Zootaxa 4029 (1): 001–142
www.mapress.com/zootaxa/
Copyright © 2015 Magnolia Press

Monograph

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.4029.1.1
http://zoobank.org/urn:lsid:zoobank.org:pub:A625A5A9-EE80-45E0-A9BE-7A183B0996B1

ZOOTAXA

4029

A taxonomic revision of South American species of the seed-harvester ant genus *Pogonomyrmex* (Hymenoptera: Formicidae). Part I

ROBERT A. JOHNSON
School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501, USA
Email: Robert.Johnson4@asu.edu, Phone: 480.897.2473, Fax: 480.727.9440

Magnolia Press
Auckland, New Zealand

Accepted by J. Longino: 28 Jul. 2015; published: 13 Oct. 2015

ROBERT A. JOHNSON

A taxonomic revision of South American species of the seed-harvester ant genus *Pogonomyrmex* (Hymenoptera: Formicidae). Part I

(*Zootaxa* 4029)

142 pp.; 30 cm.

13 Oct. 2015

ISBN 978-1-77557-811-6 (paperback)

ISBN 978-1-77557-812-3 (Online edition)

FIRST PUBLISHED IN 2015 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: zootaxa@mapress.com

http://www.mapress.com/zootaxa/

© 2015 Magnolia Press

All rights reserved.

No part of this publication may be reproduced, stored, transmitted or disseminated, in any form, or by any means, without prior written permission from the publisher, to whom all requests to reproduce copyright material should be directed in writing.

This authorization does not extend to any other kind of copying, by any means, in any form, and for any purpose other than private research use.

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

Table of contents

ABSTRACT

South American species in the seed-harvester ant genus *Pogonomyrmex* (subfamily Myrmicinae) are interesting biologically because of their numerous queen phenotypes and life histories. This paper provides a taxonomic revision and reviews the natural history for 21 South American species of *Pogonomyrmex* so that we can better study their rich and interesting ecology, life history, and evolution. Species treated herein comprise all South American species-groups except for the *brevibarbis* and *rastratus*-groups. The following taxa are raised to species: *pencosensis* Forel 1914 and *serpens* Santschi 1922. The following new synonomies are proposed: *bruchi* Forel 1913 is synonomized under *coarctatus* Mayr 1868 and *cunicularius carnivora* Santschi 1925 under *serpens* Santschi 1922. The following new species is described: *tinogasta.* This paper redescribes workers of all species, and I describe queens and diagnose males for the following species: *bispinosus* (ergatoid queen, male), *inermis* (queen, male), *laticeps* (male), *lobatus* (queen, male), *micans* (queen), *naegelii* (ergatoid queen), *pencosensis* (ergatoid queen), *serpens* (ergatoid queen), *tinogasta* (brachypterous queen), and *uruguayensis* (queen, male). A neotype was designated for the untraceable or possibly lost type of *P. bispinosus*, and a holotype or lectotype was designated from syntypes for all other previously described taxa in order to provide a single name-bearing specimen and to facilitate future taxonomic studies. Of the 21 species treated herein, five species have ergatoid (wingless) queens (*bispinosus*, *cunicularius, pencosensis, serpens, mayri*), two have brachypterous (short-winged) queens (*mendozanus, tinogasta*), and two have dimorphic queens (winged and ergatoid in *naegelii*, brachypterous and ergatoid in *laticeps*). I also provide keys for workers and queens (in English and Spanish), photographs of all castes, distribution maps, and a summary of known biology.

Key words: *Pogonomyrmex*, South America, seed-harvester ants, key to species, queen phenotypes, taxonomic revision

RESUMEN

Las hormigas del género *Pogonomyrmex* (subfamilia Myrmicinae) de Sudamérica son biológicamente interesantes por los variados fenotipos que poseen sus reinas y diversos historias de vida. Este documento ofrece una revisión taxonómica y revisa la historia natural de 21 especies de Sudamérica de *Pogonomyrmex* para que podamos estudiar mejor su rica e interesante ecología, historia de vida, y la evolución. Las especies incluidas en este trabajo comprenden todos los grupos de Sudamérica excepto las pertenecientes a los grupos *brevibarbis* y *rastratus*. Los siguientes taxa fueron elevados a especies: *pencosensis* Forel 1914 y *serpens* Santschi 1922. Se proponen las siguientes sinonimias: *bruchi* Forel 1913 es sinonomizado bajo *coarctatus* Mayr 1868 y *cunicularius carnivora* Santschi 1925 bajo *serpens* Santschi 1922. Se describe una nueva especie: *tinogasta*. En este trabajo se redescriben las obreras de todas las especies, y se describen las reinas y se brinda la diagnosis de los machos de las siguientes especies: *bispinosus* (reina ergatoide, macho), *inermis* (reina, macho), *laticeps* (macho), *lobatus* (reina, macho), *micans* (reina), *naegelii* (reina ergatoide), *pencosensis* (reina ergatoide), *serpens* (reina ergatoide), *tinogasta* (reina brachíptera), y *uruguayensis* (reina, macho). Se proporcionó un neotipo para el tipo de *P. bispinosus* que fue posible localizar o posiblemente esté perdido. Un holotipo o lectotipo fue designado a partir de los sintipos, para el resto de los taxones descritos previamente, con el fin de proporcionar un único individuo portador de nombre para facilitar futuros estudios taxonómicos. De las 21 aquí tratadas, cinco poseen reinas ergatoides (*bispinosus, cunicularius, pencosensis, serpens, mayri*), dos tienen reinas braquípteras (*mendozanus, tinogasta*) y en dos especies existen reinas dimórficas (aladas y ergatoides en *naegelii*, braquípteras y ergatoides en *laticeps*). También se provee de las claves para las obreras y reinas (en inglés y en español), fotografías de todas las castas, mapas de distribución, y un resumen de la biología conocida.

Palabras Claves: *Pogonomyrmex*, Sudamérica, hormigas colectoras de semillas, claves a especies, fenotipos de reinas, revisión taxonomía

INTRODUCTION

The seed-harvester ant genus *Pogonomyrmex* (subfamily Myrmicinae) consists of 69 described species that occur as three biogeographic faunas, one in North America (32 species) (Bolton, 2014), one on the Caribbean island of Hispaniola (3 species) (Johnson & Cover, 2015), and one in South America (34 species) (Bolton, 2014; http://www.antwiki.org/wiki/Pogonomyrmex_species_by_Country; http://www.antwiki.org/wiki/Checklist_of_Pogonomyrmex_species). No species are common to any two areas. The genus has a long history in both North and South America, but taxonomic progress on South American species has lagged because of the paucity of native taxonomists and ecologists. The last revision of South American species was by Kusnezov (1951), but it included only the *Pogonomyrmex* of Argentina. The only additions since that revision were descriptions of five new species by various authors (Cuezzo & Claver, 2009; Fernández & Palacio, 1998; Lattke, 1991, 2006), and a review of the entire genus by Taber (1998) which provided a key and distribution maps but did not address taxonomy for any species.

The revision presented here is the first of an anticipated series that attempts to stabilize taxonomy for South American species of *Pogonomyrmex* to facilitate research on their rich and interesting ecology, life history, and evolution. This is especially necessary given that researchers in Argentina (e.g., Aranda-Rickert & Fracchia, 2012; Nobua Behrmann, Milesi, Lopez de Casenave, Pol, & Pavan, 2010; Pirk & Lopez de Casenave, 2006, 2011; Pol, Lopez de Casenave, Feldhaar, Milesi, & Gadau, 2008; Pol, Lopez de Casenave, & Milesi, 2015) and Chile (Torres-Contreras, Olivares-Donoso, & Niemeyer, 2007, 2009) have begun to study this genus. Most South American species can be placed in nine species groups. This paper treats all South American species except those in two of those groups: the *P. brevibarbis*-group and the *P. rastratus*-group. To date, South American species have been described in six languages, often with brief descriptions that sometimes consisted of only one sentence. Consequently, I redescribe workers of all species so as to provide a homogenous treatment in one language.

Historical resume

The history of *Pogonomyrmex* began with descriptions of two species that were initially placed in other genera, *Formica badia* (Latreille, 1802) from Carolina, United States, and *Atta bispinosu*s from Chile (Spinola, 1851). It was not until 1868 that Gustav Mayr (1868) erected the genus *Pogonomyrmex* wherein he described three new species from Argentina (*P. coarctatus*, *P. rastratus, P. carbonarius*); the latter two species would pose taxonomic

problems and their identities would remain in confusion for the next 140+ years. Mayr published two additional papers on South American *Pogonomyrmex* (Mayr, 1870, 1887); the first paper described *P. angustus*, transferred *Atta bispinosus*, *Formica badia*, and *Myrmica crudelis* (= *Atta crudelis*) to *Pogonomyrmex*, and he described two additional forms from North America (*P. opaciceps* [= *P. occidentalis*] and *P. subdentatus*), thus establishing *Pogonomyrmex* as a New World genus that occurred in both North and South America. The second paper described two additional species (*P. uruguayensis* and *P. cunicularius*) and (erroneously) placed *P. carbonarius* as a junior synonym of *P. rastratus*. Overall, Mayr defined the early history of *Pogonomyrmex* and he described six species from South America. Only three additional species were described prior to 1900 (*P. mayri, P. theresiae* [described twice] and *P. naegelii*) (Forel, 1886, 1899a, 1899b, 1899c), though Emery (1878) previously had made available the name *P. naegelii*. The only other substantive paper during this era was a catalogue for Hymenoptera of the world (Dalle Torre, 1893).

The next era for South American *Pogonomyrmex* was dominated by three European entomologists, Auguste Forel (Swiss), Carlos Emery (Italian), and Felix Santschi (Swiss). This era began with the description of several species by Emery (1906) and ended with Santschi's last work on *Pogonomyrmex* in 1936. These three individuals collectively described 34 of the 59 forms (7 by Emery, 9 by Forel, 18 by Santschi) of South American *Pogonomyrmex* known prior to the current revision (**Figure 1**). Throughout this period, none of these authors saw any of these species in the field, but rather specimens were collected by South American naturalists (mostly Strobel, Dr. Charles Bruch, Dr. Carrete, Dr. Weiser, C. Berg) who sent numerous specimens to Europe for identification and/or description. There was a lull in species descriptions following the death of these three taxonomists.

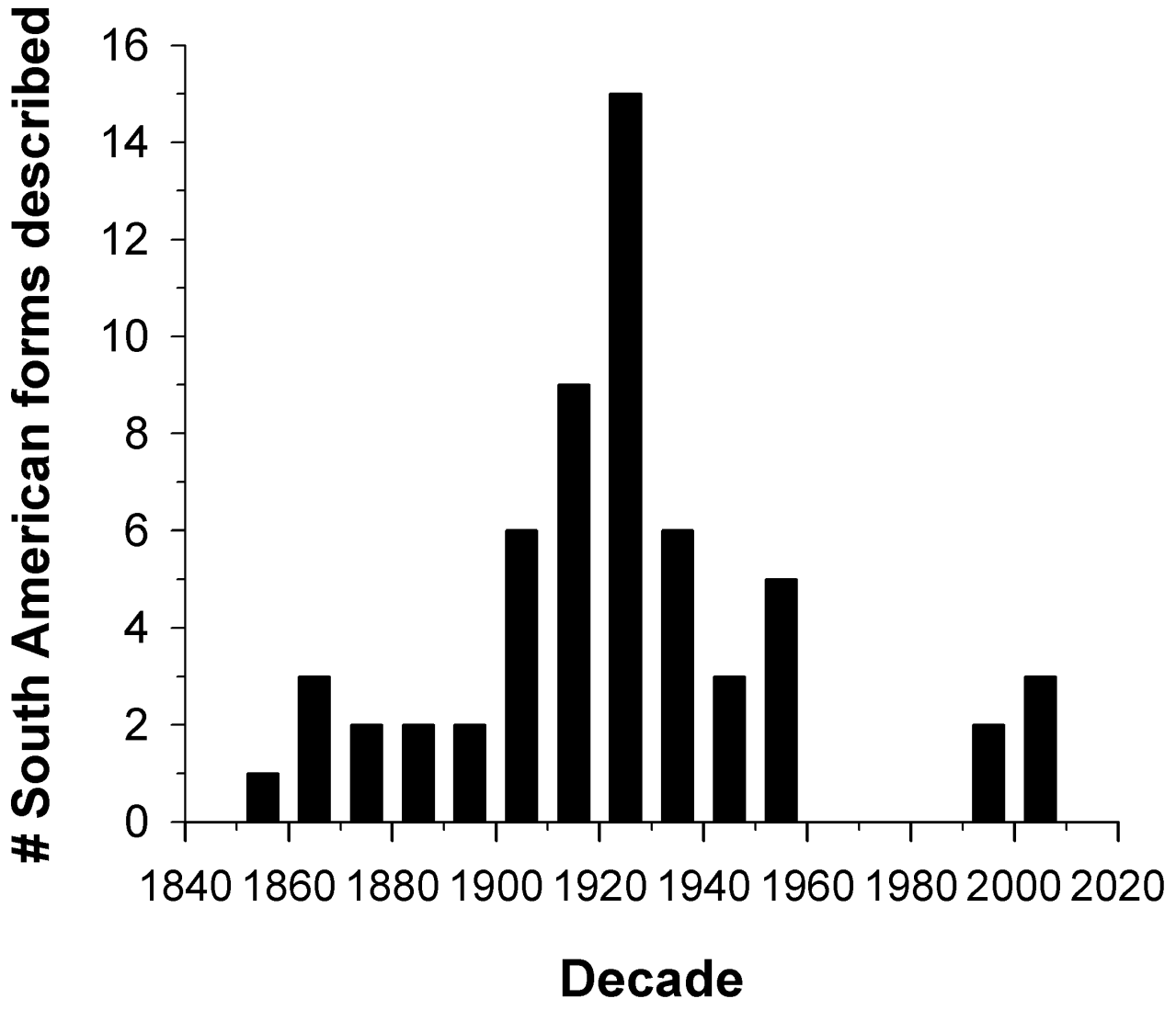

FIGURE 1. Number of South American forms of *Pogonomyrmex* described by decade.

From the mid 1930's to mid 1940's, several additional forms were described by other individuals: *P. ater* from Argentina (Donisthorpe, 1933), *P. bispinosus* var. *intermedia* from Chile (Menozzi, 1935), and *P. venezuelensis* and *P. venezuelensis* ssp. *rupununi* from Venezuela (Weber, 1943). However, Angel Gallardo (from Argentina) was the first native taxonomist to describe South American species of *Pogonomyrmex* (*P. catanlilensis* and *P. longibarbis* from Argentina) (Gallardo, 1931). Problematically, the piecemeal approach used by these authors resulted in many of these species later being synonomized under previously described species. Gallardo (1932) also wrote a review of the *Pogonomyrmex* of Argentina, which was significant because: (1) it collated information on this genus into one paper, and (2) it translated all previous descriptions into one language (Spanish) with the exception of three species that had been described in Latin (*P. coarctatus, P. carbonarius, P. rastratus*).

The lack of native South American ant taxonomists changed by the late 1940's with the arrival of Walter Kempf and Nicholas Kusnezov. Kempf contributed little to our understanding of *Pogonomyrmex* because he worked mostly in Brazil, where there are few species of *Pogonomyrmex*. In contrast, Kusnezov worked in Argentina, where he spent extensive time in the field collecting and observing species of *Pogonomyrmex*. Kusnezov described seven forms of *Pogonomyrmex* (six from Argentina, one from Bolivia) (Kusnezov, 1949, 1951, 1953, 1954), and he wrote the first taxonomic revision (in Spanish) for the *Pogonomyrmex* of Argentina (Kusnezov, 1951). More importantly Kusnezov was the first author to link ecology and evolutionary history for species in North and South America. Kusnezov (1978) updated his first key to the *Pogonomyrmex* of Argentina, which was updated again by Taber (1998) and yet again by Cuezzo & Claver (2009). However, all of these keys are difficult to use and/or are generally unsatisfactory for obtaining correct identifications.

The only subsequent revisionary work was a treatment of the ants of Chile (Snelling & Hunt, 1975), which included taxonomic updates, distribution maps, and a key to the five species of *Pogonomyrmex* known to occur in Chile (*P. bispinosus, P. vermiculatus, P. angustus, P. laevigatus, P. odoratus*). The true identity of *P. vermiculatus* has also been in a state of confusion since its description (Snelling & Hunt, 1975). There was a subsequent lull of work on South American *Pogonomyrmex*, despite a sharp upturn of research on the genus in North America beginning in the late 1960's. Since that time, five species have been described by South American taxonomists, two from Venezuela (*P. sylvestris, P. stefani*) (Lattke, 1991, 2006), one from Columbia (*P. striatinodis*) (Fernández & Palacio, 1998), and two from Argentina (*P. kusnezovi* and *P. mendozanus*) (Cuezzo & Claver, 2009).

Over this time, few studies examined the natural history and ecology of *Pogonomyrmex* in South America. Carlos Bruch was the first investigator to contribute information on the natural history of *Pogonomyrmex* (Bruch, 1916, 1917) by describing the nest structure of several species. Later studies included those by Marcus on ecology and internal anatomy (Marcus, 1953; Marcus & Marcus, 1951) and studies by Kusnezov on distribution and habitat affiliations (Kusnezov, 1949, 1951). Several studies on *Pogonomyrmex* also were conducted in Chile that mostly examined distribution, abundance, habitat use, foraging behavior, activity patterns, and orientation (Medel & Fuentes, 1995; Torres-Contreras, 2001; Torres-Contreras *et al.*, 2007).

Beginning in the early 2000's, a research group from Buenos Aires, Argentina, under the direction of Javier Lopez de Casanave, began studies on the ecology of seed predation by *Pogonomyrmex* in the Monte Desert (Mendoza Province). However, there were identification problems with these studies as two of the three species were misidentified—*P. mendozanus* as *P. pronotalis* and an apparently undescribed species as *P. rastratus* (e.g., Claver & Fowler, 1993; Pirk & Lopez de Casenave, 2006; Pirk, Lopez de Casenave, & Pol, 2004; Pol & Lopez de Casenave, 2004; Pol *et al.*, 2008). Other recent studies include seed predation by *P. pencosensis* in the Monte Desert (Aranda-Rickert & Fracchia, 2011, 2012), colony founding by *P. cunicularius* and *P. pencosensis* (Johnson, 2010), and morphology of the two queen phenotypes in *P. laticeps* (Peeters, Johnson, & Keller, 2012). Taber (1998) also provided a phylogeny based on morphological characters, distribution maps, and a key to the *Pogonomyrmex* of North America, South America, and Hispaniola. A detailed phylogeny for the entire genus is underway (C.S. Moreau & R.A. Johnson, unpub. data).

For much of its history, *Pogonomyrmex* has been divided into several subgenera. Forel's (1899a) description of *P. mayri* was significant because he placed this species into a new subgenus (*Janetia*) based on its unique morphology. The name *Janetia* was later replaced by *Forelomyrmex* because *Janetia* was a junior homonym (Wheeler, 1913). In 1902, Wheeler described *P. imberbiculus* from the United States, but this description also influenced taxonomy of South American species because he placed *P. imberbiculus* and *P. naegelii* in his new subgenus *Ephebomyrmex* (Wheeler, 1902). Forel (1912) later described *Hylomyrma* as a fourth subgenus from South America. *Hylomyrma* was subsequently elevated to generic status (Wheeler 1922) where it remains (Bolton, 2014; Ward, Brady, Fisher, & Schultz, 2015); *Hylomyrma* is considered to be the sister genus to *Pogonomyrmex*

(Jansen & Savolainen, 2010; Ward *et al.*, 2015). The other two subgenera (*Ephebomyrmex*, *Forelomyrmex*) remained valid for several decades. However, *Forelomyrmex* was later provisionally synonomized under *Pogonomyrmex* without discussion (Brown, 1973), and Snelling (1981) finalized the synonomy, again without discussion. Taber (1990) resurrected *Forelomyrmex* to generic status, and Lattke (1991) placed it back into synonomy under *Pogonomyrmex*. *Ephebomyrmex* also oscillated between generic and subgeneric status during this same period.

Significantly, several recently described species from northern South America influenced the status of subgenera within *Pogonomyrmex*. The first of these species, *P. sylvestris*, was collected from humid tropical forests in Venezuela, and it shared characters with all three subgenera (Lattke, 1991), resulting in *Ephebomyrmex* being placed as a junior synonym of *Pogonomyrmex* (Bolton, 1995). Two additional species were subsequently described from forests in northern South America (*P. striatinodis, P. stefani*); both species showed morphological intermediacy across the three subgenera that further supported subsuming *Ephebomyrmex* and *Forelomyrmex* under *Pogonomyrmex*. These three species were also considered morphologically primitive for the genus, which was used to suggest that the genus evolved in humid tropical habitats of South America (Fernández & Palacio, 1998; Lattke, 2006; Taber, 1998).

Lastly, three species from southern Argentina and southern and southcentral Chile (*P. angustus, P. laevigatus,* and *P. odoratus*) will be transferred to a new genus based on a molecular phylogeny indicating that the *P. angustus*-group is sister to a clade containing *Hylomyrma* and the remaining *Pogonomyrmex* (Ward *et al.*, 2015). These three species are excluded from this revision.

METHODS

Morphological characters were photographed using a Spot Insight QE camera attached to a Leica MZ 12$_5$ 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 0.1 mm increments. All measurements are given in mm (minimum—maximum). The following standard measurements were 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**: (HW/HL) × 100.

MOD **Maximum Ocular Diameter**: maximum diameter of the eye measured with the head in full lateral aspect.

OI **Ocular Index**: (MOD/HW) × 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**: (SL/HW) × 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**: measured along the dorsal margin from the articulation with the trochanter to most distal tip of the femur.

HFI **Hind Femur Index**: (HFL/HW) × 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:

ALWC	Alex Wild Collection, Austin, Texas, USA
AMNH	American Museum of Natural History, New York, USA
CAS	California Academy of Sciences, San Francisco, California, USA
CISEC	Colección de Invertebrados del Sur del Ecuador, Universidad Técnica Particular de Loja, Loja, Ecuador
CSC	Chris Smith Collection, Earlham College, Richmond, Indiana, USA
FML	Fundación Miguel Lillo, Tucumán, Tucumán Province, Argentina
IADIZA	Instituto Argentino de Investigaciones de Zonas Aridas, Mendoza, Mendoza 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
MNHN	Museo Nacional de Historia Natural, Santiago, Chile
MIZA	Museo del Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Aragua, Venezuela
MLPA	Museo de La Plata, La Plata, Buenos Aires Province, Argentina
MSNG	Museo Civico di Storia Naturale di Genova "Giacomo Doria", Genova, Italy
MZUSP	Museu de Zoologie, Universidade de São Paulo, São Paulo, Brazil
NHMB	Naturhistorisches Museum, Basel, Switzerland
NMW	Naturhistorisches Museum, Vienna, Austria
RAJC	Robert A. Johnson Collection, Tempe, Arizona, USA
RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Belgium
RGPC	Rodrigo G. Pol Collection, Mendoza, Mendoza Province, Argentina
UNCB	Universidad Nacional de Colombia, Medellín, Colombia
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
ZSM	Zoologische Staatssammlung, München, Germany

Latitude and longitude data were rarely available from older collections. To create distribution maps, these data were approximated using Google Earth (https://www.google.com/earth/), Geonames (http://www.geonames.org/), and/or directory of cities and towns in the world (http://www.fallingrain.com/world/index.html). The known geographical distribution of each species is also discussed relative to ecoregions of occurrence as defined by Olson *et al*. (2001). Most elevation data are based on approximately 300 series collected by RAJ. High resolution photographs of holotypes, lectotypes, paralectotypes, and non-type specimens are available at http://www.antweb.org/ and http://www.asu.edu/clas/sirgtools/pogonomyrmex/SOUTHAMERICANPOGOS.htm. Both web sites also display high-resolution photographs for wings of queens and for wings and genitalia of males; the latter site also shows type locality and/or habitat photos for some of the species treated herein.

RESULTS

Synonymic list of South American species of Pogonomyrmex, *known castes, and countries in which each species is known to occur* (excluding species in the *P. brevibarbis* and *P. rastratus*-groups)

***P. coarctatus*-group**

P. coarctatus Mayr 1868: 170 (w.q.m). Argentina, Uruguay.
= *coarctatus* var. *striaticeps* Emery 1906: 157 (w). Argentina (Santa Fe).
= *bruchi* Forel 1913: 217 (w). Argentina (Buenos Aires). **NEW SYNONOMY**
P. lobatus Santschi 1921: 96 (w.q.m). Argentina, Brazil, Uruguay.
P. marcusi Kusnezov 1951: 260 (w.q.m.l). Bolivia.
P. micans Forel 1914: 268 (w.q.m). Argentina, Paraguay.

***P. cunicularius*-group**

P. cunicularius Mayr 1887: 613 (w.q.m). Argentina, Uruguay.
= *brevispina* Santschi 1931: 275 (w.q). Argentina (Entre Ríos).
P. pencosensis Forel 1914: 265 (w.q.m). Argentina. **NEW STATUS**
P. serpens Santschi 1922: 349 (w.q). Argentina, Bolivia, Paraguay. **NEW STATUS**
= *carnivora* Santsch 1925a: 155 (w). Argentina (Santa Fe). **NEW SYNONOMY**

***P. bispinosus*-group**

P. bispinosus (Spinola 1851): 244 (w.q.m). Chile.
P. inermis Forel 1914: 267 (w.q.m). Argentina.
P. uruguayensis Mayr 1887: 615 (w.q.m). Argentina, Paraguay, Uruguay.

***P. laticeps*-group**

P. laticeps Santschi 1922: 350 (w.q.m). Argentina.
P. mendozanus Cuezzo & Claver 2009: 101 (w.q.m). Argentina.
P. tinogasta Johnson (w.q). Argentina. **NEW SPECIES**

***P. mayri*-group**

P. mayri Forel 1899a: 61 (w.q.m). Colombia.

***P. naegelii*-group**

P. abdominalis Santschi 1929: 278 (w.q). Argentina, Bolivia, Brazil.
P. naegelii Emery 1878: x (w.q.m.l). Argentina, Bolivia, Brazil, Colombia, Guyana, Paraguay, Peru, Uruguay, Venezuela.
= *venezuelensis* Weber 1943: 69 (w). Venezuela (Anzoátegui).
= *venezuelensis* ssp. *rupunini* Weber 1943: 71 (w). Guyana (Upper Takutu-Upper Essequibo).
P. tenuipubens Santschi 1936: 403 (w). Argentina, Paraguay.

***P. sylvestris*-group**

P. stefani Lattke 2006: 53 (w.m). Venezuela.
P. striatinodis Fernández & Palacio 1997: 1650 (w). Colombia, Ecuador.
P. sylvestris Lattke 1991: 305 (w). Venezuela.

Unplaced species

P. theresiae Forel 1899b: 303 (w). Ecuador.

Key to workers for Pogonomyrmecini genera and species groups of *Pogonomyrmex*

1 Psammophore poorly-developed, consisting of numerous short to long hairs scattered over ventral surface of head **2**
- Psammophore well-developed, consisting of numerous long, curved hairs along basolateral margin of head (***Pogonomyrmex*-part)** **8**
2 Inferior propodeal spines biaculeate, upper and lower portions both acuminate; apical (masticatory) margin of mandible markedly oblique in frontal 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 frontal view (***Pogonomyrmex*-part**) **3**
3 Anterior surface of petiolar node striate . . . . . ***P. mayri*-group**
- Anterior surface of petiolar node smooth and shining to moderately coriarious **4**
4 In profile, head and mesosoma with numerous long, flexuous hairs with length >MOD . . . . . ***P. sylvestris*-group**
- In profile, hairs on head and mesosoma usually short to medium-length, relatively stiff, longest rarely >MOD **5**
5 In frontal view, head elongate (CI < 90); hind femur long, HFI > 120 and HFL > 2.00 mm; entire scape strongly striate . . . . . ***P. cunicularius*-group**
- In frontal view for most to all workers in a series, head subquadrate to quadrate (CI > 90) ***and*** hind femur shorter, HFI rarely > 100 and HFL rarely > 2.00 mm; scape smooth to moderately striate **6**
6 Posterior surface of petiolar node with transverse to oblique rugae or rugoreticulate; dorsum of postpetiole with longitudinal to

oblique rugae or rugoreticulate ***or*** strongly granulate-punctate, dull; head and mesosoma concolorous tan to brown . . . . . ***P. naegelii*-group**

- Posterior surface of petiolar node and dorsum of postpetiole smooth and shining to moderately coriarious, weakly shining; head and mesosoma concolorous orangish or dark brown to black, rarely bicolored (head orangish, mesosoma blackish) . . . **7**

7 In frontal view, anterior margin of clypeus convex; in profile, clypeus strongly convex; anteroventral margin of peduncle of petiole with small, acuminate spine; promesonotum smooth and shining ***or*** if rugose to rugoreticulate, then promesonotal interugae strongly granulate, dull . . . . . ***P. angustus*-group**

- In frontal view, anterior margin of clypeus flat to concave; in profile, clypeus flat to weakly convex; anteroventral margin of peduncle of petiole with triangular process or rarely with weakly acuminate triangular spine; promesonotum rugoreticulate, interrugae smooth and shining to moderately coriarious, weakly shining . . . . . ***P. brevibarbis*-group**

8 Fine, dense, incised striae (usually longitudinal) cover anterior one-third to all of first gastral tergum . . . . . ***P. rastratus*-group (part)**

- Fine, dense, incised striae lacking on first gastral tergum or restricted to base **9**

9 Cephalic dorsum with scattered small foveae (use >50x magnification) (**Figures 3A, 8A**); part to all of cephalic dorsum with fine longitudinal striae (**Figures 3A, 8A**); antennal scapes short, extending beyond eye less than one-third the distance from posterior margin of eye to posterior corner of head . . . . . ***P. coarctatus*-group**

- Cephalic dorsum lacking foveae (**Figures 27A, 38A**); cephalic dorsum with prominent longitudinal rugae (**Figures 27A, 38A**); antennal scapes longer, extending beyond eye by more than one-half the distance from posterior margin of eye to posterior corner of head **10**

10 Dorsum of postpetiole weakly to strongly coriarious, if present rugae are faint and discontinuous . . . . . ***P. bispinosus*-group**

- Dorsum of postpetiole with transverse rugae that traverse the entire surface **11**

11 Superior propodeal spines consist of small tubercles or denticles **(unplaced)**. . . . . ***P. theresiae***

- Superior propodeal spines long, well-developed, length >0.5x distance between their bases **12**

12 Head broader than long (CI > 100); rugae on cephalic dorsum incised, closely-spaced, regular, width of rugae and interrugae similar ***or*** rugae on cephalic dorsum prominent, coarse, interrugae smooth to moderately coriarious, weakly shining to shining . . . . . ***P. laticeps*-group**

- Head variable, but head longer than broad for at least some workers in a series; rugae on cephalic dorsum prominent, coarse, interrugae usually strongly granulate-punctate, dull to weakly shining, often with a beaded appearance . . . . . ***P. rastratus*-group (part)**

Clave para obreras de los generos de Pogonomyrmecini y grupos de especies de *Pogonomyrmex*

Mediciones estándar utilizados en los claves de Español:

AC **Ancho Cefálico:** ancho máxima de la cabeza inmediatamente posterior a los ojos, medido en vista de cara completa.

LC **Longitud Cefálico**: longitud de la cápsula de la cabeza excluyendo mandíbulas, en vista frontal, desde el punto medio del margen clipeal anterior a la punto medio del margen posterior.

DMO **Diámetro Máximo Ocular:** diámetro máximo del ojo medido con la cabeza en perspectiva lateral.

IC **Índice Cefálico:** (AC/LC) × 100.

LFP **Longitud del Fémur Posterior:** medida a lo largo del margen dorsal del metafemur desde la articulación con el trocánter hasta su punto más distal.

IFP **Índice del Fémur Posterior:** (LMP/AC) × 100.

1 Psamóforo poco desarrollado, con numerosos pelos, cortos hasta largos, dispersos sobre la superficie ventral cefálica **2**

- Psamóforo bien desarrollado, con numerosos pelos largos y arqueados dispuestos sobre el margen laterobasal de la cabeza (***Pogonomyrmex*-en parte**) **8**

2 Espinas inferiores propodeales bífidas, tanto la porción superior como inferior puntiagudas; margen apical (masticador) mandibular bien oblicuo en vista frontal . . . . . ***Hylomyrma***

- Espinas inferiores propodeales redondeadas, triangulares o espiniformes; si son prominentes siempre terminan en una sola punta, jamás son bífidas; margen apical (masticador) de la mandíbula perpendicular, o casi, en vista frontal (***Pogonomyrmex*-en parte**) **3**

3 Superficie anterior del nodo peciolar estriada . . . . . **grupo de *P. mayri***

- Superficie anterior del nodo peciolar desde lisa y brillante hasta con finas líneas anastomizantes **4**

4 Cabeza y mesosoma en vista lateral con numerosos pelos largos y sedosos de una longitud > DMO . . . **grupo de *P. sylvestris***

- Pelos de la cabeza y el mesosoma en vista lateral relativamente tiesos y usualmente cortos a medianos, los más largos rara vez > DMO **5**

5 En vista frontal la cabeza es alargada (IC < 90); el fémur posterior es largo, IFP > 120 y LFP > 2.00 mm; todo el escapo con estriaciones fuertes . . . . . **grupo de *P. cunicularius***

- Para todas las obreras de una serie, o la mayoría, la cabeza en vista en vista frontal es semicuadrada a cuadrada (IC > 90) ***y también*** el fémur posterior es más breve, IFP rara vez > 100 e LFP rara vez > 2.00 mm; el escapo es liso a moderadamente estriado **6**

6 La superficie posterior del nudo peciolar presenta arrugas transversales hasta oblicuas o arrugas con reticulaciones; el dorso del pospeciolo tiene arrugas longitudinales hasta oblicuas o arrugas con reticulaciones, o de lo contrario, tiene un esculpido mate fuertemente granuloso y punteado; cabeza y mesosoma uniformemente tostado a castaño . . . . . **grupo de *P. naegelii***

- Superficies posterior del nudo peciolar y dorsal del pospecíolo varian desde lisas y brillantes hasta de poco brillo con líneas moderadas anastomizantes; cabeza y mesosoma uniformemente anaranjado o castaño oscuro hasta negro, rara vez con dos colores (cabeza anaranjada y mesosoma negruzco) **7**

7 En vista frontal, el margen anterior del clípeo es convexo y visto de perfil el clípeo es fuertemente convexo; el margen anteroventral del pedúnculo del pecíolo presenta una pequeña espina puntiaguda; el promesonoto es liso y brillante pero si es arrugado o arrugado con reticulaciones entonces el espacio entre las arrugas es fuertemente granuloso y mate . . . . . **grupo de *P. angustus***

- En vista frontal, el margen anterior del clípeo es transversal o cóncavo y en perfil el clípeo es plano a ligeramente convexo; el margen anteroventral del pedúnculo del pecíolo presenta un proceso triangular, rara veces con una espina triangular puntiaguda; el promesonoto presenta arrugas con reticulaciones, los espacios entre las arrugas varían desde lisos y brillantes hasta débilmente brillantes con líneas moderadas anastomizantes . . . . . **grupo de *P. brevibarbus***

8 Estrías finas y densas, bien talladas y usualmente longitudinales cubren el primer tergo gastral totalmente o por lo menos hasta la tercera parte anterior . . . . . **grupo de *P. rastratus* (parte)**

- El primer tergo gastral carece de estrías bien talladas, finas y densas. A lo sumo su presencia se limita a la base **9**

9 Dorso cefálico con pequeñas fosetas dispersas (use aumentos >50x) (**Figuras 3A, 8A**); una parte o todo del dorso cefálico con estrías finas longitudinales (**Figuras 3A, 8A**); escapos antenales breves, extendiéndose más allá del ojo por una distancia menor a la tercera parte de la distancia entre el margen posterior ocular hasta la esquina posterior cefálica . . . . . **grupo de *P. coarctatus***

- Dorso cefálico carece de fosetas (**Figuras 27A, 38A**); dorso cefálico con arrugas longitudinales prominentes (**Figuras 27A, 38A**); escapos antenales más largos, se extienden más allá del ojo por una distancia mayor a la mitad de la distancia entre el margen posterior ocular hasta la esquina posterior cefálica **10**

10 Dorso del pospecíolo con estrías anastomizantes finas a bien talladas, también pueden haber arrugas pero en tal caso son débiles y no continuas . . . . . **grupo de *P. bispinosus***

- Dorso del pospecíolo con arrugas transversales que cubren toda la superficie **11**

11 Espinas propodeales superiores parecen pequeños tubérculos o dentículos (**sin ubicación**) . . . . . ***P. theresiae***

- Espinas propodeales superiores largas y bien desarrolladas, su longitud > 0.5x la distancia entre sus bases **12**

12 Cabeza más ancha que larga (IC > 100); las arrugas sobre el dorso cefálico están bien talladas, cercanas entre sí y regulares; el ancho tanto de cada arruga como del espacio entre ellas es similar ***o*** las arrugas del dorso cefálico son prominentes y toscas con los espacios entre ellas lisos o con líneas finas anastomizantes, de brillo débil a fuerte . . . . . **grupo de *P. laticeps***

- Cabeza variable pero más larga que ancha en por lo menos algunas obreras de una serie; arrugas del dorso cefálico son prominentes y toscas; los espacios entre ellas son fuertemente granulosos a punteados, opacos o con brillo muy débil, frecuentemente con apariencia granulosa . . . . . **grupo de *P. rastratus* (parte)**

Key to workers for *Pogonomyrmex* species occurring in South America (*P. brevibarbis* and *P. rastratus*-groups included but not to species)

1 Fine, dense, incised striae lacking on first gastral tergum or restricted to base **2**

- Fine, dense, incised striae (usually longitudinal) cover anterior one-third to all of first gastral tergum **23**

2 Cephalic dorsum with scattered small foveae (use >50x magnification) (**Figures 3A, 8A**); part to all of cephalic dorsum with fine longitudinal striae (**Figures 3A, 8A**); antennal scapes short, extending beyond eye less than one-third the distance from posterior margin of eye to posterior corner of head (***coarctatus*-group**) **3**

- Cephalic dorsum lacking foveae (**Figures 27A, 38A, 58A**); cephalic dorsum with prominent longitudinal rugae or rugoreticulate (**Figures 27A, 38A, 58A**); antennal scapes longer, extending beyond eye by more than one-half the distance from posterior margin of eye to posterior corner of head **6**

3 Striae cover only part of cephalic dorsum, areas lacking striae shining to strongly shining **4**

- Striae cover entire cephalic dorsum, entire dorsum weakly shining **5**

4 Workers usually larger, strongly polymorphic with supermajors (HW = 1.94–3.54 mm); some weak to moderately coarse transverse rugae on posterior surface of petiolar node; rugae on dorsum of postpetiole often absent, if present usually restricted to posterior margin; inferior propodeal spines lacking or very reduced in size, broadly rounded; interrugae on mesosoma finely granulate, moderately shining . . . . . ***coarctatus***

- Workers smaller, monomorphic (HW = 1.91–2.33 mm); coarse rugae cover posterior surface of petiolar node; weak to moderately coarse transverse rugae on dorsum of postpetiole; inferior propodeal spines present, wider than long, apex bluntly angulate to acuminate; interrugae on mesosoma not granulate, smooth and strongly shining . . . . . ***marcusi***

5 In profile, lateral lobe of clypeus massively enlarged, with narrow gap (much less than width of antennal scape) between clypeal lobe and frontal lobe; concolorous ferruginous orange to orange-red. . . . . ***lobatus***

- In profile, lateral lobe of clypeus not enlarged with broad gap (similar to width of antennal scape) between clypeal lobe and frontal lobe; bicolored, head dark red to reddish-black, gaster blackish . . . . . ***micans***

6 In frontal view, head elongate (CI < 90); hind femur long, HFI > 120; entire scape strongly striate; psammophore poorly-developed, consisting of hairs scattered over ventral side of head (***cunicularius*-group**) **7**

- In frontal view, for most to all workers in a series head subquadrate to quadrate (CI > 90) ***and*** hind femur rarely long, HFI rarely > 100; scape smooth to moderately striate; psammophore poorly to well-developed **9**

7 In profile, petiolar node rounded; inferior propodeal spines wider than high, broadly rounded; first gastral tergum smooth and polished, strongly shining; superior propodeal spines shorter than distance between their bases . . . . . ***cunicularius***

- In profile, petiolar node angulate; inferior propodeal spines about as wide as high, acuminate; first gastral tergum moderately to strongly coriarious, dull to weakly shining; superior propodeal spines longer than distance between their bases **8**

8 Promesonotal dorsum weakly rugoreticulate to transversely rugose, rugae strongest on anterior pronotal dorsum; propodeal dorsum consistently transversely rugose (**Figure 22C**); body concolorous tannish-red . . . . . ***pencosensis***

- Promesonotal dorsum coarsely and consistently rugoreticulate; propodeal dorsum rugoreticulate to transversely rugose (**Figure 25C**); bicolored, mesosoma and petiolar node medium to dark orangish-brown to reddish-brown, rest of body lighter . . . . . ***serpens***

9 Superior propodeal spines absent ***or*** consisting of small to moderate sized denticles or tubercles **10**

- Superior propodeal spines present, length usually ≥0.5x the distance between their bases **11**

10 Dorsum of postpetiole with regular to wavy transverse rugae . . . . . ***theresiae***

- Dorsum of postpetiole lacking transverse rugae . . . . . ***inermis***

11 Superior and inferior propodeal spines long, acuminate; in profile, posterior surface of petiolar node with crest along anterior margin; anteroventral margin of peduncle of petiole with acuminate spine; mesosoma with at least several long, flexuous hairs; anterior margin of clypeus with minute medial tooth (***sylvestris*-group**) **12**

- Superior and inferior propodeal spines rarely long and acuminate; in profile, posterior surface of petiolar node rarely with crest along anterior margin; anteroventral margin of peduncle of petiole straight or with triangular process, but usually lacking acuminate spine; mesosoma rarely with long, flexuous hairs; anterior margin of clypeus lacking minute medial tooth **14**

12 Larger species (HW > 1.55 mm); mandible with seven teeth; compound eye lacking hairs between ommatidia; clypeus with prominent medial carina; in profile, anterodorsal margin of postpetiole not offset from helcium . . . . . ***striatinodis***

- Smaller species (HW < 1.35 mm); mandible with six teeth; compound eye with hairs between ommatidia; clypeus lacking prominent medial carina; in profile, anterodorsal margin of postpetiole offset from helcium **13**

13 Lateral surface of petiolar node longitudinally rugose; in profile, procoxae transversely striate; femur and tibiae smooth to weakly coriarious, weakly shining to shining; medial clypeal region between antennal insertions with 9–12 fine, closely-spaced, longitudinal rugae, interrugae dull to weakly shining . . . . . ***stefani***

- Lateral surface of petiolar node mostly smooth and shining; in profile, procoxae finely imbricate; femur and tibiae very strongly coriarious, dull; medial clypeal region between antennal insertions with 4–8 coarse, sometimes wavy, longitudinal rugae, interrugae more or less shining . . . . . ***sylvestris***

14 Hairs on head (including psammophore) and mesosoma very short, maximal length similar to or slightly greater than width of cephalic interrugae (note that one to few long, coarse, stiff hairs are occasionally present along posterior margin of head and/or pronotum) . . . . . ***tenuipubens***

- Hairs on head (including psammophore) and mesosoma moderately long, maximal length much longer than width of cephalic interrugae **15**

15 Dorsum of mesosoma and posterior surface of petiolar node rugoreticulate to vermiculate **16**

- Dorsum of mesosoma usually rugose, sometimes rugoreticulate to vermiculate; posterior surface of petiolar node with transverse or oblique rugae or otherwise, but never rugoreticulate to vermiculate **17**

16 Small lobe projects dorsally from anterior margin of antennal fossa, best viewed from posterior margin of head looking down onto dorsum of lateral clypeal lobes (**Figure 54A**); in dorsal view, posterior surface of petiolar node narrow, usually about as wide as distance between tips of superior propodeal spines; mesosomal hairs moderately short, longest rarely >0.7–0.8x MOD . . . . . ***naegelii* (part)**

- Lacking small lobe that projects dorsally from anterior margin of antennal fossa (**Figure 54B**); in dorsal view, posterior surface of petiolar node broader, distinctly wider than distance between tips of superior propodeal spines; mesosomal hairs longer, longest approaching to slightly exceeding MOD . . . . . ***abdominalis***

17 Dorsum of postpetiole smooth and shining, granulate, punctate, or otherwise, but lacking transverse rugae (rarely with one to few longitudinal rugae) **18**

- Dorsum of postpetiole with transverse rugae **20**

18 Posterior surface of petiolar node lacking rugae ***or*** rarely with few weak longitudinal rugae; head and mesosoma usually concolorous dark brown to black, rarely with blackish head and orangish mesosoma; metanotal sulcus usually present, weakly to strongly impressed; inferior propodeal spines well-developed, usually acuminate; propodeal spiracles circular . . . . . ***brevibarbis*-group**

- Posterior surface of petiolar node with weak to moderately coarse transverse rugae; head and mesosoma concolorous light to dark ferruginous orange; metanotal sulcus rarely present; inferior propodeal spines absent to poorly-developed; propodeal spiracles narrowly ovate **19**

19 Workers usually larger (HW = 1.75–2.05 mm); body concolorous ferruginous orange to reddish-orange; frontal lobes enlarged, lateral margins convex, projecting at a strong vertical orientation from cephalic dorsum, both in frontal view (**Figure 27A**) and from posterior margin of head looking down over cephalic dorsum (**Figure 28A**) . . . . . ***bispinosus***

- Workers smaller (HW = 1.24–1.61 mm); head and mesosoma concolorous ferruginous orange, gaster sometimes blackish; frontal lobes small, lateral margins subparallel, projecting nearly parallel to cephalic dorsum, both in frontal view (**Figure 35A**) and from posterior margin of head looking down over cephalic dorsum (**Figure 28B**) . . . . . ***uruguayensis***

20 Deeply incised, fine, closely-spaced, regular rugae cover cephalic dorsum and mesosoma, interrugae only slightly wider than rugae (**Figure 43A–C**); head and mesosoma black, gaster dark ferruginous orange . . . . . ***mendozanus***

\- Rugae on cephalic dorsum coarser, wavy to slightly irregular; rugae on mesosoma irregular or rugoreticulate to vermiculate; interrugae on head and mesosoma distinctly wider than rugae (**Figure 38A–C**); color variable, ***but*** if head and mesosoma black and gaster dark orange, then interrugae on cephalic dorsum are strongly granulate **21**

21 Interrugae on cephalic dorsum moderately to strongly granulate, dull. . . . . ***rastratus*-group (part)**

\- Interrugae on cephalic dorsum smooth to moderately coriarious, weakly shining to shining **22**

22 Body concolorous black except for dark reddish band encircling eye; rugae on promesonotum longitudinal, usually regular; rugae at medial posterior margin of head longitudinal, rarely rugoreticulate. . . . . ***tinogasta***

\- Head and mesosoma dark reddish-black, gaster black; rugae on promesonotum transverse, oblique, or irregular, rarely longitudinal; rugae along medial posterior margin of head usually partly rugoreticulate . . . . . ***laticeps***

23 Head and mesosoma with fine, dense, deeply incised, subparallel-parallel rugae; anterior margin of clypeus with small medial tooth. . . . . ***mayri***

\- Head and mesosoma with prominent irregular to regular, longitudinal rugae, interrugae usually wider than rugae; anterior margin of clypeus entire **24**

24 Dorsum of mesosoma and posterior surface of petiolar node rugoreticulate to vermiculate . . . . . ***naegelii* (part)**

\- Dorsum of mesosoma usually rugose, sometimes rugoreticulate to vermiculate; posterior surface of petiolar node with transverse or oblique rugae or otherwise, but never rugoreticulate to vermiculate . . . . . ***rastratus*-group (part)**

Pogonomyrmex de Sur América; clave a las especies basada en las obreras (grupos *P. brevibarbis* and *P. rastratus* incluido pero no a las especies)

1 Usualmente sin estrías finas y densas sobre el primer tergo gastral; en caso contrario las estrías están restringidas a la base del tergo **2**

\- Estrías finas y densas (generalmente longitudinales) cubren hasta la tercera parte o todo el primer tergo gastral **23**

2 Dorso cefálico con pequeñas fosetas dispersas (use >50x aumentos) (**Figuras 3A, 8A**); una parte a todo el dorso cefálico presenta finísimas estrías longitudinales (**Figuras 3A, 8A**); escapos antenales cortos, que se extiende menos de un tercio de la distancia desde el margen posterior del ojo a la esquina posterior de la cabeza (**grupo *coarctatus***) **3**

\- Dorso cefálico carece de fosetas (**Figuras 27A, 38A, 58A**); el dorso cefálico rugoreticulado o con rugosidades longitudinales prominentes (**Figuras 27A, 38A, 58A**); escapos antenales más largos, que se extiende más de la mitad de la distancia desde el margen posterior del ojo a la esquina posterior de la cabeza **6**

3 Estrías cubren sólo una parte del dorso cefálico, zonas sin estrías son brillantes a fuertemente brillantes **4**

\- Estrías cubren todo el dorso cefálica, superficie dorsal brilla débilmente **5**

4 Obreras generalmente más grandes, fuertemente polimórficas con supermayores (AC = 1,94–3,54 mm); rugosidades transversales débiles a moderadamente gruesas presentes en la superficie posterior del nodo del pecíolo; rugosidades del dorso del postpecíolo a menudo ausente, si está presente generalmente se restringen al margen posterior; espinas propodeales inferiores inexistentes o muy reducidos en tamaño, ampliamente redondeadas; interrugosidades del mesosoma finamente granulados y moderadamente brillantes . . . . . ***coarctatus***

\- Obreras más pequeñas, monomórficas (AC = 1,91–2,33 mm); superficie posterior del nodo del pecíolo cubierto de rugosidades gruesas; dorso del postpecíolo con rugosidades transversales débiles a moderadamente gruesas; espinas propodeales inferiores presentes, más anchas que altas, forma del ápice varía desde ángulo romo hasta puntiagudo; interrugosidades del mesosoma no son granulados, de aspecto liso y fuertemente brillante . . . . . ***marcusi***

5 De perfil, lóbulo lateral del clípeo sumamente engrosado con una estrecha brecha (mucho menos del ancho del escapo antenal) entre el lóbulo del clípeo y el lóbulo frontal; coloración uniforme naranja ferruginosa a naranja rojiza . . . . . ***lobatus***

\- De perfil, lóbulo lateral de clípeo no engrosado y con amplia brecha (similar al ancho del escapo antenal) entre el lóbulo de clípeo y el lóbulo frontal; cuerpo de dos colores, cabeza roja oscura a negro-rojizo, gáster negruzco . . . . . ***micans***

6 En vista frontal, la cabeza luce alargada (IC < 90); fémur posterior largo, IFP > 120; todo el escapo fuertemente estriado; psamóforo poco desarrollado, reducido a pelos dispersos en la parte ventral de la cabeza (**grupo *cunicularius***) **7**

\- En vista frontal, para la mayoría de todos los trabajadores en una serie la cabeza es semicuadrada a cuadrada (IC > 90) ***y*** fémur posterior rara vez largo, IFP rara vez > 100; escapos lisos a moderadamente estriados; psamóforo poco a bien desarrollado **9**

7 En perfil, el nodo del pecíolo redondeado; espinas propodeales inferiores mas anchas que altas, ampliamente redondeadas; primer tergo gastral liso y pulido, fuertemente brillante; longitud de espinas propodeales superiores menor a la distancia entre sus bases . . . . . ***cunicularius***

\- En perfil, el nodo del pecíolo angulado; espinas propodeales inferiores tan anchas como altas, acuminadas; primer tergo gastral con finas lineas anastomizantes bien desarrolladas, mate a débilmente brillante; espinas propodeales superiores más largas que la distancia entre sus bases **8**

8 Dorso promesonotal débilmente rugoreticulado a transversalmente rugoso, rugosidades más fuertes anteriormente; dorso del propodeo consistentemente transversalmente rugoso (**Figura 22C**); cuerpo uniforme marrón claro-rojo . . . . . ***pencosensis***

