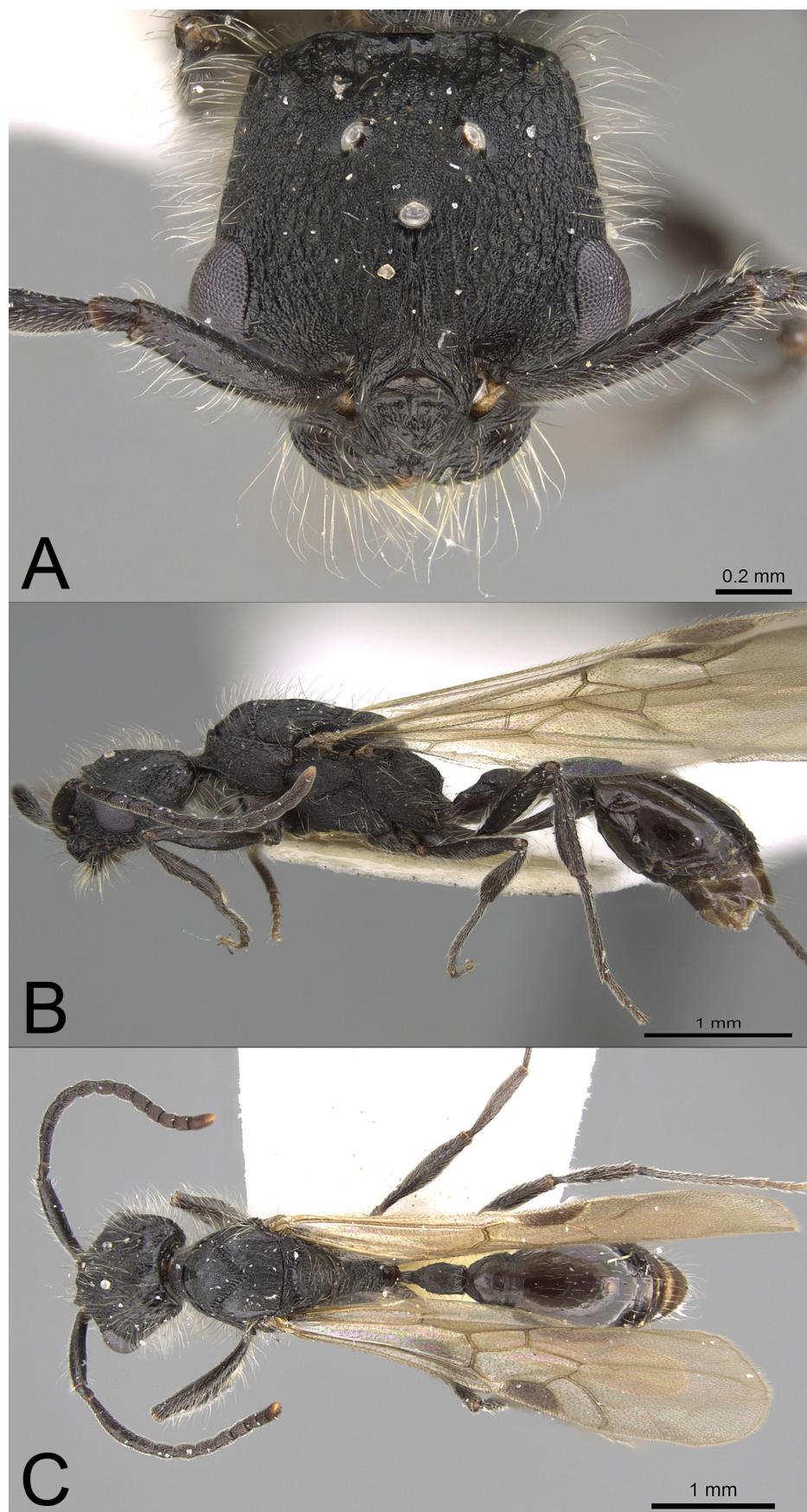


FIGURE 4. Photograph of *Patagonomyrmex angustus* (Mayr) male: (A) frontal view of head, (B) lateral view of body, (C) dorsal view of body (LACMENT273603). Photos taken by Michele Esposito and www.antweb.com.

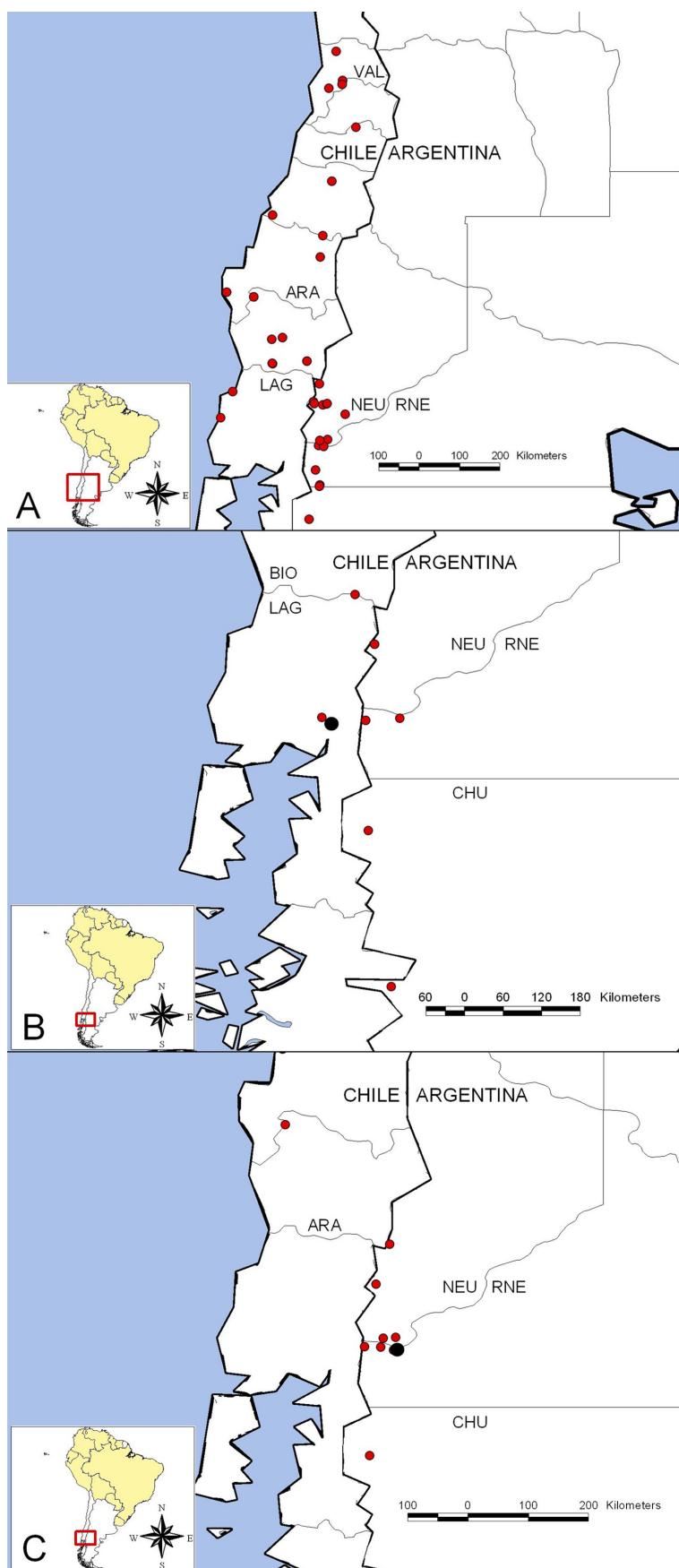


FIGURE 5. Geographic distribution of: (A) *Patagonomyrmex angustus* (Mayr), (B) *Patagonomyrmex laevigatus* (Santschi), and (C) *Patagonomyrmex odoratus* (Kusnezov); the larger filled black circle in each panel (when present) denotes the type locality.

Measurements—(n = 11). HL 1.10–1.39; HW 0.99–1.22; MOD 0.26–0.31; OMD 0.18–0.30; SL 0.82–1.03; PNW 0.71–0.97; HFL 1.06–1.28; ML 1.57–1.87; PW 0.33–0.38; PPW 0.46–0.59. Indices: SI 79.66–87.27; CI 82.58–94.40; OI 22.13–28.44; HFI 99.15–110.09.

Male. Diagnosis. This caste is diagnosed by: (1) mesopleura, metapleura, pronotal sides, and dorsum of propodeum strongly granulate, dull, with a beaded appearance, (2) at least several hairs on ventral surface of head approach or exceed MOD, and (3) scape length sometimes >0.6 mm, SI > 70.0 (**Figure 4**).

Measurements—(n = 6). HL 1.03–1.19; HW 0.88–1.01; MOD 0.35–0.42; OMD 0.11–0.22; SL 0.28–0.78; HFL 1.11–1.23; ML 1.54–1.71; PW 0.26–0.30; PPW 0.42–0.49. Indices: SI 31.82–80.41; CI 84.62–92.59; OI 36.08–43.18; HFI 117.00–126.14.