\- Dorso promesonotal totalmente con rugoreticulacion gruesa; dorso del propodeo rugoreticulado a transversalmente rugoso (**Figura 25C**); cuerpo de dos colores, mesosoma y nodo del pecíolo oscuro anaranjado-marrón a marrón rojizo, resto del cuerpo más claro . . . . . ***serpens***

9 Espinas propodeales superiores ausentes ***o*** forman dentículos o tubérculos pequeños a moderados en tamaño **10**

- Espinas propodeales superiores presente, su longitud generalmente ≥0,5x la distancia entre sus bases **11**

10 Dorso del postpecíolo con rugosidades regulares a transversalmente onduladas . . . . . ***theresiae***

- Dorso del postpecíolo carece de rugosidades transversales . . . . . ***inermis***

11 Espinas propodeales superiores e inferiores largas y puntiagudas; en perfil, superficie posterior del nodo del peciolo con cresta en margen anterior; margen anteroventral del pedúnculo del pecíolo con una espina acuminada; mesosoma con al menos varios pelos largos flexuosos; margen anterior del clípeo con diente mediano minuto (**grupo *sylvestris***). **12**

- Espinas propodeales superiores e inferiores rara vez largas y puntiagudas; en perfil, la cara posterior del nodo del pecíolo rara vez con cresta en el margen anterior; margen anteroventral del pedúnculo de pecíolo recto o con un triangular, nunca con espina puntiaguda; mesosoma rara vez con pelos largos, flexuosos; margen anterior del clípeo sin diente medio diminuto **14**

12 Especies más grandes (AC > 1,55 mm); mandíbula con siete dientes; ojo compuesto sin pelos entre los omatidios; clípeo con carena media prominente; en perfil, el margen anterodorsal de postpecíolo no esta desplazado del helcio . . . . . ***striatinodis***

- Especies más pequeñas (AC < 1,35 mm); mandíbula con seis dientes; ojo compuesto con pelos entre los omatidios; clípeo carece de una carena prominente medial; en perfil, el margen anterodorsal de postpecíolo esta desplazado del helcio **13**

13 Superficie lateral del nodo del pecíolo longitudinalmente rugosa; en perfil, procoxas transversalmente estriadas; femures y tibias lisas o con lineas muy finas y someras anastomisantes, poco brillantes a brillantes; medio del clípeo entre inserciones antenales con 9–12 rugosidades longitudinales, finas, estrechamente espaciadas, interrugosidades mate a débilmente brillante . . . . . ***stefani***

- Superficie lateral del nodo del pecíolo principalmente lisa y brillante; en perfil, procoxas finamente imbricadas; femures y tibias con líneas finas y bien talladas anastomizantes, mate; medio del clípeo entre inserciones antenales con 5–8 rugosidades longitudinales gruesas, a veces onduladas, interrugosidades más o menos brillantes . . . . . ***sylvestris***

14 Los pelos cefálicos (incluyendo el psamóforo) y del mesosoma muy cortos, sus longitudes máximas similar o ligeramente mayor al ancho de las interrugosidades cefálicas (téngase en cuenta que uno a pocos pelos rígidos, gruesos y largos ocasionalmente están juntos al margen posterior de la cabeza y / o pronoto) . . . . . ***tenuipubens***

- Los pelos cefálicos (incluyendo el psamóforo) y del mesosoma moderadamente largas, sus longitudes máximas mucho más largas que el ancho de las interrugosidades cefálicas **15**

15 Dorso del mesosoma y superficie posterior del nodo del peciólo rugoreticulada a vermiculada **16**

- Dorso del mesosomo generalmente rugosa, a veces rugoreticulada a vermiculada; superficie posterior del nodo del peciólo con rugosidades transversales u oblícuas o de otra manera, pero nunca rugoreticulada a vermiculada **17**

16 Un lóbulo pequeño se proyecta dorsalmente del margen anterior de la foseta antenal, mejor visto desde el margen posterior de la cabeza mirando hacia el dorso de los lóbulos laterales del clípeo (**Figura 54A**); en vista dorsal, superficie posterior del nodo del peciólo estrecha, por lo general más o por lo menos tan ancha como la distancia entre las puntas de las espinas propodeales superiores; pelos del mesosoma moderadamente cortos, rara vez algunos más largos >0.7–0.8x DMO . . . . . ***naegelii*** **(parte)**

- Sin un pequeño lóbulo que se proyecta dorsalmente del margen anterior de la foseta antenal (**Figura 54B**); en vista dorsal, superficie posterior del nodo del peciólo más amplia, claramente más ancha que la distancia entre las puntas de las espinas propodeales superiores; pelos del mesosomo más largos, los más largos aproximándose o ligeramente superiores a DMO . . . . . ***abdominalis***

17 Dorso del postpecíolo liso y brillante, granulado, punteada o de otro modo, pero sin rugosidades transversales (rara vez con una a pocas rugosidades longitudinales) **18**

- Dorso del postpecíolo con rugosidades transversales **20**

18 Superficie posterior del nodo del peciólo carece rugosidades o rara vez con pocas rugosidades longitudinales débiles; cabeza y mesosoma generalmente uniformemente marrón oscuro a negro, rara vez con la cabeza negruzca y mesosomo anaranjado; surco metanotal suele estar presente, impreso débil a fuertemente; espinas propodeales inferiores bien desarrolladas, usualmente puntiagudas; espiráculos propodeales circulares . . . . . **grupo *brevibarbis***

- Superficie posterior del nodo del peciólo con rugosidades transversales débiles a moderadamente gruesas; cabeza y mesosoma uniformemente ferruginosa clara a naranja oscura; surco metanotal rara vez presente; espinas propodeales inferiores ausentes a poco desarrolladas; espiráculos propodeales estrechamente ovalados **19**

19 Obreras generalmente más grandes (AC = 1,75–2,05 mm); cuerpo uniformemente naranja ferruginosa a rojizo-anaranjado; los lóbulos frontales son agrandados, sus márgenes laterales convexos, proyectándose fuertemente de manera vertical sobre el dorso cefálico, tanto en vista frontal (**Figura 27A**) como mirando desde el margen posterior de la cabeza sobre el dorso cefálico (**Figura 28A**) . . . . . ***bispinosus***

- Obreras más pequeña (AC = 1,24–1,61 mm); cabeza y mesosoma uniformemente ferruginosa anaranjada, gáster a veces negruzco; los lóbulos frontales son pequeños, sus márgenes laterales semiparalelos, proyectándose casi paralelos al dorso cefálico, tanto en vista frontal (**Figura 35A**) como mirando desde el margen posterior de la cabeza sobre el dorso cefálico (**Figura 28B**) . . . . . ***uruguayensis***

20 Dorso cephálico y mesosoma con rugosidades uniformes y muy próximas entre sí, profundamente talladas, interrugosidades ligeramente más anchas que rugosidades (**Figura 43A–C**); cabeza y mesosoma negros, gáster ferruginoso a naranja oscuro . . . . . ***mendozanus***

- Rugosidades del dorso cefálica y mesosoma más gruesas, onduladas o ligeramente irregulares; rugosidades del mesosoma irregulares o rugoreticuladas a vermiculadas; interrugosidades de la cabeza y mesosoma claramente más amplias que rugosidades (**Figura 38A–C**); color variable, ***pero*** si la cabeza y mesosoma son negras y el gáster naranja oscuro, entonces las interrugosidades del dorso cefálica son fuertemente granulados **21**

21 Interrugosidades del dorso cefálica moderadamente a fuertemente granulados, mates . . . . . **grupo *rastratus* (parte)**

- Interrugosidades del dorso cefálica lisas o con líneas finas anastomizantes, débilmente brillantes a brillantes **22**

22 Cuerpo uniformemente negro exceptuando una banda rojiza oscura que rodea el ojo; rugosidades promesonotales longitudinales y por lo general regulares; rugosidades del margen posteromedio cefálico longitudinales, rara vez rugoreticuladas . . . . . ***tinogasta***

- Cabeza y mesosoma oscuro rojizo-negro, gáster negro; rugosidades promesonotales transversales, oblicuas, o irregulares, rara vez longitudinales; rugosidades del margen posteromedio cefálico generalmente rugoreticuladas parcialmente . . . . . ***laticeps***

23 Cabeza y mesosoma con rugosidades finas y denso, profundamente talladas, semiparalelas a paralelas; margen anteromedio del clípeo con un dentículo . . . . . ***mayri***

- Cabeza y mesosoma con prominente, irregular a regular rugosidades longituinales; margen anterior del clípeo uniforme, sin un dentículo en el medio **24**

24 Dorso del mesosoma y superficie posterior del nodo del pecíolo rugoreticulado a vermiculado. . . . . ***naegelii* (parte)**

- Dorso del mesosoma generalmente rugoso, a veces rugoreticulado a vermiculado; superficie posterior del nodo del pecíolo con rugosidades transversales u oblicuas, o de otra manera, pero nunca rugoreticuladas a vermiculadas . . **grupo *rastratus* (parte)**

Key to queens for *Pogonomyrmex* species occurring in South America (*P. brevibarbis* and *P. rastratus*-groups included but not to species)

1 Ergatoid (wingless) **2**

- Winged (including brachypterous) **10**

2 Queens small (HW < 1.30 mm); mesoscutum, mesoscutellum, and posterior surface of petiolar node rugoreticulate; in profile, mesosoma discontinuous between the metanotum and propodeum . . . . . ***naegelii* (part)**

- Queens larger (HW > 1.40 mm); mesoscutum, mesoscutellum, and posterior surface of petiolar node usually rugose, rarely rugoreticulate; in profile, mesosoma continuous or nearly so between metanotum and propodeum **3**

3 Anterior clypeal margin with small medial tooth; anterior surface of petiolar node striate . . . . . ***mayri***

- Anterior clypeal margin entire, lacking a medial tooth; anterior surface of petiolar node usually smooth and shining, never striate **4**

4 Fine, dense, incised striae (usually longitudinal) cover anterior one-third or more of first gastral tergum . . . . . ***rastratus*-group (part)**

- First gastral tergum smooth and shining to moderately coriarious, weakly shining, lacking striae except occasionally at base **5**

5 Queens larger (HW > 2.40 mm); in dorsal view, petiolar node only slightly longer than wide, anterior margin broadly rounded; in dorsal view, postpetiole wider than long . . . . . ***bispinosus***

- Queens smaller (HW < 2.35 mm); in dorsal view, petiolar node notably longer than wide, anterior margin spatulate to angulate; in dorsal view, postpetiole longer than wide **6**

6 Eyes large (OI > 27.5); posterior surface of petiolar node and dorsum of postpetiole weakly coriarious, posterior surface of petiolar node sometimes with few longitudinal rugae; in profile, apex of petiolar node usually angulate with a small crest along anterior margin; propodeal spiracles circular or nearly so . . . . . ***brevibarbis*-group (part)**

- Eyes small (OI < 26.0); posterior surface of petiolar node and/or dorsum of postpetiole with transverse rugae; in profile, apex of petiolar node usually rounded to subangulate and lacking a small crest along anterior margin; propodeal spiracles narrowly ovate **7**

7 Anterior margin of clypeus concave; gaster blackish to black; psammophore well-developed, consisting of long hairs along basolateral margin of head . . . . . ***laticeps* (part)**

- Anterior margin of clypeus flat to weakly convex; gaster tannish-brown, reddish-brown, or brown; psammophore poorly-developed, consisting of short to medium-length hairs scattered across ventral side of head (***cunicularius*-group**) **8**

8 In profile, petiolar node rounded; inferior propodeal spines wider than high, broadly rounded; first gastral tergum smooth and polished, strongly shining . . . . . ***cunicularius***

- In profile, petiolar node angulate; inferior propodeal spines about as wide as high, acuminate; first gastral tergum moderately to strongly coriarious, dull to weakly shining **9**

9 Sculpturing on dorsum of mesosoma and posterior surface of petiolar node weak to moderately strong, irregularly rugose to moderately rugoreticulate; body concolorous tannish-red . . . . . ***pencosensis***

- Sculpturing on dorsum of mesosoma and posterior surface of petiolar node coarse, rugoreticulate to vermiculate; bicolored, mesosoma and petiolar node medium to dark orangish-brown to reddish-brown, rest of body lighter . . . . . ***serpens***

10 Queens small (HW < 1.35 mm); psammophore poorly-developed, consisting of scattered short hairs on ventral side of head **11**

- Queens larger (HW > 1.40 mm); psammophore well-developed, consisting of numerous, long hairs along basolateral margin of head **12**

11 Cephalic dorsum, mesoscutum, mesoscutellum, and posterior surface of petiolar node at least partly rugoreticulate to vermiculate; hairs short, all hairs on mesosoma, posterior surface of petiolar node, dorsum of postpetiole, and gaster shorter than MOD . . . . . ***naegelii* (part)**

- Cephalic dorsum, mesoscutum, and mesoscutellum with regular to weakly irregular longitudinal rugae, posterior surface of petiolar node granulate-punctate; hairs longer, longest hairs on mesosoma, posterior surface of petiolar node, dorsum of postpetiole, and gaster >MOD . . . . . ***abdominalis***

12 Fine, dense, incised striae (usually longitudinal) cover anterior one-third or more of first gastral tergum . . . . . ***rastratus*-group (part)**

- First gastral tergum smooth and shining to moderately coriarious, weakly shining, lacking striae except occasionally at base .

. . . . . **13**

13 Queen larger (HW > 2.90 mm); cephalic dorsum with scattered foveae (use >50x magnification) (**Figures 4A, 9A**); part to all of cephalic dorsum with longitudinal striae (**Figures 4A, 9A**); antennal scapes short, extending beyond eye less than one-third the distance from posterior margin of eye to posterior corner of head (***coarctatus*-group**) **14**

- Queens small (HW < 2.70 mm); cephalic dorsum lacking scattered foveae (**Figures 36A, 44A, 48A**); cephalic dorsum with prominent longitudinal rugae (**Figures 36A, 44A, 48A**); antennal scapes longer, extending beyond eye by more than one-half the distance from posterior margin of eye to posterior corner of head **17**

14 Fine striae cover only part of cephalic dorsum, areas lacking striae shining to strongly shining. **15**

- Fine striae cover cephalic dorsum, entire dorsum weakly shining **16**

15 Queens larger (HW > 3.6 mm); cephalic dorsum mostly lacking fine striae; inferior propodeal spines poorly-developed, wider than tall, broadly rounded . . . . . ***coarctatus***

- Queens smaller (HW < 3.1 mm); most of cephalic dorsum covered by moderately dense striae; inferior propodeal spines well-developed, triangular, apex bluntly angulate to acuminate . . . . . ***marcusi***

16 In profile, lateral lobe of clypeus massively enlarged with narrow gap (much less than width of antennal scape) between clypeal lobe and frontal lobe; concolorous ferruginous orange to orange-red. . . . . ***lobatus***

- In profile, lateral lobe of clypeus not enlarged with broad gap (similar to width of antennal scape) between clypeal lobe and frontal lobe; bicolored, head dark red to reddish-black, gaster blackish . . . . . ***micans***

17 Brachypterous; in dorsal view, pronotum large and well-developed; mesoscutum poorly-developed, anterior margin barely surpassing humeral shoulders of pronotum; in profile, the pronotum rises at an approximately 45° angle to meet the mesoscutum. **18**

- Wings fully-developed; in dorsal view, pronotum small, poorly-developed; mesoscutum well-developed, anterior margin extending to or near pronotal collar; in profile, the pronotum rises nearly vertically to meet the mesonotum **20**

18 Gaster dark ferruginous orange . . . . . ***mendozanus***

- Gaster black. **18**

19 Head and mesosoma dark reddish-black, gaster black . . . . . ***laticeps* (part)**

- Concolorous black except for reddish area encircling eye . . . . . ***tinogasta***

20 Posterior surface of petiolar node and dorsum of postpetiole smooth and shining to moderately coriarious, weakly shining, rarely with few longitudinal or transverse rugae; head, mesosoma, and gaster concolorous dark brown to black; inferior propodeal spines well-developed, acuminate; propodeal spiracles circular or nearly so . . . . . ***brevibarbis*-group (part)**

- Posterior surface of petiolar node and usually dorsum of postpetiole with numerous transverse rugae; color variable, usually orangish or orange and black but never concolorous dark brown to black; inferior propodeal spines poorly-developed, tips usually subangulate to broadly rounded; propodeal spiracles narrowly ovate **21**

21 Transverse rugae cover dorsum of postpetiole; lateral margins of propodeal declivity lacking numerous fine, delicate hairs . . . . . ***rastratus*-group (part)**

- Transverse rugae on dorsum of postpetiole lacking, discontinuous, or only present on lateral margins, faint to absent medially; numerous fine, delicate hairs usually present along lateral margin of propodeal declivity **22**

22 Superior propodeal spines present . . . . . ***uruguayensis***

- Superior propodeal spines absent . . . . . ***inermis***

Pogonomyrmex de Sur América; clave a las especies basada en las reinas (grupos *P. brevibarbis* and *P. rastratus* incluido pero no a las especies)

1 Ergatoide (áptera) **2**

- Con alas (incluyendo formas braquípteras). **10**

2 Hembras pequeñas (AC < 1,30 mm); mesoscuto, escutelo y superficie posterior del nodo del pecíolo rugoreticulado; mesosoma de perfil presenta una discontinuidad entre el metanoto y propodeo . . . . . ***naegelii* (parte)**

- Hembras más grandes (AC > 1,40 mm); mesoscuto, escutelo y superficie posterior del nodo del pecíolo generalmente arrugado, rara vez rugoreticulado; mesosoma de perfil continua, o casi, entre metanoto y propodeo **3**

3 Margen anteromedio del clípeo con diente pequeño; superficie anterior del nodo del pecíolo estriado . . . . . ***mayri***

- Margen anteromedio del clípeo entero, sin diente; superficie anterior del nodo del pecíolo generalmente lisa y brillante, nunca estriado **4**

4 Estrías finas y densas, talladas (generalmente longitudinales) cubren la tercera parte anterior, o más, del primer tergo gastral. . . . . **grupo *rastratus* (parte)**

- Primer tergo gastral liso y brillante o con finas líneas anastomizantes, poco brillante, sin estrías excepto ocasionalmente en la base **5**

5 Hembras más grandes (AC > 2,40 mm); el nodo del pecíolo en vista dorsal ligeramente más largo que ancho, su margen anterior ampliamente redondeado; postpecíolo más ancho que largo en vista dorsal . . . . . ***bispinosus***

- Hembras pequeñas (AC < 2,35 mm); el nodo del pecíolo notablemente más largo que ancho en vista dorsal, su margen anterior espatulado a angulado; postpecíolo más largo que ancho en vista dorsal **6**

6 Ojos grandes (IO > 27,5); superficie posterior del nodo del pecíolo y el dorso de postpecíolo con débiles líneas anastomizantes, pecíolo a veces con pocas arrugas longitudinales; ápice del nodo del pecíolo de perfil generalmente angular con una pequeña cresta a lo largo del margen anterior; espiráculo propodeal aproximadamente circular. . . . . **grupo *brevibarbis* (parte)**

- Ojos pequeños (IO < 26,0); superficie posterior del nodo del pecíolo y / o dorso de postpecíolo con arrugas transversales; el

ápice del nodo del pecíolo de perfil normalmente redondeado a semi-angular y sin una pequeña cresta a lo largo del margen anterior; espiráculo propodeal estrechamente ovalado **7**

7 Margen anterior del clípeo cóncavo; gáster negruzco a negro; psamóforo bien desarrollado, con pelos largos a lo largo del margen basolateral de la cabeza . . . . . ***laticeps* (parte)**

- Margen anterior del clípeo recto a ligeramente convexo; gáster marrón claro, marrón rojizo o marrón; psamóforo con poco desarrollado, los pelos cortos a mediano y esparcidos por la parte ventral cefálica (**grupo *cunicularius***) **8**

8 De perfil, el nodo del pecíolo es redondeado; espinas propodeales inferiores mas anchas que altas, ampliamente redondeados; primer tergo gastral liso y pulido, fuertemente brillante . . . . . ***cunicularius***

- De perfil, el nodo del pecíolo angulado; espinas propodeales inferiores tan anchas como altas, puntiagudas; primer tergo gastral con líneas finas anastomizantes moderadamente a fuertemente talladas, brillo mate a débilmente resplandeciente **9**

9 Esculpido del dorso mesosomal y superficie posterior del nodo del pecíolo débil a moderadamente fuerte, rugoso e irregular a moderadamente rugoreticulado; cuerpo uniformemente marrón claro a rojo . . . . . ***pencosensis***

- Esculpido del dorso mesosomal y superficie posterior del nodo del pecíolo grueso, rugoreticulado a vermiculado; cuerpo de dos colores, mesosoma y superficie posterior del nodo peciolar de medio a oscuro un anaranjado-marrón claro u oscuro hasta marrón rojizo, el resto del cuerpo más claro . . . . . ***serpens***

10 Hembras pequeña (AC < 1,35 mm); psamóforo con poco desarrollado, que consiste de pelos cortos dispersos en el lado ventral de la cabeza **11**

- Hembras más grande (AC > 1,40 mm); psamóforo bien desarrollado, que consiste de numerosos pelos largos a lo largo de margen basolateral de la cabeza **12**

11 Dorso cefálico, mesoscuto, mesoscutelo y la superficie posterior del nodo del pecíolo por lo menos parcialmente rugoreticulada a vermiculada; pelos cortos, todos los pelos del mesosoma, superficie posterior del nodo peciolar, dorso de postpecíolo y gáster más corto que DMO . . . . . ***naegelii* (parte)**

- Dorso cefálico, mesoscuto y mesoscutelo con arrugas longitudinales irregulares discernibles a débiles, superficie posterior del nodo del pecíolo granular-punteado; pelos más largos, los pelos más largos del mesosoma, de la superficie posterior del nodo del pecíolo, del dorso de postpecíolo y gáster >DMO . . . . . ***abdominalis***

12 Estrías finas y densas (generalmente longitudinales) y talladas cubren la tercera parte anteior o mas del primer tergo gastral . . . . . **grupo *rastratus* (parte)**

- Primer tergo gastral liso y brillante o con líneas finas anastomizantes, poco brillante, sin estrías excepto ocasionalmente en la base **13**

13 Hembras más grandes (AC > 2,90 mm); dorso cefálico con fosetas dispersas (use aumentos >50x) (**Figuras 4A, 9A**); parte a todo el dorso cefálico con estrías longitudinales (**Figuras 4A, 9A**); escapos antenales cortos, que se extiende menos de un tercio de la distancia desde el margen posterior del ojo a la esquina posterior de la cabeza (**grupo *coarctatus*)** **14**

- Hembras pequeñas (AC < 2,70 mm); dorso cefálico sin fosetas dispersas (**Figuras 43A, 47A**); dorso cefálico con prominentes arrugas longitudinales (**Figuras 43A, 47A**); escapos antenales más largos, que se extiende más de la mitad de la distancia desde el margen posterior del ojo a la esquina posterior de la cabeza **17**

14 Sólo una parte del dorso cefálica cubierto por estrías finísimas, zonas sin estrías brillantes a fuertemente brillantes **15**

- Dorso cefálico cubierto por estrías finísimas, todo el dorso débilmente brillante **16**

15 Hembras más grandes (AC > 3,6 mm); mayor parte del dorso cefálica sin finas estrías; espinas propodeales inferiores poco desarrolladas, más anchas que altas, ampliamente redondeadas. . . . . ***coarctatus***

- Hembras pequeñas (AC < 3,1 mm); la mayor parte del dorso cefálica cubiertos por estrías moderadamente densas; espinas propodeales inferiores bien desarrolladas, triangulares, sus ápices puntiagudos o forma de ángulo romo . . . . . ***marcusi***

16 De perfil, lóbulo lateral del clípeo muy engrosado, con una estrecha brecha (mucho menor que el ancho del escapo) entre el lóbulo del clípeo y el lóbulo frontal; uniformemente anaranjado ferruginoso a naranja-rojo . . . . . ***lobatus***

- De perfil, lóbulo lateral del clípeo no engrosado y con una amplia brecha (similar al ancho del escapo) entre el lóbulo de clípeo y el lóbulo frontal; cuerpo de dos colores, cabeza rojo oscuro a rojizo-negro, gáster negruzco. . . . . ***micans***

17 Braquípteros; en vista dorsal, pronoto grande y bien desarrollado; mesoscuto poco desarrollado, su margen anterior apenas supera los "hombros" del húmero de pronoto; de perfil el pronoto se eleva formando un ángulo de aproximadamente 45º para unirse con el mesoscuto. **18**

- Alas completamente desarrolladas; en vista dorsal, pronoto pequeño, con poco desarrollado; mesoscuto bien desarrollado, su margen anterior se extiende hasta o cerca del cuello pronotal; de perfil el pronoto se eleva casi verticalmente para unirse con el mesoscuto **20**

18 Gáster naranja pardo oscuro . . . . . ***mendozanus***

- Gáster negro **19**

19 Cabeza y mesosoma oscuro rojizo-negro, gáster negro . . . . . ***laticeps* (parte)**

- Cuerpo concoloros negro excepto la zona que rodea el ojo rojizo . . . . . ***tinogasta***

20 Superficie posterior del nodo del pecíolo y dorso del postpecíolo liso y brillante o con fina líneas anastomizantes moderadamente, con poco resplandor, raramente con algunas arrugas longitudinales o transversales; cabeza, mesosoma y gáster uniformemente marrón oscuro a negro; espinas propodeales inferiores bien desarrolladas, puntiagudas; espiráculos propodeales circulares o ampliamente ovaladas . . . . . **grupo *brevibarbis* (parte)**

- Superficie posterior del nodo del pecíolo y generalmente el dorso del postpecíolo con numerosas arrugas transversales; color variable, generalmente anaranjado o naranja y negro pero nunca uniformemente marrón oscuro a negro; espinas propodeales inferiores poco desarrolladas, sus ápices generalmente subangulares a redondeadas; espiráculos propodeales estrechamente ovaladas **21**

21 Dorso de postpecíolo cubierto por arrugas transversales; márgenes laterales de la declividad propodeal sin numerosos pelos

bien delicados . . . . . .**grupo *rastratus* (parte)**
- Arrugas transversales en el dorso de postpecíolo ausentes, discontinuas, o sólo presentes en los márgenes laterales, débil o ausente medialmente; numerosos pelos finos y delicados normalmente presentes a lo largo del margen lateral de la declividad del propodeo **22**

22 Espinas propodeales superiores presentes. . . . . ***uruguayensis***
- Espinas propodeales superiores ausentes . . . . . ***inermis***

For species in which males are known I provide a brief diagnosis using salient characters, measurements, and photos.

SPECIES ACCOUNTS

Pogonomyrmex coarctatus-group

Workers in the *P. coarctatus*-group are diagnosed by the following characters: (1) first gastral tergum lacking striae, (2) large (HW = 1.97–3.99 mm), sometimes polymorphic, (3) numerous small, hair-bearing foveae scattered across cephalic dorsum (best viewed at >50x magnification) (**Figures 3A, 8A**), (4) part to all of cephalic dorsum with very fine, dense, longitudinal striae, (5) antennal scapes short, extending less than one-third the distance from posterior margin of eye to posterior corner of head, and (6) posterolateral margin of head with a carina that is much coarser than rugae on cephalic dorsum. All of these characters also diagnose queens, which are larger than those of all South American congeners (HW = 2.91–4.06 mm).

Pogonomyrmex coarctatus

(Figures 2–5)

Pogonomyrmex coarctatus Mayr, 1868: 170 (worker). Syntypes examined: 2 workers [NMW], ARGENTINA, Buenos Aires: Bahía Blanca (Strobel leg.); Mayr, 1887: 614 (queen); Bruch, 1917: 303, figs. 1, 2 (male). See also Gallardo, 1932: 150, figs. 33–36. NMW worker here designated **LECTOTYPE** [CASENT0173362].

Pogonomyrmex coarctatus Mayr var. *striaticeps* Emery, 1906: 157 (worker, in footnote). Syntypes examined: 3 workers [MACN], ARGENTINA, Santa Fe: Rosario, #1609 (Hubrich leg.); Kusnezov, 1951: 253 (synonomy under *coarctatus*; here confirmed). See also Gallardo, 1932: 156, figs. 37–38. MACN worker here designated **LECTOTYPE** [CASENT0249049].

Pogonomyrmex coarctatus race *bruchi* Forel, 1913: 217 (worker). Syntypes examined: 3 workers [MHNG], ARGENTINA, Buenos Aires: Bahía Blanca, Puerto Militar (Ingenieur Zelenka leg., 19 November 1913); 2 workers [MHNG], Buenos Aires: Estación Verónica, south of La Plata (Schuel leg.); 1 worker [MLPA], Buenos Aires. MHNG worker from Bahía Blanca here designated **LECTOTYPE** [CASENT0173345]. **NEW SYNONOMY**

Pogonomyrmex bruchi: Forel, 1914: 268, raised to species. See also Gallardo, 1932: 157, fig. 39.

Worker. Diagnosis. Within the *P. coarctatus*-group, the combination of: (1) strongly polymorphic with supermajors, (2) very fine longitudinal striae cover most of the cephalic dorsum, areas lacking rugae weakly shining to shining, (3) in profile, lateral lobe of clypeus not enlarged with wide gap between clypeal lobe and frontal lobe (gap width similar to width of antennal scape), (4) interrugae on mesosoma weakly to moderately granulate, weakly shining, (5) weak to moderately coarse rugae on posterior surface of petiolar node, (6) rugae on dorsum of postpetiole lacking or with weak transverse rugae near posterior margin, (7) inferior propodeal spines lacking or very reduced in size and broadly rounded, and (8) body mostly concolorous reddish-orange to reddish-brown uniquely characterize this species (**Figures 2–3**).

Measurements—lectotype (n = 41). HL 3.37 (1.94–3.54); HW 3.66 (1.97–3.99); MOD 0.63(0.39–0.63); OMD 0.74 (0.42–0.94); SL 1.79 (1.28–2.10); PNW 1.97 (1.28–2.29); HFL 2.77 (1.75–2.90); ML 3.27 (2.20–3.54); PW 0.84 (0.43–0.95); PPW 0.98 (0.64–1.20). Indices: SI 48.91 (51.13–67.50); CI 108.61 (100.50–115.31); OI 17.21 (13.93–21.61); HFI 75.68 (71.57–91.88).

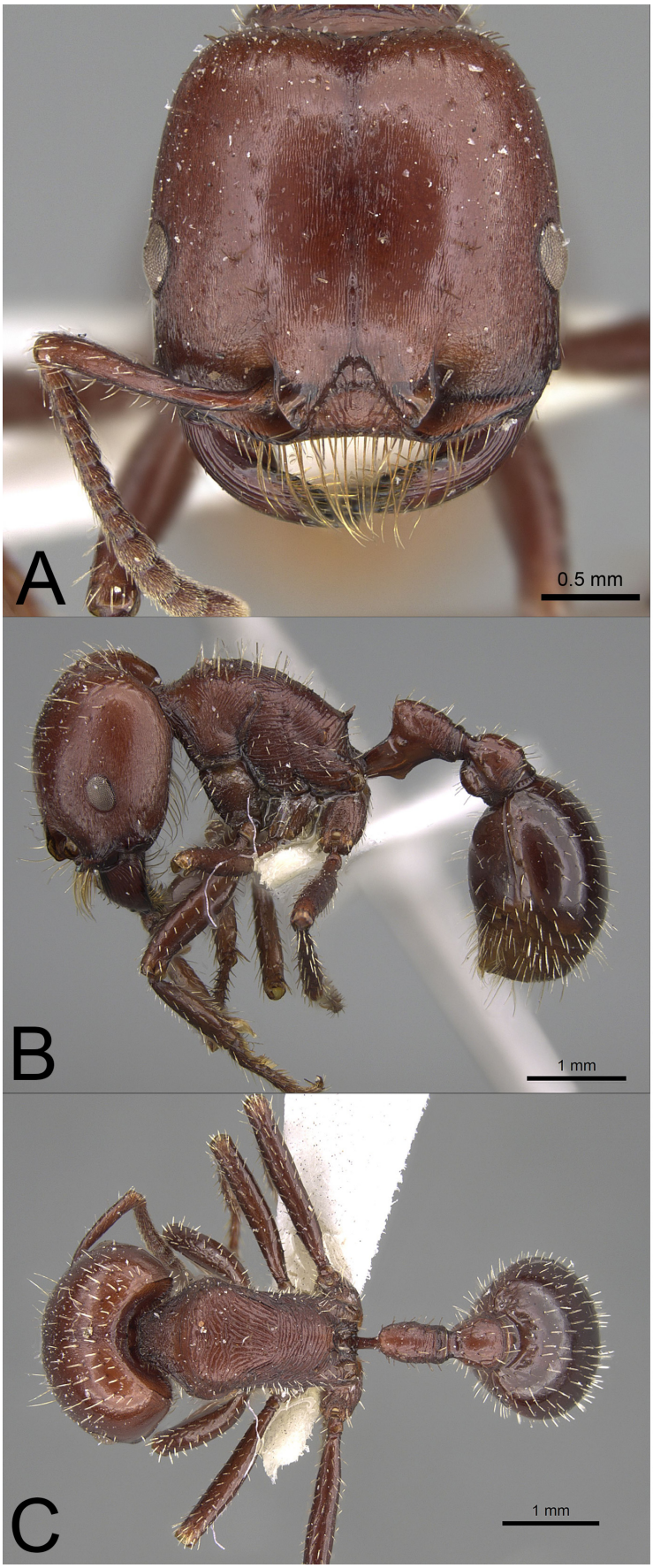

FIGURE 2. Photograph of *Pogonomyrmex coarctatus* Mayr minor worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0914114)**.** Photographs by Michele Esposito from www.AntWeb.org**.**

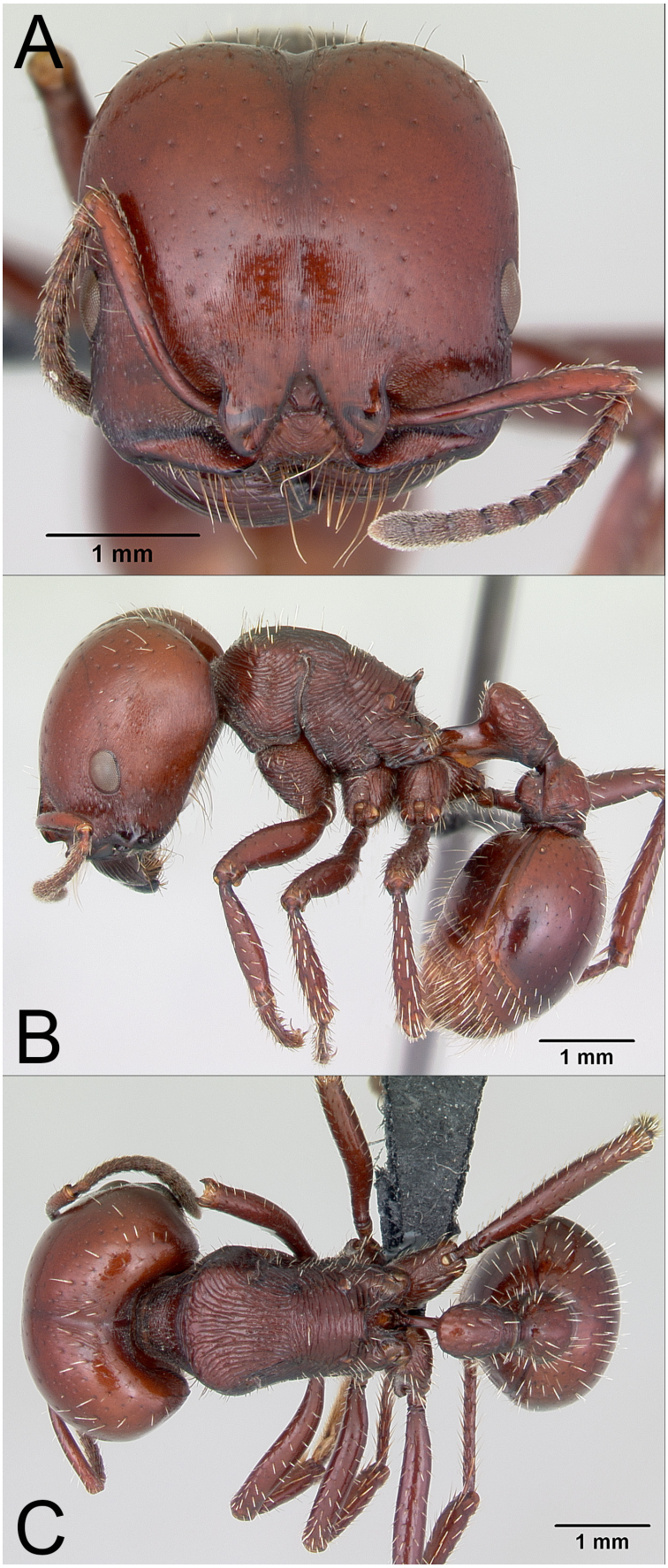

FIGURE 3. Photograph of *Pogonomyrmex coarctatus* Mayr supermajor worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0172632)**.** Photographs by April Nobile from www.AntWeb.org**.**

Redescription. Highly polymorphic with supermajors. Head shape varies with worker size, quadrate in minors, increasingly wider than long in majors and supermajors (CI = 100.5–115.3, positively associated with head width, $n = 42$, $R^2 = 0.69$, $P < 0.0001$; CI = 4.92*HW + 92.29); posterior margin concave medially in full-face view. Longitudinal cephalic striae very fine and dense, covering part to most of head but often indistinct, width of striae and interstriae similar; in full-face view, medial striae not diverging toward posterior corners of head. Cephalic interstriae weakly shining to shining. Vertex weakly striate, weakly shining to smooth and shining. Anterior margin of clypeus flat to weakly concave; dorsal surface with several moderately coarse, subparallel, longitudinal, oblique, or arcuate rugae. In profile, lateral lobe of clypeus not enlarged with wide gap between clypeal lobe and frontal lobe (gap width similar to width of antennal scape). Numerous long, curved, bristle-like, yellowish macrochaetae project from anterior margin of clypeus and ventral side of mandibles. Mandible with six teeth; mandibular dorsum coarsely rugose. MOD ranging from 0.15–0.23x HL. In profile, eyes situated anterior to middle of head, OMD = 1.00–1.58x MOD. Antennal scapes short (SI = 48.91–70.92), extending less than one-third the distance from posterior margin of eye to posterior corner of head. Base of antennal scapes smooth and shining, distal portion sometimes weakly granulate or weakly striate, weakly shining to shining; basal flange well-developed with carinate margin. Psammophore well-developed.

Mesosomal profile weakly to moderately convex; all mesosomal surfaces with prominent coarse, subparallel, weakly wavy to irregular, widely-spaced rugae. In dorsal view, humeral shoulders of pronotum weakly rounded to knoblike. Dorsum of promesonotum with longitudinal rugae that diverge anterad toward humeral shoulders of pronotum; transverse rugae on anterior surface of pronotum continue obliquely or longitudinally on pronotal sides; rugae on mesopleura angle posterodorsally. Superior propodeal spines moderately long, acuminate, connected by well-defined keel; spine length less than width between their bases; regular to weakly wavy transverse rugae on propodeal dorsum traverse ventrally or anteroventrally on sides. Inferior propodeal spines absent or very reduced in size, broadly rounded. Propodeal spiracles narrowly ovate facing posterad. Interrugae on mesosoma moderately granulate, weakly shining. Legs weakly granulate, weakly shining to smooth and strongly shining.

Peduncle of petiole about 0.7x as long as petiolar node, anteroventral margin with broadly rounded process. In profile, posterior surface of petiolar node weakly convex; node asymmetrical with anterior surface shorter than posterior surface, apex rounded. In dorsal view, petiolar node longer than wide, sides subparallel, slightly wider near middle, narrowing to spatulate to rounded anterior margin. Sides and posterior surface of petiolar node mostly smooth or with weak to moderately coarse, wavy to irregular, transverse, oblique, or longitudinal rugae, weakly shining. Dorsum of postpetiole convex in profile; in dorsal view, widest near posterior margin, narrowing to anterior margin, maximum width about equal to length; weakly to moderately granulate-punctate, occasionally with weak transverse rugae near posterior margin, weakly shining. First gastral tergum moderately coriarious, weakly shining to shining.

Erect white to yellowish pilosity sparse to moderately abundant on head, mostly similar in length, arising from foveae; longest hairs not exceeding MOD, few >0.5x MOD. Moderately abundant suberect pilosity on scape; abundant decumbent hairs on funicular segments. Legs with moderately abundant suberect to decumbent setae. Mesosoma with moderately dense erect setae that are mostly similar in length, longest approaching MOD; petiolar node, postpetiole, first gastral tergum with moderately dense erect setae that are mostly similar in length, longest notably shorter than MOD; long hairs on margins of posterior gastral terga often >MOD. Body mostly concolorous reddish-orange to reddish-brown (**Figures 2–3**).

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) large size (HW > 3.65 mm), (3) striae mostly lacking on cephalic dorsum, (4) inferior propodeal spines poorly-developed, wider than high, broadly rounded, and (5) body mostly concolorous reddish-orange to reddish-brown (**Figure 4**).

Measurements—(n = 12). HL 3.35–3.61; HW 3.69–4.06; MOD 0.55–0.64; OMD 0.69–0.86; SL 1.79–2.09; PNW 2.21–2.49; HFL 2.42–2.89; ML 3.73–4.29; PW 1.01–1.20; PPW 1.37–1.49. Indices: SI 45.43–55.03; CI 107.93–114.87; OI 14.21–16.93; HFI 61.42–74.04.

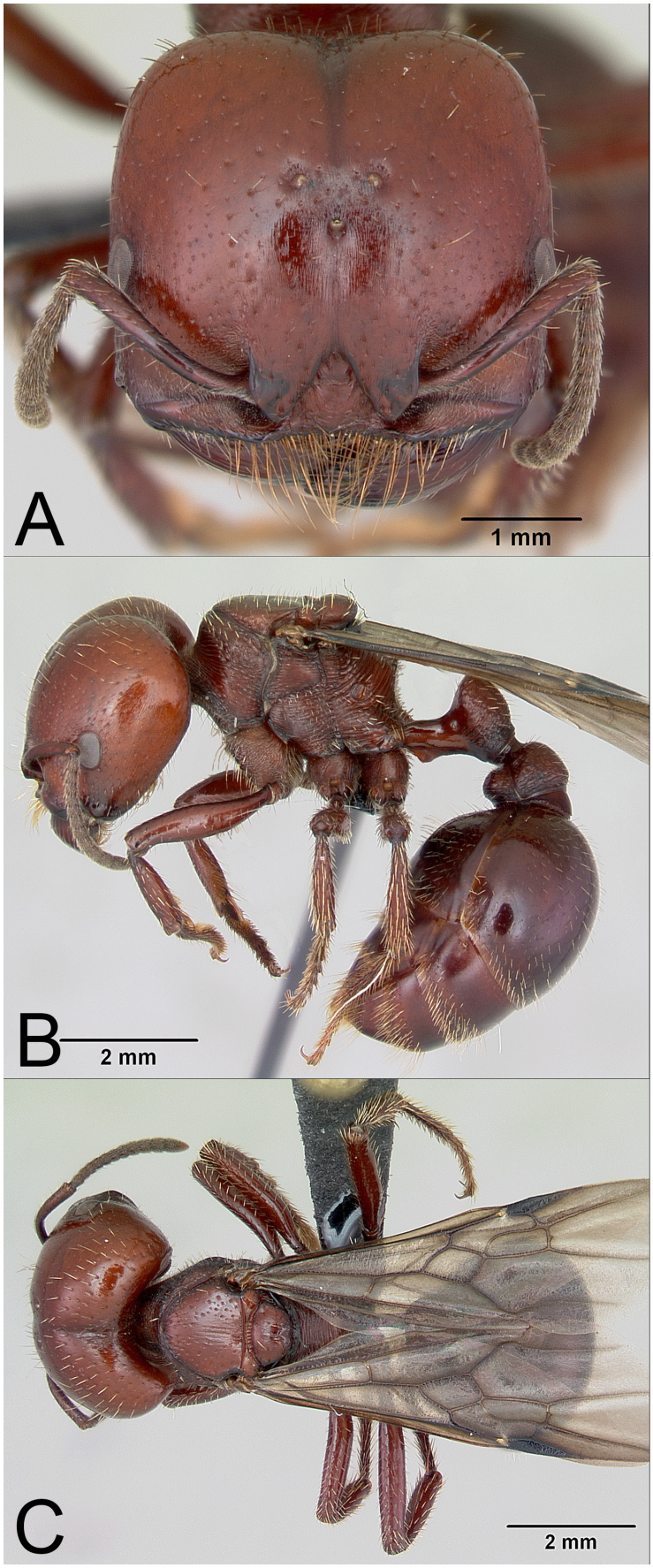

FIGURE 4. Photograph of *Pogonomyrmex coarctatus* Mayr alate queen: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0172633)**.** Photographs by April Nobile from www.AntWeb.org**.**

Male. Diagnosis. This caste is diagnosed by: (1) first gastral tergum lacking striae, (2) large (HW > 1.75 mm; HL > 1.70 mm; ML > 3.20 mm), (3) hairs on head (especially posterior to eyes) and dorsum of mesosoma moderately dense, moderately long and flexuous, longest hairs rarely >0.5–0.8x MOD, (4) transverse rugae on dorsum of postpetiole weak, restricted to posterior margin, anterad portion strongly coriarious, dull, (5) rugae posterior to eyes and ocelli absent or weak, and (6) at least one and usually both mandibles with three teeth (**Figure 5**).

Measurements—(*n* = 12). HL 1.70–2.04; HW 1.79–2.05; MOD 0.58–0.73; OMD 0.19–0.36; SL 0.44–0.57; HFL 2.05–2.45; ML 3.21–3.78; PW 0.72–0.80; PPW 0.88–0.99. Indices: SI 23.23–29.38; CI 99.50–110.00; OI 32.22–36.87; HFI 103.02–131.11.

Additional material examined. ARGENTINA: ***Buenos Aires***: Reserva Otamendi, 50', Jan 21, 1999 & Nov 13, 2003 (CASC; CSC; RAJC); Tandil, Nov 20, 1959 (FML; LACM; MACN); Patagones, Jan 9, 1950 (FML); Bahía Blanca, Jan 3, 1964 & no date (MACN; MHNG; MZUSP; NMW); Medanos, Feb 4, 1938 (MLPA); San José Libertad, no date (MACN; MLPA); Azul, Apr 26, 1962 (USNM); Rosas, no date (USNM); Sierra Bayas, no date (LACM; MACN); Punta Picada, no date (MACN); Puerto Militar, no date (MACN); Punta Piedras, no date (MACN); Sierra de la Ventana, Nov 19, 2005 & no date (CSC; MACN; MCZ; MLPA); Coronel Suárez, Mar 1920 (MACN); Tres Arroyos, Mar 31, 1938 (MLPA); Monte Hermoso, no date (MACN; MLPA); Rt 33 at 14 km N Bahía Blanca, Nov 20, 2005 (CSC); 15 km SE Olavarría, Nov 18, 2005 (CSC); 32 km S Pehuajó, Nov 19, 2005 (CSC); Tornquist, Feb 7, 1947 (FML); no loc, no date (MACN; MLPA). ***Córdoba***: Rt 9 at 6.5 mi E Bell Ville, 390', Dec 21, 2005 (CSC; RAJC); Nono, 2940', Jan 17, 2008 (RAJC); Rt 20 at 1.0 km N Nono, 2920', Jan 23, 2006 (RAJC); Rt 9 at 3.5 km E Marcos Juárez, 330', Jan 14, 2010 (RAJC); Alta Gracia La Granja, Sierras Córdoba, no date (MACN); Unguillo, no date (MLPA); no loc, no date (MACN). ***Entre Ríos***: Parque Nacional El Palmar, Jan 6, 2006 (RGPC); Gualeguay, no date (MACN); Diamante, Mar 29, 1918 (MACN); San José de Feliciano, Dec 1972 (MACN); Rt 14 at 5.1 mi N Gualeguychú, 60', Dec 17, 2005 (RAJC); Rt 39 at 36.1 km SE Basavilbaso, 160', Feb 13, 2010 (RAJC); Estancia Sosa, no date (MACN; MLPA; USNM); La Picada, May 24, 1951 (FML; MCZ; MZUSP; USNM); 10.3 km S Jct Rts 14 & 39, 60', Dec 17, 2005 (RAJC); Jct Rts 14 & 130, 70', Dec 18, 2005 (CASC; MCZ; RAJC); Rt 16 at 6.1 km E Larroque, 190', Jan 13, 2010 (RAJC); Rt 14 at 13.0 km N Ubajuay, 70', Dec 18, 2005 (RAJC); Rt 18 at 7.3 mi SW San Salvador, 220', Dec 19, 2005 (RAJC); Rt 18 at 20 km E Villaguay, 160', Dec 19, 2005 (RAJC); Villaguay, 200', Dec 19, 2005 (RAJC); Rt 18 at 3.3 mi NW Villaguay, 210', Dec 19, 2005 (RAJC); Rt 18 at 12.8 mi W Villaguay, 150', Dec 20, 2005 (RAJC); Rt 18 at 33.9 mi W Villaguay, 320', Dec 20, 2005 (CSC; RAJC); Rt 127 at 2.0 km SW Federal, 230', Jan 13, 2011 (RAJC); Polideportive Municipal General San Martín, Oct 28, 1954 (FML); Arroyo Tres Sauces, Jun 3, 1951 (FML); no loc, no date (USNM). ***La Pampa***: Rt 188 at 28.1 km W Rancul, 950', Jan 27, 2008 (RAJC); Monte Nievas, no date (MACN; USNM); Río Colorado, no date (MACN; MLPA); central La Pampa, no date (MACN). ***Río Negro***: 35.6 km NW Jct Rts 251 & 2, 360', Jan 22, 2011 (RAJC); Rt 22 at 15 km E Choele Choel, 400', Jan 22, 2011 (RAJC); Rt 251 at 16.6 km N General Conesa, 390', Jan 21, 2011 (RAJC); Rt 251 at 9.7 km S General Conesa, 230', Jan 21, 2011 (RAJC); Sauce Blanco, no date (FML; LACM; MCZ; MZUSP); 51 km E Río Colorado, Nov 20, 2005 (CSC); no loc, no date (MACN; MLPA). ***San Luis***: Cortaderas, Jan 29, 1958 (FML; LACM). ***Santa Fe***: Rt 19 at 14.5 mi W Santa Clara de Buen Vista, 240', Dec 20, 2005 (CSC; RAJC); Rt 34 at Cañada Rosquín, 230', Dec 21, 2005 (CSC; RAJC); Rosario, no date (MACN); Fives Lille, no date (MCZ); Saladillo, no date (USNM). **URUGUAY**: no loc, no date (MCZ; MLPA; USNM). ***Florida***: Florida, Jan 1952 (FML). ***Lavelleja***: Villa Serrana, Jun 7, 1961 (USNM); Arequita, Jan 6, 1951 (FML). ***Maldonado***: Maldonado, Feb 15, 1960 (FML). ***Montevideo***: Montevideo, no date (MACN); near Montevideo, Feb 20, 1976 (LACM). ***Treinta y tres***: Santa Clara de Olimar, Jan 9, 1960 (FML). ***Locations not found.*** **ARGENTINA:** ***Buenos Aires***: Tuzumba, no date (MLPA); Punta dellnolio (?), Dec 1, 1957 (USNM). ***Río Negro:*** Menatia, Oct 2, 1914 (MLPA). **URUGUAY:** ***Canelones***: Crizicon Falzon, no date (MLPA). ***Paysandú***: Rt 30, km 476, Feb 25, 1961 (FML). ***Río Negro***: Rt 24, Feb 25, 1961 (FML). ***Depto Unknown***: Rt 2, km 214, Feb 26, 1961 (FML); C Mazangano, km 20, no date (FML); C de Amaro, Rt 8, Feb 18, 1961 (FML). ***Questionable locales*** **(appear to be outside of geographic range): ARGENTINA:** ***Catamarca***: central Catamarca, no date (MACN). ***Mendoza***: no loc, no date (MACN) (**Figure 6A**).

Etymology. Mayr (1868) did not discuss the naming of this species, and his reasoning for this name is unclear. The epithet *coarctatus* (from Latin, *coarct* = compressed, confined, or drawn close together, and *–atus* = suffix to denote provided with) apparently refers to an unknown structure that Mayr determined to be compressed or drawn close together.

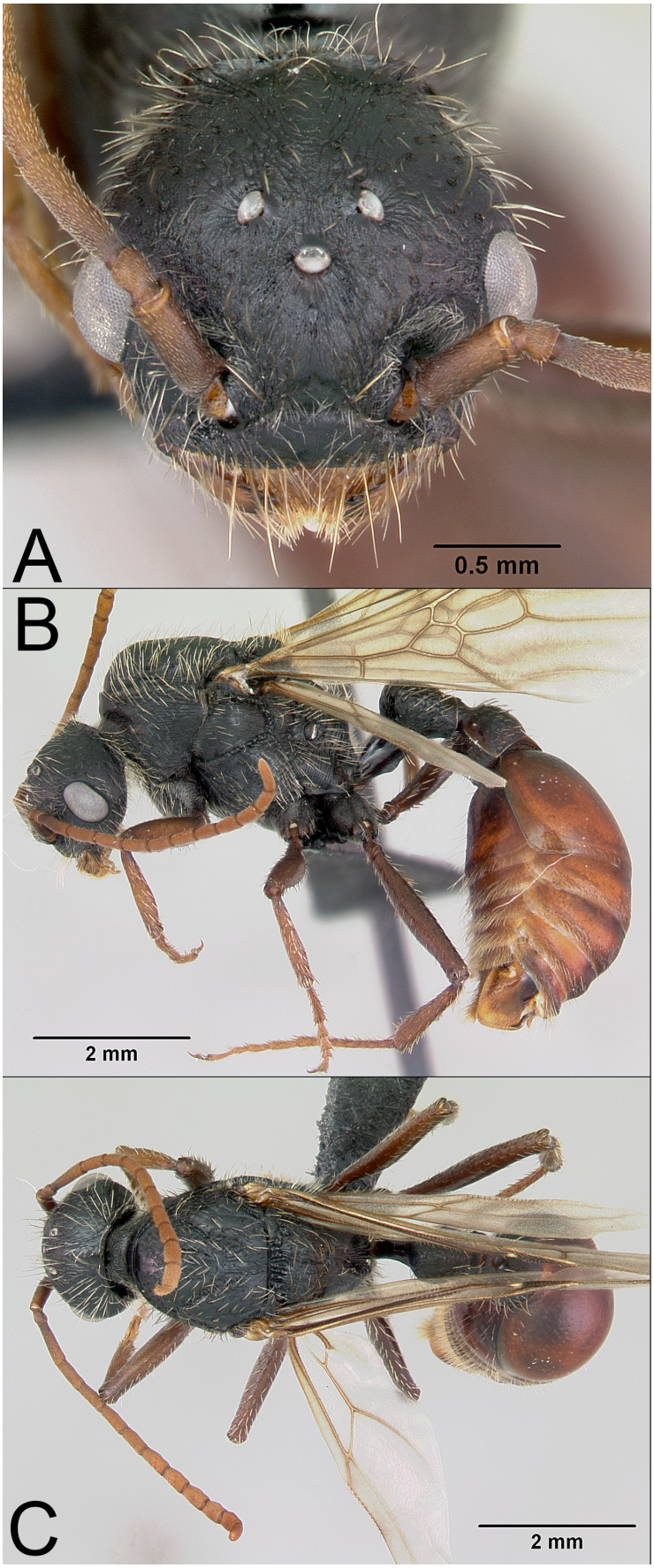

FIGURE 5. Photograph of *Pogonomyrmex coarctatus* Mayr male: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0172634)**.** Photographs by April Nobile from www.AntWeb.org**.**

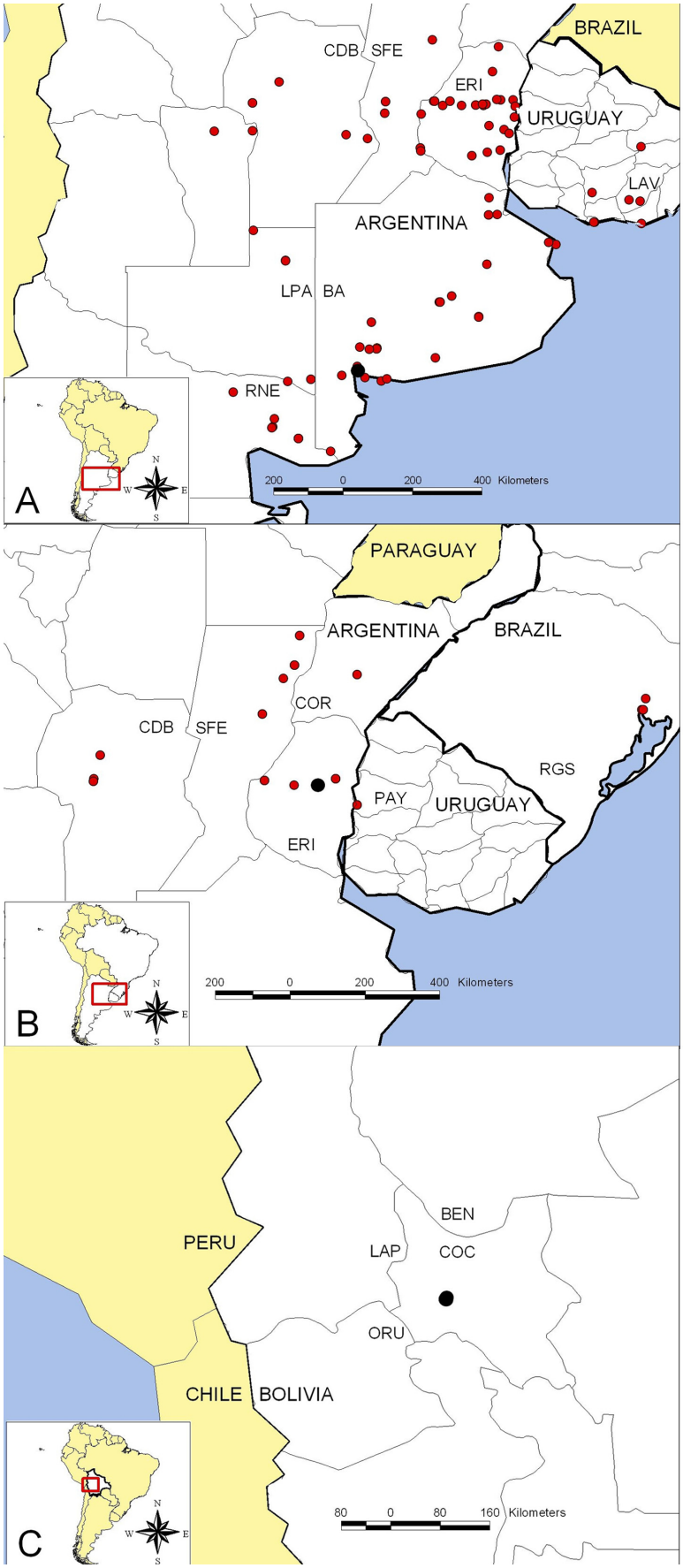

FIGURE 6. Geographic distribution of: (**A**) *Pogonomyrmex coarctatus* Mayr, (**B**) *Pogonomyrmex lobatus* Santschi, and (**C**) *Pogonomyrmex marcusi* Kusnezov. The larger black circle in each panel denotes the type locality.

Discussion. *Pogonomyrmex coarctatus* co-occurs with two other *P. coarctatus*-group species, *P. lobatus* and *P. micans*. *Pogonomyrmex coarctatus* can be distinguished from these two species based on the following characters: (1) *P. coarctatus* has fine, dense, longitudinal striae that are often indistinct and cover part to most of cephalic dorsum, (2) in profile, lateral lobe of clypeus not enlarged, with a wide gap between the clypeal lobe and frontal lobe (similar to width of antennal scape), (3) dorsum of postpetiole weakly to moderately granulate-punctate, occasionally with weak rugae near posterior margin, and (4) body mostly concolorous reddish-orange to reddish-brown. In *P. lobatus*, the cephalic dorsum is covered with very fine, dense striae, and the lateral lobe of clypeus is massively enlarged, nearly contacting the frontal lobe. In *P. micans*, the cephalic dorsum is covered with very fine, dense striae, the dorsum of postpetiole has prominent moderately coarse transverse rugae, and workers are bicolored (dark red and blackish). *Pogonomyrmex marcusi* is only known from mid- to higher elevations in central Bolivia, and thus is geographically isolated from *P. coarctatus*; these two species can be separated using characters in the key.

Pogonomyrmex coarctatus var. *striaticeps* was erected because its cephalic sculpturing was more fine and dense than that on the type specimen (see also Gallardo, 1932). Kusnezov (1951) synonomized *P. coarctatus* var. *striaticeps* without discussion. I concur with this synonomy because the degree of cephalic sculpturing in syntypes of *P. coarctatus* var. *striaticeps* occurs within colonies of *P. coarctatus*.

Kusnezov (1951) provided a thorough discussion on *P. bruchi*, indicating that it was closely related to *P. coarctatus*, and that it could be distinguished from the latter species by its smaller size, but more importantly by its much weaker degree of worker polymorphism. He also noted that the geographic range of *P. bruchi* occurred within that of *P. coarctatus* suggesting two possibilities: (1) *P. bruchi* was a distinct species given that its geographic range was entirely contained within that of *P. coarctatus*, and (2) *P. bruchi* was an insignificant variety of *P. coarctatus* in the event that the two taxa lacked morphological differences.

In his key to South American *Pogonomyrmex*, Taber (1998) noted that *P. coarctatus* and *P. bruchi* differed in the size of the trough at the base of the scape (conspicuous in *P. coarctatus*, absent to weak in *P. bruchi*), the thickness of the femur on the foreleg (weakly incrassate in *P. coarctatus*, strongly incrassate in *P. bruchi*), and in the keel between the superior propodeal spines (keel lacking in *P. coarctatus*, keel present in *P. bruchi*). Cuezzo and Claver (2009) used these same characters to separate *P. coarctatus* and *P. bruchi*.

I have examined syntypes of *P. coarctatus* and *P. bruchi*, and there are no consistent differences between these two taxa. None of the characters discussed by Taber (1998) consistently differ between the two taxa, and variation that he noted occurs within colonies of *P. coarctatus*. Thus, I place *P. bruchi* as a junior synonym of *P. coarctatus*. Moreover, erecting *P. bruchi* as a species likely resulted from collecting few specimens and/or not examining nests to determine if workers were polymorphic.

Biology. Nests of *P. coarctatus* generally consist of a small hole in the ground, with a tumulus up to 10–15 cm in diameter. Nests are placed in open, exposed sites and they sometimes are surrounded by a small midden of seed chaff. Nests are most easily located by following baited workers to the nest. Foragers often form very loose columns with scattered individuals that harvest the seeds of various species. Foragers often climb vegetation to cut seeds directly from plants (pers. obs.). Colonies of *P. coarctatus* contain approximately 2000 workers (C. Smith, unpub. data).

Pogonomyrmex coarctatus is the only polymorphic species of *Pogonomyrmex* in South America. One feature of the *P. coarctatus*-group species is that they exhibit a graded polymorphism that results from extending worker sizes, while maintaining the same allometry (**Figure 7**). These species range from the monomorphic *P. marcusi* and *P. micans*, to the moderately polymorphic *P. lobatus* that lacks supermajors, to the polymorphic *P. coarctatus* that has supermajors (also see below—life history and phenotypic diversity).

Sexuals have been collected in nests from 18-20 December, mating flights were observed during late morning on 18 December, and foundresses have been collected from the ground on 21–23 January. Kusnezov (1951) observed a mating flight near mid-day on Jan 9, 1950, noting that it was a sunny, windless day and that isolated individuals flew from the nest. Queens of *P. coarctatus* are polyandrous with a mean ($\bar{x}$ ± SE) effective mating frequency of 8.5 ± 1.7 (range = 3.2–17.2, n = 10 colonies) (C. Smith, unpub. data). One queen of *P. coarctatus* had 27 ovarioles; queen dry mass averaged ($\bar{x}$ ± SE) 29.9 ± 1.8 mg (n = 3) (R.A. Johnson, unpub. data).

Pogonomyrmex coarctatus is a lowland species that occurs at elevations from 15–890 m. This species occurs throughout the Humid Pampas and Espinal ecoregions as well as the southern Uruguayan Savanna and southern portions of the Humid Chaco, Dry Chaco, and Low Monte Desert ecoregions as defined by Olson *et al*. (2001).

Overall, *P. coarctatus* occurs in more mesic habitats than most congeners in Argentina, but it also reaches into the Low Monte Desert habitats in southern Buenos Aires Province (**Figure 6A**).

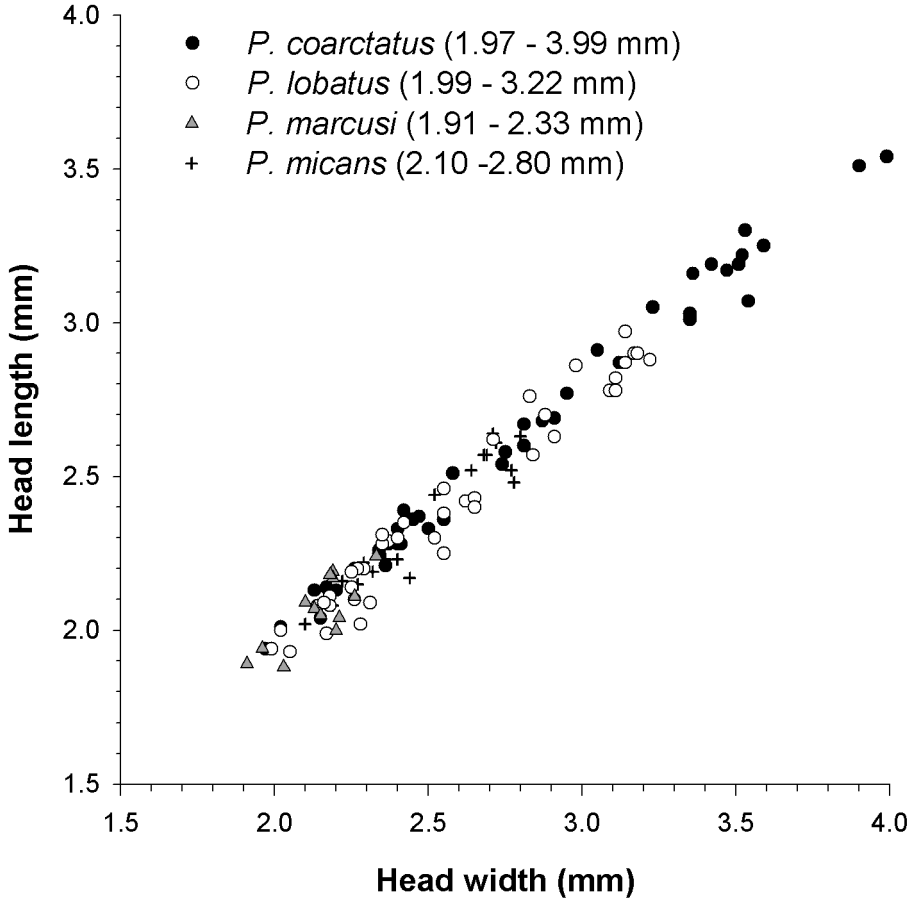

FIGURE 7. Bivariate plot of head width versus head length for the four species in the *Pogonomyrmex coarctatus*-group: *P. coarctatus*—polymorphic with supermajors (n = 42), *P. lobatus*—moderately polymorphic, but lacks supermajors (n = 42), *P. marcusi*—monomorphic (n = 13), and *P. micans*—monomorphic (n = 22).

Pogonomyrmex lobatus

(Figures 8–10)

Pogonomyrmex lobatus Santschi, 1921: 96 (worker). Syntypes examined: 6 workers [MACN], 1 worker [MCZ], 1 worker [MZUSP], ARGENTINA, Entre Ríos: Villaguay (Charles Bruch leg.). See also Gallardo, 1932: 160, fig. 41; Kusnezov, 1951: figs. 13b, 13c. MCZ worker here designated **LECTOTYPE** [CASENT0217260].

Worker. Diagnosis. Within the *P. coarctatus*-group, the combination of: (1) fine, dense, longitudinal striae cover cephalic dorsum, (2) in profile, lateral lobe of clypeus massively enlarged with narrow gap between lateral lobe and frontal lobe, the latter two structures nearly in contact, and (3) body mostly concolorous reddish-orange to reddish-brown uniquely characterize this species (**Figure 8**).

Measurements—lectotype (n = 41). HL 2.31 (1.93–2.97); HW 2.39 (1.99–3.22); MOD 0.43 (0.38–0.60); OMD 0.43 (0.46–0.74); SL 1.42 (1.27–1.90); PNW 1.42 (1.26–1.93); HFL 1.94 (1.81–2.55); ML 2.66 (2.13–3.45); PW 0.52 (0.47–0.85); PPW 0.69 (0.66–1.13). Indices: SI 59.41 (55.21–70.00); CI 103.46 (101.00–113.33); OI 17.99 (14.91–21.37); HFI 81.17 (75.00–99.01).

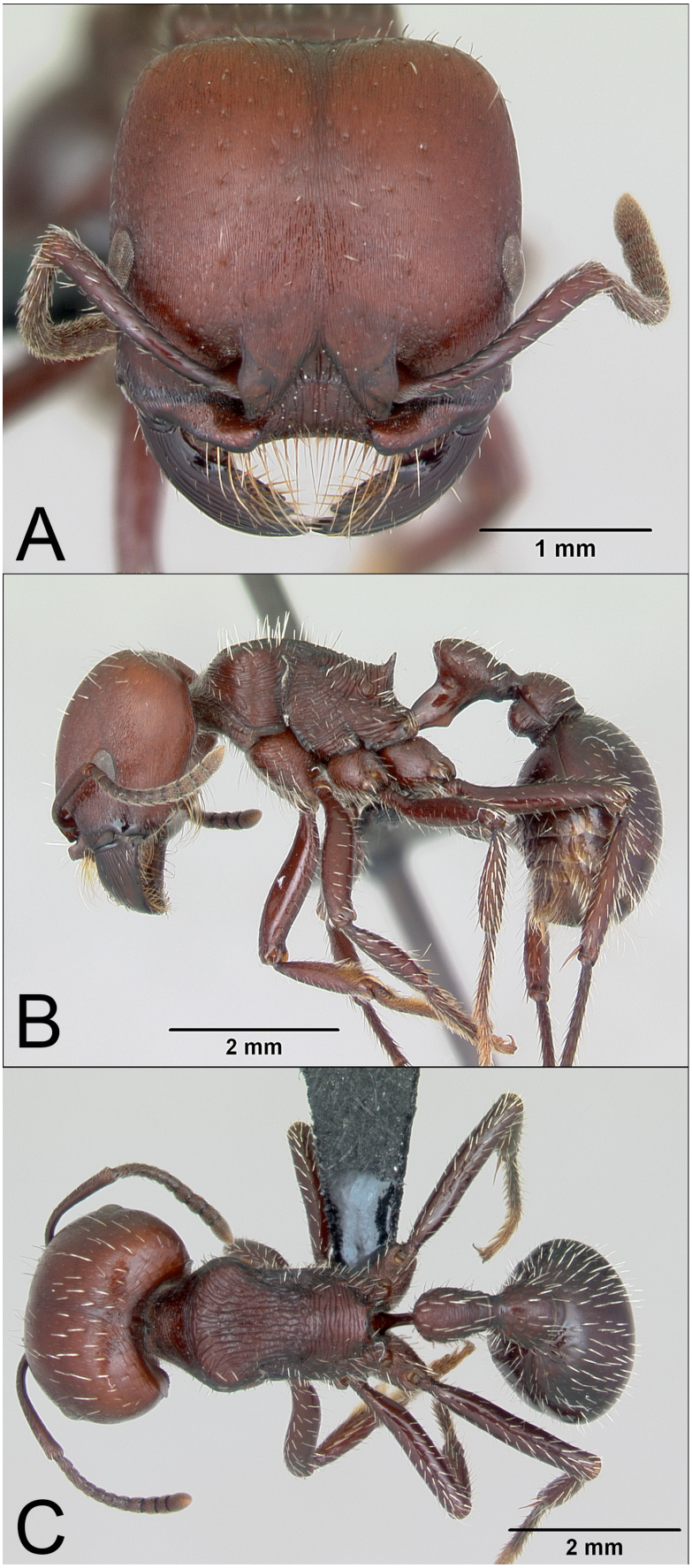

FIGURE 8. Photograph of *Pogonomyrmex lobatus* Santschi worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0172684)**.** Photographs by April Nobile from www.AntWeb.org**.**

Redescription. Moderately polymorphic, but lacking supermajors. Head shape varies with worker size, quadrate in minors and increasingly wider than long in majors (CI = 101.00–113.33, positively associated with head width, $n = 42$, $R^2 = 0.28$, $P < 0.001$); posterior margin weakly concave medially in full-face view. Fine, dense, longitudinal striae cover cephalic dorsum, width of striae and interstriae similar; in full-face view, medial striae not diverging toward posterior corners of head. Cephalic interstriae dull to weakly shining. Vertex with fine, dense striae, interstriae weakly shining to smooth and shining. In full-face view, entire cephalic dorsum with silky appearance. Anterior margin of clypeus concave; dorsal surface with numerous moderately coarse, subparallel, longitudinal to oblique rugae. In profile, lateral lobe of clypeus massively enlarged with narrow gap (much less than width of antennal scape) between clypeal lobe and frontal lobe, the latter two structures nearly in contact. Numerous long, curved, bristle-like, yellowish macrochaetae project from anterior margin of clypeus and ventral side of mandibles. Mandible with six teeth; mandibular dorsum strongly rugose. MOD ranging from 0.16–0.23x HL. In profile, eyes situated anterior to middle of head, OMD = 1.00–1.51x MOD. Antennal scapes short (SI = 55.21–70.00), extending less than one-third the distance from the posterior margin of the eye to the posterior corner of head. Base of antennal scapes smooth and shining, distal portion sometimes weakly granulate or weakly striate, weakly shining to shining; basal flange well-developed with carinate margin. Psammophore well-developed.

Mesosomal profile weakly to moderately convex; all mesosomal surfaces with prominent coarse, subparallel, weakly irregular, widely-spaced rugae. In dorsal view, humeral portion of pronotum rounded to knoblike. Dorsum of promesonotum with longitudinal rugae that rarely diverge toward humeral shoulders of pronotum; transverse rugae on anterior surface of pronotum continue obliquely or longitudinally onto pronotal sides; rugae on mesopleura angle posterodorsally. Superior propodeal spines long, acuminate, connected by well-defined keel; spine length about equal to or slightly less than width between their bases; regular to weakly wavy, transverse rugae on propodeal dorsum traverse ventrally or anteroventrally on sides. Inferior propodeal spines wider than long, apex broadly rounded. Propodeal spiracles narrowly ovate facing posterad. Interrugae on mesosoma weakly to moderately granulate, weakly shining to shining. Legs weakly granulate, weakly shining.

Peduncle of petiole about 0.7x as long as petiolar node, anteroventral margin with broadly rounded to angulate process. In profile, posterior surface of petiolar node weakly convex; node asymmetrical with anterior surface notably shorter than posterior surface, apex rounded. In dorsal view, petiolar node longer than wide, widest near center, narrowing to rounded or spatulate anterior margin. Sides and posterior surface of petiolar node with weak to moderately coarse, wavy to irregular transverse rugae. Dorsum of postpetiole convex in profile; in dorsal view, widest near posterior margin, narrowing to anterior margin, maximum width about equal to length, weakly to moderately punctate, rarely with weak irregular, transverse rugae posterad. Interrugae on posterior surface of petiolar node and dorsum of postpetiole weakly to moderately granulate, dull to weakly shining. First gastral tergum moderately coriarious, weakly shining to smooth and shining.

Erect white to yellowish pilosity moderately abundant on head, variable in length and arising from foveae; longest hairs not exceeding MOD. Moderately abundant suberect pilosity on scape; abundant decumbent hairs on funicular segments. Legs with moderately abundant suberect to decumbent setae. Mesosoma, petiolar node, postpetiole, first gastral tergum with moderately dense erect setae, longest about equal to MOD; abundant long hairs on posterior margins of gastral terga, longest >MOD. Body mostly concolorous reddish-orange to reddish-brown (**Figure 8**).

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) large size (HW = 3.41–3.55 mm), (3) striae cover cephalic dorsum, and (4) in profile, lateral lobe of clypeus massively enlarged with narrow gap (much less than width of antennal scape) between clypeal lobe and frontal lobe (**Figure 9**).

Measurements—(n = 5). HL 3.09–3.24; HW 3.41–3.55; MOD 0.53–0.60; OMD 0.67–0.77; SL 1.87–1.93; PNW 2.37–2.51; HFL 2.61–2.77; ML 3.74–4.44; PW 1.02–1.16; PPW 1.25–1.33. Indices: SI 53.12–56.27; CI 105.25–114.89; OI 15.45–17.01; HFI 75.65–78.69.

Description. Large species (HW = 3.41–3.55 mm) with caste-specific morphology of the mesosoma related to wing-bearing and presence of ocelli on head. In full-face view, head wider than long (CI = 105.2–114.9), posterior margin weakly concave medially. Fine, dense, longitudinal striae cover cephalic dorsum; striae on vertex often less abundant and/or less prominent, interstriae weakly shining to shining. Mandible with six teeth, dorsal surface coarsely rugose. In profile, lateral lobe of clypeus massively enlarged with narrow gap (much less than width of antennal scape) between clypeal lobe and frontal lobe, the latter two structures nearly in contact. Psammophore well-developed.

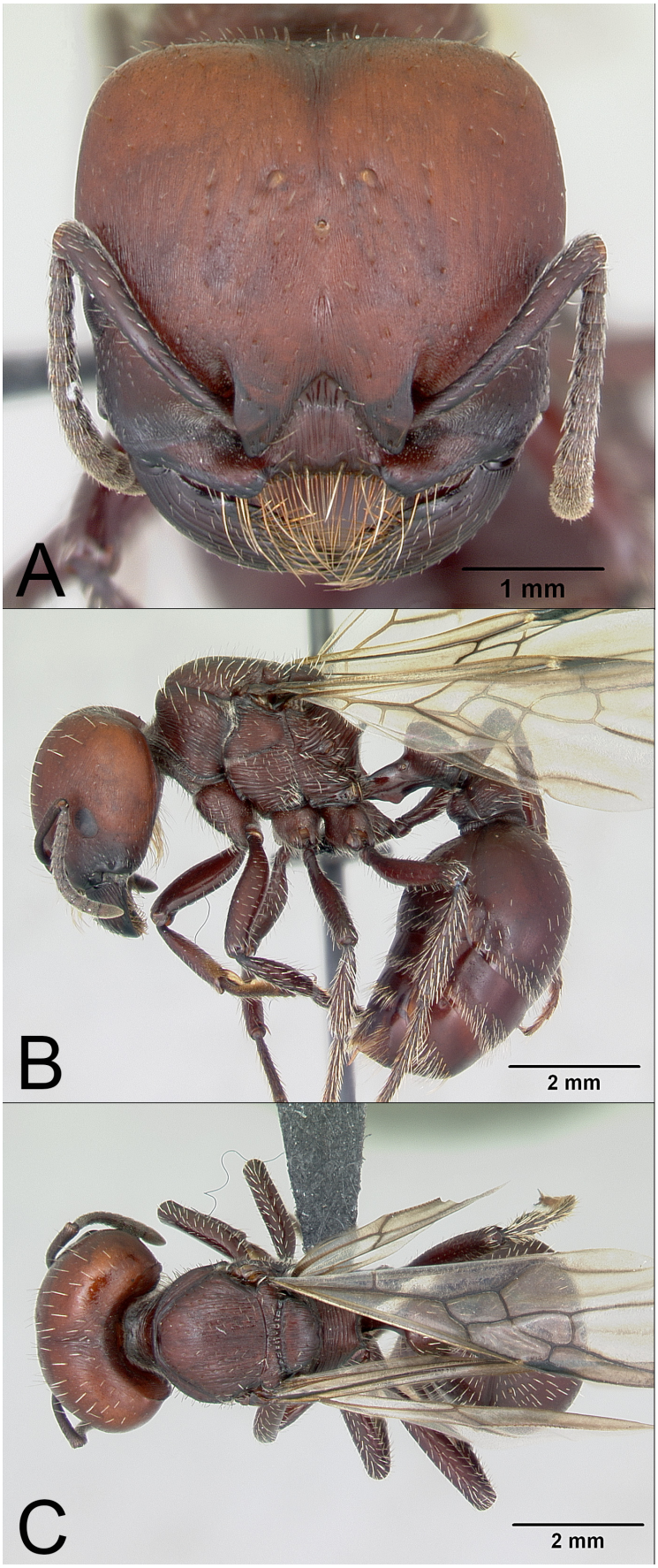

FIGURE 9. Photograph of *Pogonomyrmex lobatus* Santschi alate queen: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0172685)**.** Photographs by April Nobile from www.AntWeb.org**.**

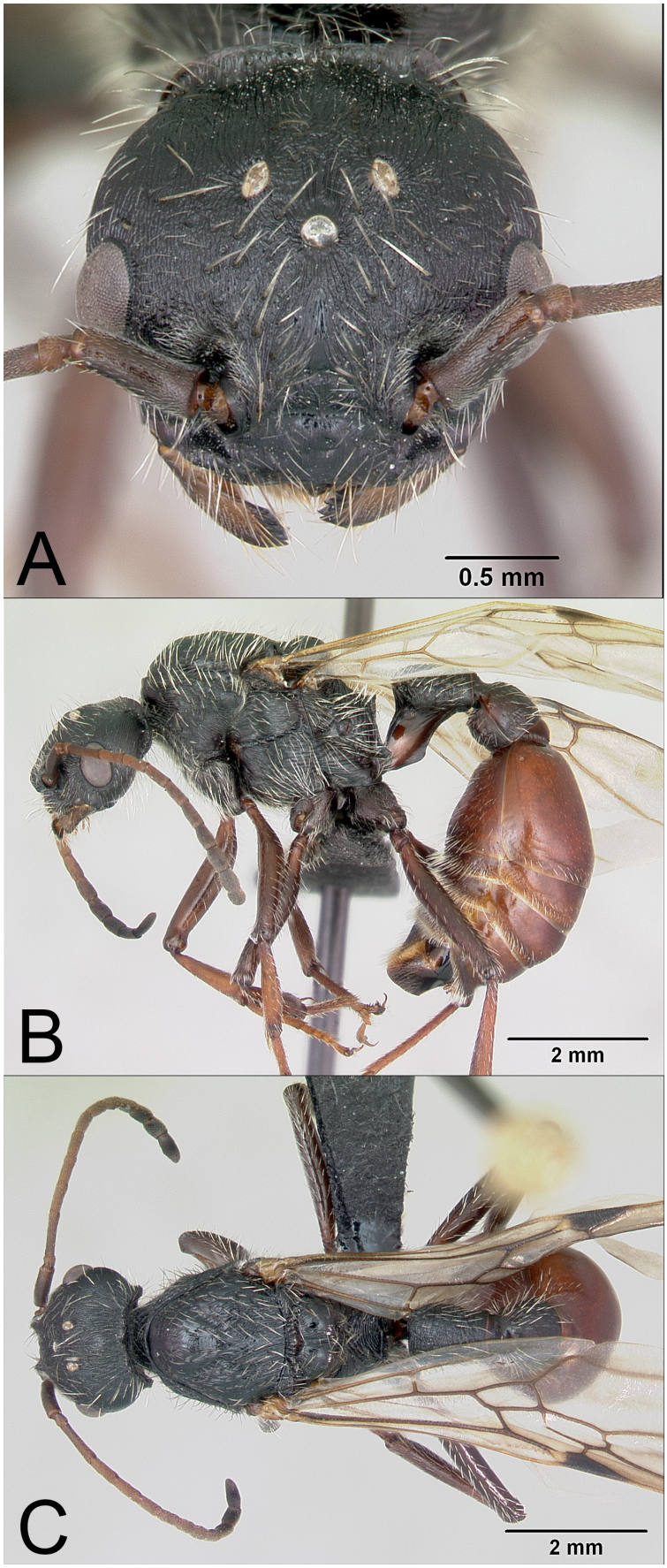

FIGURE 10. Photograph of *Pogonomyrmex lobatus* Santschi male: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0172686)**.** Photographs by April Nobile from www.AntWeb.org**.**

All mesosomal surfaces with subparallel, weakly irregular rugae; superior propodeal spines short. Peduncle of petiole about as long as petiolar node, anteroventral margin often with blunt to angulate process. In profile, petiolar node asymmetrical with anterior surface notably shorter than posterior surface, apex rounded. Postpetiole slightly wider than long. Posterior surface of petiolar node and dorsum of postpetiole with weak to moderately strong, wavy to irregular, transverse rugae; interrugae weakly to moderately punctate, weakly shining. Gastral terga smooth, weakly shining to shining. Most body surfaces with moderately abundant short, suberect to erect, white to yellowish setae. Body mostly concolorous reddish-orange to reddish-brown, head often slightly lighter (**Figure 9**).

Male. Diagnosis. This caste is diagnosed by: (1) first gastral tergum lacking striae, (2) large (HW > 1.75 mm; HL > 1.80 mm; ML > 3.30 mm), (3) hairs on head (especially posterior to eyes) and dorsum of mesosoma moderately dense, moderately long and flexuous, longest hairs rarely >0.5–0.8x MOD, (4) transverse rugae on dorsum of postpetiole weak, present on posterior one-half of segment, often extending anterad (sometimes oblique or longitudinal more anterad), (5) rugae posterior to eyes and ocelli prominent, and (6) at least one and usually both mandibles with four teeth (**Figure 10**).

Measurements—(*n* = 12). HL 1.83–2.06; HW 1.78–2.14; MOD 0.56–0.70; OMD 0.21–0.36; SL 0.45–0.61; HFL 2.18–2.61; ML 3.39–4.04; PW 0.74–0.93; PPW 0.90–1.12. Indices: SI 22.39–30.90; CI 93.47–105.94; OI 29.47–36.52; HFI 109.95–129.83.

Additional material examined. ARGENTINA: ***Córdoba***: Rt 5 at 3.4 km S Alta Gracia, 1830', Jan 23, 2006 (RAJC); Estancia Santo Domingo (Salsipuedes), Feb 24, 2009 (RGPC); Anisacate, no date (FML). ***Corrientes***: Mercedes, no date (MACN). ***Entre Ríos***: Rt 18 at 7.3 mi SW San Salvador, 220', Dec 19, 2005 (CASC; CSC; MCZ; RAJC); La Picada, May 14, 1951 (FML; LACM); Rt 18 at 33.9 mi W Villaguay, 320', Dec 20, 2005 (MCZ; RAJC); Villaguay, no date (MACN; MLPA). ***Santa Fe***: 22 km S Reconquista, 45 m, Nov 15, 2003 (RAJC); 23.2 km NW Reconquista, Dec 5, 2005 (CSC); Villa Guillermina, no date (FML); Fives Lille, no date (MACN). **BRAZIL:** ***Río Grande do Sul***: Porto Alegre, Mar 24, 1971 (LACM; MCZ; MZUSP); São Leopoldo, no date (MCZ). **URUGUAY:** ***Paysandú***: Paysandú, Apr 25, 1961 & Feb 25, 1961 (FML; LACM). ***Questionable locales*** **(appear to be outside of geographic range): ARGENTINA:** ***Buenos Aires***: Monte Hermoso, no date (MLPA) (**Figure 6B**).

Etymology. The specific epithet, *lobatus* (from Latin, *lobat* = lobed), refers to the massively enlarged lateral lobes of the clypeus.

Discussion. *Pogonomyrmex lobatus* co-occurs with *P. coarctatus*, and it is likely to co-occur with *P. micans. Pogonomyrmex lobatus* can be distinguished from *P. coarctatus* using the following characters: (1) *P. lobatus* has a massively enlarged lateral lobe of the clypeus, with the lobe nearly contacting the frontal lobe, and (2) the cephalic dorsum is covered with very fine, dense, longitudinal striae. In *P. coarctatus,* the lateral lobe of the clypeus is not enlarged, with a wide gap between the clypeal lobe and frontal lobe, and the very fine, dense, longitudinal striae are often indistinct and cover only part to most of cephalic dorsum. In *P. micans* the lateral lobe of the clypeus is not enlarged, the dorsum of the postpetiole has prominent moderately coarse rugae, and workers are bicolored (dark red and blackish). In *P. lobatus*, the lateral lobe of the clypeus is massively enlarged, workers are a concolorous reddish-orange to reddish-brown, and the dorsum of the postpetiole is weakly to moderately punctate, rarely with weak rugae posterad. *Pogonomyrmex marcusi* is only known from mid- to higher elevations in central Bolivia and thus is geographically isolated from *P. lobatus*; these two species can be separated using characters in the key.

Biology. *Pogonomyrmex lobatus* appears to be a relatively uncommon species that is a solitary forager, though it sometimes forms very loose foraging columns with few, scattered workers, similar to those seen in *P. coarctatus*. Nests range from a cryptic entrance to a 15 cm tumulus, and they sometimes have a small midden of seed chaff. Colonies of *P. lobatus* are probably similar in size to those of *P. coarctatus*, suggesting that they range up to about 2000 workers. Sexuals have been collected from nests and dealate queens from the ground on 19 December, indicating that mating flights occur during the austral summer.

Pogonomyrmex lobatus is a lowland species that occurs at elevations from 45–555 m. This species occurs in the Uruguayan Savanna, northern Espinal, southern Humid Chaco, and along the southeastern edge of the Dry Chaco ecoregions as defined by Olson *et al*. (2001) (**Figure 6B**).

Pogonomyrmex marcusi
(Figures 11–13)

Pogonomyrmex marcusi Kusnezov, 1951: 260, fig. 13a (worker, diagnosis in key). Syntypes examined: 3 workers [LACM], 3 workers [MZUSP], 16 workers [USNM], BOLIVIA, Cochabamba: Cochabamba (H. Marcus leg., 19 December 1945 & 4 May 1946). Kusnezov, 1954: 82, figs. 1–4 (queen, male); Marcus, 1953: 43, figs. 33–41 (larvae); Wheeler & Wheeler, 1960: 3 (redescription of larvae). See also Marcus and Marcus, 1951: 117, figs. 8–11; Marcus, 1953: 43, figs. 30–32. USNM worker here designated **LECTOTYPE** [CASENT0914118].

Worker. Diagnosis. Within the *P. coarctatus*-group, the combination of: (1) longitudinal striae cover part to most of cephalic dorsum, areas lacking striae shining to strongly shining, (2) in profile, lateral lobe of clypeus weakly enlarged, (3) interrugae on mesosoma smooth, strongly shining, (4) inferior propodeal spines wider than long, apex bluntly angulate to acuminate, and (5) head reddish-orange, first gastral tergum reddish-brown; rest of body reddish-orange to reddish-black uniquely characterize this species (**Figure 11**).

Measurements—lectotype (n = 5 plus 8 paralectotypes). HL 1.94 (1.88–2.24); HW 2.04 (1.91–2.33); MOD 0.41 (0.38–0.44); OMD 0.40 (0.39–0.48); SL 1.37 (1.10–1.55); PNW 1.30 (1.14–1.44); HFL 1.75 (1.69–2.15); ML 2.08 (2.20–2.75); PW 0.44 (0.44–0.53); PPW 0.59 (0.59–0.69). Indices: SI 67.16 (57.59–70.92); CI 105.15 (100.000–110.00); OI 20.10 (18.03–20.95); HFI 85.78 (83.18–95.13).

Redescription. Monomorphic, head quadrate to wider than long (CI = 100.00–110.00), posterior margin flat to weakly concave in full-face view. Fine, dense, longitudinal striae cover only part of cephalic dorsum, width of striae and interstriae similar; in full-face view, medial striae not diverging toward posterior corners of head. Cephalic interstriae, most of cephalic dorsum, and vertex smooth, strongly shining. Anterior margin of clypeus flat to weakly concave; dorsal surface with several moderately coarse subparallel, longitudinal, oblique, or arcuate rugae. In profile, lateral lobe of clypeus usually weakly enlarged. Numerous long, curved, bristle-like, yellowish macrochaetae project from anterior margin of clypeus and ventral side of mandibles. Mandible with six teeth; mandibular dorsum coarsely rugose. MOD ranging from 0.18–0.22x HL. In profile, eyes situated anterior to middle of head, OMD = 0.88–1.18x MOD. Antennal scapes short (SI = 57.59–70.92), extending less than one-third the distance from posterior margin of eye to posterior corner of head. Antennal scapes smooth and shining; basal flange well-developed with carinate margin. Psammophore well-developed.

Mesosomal profile weakly to moderately convex; all mesosomal surfaces with prominent coarse, subparallel, weakly wavy to irregular, widely-spaced rugae. In dorsal view, humeral shoulders of pronotum weakly rounded to knoblike. Dorsum of promesonotum with longitudinal rugae that diverge anteriorly toward humeral shoulders of pronotum; transverse rugae on anterior surface of pronotum continue obliquely or ventrally on pronotal sides; rugae on mesopleura angle posterad or posterodorsally. Superior propodeal spines long, acuminate, connected by well-defined keel; spine length slightly less than width between their bases; regular to weakly wavy, transverse rugae on propodeal dorsum traverse ventrally or anteroventrally on sides. Inferior propodeal spines wider than long, apex bluntly angulate to acuminate. Propodeal spiracles narrowly ovate facing posterad. Interrugae on mesosoma smooth, strongly shining. Legs weakly granulate, weakly shining to smooth and strongly shining.

Peduncle of petiole about 0.7x as long as petiolar node, anteroventral margin with broadly rounded process. In profile, posterior surface of petiolar node weakly convex; node asymmetrical with anterior surface notably shorter than posterior surface, apex rounded. In dorsal view, petiolar node longer than wide, sides subparallel, slightly wider near middle, narrowing to spatulate anterior margin. Sides and posterior surface of petiolar node with coarse, wavy to irregular transverse, oblique, or longitudinal rugae. Dorsum of postpetiole convex in profile; in dorsal view, widest near posterior margin, narrowing to anterior margin, maximum width about equal to length. Regular to wavy, weak to moderately coarse, transverse rugae on dorsum of postpetiole, sometimes weakening or lacking near anterior margin; interrugae on posterior surface of petiolar node and dorsum of postpetiole smooth to moderately granulate, weakly shining to shining. First gastral tergum smooth and strongly shining.

Erect white to yellowish pilosity sparse to moderately abundant on head, mostly similar in length and arising from foveae; longest hairs not exceeding MOD, few >0.5x MOD. Moderately abundant suberect pilosity on scape; abundant decumbent hairs on funicular segments. Legs with moderately abundant suberect to decumbent setae. Mesosoma with moderately dense, erect setae that are mostly similar in length, longest approaching MOD; petiolar node, postpetiole, first gastral tergum with moderately dense, erect setae that are mostly similar in length, longest notably shorter than MOD; length of hairs on margins of posterior gastral terga often >MOD. Head reddish-orange, first gastral tergum reddish-brown; rest of body reddish-orange to reddish-black (**Figure 11**).

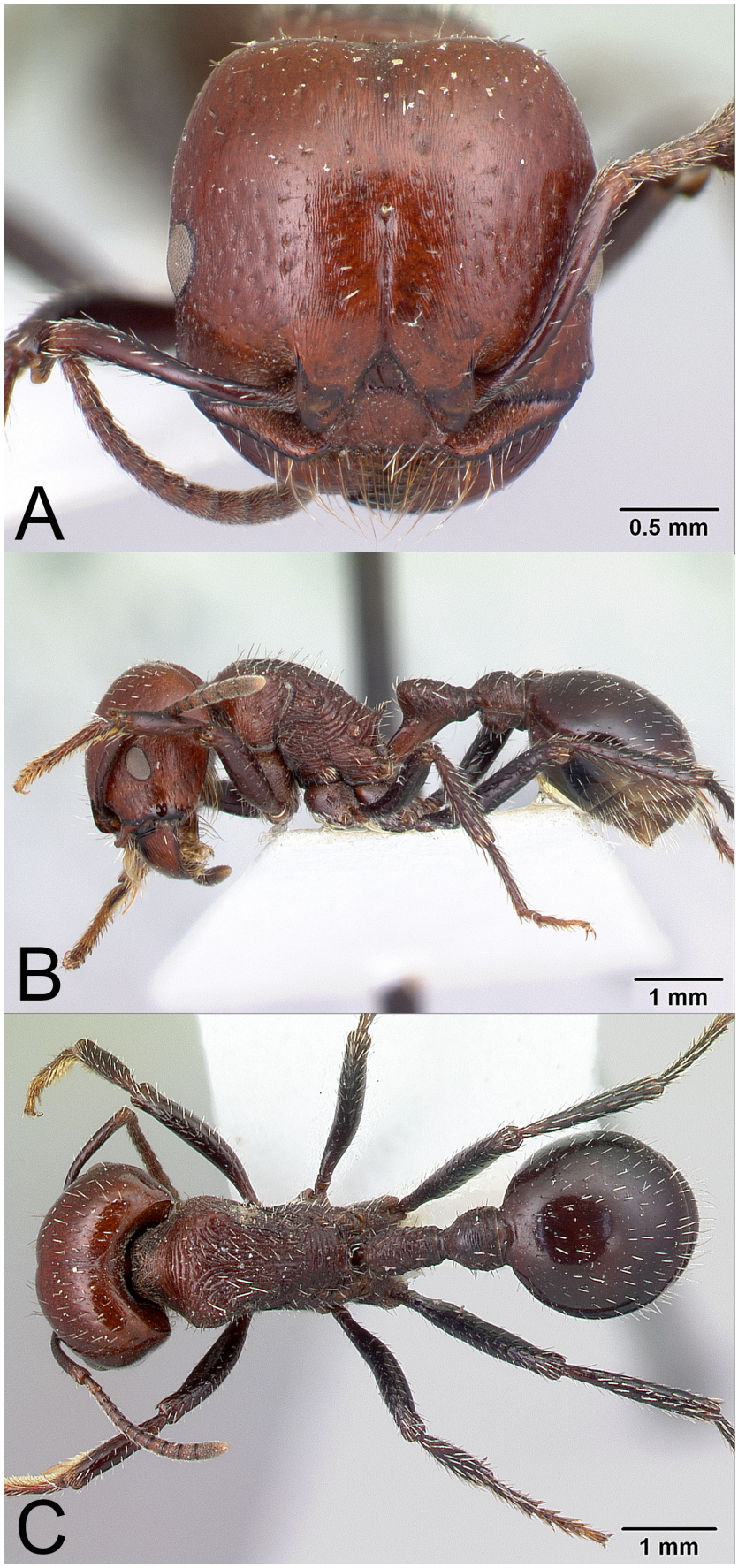

FIGURE 11. Photograph of *Pogonomyrmex marcusi* Kusnezov worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0217259)**.** Photographs by Erin Prado from www.AntWeb.org**.**

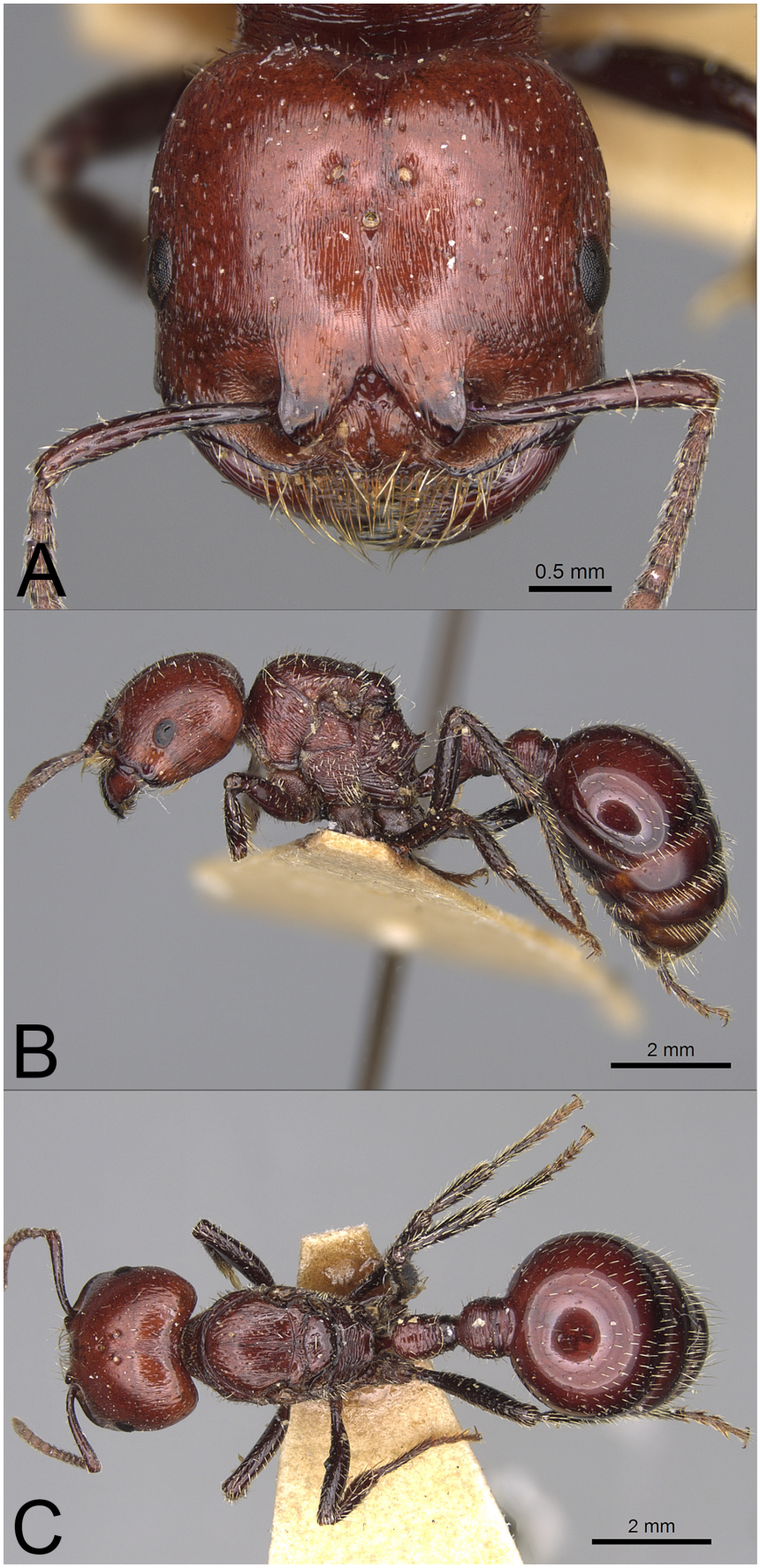

FIGURE 12. Photograph of *Pogonomyrmex marcusi* Kusnezov dealate queen: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0914201)**.** Photographs by Michele Esposito from www.AntWeb.org**.**

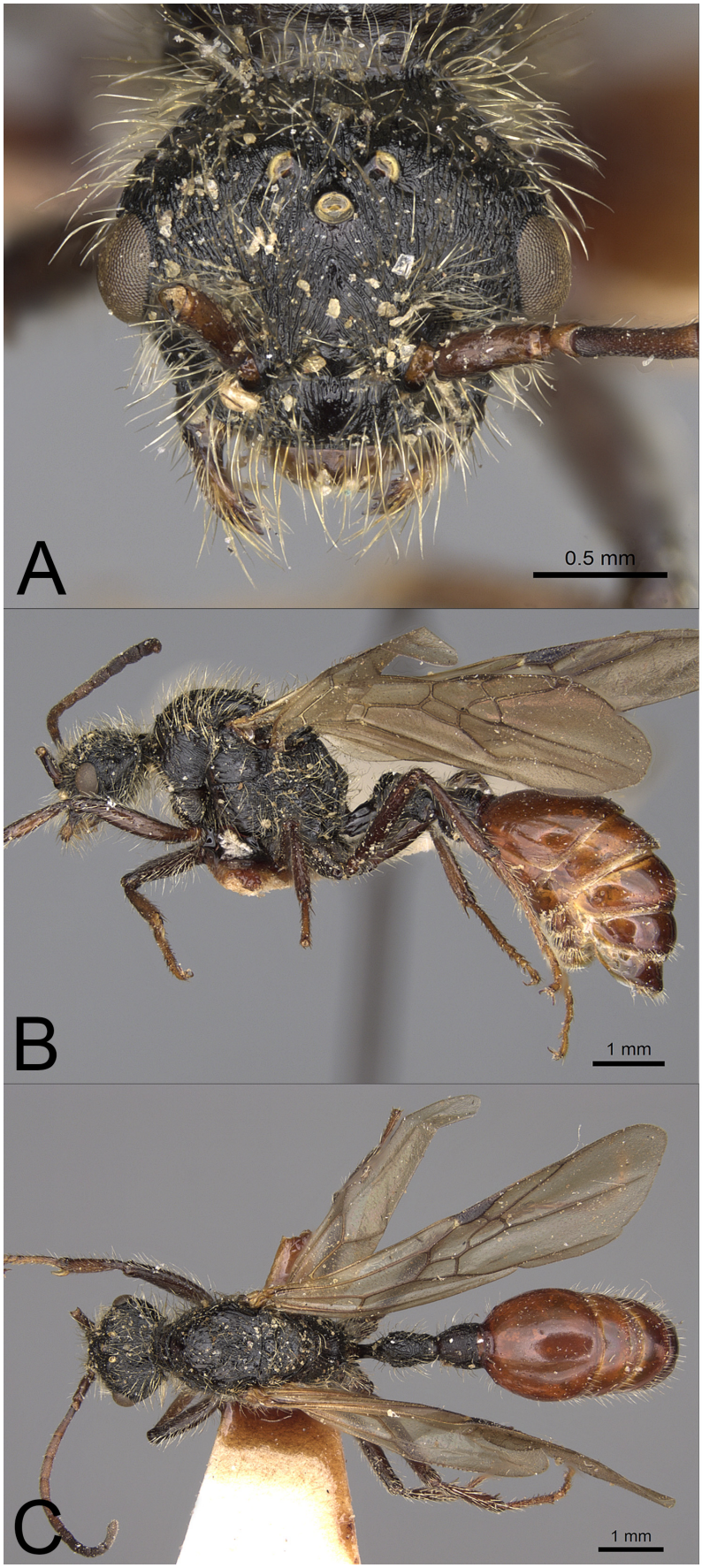

FIGURE 13. Photograph of *Pogonomyrmex marcusi* Kusnezov male: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0914205)**.** Photographs by Michele Esposito from www.AntWeb.org**.**

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) large size (HW = 2.91 mm), (3) striae cover most of cephalic dorsum, and (4) inferior propodeal spines well-developed, triangular, apex bluntly angulate to acuminate (**Figure 12**).