Additional material examined. ARGENTINA: *Chubut*: El Bolsón, Feb 12, 1949 (FML; LACM; MHNG); Lago Menéndez, no date (USNM). *Neuquén*: Lago Brazo Huemul Nahual Huapi, 2840', Jan 26, 2011 (MCZ; RAJC); Río Caleufu, 20 mi W Collon-Curá, Mar 9–14, 1980 (CASC); Hua Hum, Jan 26, 1949 (CASC; LACM; MHNG); Quilaquina, no date (MACN); San Martín de los Andes, 800 m, Jan 8, 1995 & no date (MCZ; MLPA; PSWC; UCDC); Pucará, no date (MHNG; MZUSP); Parque Nacional Lanín, Lago Paimun-La Cascada, Jan 26, 1999 (FML). *Río Negro*: Cerro Lopez, 1003 m, Jan 2005 (MCZ; RAJC); 11.4 km E Llao Llao, 760 m, Nov 16, 1966 (CASC); 5.6 km N Río Foyel, 920 m, Nov 18, 1966 (CASC); Victoria Nahuel Huapi, May 27, 1971 (MZUSP). CHILE: *La Araucanía*: Cerro de Naguelbuta, Angol, 620 m & 650 m, Oct 12, 1931 (MCZ); 10 km E Pucon, Jan 12, 1951 (CASC; LACM); Temuco, no date (MCZ); 20 km E Temuco, Jan 8, 1951 (CASC; USNM); 12.3 km N Loncoche, 280 m, Nov 10–16, 1966 (CASC; LACM). *Biobío*: Chillan Cordillera, Mar 12, 2005 (CASC); Cordillera Nahuelbuta, 20 km W Caramávida, 750 m, Jan 31, 1967 (CASC); 50 km E San Carlos, Dec 26, 1950 (MCZ). *Los Lagos*: Pucatrihue, 0 m, Feb 4, 1967 (CASC). *Los Ríos*: Puerto de Corral, Mar 1904 (MHNG); Corral, no date (MHNG); Valdivia, Feb 1879 & no date (MCZ; MLPA). *Maule*: Cuyurranquill, 400 m, Jan 23–31, 1981 (USNM); Cajón de Río Claro, SE Los Queñes, 1000 m, Oct 9, 1966 (CASC). *Metropolitán*: Cuesta de la Dormida, 1000 m, Nov 1, 1966 (CASC; LACM); Cerro el Roble, ca 2000 m, Oct 22, 1972 (LACM); Reserva Nacional Río Clarillo, comuna Pirque (not examined, literature record from Solervicens, Estrada, & Márquez, 1991). *O'Higgins*: 3 km N Callejones, Jan 22, 1967 (CASC). *Valparaíso*: 90 km S Illapel, Nov 28, 1950 (CASC); Río Marga Marga, Los Perales, 330 m, Oct 13, 1966 (CASC); Parque Nacional La Campana (not examined, literature record from Ipinza-Regla, 1985 & Sáiz & Carvajal, 1990). *Region Unknown*: no loc, no date (USNM) (**Figure 5A**).

Etymology. The name of this species, *angustus* (from Latin, *angustus* = narrow, small), is derived from the narrow body, as discussed in the description by Mayr.

Discussion. *Patagonomyrmex angustus* co-occurs with both *Pa. laevigatus* and *Pa. odoratus*. It is distinguished from the latter two species based on the following characters: (1) dorsum of promesonotum and posterior surface of petiolar node strongly granulate-punctate, weakly shining (dorsum of promesonotum and posterior surface of petiolar node smooth and shining in *Pa. laevigatus* and *Pa. odoratus*), and (2) inferior propodeal spines elongate, length similar to that of superior propodeal spines (the inferior propodeal spines are triangular and notably shorter than superior propodeal spines in *Pa. laevigatus* and *Pa. odoratus*). We did not find any morphological measurements that could be used to separate *Pa. angustus* from its two congeners.

Mayr (1870) described the worker of *Pa. angustus* in a key with no additional information, and he later described the queen and male (Mayr, 1887) listing the type locality as “Valdivia in Chile”. As noted by Kusnezov (1949), this vague location does not indicate if the type locality was in the city or province of Valdivia.

Patagonomyrmex laevigatus NEW COMBINATION

(Figures 6–8)

Pogonomyrmex (Ephebomyrmex) laevigatus Santschi, 1921: 97 (worker). Syntypes examined: 5 workers [MACN], 2 workers [ZSM], #1077, CHILE, Llanquihue Province: Cayutué (Dr. Wolffhügel leg.); Kusnezov, 1949: 301 (male, in key). MACN worker here designated LECTOTYPE [CASENT0217258].

Ephebomyrmex laevigatus (Santschi); Kusnezov, 1960: 354, first combination in *Ephebomyrmex*.

Pogonomyrmex laevigatus Santschi; Snelling & Hunt, 1976: 75, revived combination in *Pogonomyrmex*.

Worker. Diagnosis. This species is uniquely characterized by the following combination of features: (1) longitudinal rugae on cephalic dorsum rarely continue to posterior margin, (2) interrugae on cephalic dorsum and

dorsum of promesonotum mostly smooth and shining, (3) posterior surface of petiolar node smooth and shining, (4) inferior propodeal spines triangular, height and width similar, notably shorter than superior spines, and (5) body mostly concolorous dark brownish-black to black (**Figure 6**).

Measurements. Lectotype ($n = 12$). HL 1.18 (1.11–1.24); HW 1.06 (0.97–1.13); MOD 0.28 (0.24–0.30); OMD 0.23 (0.20–0.25); SL 0.96 (0.84–0.95); PNW 0.73 (0.66–0.76); HFL 1.10 (0.99–1.16); ML 1.57 (1.32–1.53); PW 0.28 (0.25–0.31); PPW 0.42 (0.41–0.49). Indices: SI 90.57 (84.07–97.94); CI 89.83 (78.86–92.79); OI 26.42 (23.76–27.84); HFI 103.77 (97.27–113.40).

Redescription. Longitudinal rugae on cephalic dorsum prominent, weakly wavy, widely-spaced, beginning on frontal lobes but rarely extending to posterior margin; posterior margin flat in full-face view. Wavy to irregular, often discontinuous rugae arc from mandibular margins to frontal lobes and traverse longitudinally above and below eyes, usually terminating before vertex; lateral rugae weaker than those on cephalic dorsum. Interrugae on cephalic dorsum smooth and shining; vertex and posterior margin of head weakly granulate-punctate, weakly shining to smooth and shining. Dorsum of clypeus with several moderately strong, subparallel, longitudinal rugae. Mandible with six teeth; mandibular dorsum strongly rugose. MOD ranging from 0.20–0.25x HL. In profile, eyes situated anterior to middle of head, OMD = 0.76–0.93x MOD. In full-face view, eyes protruding slightly beyond lateral margins of head. Antennal scapes long (SI = 84.07–97.94), surpassing vertex by less than length of second funicular segment; scapes weakly to moderately granulate-punctate, often with faint striae, weakly shining; basal flange moderately well-developed with carinate margin.

Mesosomal profile strongly convex; dorsum of promesonotum smooth and shining; longitudinal rugae on mesospleura and metapleura wavy to irregular, interrugae weakly to moderately granulate-punctate, weakly shining. Promesonotal suture absent to weakly impressed on occasional individuals. Superior propodeal spines long, narrowing to blunt tip, length rarely >0.7 –0.8x the distance between their bases; inferior propodeal spines moderately well-developed, triangular, acuminate, length and width similar, distinctly shorter than superior spines. Propodeal spiracles weakly ovate to circular facing posterad. Legs weakly granulate, weakly shining to smooth and shining.

Peduncle of petiole about as long as petiolar node, anteroventral margin of peduncle of petiole with a small, acuminate spine. In profile, posterior surface of petiolar node weakly convex; petiolar node asymmetrical with anterior surface shorter than posterior surface, apex bluntly angulate to rounded. In dorsal view, petiolar node longer than wide, sides subparallel, narrowing to rounded to bluntly angulate anterior margin. Dorsum of postpetiole convex in profile; in dorsal view, widest near posterior margin, narrowing to anterior margin, maximum width and length similar; posterior surface and sides of petiolar node and dorsum and sides of postpetiole smooth and shining; first gastral tergum smooth and shining.

Erect, short to long, copperish-brown hairs abundant on head, one to few approaching to slightly exceeding MOD. Moderately abundant subdecumbent to decumbent hairs on antennal scapes; abundant decumbent to appressed hairs on funicular segments. Legs with moderately abundant subdecumbent to decumbent setae. Mesosoma with moderately dense, medium to long, erect setae, longest approaching MOD; petiolar node, postpetiole, gastral terga with moderately dense, erect setae, mostly similar in length, longest notably shorter than MOD. Body mostly concolorous dark brownish-black to black (**Figure 6**).

Queen. Diagnosis. This caste is diagnosed by: (1) caste-specific morphology of the mesosoma related to wing-bearing and presence of ocelli on head, (2) mesoscutum and mesoscutellum smooth and shiny, (3) inferior propodeal spines triangular, much shorter than superior propodeal spines, and (4) body mostly concolorous dark brownish-black to black (**Figure 7**).

Measurements. ($n = 2$). HL 1.25–1.30; HW 1.02–1.12; MOD 0.26–0.33; OMD 0.20–0.24; SL 0.80–0.91; PNW 0.92–0.93; HFL 1.08–1.12; ML 1.56–1.63; PW 0.32–0.34; PPW 0.51–0.53. Indices: SI 71.43–89.22; CI 78.46–89.60; OI 25.49–29.46; HFI 100.00–105.88.

Description. With caste-specific morphology of the mesosoma related to wing-bearing and presence of ocelli on head. In full-face view, head elongate (CI = 78.46–89.60), posterior margin flat. Longitudinal rugae on cephalic dorsum extending to near posterior margin, rugae fine and dense medially, density decreasing laterally and becoming weakly rugoreticulate; vertex weakly rugoreticulate. Interrugae on cephalic dorsum weakly to moderately coriarious, weakly shining. Mandible with five to six teeth, dorsal surface convex, coarsely rugose, anterior margin flat to weakly convex. Psammophore poorly-developed, consisting of short to medium-length hairs scattered across ventral surface of head.