Measurements—(*n* = 1). HL 2.74; HW 2.91; MOD 0.56; OMD 0.63; SL 1.61; PNW 2.06; HFL 2.43; ML 3.35; PW 0.87; PPW 1.17. Indices: SI 55.33; CI 106.20; OI 19.24; HFI 83.51.

Male. Diagnosis. This caste is diagnosed by: (1) first gastral tergum lacking striae, (2) large (HW > 1.65 mm; HL > 1.75 mm; ML > 2.95 mm), (3) hairs on head (especially posterior to eyes) and dorsum of mesosoma dense, long and flexuous, length of numerous hairs approach to exceed MOD, (4) mandibles with three teeth, and (5) interrugae on katepisternum weakly shining to shining (**Figure 13**).

Measurements—(*n* = 1). HL 1.69; HW 1.77; MOD 0.54; OMD 0.31; SL 0.45; HFL 2.09; ML 2.97; PW 0.63; PPW 0.78. Indices: SI 25.42; CI 104.73; OI 30.51; HFI 118.08.

Additional material examined. BOLIVIA: *Cochabamba*: Cochabamba, Jan 24–28, 1954 (FML; LACM; MCZ; USNM; ZSM); Temporal, Mar 10, 1946 (FML) (**Figure 6C**).

Etymology. Kuznezov named this species after Dr. Harry Marcus, who collected the syntypes and studied this species.

Discussion. *Pogonomyrmex marcusi* is not known to occur near any *P. coarctatus*-group species or any other species of *Pogonomyrmex.* Additionally, *P. marcusi* is the only *P. coarctatus*-group species that occurs at mid- to high elevations (2660 m), while the other three species are only known to occur below 1000 m. *Pogonomyrmex marcusi* is easily distinguished from other *P. coarctatus*-group species using characters given in the key.

Biology. *Pogonomyrmex marcusi* is a solitary forager that travels up to 20 m from the nest to harvest the seeds of various grass species, but a file of foragers was observed returning to nests (Marcus & Marcus, 1951). Nests are cryptic and difficult to locate without finding a forager to follow back to the nest. Nests usually have several entrances that are placed under or at the edge of stones or under plants (Marcus & Marcus, 1951). Nest excavations indicate that *P. marcusi* colonies contain 600–700 workers plus 200 larvae and pupae (Marcus, 1953; Marcus & Marcus, 1951).

Sexuals of *P. marcusi* have been collected on 28 January, suggesting that mating flights occur during the austral summer. Marcus and Marcus (1951) also noted that several nests contained ergatogynes in addition to workers. It is unclear what they meant by ergatogynes, which they described only as having well-developed ovaries. By comparison, they indicated that workers had a smaller gaster and poorly-developed ovarioles with small eggs. I did not encounter any ergatogynes while examining individuals during this study.

Pogonomyrmex marcusi is only known from arid habitats near Cochabamba, Bolivia, at elevations of approximately 2660 m (Marcus & Marcus, 1951). This species occurs in the Bolivian Montane Dry Forest ecoregion as defined by Olson *et al*. (2001) (**Figure 6C**). I also have an unverified record of *P. marcusi* (collection at Universidade Estadual de Santa Cruz, Brazil) from Valle Sagrado, near Cusco, Peru. Overall, *P. marcusi* is the only *P. coarctatus*-group species that occurs at mid- to high elevations.

Pogonomyrmex micans

(Figures 14–16)

Pogonomyrmex bruchi Forel r. *micans* Forel, 1914: 268 (worker, male). Syntypes examined: 26 workers, 2 males [MHNG], 2 workers [MLPA], ARGENTINA, San Luis: Alto Pencoso near La Plata, #224 (Bruch leg.). See also Gallardo, 1932: 158, fig. 40. MLPA worker here designated **LECTOTYPE [**CASENT0217254].

Pogonomyrmex micans Forel: Kusnezov, 1951: 254, raised to species.

Worker. Diagnosis. Within the *P. coarctatus*-group, the combination of: (1) fine, dense, longitudinal striae cover cephalic dorsum, (2) coarse rugae on posterior surface of petiolar node, rugae less coarse and more dense on dorsum of postpetiole, (3) in profile, lateral lobe of clypeus poorly-developed with broad gap between clypeal lobe and frontal lobe (gap as wide as to wider than antennal scape), and (4) bicolored—head reddish-brown; mesosoma, petiolar node, postpetiole reddish-brown to blackish-red; gaster reddish-black to nearly black uniquely characterize this species (**Figure 14**).

Measurements—lectotype (*n* = 20). HL 2.09 (2.02–2.64); HW 2.25 (2.10–2.80); MOD 0.45 (0.42–0.56); OMD 0.41 (0.40–0.60); SL 1.48 (1.23–1.73); PNW 1.48 (1.31–1.79); HFL 1.67 (1.81–2.32); ML 2.10 (2.17–2.80);

PW 0.51 (0.49–0.70); PPW 0.70 (0.63–0.91). Indices: SI 65.78 (52.50–63.84); CI 107.66 (102.65–112.44); OI 20.00 (15.88–22.03); HFI 74.22 (68.95–89.05).

Redescription. Monomorphic, head slightly wider to wider than long (CI = 102.65–112.44), posterior margin flat to weakly concave in full-face view. Fine, dense, longitudinal striae cover cephalic dorsum, width of striae and interstriae similar; medial striae not diverging toward posterior corners of head. Cephalic interstriae dull to weakly shining; vertex smooth and shining or with very fine, dense striae; interstriae smooth, weakly shining to shining; entire cephalic dorsum with silky appearance. Anterior margin of clypeus concave; dorsal surface with numerous moderately coarse subparallel, longitudinal to oblique rugae. Numerous long, curved, bristle-like, yellowish macrochaetae project from anterior margin of clypeus and ventral surface of mandibles. Mandible with six teeth, rarely with an additional denticle between 4th and 5th teeth; mandibular dorsum coarsely rugose. MOD ranging from 0.17–0.23x HL. In profile, eyes situated anterior to middle of head, OMD = 0.88–1.13x MOD. Antennal scapes short (SI = 52.50–63.84), extending less than one-third the distance from posterior margin of eye to posterior corner of head. Base of antennal scapes smooth and shining, distal portion weakly striated, weakly to strongly shining; basal flange well-developed with carinate margin. Psammophore well-developed.

Mesosomal profile weakly to moderately convex; all mesosomal surfaces with prominent coarse, subparallel, weakly irregular, widely-spaced rugae. In dorsal view, humeral shoulders of pronotum rounded to knoblike. Dorsum of promesonotum with longitudinal rugae that diverge anteriorly toward humeral shoulders of pronotum; transverse rugae on anterior surface of pronotum continue obliquely or longitudinally on pronotal sides; rugae on mesopleura angle posterodorsally. Superior propodeal spines long, acuminate, connected by well-defined keel; spine length about equal to width between their bases; regular to weakly wavy, transverse rugae on propodeal dorsum traverse ventrally or anteroventrally on sides. Inferior propodeal spines wider than long, apex rounded to angulate. Propodeal spiracles narrowly ovate facing posterad. Interrugae on mesosoma weakly to moderately granulate, weakly shining to shining. Legs weakly granulate, weakly shining.

Peduncle of petiole about 0.8x as long as petiolar node, anteroventral margin with broadly rounded process. In profile, posterior surface of petiolar node weakly convex; node asymmetrical with anterior surface notably shorter than posterior surface, apex rounded. In dorsal view, petiolar node longer than wide, widest near middle, narrowing to spatulate to weakly acute anterior margin. Sides and posterior surface of petiolar node with coarse, wavy to irregular, transverse rugae. Dorsum of postpetiole convex in profile; in dorsal view, widest near posterior margin, narrowing to anterior margin, maximum width about equal to length. Regular to wavy, fine, dense, transverse rugae on dorsum of postpetiole, sometimes lacking on anterior margin; interrugae on posterior surface of petiolar node and dorsum of postpetiole weakly to moderately granulate, dull to weakly shining. First gastral tergum moderately coriarious, weakly shining to smooth and shining.

Erect white to yellowish pilosity moderately abundant on head, variable in length and arising from foveae; longest hairs not exceeding MOD, few >0.5x MOD. Moderately abundant suberect pilosity on scape; abundant decumbent hairs on funicular segments. Legs with moderately abundant suberect to decumbent setae. Mesosoma, petiolar node, postpetiole, first gastral tergum with moderately dense erect setae that are similar in length, longest hairs shorter than MOD; length of hairs on margins of posterior gastral terga occasionally >MOD. Head reddish-brown; mesosoma, petiolar node, postpetiole reddish-brown to blackish-red; antennae, legs, gaster reddish-brown to nearly black (**Figure 14**).

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) large size (HW = 2.94–3.09 mm), (3) striae cover cephalic dorsum, (4) in profile, lateral lobe of clypeus not enlarged with broad gap (similar to the width of antennal scape) between clypeal lobe and frontal lobe, and (5) bicolored—head reddish-orange; gaster reddish-brown to nearly black (**Figure 15**).

Measurements—(*n* = 7). HL 2.50–2.84; HW 2.94–3.09; MOD 0.55–0.64; OMD 0.59–0.64; SL 1.52–1.68; PNW 2.01–2.23; HFL 2.20–2.47; ML 3.46–3.62; PW 0.77–0.91; PPW 1.04–1.19. Indices: SI 49.19–55.08; CI 108.10–122.13; OI 18.71–20.85; HFI 71.66–80.98.

Description. Large species (HW = 3.94–3.09 mm) with caste-specific morphology of the mesosoma related to wing-bearing and presence of ocelli on head. In full-face view, head wider than long (CI = 108.1–122.1), posterior margin weakly concave medially. Fine, dense, longitudinal striae cover cephalic dorsum; striae on vertex often less abundant or absent. Interstriae weakly shining to shining. Mandible with six teeth, dorsal surface coarsely rugose. Psammophore well-developed.

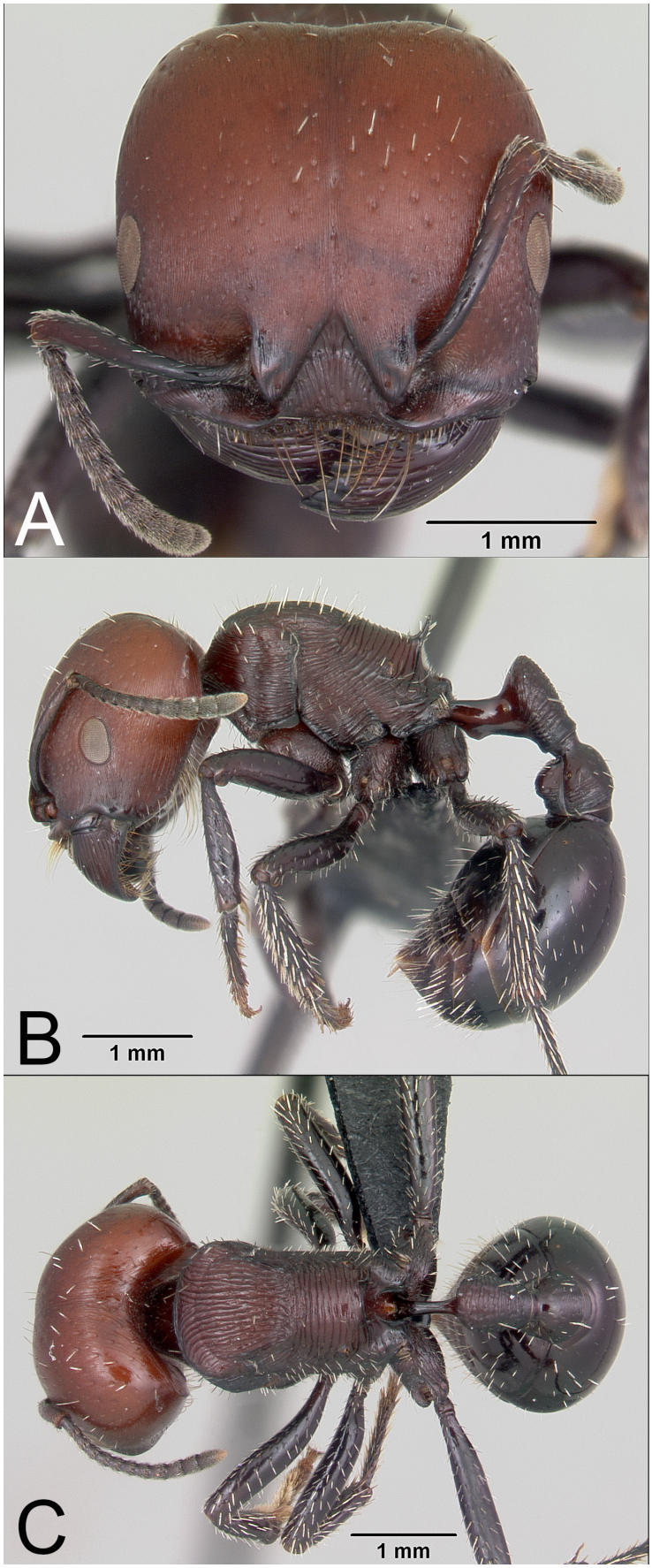

FIGURE 14. Photograph of *Pogonomyrmex micans* Forel worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0103265)**.** Photographs by April Nobile from www.AntWeb.org**.**

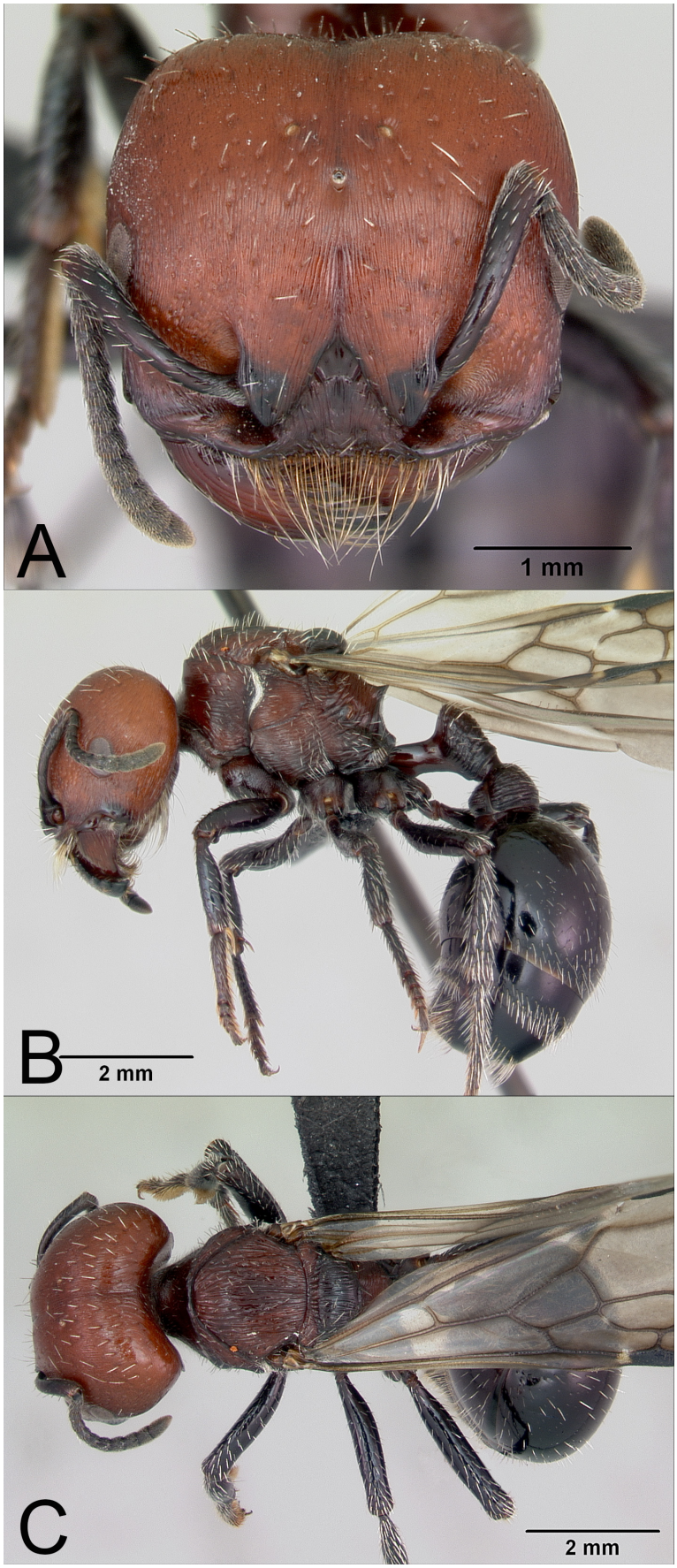

FIGURE 15. Photograph of *Pogonomyrmex micans* Forel alate queen: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0172675)**.** Photographs by April Nobile from www.AntWeb.org**.**

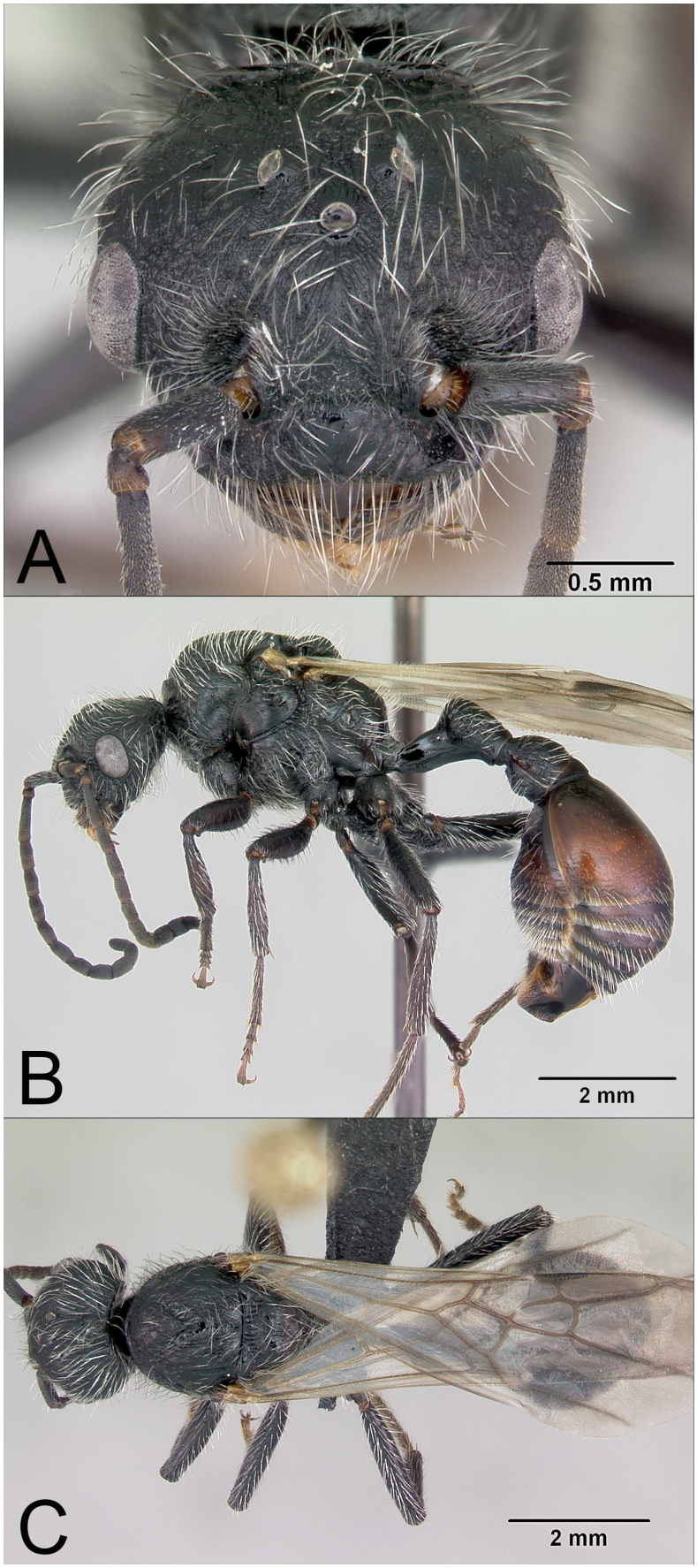

FIGURE 16. Photograph of *Pogonomyrmex micans* Forel male: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0172676)**.** Photographs by April Nobile from www.AntWeb.org**.**

All mesosomal surfaces with subparallel, weakly irregular rugae. Superior propodeal spines short. Peduncle of petiole slightly shorter than petiolar node, anteroventral margin with blunt to angulate process. In profile, petiolar node asymmetrical with anterior surface notably shorter than posterior surface, apex rounded. Postpetiole slightly wider than long. Posterior surface of petiolar node and dorsum of postpetiole with wavy to irregular transverse rugae, rugae coarser on petiolar node than postpetiole; interrugae weakly punctate, weakly shining. Gastral terga smooth, weakly shining to shining. Most body surfaces with moderately abundant suberect to erect, short white to yellowish setae. Head reddish-orange; mesosoma, petiolar node, postpetiole reddish-brown to blackish-red; gaster reddish-brown to nearly black (**Figure 15**).

Male. Diagnosis. This caste is diagnosed by: (1) first gastral tergum lacking striae, (2) large (HW > 1.80 mm; HL > 1.65 mm; ML > 2.75 mm), (3) hairs on head (especially posterior to eyes) and dorsum of mesosoma dense, long and flexuous, length of numerous hairs approach to exceed MOD, (4) mandibles with four teeth, and (5) interrugae on katepisternum dull (**Figure 16**).

Measurements—(*n* = 12). HL 1.67–1.95; HW 1.82–2.11; MOD 0.59–0.68; OMD 0.20–0.38; SL 0.44–0.56; PNW 1.64–1.99; HFL 1.81–2.20; ML 2.99–3.49; PW 0.68–0.83; PPW 0.82–1.02. Indices: SI 22.34–29.26; CI 100.00–126.35; OI 30.41–35.29; HFI 95.90–115.51.

Additional material examined. **ARGENTINA:** ***Catamarca***: Rt 157 at 25.2 km NNW Jct Rt 60, 750', Mar 21, 2015 (RAJC); Rt 20 at 0.7 km NE Esquiú, 800', Mar 21, 2015 (RAJC). ***Córdoba***: Rt 34 at Minas Clavero, 3005', Dec 18, 2006 (RAJC); 2.6 km N Nono, Dec 19, 2006 (CSC); 5 mi N Deán Funes, Feb 8, 1951 (CASC); Rt 16 at 6.1 km NE Jct Rt 38, 1630', Mar 20, 2015 (RAJC); Rt 16 at 15.2 km N Chuña, 1670', Mar 20, 2015 (RAJC); Rt 60 at 27.7 km NW Quilino, 700', Mar 21, 2015 (RAJC). ***Jujuy***: Valle Grande, Feb 11, 1951 (FML). ***La Rioja***: 4.2 km S Jct Rts 79 & 73, 1620', Jan 22, 2006 (RAJC); Rt 38 at 8.1 km W of Córdoba-La Rioja border, 710', Jan 14, 2010 (RAJC); Rt 38 at 9.2 km E Chamical, 1500', Jan 14, 2010 (RAJC); Rt 38 at 15.4 km SE Chamical, 1400', Mar 19, 2015 (RAJC); Rt 38 at 1.6 km W Chamical, 1490', Mar 20, 2015 (RAJC); Rt 79 at 1.5 km S Catuna, 1610', Jan 22, 2010 (RAJC); Rt 79 at 14.2 km S Catuna, 1810', Mar 19, 2015 (RAJC); Rt 79 at 34.6 km S Catuna, 2050', Jan 22, 2006 (RAJC); Rt 79 at 6.9 km SE Ulapes, 1250', Jan 22, 2006 (RAJC); Rt 79 at 26.8 km SE Ulapes, 960', Mar 19, 2015 (RAJC); Rt 79 at 2.6 km N Ulapes, 1360', Mar 18, 2015 (RAJC); Rt 141 at 1.7 km E Chepes, 2150', Mar 17, 2015 (RAJC); Rt 141 at 30.8 km E Chepes, 1880', Mar 18, 2015 (RAJC), Rt 79 at 4.2 km S Jct Rt 141, 1750', Mar 19, 2015 (RAJC); Rt 79 at 55.1 km NE Jct Rt 38, 1240', Mar 22, 2015 (RAJC); Rt 60 at 15.4 km NE Jct Rt 20, 660', Mar 23, 2015 (RAJC). ***Mendoza***: Rt 7 at 5.8 km W Desaguadero, 1530', Dec 28, 2005 (RAJC); no loc, no date (MACN). ***Salta***: Piedras Lumbrera, May 24, 1949 (FML); Lumbreras, no date (LACM); Rt 9 at 1.2 km N turnoff to Lumbrera, 2390', Apr 4, 2015 (RAJC); Piedras, no date (USNM). ***San Luis***: La Tranca, Feb 10, 2009 (RGPC); La Punta, 2790', Mar 6, 2005 & Dec 27, 2005 (RAJC); Rt 20 at 1 km NE Luján, 1940', Dec 26, 2005 (CASC; RAJC); Rt 20 at 38.8 km W Luján, 2030', Dec 27, 2005 (RAJC); Rt 20 at 75.6 km W Luján, 1570', Dec 27, 2005 (CASC; MCZ; RAJC); Rt 20 at 1 km SW Quines, 1670', Dec 26, 2005 (RAJC); 3.7 km SE Jct Rts 20 & 147, 2380', Dec 27, 2005 (RAJC); Rt 7 at Alto Pencoso, 2330', Dec 27, 2005 & Dec 20, 2006 (RAJC); Rt 7 at 3.5 km W Alto Pencoso, Dec 19, 2006 (CSC); 38.8 km N Jct Rts 20 & 79, 1240', Jan 22, 2006 (RAJC); no loc, no date (MACN; MLPA; USNM); Rt 147 at 1.3 km NW turnoff to Parque Nacional Las Quijadas, 2300', Mar 16, 2015 (RAJC). ***Santa Fe***: Ruta 34 at 3 km W Santa Ana, 145 m, Dec 20, 2004 (RAJC). ***Santiago del Estero***: Rt 130 at 11.5 km NW Jct Rt 34, 870', Apr 7, 2015 (RAJC); Rt 64 at 3.7 km W Jct Rt 157, 870', Apr 9, 2015 (RAJC). ***Tucumán***: Ticucho, Dpto Trancas, Nov 6, 1965 (MZUSP); Uruena, Dec 5, 1959 (FML). **PARAGUAY:** ***Boquerón***: Ruta Trans-Chaco, 180 m, Dec 4, 2002 (ALWC) (**Figure 17**).

Etymology. The specific epithet, *micans* (from Latin, *micans* = shining, gleaming, or sparkling), apparently refers to the head, which Forel described as subopaque with a silky aspect.

Discussion. *Pogonomyrmex micans* co-occurs with *P. coarctatus,* and it likely co-occurs with *P. lobatus. Pogonomyrmex micans* is distinguished from *P. coarctatus* using the following characters: (1) in *P. micans*, fine, dense, longitudinal striae cover the cephalic dorsum, (2) dorsum of postpetiole has prominent moderately coarse rugae, and (3) workers are bicolored (dark red and blackish). In *P. coarctatus*: (1) the very fine, dense, longitudinal striae are often indistinct and cover only part to most of head, (2) dorsum of postpetiole is weakly to moderately granulate-punctate, occasionally with weak rugae near posterior margin, and (3) the body is mostly concolorous reddish-orange to reddish-brown. *Pogonomyrmex micans* is distinguished from *P. lobatus* by the following characters: (1) the lateral lobe of clypeus not enlarged, (2) the dorsum of the postpetiole has prominent moderately coarse rugae, and (3) workers are bicolored (dark red and blackish). In *P. lobatus*: (1) the lateral lobe of clypeus is

massively enlarged, nearly contacting the frontal lobe, (2) dorsum of postpetiole weakly to moderately granulate, rarely with weak transverse rugae posteriorly, and (3) workers are concolorous reddish-orange to reddish-brown. *Pogonomyrmex marcusi* is only known from mid- to higher elevations in central Bolivia and thus is geographically isolated from *P. micans*; these two species can be separated using characters in the key.

Biology. *Pogonomyrmex micans* is a solitary forager that harvests the seeds of various grass and nongrass species, but very loose columns of scattered foragers also have been observed. Nests are variable, ranging from entrances lacking a tumulus to ones with a tumulus up to 15 cm in diameter. Colonies of *P. micans* are probably similar in size to those of *P. coarctatus* suggesting that they contain up to about 2000 workers.

Collection dates for sexuals range from 26 December to 22 January, suggesting that mating flights occur during the austral summer (January–February). Queens of *P. micans* contained an average of 12.5 ovarioles ($n = 2$); queen dry mass averaged ($\bar{x}$ ± SE) 20.7 ± 0.4 mg ($n = 5$) (R.A. Johnson, unpub. data).

Pogonomyrmex micans is a lowland species that inhabits elevations from 145–910 m. This species is most common in the Dry Chaco, but it also ranges into the Humid Chaco and the eastern edge of the Low Monte Desert ecoregion as defined by Olson *et al*. (2001). The Jujuy record appears to be an outlier at the edge of the Central Andean Puna/Southern Andean Yungas ecoregions; these specimen were probably collected in a valley at lower elevations (**Figure 17**).

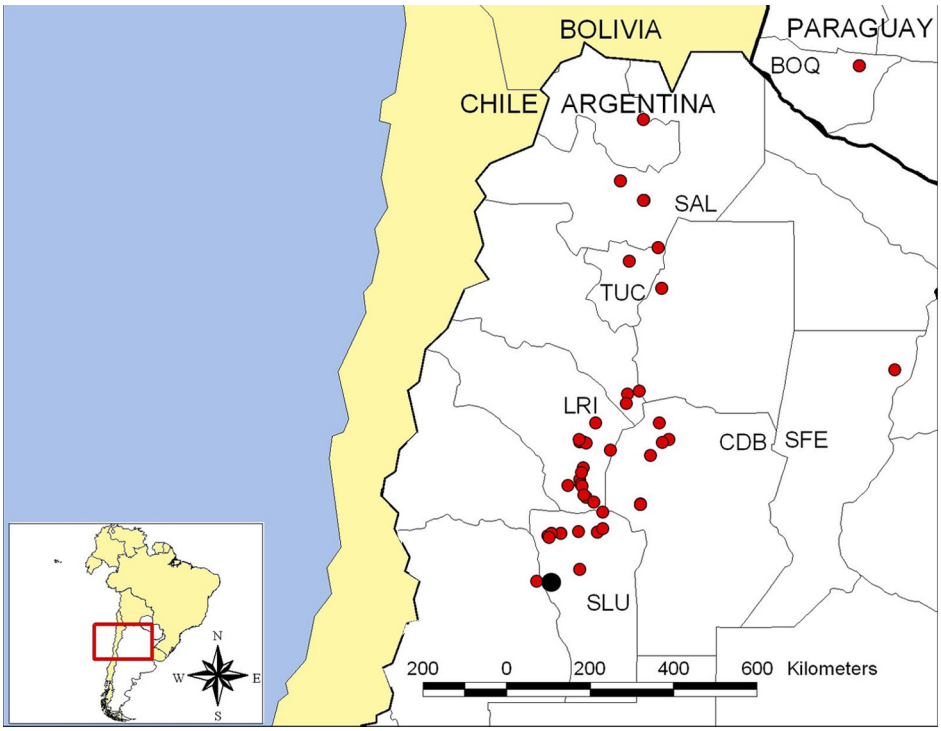

FIGURE 17. Geographic distribution of *Pogonomyrmex micans* Forel. The larger black circle denotes the type locality.

Pogonomyrmex cunicularius-group

Workers in the *P. cunicularius*-group are diagnosed by the following characters: (1) psammophore poorly-developed, consisting of short to medium-length hairs scattered across ventral side of head, (2) first gastral tergum lacking striae, (3) head elongate (CI < 90.0), (4) femur long (HFL > 2.05 mm; HFI > 118.0), (5) scapes long, surpassing posterior corners of head; entire scape with pronounced longitudinal striae, (6) eyes small, ranging from 0.15–0.19x HL, and (7) anterior margin of clypeus flat to weakly convex, apron lacking clypeal teeth.

Queens are diagnosed by: (1) ergatoid, with morphology similar to workers except for presence of ocelli and slightly larger size compared to workers, (2) psammophore poorly-developed, consisting of short to medium-length hairs scattered across ventral side of head, (3) first gastral tergum lacking striae, (4) mesosoma weakly to moderately enlarged, mesosomal segments fused, metanotal groove weakly to moderately impressed, (5) head elongate (CI < 94.0), and (6) femur long (HFI > 116.0).

Pogonomyrmex cunicularius
(Figures 18–20)

Pogonomyrmex cunicularius Mayr, 1887: 613 (worker, male). Syntypes examined: 3 workers [MSNG], 2 workers [NMW], URUGUAY, no location; 1 male [NMW], URUGUAY, Montevideo: Montevideo; 2 workers [NMW], ARGENTINA, Buenos Aires (Prof. Berg leg.). See also Gallardo, 1932: 120, fig. 13; Johnson, 2010: 169, fig. 2. NMW worker from URUGUAY here designated **LECTOTYPE** [CASENT0173372].

Pogonomyrmex cunicularis var. *brevispinus* Santschi, 1931: 275 (worker, ergatoid queen). Syntypes examined: 1 worker, 1 ergatoid queen [MACN], ARGENTINA, Entre Ríos: Estación Sosa (Mac Donagh leg.). Kusnezov, 1951: 251 (synonomy under *cunicularius*; here confirmed). See also Gallardo, 1932: 123. MACN worker here designated **LECTOTYPE** [CASENT0249048].

Worker. Diagnosis. Within the *P. cunicularius*-group, the combination of: (1) in profile, petiolar node broadly rounded, (2) inferior propodeal spines rounded, (3) superior propodeal spines moderately long, shorter than distance between their bases, and (4) first gastral tergum smooth and strongly shining uniquely characterize this species (**Figure 18**).

Measurements—lectotype (n = 16). HL 2.38 (1.85–2.47); HW 2.07 (1.52–2.10); MOD 0.38 (0.31–0.42); OMD 0.62 (0.45–0.69); SL 1.55 (1.44–1.92); PNW 1.44 (1.04–1.47); HFL 2.57 (2.09–2.68); ML 2.83 (2.05–2.87); PW 0.50 (0.40–0.54); PPW 0.72 (0.55–0.76). Indices: SI 74.88 (79.40–100.00); CI 86.97 (81.01–88.21); OI 18.36 (17.79–21.16); HFI 124.15 (119.23–139.38).

Redescription. Head elongate (CI = 81.01–88.21), widest immediately posterior to mandibles, narrowing posterior to eyes; posterior margin flat to weakly convex in full-face view. Cephalic dorsum with weak to moderately strong, wavy or irregular longitudinal rugae to weakly rugoreticulate, rugae often weaker to indistinct near posterior margin; in full-face view, medial rugae diverging weakly toward posterior corners of head. Cephalic interrugae weakly to moderately granulate, weakly shining. Vertex weakly rugose to weakly to moderately granulate, dull to weakly shining. Anterior margin of clypeus flat to weakly convex; dorsal surface with at least several subparallel longitudinal or oblique rugae. Mandibles with six teeth; mandibular dorsum coarsely rugose. Eyes small, MOD ranging from 0.15–0.18x HL. In profile, eyes situated anterior to middle of head, OMD = 1.36–1.77x MOD. Antennal scapes long (SI = 74.88–100.00), surpassing vertex by less than length of first funicular segment; entire scape with longitudinal striae. Basal flange of scape well-developed with carinate margin. Psammophore poorly-developed, consisting of short to medium-length hairs scattered across ventral surface of head.

Promesonotal profile moderately convex, propodeum flat; all mesosomal surfaces with subparallel, irregular rugae to weakly rugoreticulate. In dorsal view, humeral shoulders of pronotum rounded. Dorsum of promesonotum and sides of pronotum with transverse, oblique to longitudinal, irregular rugae to rugoreticulate; mesopleura with irregular rugae that angle posterodorsally. Superior propodeal spines moderately long, acuminate, shorter than distance between their bases; spines connected by well-defined keel; wavy to irregular transverse rugae on propodeal dorsum traverse ventrally or anteroventrally on sides. Inferior propodeal spines well-developed, triangular, wider than high, tips broadly rounded to bluntly angulate. Propodeal spiracles narrowly ovate facing posterad. Interrugae on mesosoma smooth to weakly granulate, weakly to strongly shining. Legs long (HFL = 2.09–2.68 mm), weakly to moderately coriarious to granulate, dull to weakly shining.

Peduncle of petiole about 0.8x length of petiolar node, anteroventral margin with bluntly angulate to angulate triangular process. In profile, posterior surface of petiolar node flattened; node asymmetrical with anterior surface shorter than posterior surface, apex broadly rounded. In dorsal view, petiolar node about 1.5x longer than wide, widest near anterior margin. Sides and posterior surface of petiolar node with weak to moderately coarse, irregular, transverse rugae, or granulate-punctate. Dorsum of postpetiole convex in profile; in dorsal view, widest near posterior margin, narrowing to anterior margin, maximum width about equal to length, strongly granulate-punctate, dull to weakly shining. First gastral tergum smooth, strongly shining.

Erect to semi-erect yellowish pilosity moderately abundant on head, variable in length, longest hairs approaching MOD. Moderately abundant suberect yellowish pilosity on scape; abundant decumbent hairs on funicular segments. Legs with moderately abundant subdecumbent to decumbent yellowish setae. Mesosoma, petiolar node, postpetiole, and gastral terga with moderately dense erect setae, mostly similar in length, longest hairs not exceeding MOD. Body concolorous tannish-orange to tannish-red (**Figure 18**).

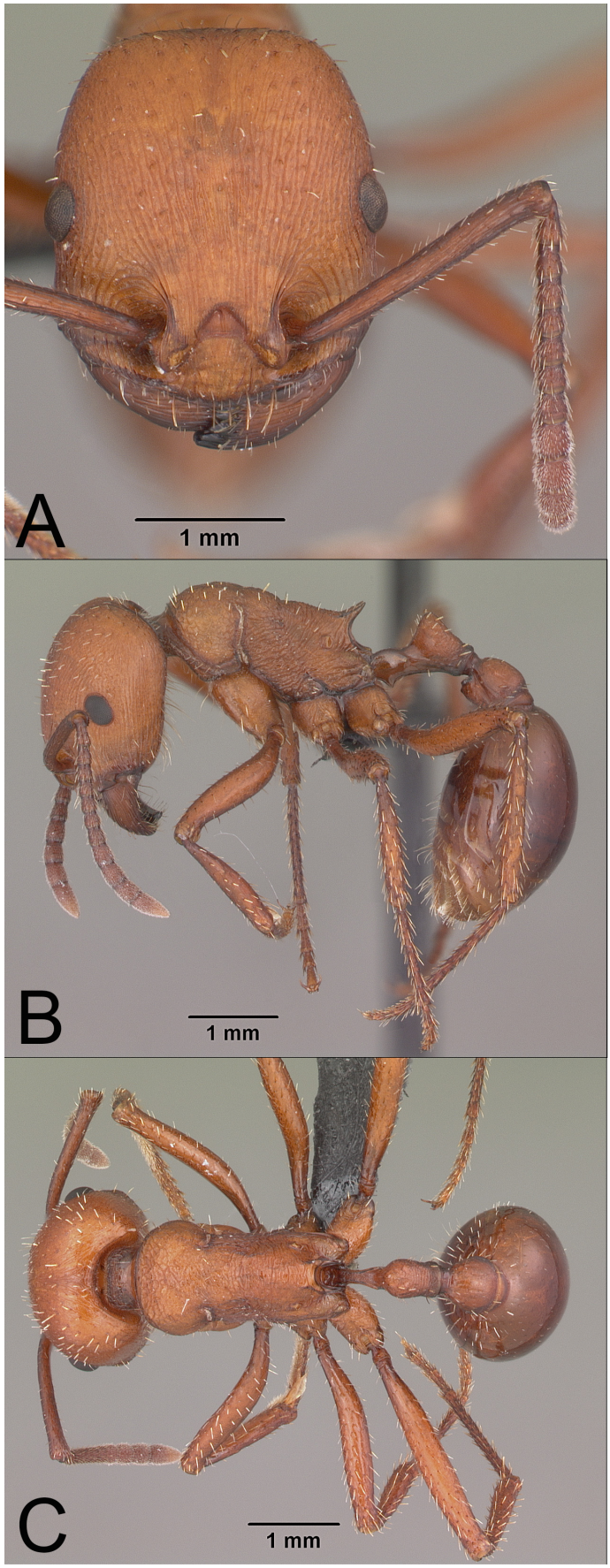

FIGURE 18. Photograph of *Pogonomyrmex cunicularius* Mayr worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0103052)**.** Photographs by April Nobile from www.AntWeb.org**.**

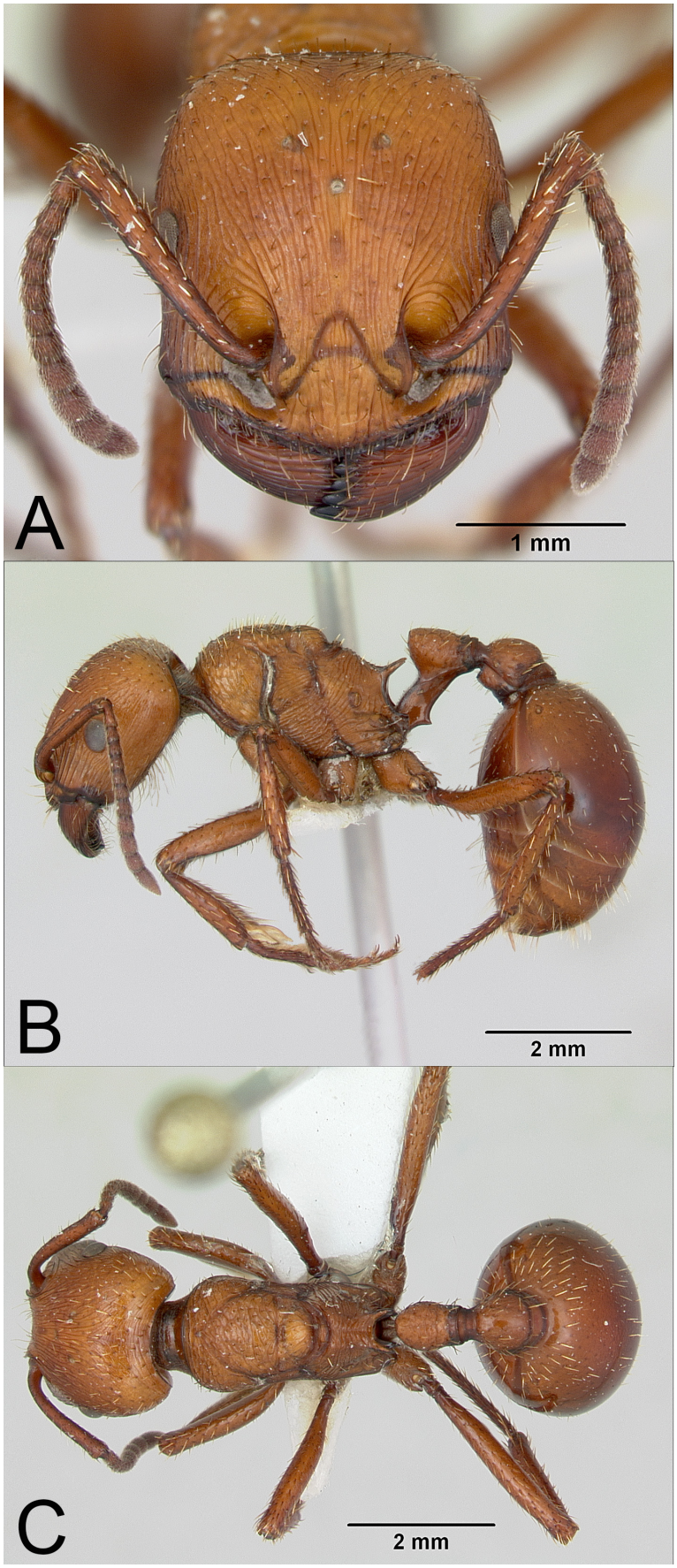

FIGURE 19. Photograph of *Pogonomyrmex cunicularius* Mayr ergatoid queen: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0173109). Photographs by April Nobile from www.AntWeb.org**.**

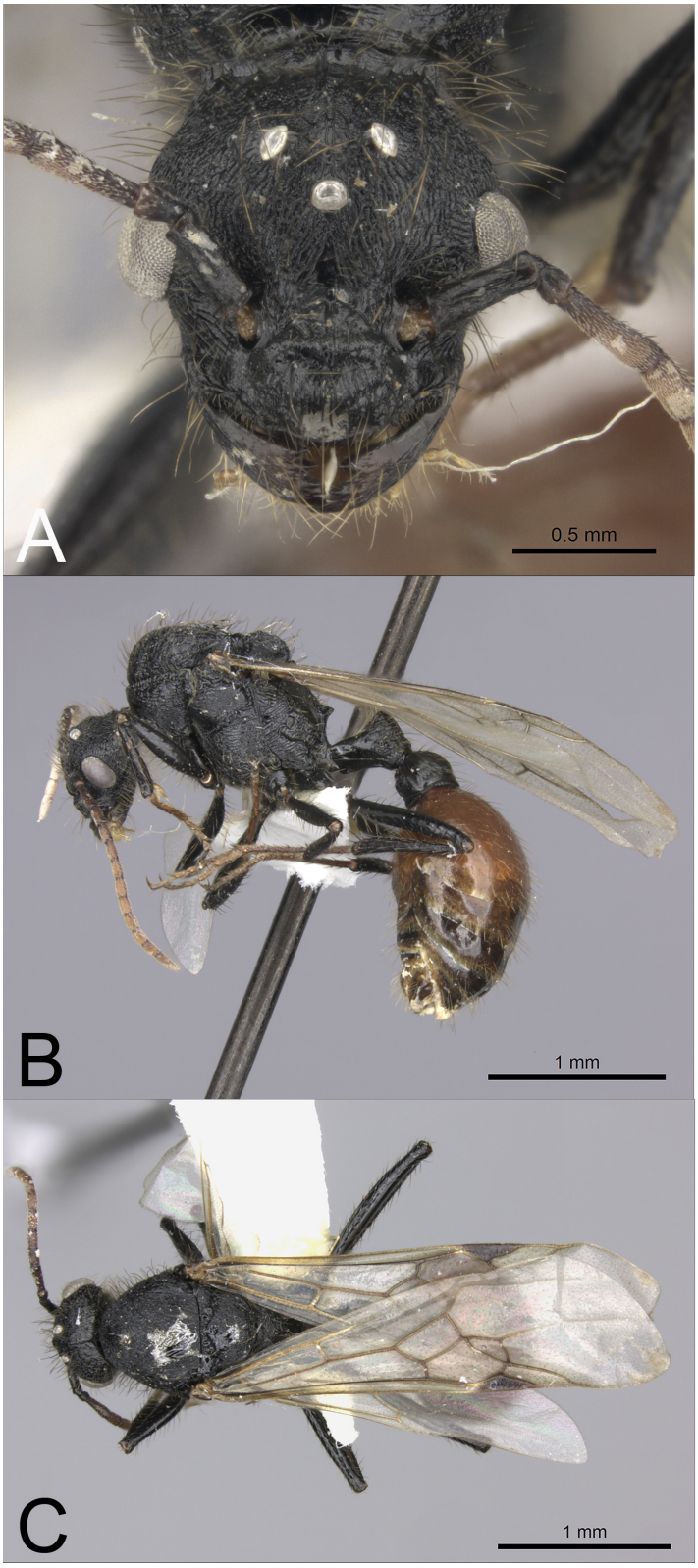

FIGURE 20. Photograph of *Pogonomyrmex cunicularius* Mayr male: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0235298)**.** Photographs by Will Ericson from www.AntWeb.org**.**

Ergatoid Queen. Diagnosis. This caste is diagnosed by: (1) ergatoid, with small ocelli on head, (2) in profile, petiolar node rounded, (3) inferior propodeal spines wider than high, apex broadly rounded, and (4) first gastral tergum smooth and polished, strongly shining (**Figure 19**).

Measurements—(*n* = 12). HL 2.26–2.66; HW 1.96–2.38; MOD 0.35–0.45; OMD 0.54–0.66; SL 1.53–1.87; PNW 1.23–1.60; HFL 2.27–2.70; ML 2.46–3.20; PW 0.51–0.67; PPW 0.71–0.93. Indices: SI 74.63–87.24; CI 85.38–90.49; OI 17.07–20.74; HFI 111.34–125.37.

Male. Diagnosis. This caste is diagnosed by: (1) first gastral tergum lacking striae, (2) femur long (HFL > 1.95 mm), HFI > 150.0, (3) head weakly elongate (CI < 100.0), (4) posterior surface of petiolar node rugose to rugoreticulate, (5) in profile, petiolar node rounded, (6) superior propodeal spines consist of teeth to short spines, and (7) notauli present (**Figure 20**).