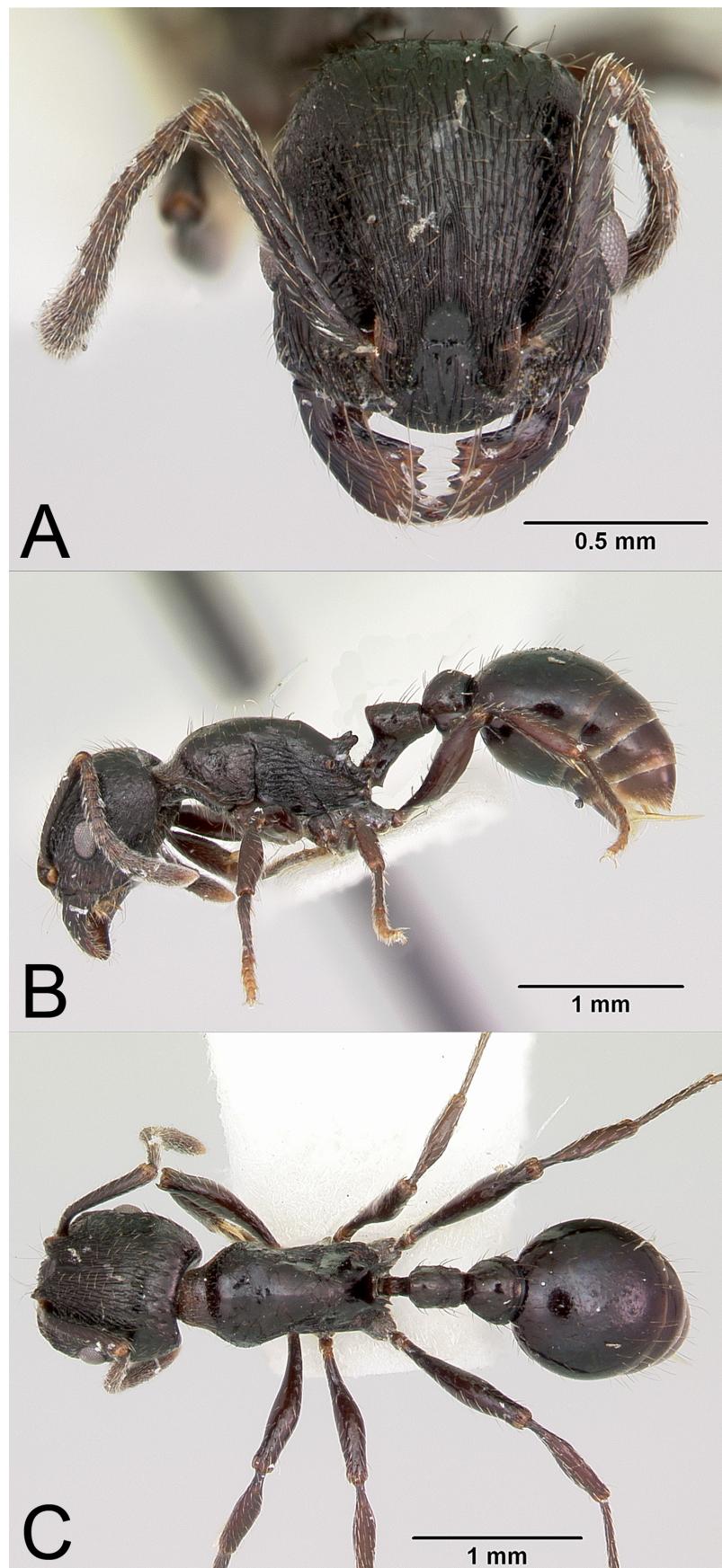


FIGURE 6. Photograph of *Patagonomyrmex laevigatus* (Santschi) worker: (A) frontal view of head, (B) lateral view of body, (C) dorsal view of body (CASENT0103393). Photos taken by April Nobile and www.antweb.com.

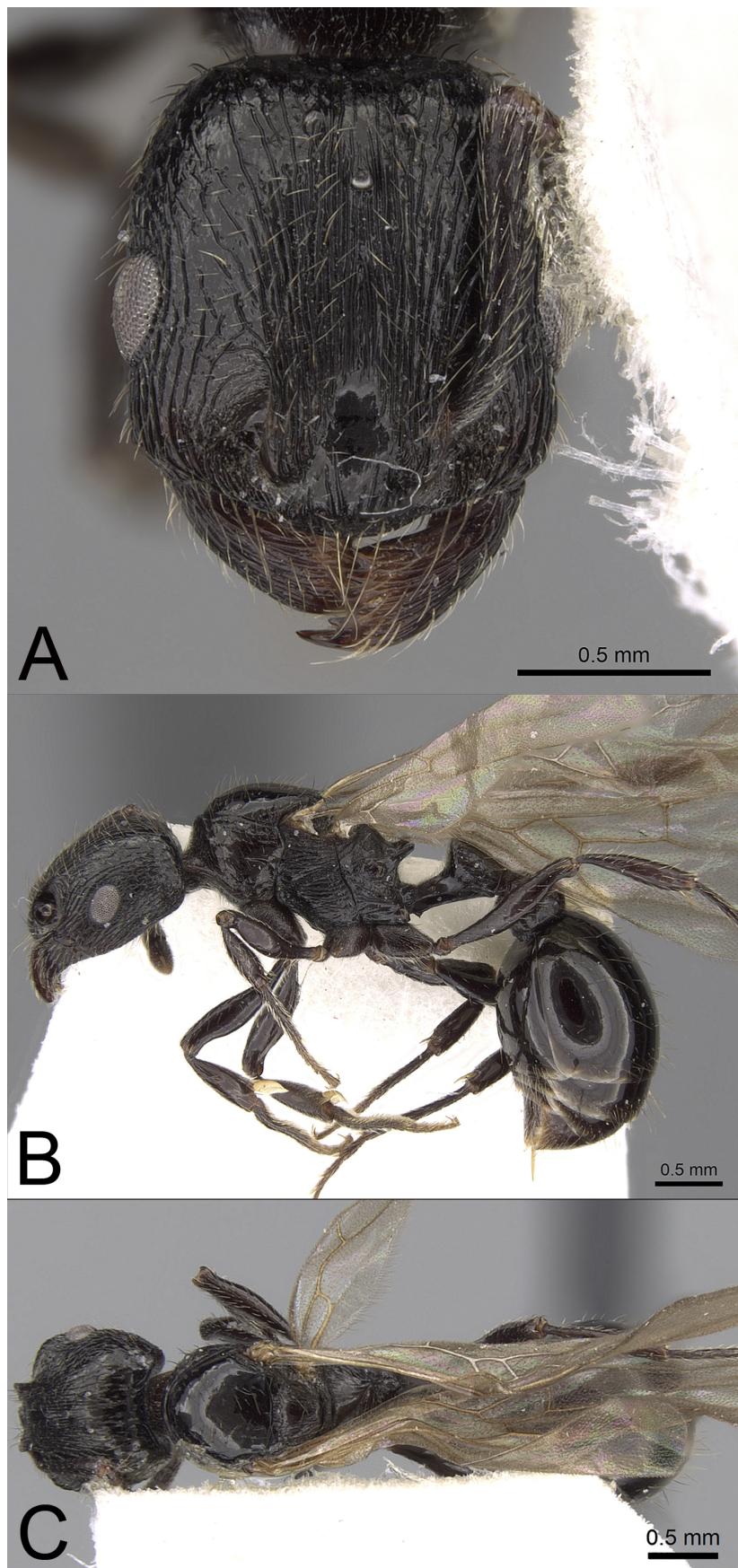


FIGURE 7. Photograph of *Patagonomyrmex laevigatus* (Santschi) alate queen: (A) frontal view of head, (B) lateral view of body, (C) dorsal view of body (CASENT0280992). Photos taken by Estella Ortega and www.antweb.com.

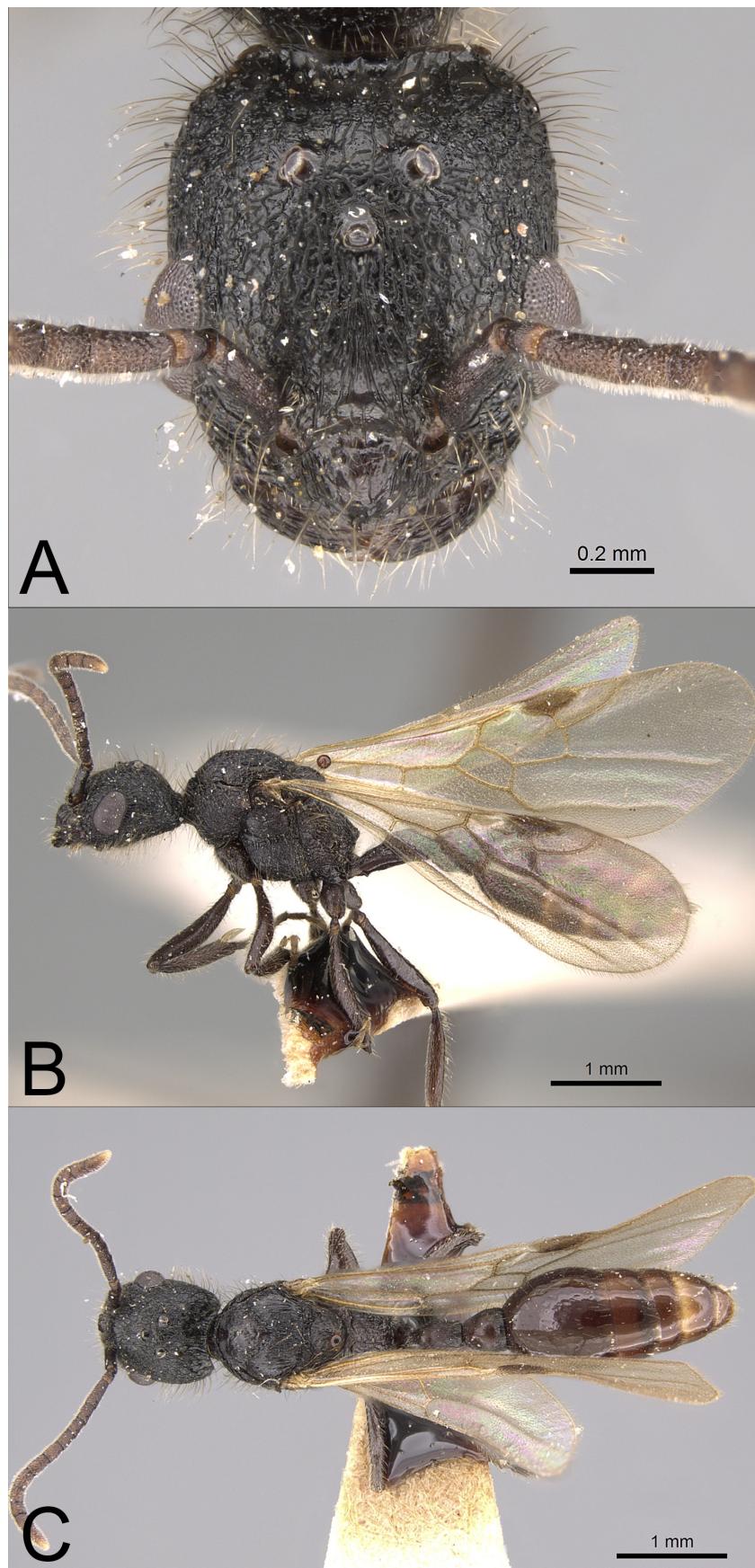


FIGURE 8. Photograph of *Patagonomyrmex laevigatus* (Santschi) male: (A) frontal view of head, (B) lateral view of body, (C) dorsal view of body (CASENT0914809). Photos taken by Michele Esposito and www.antweb.com.

Mesoscutum, mesoscutellum, dorsum of propodeum smooth and shining; mesoplura, metapluera, propodeal sides longitudinally rugose; interrugae weakly coriarious, weakly shining. Superior propodeal spines well-developed with blunt tips, inferior propodeal spines triangular, wider than tall, about 0.5–0.7x the length of superior spines. In profile, petiolar node asymmetrical with anterior surface shorter than posterior surface, apex subangulate. In dorsal view, postpetiole wider than long. Posterior surface of petiolar node and dorsum of postpetiole weakly coriarious, weakly shining to smooth and shining. First gastral tergum smooth and shining. Most body surfaces with moderately abundant suberect to erect, yellowish setae; gaster with fewer setae. Entire body dark brownish-black to black; legs, posterior gastral terga often with brownish infusion (**Figure 7**).

Male. Diagnosis. This caste is diagnosed by: (1) mesopleura, metapleura, pronotal sides and/or dorsum of propodeum with weak to strong rugae, (2) no hairs on ventral surface of head or those protruding from mandibles approach MOD, and (3) in profile, juncture between cephalic dorsum and posterior declivity (near posterior margin of ocelli) weakly angulate to rounded, posterior declivity weakly convex to weakly concave (**Figure 8**).

Measurements—($n = 4$). HL 1.06–1.19; HW 0.93–1.01; MOD 0.39–0.43; OMD 0.14–0.18; SL 0.29–0.35; HFL 1.15–1.25; ML 1.62–1.73; PW 0.27–0.30; PPW 0.40–0.43. Indices: SI 30.21–37.63; CI 80.87–90.57; OI 41.58–46.24; HFI 123.66–126.88.

Additional material examined. ARGENTINA: *Chubut*: Lago Fontana, Mar 4, 1948 (FML). *Río Negro*: Tronador, no date (MACN); San Carlos de Bariloche, Feb 8, 1964 (MZUSP). *Neuquén*: Hua Hum, no date & Jan 25, 1949 (FML; MHNG). CHILE: *La Araucanía*: Pucón, Volcán Villarica, >1000 m, Dec 3, 1989 (LACM). *Los Lagos*: Petrohue, Mar 1922 (MLPA) (**Figure 5B**).

Etymology. The specific epithet, *laevigatus* (from Latin, *laevigatus* = smooth, glossy), is derived from the smooth, shiny surface over most of the body of this species.

Discussion. *Patagonomyrmex laevigatus* co-occurs with *Pa. angustus* and *Pa. odoratus*. *Patagonomyrmex laevigatus* is distinguished from *Pa. angustus* based on the following characters: (1) dorsum of promesonotum and posterior surface of petiolar node smooth and shining (both structures strongly granulate in *Pa. angustus*), and (2) inferior propodeal spines triangular, shorter than superior propodeal spines (inferior propodeal spines elongate, length similar to that of superior propodeal spines in *Pa. angustus*). In his key, Kusnezov (1951) separated *Pa. laevigatus* from *Pa. odoratus* based on the mostly concolorous blackish to black body (body orangish-brown with the gaster slightly darker in *Pa. odoratus*). Kusnezov (1949, 1951) also indicated that longitudinal rugae on the cephalic dorsum were coarser in *Pa. laevigatus* than in *Pa. odoratus*, but I could not discern this difference. He also indicated the angle between the peduncle of the petiole and the anterior surface of the petiolar node was more rounded in *Pa. laevigatus*, and more angulate in *Pa. odoratus*. This character appeared to be very subtle and inconsistent, and thus was not a useful diagnostic trait. We did not find any morphological measurements that could be used to separate *Pa. laevigatus* from its two congeners.

***Patagonomyrmex odoratus* NEW COMBINATION**

(Figures 9–11)

Pogonomyrmex (Ephebomyrmex) odoratus Kusnezov, 1949: 302, figs. 1, 2 (worker, queen, male). Syntypes examined: 6 workers, 3 alate queens [FML], 11 workers, 7 alate queens [LACM], 2 workers, 1 alate queen [MLPA], 12 workers, 4 alate queens, 2 males [USNM], ARGENTINA, Río Negro: Bariloche, Cerro Otto, #3554 (N. Kusnezov leg., 6 February 1949); #3553—same data as lectotype: 6 workers, 3 males [FML]. See also Kusnezov, 1960: fig. unnumbered, pg. unnumbered. USNM worker here designated **LECTOTYPE** [CASENT0914807].

Ephebomyrmex odoratus (Kusnezov); Kusnezov, 1960: 354, first combination in *Ephebomyrmex*.

Pogonomyrmex odoratus Kusnezov; Snelling & Hunt, 1976: 75, fig. 25, revived combination in *Pogonomyrmex*.

Worker. Diagnosis. This species is uniquely characterized by the following combination of features: (1) longitudinal rugae on cephalic dorsum rarely continue to posterior margin, (2) interrugae on cephalic dorsum and dorsum of promesonotum mostly smooth and shining, (3) posterior surface of petiolar node smooth and shining, (4) inferior propodeal spines triangular, length and width similar, notably shorter than superior spines, and (5) head and mesosoma mostly concolorous amber-orange to brownish-orange, gaster usually darker orangish-black (**Figure 9**).

Measurements. Lectotype ($n = 4 + 9$ paratypes). HL 1.27 (1.00–1.25); HW 1.11 (0.86–1.08); MOD 0.27

(0.24–0.29); OMD 0.18 (0.15–0.24); SL 0.91 (0.79–0.96); PNW 0.74 (0.62–0.73); HFL 1.12 (0.94–1.15); ML 1.52 (1.18–1.60); PW 0.30 (0.20–0.30); PPW 0.47 (0.39–0.45). Indices: SI 81.98 (79.63–96.00); CI 87.05 (82.46–95.50); OI 24.32 (24.53–27.91); HFI 100.90 (91.43–110.64) (see also Kusnezov, 1949).

Redescription. Longitudinal rugae on cephalic dorsum prominent, widely-spaced, weakly wavy, beginning on frontal lobes but rarely extending to posterior margin; posterior margin flat in full-face view. Wavy to irregular, often discontinuous rugae arc from mandibular margins to frontal lobes and traverse longitudinally above and below eyes, usually terminating before reaching vertex; lateral rugae weaker than those on cephalic dorsum. Interrugae on cephalic dorsum smooth and shining; vertex and posterior margin of head weakly granulate-punctate, weakly shining to smooth and shining. Dorum of clypeus with several moderately coarse, subparallel, longitudinal rugae. Mandible with six teeth; mandibular dorsum strongly rugose. MOD ranging from 0.21–0.25x HL. In profile, eyes situated anterior to middle of head, OMD = 0.57–0.89x MOD. In full-face view, eyes protruding slightly beyond lateral margins of head. Antennal scapes long (SI = 79.63–96.00), surpassing vertex by less than length of second funicular segment; scapes weakly to moderately granulate-punctate, often with faint striae, weakly shining; basal flange moderately well-developed with carinate margin.

Mesosomal profile strongly convex; dorsum of promesonotum smooth and shining; longitudinal rugae on mesospleura and metapleura wavy to irregular, interrugae weakly to moderately granulate-punctate, weakly shining. Promesonotal suture absent to weakly impressed on occasional individuals. Superior propodeal spines long, narrowing to blunt tip, length rarely exceeding 0.6–0.7x the distance between their bases; inferior propodeal spines moderately well-developed, triangular, acuminate to bluntly tipped, length and width similar, distinctly shorter than superior spines. Propodeal spiracles weakly ovate to circular facing posterad. Legs weakly granulate to smooth, weakly shining to shining.