Measurements—(*n* = 12). HL 1.30–1.77; HW 1.17–1.54; MOD 0.51–0.64; OMD 0.21–0.32; SL 0.38–0.49; HFL 1.98–2.48; ML 2.51–3.25; PW 0.48–0.67; PPW 0.63–0.97. Indices: SI 24.84–35.66; CI 82.89–92.81; OI 39.61–47.86; HFI 154.69–182.05.

Additional material examined. ARGENTINA: ***Corrientes***: Rt 14 at km 423, 90 m, Feb 27, 2003 (CASC; RAJC); Mercedes, Feb 1918 (MACN; USNM). ***Entre Ríos***: Pueblo Liebig, 70', Dec 17, 2005 & Feb 13, 2010 (CSC; MCZ; RAJC); Rt 14 at 4.5 km N San José/Colón exit, 80', Dec 13, 2006 (RAJC); Rt 14 at 5.1 mi N Gualeguychú, 60', Dec 17, 2005 (RAJC); Estancia Sosa, no date (MACN; MLPA); Hernandarias, Jun 7, 1951 (FML; MZUSP); El Palmar, Nov 24, 2005 (CSC); Parque Nacional El Palmar, Jan 5, 2006 (RGPC); La Picada, May 1951 (FML). **URUGUAY:** ***Artigas***: Pintado Grande, Feb 22, 1969 (FML; LACM); Grutas de Chiflero, Feb 22, 1961 & no date (FML; LACM); R de Chiflero, Feb 22, 1961 (FML); Rt 30, no date (FML). ***Colonia***: Colonia Suissa (= Nueva Helvecia), Mar 11, 1969 (LACM). ***Maldonado***: La Sierra, no date (LACM; MCZ; MSNG). ***Montevideo***: Montevideo, no date (MCZ; MLPA; USNM). ***Paysandú***: Paysandú, Feb 25, 1961 (FML) (**Figure 21A**).

Etymology. The specific epithet, *cunicularius*, (from Latin *cunicul*-, which indicates a miner or burrower, plus the Latin suffix -*arius*, which denotes belonging to) apparently refers to the soil nests excavated by this species. Mayr did not discuss the naming of this species, but Kusnezov (1949) wrote that *P. cunicularius* was the only Argentinian species of *Pogonomyrmex* that constructed a nest crater.

Discussion. *Pogonomyrmex cunicularius* is not known to co-occur with any other *P. cunicularius*-group species but additional collections may show it co-occurs with both *P. pencosensis* and *P. serpens*. *Pogonomyrmex cunicularius* can be distinguished from these two species based on the following characters: (1) in profile, petiolar node broadly rounded, (2) inferior propodeal spines rounded, and (3) first gastral tergum smooth and strongly shining. In *P. pencosensis* and *P. serpens*: (1) in profile, the petiolar node is angulate, (2) inferior propodeal spines are acuminate, and (3) first gastral tergum is weakly to moderately coriarious, dull to weakly shining.

Santschi erected *P. cunicularius* var. *brevispinus* because, compared to the type specimen, the propodeal spines were shorter (no longer than maximum eye diameter), the petiolar node was narrower, and the postpetiole was slightly longer than wide along the posterior margin. Kusnezov (1951) synonomized *P. cunicularius* var. *brevispinus* under *P. cunicularius* without discussion, and I concur with his synonomy. The propodeal spines were slightly shorter in the syntype worker of *P. cunicularius* var. *brevispinus* that I examined, but their length was within the range of variation observed among workers. The width of the petiolar node and shape of the postpetiole also were within the range of variation observed among workers. Finally, the syntype ergatoid queen of *P. cunicularius* var. *brevispinus* and queens of *P. cunicularius* did not display noticeable differences.

Biology. The biology of *P. cunicularius* is poorly known but it is likely similar to that of *P. pencosensis*. This species is a solitary forager that can travel >25 m from the nest. Nests of *P. cunicularius* usually have a pebble tumulus up to 25 cm in diameter with a nest entrance that is up to 2–3 cm in diameter. Colonies of *P. cunicularius* probably contain 500 to >1000 workers, and they can produce >100 ergatoid queens and numerous males (pers. obs.).

Sexuals have been collected from nests from 13 December to 13 February, and one founding queen was excavated on 17 February, indicating the mating flights occur during the austral summer. The large number of ergatoid queens produced by colonies (>100) infers that queens use independent colony founding (see Peeters *et al.*, 2012), which is an unusual behavior for ergatoid queens (see Johnson, 2010). One excavated queen was haplometrotic, and founding queens are probably semi-claustral (they forage) (see Johnson, 2010). Queens contained 9–12 ovarioles (*n* = 3), compared to four in workers (*n* = 6).

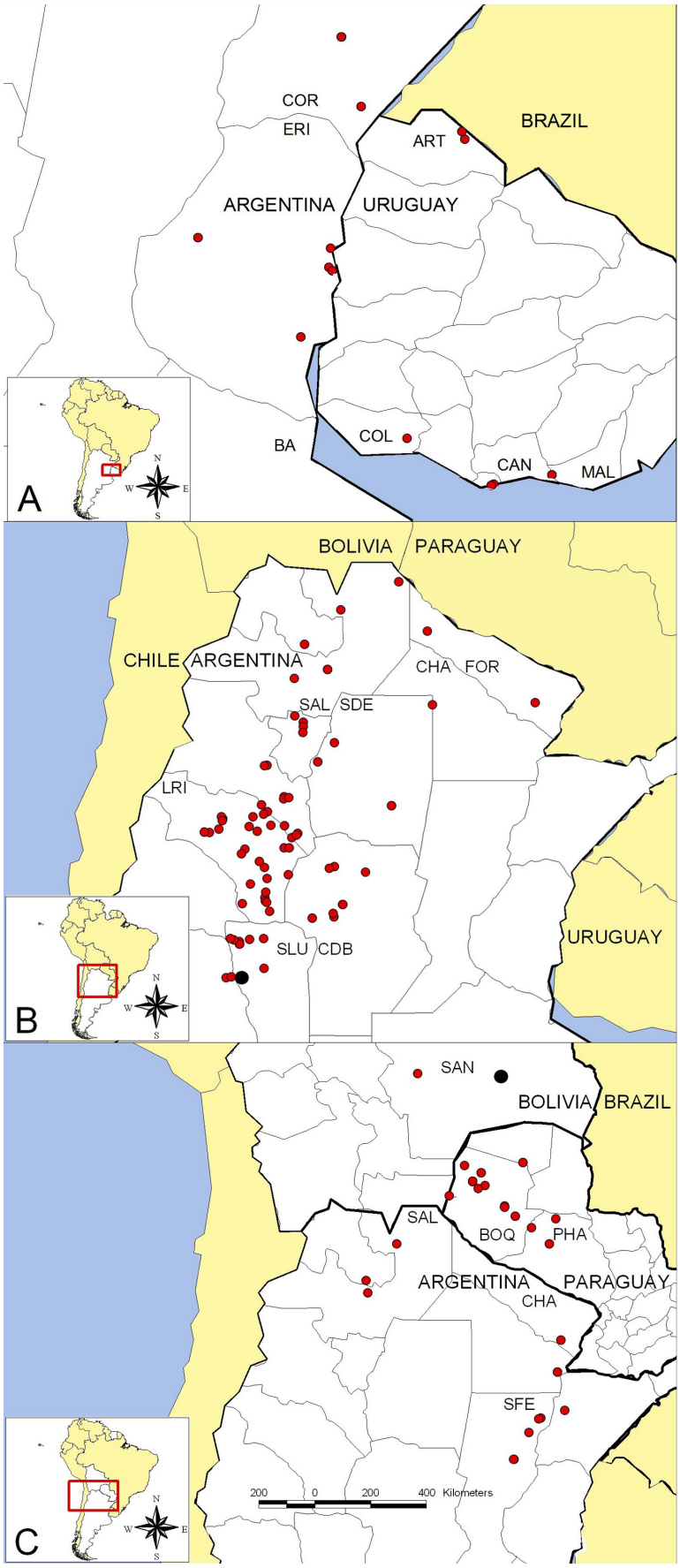

FIGURE 21. Geographic distribution of: (**A**) *Pogonomyrmex cunicularius* Mayr, (**B**) *Pogonomyrmex pencosensis* Forel, and (**C**) *Pogonomyrmex serpens* Santschi. The larger black circle in each panel (when present) denotes the type locality.

Pogonomyrmex cunicularius is a lowland species that occurs at elevations from 20–90 m. This species is only known to occur east and north of Río Paraná in the Espinal, Uruguayan Savanna, and Humid Pampas ecoregions as defined by Olson *et al*. (2001) (**Figure 21A**). The very wide Río Paraná may act as a barrier to dispersal by ergatoid queens. At present, *P. cunicularius* appears to be rare with very fragmented populations that likely result from intense and widespread agricultural use over most of its historic range (**Figure 21A**).

Pogogonomyrmex pencosensis **NEW STATUS**

(Figures 22–24)

Pogonomyrmex cunicularius pencosensis Forel, 1914: 265 (worker, male). Syntypes examined: 24 workers, 1 ergatoid queen, 1 male [MHNG], 1 worker [MLPA], ARGENTINA, San Luis: Alto Pencoso, #1555 (Bruch leg.); Kusnezov, 1951: 251 (synonomy under *cunicularius*; not confirmed here). See also Gallardo, 1932: 125, figs. 16, 17; Johnson, 2010: 169, fig. 1. MLPA worker here designated **LECTOTYPE** [CASENT0217253].

Pogonomyrmex cunicularius pencosensis var. *dubia* Forel, 1914: 267 (worker) [UNAVAILABLE NAME]. Material examined: 1 worker [MHNG], 1 worker [MLPA], ARGENTINA, San Luis: Alto Pencoso (Bruch leg.); Kusnezov, 1951: 251 (material referred to *P. cunicularius*; material herein referred to *pencosensis*). See also Gallardo, 1932: 128.

Worker. Diagnosis. Within the *P. cunicularius*-group, the combination of: (1) in profile, apex of petiolar node weakly rounded to angulate, (2) inferior propodeal spines acuminate, (3) superior propodeal spines long, length notably greater than distance between their bases, (4) first gastral tergum moderately coriarious, dull to weakly shining, (5) sculpturing on dorsum of promesonotum and posterior surface of petiolar node weak to moderately strong, rugae irregular to moderately rugoreticulate, (6) propodeal dorsum consistently transversely rugose, and (7) entire body concolorous tannish-red uniquely characterize this species (**Figure 22**).

Measurements—lectotype (n = 12). HL 1.88 (1.79–2.27); HW 1.51 (1.57–1.95); MOD 0.30 (0.31–0.40); OMD 0.41 (0.44–0.63); SL 1.43 (1.35–1.85); PNW 0.95 (1.10–1.31); HFL 2.30 (2.21–2.78); ML 2.22 (2.30–2.82); PW 0.38 (0.39–0.47); PPW 0.54 (0.51–0.63). Indices: SI 94.70 (79.26–98.92); CI 80.32 (81.53–88.27); OI 19.87 (17.84–22.70); HFI 152.32 (130.85–151.38).

Redescription. Head elongate (CI = 80.32–88.27), widest immediately posterior to mandibles, narrowing posterior to eyes; posterior margin flat to weakly convex in full-face view. Cephalic dorsum with weak to moderately coarse, wavy to irregular longitudinal rugae to weakly rugoreticulate, rugae often weaker to indistinct near posterior margin; in full-face view, medial rugae diverging weakly toward posterior corners of head. Cephalic interrugae weakly to strongly granulate, dull to weakly shining. Vertex weakly to moderately rugose or granulate, dull to weakly shining. Anterior margin of clypeus flat; dorsal surface with at least several subparallel longitudinal or oblique rugae. Mandibles with six teeth; mandibular dorsum coarsely rugose. Eyes small, MOD ranging from 0.15–0.19x HL. In profile, eyes situated anterior to middle of head, OMD = 1.19–1.80x MOD. Antennal scapes long (SI = 79.26–98.92), surpassing vertex by less than length of first funicular segment; entire scape with longitudinal striae. Basal flange of scape well-developed with carinate margin. Psammophore poorly-developed, consisting of short to medium-length hairs scattered across ventral surface of head.

Promesonotal profile weakly convex, propodeum flat; all mesosomal surfaces with subparallel, irregular rugae to weakly rugoreticulate. In dorsal view, humeral shoulders of pronotum rounded. Dorsum of promesonotum with transverse or oblique, irregular rugae to rugoreticulate, weaker or mostly absent to weakly to moderately granulate on pronotal sides; mesopleura with irregular rugae that angle posterodorsally. Superior propodeal spines long, strongly tapered, acuminate, notably longer than width between their bases; spines connected by well-defined keel; irregular transverse rugae on propodeal dorsum traverse ventrally or anteroventrally on sides. Inferior propodeal spines well-developed, triangular, wider than high, with angulate to acuminate tip. Propodeal spiracles narrowly ovate facing posterad. Interrugae on mesosoma smooth to moderately granulate, weakly to strongly shining. Legs long (HFL = 2.21–2.78 mm), strongly coriarious to granulate, dull.

Peduncle of petiole about as long as petiolar node, anteroventral margin with an acuminate spine. In profile, petiolar node asymmetrical with anterior surface notably shorter than posterior surface; apex weakly rounded to angulate, usually weakly elevated above the flattened posterior surface of petiolar node. In dorsal view, petiolar node about 1.5x longer than wide, widest near weakly to moderately acute anterior margin. Sides and posterior surface of petiolar node with irregular, transverse rugae, rugoreticulate, or granulate-punctate. Dorsum of

postpetiole convex in profile; in dorsal view, widest near posterior margin, narrowing to anterior margin, slightly longer than wide, strongly granulate-punctate, dull to weakly shining. First gastral tergum moderately to strongly coriarious, dull to weakly shining.

Erect to semi-erect yellowish pilosity moderately abundant on head, variable in length, longest hairs notably shorter than MOD. Moderately abundant suberect, yellowish pilosity on scape; abundant decumbent hairs on funicular segments. Legs with moderately abundant subdecumbent to decumbent white to yellowish setae. Mesosoma, petiolar node, postpetiole, and gastral terga with moderately dense, erect setae, mostly similar in length, longest hairs shorter than MOD. Body concolorous tannish-red, often with darker transverse bands on gastral terga (**Figure 22**).

Ergatoid Queen. Diagnosis. This caste is diagnosed by: (1) ergatoid, with small ocelli on head, (2) in profile, petiolar node angulate, (3) inferior propodeal spines about as wide as high, acuminate, (4) first gastral tergum moderately coriarious, dull to weakly shining, and (5) sculpturing on dorsum of mesosoma and posterior surface of petiolar node weak to moderately coarse, rugae irregular to moderately rugoreticulate (**Figure 23**).

Measurements—(*n* = 12). HL 2.24–2.58; HW 1.99–2.26; MOD 0.38–0.43; OMD 0.51–0.65; SL 1.70–1.91; PNW 1.27–1.50; HFL 2.45–2.86; ML 2.62–3.13; PW 0.45–0.57; PPW 0.68–0.82. Indices: SI 77.63–86.93; CI 85.78–92.41; OI 16.81–21.61; HFI 108.41–143.72.

Description. Ergatoid, very similar to workers except for presence of ocelli on head and slightly larger size (HL = 2.24–2.58, HW = 1.99–2.26 for queens: HL = 1.79–2.27, HW = 1.57–1.95 for workers). In full-face view, head elongate (CI = 85.78–92.41), sides of head from mandible to lower eye margin parallel, usually slightly wider immediately behind eyes than posterior to mandibles, posterior margin flat. Cephalic dorsum with wavy to weakly irregular longitudinal rugae, interrugae moderately to strongly granulate-punctate, dull to weakly shining; vertex with weaker to faintly visible rugae, weakly shining to shining. Mandible with six teeth, dorsal surface coarsely rugose. Psammophore poorly-developed, consisting of short to medium-length hairs scattered across ventral surface of head.

Mesosomal segments fused, occasionally with weakly impressed promesonotal and/or mesoepinotal suture, lacking all morphological structures related to wings. All mesosomal surfaces with wavy to weakly irregular rugae. Superior propodeal spines long; spines longer than width between their bases; inferior propodeal spines well-developed, triangular, wider than high, with angulate to acuminate tip. Peduncle of petiole about as long as petiolar node, anteroventral margin with an acute spine-like process. In profile, petiolar node asymmetrical with anterior surface notably shorter than posterior surface, apex angulate. Posterior surface of petiolar node with wavy to moderately irregular transverse rugae; interrugae weakly punctate, weakly shining. Postpetiole convex in profile; in dorsal view, maximum width about equal to length; dorsum moderately to strongly granulate-punctate or with weak irregular, transverse to oblique rugae, dull to weakly shining. First gastral tergum moderately to strongly coriarious, dull to weakly shining. Most body surfaces with moderately abundant suberect to erect, short white to yellowish setae. Body concolorous tannish-red, gaster often slightly darker with one or more darker transverse bands (**Figure 23**).

Male. Diagnosis. This caste is diagnosed by: (1) first gastral tergum lacking striae, (2) femur long (HFL > 1.95 mm), HFI > 135.0, (3) head weakly elongate (CI < 100.0), (4) posterior surface of petiolar node rugose to rugoreticulate, (5) superior propodeal spines consist of teeth to short spines, (6) in profile, petiolar node angulate to sharply angulate, and (7) notauli present (**Figure 24**).

Measurements—(*n* = 12). HL 1.36–1.66; HW 1.10–1.44; MOD 0.50–0.62; OMD 0.18–0.33; SL 0.34–0.53; HFL 1.97–2.64; ML 2.37–3.25; PW 0.44–0.63; PPW 0.62–0.89. Indices: SI 29.50–41.09; CI 80.88–97.96; OI 38.85–45.74; HFI 136.81–195.56.

Additional material examined. ARGENTINA: ***Catamarca***: Jct Rts 46 & 60, 2830', Jan 17, 2006 (RAJC); Joyango, Dec 30, 1973 (LACM; USNM); Villa Vil, Feb 11, 1974 (LACM); Andagalá, Feb 10, 1945 (USNM); Chumbicha, no date (MACN); Rt 20 at 13.9 km SW Esquiú, 870', Mar 21, 2015 (RAJC); Rt 20 at 20.6 km SW Esquiú, 850', Mar 21, 2015 (RAJC); Rt 38 at 6.5 km SE Jct Rt 1, 2000', Apr 9, 2015 (RAJC). ***Córdoba***: Nono, 2940', Jan 17, 2008 (RAJC); Rt 20 at 1.0 km N Nono, 2920', Jan 23, 2006 (RAJC); Córdoba, Nov 20, 1948 (FML); Anisacate, no date (FML); 5 mi N Deán Funes, Feb 8, 1951 (CASC); 24 mi S El Recreo, Feb 9, 1951 (CASC); Rt 16 at 15.2 km N Chuña, 1670', Mar 20, 2015 (RAJC); Rt 38 at 0.6 km S entrance to Catamarca, 1630', Mar 22, 2015 (RAJC); Alta Gracia, Apr 1930 (MACN); Alta Gracia La Granja, Sierras de Córdoba, no date (USNM); no loc, no date (LACM; MACN; MCZ; MLPA). ***Formosa***: Ingeniero Juárez, Mar 13, 1948 (FML). ***Jujuy***: Palpalá, Jan

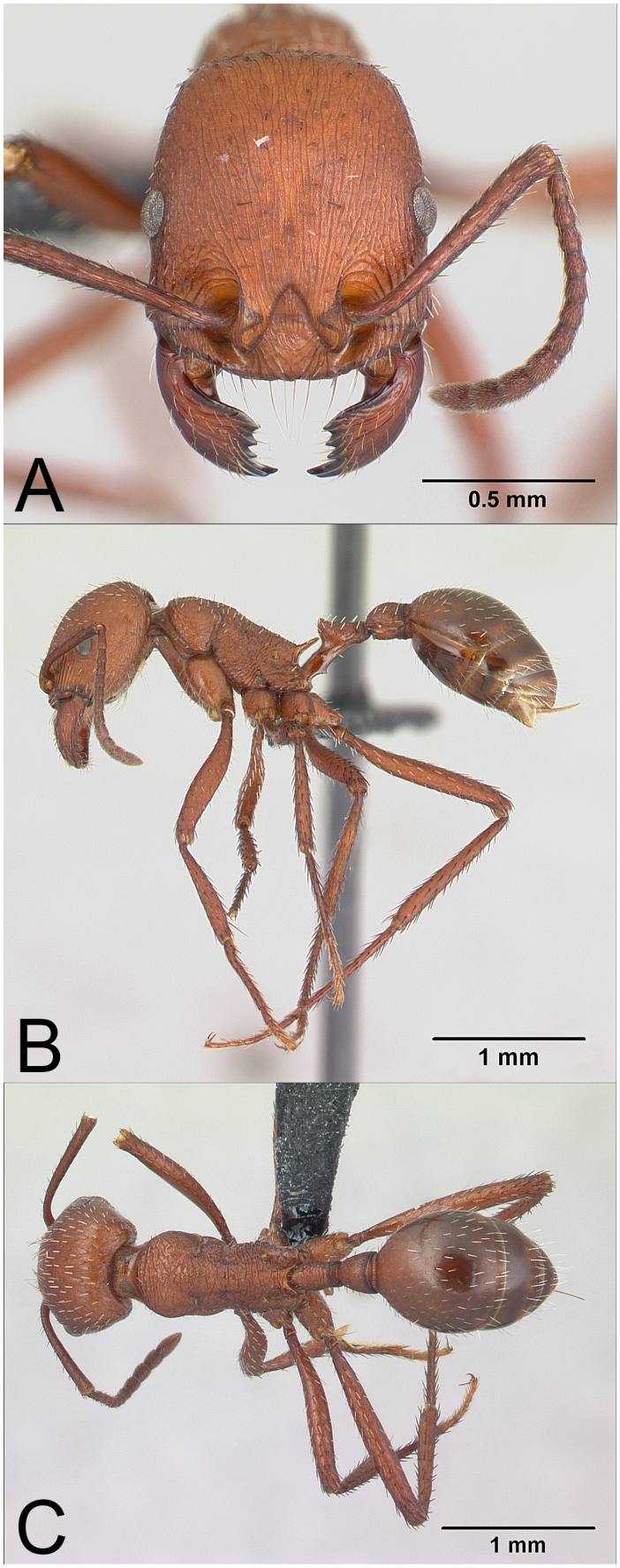

FIGURE 22. Photograph of *Pogonomyrmex pencosensis* Forel worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0178878). Photographs by Erin Prado from www.AntWeb.org**.**

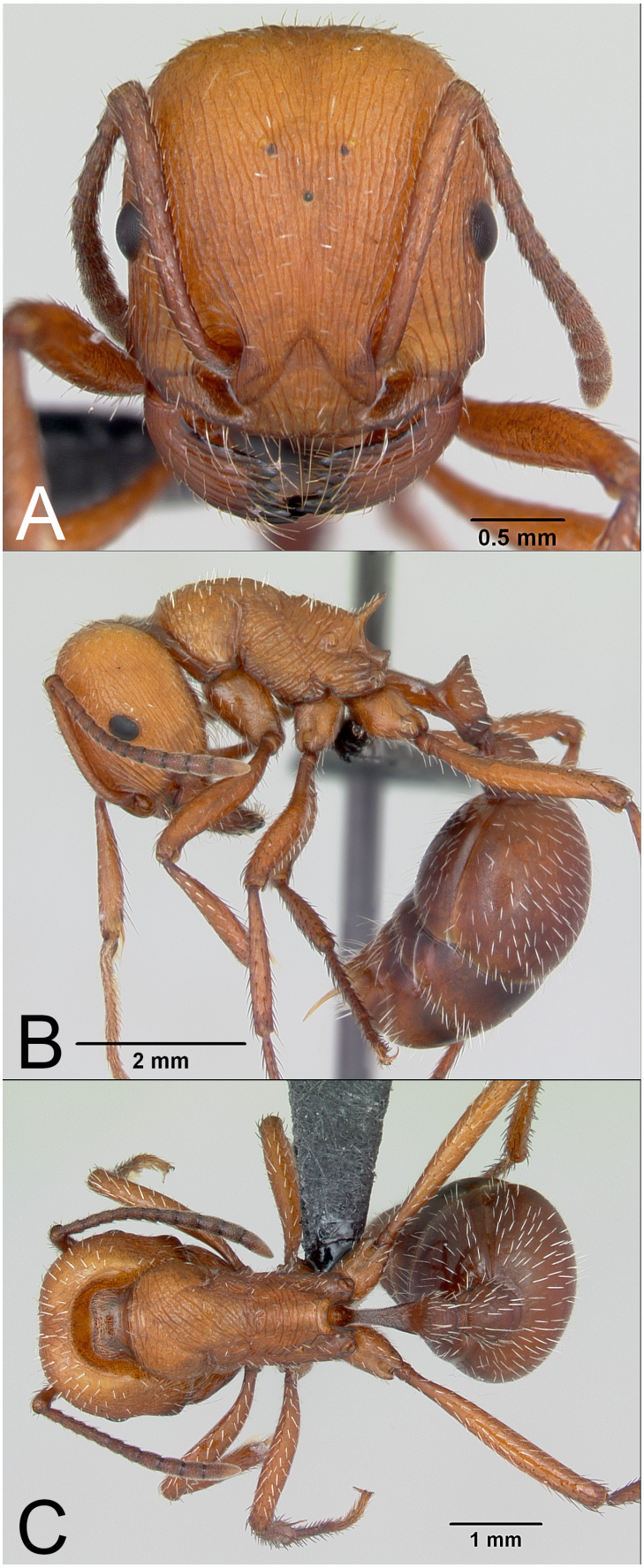

FIGURE 23. Photograph of *Pogonomyrmex pencosensis* Forel ergatoid queen: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0172682). Photographs by April Nobile from www.AntWeb.org**.**

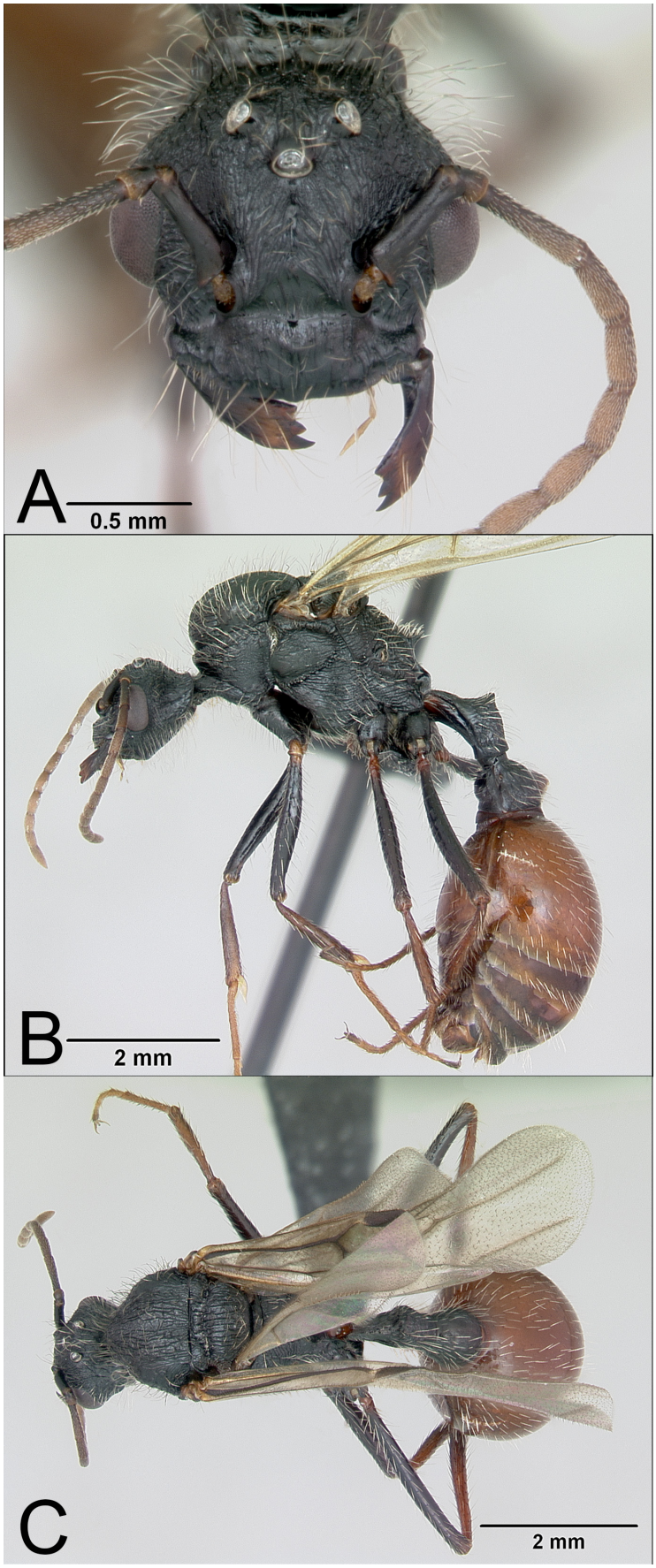

FIGURE 24. Photograph of *Pogonomyrmex pencosensis* Forel male: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0172683). Photographs by April Nobile from www.AntWeb.org.

25, 1948 (FML). ***La Rioja***: 30.8 km E Jct Rts 5 & 38, 1160', Jan 21, 2006 (RAJC); 36.3 km E Jct Rts 5 & 60, 1080', Jan 21, 2006 (RAJC); Rt 38 at 11.5 km SW Jct Rt 60, 1300', Mar 22, 2015 (RAJC); 4.2 km S Jct Rts 79 & 73, 1620', Jan 22, 2006 (RAJC); 4.3 km SE Jct Rts 5 & 60, 960', Jan 21, 2006 (RAJC); 47.0 km SE Jct Rts 5 & 60, 850', Jan 21, 2006 (RAJC); 96.8 km N Jct Rts 9 & 38, 1750', Jan 7, 2006 (RAJC); Rt 38 at 24.7 km N La Rioja, 1400', Jan 7, 2006 (RAJC); Rt 38 at 15.8 km N Patquía, 1580', Jan 20, 2006 (RAJC); 7.4 km N Jct Rts 38 & 74, 1490', Jan 15, 2010 (RAJC); Rt 38 at 8.1 km W of Córdoba-La Rioja border, 710', Jan 14, 2010 (RAJC); Rt 40 at 1.3 km W Los Tambillos, 5240', Jan 3, 2006 (RAJC); Rt 40 at 6.0 km N Chilecito, 3200', Jan 3, 2006 (RAJC); Rt 40 at 11.3 km N Chilecito, 3230', Feb 6, 2010 (RAJC); Rt 40 at 14.0 km N Chilecito, 3410', Feb 4, 2010 (MCZ; RAJC); Rt 40 at 49.1 km S Pituil, 4270', Jan 20, 2006 (RAJC); Rt 40 at 5.7 km SW Nonogasta, 3690', Jan 3, 2006 (RAJC); Rt 73 at 83.8 km NE Chamical, 1110', Jan 21, 2006 (RAJC); Rt 38 at 19.2 km NW Chamical, 1630', Mar 22, 2015 (RAJC); Rt 79 at 30.1 km N Catuna, 1690', Mar 19, 2105 (RAJC); Rt 79 at 14.2 km S Catuna, 1810', Mar 19, 2015 (RAJC); Rt 79 at 34.6 km S Catuna, 2050', Jan 22, 2006 (RAJC); Rt 79 at 6.9 km SE Ulapes, 1250', Jan 22, 2006 (RAJC); Rt 79 at 95.0 km NE Jct Rt 38, 700', Mar 23, 2015 (RAJC); Rt 40 at 30.0 km E Villa Unión, 4560', Jan 3, 2006 (CASC; RAJC); no loc, no date (MACN). ***Mendoza***: Rt 7 at 19.8 km E La Paz, 1520', Jan 23, 2008 (RAJC); Rt 7 at 5.8 km W Desaguadero, 1530', Dec 28, 2005 (RAJC). ***Salta***: 50 km NE Joaquín V Gonzáles, Mar 4, 1992 (LACM); San Bernardo, Jan 19, 1948 (FML); Osma, Jan 27, 1948 (FML); Pichanal, Nov 27, 1948 (FML). ***San Luis***: La Tranca, Feb 10, 2009 (RGPC); Portezuelo, Apr 16, 2009 (RGPC); 3.7 km SE Jct Rts 20 & 147, 2380', Dec 27, 2005 (RAJC); Rt 20 at 24.6 km NW Jct Rt 147, 1630', Mar 16, 2015 (RAJC); La Punta, 2790', Dec 27, 2005 (RAJC); Parque Nacional Sierra las Quijadas, 2610' & 2720', Mar 6, 2005 (RAJC); Rt 20 at 38.8 km W Luján, 2030', Dec 27, 2005 (RAJC); Rt 20 at 75.6 km W Luján, 1570', Dec 27, 2005 (RAJC); Rt 7 at Alto Pencoso, 2330', Dec 27, 2005 (MACN; RAJC); no loc, no date (MLPA); Rt 141 at 17.2 km E border with San Juan, Mar 17, 2015 (RAJC); Rt 141 at 30.8 km E Chepes, 1880', Mar 18, 2015 (RAJC); Rt 79 at 4.2 km S Jct Rt 141, 1750', Mar 19, 2015 (RAJC). ***Santiago del Estero***: Pampa de los Guanacos, 142 m, Apr 2009 (RAJC); Lago Muyo, Apr 1957 (LACM); Río Hondo, Jan 14, 1948 (FML). ***Tucumán***: 9 km SSE Las Cejas, 330 m, Feb 4, 1995 (MCZ); Ticucho, Dpto Trancas, Dec 1, 1965 (MZUSP); Saladillo, no date (USNM); San Pedro de Colalao, no date (FML); Tapia-Trancas, Nov 19, 1998 (FML); Depto Leales, Mar 26, 1948 (FML); no loc, no date (USNM). ***Locations not found. Salta***: Rt 34, no date (FML). ***Tucumán***: Reserva Forestal, Mar 2–4, 1948 (FML). ***Questionable locales. Catamarca***: Agudos, Feb 4, 1967 (MCZ) (**Figure 21B**).

Etymology. The specific epithet, *pencosensis* (Latinization of Pencoso, and -*ensis* = adjectival suffix for belonging to), refers to the syntype series being collected at Alto Pencoso, San Luis Province, Argentina.

Discussion. *Pogonomyrmex pencosenis* is not known to co-occur with any other *P. cunicularius*-group species. However, additional collections may show it co-occurs with *P. cunicularius* and *P. serpens*. *Pogonomyrmex pencosensis* can be distinguished from *P. cunicularius* based on the following characters: (1) petiolar node angulate in profile, (2) superior propodeal spines longer than distance between their bases, (3) inferior propodeal spines about as wide as high, acuminate, and (4) first gastral tergum coriarious, dull to weakly shining. In *P. cunicularius*, the petiolar node is rounded in profile, superior propodeal spines are shorter than the distance between their bases, inferior propodeal spines are wider than high, broadly rounded, and the first gastral tergum is smooth and polished, strongly shining. *Pogonomyrmex pencosensis* is distinguished from *P. serpens* based on the following characters: (1) sculpturing on dorsum of the mesosoma and posterior surface of petiolar node weak, rugae irregular to moderately rugoreticulate, and (2) body concolorous tannish-red. In *P. serpens*, sculpturing on the dorsum of the mesosoma and posterior surface of petiolar node is coarse, rugoreticulate to vermiculate, and the body is bicolored with mesosoma and petiolar node orangish-brown to reddish-brown, the rest slightly lighter.

In describing *P. cunicularius* race *pencosensis*, Forel indicated it to be smaller and more slender, the sculpturing more dense, the head more dull, and the inferior propodeal spines longer and more acute than in *P. cunicularius.* Indeed, workers and ergatoid queens of *P. pencosensis* are morphologically distinct and easily distinguished from *P. cunicularius* and *P. serpens*. Thus, I raise *P. pencosensis* from synonomy to rank as a valid species.

Biology. *Pogonomyrmex pencosensis* is one of the more well-studied species of *Pogonomyrmex* in Argentina. This species is a solitary forager that can travel >25 m from the nest. Unlike most congeners, *P. pencosensis* is a scavenger, with insects (mostly dead ants) comprising most of the diet (62%), followed by seeds (22%), and plant parts (12%). Most harvested seeds are those produced by shrubs and trees in which the seed possesses an aril, elaisome, or other attractant body; this species is also a key disperser for the shrub *Japtropha excisa*, which

produces myrmecochorous seeds with an elaisome (Aranda-Rickert & Fracchia, 2011, 2012). Nests of *P. pencosensis* can be cryptic and lack a tumulus or they can have a pebble tumulus up to 25 cm in diameter, occasionally with a small chaff midden and a 2–3 cm nest entrance. Nests of *P. pencosensis* have 10–30 chambers, reach a depth of 60–70 cm, and contain 500 to >1000 workers along with >100 ergatoid queens and numerous males (Aranda-Rickert & Fracchia, 2012; R.A. Johnson, pers. obs.).

Pogonomyrmex penscosensis is remarkable among species within phylogenetically advanced subfamilies of ants because the external morphology of the queen is virtually identical to that of workers, except that queens are slightly larger and they have ocelli and a weakly impressed promesonotal suture (**Figure 23**). Queens also possess 8–13 ovarioles compared to four in workers (see also Johnson, 2010). The morphological similarity between ergatoid queens and workers is also evidenced in that the Forel collection (MHNG) contained one syntype ergatoid queen that previous authors had presumably judged to be a large worker.

Sexuals have been collected from nests from 28 December to 6 February, and foundresses (or foraging ergatoid queens presumed to be foundresses) have been collected from 27 December to 21 January. The large number of ergatoid queens produced by colonies (>100) suggests that queens use independent colony founding (see Peeters *et al.*, 2012), which is an unusual behavior for ergatoid queens (see Johnson, 2010). Additionally, one captured founding queen was semi-claustral (it foraged) and haplometrotic. Ergatoid queens also have been observed foraging outside the nest, but reproductive status was not determined for these individuals (see Johnson, Holbrook, Strehl, & Gadau, 2007). Additional research should examine mating, reproductive, and nest founding behavior of this species.

Pogonomyrmex pencosensis inhabits sites at elevations from 140–1590 m. This species is common in the Dry Chaco ecoregion, but it also occurs in the Humid Chaco, central portions of the High Monte Desert, and along the northeastern edge of the Low Monte Desert ecoregions as defined by Olson *et al.* (2001) (**Figure 21B**).

Pogonomyrmex serpens **NEW STATUS**

(Figures 25–26)

Pogonomyrmex cunicularis var. *serpens* Santschi, 1922: 349 (worker). Syntypes examined: 2 workers [MACN], BOLIVIA, San José, at two hours on the path to Carumba, #1073 (Lizer and Delétang leg.). Kusnezov, 1951: 251 [synonomy under *cunicularius*; not confirmed here]. See also Gallardo, 1932: 123, fig. 15. MACN worker here designated **LECTOTYPE** [CASENT0235269].

Pogonomyrmex cunicularis var. *carnivora* Santschi, 1925a: 155, fig. 2 (worker). Syntypes examined: 6 workers [MACN], 1 worker [MZUSP], ARGENTINA, Santa Fe: Fives Lille, #1614 (Weiser leg.). Kusnezov, 1951: 251 (synonomy under *cunicularius*); Wheeler & Wheeler 1972: 236 (revived from synonomy, raised to species); Bolton, 1995: 340 (resynonomized under *cunicularius*; not confirmed here). See also Gallardo, 1932: 123, fig. 14. MACN worker here designated **LECTOTYPE** [CASENT0249054]. **NEW SYNONOMY**

Worker. Diagnosis. Within the *P. cunicularius*-group, the combination of: (1) in profile, apex of petiolar node weakly rounded to angulate, (2) inferior propodeal spines acuminate, (3) superior propodeal spines long, length greater than distance between their bases, (4) first gastral tergum moderately coriarious, weakly shining, (5) sculpturing on dorsum of promesonotum and posterior surface of petiolar node coarse, rugoreticulate to vermiculate, (6) propodeal dorsum rugoreticulate to transversely rugose, and (7) bicolored—mesosoma and petiolar node darker than rest of body uniquely characterize this species (**Figure 25**).

Measurements—lectotype (n = 12). HL 2.40 (2.00–2.33); HW 2.02 (1.65–2.00); MOD 0.37 (0.32–0.42); OMD 0.76 (0.46–0.62); SL 1.74 (1.58–1.81); PNW 1.38 (1.15–1.34); HFL 2.71 (2.22–2.79); ML 2.77 (2.41–2.76); PW 0.49 (0.43–0.52); PPW 0.66 (0.56–0.72). Indices: SI 86.14 (89.07–97.21); CI 84.17 (81.13–87.50); OI 18.32 (17.88–22.42); HFI 134.16 (127.59–143.96).

Redescription. Head elongate (CI = 81.13–87.50), widest immediately posterior to mandibles, narrowing posterior to eyes; posterior margin flat to weakly convex in full-face view. Cephalic dorsum with moderately coarse, wavy to irregular longitudinal rugae or weakly rugoreticulate; in full-face view, medial rugae diverging weakly toward posterior corners of head. Cephalic interrugae weakly to moderately granulate, weakly shining. Vertex weakly to moderately rugose, dull to weakly shining. Anterior margin of clypeus flat to weakly convex; dorsal surface with several subparallel longitudinal or oblique rugae. Mandibles with six teeth; mandibular dorsum coarsely rugose. Eyes small, MOD ranging from 0.15–0.19x HL. In profile, eyes situated anterior to middle of

head, OMD = 1.27–1.75x MOD. Antennal scapes long (SI = 86.14–97.21), surpassing vertex by less than length of first funicular segment; entire scape with longitudinal striae. Basal flange of scape well-developed with carinate margin. Psammophore poorly-developed, consisting of short to medium-length hairs scattered across ventral side of head.

Promesonotal profile weakly convex, propodeum flat; all mesosomal surfaces with irregular rugae or rugoreticulate to vermiculate. In dorsal view, humeral shoulders of pronotum rounded. Dorsum of promesonotum and sides of pronotum rugoreticulate to vermiculate, dorsum of pronotum sometimes transversely rugose; mesopleura with irregular rugae that angle posterodorsally. Superior propodeal spines long, narrowing to acuminate tip, length greater than distance between their bases; spines connected by well-defined keel; irregular transverse rugae to rugoreticulate on propodeal dorsum, rugae traverse ventrally or anteroventrally on sides. Inferior propodeal spines well-developed, triangular, wider than high, with angulate to acuminate tip. Propodeal spiracles narrowly ovate facing posterad. Interrugae on mesosoma smooth to weakly granulate, weakly shining to shining. Legs long (HFL = 2.22–2.79 mm), weakly to moderately coriarious to granulate, weakly shining.

Peduncle of petiole about 0.8x as long as petiolar node, anteroventral margin with acuminate spine. In profile, posterior surface of petiolar node flattened; node asymmetrical with anterior surface shorter than posterior surface, apex weakly rounded to angulate, usually weakly elevated above posterior surface. In dorsal view, petiolar node about 1.5x longer than wide, widest near anterior margin. Posterior surface of petiolar node with coarse, irregular rugae to rugoreticulate, interrugae weakly to moderately punctate, weakly shining. Dorsum of postpetiole convex in profile; in dorsal view, widest near posterior margin, narrowing towards anterior margin, maximum width about equal to length, strongly granulate-punctate or with weak irregular, transverse rugae, dull to weakly shining. First gastral tergum moderately coriarious, weakly shining.

Erect to semi-erect yellowish pilosity moderately abundant on head, variable in length. Moderately abundant suberect yellowish pilosity on scape; abundant decumbent hairs on funicular segments. Legs with moderately abundant subdecumbent to decumbent yellowish setae. Mesosoma, petiolar node, postpetiole, and first gastral tergum with moderately dense, erect setae, mostly similar in length, longest hairs on posterior gastral terga; longest hairs on rest of body rarely >0.5x MOD. Bicolored with mesosoma and petiolar node darker than rest of body, but color varies geographically. In Argentina, the mesosoma and petiolar node are reddish-orange to reddish-brown, rest of body ferruginous orange. Specimens from Paraguay were darker, with the mesosoma brownish to brownish-orange, rest of body lighter reddish-orange to reddish-brown (**Figure 25**).

Ergatoid Queen. Diagnosis. This caste is diagnosed by: (1) ergatoid, with small ocelli on head, (2) in profile, petiolar node angulate, (3) inferior propodeal spines about as wide as high, acuminate, (4) first gastral tergum moderately coriarious, dull to weakly shining, (5) sculpturing on dorsum of mesosoma and posterior surface of petiolar node weak to moderately strong, rugae irregular to moderately rugoreticulate, and (7) bicolored—mesosoma dark red-orange; head, legs, petiolar node, postpetiole, gaster lighter red-orange (**Figure 26**).

Measurements—(*n* = 5). HL 1.97–2.41; HW 1.63–2.20; MOD 0.35–0.43; OMD 0.42–0.66; SL 1.46–1.84; PNW 1.11–1.37; HFL 2.17–2.68; ML 2.37–2.70; PW 0.43–0.53; PPW 0.58–0.74. Indices: SI 73.64–89.57; CI 82.74–93.62; OI 17.27–21.47; HFI 110.00–133.13.

Description. Ergatoid, very similar to workers except for presence of ocelli on head and slightly larger size (HL = 1.97-2.41, HW = 1.63–2.20 for queens: HL = 2.00–2.40, HW = 1.65–2.02 for workers). In full-face view, head elongate (CI = 82.74–93.62), sides of head from mandible to lower eye margin parallel or diverging weakly toward mandibular insertion; posterior margin flat to weakly convex. Cephalic dorsum with longitudinal, wavy to moderately irregular rugae, sometimes becoming rugoreticulate near posterior margin, interrugae weakly to strongly granulate-punctate, dull to weakly shining; vertex rugose, weakly shining to shining. Mandible with six teeth, dorsal surface coarsely rugose. Psammophore poorly-developed, consisting of short to medium-length hairs scattered across ventral side of head.

Mesosomal segments fused, mesoepinotal suture often weakly impressed, lacking all morphological structures related to wings. Promesonotum mostly rugoreticulate to vermiculate; propodeum with irregular transverse rugae that traverse ventrally on sides. Superior propodeal spines long; spine length similar to or slightly longer than distance between their bases; inferior propodeal spines well-developed, triangular, wider than high, with angulate to acuminate tip. Peduncle of petiole about as long as petiolar node, anteroventral margin with acute spine-like process. In profile, petiolar node asymmetrical with anterior surface notably shorter than posterior surface, apex angulate. Posterior surface of petiolar node with irregular transverse rugae to rugoreticulate-vermiculate; interrugae

weakly punctate, weakly shining to smooth and shining. Postpetiole convex in profile; in dorsal view, maximum width about equal to length; dorsum moderately to strongly granulate-punctate, with weak irregular transverse rugae, or rugoreticulate, dull to weakly shining. First gastral tergum moderately to strongly coriarious, dull to weakly shining. Most body surfaces with moderately abundant suberect to erect, short, yellowish setae. Bicolored—mesosoma dark red-orange; head, legs, petiolar node, postpetiole, gaster lighter red-orange (**Figure 26**).

Male. Unknown.

Additional material examined. ARGENTINA: ***Chaco***: Colonia Benítez, Dec 1–7, 1948 & no date (FML; LACM; MHNG). ***Corrientes***: San Roque, no date (MACN); no loc, Feb 1920 (MACN; USNM); no loc, no date (USNM). ***Formosa***: Reserva El Bagual, 151 m, Apr 2005 (FML; MCZ; RAJC); Gran Guardia, Nov 25–Dec 15, 1952 (FML)**.** ***Jujuy***: Rt 66 at 11.8 km N Jct Rt 34, 2980', Apr 4, 2015 (RAJC). ***Misiones***: no loc, Dec 1920 (MACN). ***Salta***: Embarcación, no date (FML); no loc, Dec 18, 1949 (FML); Rt 9 at 3.0 km N Cabeza de Buey, 2520', Apr 4, 2015 (RAJC). ***Santa Fe***: Ruta 11 at 23 mi S Villa Ocampo, 140 m, Dec 20, 2004 (RAJC); 22 km S Reconquista, 45 m, Nov 15, 2003 (RAJC); Ruta 34 at 3 km W Santa Ana, 145 m, Dec 20, 2004 (RAJC); Fives Lille, no date (MACN; MZUSP). **BOLIVIA:** ***Santa Cruz***: Los Negros, Oct 10, 1962 (LACM). **PARAGUAY**: ***Boquerón***: Nueva Asunción, 1050', Nov 2–6, 2001 (RAJC; RBINS); Enciso, 830', Nov 4–6, 2001 (ALWC; RAJC); Estancia Maria Vicenta, 780', Sep 27–29, 2004 (RAJC; RBINS); Fortin Mayor Infante Rivarola, 910', Oct 1–4, 2004 (RAJC; RBINS); Garrapatal, 710', Nov 5–6, 2001 (RAJC; RBINS); Mister Long, 460', Sep 17–18, 2003 (RAJC; RBINS); Laguna Salada de Salazan, Dec 5, 1993 (ALWC); Ruta Trans-Chaco, 180 m, Dec 4, 2002 (ALWC); Mariscal Estigarribia, Sep 22, 1994 (ALWC); 4 km NW Mariscal Estigarribia, 180 m, Dec 12, 2002 (ALWC); 80 km SW Destacamento Teniente Pico, Aug 6, 1994 (ALWC); Parque Nacional Teniente Enciso, Park Administration area, Aug 6–7, 1994 (ALWC). ***President Hayes***: Los Pioneros, 420', Oct 9–11, 2003 (RAJC; RBINS); Río Verde, 350', Oct 15–16, 2003 (RAJC; RBINS); Ruta Trans-Chaco, 120 m, Dec 5, 2002 (ALWC) (**Figure 21C**).

Etymology. The specific epithet, *serpens* (from Latin, *serpens* = serpent), apparently refers to a snake. Santschi did not discuss the naming of this species, so its derivation is unclear. The name might refer to the narrow, elongate body of this species.

Discussion. *Pogonomyrmex serpens* is not known to co-occur with any other *P. cunicularius*-group species but it is likely to co-occur with both *P. cunicularius* and *P. pencosensis*. *Pogonomyrmex serpens* can be distinguished from *P. cunicularius* by the combination of: (1) petiolar node angulate in profile, (2) inferior propodeal spines about as wide as high with an acuminate tip, (3) first gastral tergum moderately to strongly coriarious, dull to weakly shining, and (4) superior propodeal spines long, length greater than distance between their bases. In *P. cunicularius*: (1) the petiolar node is rounded in profile, (2) the inferior propodeal spines are wider than high with a broadly rounded apex, (3) the first gastral tergum is smooth and polished, strongly shining, and (4) superior propodeal spines are short, length less than distance between their bases. *Pogonomyrmex serpens* can be distinguished from *P. pencosensis* by the combination of: (1) sculpturing on dorsum of mesosoma and posterior surface of petiolar node coarse, rugoreticulate to vermiculate, and (2) body bicolored with mesosoma and petiolar node medium to dark orangish-brown to reddish-brown, rest of body lighter. In *P. pencosensis*: (1) sculpturing on the dorsum of the mesosoma and posterior surface of petiolar is weak to moderately strong, rugae are irregular to moderately rugoreticulate, and (2) the body is concolorous tannish-red.

In describing *P. cunicularius* var. *serpens*, Santschi did not note specific differences from the other two forms, but said only that the head was a dark reddish-brown and that sculpturing on both the dorsum and sides of the mesosoma consisted of irregular to vermiculate rugae. The bicolored body and the much stronger and more irregular to vermiculate sculpturing on the mesosoma make this form morphologically distinct from both *P. cunicularius* and *P. pencosensis*. Thus, I raise *P. serpens* from synonomy to rank as a valid species.

Santschi described *P. cunicularius* var. *carnivora* as very similar to variety *serpens*, except that *carnivora* was slightly larger and had much longer superior propodeal spines (length twice the distance between their bases compared to similar to distance between the bases in *serpens*). Examination of numerous series of *P. serpens* demonstrate that the variation in body size and spine length described by Santschi occurs within colonies.