Peduncle of petiole about as long as petiolar node, anteroventral margin of peduncle of petiole with a small, acuminate spine. In profile, posterior surface of petiolar node weakly convex; petiolar node asymmetrical with anterior surface shorter than posterior surface, apex rounded to bluntly angulate. In dorsal view, petiolar node longer than wide, sides subparallel, narrowing to rounded to bluntly angulate anterior margin. Dorsum of postpetiole convex in profile; in dorsal view, widest near posterior margin, narrowing to anterior margin, maximum width and length similar; posterior surface and sides of petiolar node and dorsum and sides of postpetiole smooth and shining; first gastral tergum smooth and shining.

Erect, short to long, copperish-brown hairs abundant on head, one to few approach to slightly exceed MOD. Moderately abundant subdecumbent to decumbent hairs on antennal scapes; abundant decumbent to appressed hairs on funicular segments. Legs with moderately abundant subdecumbent to decumbent setae. Mesosoma with moderately dense, medium to long, erect setae, longest approaching MOD; petiolar node, postpetiole, gastral terga with moderately dense erect setae, mostly similar in length, longest notably shorter than MOD. Body other than gaster mostly concolorous amber-orange to brownish-red, medial portion of cephalic dorsum usually slightly darker than rest of head; gaster dark orangish-black to brownish-black (**Figure 9**).

Queen. Diagnosis. This caste is diagnosed by: (1) caste-specific morphology of the mesosoma related to wing-bearing and presence of ocelli on head, (2) mesoscutum and mesoscutellum smooth and shiny, (3) inferior propodeal spines triangular, much shorter than superior propodeal spines, and (4) body orangish-brown, gaster slightly darker (**Figure 10**).

Measurements—($n = 9 + 3$ paralectotypes). HL 1.21–1.26; HW 1.05–1.12; MOD 0.30–0.33; OMD 0.17–0.24; SL 0.83–0.97; PNW 0.85–0.93; HFL 1.03–1.14; ML 1.52–1.77; PW 0.26–0.33; PPW 0.49–0.54. Indices: SI 79.05–89.81; CI 83.33–92.56; OI 27.52–30.28; HFI 96.26–106.67 (see also Kusnezov, 1949).

Male. Diagnosis. This caste is diagnosed by: (1) mesopleura, metapleura, pronotal sides and/or dorsum of propodeum with weak to strong rugae, (2) no hairs on ventral surface of head or those protruding from mandibles approach MOD, and (3) in profile, juncture between cephalic dorsum and posterior declivity (near posterior margin of ocelli) strongly angulate; posterior declivity strongly concave (**Figure 11**).

Measurements—($n = 2 + 1$ paralectotype). HL 1.08–1.22; HW 0.90–1.01; MOD 0.41–0.45; OMD 0.16–0.19; SL 0.28–0.33; HFL 0.98–1.17; ML 1.71–1.75; PW 0.23–0.27; PPW 0.38–0.42. Indices: SI 29.17–36.67; CI 82.79–85.71; OI 43.75–45.56; HFI 102.08–123.33 (see also Kusnezov, 1949).

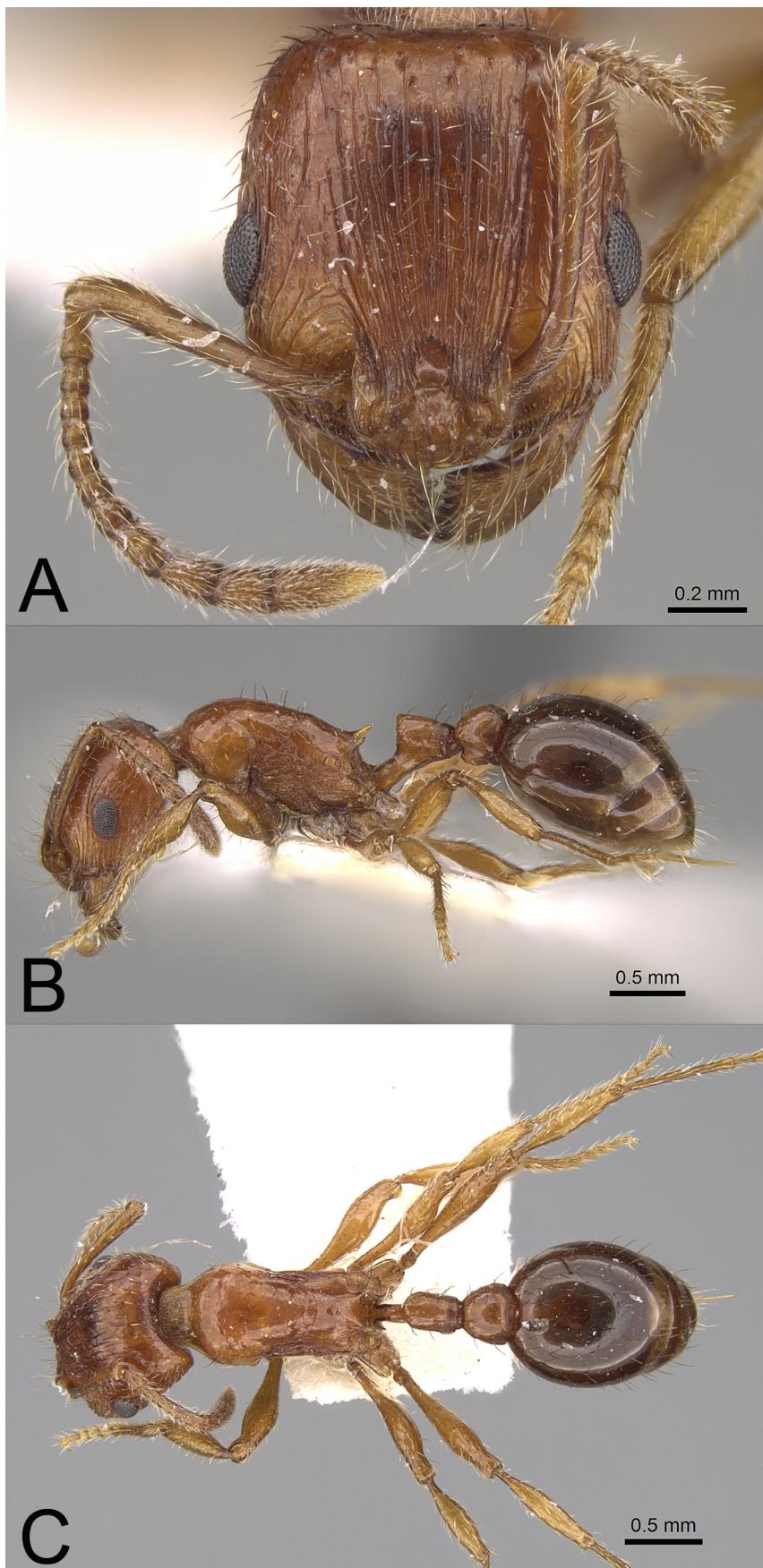


FIGURE 9. Photograph of *Patagonomyrmex odoratus* (Kusnezov) lectotype worker: (A) frontal view of head, (B) lateral view of body, (C) dorsal view of body (CASENT0914807). Photos taken by Michele Esposito and www.antweb.com.

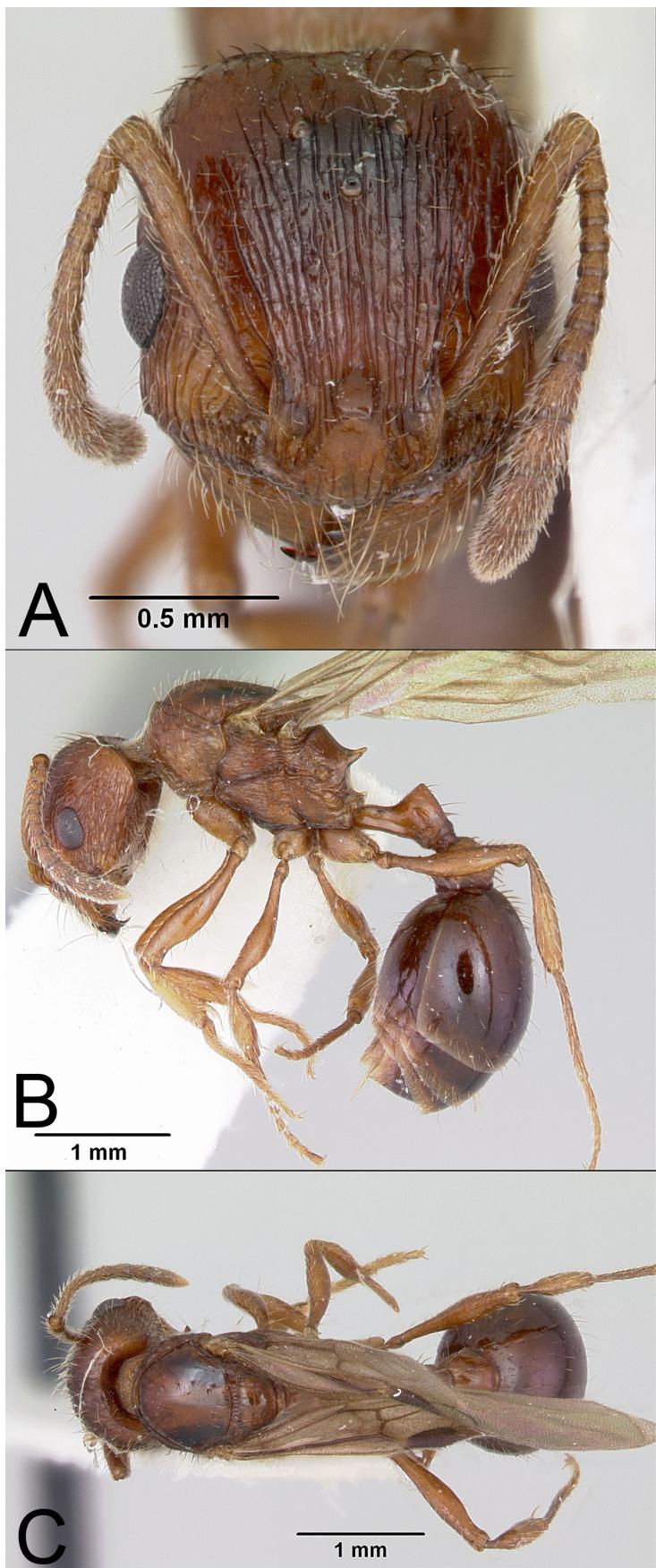


FIGURE 10. Photograph of *Patagonomyrmex odoratus* (Kusnezov) paralectotype alate queen: (A) frontal view of head, (B) lateral view of body, (C) dorsal view of body (CASENT0103396). Photos taken by April Nobile and www.antweb.com.

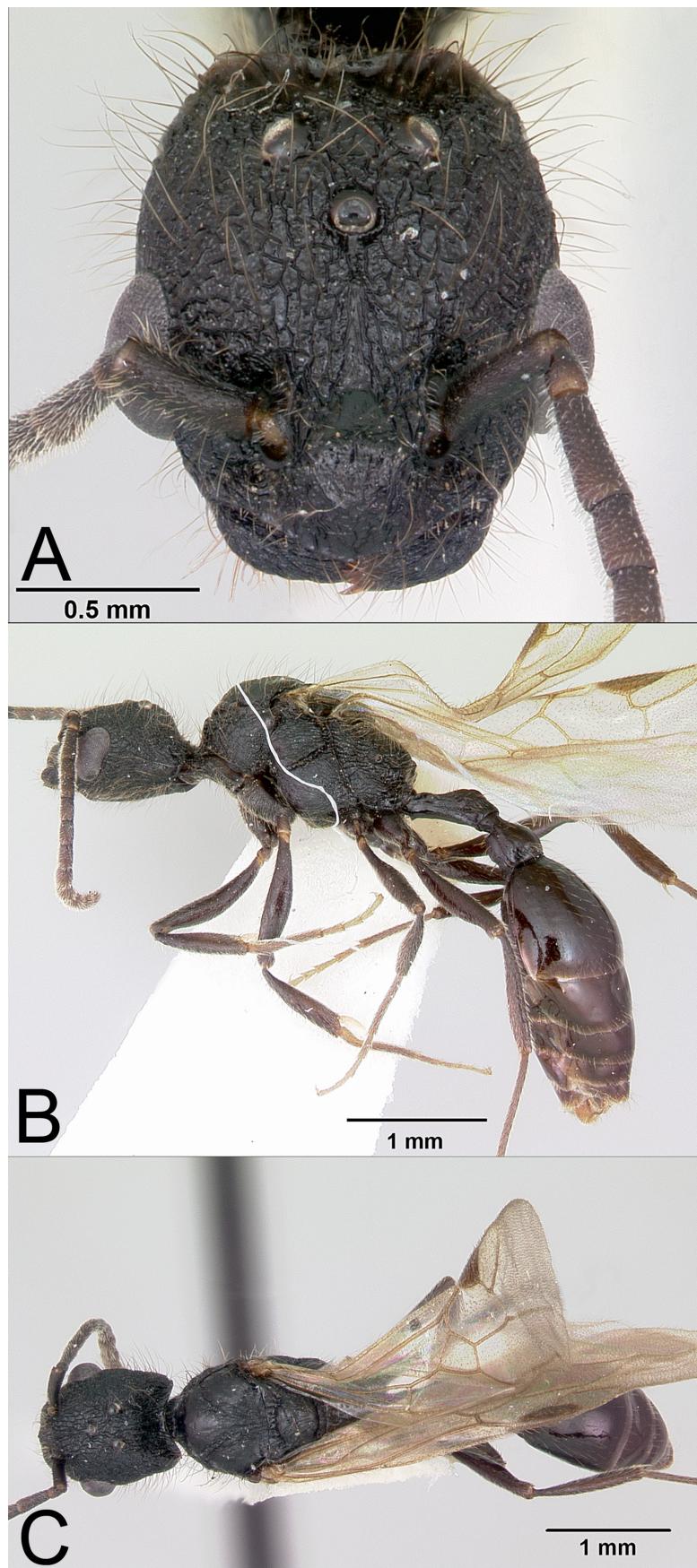


FIGURE 11. Photograph of *Patagonomyrmex odoratus* (Kusnezov) paralectotype male: (A) frontal view of head, (B) lateral view of body, (C) dorsal view of body (CASENT0103405). Photos taken by April Nobile and www.antweb.com.

Additional material examined. ARGENTINA: *Chubut*: Laguna Verde, Feb 17, 1949 (LACM). *Neuquén*: Lago Tromen, 1050 m, Jan 9, 1995 (MCZ; PSWC; UCDC); Parque Nacional Lanín, Pucara, Jan 24, 1999 (FML); Brazo Huemel Nahual Huapi Lago, 2840', Jan 26, 2011 (MCZ; RAJC). *Río Negro*: Bariloche, Jun 2, 1949 & Feb 6, 1949 (LACM; MCZ; MLPA); Laguna Frías, 760 m, Nov 16, 1966 (CASC); Isla Victoria Bariloche, Jan 15, 1972 (MZUSP); Cerro Lopez, 1700 m, Jan 2005 (RAJC). CHILE: *La Araucanía*: Parque Nacional Nahuelbuta, Dec 14, 1972 (LACM). *Metropolitan*: La Reserva Nacional Río Clarillo, comuna Pirque ($33^{\circ} 41' S$, $70^{\circ} 34' W$) (not examined, literature record from Solervicens *et al.*, 1991). *O'Higgins*: Baños de Flaco, 1940 m (not examined, literature record from Ipinza-Regla, Covarrubias, & Guevara, 1983) (Figure 5C).

Etymology. In his description, Kusnezov did not give information regarding the naming of this species. However, Kunezov (1960) indicated that the name was derived from the odor emitted by the species.

Discussion. *Patagonomyrmex odoratus* co-occurs with *Pa. angustus* and *Pa. laevigatus*. *Patagonomyrmex odoratus* can be distinguished from *Pa. angustus* based on the following characters: (1) dorsum of promesonotum and posterior surface of petiolar node smooth and shining (both structures moderately granulate in *Pa. angustus*), and (2) inferior propodeal spines triangular, shorter than superior propodeal spines (inferior propodeal spines elongate with length similar to that of superior propodeal spines in *Pa. angustus*). In his key, Kusnezov (1951) separated *Pa. odoratus* from *Pa. laevigatus* based on the orangish-brown body with a slightly darker gaster in *Pa. odoratus* versus mostly concolorous blackish to black body in *Pa. laevigatus*. Kusnezov (1949, 1951) also indicated that the longitudinal rugae on the cephalic dorsum were less coarse in *Pa. odoratus* than in *Pa. laevigatus*, but I could not discern this difference. He also indicated the angle between the peduncle of the petiole and the anterior surface of the petiolar node was more rounded in *Pa. laevigatus*, and more angulate in *Pa. odoratus*. This character appeared to be very subtle and inconsistent, and thus was not a useful diagnostic trait. We did not find any morphological measurements that could be used to separate *Pa. odoratus* from its two congeners.

In his description of this species, Kusnezov (1951) listed six localities at which *Pa. odoratus* had been collected, but he did not designate a type locality. In their treatment of the ants of Chile, Snelling & Hunt (1975) chose Hua Hum as the type locality because it was the first of six localities listed by Kusnezov (1949). Our designation of a lectotype supercedes this act, and the type locality is now Cerro Otto, Río Negro Province, Argentina.

Discussion

Taxonomy and identification. *Patagonomyrmex* workers share several characters with species in the former subgenus *Ephebomyrmex* including small size, poorly-developed psammophore, antenna with 12 segments, and hind legs with finely pectinate tibial spurs. However, our molecular phylogram confirms that *Patagonomyrmex* represents a distinct lineage of ants, especially given our inclusion of sequences from numerous species of *Pogonomyrmex* from North America, South America, and Hispaniola, including most species previously assigned to *Ephebomyrmex*. Our phylogram also supports the hypothesis that *Patagonomyrmex* is the sister group to all other pogonomyrmecines (see also Ward *et al.*, 2015). These results also demonstrate the value of conducting molecular phylogenetic studies on large numbers of species to determine if they are monophyletic or morphologically convergent (Brady, Schultz, Fisher, & Ward, 2006; Moreau *et al.*, 2006; Schmidt & Shattuck, 2014; Ward *et al.*, 2015).

One morphological difference between *Patagonomyrmex* and *Pogonomyrmex* regards palp formula. Ward *et al.* (2015) indicated that the palp formula (maxillary, labial) was 5,4 or 4,3 for genera in the tribe Pogonomyrmecini. In his revision of North American *Pogonomyrmex*, Cole (1968) listed the palp formula for *Pa. angustus* and *Pa. odoratus*, and for numerous species of *Pogonomyrmex* from North America, South America, and Hispaniola. Part of his discussion follows: "my examination of mouthparts from long series of workers of our North American species of *Ephebomyrmex* has failed to reveal a single case of either 5-segmented maxillary palps or 4-segmented labial palps (Cole, 1968, pg. 27), followed by "my studies of mouthparts of all castes of all species of the subgenus *Pogonomyrmex* that have been available to me have shown a constant number of 4 maxillary and 3 labial palp segments" (pg. 28). Cole (1968) also listed a palp formula of 4,3 for two species from Hispaniola, *Po. saucius* and *Po. schmitti*. The only exception listed by Cole (1968) was a palp formula of 5,4 for workers of *Pa. angustus* and *Pa. odoratus*. Examination of palps by the senior author also found a palp formula of 4,3 for *Pogonomyrmex* and 5,4 for *Patagonomyrmex*.