In regard to the type locality, Santschi gave a vague description, saying it was San José, two hours from Carumba, which is likely Corumba, Mato Grosso, Brazil. San José de Chiquitos is the only San José in this part of Bolivia, and it is about 350 km WNW of Corumba. Consequently, I assume that San José de Chiquitos is the type locality.

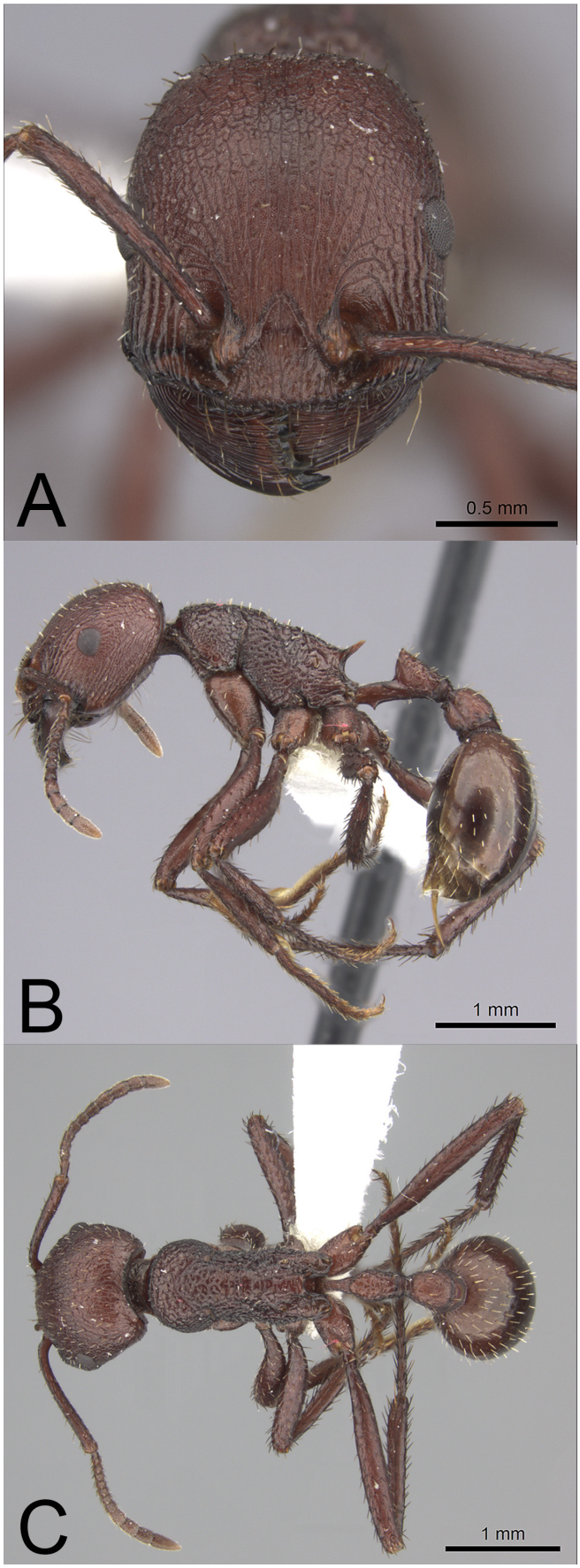

FIGURE 25. Photograph of *Pogonomyrmex serpens* Santschi worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0235271). Photographs by Will Ericson from www.AntWeb.org**.**

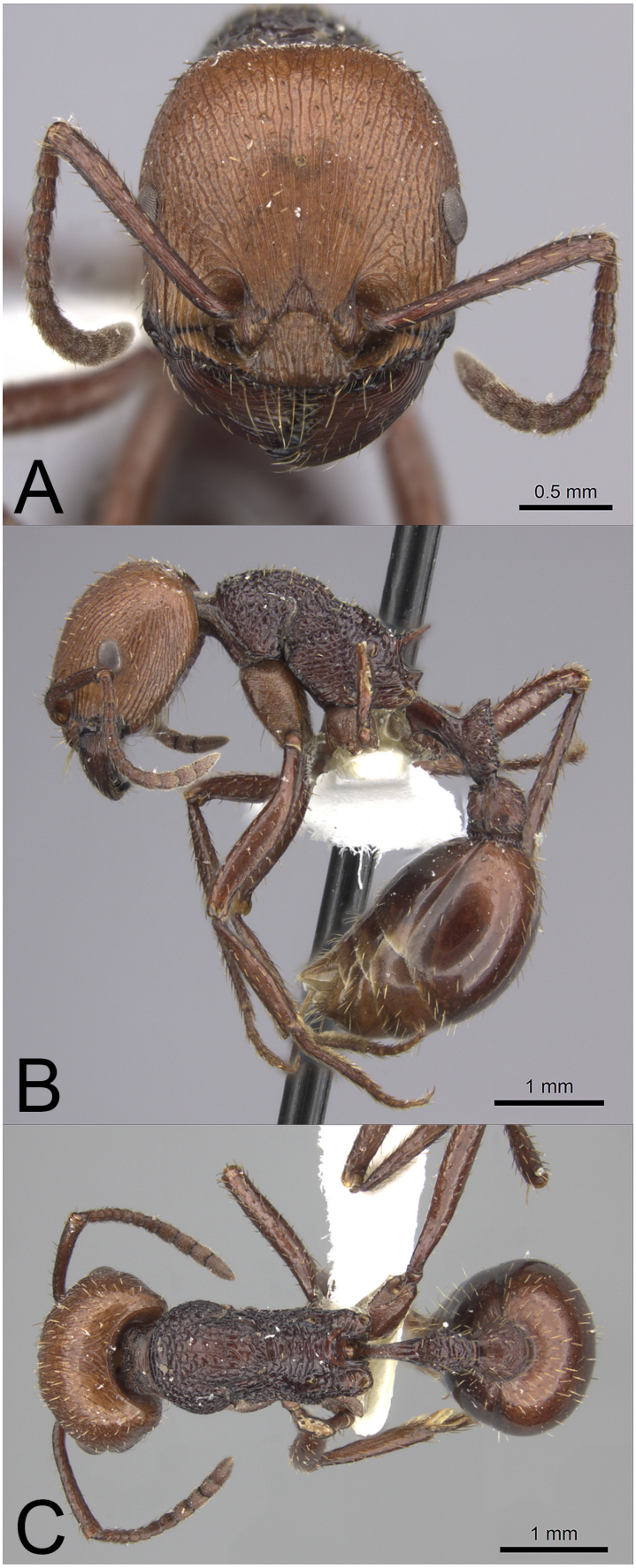

FIGURE 26. Photograph of *Pogonomyrmex serpens* Santschi ergatoid queen: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0235270). Photographs by Will Ericson from www.AntWeb.org.

Biology. Nothing is known regarding the biology of *P. serpens* but it is likely to be similar to that of *P. cunicularius* and *P. pencosensis*. The only literature note is from Santschi's (1925) description of var. *carnivora* saying that Bruch told him that workers collected insects to provision the nest.

Pogonomyrmex serpens is a lowland species that inhabits sites at elevations from 45–905 m. This species is mostly restricted to the Humid Chaco and northern portions of the Dry Chaco ecoregions as defined by Olson *et al*. (2001), with three additional records outside the northern and western edges of the Dry Chaco (**Figure 21C**).

Pogonomyrmex bispinosus-group

Workers in the *P. bispinosus*-group are diagnosed by the following characters: (1) psammophore well-developed, (2) first gastral tergum lacking striae, (3) posterior surface of petiolar node with transverse rugae or rugoreticulate, and (4) dorsum of postpetiole lacking rugae. Queens have: (1) psammophore well-developed, (2) weak transverse, but usually incomplete rugae on dorsum of postpetiole, and (3) short, delicate hairs along the lateral margin of propodeal declivity.

Pogonomyrmex bispinosus
(Figures 27–30)

Atta bispinosus Spinola *in* Gay, 1851: 244. Neotype worker [ANTWEB1008879] by present designation [LACM]. CHILE, Valparaíso: Petorca Province, 3 km N Zapallar, 28 October 1972, J.H. Hunt, #952 (previous holotype worker from CHILE, Santa Rosa, presumed lost or destroyed).

Pogonomyrmex bispinosus (Spinola): Mayr, 1870: 971. First combination in *Pogonomyrmex*. See also Gallardo, 1932: 130; Snelling & Hunt, 1976: 75, figs. 24, 27, 28.

Workers associated with the neotype: (7 workers) same data as neotype. **Diagnosis**. Within the *P. bispinosus*-group, the combination of: (1) superior propodeal spines well-developed, (2) larger (HW = 1.75–2.05 mm), (3) body concolorous tannish-brown to reddish-brown, (4) in frontal view and from posterior margins of head looking down over cephalic dorsum, frontal lobes enlarged, lateral margins convex, projecting at a strong vertical orientation relative to cephalic dorsum uniquely characterize this species (**Figures 27–28**).

Measurements—neotype (n = 11). HL 1.90 (1.67–2.00); HW 1.88 (1.75–2.05); MOD 0.38 (0.32–0.40); OMD 0.40 (0.36–0.45); SL 1.50 (1.27–1.48); PNW 1.15 (1.06–1.27); HFL 1.79 (1.59–1.98); ML 1.96 (1.86–2.17); PW 0.47 (0.46–0.54); PPW 0.68 (0.60–0.74). Indices: SI 79.79 (67.32–77.47); CI 98.95 (97.47–105.59); OI 20.21 (15.61–20.21); HFI 95.21 (84.13–100.00).

Redescription. Head subquadrate to quadrate (CI = 97.47–105.59), widest just posterior to eyes; posterior margin flat to weakly concave in full-face view. Longitudinal rugae on cephalic dorsum prominent, wavy to irregular; in full-face view, medial rugae diverging weakly toward posterior corners of head. In profile, rugae posterior to eyes converging near vertex. Cephalic interrugae strongly granulate-punctate, dull to weakly shining; vertex rugose. In frontal view and from posterior margins of head looking down over cephalic dorsum, frontal lobes enlarged, lateral margins convex, projecting at a strong vertical orientation relative to cephalic dorsum. Anterior margin of clypeus concave; lateral lobes with broad, blunt, sometimes inconspicuous tooth-like process below each antennal socket; dorsal surface with several subparallel, longitudinal rugae. Mandible with six teeth; mandibular dorsum coarsely rugose. MOD ranging from 0.16-21x HL. In profile, eyes situated slightly anterior to middle of head, OMD = 1.00–1.30x MOD. Antennal scapes moderately long (SI = 67.32–79.79), failing to reach vertex by length of basal funicular segment; base of scape flattened dorsoventrally, ventral surface widened at base with moderately well-developed inferior basal flange, margin of flange weakly carinate; entire scape with weak longitudinal striae, moderately granulate-punctate, weakly shining. Psammophore well-developed.

Mesosomal profile weakly convex; all mesosomal surfaces with prominent irregular rugae to rugoreticulate. Dorsum of pronotum with irregular, transverse rugae to rugoreticulate, pronotal sides rugoreticulate or with coarse, irregular rugae traversing posteroventrally; dorsum of mesonotum and propodeum with irregular longitudinal rugae, irregular rugae on mesopleura longitudinal or traversing posterodorsally. Interrugae on mesosoma weakly to strongly granulate, dull to weakly shining. Superior propodeal spines moderately well-developed, length about

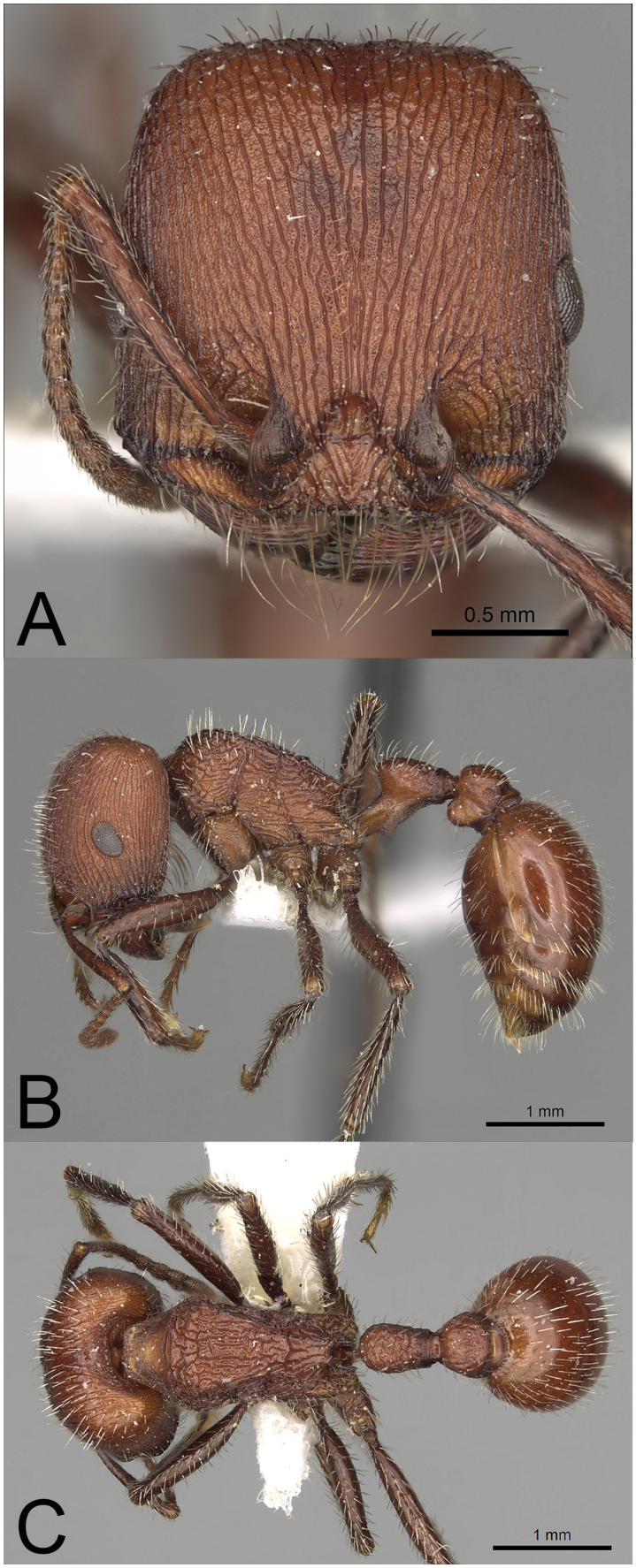

FIGURE 27. Photograph of *Pogonomyrmex bispinosus* (Spinola) worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0281087). Photographs by Shannon Hartman from www.AntWeb.org.

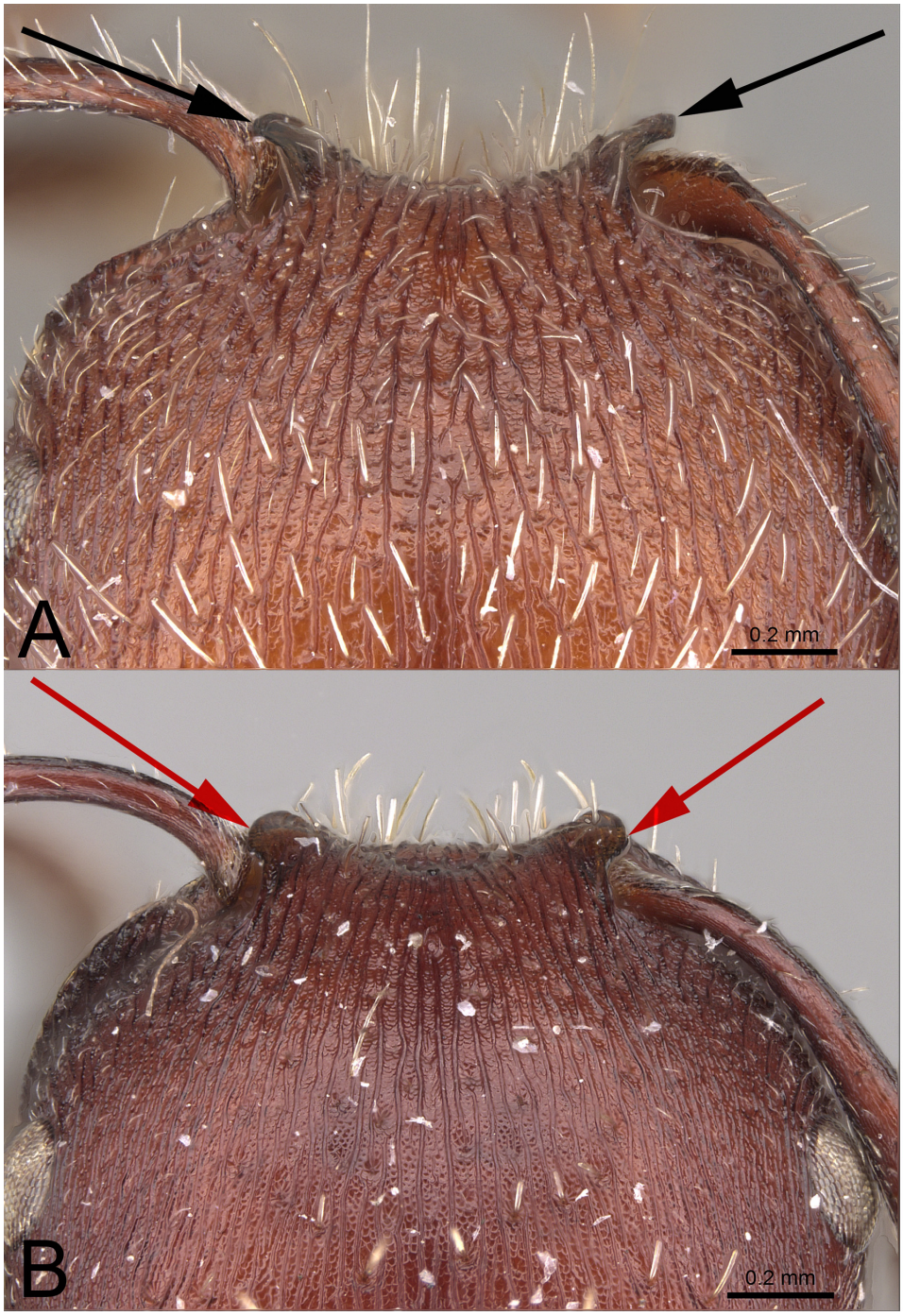

FIGURE 28. Photograph from posterior margin of head looking down over cephalic dorsum: (A) *Pogonomyrmex bispinosus* (Spinola)—black arrows show enlarged frontal lobes with convex lateral margins projecting from cephalic dorsum at a strong vertical orientation (CASENT0281087), and (B) *Pogonomyrmex uruguayensis* Mayr—red arrows show frontal lobes not enlarged with lateral margins mostly subparallel and projecting nearly parallel to cephalic dorsum (CASENT0914810). Photographs by Michele Esposito from www.AntWeb.org.

0.6–0.8x distance between their bases. Inferior propodeal spines poorly-developed, consisting of a broadly rounded process. Propodeal spiracles narrowly ovate facing posterad. Legs weakly to moderately coriarious, weakly shining.

Peduncle of petiole about 0.8x as long as petiolar node, anteroventral margin with poorly to well-developed rounded process. In profile, petiolar node asymmetrical with anterior surface shorter than posterior surface; apex broadly rounded. In dorsal view, petiolar node longer than wide, widest near spatulate anterior margin. Posterior surface of petiolar node with weak to coarse, irregular, longitudinal, oblique, or transverse rugae to rugoreticulate; interrugae on all surfaces weakly to moderately granulate-punctate, weakly shining. Dorsum of postpetiole convex

in profile; in dorsal view, widest near posterior margin, narrowing to anterior margin, maximal width usually greater than length, weakly to moderately coriarious, weakly shining. First gastral tergum moderately coriarious, weakly shining to smooth and shining.

Erect whitish to cream colored pilosity moderately abundant on head, short and similar in length, usually longer along posterior margin; longest hairs not exceeding MOD. Moderately abundant erect to semidecumbent pilosity on scape; abundant decumbent hairs on funicular segments. Legs with moderately abundant, long, semidecumbent, whitish to cream colored setae. Mesosoma, petiolar node, postpetiole, first gastral tergum with moderately dense, erect, whitish to cream colored setae, often similar in length, longest hairs approaching to exceeding MOD. Body concolorous tannish-brown to reddish-brown (**Figures 27–28**).

Ergatoid Queen. Diagnosis. This caste is diagnosed by: (1) ergatoid, with small ocelli on head and mesosoma lacking all morphological structures related to wings, (2) in dorsal view, pronotum large, well-developed; mesoscutum poorly-developed, anterior margin barely surpassing humeral shoulders of pronotum, (3) superior propodeal spines well-developed, length greater than 0.6x distance between their bases, (4) inferior spines well-developed, wider than tall, broadly rounded, (5) in dorsal view, petiolar node globular, anterior margin broadly rounded, (6) in dorsal view, postpetiole notably wider than long, (7) rugae on dorsum of postpetiole lacking or faint to weak, rarely crossing entire surface, and (8) body mostly concolorous tannish-brown to reddish-brown (**Figure 29**).

Measurements—(*n* = 2). HL 2.27–2.29; HW 2.43–2.57; MOD 0.38–0.46; OMD 0.54–0.55; SL 1.61–1.61; PNW 1.40–1.52; HFL 2.06–2.08; ML 2.85–2.83; PW 0.77–0.79; PPW 1.06–1.09. Indices: SI 62.65–62.65; CI 106.11–113.22; OI 14.79–18.93; HFI 80.93–84.77.

Description. Ergatoid, with small ocelli on head. In full-face view, head slightly wider to wider than long (CI = 106.11–113.22), widest just posterior to eyes, posterior margin weakly concave. Longitudinal rugae on cephalic dorsum prominent, wavy to irregular; in full-face view, medial rugae diverging weakly toward posterior corners of head; vertex weakly to moderately rugose; interrugae on cephalic dorsum and vertex weakly to moderately granulate-punctate, weakly shining. Mandible with six teeth, dorsal surface coarsely rugose. Psammophore well-developed.

Mesosomal segments largely fused, lacking all morphological structures related to wings. In dorsal view, pronotum large, well-developed; mesoscutum poorly-developed, anterior margin barely surpassing humeral shoulders of pronotum. All mesosomal surfaces with subparallel, regular, wavy, or irregular rugae; interrugae weakly to moderately granulate-punctate, weakly shining; propodeum with well-developed superior and inferior spines; inferior spines wider than tall, broadly rounded. Peduncle of petiole about 0.8x as long as petiolar node, anteroventral margin with weak process. In profile, petiolar node asymmetrical with anterior surface notably shorter than posterior surface, apex subangulate to rounded. In dorsal view, petiolar node globular, posterior surface with irregular rugae, interrugae weakly to moderately granulate-punctate, weakly shining. In dorsal view, postpetiole wider than long; dorsum with faint to weak irregular rugae, moderately granulate-punctate, weakly shining. First gastral tergum weakly coriarious, weakly shining to smooth and shining. Most body surfaces with moderately abundant suberect to erect, medium-length, white to yellowish setae. Body concolorous tannish-brown to reddish-brown (**Figure 29**).

Male. Diagnosis. This caste is diagnosed by: (1) first gastral tergum lacking striae, (1) in dorsal view, anteromedial surface of petiolar node and usually apex weakly to strongly concave, (2) dorsum of postpetiole with weak longitudinal rugae, (3) transverse rugae usually present between frontal lobes, and (4) notauli present (**Figure 30**).

Measurements—(*n* = 6). HL 1.37–1.63; HW 1.41–1.71; MOD 0.46–0.55; OMD 0.20–0.27; SL 0.41–0.51; HFL 1.82–2.13; ML 2.41–2.71; PW 0.50–0.65; PPW 0.69–0.86. Indices: SI 26.28–32.00; CI 102.92–107.24; OI 31.58–34.67; HFI 114.47–132.62.

Additional material examined. CHILE: ***Metropolitan***: El Coipo, Jan 12, 1968 (LACM; MNHN); Río Maipo, El Peumo, Nov 1951 & Nov 23, 1967 (LACM; MNHN); Quebrada el Peumo, Nov 21, 1966 (LACM; MNHN); Cajon el Maipo, Dec 15–18, 1969 & Sept 23, 2000 & no date (LACM; MNHN); San José de Maipo, Jan 25–29, 1970 (MNHN); El Manzano, Dec 1, 1966 (LACM; MNHN); El Canelo, Dec 15, 1954 & Jan 9, 1967 (LACM; MNHN); Fundo Santa Laura near Cuesta de la Dormida, Dec 2, 1972 (LACM); Cerro Manquehue, Dec 1997 (MNHN); El Peñón, Dec 8, 1952 (MNHN). ***Valparaíso***: 10 km E Papudo, Nov 28, 1950 (CASC); Viña del Mar, no date (MSNG); Laguna Verde, Dec 13, 2001 (RAJC; UCDC); Los Molles, Oct 26, 1971 (MNHN); Santa Rosa (= Santa Rosa del Los Andes), not examined (syntype from Spinola description). ***Region Unknown***: no loc, no date (USNM) (**Figure 31A**).

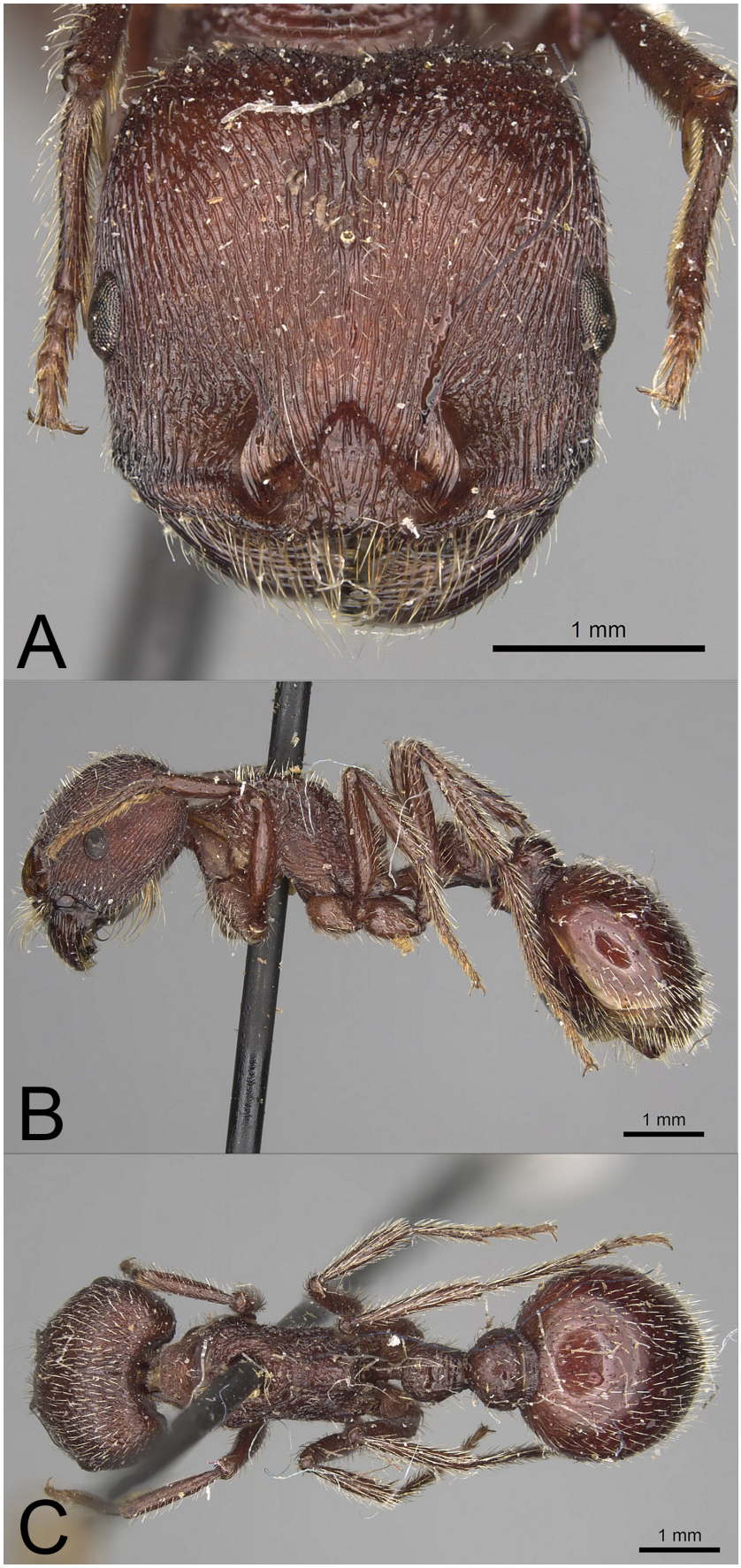

FIGURE 29. Photograph of *Pogonomyrmex bispinosus* (Spinola) ergatoid queen: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (LACMENT273679). Photographs by Shannon Hartman from www.AntWeb.org.

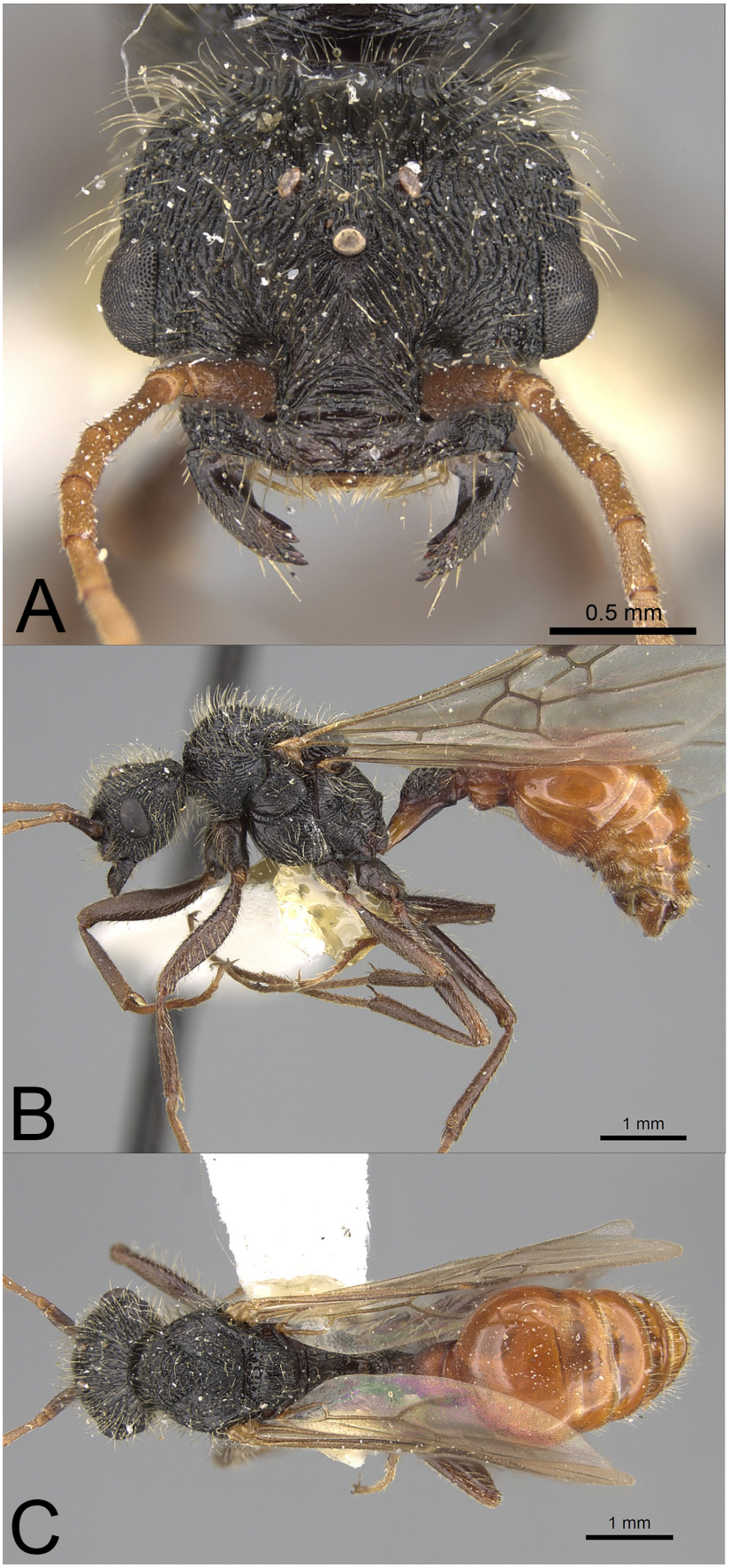

FIGURE 30. Photograph of *Pogonomyrmex bispinosus* (Spinola) male: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (LACMENT273583). Photographs by Michele Esposito from www.AntWeb.org**.**

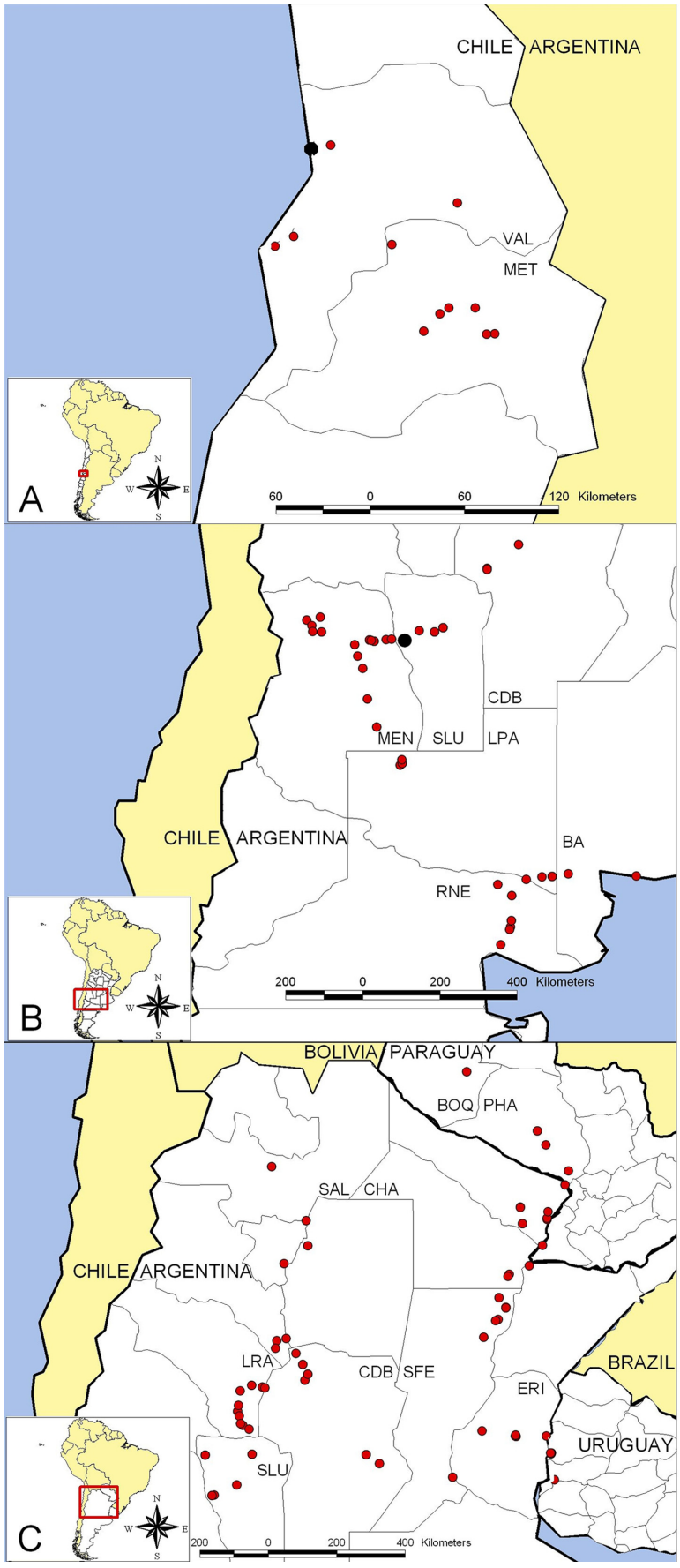

FIGURE 31. Geographic distribution of: (**A**) *Pogonomyrmex bispinosus* (Spinola), (**B**) *Pogonomyrmex inermis* Forel, and (**C**) *Pogonomyrmex uruguayensis* Mayr. The larger black circle in each panel (when present) denotes the type locality.

Etymology. The naming of this species apparently refers to the two well-developed superior propodeal spines, which Spinola described as two dorsal spines, straight and equally vertical, slightly in front of posterior border.

Discussion. *Pogonomyrmex bispinosus* is restricted to Chile, and it is distinguished from all Chilean congeners by: (1) well-developed psammophore, (2) first gastral tergum lacks striae, (3) dorsum of postpetiole lacks transverse striae, (4) body concolorous tannish-brown to reddish-brown, and (5) in frontal view and from posterior margins of head looking down over cephalic dorsum, the frontal lobes are enlarged and the lateral margins are convex, projecting at a strong vertical orientation relative to the cephalic dorsum.

Spinola (1851) described *P. bispinosus* from one worker that was collected at Santa Rosa, Chile (= Santa Rosa de los Andes, Valparaíso Region), and from sexuals (queens and males) taken during a mating flight at Tucapel, Chile. Emery (1906) believed the worker and sexuals were different species, and he assigned the sexuals as *P. bispinosus* var. *spinolae*. I concur with Emery (1906) that the queens and males described by Spinola (1851) are not conspecific with workers; the sexuals are in the *P. rastratus*-group and are not treated herein.

The type of *P. bispinosus* was not located during this study and it is presumably lost or destroyed. However, salient features of the present species correspond with the description by Spinola (1851): (1) entirely ferruginous red, (2) dorsum of postpetiole strongly punctate (lacking transverse rugae), and (3) first gastral tergum smooth and shining. In combination, these characters uniquely characterize *P. bispinosus* from all Chilean congeners. In addition, all material examined during this study was from the Metropolitan and Valparaíso Regions, which meets the geographical criteria for *P. bispinosus*. Snelling & Hunt (1975) also identified these same workers as *P. bispinosus*, listing diagnostic characters as: (1) dorsum of postpetiole punctate and lacking transverse striae, and (2) scape thickened near the base. Moreover, Spinola's description of *P. bispinosus*, along with absence of morphologically similar congeners in Chile, leave no doubt as to the identity of *P. bispinosus* (see also Snelling & Hunt, 1975).

The three examined queens were not collected with workers but correspond with workers in several respects: (1) concolorous dark ferruginous red-orange to reddish-brown, (2) first gastral tergum smooth and shining, (3) dorsum of the postpetiole lacking transverse rugae, and (4) geographic proximity to worker collections. Males were collected with queens at one site, and these males undoubtedly are those of *P. bispinosus* given their large size and smooth, shining first gastral tergum. Snelling & Hunt (1975) also determined these sexuals to be *P. bispinosus*.

Biology. Nothing is known about the biology of *P. bispinosus* other than that males and/or ergatoid queens have been collected from 21 November to 29 January. It would be fruitful to study mating and colony founding behavior of this species given that they have ergatoid queens.

Pogonomyrmex bispinosus is only known from central portions of Chile (Valparaíso and Metropolitan Regions) at elevations estimated to range from sea level to >1000 m in the Valdivian Temperate Forests and Chilean Matorral ecoregions as defined by Olson *et al*. (2001) (**Figure 31A**).

Pogonomyrmex inermis

(Figures 32–34)

Pogonomyrmex inermis Forel, 1914: 267 (worker). Syntypes examined: 2 workers [MACN], 8 workers [MHNG], 1 worker [MLPA], ARGENTINA, San Luis: Alto Pencoso, #204 (C. Bruch leg.). See also Gallardo, 1932: 128, fig. 18; Kusnezov, 1951: figs. 9a, 9b. MACN worker here designated **LECTOTYPE** [CASENT0217257].

Worker. Diagnosis. Within the *P. bispinosus*-group, the combination of: (1) superior propodeal spines absent or consisting of small denticles or tubercles uniquely characterize this species (**Figure 32**).

Measurements—lectotype (n = 12). HL 1.74 (1.59–1.79); HW 1.86 (1.59–1.84); MOD 0.33 (0.30–0.39); OMD 0.37 (0.38–0.50); SL 1.26 (1.16–1.35); PNW 1.21 (1.04–1.19); HFL 1.78 (1.59–1.87); ML 1.85 (1.91–2.18); PW 0.50 (0.39–0.47); PPW 0.61 (0.53–0.63). Indices: SI 67.74 (66.67–76.10); CI 106.90 (98.18–106.98); OI 17.74 (17.34–22.16); HFI 95.70 (92.13–103.77).

Redescription. Head quadrate to slightly wider than long (CI = 98.18– 106.98), widest just posterior to eyes; posterior margin flat to weakly concave in full-face view. Longitudinal rugae on cephalic dorsum prominent, wavy to irregular, often moderately rugoreticulate toward posterior margin; in full-face view, medial rugae diverging weakly toward posterior corners of head. In profile, rugae posterior to eyes converging near vertex. Cephalic interrugae strongly granulate, dull; vertex rugose. Anterior margin of clypeus concave; dorsal surface with several

subparallel, longitudinal rugae. Mandible with six teeth; mandibular dorsum coarsely rugose. MOD ranging from 0.18–0.23x HL. In profile, eyes situated slightly anterior to middle of head, OMD = 1.10–1.54x MOD. Antennal scapes moderately long (SI = 66.67–76.10), failing to reach vertex by length of basal funicular segment; entire scape with longitudinal striae. Psammophore well-developed.

Mesosomal profile strongly convex; all mesosomal surfaces with prominent irregular rugae to rugoreticulate. Anterior margin of pronotal dorsum with irregular transverse rugae that traverse posteroventrally or become rugoreticulate on pronotal sides; dorsum of mesonotum with irregular longitudinal rugae, or rugoreticulate to vermiculate; rugae on mesopleura longitudinal or traversing posterodorsally; dorsum of propodeum with irregular transverse rugae that traverse ventrally or anteroventrally on propodeal sides. Interrugae on mesosoma weakly to strongly granulate, dull to weakly shining. Superior propodeal spines absent or consisting of small denticles or tubercles. Inferior propodeal spines lacking. Propodeal spiracles narrowly ovate facing posterad. Legs moderately to strongly coriarious, weakly shining.

Peduncle of petiole about 0.8x as long as petiolar node, anteroventral margin often with poorly-developed, broadly rounded process. In profile, petiolar node asymmetrical with anterior surface shorter than posterior surface; apex broadly rounded. In dorsal view, petiolar node longer than wide, widest near spatulate anterior margin. Sides and posterior surface of petiolar node with coarse, irregular, transverse rugae or rugoreticulate; interrugae weakly to moderately granulate, weakly shining to shining. Dorsum of postpetiole convex in profile; in dorsal view, widest near posterior margin, narrowing to anterior margin, maximal width about equal to length, moderately to strongly coriarious, dull to weakly shining. First gastral tergum moderately to strongly coriarious, weakly shining.

Erect whitish to yellowish pilosity moderately abundant on head, variable in length, longest hairs not exceeding MOD. Moderately abundant suberect to semidecumbent pilosity on scape; abundant decumbent hairs on funicular segments. Legs with moderately abundant suberect to decumbent white setae. Mesosoma, petiolar node, postpetiole, first gastral tergum with moderately dense, erect, white setae, often similar in length, longest hairs on mesosoma approaching MOD. Body tannish-brown to reddish-brown, posterior portion of petiolar node and postpetiole often darker brown, gaster dark brown to blackish (**Figure 32**).

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) superior propodeal spines absent or consisting of small denticles, (3) inferior propodeal spines lacking, (4) in dorsal view, dorsum of postpetiole lacking transverse rugae, or rugae few and incomplete, and (5) body usually bicolored, with gaster noticeably darker than rest of body (**Figure 33**).

Measurements—(*n* = 12). HL 1.74–2.02; HW 1.79–2.19; MOD 0.39–0.47; OMD 0.39–0.56; SL 1.23–1.39; PNW 1.28–1.51; HF 1.72–2.06; ML 2.29–2.65; PW 0.48–0.57; PPW 0.68–0.83. Indices: SI 60.98–73.33; CI 101.60–108.42; OI 18.26–23.50; HFI 86.76–103.52.

Description. With caste-specific morphology of the mesosoma related to wing-bearing and presence of ocelli on head. In full-face view, head quadrate to wider than long (CI = 101.60–108.42), widest just posterior to eyes, posterior margin flat. Longitudinal rugae on cephalic dorsum prominent, wavy to irregular; in full-face view, medial rugae not diverging toward posterior corners of head, interrugae weakly to moderately granulate-punctate, weakly shining; vertex rugose, interrugae moderately granulate-punctate, dull to weakly shining. Mandible with six teeth, dorsal surface coarsely rugose. Psammophore well-developed.

All mesosomal surfaces with subparallel, regular, wavy, or irregular rugae; interrugae weakly to moderately granulate-punctate, weakly shining; propodeum unarmed or with small denticles; inferior propodeal spines absent. Peduncle of petiole about as long as petiolar node, anteroventral margin straight or with a weak process. In profile, petiolar node asymmetrical with anterior surface notably shorter than posterior surface, apex rounded to weakly angulate. Posterior surface of petiolar node with irregular transverse rugae; dorsum of postpetiole with very weak, usually incomplete transverse or oblique rugae, and/or mostly granulate-punctate; interrugae on posterior surface of petiolar node and dorsum of postpetiole weakly to moderately granulate-punctate, weakly shining. First gastral tergum weakly to moderately coriarious, weakly shining. Most body surfaces with moderately abundant suberect to erect, medium-length, white to yellowish setae; moderately abundant suberect to erect hairs on first gastral tergum, those on second and third terga restricted to posterior margin. Head, mesosoma, petiolar node, and postpetiole tannish-brown; gaster blackish-brown (**Figure 33**).

Male. Diagnosis. This caste is diagnosed by: (1) first gastral tergum lacking striae, (2) in full-face view, external margin of apical tooth curved inward, (3) dorsum of postpetiole strongly granulate, dull, to occasionally weakly rugoreticulate-vermiculate, interrugae dull, (4) rugae on cephalic dorsum prominent, subparallel, (5)

pronotal sides and mesopleura with longitudinal rugae, (6) interrugae on cephalic dorsum, pronotal sides, and mesopleura weakly shining to shining, and (7) notauli present (**Figure 34**).

Measurements—(n = 12). HL 1.42–1.73; HW 1.43–1.70; MOD 0.46–0.59; OMD 0.20–0.31; SL 0.36–0.49; HFL 1.63–1.90; ML 2.30–2.78; PW 0.46–0.63; PPW 0.62–0.83. Indices: SI 24.16–31.33; CI 92.55–102.11; OI 30.87–38.00; HFI 109.40–127.70.

Additional material examined. ARGENTINA: ***Buenos Aires***: Monte Hermoso, no date (MLPA); Rt 22 at 36.3 km W Medanos, Jan 20, 2011 (RAJC); no loc, no date (MACN). ***Córdoba***: Estancia Santo Domingo, Feb 24, 2009 (RGPC); Nono, 2940', Jan 17, 2008 (RAJC); 2.6 km N Nono, Dec 18, 2006 (CSC); no loc, no date (MCZ). ***La Pampa***: Santa Isabel, Jan 30, 2010 (RGPC); Rt 143 at 4.5 km NW Santa Isabel, Feb 13, 2014 (RAJC); 8 km S Jct Hwys 151 & 143, 1100', Dec 9, 2003 (RAJC); Río Colorado, no date (MACN); 51 km E Río Colorado, Nov 20, 2005 (CSC); Rt 22 at 90.5 km W Medanos, 320', Jan 21, 2011 (RAJC); Rt 251 at 35.8 km S Jct Rt 22, 320', Jan 21, 2011 (RAJC). ***Mendoza***: Ugarteche, Dec 27, 2008 (RGPC); 59 km SE San Martín, Nov 22, 2005 (CSC); 24 km S Monte Coman, 1640', Dec 9, 2003 (RAJC); Reserva Nancuñan, Oct 30, 2008 (RGPC); Hwy 7 at 20 km E La Paz, 1640', Dec 12, 2003 (CASC; MCZ; RAJC); Rt 7 at 5.8 km W Desaguadero, 1530', Dec 28, 3005 (RAJC); Rt 7 at 21.7 km E La Dormida, 1740', Dec 28, 2005 (RAJC); Rt 7 at 17.8 km E La Dormida, 1670', Jan 23, 2008 (RAJC); Rt 7 at 29.8 km E La Dormida, 1610', Jan 23, 2008 (RAJC); Rt 7 at Arroyo de las Minas, 4130', Dec 29, 2005 (RAJC); Rt 86 at 20 km NE Tupangato, 4510', Jan 21, 2008 (RAJC); 61.4 km S Jct Rts 7 & 153, 1910', Jan 23, 2008 (RAJC); Portrerillos, Dec 12, 1950 (FML); Cerro de la Gloria, Dec 3, 1950 (LACM; USNM); no loc, no date (FML; MZUSP). ***Río Negro***: 35.6 km NW Jct Rts 251 & 2, 360', Jan 22, 2011 (RAJC); Rt 251 at 16.6 km N General Conesa, 390', Jan 21, 2011 (RAJC); General Conesa, no date (FML). ***San Luis***: Potrero de los Funes, 3030', Dec 25, 2005 (RAJC); La Florida, 3310', Dec 25, 2005 (RAJC); Rt 7 at Alto Pencoso, 2330', Dec 27, 2005 (RAJC); Rt 15 at 16.9 km N Balde, 1670', Mar 15, 2015 (RAJC); no loc, no date (MACN; MLPA). ***Questionable locales*** **(appear to be outside geographic range):** ***Catamarca***: no loc, no date (MACN; MLPA); El Pucare, no date (LACM). ***Entre Ríos***: El Palmer, no date (FML) (**Figure 31B**).

Etymology. The specific epithet, *inermis* (from Latin, *inermis* = unarmed), refers to this species lacking superior propodeal spines.

Discussion. *Pogonomyrmex inermis* co-occurs with *P. uruguayensis*, and it is distinguished from *P. uruguayensis* by absence of superior propodeal spines (reduced to denticles or small tubercles), which are present in *P. uruguayensis*. Additionally, workers of *P. inermis* are typically larger (HW = 1.59–1.86 mm) than those of *P. uruguayensis* (HW = 1.24–1.61 mm). Absence of superior propodeal spines and absence of striae on the first gastral tergum distinguish *P. inermis* from all congeners in Argentina.

Biology. *Pogonomyrmex inermis* is one of the more well-studied species of *Pogonomyrmex* in Argentina. This species harvests the seeds of various grass and nongrass species (Pirk & Lopez de Casenave, 2010, 2011; Pirk, Lopez de Casenave, & Marone, 2007; Pirk, Lopez de Casenave, Pol, Marone, & Milesi, 2009; Pol, Lopez de Casenave, & Pirk, 2011). Workers are solitary foragers, but additional observations show that foragers leave the nest to travel in few directions; they do not form a conspicuous trail, and they do not recruit nestmates to high-density seed patches (Pol *et al.*, 2015). Five colonies averaged 47–70 foragers, which consisted of about 15% of all workers in nests (Nobua-Behrmann, Lopez de Casenave, Milesi, & Pavan, 2013). Nests are typically distinguished by the large midden of seed chaff (15–20 cm in diameter) that surrounds or is adjacent to the nest entrance. Nests sometimes have 2–3 entrances with a tumulus that ranges up to 15 cm in diameter. Colonies of *P. inermis* are relatively small: two excavated colonies contained an average of 299 workers and 54 larvae and pupae (Nobua Behrmann *et al.*, 2010).

Collection dates for sexuals range from 18 December to 23 January. Mating flights have not been observed, but they occur during the austral summer (December–January) based on finding two dealate queens on the ground on 21–22 January, and excavating queens from incipient nests on 25 December; all excavated queens (n = 7) were haplometrotic (R.A. Johnson, unpub. data). Queens of *P. inermis* are polyandrous with a mean ($\bar{x}$ ± SE) effective mating frequency of 6.52 ± 2.77 (range = 2–12; n = 20) (Pol *et al.*, 2008).