Pogonomyrmex contains several species groups in which workers possess a poorly-developed psammophore and thus might be confused with *Patagonomyrmex*. The best characters to separate *Patagonomyrmex* from these species are: (1) clypeus strongly convex in profile, and (2) anterior margin of clypeus convex in full-face view (**Figures 2A, 6A, 9A**). No species of *Pogonomyrmex* with a poorly-developed psammophore have a clypeus that is convex in profile, and only species in the *Po. cunicularius*-group have a clypeus with the anterior margin weakly convex in full-face view. The small, acuminate spine on the anteroventral margin of the peduncle of the petiole is also distinctive: only species in the *Po. sylvestris*-group and sometimes *Po. cunicularius*-group possess this character.

Species of *Patagonomyrmex* also are geographically restricted to southern Argentina and southern and southcentral Chile. No species of *Pogonomyrmex* with a poorly-developed psammophore occur in Chile and only species in the *Po. naegelii*-group, *Po. brevibarbis*-group, and *Po. cunicularius*-group occur in Argentina (Johnson, 2015; R.A. Johnson, unpub. data). Of these species, only those in the *Po. brevibarbis*-group occur in provinces inhabited by *Patagonomyrmex* (Neuquén, Río Negro, Chubut). The most southern occurrence for species in the *Po. naegelii*-group (*abdominalis*, *naegelii*, *tenuipubens*) is central Argentina (Mendoza, San Luis, La Pampa Provinces), about 600 km north of the nearest locale for *Patagonomyrmex* (see Johnson, 2015).

One notable morphological trait was variable scape length in *Pa. angustus* males. Most males had longer scapes (0.73–0.78 mm; SI = 74.26–80.41 [n = 4] versus 0.28–0.33; SI = 31.82–32.00 [n = 2]; [**Figure 4**]), whereas scapes were short in all males of *Pa. laevigatus* (0.28–0.33 mm; SI 29.17–36.67 [n = 4]; [**Figure 8**]) and *Pa. odoratus* (0.28–0.33 mm; SI 29.17–36.67 [n = 3]; [**Figure 11**]). Additional males of all three species should be collected to determine consistency of male scape length within and among colonies.

Biology. Little is known about the biology of *Patagonomyrmex* other than observations made by Kusnezov (1949, 1953, 1960). Most of his observations were for *Pa. odoratus*, but the biology of these three species appears similar, and thus all three species are discussed together. Nests are variable, ranging from an entrance lacking a tumulus to one that is 10–12 cm in diameter. Typically, nests are located in open areas or under stones or other objects. Workers of all three species are diurnal, slow-moving, solitary foragers that are timid and non-aggressive. Little information is available on food items collected, though Kusnezov (1960) indicated that they were granivores. Colonies of *Pa. odoratus* probably contain fewer than 300–400 workers (Kusnezov, 1949); colony size for *Pa. angustus* and *Pa. laevigatus* appears to be similar (Kusnezov, 1949; 1960; pers. obs.).

Alate queens and males are known for all three species; collection dates for sexuals range from October 9 to May 27 for *Pa. angustus* (October 9–22 in Chile; November 16 to May 27 in Argentina), January 25 to February 17 for *Pa. laevigatus*, and January 15 to February 18 for *Pa. odoratus* (Kusnezov, 1949; R.A. Johnson, unpub. data). Number of sexuals in nests ranged from 1–18 alate queens and 1–7 males in *Pa. angustus*, 4–5 alate queens and 5–19 males in *Pa. laevigatus*, and 1–54 alate queens and 1–19 males in *Pa. odoratus* (Kusnezov, 1949). Mating flights are unknown for all three species, but the above dates suggest that flights occur during the austral summer, probably from late January through March or later. The trigger for mating flights is unknown. Nest excavations indicate that colonies of all three species typically contain 1–2 reproductive (dealate) queens (*Pa. odoratus*: 1 queen [n = 1], 2 queens [1]; *Pa. laevigatus*: 1 queen [1]; *Pa. angustus*: 1 queen [3], 2 queens [1]) (see Kusnezov, 1949; R.A. Johnson, unpub. data).

All three species of *Patagonomyrmex* are restricted to cool, relatively humid, short growing-season climates in southern Argentina and southern to southcentral Chile, typically in habitats dominated by *Nothofagus* or *Austrocedrus* (= *Libocedrus* in Kusnezov, 1949). *Patagonomyrmex laevigatus* has the most restrictive distribution as it is only known from shady areas in well-developed mesophilic coihue (*Nothofagus dombeyi*) forests, i.e., it is absent from arid and semi-arid habitats including *Austrocedrus* forests (Kusnezov, 1949) (see also Table 2; **Figure 5**). *Patagonomyrmex angustus* and *Pa. odoratus* also have relatively localized distributions in Argentina, but both species have broader distributions in Chile (**Figure 5**); *Pa. odoratus* occurs north to near Santiago (Solervicens *et al.*, 1991; specimens not examined), and *Pa. angustus* is common to as far north as the Valparaíso Region (**Figure 5**). Both *Pa. odoratus* and *Pa. angustus* occur in several biogeographic zones-bioclimatic regions in Chile, whereas *Pa. laevigatus* has a very restricted distribution (Table 2). Using the ecoregions defined by Olson *et al.* (2001), *Pa. angustus* occurs in the Valdivian Temperate Forest and Chilean Matorral ecoregions, with one record from the western edge of the Patagonian Steppe; both *Pa. laevigatus* and *Pa. odoratus* are restricted to the Valdivian Temperate Forest ecoregion.

TABLE 2. Biogeographic communities and bioclimatic regions for occurrence of *Patagonomyrmex* in Chile (from Ipinza-Regla & Covarrubias, 1982).

Species	Biogeographic communities	Bioclimatic regions*
<i>angustus</i>	forest, savannah	1–6
<i>laevigatus</i>	forest	1
<i>odoratus</i>	forest, montane, savannah	2–3, 5–6

*¹ocean with Mediterranean influence, ²arid Mediterranean, ³semiarid Mediterranean, ⁴subhumid Mediterranean, ⁵humid Mediterranean, ⁶very humid Mediterranean.

All three species of *Patagonomyrmex* can be sympatric, but each species more typically occurs in different microhabitats. *Patagonomyrmex odoratus* sometimes co-occurs with *Pa. laevigatus* in shaded *Nothofagus* forests, but it is more common in exposed, slightly drier microsites such as open areas with low densities of Chilean cedar (*Austrocedrus chilensis*) (Kusnezov, 1949). *Patagonomyrmex angustus* occurs over the widest range of microhabitats, including the *Araucaria*, *Nothofagus*, and *Austrocedrus* zones, largely in more exposed, drier microhabitats than those used by both *Pa. laevigatus* and *Pa. odoratus*. *Patagonomyrmex laevigatus* occurs at elevations from ~220->1000 m in Chile and 560–950 m in Argentina, *Pa. odoratus* ranges from 540–1700 m in Argentina and from ~1000–1940 m in Chile, and *Pa. angustus* ranges from 390–1005 m in Argentina, and from 0–2000 m in Chile.

Acknowledgments

The following individuals (museums) provided specimens used in this study: Brian Fisher (CASC), Fabianna Cuezzo (FML), Stefan Cover (MCZ), Brian Brown (LACM), Ted Schultz (USNM), Stefan Schmidt (ZSM), Beto Brandão (MZUSP), Arturo Roig-Alsina (MACN), Bernard Landry (MHNG), Manuela Vizek (NMW), Alberto Abrahamovich (MLPA), and Phil Ward (UCDC). This project was funded partly by the Ernst Mayr Travel Grant in Animal Systematics from the Museum of Comparative Zoology at Harvard University. RAJ also thanks Gary Alpert for his hospitality during visits to Harvard University, Brendon Boudinot for comments that improved the manuscript, and John Lattke for translating the abstract and keys into Spanish. We also thank Brian Fisher and AntWeb.org for use of species images.

References cited

- Anderson, K.E., Gadau, J., Mott, B.M., Johnson, R.A., Altamirano, A., Strehl, C. & Fewell, J.H. (2006) Distribution and evolution of genetic caste determination in *Pogonomyrmex* seed-harvester ants. *Ecology*, 87, 2171–2184.
[http://dx.doi.org/10.1890/0012-9658\(2006\)87\[2171:DAEOGC\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2006)87[2171:DAEOGC]2.0.CO;2)
- Bolton, B. (1994) *Identification Guide to the Ant Genera of the World*. Harvard University Press, Cambridge, Massachusetts. 222 pp.
- Bolton, B. (2014) *An Online Catalog of the Ants of the World*. Available from: <http://antcat.org> (accessed 22 March 2016)
- Brady, S.G., Schultz, T.D., Fisher, B.L. & Ward, P.S. (2006) Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proceedings of the National Academy of Science USA*, 103, 18172–18177.
<http://dx.doi.org/10.1073/pnas.0605858103>
- Cole, A.C. (1968) *Pogonomyrmex Harvester Ants: A Study of the Genus in North America*. University of Tennessee Press, Knoxville, Tennessee, 222 pp.
- Cole, B.J. & Wiernasz, D.C. (1999) The selective advantage of low relatedness. *Science*, 285, 891–893.
<http://dx.doi.org/10.1126/science.285.5429.891>
- Drummond, A.J., Ashton, B., Buxton, S., Cheung, M., Cooper, A., Duran, C., Field, M., Heled, J., Kearse, M., Markowitz, S., Moir, R., Stones-Havas, S., Sturrock, S., Thierer, T. & Wilson, A. (2012) Geneious v5.6. Available from: <http://www.geneious.com> (Accessed 15 Jul. 2016)
- Emery, C. (1921) Hymenoptera, Family Formicidae, Subfamily Myrmicinae [part]. *Genera Insectorum*, 174A, 1–94.
- Gordon, D.M. & Kulig, A.W. (1996) Founding, foraging, and fighting: colony size and the spatial distribution of harvester ant nests. *Ecology*, 77, 2393–2409.
<http://dx.doi.org/10.2307/2265741>

- Hölldobler, B. (1971) Homing in the harvester ant *Pogonomyrmex badius*. *Science*, 171, 1149–1151.
<http://dx.doi.org/10.1126/science.171.3976.1149>
- Hölldobler, B. (1976) Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. *Behavioral Ecology and Sociobiology*, 1, 3–44.
<http://dx.doi.org/10.1007/BF00299951>
- Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogeny. *Bioinformatics*, 17, 754–755.
<http://dx.doi.org/10.1093/bioinformatics/17.8.754>
- Ipinza-Regla, J.H. (1985) Formicidos en el contenido gástrico de *Liolaemus monticola*. *Revista Chilena de Entomología*, 12, 165–168.
- Ipinza-Regla, J.H. & Covarrubias, R. (1982) Distribución de especies de la subfamilia Myrmicinae Formicidae en Chile. *Revista Española de Entomología*, 58, 135–141.
- Ipinza-Regla, J.H., Covarrubias, R. & Guevara, R.F.L. (1983) Distribucion altitudinal de Formicidae en Los Andes de Chile central. *Folia Entomologica Mexicana*, 55, 103–128.
- Johnson, R.A. (2001) Biogeography and community structure of North American seed-harvester ants. *Annual Review of Entomology*, 46, 1–29.
<http://dx.doi.org/10.1146/annurev.ento.46.1.1>
- Johnson, R.A. (2002) Semi-claustral colony founding in the seed-harvester ant *Pogonomyrmex californicus*: a comparative analysis of founding strategies. *Oecologia*, 132, 60–67.
<http://dx.doi.org/10.1007/s00442-002-0960-2>
- Johnson, R.A. (2006) Capital and income breeding and the evolution of colony founding strategies in ants. *Insectes Sociaux*, 53, 316–322.
<http://dx.doi.org/10.1007/s00040-006-0874-9>
- Johnson, R.A. (2015) A taxonomic revision of South American species of the seed-harvester ant genus *Pogonomyrmex* (Hymenoptera: Formicidae). Part I. *Zootaxa*, 4029 (1), 1–142.
<http://dx.doi.org/10.11646/zootaxa.4029.1.1>
- Johnson, R.A. & Cover, S.P. (2015) A taxonomic revision of the seed-harvester ant genus *Pogonomyrmex* (Hymenoptera: Formicidae) on Hispaniola. *Zootaxa*, 3972 (2), 231–249.
<http://dx.doi.org/10.11646/zootaxa.3972.2.5>
- Johnson, R.A. & Overson, R.P. (2009) A new North American species of *Pogonomyrmex* (Hymenoptera: Formicidae) from the Mohave Desert of central California and western Nevada. *Journal of Hymenoptera Research*, 18, 305–314.
- Johnson, R.A., Overson, R.P. & Moreau, C.S. (2013) A new species of seed-harvester ant, *Pogonomyrmex hoelldobleri* (Hymenoptera: Formicidae), from the Mohave and Sonoran Deserts of North America. *Zootaxa*, 3646 (3), 201–227.
<http://dx.doi.org/10.11646/zootaxa.3646.3.1>
- Kusnezov, N. (1949) *Pogonomyrmex* del grupo *Ephebomyrmex* en la fauna de la Patagonia (Hymenoptera, Formicidae). *Acta Zoologica Lilloana*, 8, 291–307.
- Kusnezov, N. (1951) El género *Pogonomyrmex* Mayr (Hym., Formicidae). *Acta Zoologica Lilloana*, 11, 227–333.
- Kusnezov, N. (1953) Las hormigas en los parques nacionales de la Patagonia y los problemas relacionados. *Anales del Museo Nahuel Huapí*, 3, 105–125.
- Kusnezov, N. (1960) La fauna de hormigas en el oeste de la Patagonia y Tierra de Fuego. *Acta Zoologica Lilloana*, 17, 321–401.
- LaPolla, J.S., Kallal, R.J. & Brady, S.G. (2012) A new ant genus from the Greater Antilles and Central America, *Zatania* (Hymenoptera: Formicidae), exemplifies the utility of male and molecular character systems. *Systematic Entomology*, 37, 2001–2214.
<http://dx.doi.org/10.1111/j.1365-3113.2011.00605.x>
- Larget, B. & Simon, D. (1999) Markov chain Monte Carlo algorithms for the Bayesian analysis of phylogenetic trees. *Molecular Biology and Evolution*, 16, 750–759.
- MacMahon, J.A., Mull, J.F. & Crist, T.O. (2000) Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. *Annual Review of Ecology and Systematics*, 31, 265–291.
<http://dx.doi.org/10.1146/annurev.ecolsys.31.1.265>
- Maddison, W.P. & Maddison, D.R. (2011) Mesquite: a molecular modular system for evolutionary analysis. Version 2.75 <http://mesquiteproject.org/>.
- Mayr, G. (1870) Neue Formiciden. *Verhandlungen Zoologisch-Botanischen Gesellschaft in Wein*, 20, 939–996.
- Mayr, G. (1887) Südamerikanische Formiciden. *Verhandlungen der k. k. Zoologisch-Botanischen Gesellschaft in Wein*, 37, 511–632.
- Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCS)*, New Orleans, Louisiana, pp. 1–8.
<http://dx.doi.org/10.1109/gce.2010.5676129>
- Moreau, C.S. (2008) Unraveling the evolutionary history of the hyperdiverse ant genus *Pheidole* (Hymenoptera: Formicidae). *Molecular Phylogenetics and Evolution*, 48, 224–239.
<http://dx.doi.org/10.1016/j.ympev.2008.02.020>
- Moreau, C.S. (2014) A practical guide to DNA extraction, PCR, and gene-based DNA sequencing in insects. *Halteres*, 5, 32–

- Moreau, C.S. & Bell, C.D. (2013) Testing the museum versus cradle biological diversity hypothesis: phylogeny, diversification, and ancestral biogeographic range evolution of the ants. *Evolution*, 67, 2240–2257.
<http://dx.doi.org/10.1111/evo.12105>
- Moreau, C.S., Bell, C.D., Vila, R., Archibald, S.B. & Pierce, N.E. (2006) Phylogeny of the ants: diversification in the age of angiosperms. *Science*, 312, 101–104.
<http://dx.doi.org/10.1126/science.1124891>
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J. A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Alnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettenberg, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience*, 51, 933–938.
[http://dx.doi.org/10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]2.0.CO;2](http://dx.doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2)
- Parker, J.D. & Rissing, S.W. (2002) Molecular evidence for the origin of workerless social parasites in the ant genus *Pogonomyrmex*. *Evolution*, 56, 2017–2028.
<http://dx.doi.org/10.1111/j.0014-3820.2002.tb00128.x>
- Posada, D. & Crandall, K.A. (2001) Selecting the best-fit model of nucleotide substitution. *Systematic Biology*, 50, 580–601.
<http://dx.doi.org/10.1080/106351501750435121>
- Rannala, B. & Yang, Z.H. (1996) Probability distribution of molecular evolutionary trees: a new method of phylogenetic inference. *Journal of Molecular Evolution*, 43, 304–311.
<http://dx.doi.org/10.1007/BF02338839>
- Sáiz, F. & Carvajal, C. (1990) Incendios forestales en el parque nacional La Campana, Sector Ocoa, V Region, Chile. V. Blattodea, Formicidae y Mutillidae. Impacto y recuperacion. *Anales del Museo de Historia Natural de Valparaíso Chile*, 21, 51–61.
- Santschi, F. (1921) Ponerinae, Dorylinae et quelques autres formicides néotropiques. *Bulletin de la Société Vaudoise des Sciences Naturelles*, 54, 81–103.
- Schmidt, C.A. & Shattuck, S.O. (2014) The higher classification of the ant subfamily Ponerinae (Hymenoptera: Formicidae), with a review of ponerine ecology and behavior. *Zootaxa*, 3817 (1), 1–242.
<http://dx.doi.org/10.11646/zootaxa.3817.1.1>
- Snelling, R.R. & Hunt, J.H. (1975) The ants of Chile (Hymenoptera: Formicidae). *Revista Chilena de Entomología*, 9, 63–129.
- Solervicens, J., Estrada, P. & Márquez, M. (1991) Notes on the insect fauna from the soil surface and foliage at the Reserva Nacional Río Clarillo, Region Metropolitana, Chile. *Acta Entomologica Chilena*, 16, 161–182.
- Stamatakis, A., Ludwig, T. & Meier, H. (2005) RAxML-III: a fast program for maximum likelihood-based inference of large phylogenetic trees. *Bioinformatics*, 21, 456–463.
<http://dx.doi.org/10.1093/bioinformatics/bti191>
- Ward, P.S. (2011) Integrating molecular phylogenetic results into ant taxonomy (Hymenoptera: Formicidae). *Myrmecological News*, 15, 21–29.
- Ward, P.S., Brady, S.G., Fisher, B.L. & Schultz, T.R. (2010) Phylogeny and biogeography of dolichoderine ants: effects of data partitioning and relict taxa on historical inference. *Systematic Biology*, 59, 342–362.
<http://dx.doi.org/10.1093/sysbio/syq012>
- Ward, P.S., Brady, S.G., Fisher, B.L. & Schultz, T.R. (2015) The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). *Systematic Entomology*, 40, 61–81.
<http://dx.doi.org/10.1111/syen.12090>
- Wiernasz, D.C. & Cole, B.J. (2003) Queen size mediates queen survival and colony fitness in harvester ants. *Evolution*, 57, 2179–2183.
<http://dx.doi.org/10.1111/j.0014-3820.2003.tb00396.x>