Pogonomyrmex inermis inhabits sites at elevations from 95–1370 m. This species is common in the Lower Monte Desert, southern Humid Chaco, southern Espinal, and southwestern Humid Pampas ecoregions as defined by Olson *et al*. (2001) (**Figure 31B**).

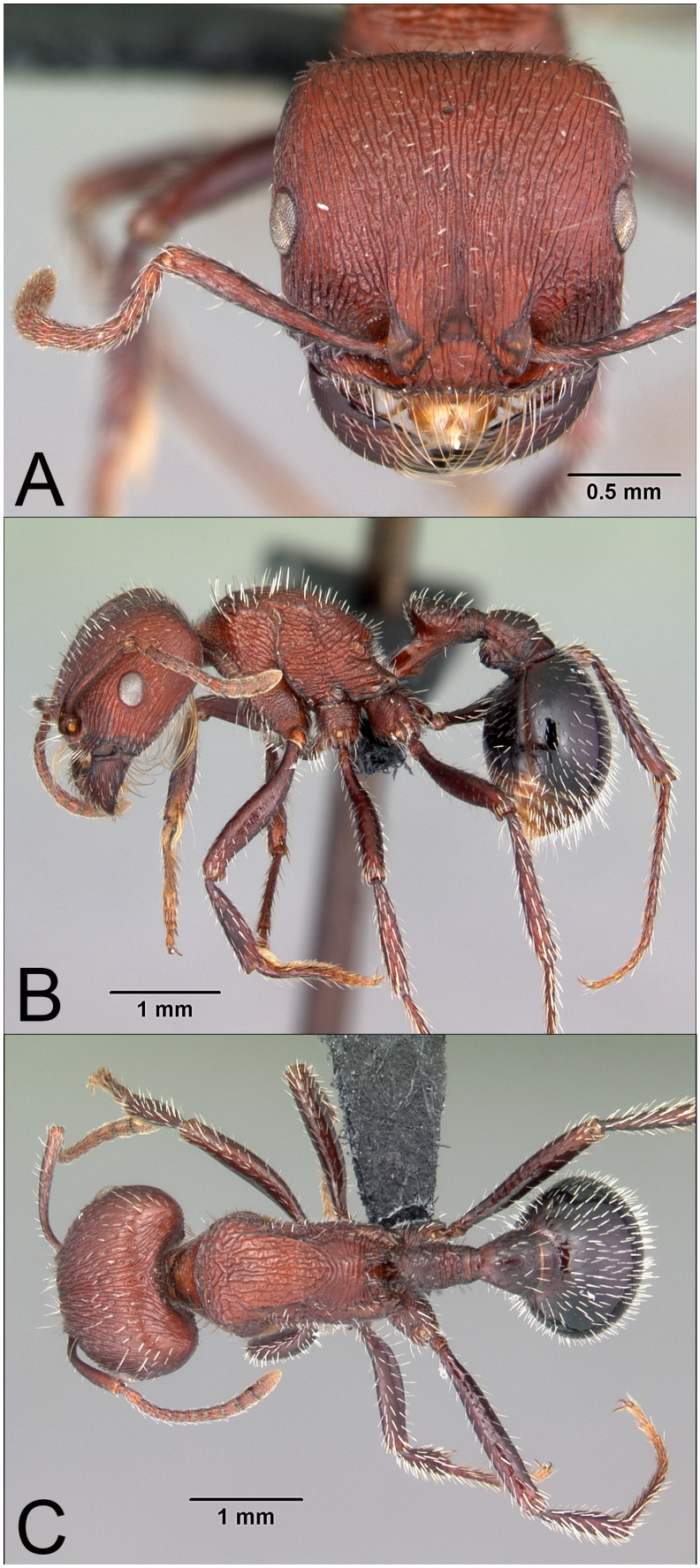

FIGURE 32. Photograph of *Pogonomyrmex inermis* Forel worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0102694). Photographs by April Nobile from www.AntWeb.org.

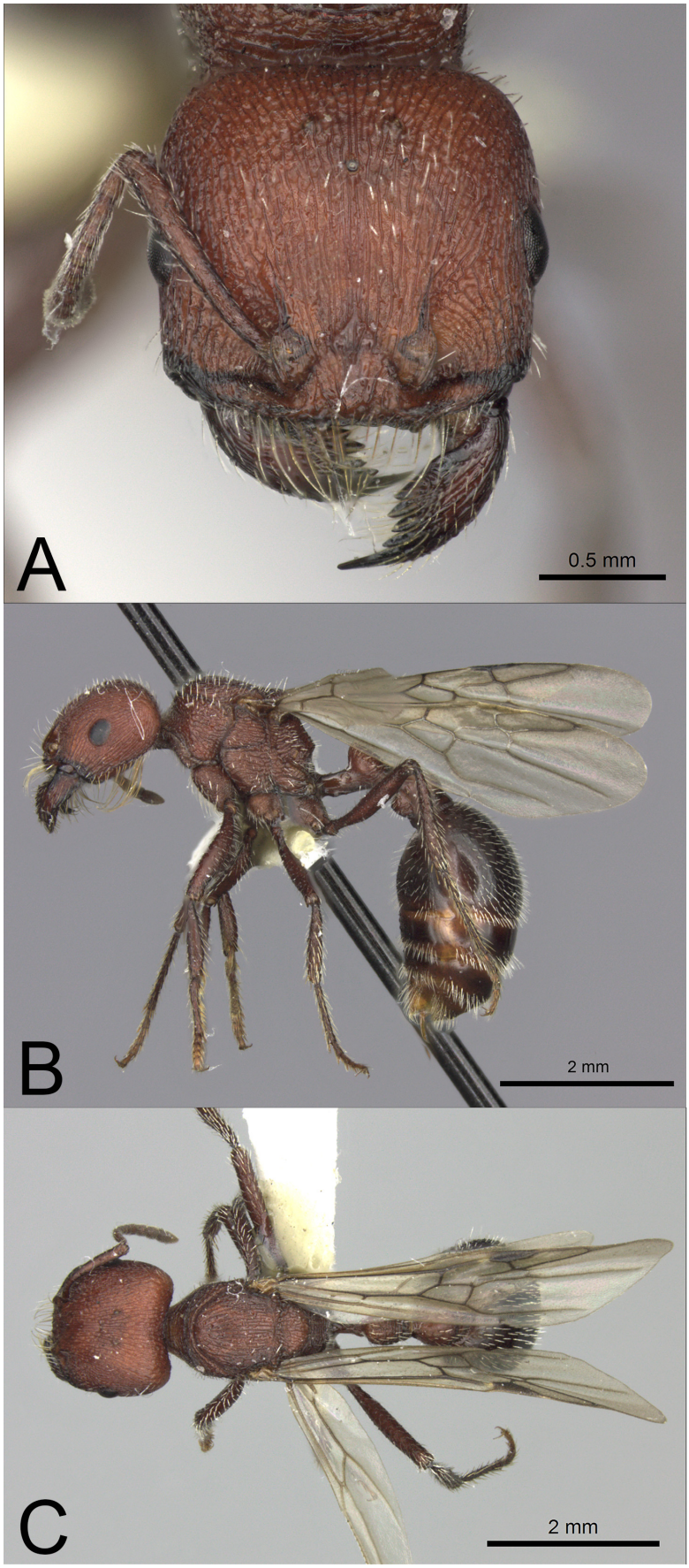

FIGURE 33. Photograph of *Pogonomyrmex inermis* Forel alate queen: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0235305). Photographs by Will Ericson from www.AntWeb.org**.**

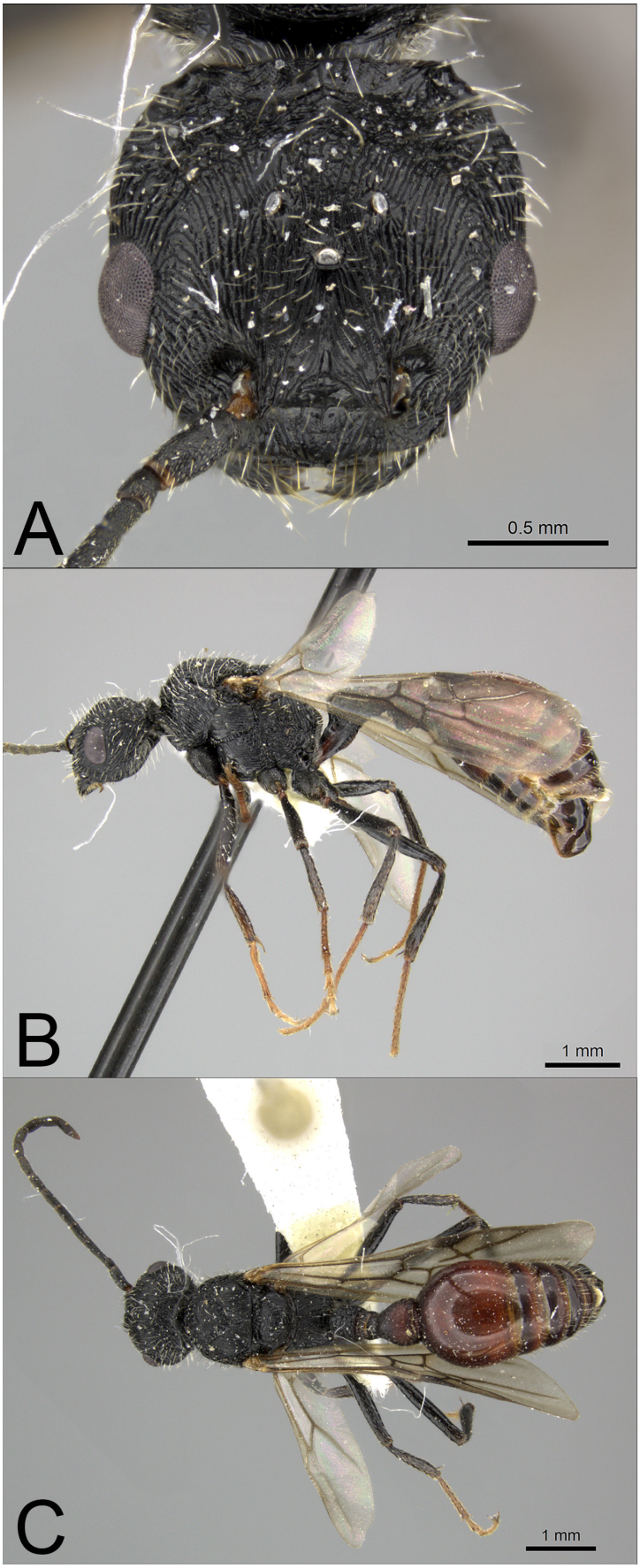

FIGURE 34. Photograph of *Pogonomyrmex inermis* Forel male: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0235306). Photographs by Estella Ortega from www.AntWeb.org.

Pogonomyrmex uruguayensis
(Figures 28, 35–37)

Pogonomyrmex uruguayensis Mayr, 1887: 614 (worker). Syntypes examined: 1 worker [MSNG], 1 worker [NMW], URUGUAY, no location (Prof. C. Berg). See also Gallardo, 1932: 148, fig. 32. NMW worker here designated **LECTOTYPE** [CASENT0173373].
Pogonomyrmex uruguensis Mayr: Santschi, 1921: 95.

Worker. Diagnosis. Within the *P. bispinosus*-group, the combination of: (1) superior propodeal spines well-developed, (2) smaller (HW = 1.24-1.61 mm), (3) in frontal view and from posterior margins of head looking down over cephalic dorsum, frontal lobes poorly-developed, lateral margins subparallel, projecting nearly parallel to cephalic dorsum uniquely characterize this species (**Figures 28 & 35**).

Measurements—lectotype (n = 21). HL 1.55 (1.28–1.62); HW 1.54 (1.24–1.61); MOD 0.33 (0.30–0.40); OMD 0.37 (0.30–0.41); SL 1.04 (0.86–1.14); PNW 1.06 (0.88–1.15); HFL 1.31 (1.19–1.57); ML 1.67 (1.51–2.05); PW 0.41 (0.33–0.50); PPW 0.55 (0.47–0.63). Indices: SI 67.53 (64.56–77.42); CI 99.35 (93.23–105.41); OI 21.43 (21.15–26.28); HFI 85.06 (84.46–100.73).

Redescription. Head subquadrate to quadrate (CI = 93.23–105.41), widest just posterior to eyes; posterior margin flat in full-face view. Longitudinal rugae on cephalic dorsum weak, wavy to irregular; in full-face view, medial rugae diverging weakly towards posterior corners of head. In profile, rugae posterior to eyes converging near vertex, occasionally weak to indistinct near vertex. Cephalic interrugae strongly granulate, dull; vertex moderately granulate or rugose, interrugae weakly to moderately granulate, weakly shining to shining. In frontal view and from posterior margins of head looking down over cephalic dorsum, frontal lobes poorly-developed, lateral margins subparallel, projecting nearly parallel to cephalic dorsum. Anterior margin of clypeus concave; dorsal surface with several subparallel longitudinal rugae. Mandible with six teeth; mandibular dorsum coarsely rugose. MOD ranging from 0.21–0.28x HL. In profile, eyes situated slightly anterior to middle of head, OMD = 0.88–1.25x MOD. Antennal scapes moderately long (SI = 64.56–77.42), failing to reach vertex by length of basal funicular segment; entire scape with longitudinal striae. Psammophore well-developed.

Mesosomal profile strongly convex; all mesosomal surfaces with prominent irregular rugae to rugoreticulate. Anterior margin of pronotal dorsum with irregular transverse rugae or moderately rugoreticulate, humeral shoulders on pronotum and pronotal sides rugoreticulate or with rugae that traverse posteroventrally or longitudinally; dorsum of mesonotum with irregular, longitudinal rugae that diverge anteriorly to rugoreticulate or vermiculate; rugae on mesopleura longitudinal or traversing posterodorsally; dorsum of propodeum with irregular transverse to oblique rugae or rugae lacking; rugae traverse ventrally or anteroventrally on propodeal sides. Interrugae on pronotum and mesonotum moderately to strongly granulate, dull to weakly shining, those on propodeum very strongly granulate, very dull to dull. Superior propodeal spines moderately long, slightly shorter than width between their bases. Inferior propodeal spines lacking. Propodeal spiracles narrowly ovate facing posterad. Legs moderately to strongly coriarious, weakly shining.

Penduncle of petiole about 0.7x as long as petiolar node, anteroventral margin with poorly-developed, broadly rounded process. In profile, petiolar node asymmetrical with anterior surface shorter than posterior surface; apex broadly rounded. In dorsal view, petiolar node longer than wide, widest near spatulate anterior margin. Sides and dorsum of petiolar node with weak, wavy to irregular, transverse rugae; interrugae moderately to strongly granulate-punctate, dull to weakly shining. Dorsum of postpetiole convex in profile; in dorsal view, widest at or near posterior margin and tapering to anterior margin, maximal width about equal to length, weakly to strongly coriarious, dull to weakly shining; sides of postpetiole often with weak transverse rugae. First gastral tergum moderately to strongly coriarious, weakly shining.

Erect whitish to yellowish pilosity moderately abundant on head, variable in length, longest hairs not exceeding MOD. Moderately abundant suberect to semidecumbent pilosity on scape; abundant decumbent hairs on funicular segments. Legs with moderately abundant suberect to decumbent white setae. Mesosoma, petiolar node, postpetiole, first gastral tergum with moderately dense erect white setae, often similar in length, longest hairs much shorter than MOD. Body concolorous tannish-brown to reddish-brown, head sometimes slightly lighter than rest of body (**Figures 28 & 35**).

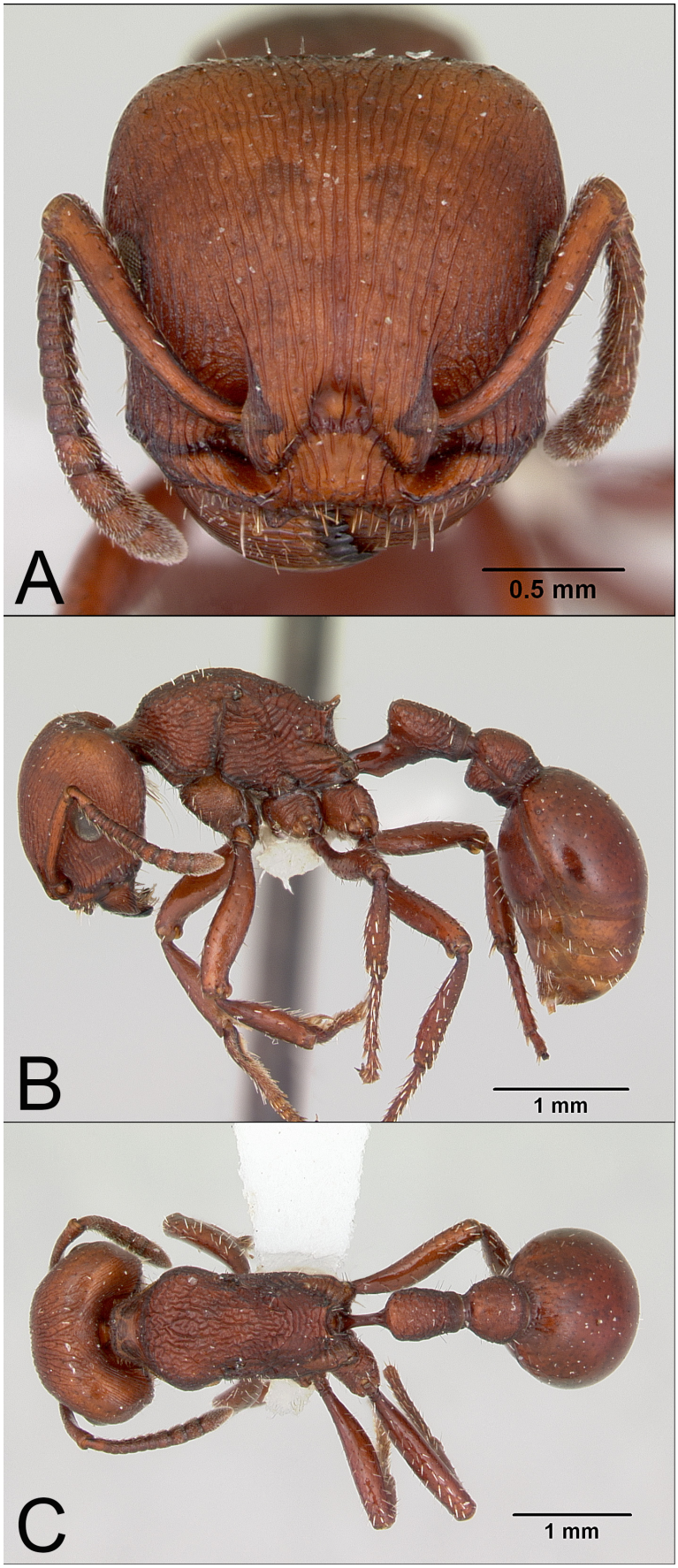

FIGURE 35. Photograph of *Pogonomyrmex uruguayensis* Mayr worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0173115). Photographs by April Nobile from www.AntWeb.org.

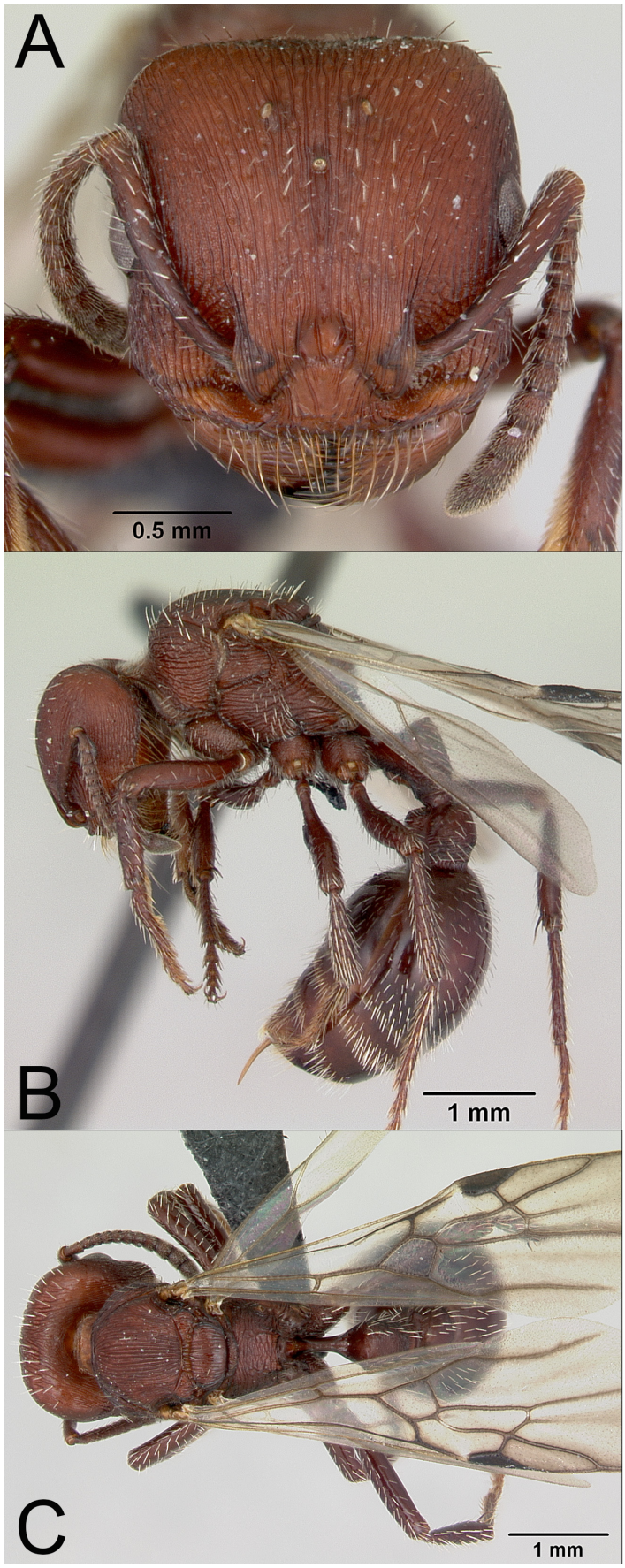

FIGURE 36. Photograph of *Pogonomyrmex uruguayensis* Mayr alate queen: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0173121). Photographs by April Nobile from www.AntWeb.org.

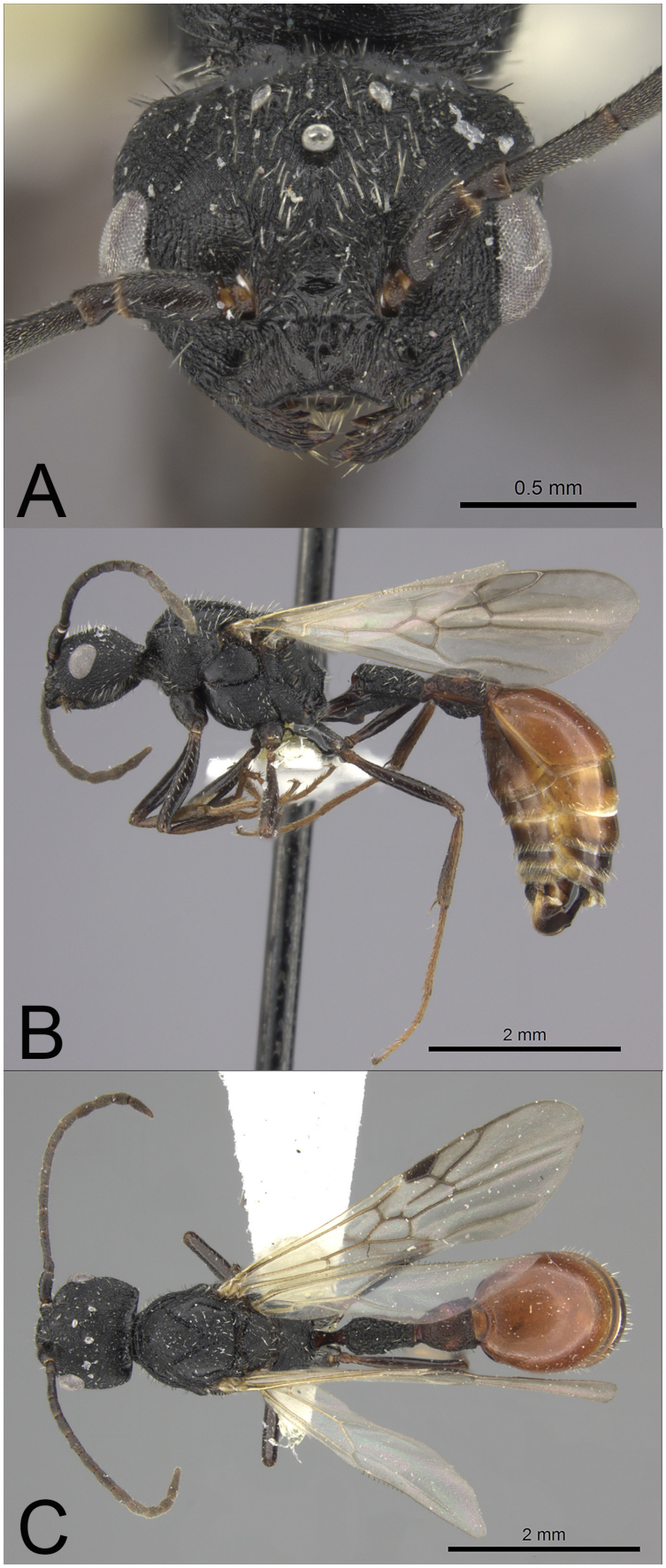

FIGURE 37. Photograph of *Pogonomyrmex uruguayensis* Mayr male: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0235274). Photographs by Will Ericson from www.AntWeb.org.

Queen. Diagnosis. This caste is diagnosed by: (1) caste-specific morphology of the mesosoma related to wing-bearing and presence of ocelli on the head, (2) superior propodeal spines present, (3) inferior propodeal spines absent, (4) rugae on cephalic dorsum wavy to irregular, interrugae distinctly wider than rugae, (5) posterior surface of petiolar node and usually dorsum of postpetiole rugose (usually transverse), rugae on dorsum of postpetiole often faint to absent medially, (6) in profile, apex of petiolar node subangulate to angulate, and (7) body concolorous tannish-brown (**Figure 36**).

Measurements—(*n* = 12). HL 1.64–1.76; HW 1.72–1.83; MOD 0.36–0.47; OMD 0.38–0.45; SL 1.08–1.18; PNW 1.27–1.48; HF 1.40–1.63; ML 2.24–2.50; PW 0.50–0.63; PPW 0.70–0.81. Indices: SI 60.34–68.60; CI 100.00–105.29; OI 20.93–27.33; HFI 81.40–93.02.

Description. With caste-specific morphology of the mesosoma related to wing-bearing and presence of ocelli on head. In full-face view, head quadrate to slightly wider than long (CI = 100.00–105.29), widest just posterior to eyes, posterior margin flat. Longitudinal rugae on cephalic dorsum prominent, wavy to irregular; in full-face view, medial rugae not diverging toward posterior corners of head, interrugae weakly granulate-punctate, weakly shining to shining; vertex rugose, interrugae weakly granulate-punctate, weakly shining to shining. Mandible with six teeth, dorsal surface coarsely rugose. Psammophore well-developed.

All mesosomal surfaces with subparallel, regular, wavy, or irregular rugae; interrugae on mesoscutum and mesoscutellum weakly coriarious, weakly shining to shining, those on propodeum moderately to strongly granulate-punctate, dull; propodeum with short superior spines; inferior propodeal spines absent. Peduncle of petiole long, anteroventral margin with weakly to moderately well-developed triangular process. In profile, petiolar node asymmetrical with anterior surface notably shorter than posterior surface, apex rounded to weakly angulate. Posterior surface of petiolar node and dorsum of postpetiole with irregular transverse rugae; rugae on postpetiole weaker, often faint to absent medially; interrugae on posterior surface of petiolar node and dorsum of postpetiole weakly granulate-punctate, weakly shining. First gastral tergum weakly coriarious, shining to strongly shining. Most body surfaces with moderately abundant suberect to erect, medium-length, white to yellowish setae; moderately abundant suberect to erect hairs on first gastral tergum, those on second and third terga restricted to posterior margin. Body mostly concolorous tannish-brown (**Figure 36**).

Male. Diagnosis. This caste is diagnosed by: (1) first gastral tergum lacking striae, (2) in full-face view, external margin of apical tooth curved inward, (3) dorsum of postpetiole strongly granulate, dull, to occasionally very weakly rugoreticulate to vermiculate, interrugae dull, (4) rugae on head usually rugoreticulate to vermiculate, (5) pronotal sides and mesopleura with occasional rugae, (6) interrugae on cephalic dorsum, pronotal sides, and mesopleura moderately to strongly granulate, dull, and (7) notauli present (**Figure 37**).

Measurements—(*n* = 3). HL 1.32–1.42; HW 1.38–1.51; MOD 0.50–0.54; OMD 0.26–0.29; SL 0.37–0.40; HFL 1.56–1.68; ML 2.60–2.68; PW 0.52–0.57; PPW 0.68–0.72. Indices: SI 24.50–27.54; CI 104.55–109.49; OI 34.67–36.23; HFI 103.31–121.01.

Additional material examined. ARGENTINA: ***Catamarca***: Rt 20 at 0.7 km NE Esquiú, 800', Mar 21, 2015 (RAJC); Rt 157 at 25.2 km NNW Jct Rt 60, 750', Mar 21, 2015 (RAJC). ***Chaco***: Rt 11 at 26.6 km S Resistencia, 170', Jan 19, 2011 (RAJC); 42 km SW Resistencia, Dec 18, 2005 (CSC). ***Córdoba***: Rt 2 at 18.9 mi E Villa María, 470', Dec 21, 2005 (CASC; CSC; RAJC); Rt 65 at 22.4 km E Villa María, Dec 18, 2005 (CSC); Rt 9 at 6.5 mi E Bell Ville, 390', Dec 21, 2005 (CSC; RAJC); Rt 16 at 15.2 km N Chuña, 1670', Mar 20, 2015 (RAJC); Rt 60 at 4.2 km SE Quilino, 1520', Mar 20, 2015 (RAJC); Rt 60 at 27.7 km NW Quilino, 700', Mar 21, 2015 (RAJC); Rt 60 at 12.3 km NW Lucio Mansilla, 680', Mar 21, 2015 (RAJC). ***Corrientes***: Rt 12 at 10.2 km E Santa Ana, 210', Jan 18, 2011 (RAJC); no loc, no date (USNM). ***Entre Ríos***: Parque Nacional El Palmar, Jan 6, 2006 (RGPC); Rt 130 at 2.7 mi S Villaguay, 190', Dec 19, 2005 (CSC; RAJC); Villaguay, no date (MACN; MLPA); no loc, no date (MACN). ***Formosa***: Reserva "El Bagual", 151 m, Apr 2009 (RAJC); Guaycolec, no date (MACN; NHMB); Estancia Sosa, no date (MACN). ***La Rioja***: Rt 79 at 30.1 km N Catuna, 1890', Mar 19, 2015 (RAJC); Rt 79 at 14.2 km S Catuna, 1810', Mar 19, 2015 (RAJC); Rt 79 at 34.6 km S Catuna, 2050', Jan 22, 2006 (MCZ; RAJC); Rt 79 at 2.6 km N Ulapes, Mar 19, 2015 (RAJC); Rt 79 at 6.9 km SE Ulapes, 1250', Jan 22, 2006 (RAJC); Rt 79 at 26.8 km SE Ulapes, 960', Mar 19, 2015 (RAJC); Rt 79 at 4.2 km S Jct Rt 141, 1750', Mar 19, 2015 (RAJC); Rt 38 at 8.1 km W of Córdoba-La Rioja border, 710', Jan 14, 2010 (RAJC); Rt 38 at 2.3 km W Córdoba border, Mar 20, 2015 (RAJC); Rt 38 at 42.1 km ESE Chamical, Mar 20, 2015 (RAJC); Rt 60 at 15.4 km NE Jct Rt 20, 660', Mar 23, 2015 (RAJC). ***Salta***: Estacion Ferrocarril Virgilio Tedin, Feb 28, 1948 (FML). ***San Luis***: Rt 7 at Alto Pencoso, 2150', Dec 20, 2006 (RAJC); La Tranca, Feb 10 & 24, 2009 (RGPC); La Punta, 2790', Mar 6, 2005 (RAJC); Rt 20

at 1 km NE Luján, 1940', Dec 26, 2005 (RAJC); Rt 7 at 3.5 km W Alto Pencoso, Dec 20, 2006 (CSC). ***Santa Fe***: Paraná River floodplain at Villa Ocampo, 45 m, Nov 21, 2004 (RAJC); Ocampo, 50 m, Nov 17, 2003 (CASC; RAJC); Rt 11 at 23 mi S Villa Ocampo, 140 m, Dec 20, 2004 (RAJC); Rt 34 at 3 km W Santa Ana, 145 m, Dec 20, 2006 (RAJC); 22 km S Reconquista, 45 m, Nov 15, 2003 (RAJC); Villa Guillermina, no date (LACM); Rosario, no date (MACN); Fives Lille, no date (MACN); 18.2 km S Los Toscas, Dec 4, 2005 (CSC). ***Santiago del Estero***: Rt 34 at 33.6 km N Pozo Hondo, 820', Apr 7, 2015 (RAJC). ***Tucumán***: Rt 34 at 70.8 km SE Jct Rt 9, 1400', Apr 7, 2015 (RAJC). **PARAGUAY:** ***Boquerón***: Rt Trans-Chaco, 180 m, Dec 4, 2002 (ALWC). ***Ñeembucú***: Pila Aeropuerto, 65 m, Dec 12, 2002 (ALWC). ***Presidente Hayes***: Rt Trans-Chaco at km 438, Dec 5, 1993 (ALWC); Rt Trans-Chaco at km 140, Dec 3, 1993 (ALWC); Rt Trans-Chaco, 90 m, Dec 3, 2002 (ALWC); Monte Lindo, Nov 15, 1993 (ALWC). **URUGUAY:** ***Paysandú***: Arroyo Sacra, Feb 25, 1961 (LACM). ***Locations not found*****: URUGUAY:** ***Rivera***: Río Negro, Feb 1941 (FML). ***Dpto. Unknown***: no loc, no date (MCZ; NMW) (**Figure 31C**).

Etymology. The specific epithet, *uruguayensis* was derived from Charles Berg collecting the series of syntype workers in Uruguay (the exact location was unspecified).

Discussion. *Pogonomyrmex uruguayensis* co-occurs with *P. inermis*. The two species are easily distinguished as *P. uruguayensis* has superior propodeal spines while these spines are lacking or reduced to small denticles or tubercles in *P. inermis*. Additionally, workers of *P. uruguayensis* are typically smaller (HW = 1.24–1.61 mm) than those of *P inermis* (HW = 1.59–1.86 mm). *Pogonomyrmex uruguayensis* is distinguished from other sympatric congeners by its well-developed psammophore and absence of transverse rugae on the dorsum of the postpetiole.

I also examined five workers that Santschi had labelled as "syntypes" of *P. uruguayensis* var. *spinosula* from Guaycubec (=Guaycolec?), Formosa, Argentina (NHMB). Santschi (1921) described this variety, but did not name it as a new variety, such that these specimens are not true syntypes and the name is unavailable.

Gallardo (1932, pg. 131) mentioned that Santschi had identified one worker of *P. bispinosus* from Formosa, Argentina, that coincided well with the description, but that it was far from all Chilean records. I did not examine this specimen, but it was undoubtedly *P. uruguayensis*.

Biology. *Pogonomyrmex uruguayensis* is a solitary forager that harvests the seeds of various grass and nongrass species, but very loose columns of scattered foragers also have been observed. Nests are cryptic or they can have a tumulus up to 10 cm in diameter; nests occasionally have a small (5–10 cm in diameter) external midden of seed chaff. Most colonies of *P. uruguayensis* appear to be small and probably contain about 300–500 workers, but sometimes reach up to approximately 1000 workers.

Collection dates for sexuals range from 30 November to 21 December. Mating flights have not been observed, but they occur during the austral summer (December–January) based on finding dealate queens on the ground on 19 & 26 December. Several dealate queens also were collected foraging outside the nest. Several ant species have queens that sometimes apparently forego mating and later perform tasks such as foraging and nest maintenance (Peeters, 1997). Reproductive status was not determined for these queens, but they are assumed to have been unmated given that foraging queens (both ergatoid and dealate) are unmated in *P. pima*, which is the only species in which such queens have been dissected (Johnson *et al.*, 2007). These observations add another *Pogonomymex* to the list of species in which queens forage outside the nest (Johnson *et al.*, 2007).

Pogonomyrmex uruguayensis inhabits sites at elevations from 50–845 m. This species occurs in the Dry Chaco, Humid Chaco, Uruguayan Savanna, northern Espinal, and northern Humid Pampas ecoregions as defined by Olson *et al*. (2001) (**Figure 31C**).

***Pogonomyrmex laticeps*-group**

Workers in the *P. laticeps*-group are diagnosed by the following characters: (1) first gastral tergum lacking striae, (2) head broader than long, (3) interrugae on cephalic dorsum and dorsum of mesosoma smooth to moderately coriarious, weakly shining to shining (granulation and/or punctation absent) ***or*** rugae incised, interrugae about as wide as rugae, (4) superior propodeal spines well-developed, and (5) inferior propodeal spines poorly-developed or lacking. The mostly smooth interrugae appear to be the best character to diagnose *P. laticeps* and *P. tinogasta*. All three species have brachypterous queens, diagnosed by: (1) poorly-developed mesoscutum, its anterior margin barely surpassing the humeral shoulders of pronotum, (2) pronotum enlarged, and (2) in profile, the pronotum rises at an approximately 45° angle to meet the mesoscutum.

Pogonomyrmex laticeps
(Figures 38–41)

Pogonomyrmex laticeps Santschi, 1922: 350 (worker). Syntypes examined: 2 workers [MACN], ARGENTINA, Catamarca: Masao, #1376 (Weiser leg., March 1921); Kusnezov, 1951: 274, figs. 10a, 10b (ergatoid queen, brachypterous queen). See also Gallardo, 1932: 161, fig. 42; Peeters, *et al*. 2012: figs. 2–4, 6–7. MACN worker here designated **LECTOTYPE** [CASENT0217255].

Worker. Diagnosis. Within the *P. laticeps*-group, the combination of: (1) head and mesosoma dark reddish-black, gaster black, (2) rugae on promesonotum transverse, oblique, or irregular, rarely longitudinal, and (3) medial rugae along posterior margin of head usually partly rugoreticulate uniquely characterize this species (**Figure 38**).

Measurements—lectotype (n = 52). HL 2.04 (1.56–2.07); HW 2.20 (1.65–2.25); MOD 0.37 (0.30–0.40); OMD 0.53 (0.39–0.64); SL 1.39 (1.08–1.59); PNW 1.38 (1.04–1.39); HFL 2.08 (1.45–2.24); ML 2.67 (1.85–2.62); PW 0.55 (0.0.39–0.59); PPW 0.79 (0.59–0.83). Indices: SI 63.18 (60.34–81.52); CI 107.84 (101.12–115.20); OI 16.82 (16.28–23.20); HFI 94.55 (81.22–110.56). See also Peeters *et al*. (2012).

Redescription. Head subquadrate to wider than long (CI = 101.12–115.20), widest just posterior to eye; posterior margin flat in full-face view. Longitudinal rugae on cephalic dorsum prominent, weakly wavy to irregular, sometimes weakly rugoreticulate on medioposterior margin; in full-face view, medial rugae diverging weakly toward posterior corners of head. In profile, rugae posterior to eyes converging toward vertex. Cephalic interrugae weakly granulate, shining; vertex rugose. Anterior margin of clypeus flat to weakly concave; dorsal surface with numerous subparallel, longitudinal rugae. Mandible with six teeth; mandibular dorsum coarsely rugose. Numerous long, curved, bristle-like, yellowish hairs project from anterior margin of clypeus and basolateral margin of mandibles. MOD ranging from 0.18–0.23x HL. In profile, eyes situated near middle of head, OMD = 1.19–1.60x MOD. Antennal scapes relatively long (SI = 60.34–81.52), failing to reach vertex by up to length of basal funicular segment; scapes smooth and shining, distal portion often weakly striate. Basal flange of scape flattened, well-developed with carinate margin. Psammophore well-developed.

Mesosomal profile flat to weakly convex; all mesosomal surfaces with prominent rugae. In profile and dorsal views, humeral shoulders of pronotum sometimes angulate, weakly elevated above medial portion of pronotum. Dorsum of promesonotum and sides of pronotum with coarse, transverse, longitudinal or oblique, irregular rugae, rugoreticulate to vermiculate; promesonotal suture weakly impressed on occasional workers. Mesopleura with wavy to irregular rugae angling posterodorsally, rugae often more irregular to rugoreticulate near anterodorsal margin. Dorsum of propodeum with transverse to irregular rugae that traverse anteroventrally on sides. Propodeum with long, acuminate spines connected by well-defined keel; spine length similar to or slightly longer than distance between their bases. Inferior propodeal spines absent or reduced to indistinct rounded or triangular process. Propodeal spiracles narrowly ovate facing posterad. Interrugae on mesosoma smooth, strongly shining. Legs moderately coriarious, weakly shining.

Peduncle of petiole about 0.8x as long as petiolar node, anteroventral margin usually with rounded to triangular tooth-like process. In profile, petiolar node asymmetrical with anterior surface about one-half as long as posterior surface; apex weakly angulate to rounded. In dorsal view, petiolar node longer than wide, sides subparallel to slightly wider near spatulate anterior margin; posterior surface and sides with moderately strong, wavy to irregular, transverse to arcuate rugae. Dorsum of postpetiole convex in profile; in dorsal view, widest near posterior margin, narrowing to anterior margin; maximal width about equal to length; dorsum and sides with wavy to irregular transverse rugae that are finer, denser than on posterior surface of petiolar node. Interrugae on posterior surface of petiolar node smooth and strongly shining, weakly to moderately granulate, weakly shining on dorsum of postpetiole. First gastral tergum moderately coriarious, weakly shining to smooth, strongly shining.

Erect whitish pilosity moderately abundant on head, variable in length, longest hairs not exceeding MOD. Moderately abundant suberect to semidecumbent pilosity on scape, abundant decumbent hairs on funicular segments. Legs with moderately abundant semidecumbent white setae. Mesosoma, petiolar node, postpetiole, and gastral terga with moderately dense, erect setae, variable in length, only those on posterior gastral terga approaching MOD. Head, mesosoma dark orangish-black to reddish-black; petiolar node, postpetiole slightly darker; legs, gaster dark brown to black (**Figure 38**).

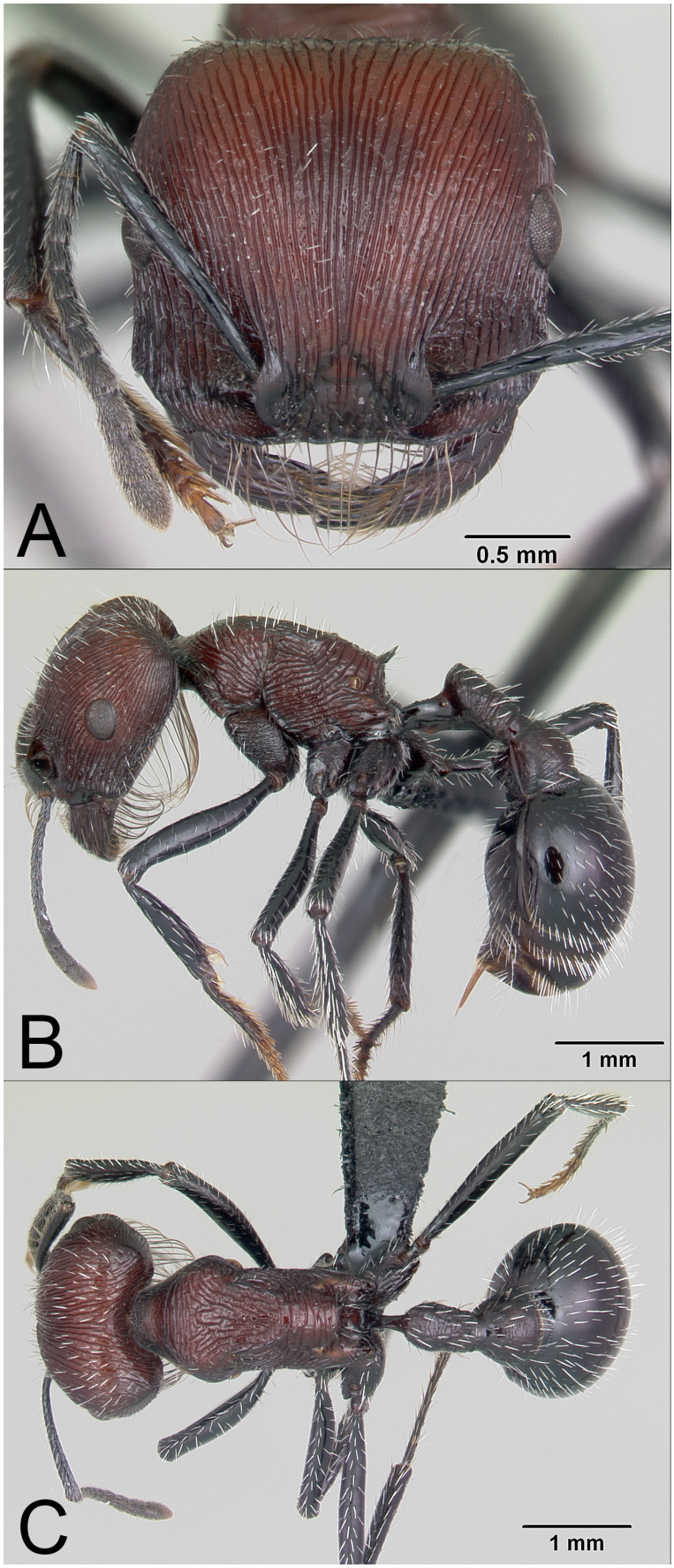

FIGURE 38. Photograph of *Pogonomyrmex laticeps* Santschi worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0103263). Photographs by April Nobile from www.AntWeb.org.

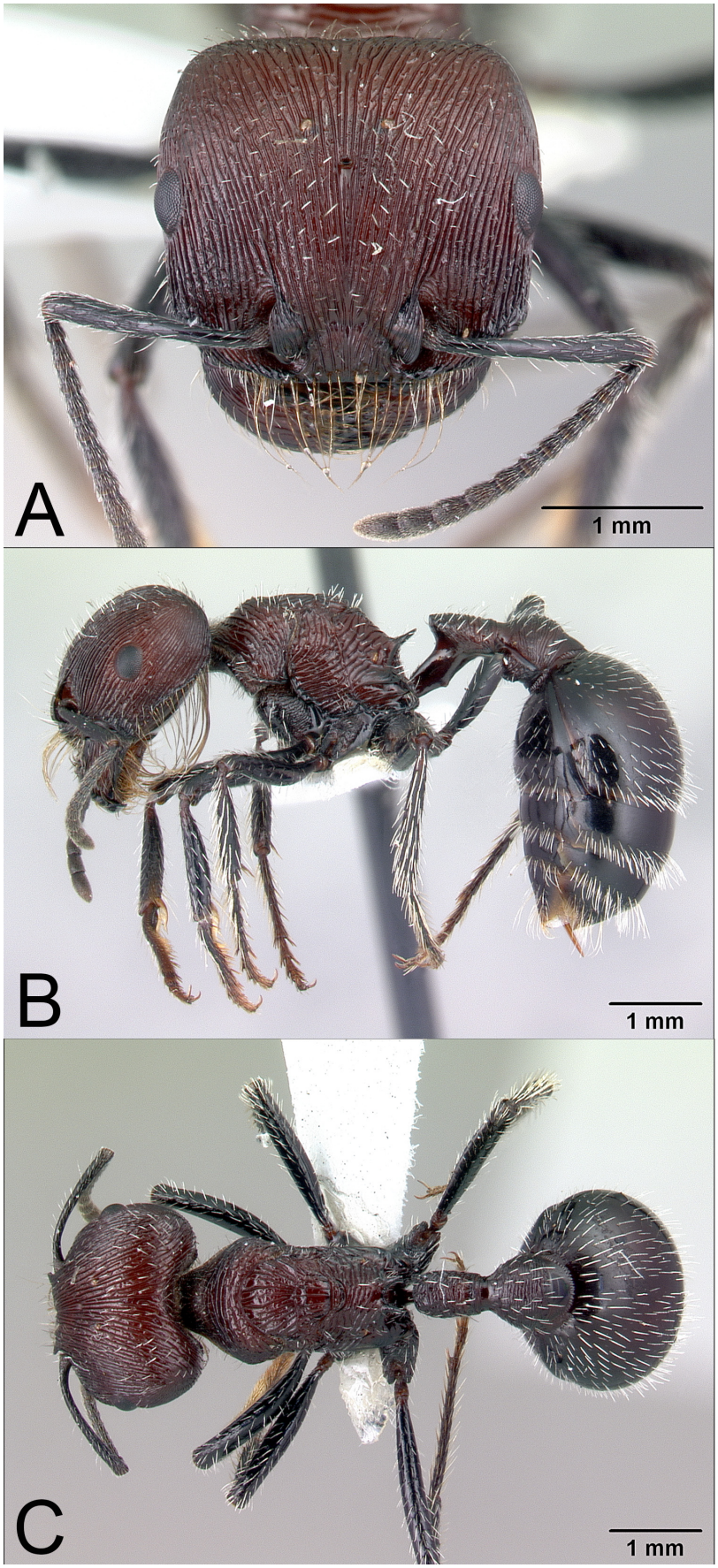

FIGURE 39. Photograph of *Pogonomyrmex laticeps* Santschi ergatoid queen: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0217266). Photographs by Erin Prado from www.AntWeb.org.

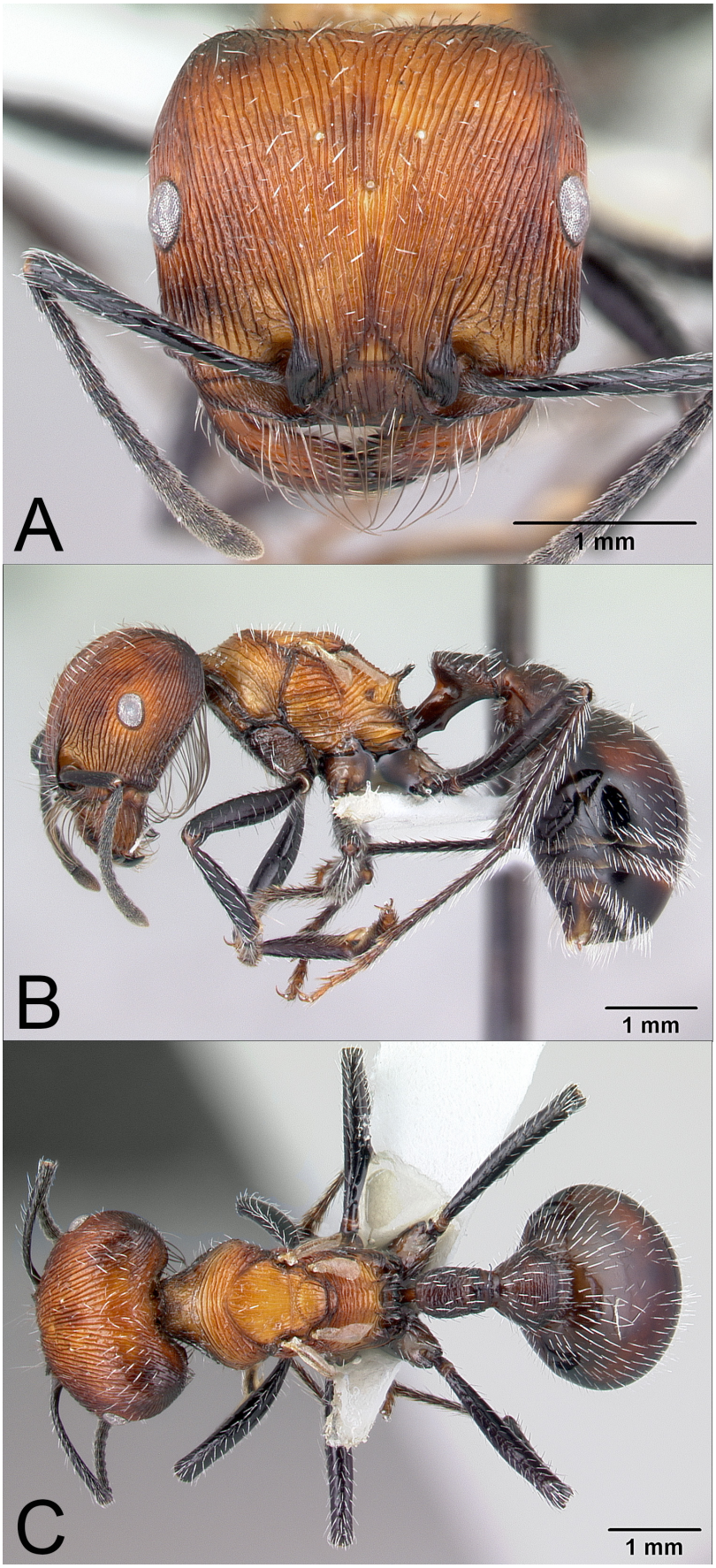

FIGURE 40. Photograph of *Pogonomyrmex laticeps* Santschi brachypterous queen: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0217265). Photographs by Erin Prado from www.AntWeb.org.

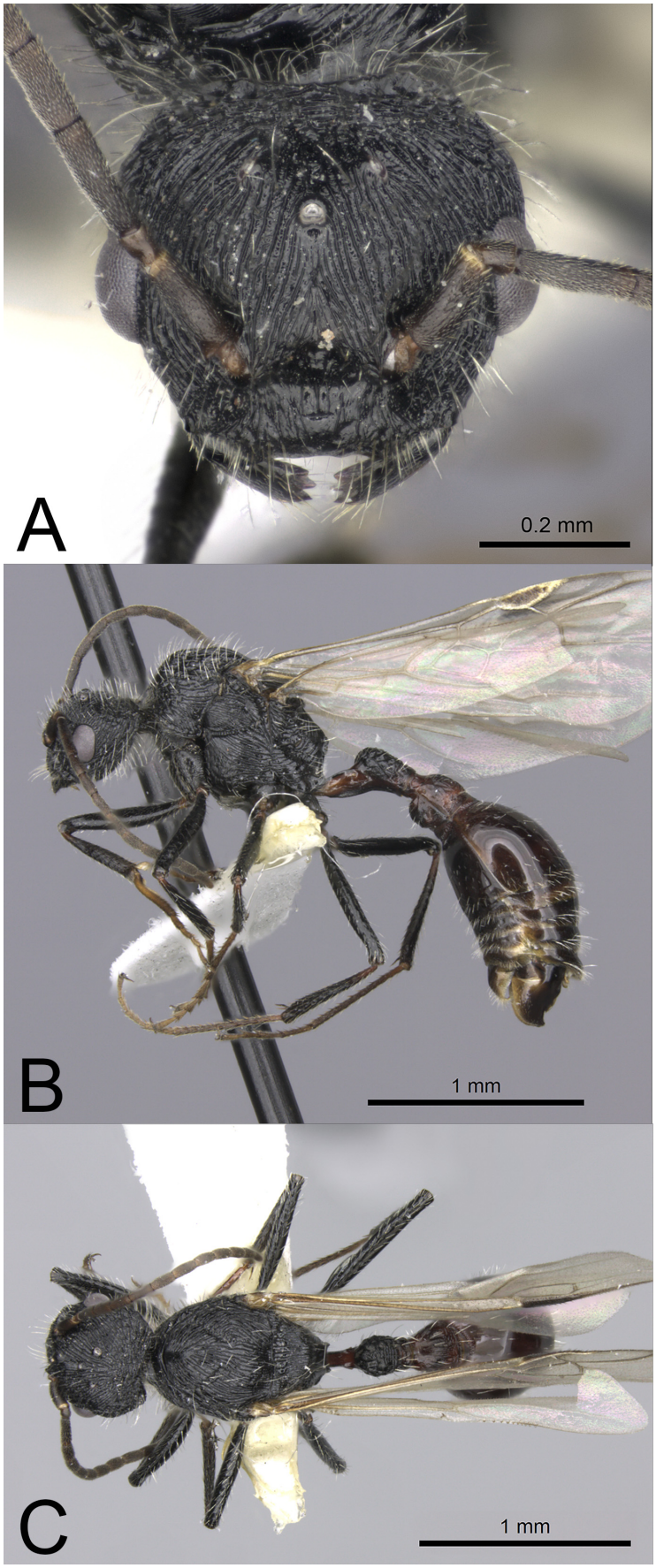

FIGURE 41. Photograph of *Pogonomyrmex laticeps* Santschi male: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0235297). Photographs by Will Ericson from www.AntWeb.org.

Ergatoid queen. Diagnosis. This caste is diagnosed by: (1) ergatoid, with small ocelli on head and mesosoma lacking morphological structures related to wings, (2) larger species (HW > 1.40 mm), (3) first gastral tergum smooth and shining to moderately coriarious, (4) interrugae on cephalic dorsum smooth and shiny, and (5) head, mesosoma, petiolar node, postpetiole dark reddish-black; gaster blackish (**Figure 39**).

Measurements—(*n* = 25). HL 1.85–2.18; HW 1.99–2.32; MOD 0.35–0.44; OMD 0.5–0.67; SL 1.25–1.65; PNW 1.28–1.45; HFL 1.83–2.24; ML 2.26–2.75; PW 0.49–0.64; PPW 0.78–0.96. Indices: SI 53.88–76.39; CI 104.19–113.00; OI 16.09–20.39; HFI 83.04–100.00. See also Peeters *et al*. (2012).

Brachypterous queen. Diagnosis. This caste is diagnosed by: (1) brachypterous with very small wings and small ocelli on head, (2) in dorsal view, mesoscutum poorly-developed, anterior margin barely surpassing humeral shoulders of pronotum, (3) pronotum well-developed, (4) in profile, the pronotum rises at an approximately 45º angle to meet the mesoscutum, and (5) head and mesosoma dark reddish-black, gaster black (**Figure 40**).

Measurements—(*n* = 30). HL 1.90–2.36; HW 2.09–2.49; MOD 0.40–0.46; OMD 0.55–0.69; SL 1.35–1.66; PNW 1.29–1.59; HFL 2.01–2.44; ML 2.26–2.87; PW 0.53–0.63; PPW 0.83–1.02. Indices: SI 57.26–70.09; CI 104.66–119.29; OI 16.46–19.66; HFI 84.10–102.14. See also Peeters *et al*. (2012).

Male. Diagnosis. The combination of: (1) first gastral tergum lacking striae, (2) rugae on dorsum of postpetiole usually longitudinal, interrugae weakly shining to shining, (3) dorsum of mesoscutum and mesoscutellum with prominent wavy to weakly irregular longitudinal rugae, interrugae weakly shining to shining, (4) in dorsal view, dorsum of propodeum depressed, lacking rugae, weakly shining to shining; prominent rugae traverse posteroventrally lateral to depression, and (5) notauli present (**Figure 41**).

Measurements—(*n* = 12). HL 1.20–1.43; HW 1.32–1.52; MOD 0.43–0.55; OMD 0.22–0.32; SL 0.34–0.42; HFL 1.50–1.96; ML 2.13–2.62; PW 0.44–0.58; PPW 0.65–0.81. Indices: SI 23.68–31.82; CI 103.50–122.58; OI 30.94–36.18; HFI 107.91–146.27.

Additional material examined. ARGENTINA: ***Catamarca***: Punta de Balasto, no date (MACN); Rt 40 at 3.8 km S Punta de Balasto, 7040', Jan 27, 2010 (MCZ; RAJC); Catamarca airport, Feb 4, 1967 (MCZ); Santa María, no date (FML; LACM; MCZ); Valle de Santa María, no date (MCZ); Rt 39 at 0.4 km N Santa María, 5930', Mar 25, 2015 (RAJC); Rt 39 at 15.1 km S Santa María, 6480', Mar 25, 2015 (RAJC); Valle Masan, no date (MCZ); Rt 60 at Casa de Piedra, 790', Mar 21, 2015 (RAJC); Rt 38 at 0.6 km S entrance to Catamarca, 1630', Mar 22, 2015 (RAJC). ***La Rioja***: El Portezuelo, Apr 16, 2009 (RGPC); Rt 29 at 38.7 km S El Portezuelo, 2250', Apr 9, 2015 (RAJC); 96.8 km N Jct Rts 9 & 38, 1750', Jan 7, 2006 (RAJC); Rt 38 at 20.8 km ESE Patquia, 1210', Mar 19, 2015 (RAJC); Rt 38 at 20.8 km ESE Patquia, 1210', Mar 22, 2015 (RAJC); Rt 38 at 30.8 km SE Patquía, 1330', Jan 15, 2010 (RAJC); Rt 38 at 44.2 km SE Patquia, 1270', Mar 22, 2015 (RAJC); 18.0 km NW Patquía, 1970', Jan 20, 2006 (RAJC); Rt 27 at 22.5 km S Patquia, 1590', Apr 9, 2015 (RAJC); Rt 27 at 69.4 km S Patquia, 1900', Apr 9, 2015 (RAJC); Rt 38 at 35.7 km N Jct Rt 74 (Patquia exit), 1410', Mar 22, 2015 (RAJC); 30.8 km E Jct Rts 5 & 38, 1160', Jan 21, 2006 (RAJC); Rt 40 at 6.0 km N Chilecito, 3200', Jan 3, 2006 (RAJC); Rt 40 at 11.3 km N Chilecito, 3230', Feb 6, 2010 (RAJC); Rt 40 at 14.0 km N Chilecito, 3410', Feb 4, 2006 (RAJC); Rt 40 at 25.4 km W Shaqui, 4070', Jan 5, 2006 (RAJC); Rt 40 at 49.1 km S Pituil, 4270', Jan 20, 2006 (RAJC); Rt 73 at 60.7 km NE Chamical, 1430', Jan 21, 2006 (RAJC); Rt 38 at 19.2 km NW Chamical, 1290', Mar 20, 2015 (RAJC); Nonogasta, no date (MACN); Rt 141 at 17.2 km E border with San Juan, 1560', Mar 17, 2015 (RAJC); Rt 141 at 2.7 km E Chepes, 2130', Mar 18, 2015 (RAJC); Rt 79 at 66.5 km NE Jct Rt 38, 1270', Mar 23, 2015 (RAJC). ***Salta***: Cafayate, Feb 20–26, 1948 (FML; LACM; MCZ); Cafayate, no date (LACM; MZUSP; USNM); Rt 40 at 5.6 km N Cafayate, 5480', Jan 11, 2006 (RAJC); Rt 40 at 28.4 km N Cafayate, 5400', Jan 11, 2006 (RAJC); Cafayate-Santa María-Frontera Salta-Tucuman, Jan 28, 1942 (FML); Rt 40 at 0.2 km N Tucumán border, 5560', Mar 24, 2015 (RAJC); Rt 40 at 13.4 km N Tucumán border, 5710', Mar 24, 2015 (RAJC); Rt 40 at 8.2 km N Jct Rt 68, 5510', Mar 26, 2015 (RAJC); Rt 40 at 2.6 km N San Carlos, 5470', Mar 26, 2015 (RAJC). ***San Juan***: Rt 141 at 14.6 km E turnoff to Marayes, 1550', Mar 17, 2015 (RAJC). ***San Luis***: 3.7 km SE Jct Rts 20 & 147, 2380', Dec 27, 2005 (RAJC); Parque Nacional Sierra las Quijadas, 2610', Mar 6, 2005 (RAJC); Rt 147 at 1.3 km NW turnoff to Parque Nacional Las Quijadas, 2300', Mar 16, 2015 (RAJC); Rt 20 at 75.6 km W Luján, 1570', Dec 27, 2005 (RAJC); La Tranca, Feb 10, 2009 (RGPC). ***Tucumán***: Rt 307 at 6.8 km NW Amaicha de Valle, 6080', Jan 27, 2010 (RAJC); Rt 40 at 9.8 km NW Amaiche del Valle, 5930', Mar 24, 2015 (RAJC); Rt 40 at 10.0 km NW Amaicha del Valle, 5940', Jan 10, 2006 (CASC; RAJC); SW Amaicha de Valle, 2100 m, Feb 3, 1995 (MCZ); Bañado de Quilmes, no date (MACN) (**Figure 42A**).

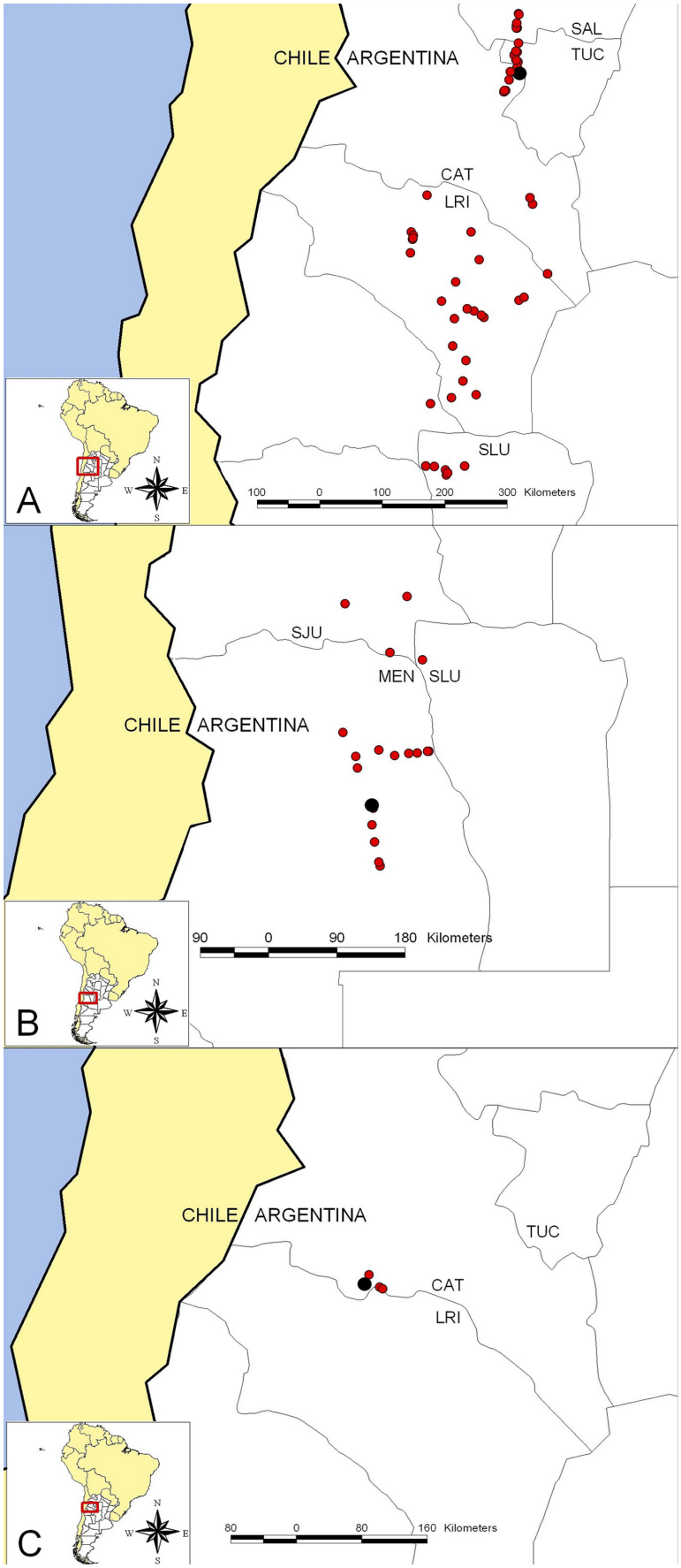

FIGURE 42. Geographic distribution of: (**A**) *Pogonomyrmex laticeps* Santschi, (**B**) *Pogonomyrmex mendozanus* Cuezzo & Claver, and (**C**) *Pogonomyrmex tinogasta* Johnson. The larger black circle in each panel denotes the type locality.

Etymology. The specific epithet, *laticeps* (from Latin, *latus* = wide, and the suffix *-ceps* = head), is derived from the wide head of this species; in his description, Santschi noted that the head was clearly wider than long.

Discussion. *Pogonomyrmex laticeps* is not known to co-occur with *P. mendozanus* or *P. tinogasta*. *Pogonomyrmex laticeps* can be distinguished from *P. mendozanus* by the coarse, irregular rugae on the head and mesosoma, whereas cephalic and mesosomal rugae on *P. mendozanus* are fine, incised, and very regular. *Pogonomyrmex laticeps* can be distinguished from *P. tinogasta* based on the following characters: (1) head and mesosoma dark reddish-black, gaster black, (2) rugae on promesonotum transverse, oblique, or irregular, rarely longitudinal, and (3) medial rugae along posterior margin of head usually partly rugoreticulate. In *P. tinogasta*: (1) the body is concolorous black except for a dark reddish band encircling the eye, (2) the promesonotal rugae are longitudinal, usually regular, and (3) the medial rugae along the posterior margin of the head are longitudinal, rarely rugoreticulate.

Several authors have misinterpreted the type locality for *P. laticeps*. In describing the species, Santschi (1922) listed the type locality as Masao, Catamarca Province, Argentina (see also Baldini & Scattolin, 1993). Alternatively, Gallardo (1932) listed the type locality as Masas, and Kempf (1972) apparently questioned the locality by indicating it as <Masao> (=Mazán?). Additionally, the label on an MCZ specimen was interpreted as Valle Masan.

Biology. *Pogonomyrmex laticeps* is a solitary forager that harvests seeds. Nests usually have a tumulus that is up to 15 cm in diameter, sometimes with an external midden of seed chaff. Colonies of *P. laticeps* are relatively small: Kusnezov (1951) estimated colony size at 25–50 workers, but I have excavated colonies with up to 200 workers (Peeters *et al.*, 2012), suggesting that colony size probably ranges up to 300–400 workers. Colonies in southern portions of the range sometimes contain up to 1000 workers, and very loose columns of scattered foragers have been observed.

This species is interesting morphologically because it has two non-flying queen phenotypes—ergatoid and brachypterous queens (Peeters *et al.*, 2012). Only one queen phenotype is produced within a colony, and both queen phenotypes have similar reproductive potentials with a spermatheca and 12–15 ovarioles (Peeters *et al.*, 2012). Colonies of both phenotypes can produce >50 queens, which Peeters *et al*. (2012) used to suggest that both queen phenotypes initiate nests using independent colony founding. Little is known about mating, but ergatoid queens have been collected from 6 February to 16 April. Brachypterous queens were larvae, pupae, or callows near the end of January and mature brachypterous queens have been collected from 20 February to 9 April. Mating has not been observed, but both ergatoid and brachypterous foundresses have been observed running on the ground (Mar 23 for ergatoid queens; Mar 24–25 for brachypterous queen), and both phenotypes exhibit independent colony founding; one haplometrotic ergatoid queen was excavated on March 22, and one haplometrotic brachypterous queen was excavated on March 24. Both ergatoid and brachypterous foundresses were observed to forage outside the nest (pers. obs.). Mating activities and colony founding appeared to have been triggered by late summer rains.

Data also indicate that the two queen phenotypes have a non-random geographic distribution; ergatoid queens are known to occur only in southern portions of their range (San Luis, La Rioja, eastern San Juan, and southeastern Catamarca Provinces), whereas brachypterous queens are only known to occur in northern portions of their range (northeastern Catamarca, southern Salta, and western Tucumán Provinces) (**Figure 42A**). These two populations may represent two closely-related species, but firm data to substantiate this hypothesis are lacking. Consequently, these two populations are retained within *P. laticeps* until additional data become available.

Pogonomyrmex laticeps inhabits sites at elevations from 240-2135 m. This species occurs from northwestern San Luis to southcentral Salta, and it is restricted to northern and central portions of the High Monte Desert and southwestern portions of the Dry Chaco ecoregions as defined by Olson *et al*. (2001) (**Figure 42A**).

Pogonomyrmex mendozanus

(Figures 43–46)

Pogonomyrmex mendozanus Cuezzo and Claver, 2009: 101, figs. 1, 2, 5–11 (worker, queen, male). Types examined: holotype worker (not examined) [IADIZA], 10 worker paratypes [FML], ARGENTINA, Mendoza: Departamento Santa Rosa, Ñancuñán (S. Claver leg., 12 February 1997).

Pogonomyrmex pronotalis Santschi: Claver & Fowler, 1993: 191; Pirk *et al*., 2004: 65; Pirk & Lopez de Casenave, 2006: 119; Pirk *et al*., 2007: 1092; Pol & Lopez de Casenave, 2004: 647; Pol *et al*., 2008: 92; Pirk *et al*., 2009: 908.

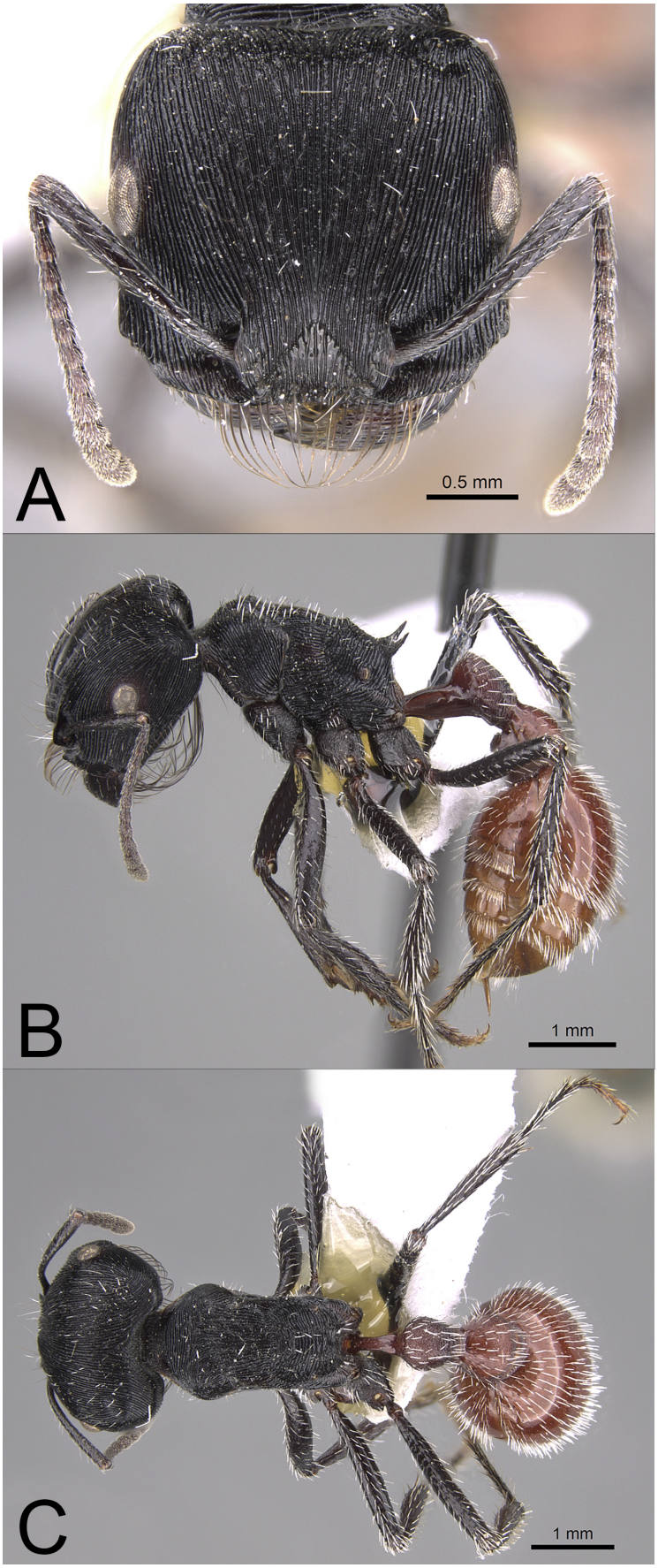

FIGURE 43. Photograph of *Pogonomyrmex mendozanus* Cuezzo & Claver worker: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0914385). Photographs by Michele Esposito from www.AntWeb.org.

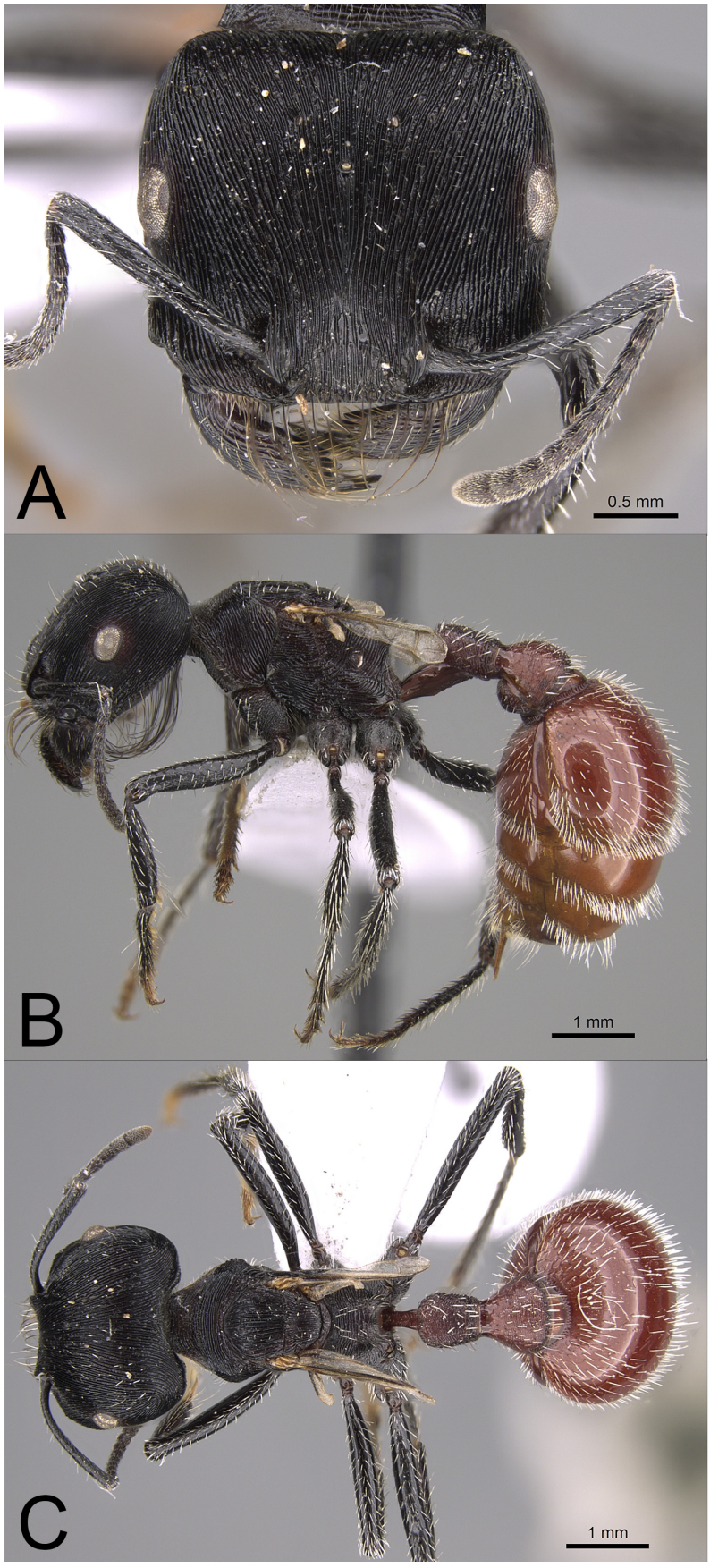

FIGURE 44. Photograph of *Pogonomyrmex mendozanus* Cuezzo & Claver brachypterous queen: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0914403). Photographs by Michele Esposito from www.AntWeb.org.

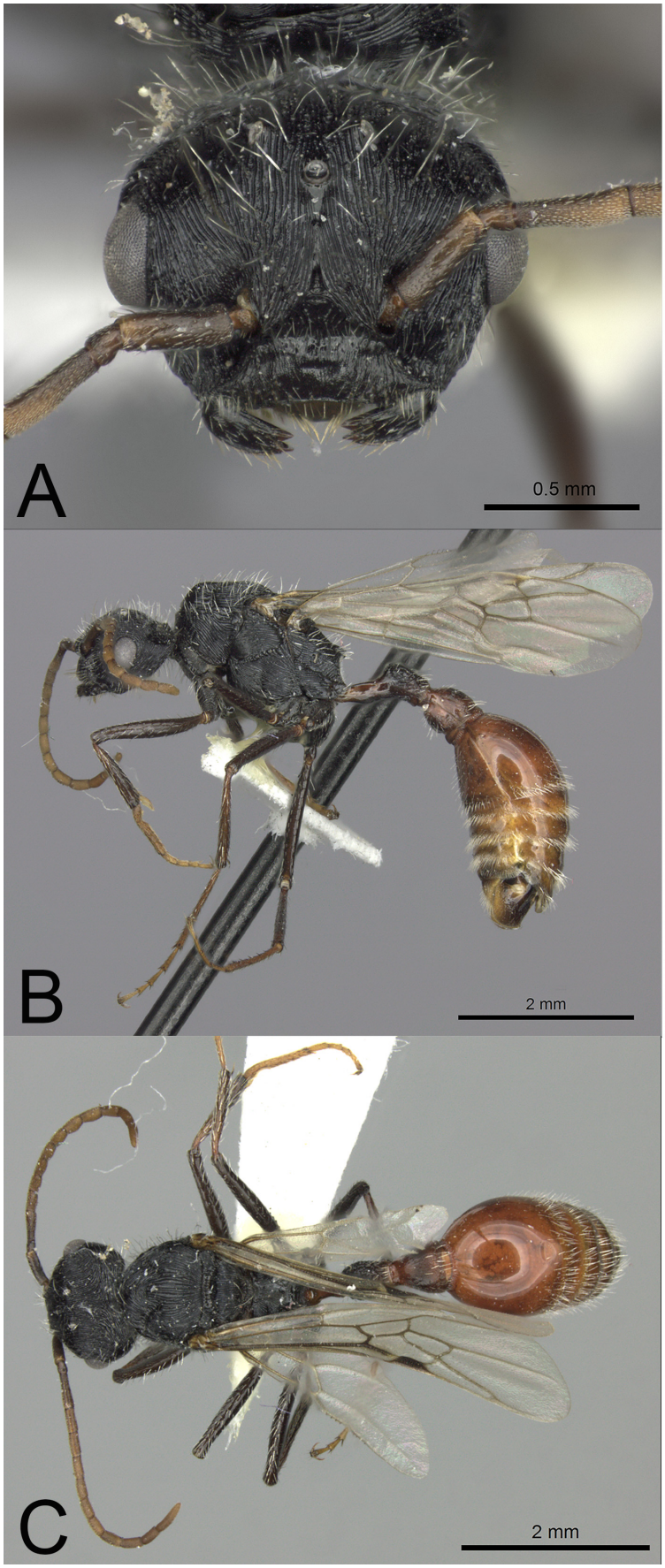

FIGURE 45. Photograph of *Pogonomyrmex mendozanus* Cuezzo & Claver male: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0235299). Photographs by Will Ericson from www.AntWeb.org**.**

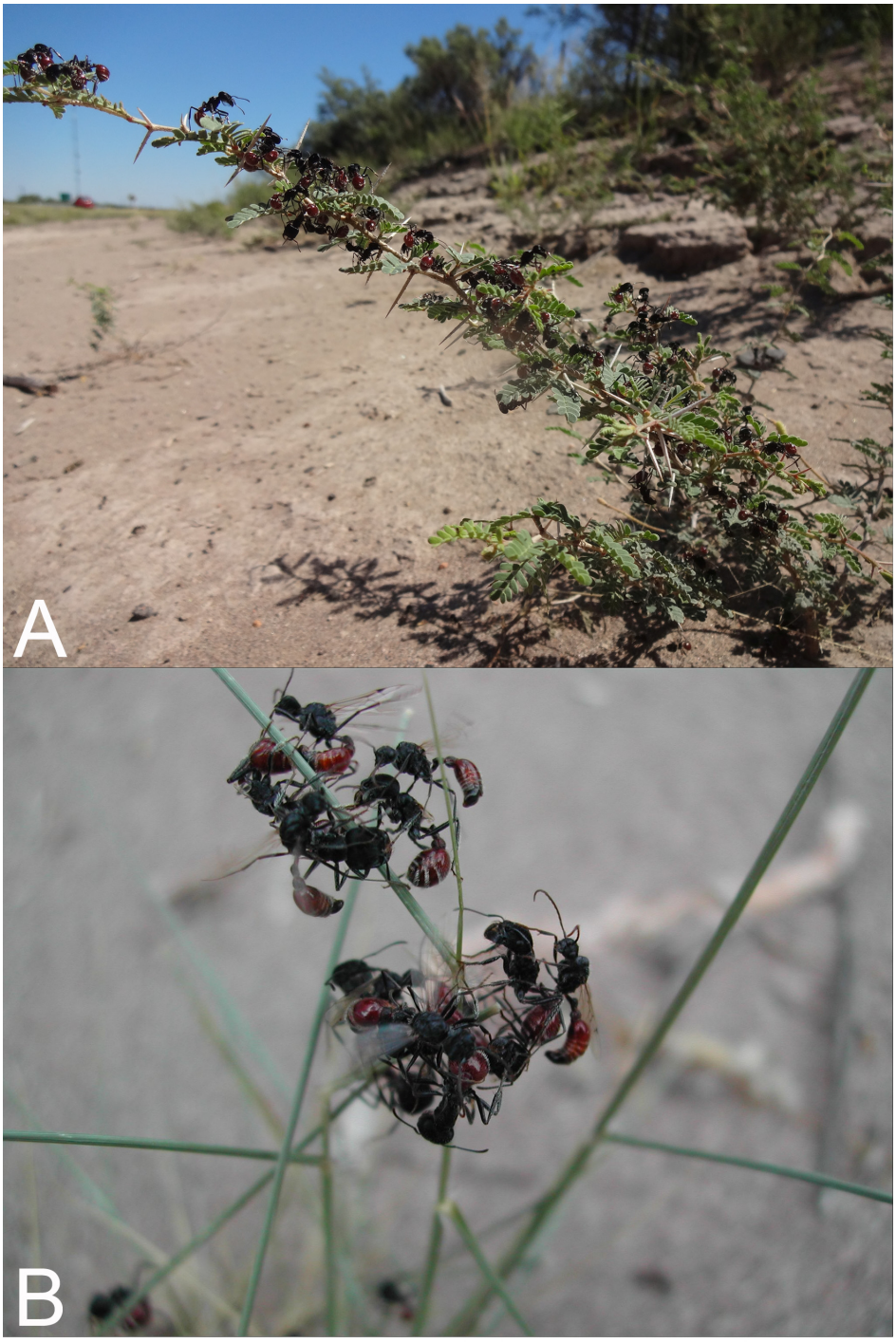

FIGURE 46. Photograph of: (**A**) numerous brachypterous queens of *Pogonomyrmex mendozanus* aggregating on a low-growing plant (< 0.3 m tall) immediately outside their natal nest (no males were observed), and (**B**) mating aggregation containing brachypterous queens of *P. mendozanus*. Bottom photograph courtesy of Rodrigo Pol.

Worker. Diagnosis. Within the *P. laticeps*-group, the combination of: (1) head and mesosoma black, gaster dark ferruginous orange, and (2) head and mesosoma covered by fine, regular, incised rugae uniquely characterize this species (**Figure 43**).

Measurements—(*n* = 16). HL 1.65–2.04; HW 1.87–2.28; MOD 0.37–0.49; OMD 0.47–0.67; SL 1.25–1.59; PNW 1.20–1.41; HF 1.79–2.28; ML 2.16–2.58; PW 0.49–0.67: PPW 0.65–0.82. Indices: SI 65.45–75.66; CI 102.50–113.33; OI 20.27–23.04; HFI 94.14–106.95. See also Cuezzo & Claver (2009).

Redescription. Head subquadrate to wider than long (CI = 102.50–113.33), widest just posterior to eyes; posterior margin flat to weakly concave in full-face view. Cephalic dorsum with fine, regular, incised, longitudinal rugae; in full-face view, medial rugae diverging weakly toward posterior corners of head. In profile, rugae posterior to eyes converging toward vertex. Cephalic interrugae appearing as furrows, weakly to moderately coriarious, weakly shining; vertex rugose. Anterior margin of clypeus weakly to moderately concave; dorsal surface with numerous subparallel, longitudinal rugae. Mandible with six teeth; mandibular dorsum coarsely rugose. Numerous long, curved, bristle-like, yellowish to brownish hairs project from anterior margin of clypeus and basolateral margin of mandibles. MOD ranging from 0.20–0.25x HL. In profile, eyes situated near middle of head, OMD = 1.24–1.43x MOD. Antennal scapes relatively long (SI = 65.45–75.66), reaching vertex or failing to reach vertex by less than length of basal funicular segment; scapes often with moderately coarse longitudinal striae. Basal flange of scape flattened with carinate margin. Psammophore well-developed.

Promesonotal profile flattened, propodeum descending; all mesosomal surfaces with prominent subparallel/parallel rugae similar to that on cephalic dorsum. In profile and dorsal views, humeral shoulders of pronotum angulate, distinctly elevated above medial portion of pronotum. Dorsum of promesonotum with longitudinal rugae that diverge anterad toward humeral shoulders of pronotum; anterior margin of pronotum with transverse rugae that traverse posteroventrally or obliquely on pronotal sides. Mesopleura with transverse rugae, those near dorsal margin often traversing posterodorsally. Dorsum and sides of propodeum with transverse rugae. Superior propodeal spines long, acuminate; spines longer than distance between their bases. Inferior propodeal spines absent or reduced to indistinct broadly rounded processes. Propodeal spiracles narrowly ovate facing posterad. Interrugae on mesosoma weakly coriarious, weakly shining to shining. Legs moderately coriarious, weakly shining.

Peduncle of petiole slightly shorter than petiolar node, anteroventral margin usually flat, lacking tooth or lobe. In profile, petiolar node asymmetrical with anterior surface shorter than posterior surface; apex weakly angulate to rounded. In dorsal view, petiolar node longer than wide, widest near spatulate anterior margin; posterior surface with numerous fine, transverse to arcuate, wavy striae that curve posteroventrally on sides. Dorsum of postpetiole convex in profile; in dorsal view, widest near posterior margin, narrowing anterad; maximal width about equal to length; dorsum and sides with numerous transverse, wavy striae that are finer, denser than those on posterior surface of petiolar node. Interrugae on posterior surface of petiolar node and dorsum of postpetiole weakly to moderately punctate or coriarious, weakly shining to shining. First gastral tergum weakly to moderately coriarious, weakly shining to shining.

Erect white pilosity moderately abundant on head, variable in length, longest hairs not exceeding MOD. Moderately abundant suberect to semidecument pilosity on scape, abundant decumbent hairs on funicular segments. Legs with moderately abundant suberect white setae. Mesosoma, petiolar node, postpetiole with moderately dense, erect white setae, often similar in length, longest on pronotum, none >MOD; gastral terga with moderately dense pilosity, only those on posterior gastral terga approaching MOD. Head, mesosoma black; petiolar node dark orangish-brown to orangish-black; postpetiole, gaster lighter orangish-brown; mandibles, circumference of eyes, tarsi often dark reddish-brown (**Figure 43**).

Brachyterous queen. Diagnosis. This caste is diagnosed by: (1) brachypterous with very small wings and small ocelli on head, (2) in dorsal view, mesoscutum poorly-developed, anterior margin barely surpassing humeral shoulders of pronotum, (3) pronotum well-developed, (4) in profile, the pronotum rises at an approximately 45º angle to meet the mesoscutum, (5) fine, regular, longitudinal rugae on head, mesoscutum, and mesoscutellum, and (6) head and mesosoma black; gaster dark ferruginous orange (**Figure 44**).

Measurements—(*n* = 3). HL 2.07–2.53; HW 2.44–2.81; MOD 0.50–0.53; OMD 0.55–0.81; SL 1.58–1.74; PNW 1.54–1.68; HFL 2.28–2.48; ML 2.59–2.76; PW 0.70–0.77; PPW 1.00–1.05. Indices: SI 61.92–66.13; CI 111.07–119.81; OI 18.86–20.56; HFI 88.26–95.16. See also Cuezzo & Claver (2009).

Male. Diagnosis. This caste is diagnosed by: (1) first gastral tergum lacking striae, (2) weakly regular to regular, subparallel rugae prominent on sides of head, pronotal sides, and mesopleura, (3) in profile, rugae forming circumocular whorls posterior to eyes, and (4) notauli present (**Figure 45**).

Measurements—(*n* = 12). HL 1.27–1.67; HW 1.44–1.68; MOD 0.46–0.56; OMD 0.23–0.40; SL 0.37–0.56; HFL 1.53–2.19; ML 2.47–2.91; PW 0.50–0.60; PPW 0.70–0.79. Indices: SI 23.42–34.15; CI 98.16–113.39; OI 29.34–33.94; HFI 106.25–133.54. See also Cuezzo & Claver (2009).

Additional material examined. ARGENTINA: ***Mendoza***: Reserva Nancuñan, 1800', Dec 12, 2003 & Oct 30, 2008 & Feb 14, 2010 (CASC; RAJC; RGPC); Fadina, Nancuñan, Feb 14, 2010 (RAJC); 115.0 km S Jct Rts 7 &

153, 1730', Jan 23, 2008 (RAJC); 138.1 km S Jct Rts 7 & 153, 1690', Jan 23, 2008 (RAJC); 22.1 km S Jct Rts 7 & 153, 1900', Jan 23, 2008 (RAJC); 38.4 km S Jct Rts 7 & 153, 1870', Jan 23, 2008 (RAJC); Rt 171 at 15.0 km SE Monte Coman, 1700', Jan 27, 2008 (RAJC); Rt 7 at 10.3 km E La Paz, 1540', Jan 23, 2008 (RAJC); Rt 7 at 9.8 km E La Dormida, 1720', Jan 23, 2008 (RAJC); Rt 7 at 29.8 km E La Dormida, 1610', Jan 23, 2008 (MCZ; RAJC); Rt 7 at 5.8 km W Desaguadero, 1530', Dec 28, 2005 (RAJC); Rt 7 at 8.5 km W Desaguadero, 1520', Mar 15, 2015 (RAJC); 20 mi SE Mendoza, Dec 26, 2006 (CSC); 8.5 km NW Real de Padre, Nov 22, 2005 (CSC); Rt 7 at 11.5 km W Santa Rosa, 2030', Mar 15, 2015 (RAJC). ***San Juan***: Nueva Castilla, Dec 1964 (MZUSP); Pie de Palo, Mar 11, 1920 (LACM; MCZ); Rt 20 near El Encón, no date (RGPC). ***San Luis***: Rt 20 at 0.6 km SE border with San Juan, 1610', Mar 16, 2015 (RAJC) (**Figure 42B**).

Etymology. The specific epithet, *mendozanus* (Latinization of Mendoza), is derived from the type locality occurring in Mendoza Province, Argentina.

Discussion. *Pogonomyrmex mendozanus* was misidentified as *P. pronotalis* in a list of ant species in Ñancuñan Biosphere Reserve (Claver & Fowler, 1993) and in subsequent publications (see above) until it was described by Cuezzo & Claver (2009). However, these two species are easily separated with coloration being one of the few characters in common. In describing *P. mendozanus*, Cuezzo & Claver (2009) listed several characters to distinguish it from *P. pronotalis*. Sculpturing on the head and mesosoma is the best character: rugae on the cephalic dorsum of *P. mendozanus* are fine, very regular, and incised, whereas they are coarse and irregular on *P. pronotalis*. Lack of striae on the first gastral tergum combined with the fine, regular, incised sculpturing on the head and mesosoma and coloration pattern separate *P. mendozanus* from all South American congeners.

Biology. *Pogonomyrmex mendozanus* is one of the more well-studied species of *Pogonomyrmex* in Argentina. This species harvests the seeds of various grass species and nongrass species to a lesser extent (Pirk & Lopez de Casenave, 2006, 2010, 2011; Pirk *et al.*, 2007; Pirk *et al.*, 2009; Pol & Lopez de Casenave, 2004; Pol *et al.*, 2011), and it is a solitary forager that recruits nestmates to high-density seed patches (Pol *et al.*, 2015). Five colonies averaged 108–186 foragers, which consisted of an estimated 10–13% of all workers in the nests (Nobua-Behrmann *et al.*, 2013). Nests have a tumulus that ranges up to 40 cm in diameter; a midden of seed chaff sometimes surrounds the nest. Colonies of *P. mendozanus* are relatively small: two excavated colonies in Reserva Ñancuñan contained an average of 615 workers plus 292 larvae and pupae (Nobua Behrmann *et al.*, 2010). Colony size was similar in another study, but varied by grazing intensity: colonies in lightly grazed areas contained 731 ± 249 (n = 12; mean ± SD) individuals including brood (535 ±105 of which were workers), while those in heavily grazed areas contained 557 ± 325 (n = 12) individuals including brood (382 ± 230 of which were workers). All colonies contained one reproductive queen (n = 19) (R.G. Pol, pers. comm.). Worker dry mass averaged 3.87 mg, while that of brachypterous queens averaged 9.16 mg; the mean queen to worker dry mass ratio was 2.37 (n = 2 colonies) (R.A. Johnson, unpub. data).

Collection dates for sexuals range from 28 December to 15 March, and mating flights have been observed on 21 January, 14–15 February, and 15 March. Flights occur during early to late afternoon on days following rain. Mating involves the brachypterous queens leaving their natal nest to mate at aggregations in low-growing vegetation at the top of or near their natal nest; aggregations are often small and contain approximately 20–30 individuals, but over 100 brachypterous queens have been observed on vegetation outside their nests (pers. obs.; R.G. Pol, pers. comm.) (**Figure 46**). Queens mate with multiple males with an average (± SD) effective mating frequency of 8.75 ± 3.26 (range = 4–16; n = 24) (Pol *et al.*, 2008). After mating, queens leave the aggregation to initiate a nest using independent colony founding (R.G. Pol, pers. comm.), which is an unusual behavior for brachypterous queens (see Johnson, 2010). No information is available, but these brachypterous queens are probably obligate foragers (see Peeters *et al.*, 2012).

Pogonomyrmex mendozanus inhabits sites at elevations from 465–545 m. This species is common from southeastern San Juan to eastcentral Mendoza, and it appears to be restricted to the northern one-third of the Low Monte Desert ecoregion as defined by Olson *et al*. (2001) (**Figure 42B**). Interestingly, the distribution of *P. mendozanus* stops at the southern boundary of the High Monte Desert ecoregion. Field observations suggest that *P. mendozanus* is restricted to deep, loose, sandy soils (pers. obs.); nests are most common in open, disturbed areas such as roadsides (Pirk *et al.*, 2004).

***Pogonomyrmex tinogasta* Johnson, NEW SPECIES**
(Figures 47–48)

Holotype worker [CASENT0914113]: ARGENTINA, Catamarca: Departamento Tinogasta, Ruta 11 at 17.5 km south of Tinogasta, 28º12.8'S 67º37.2'W, 4390 feet (1330 m), 4 January 2006 (R.A. Johnson #3754) [MACN]. Paratypes, same data as holotype: FML (3w), MACN (9w), RAJC (9w), UCDC (3w). Additional paratype series from the same locality and date—RAJ #3753: CASC (1w), FML (3w), MACN (9w), LACM (3w), MCZ (3w), RAJC (9w), USNM (3w); RAJ #3755: MACN (9w), RAJC (9w).

Worker. Diagnosis. Within the *P. laticeps*-group, the combination of: (1) body concolorous black except for dark reddish band encircling eye, (2) rugae on promesonotum longitudinal, usually regular, and (3) medial rugae along posterior margin of head longitudinal, rarely rugoreticulate uniquely characterize this species (**Figure 47**).

Measurements—holotype (*n* = 13 paratypes). HL 1.87 (1.74–2.02); HW 1.98 (1.79–2.23); MOD 0.40 (0.36–0.45); OMD 0.51 (0.45–0.58); SL 1.45 (1.33–1.57); PNW 1.24 (1.12–1.39); HFL 2.03 (1.90–2.13); ML 2.12 (2.16–2.60); PW 0.50 (0.48–0.57); PPW 0.74 (0.69–0.84). Indices: SI 73.23 (62.44–76.54); CI 105.88 (102.87–113.78); OI 20.20 (18.18–22.35); HFI 102.53 (92.66–107.58).

Description. Head subquadrate to wider than long (CI = 102.87–113.78), widest just posterior to eye; posterior margin flat in full-face view. Longitudinal rugae on cephalic dorsum prominent, weakly wavy to irregular; in full-face view, medial rugae diverging weakly toward posterior corners of head. In profile, rugae posterior to eyes converging toward vertex; vertex rugose. Cephalic interrugae weakly to moderately granulate-punctate, weakly shining to shining. Anterior margin of clypeus flat to weakly concave; dorsal surface with numerous subparallel, longitudinal rugae. Mandible with six teeth; mandibular dorsum coarsely rugose. Numerous long, curved, bristle-like, yellowish to brownish hairs project from anterior margin of clypeus and basolateral margin of mandibles. MOD ranging from 0.19–0.24x HL. In profile, eyes situated near middle of head, OMD = 1.09–1.39x MOD. Antennal scapes relatively long (SI = 62.44–76.54), failing to reach vertex by up to length of basal funicular segment, smooth and shining, distal portion often weakly striate. Basal flange of scape flattened, well-developed with carinate margin. Psammophore well-developed.

Mesosomal profile flat to weakly convex; all mesosomal surfaces with prominent rugae. In profile and dorsal views, humeral shoulders of pronotum angulate, occasionally weakly elevated above medial portion of pronotum. Dorsum of promesonotum with wavy to irregular longitudinal rugae that diverge anterad toward humeral shoulders of pronotum, occasionally weakly rugoreticulate or irregularly transverse; anterior margin of pronotum with wavy to irregular transverse rugae that traverse ventrally on pronotal sides. Mesopleura with wavy to irregular rugae angling posterodorsally, rugae often more irregular to rugoreticulate near anterodorsal margin. Posterior surface of propodeum with transverse to weakly irregular rugae that traverse anteroventrally on sides. Propodeum with long, acuminate spines connected by well-defined keel; spines longer than distance between their bases. Inferior propodeal spines absent or reduced to indistinct broadly rounded processes. Propodeal spiracles narrowly ovate facing posterad. Interrugae on mesosoma weakly to moderately punctate to coriarious, weakly shining. Legs moderately coriarious, weakly shining.

Peduncle of petiole slightly shorter than petiolar node, anteroventral margin with bluntly angulate tooth-like process. In profile, petiolar node asymmetrical with anterior surface shorter than posterior surface; apex weakly angulate to rounded. In dorsal view, petiolar node longer than wide, sides subparallel to slightly wider near spatulate anterior margin; posterior surface and sides with moderately strong, wavy to irregular, transverse to arcuate rugae. Dorsum of postpetiole convex in profile; in dorsal view, widest near posterior margin, narrowing toward anterior margin; maximal width about equal to length; dorsum and sides with wavy to irregular transverse rugae that are finer, denser than those on posterior surface of petiolar node. Interrugae weakly coriarious, weakly shining on posterior surface of petiolar node, weakly to moderately coriarious, dull to weakly shining on dorsum of postpetiole. First gastral tergum weakly to moderately coriarious, weakly shining to shining.

Erect whitish pilosity moderately abundant on head, variable in length, longest hairs shorter than MOD. Moderately abundant suberect to semidecumbent pilosity on scape, abundant decumbent hairs on funicular segments. Legs with moderately abundant semidecumbent white setae. Mesosoma, petiolar node, postpetiole, gastral terga with moderately dense, erect setae, mostly similar in length, only those on posterior gastral terga approaching MOD. Body concolorous black, often with dark reddish to brownish hue except for dark reddish-black band that usually encircles eyes (**Figure 47**).

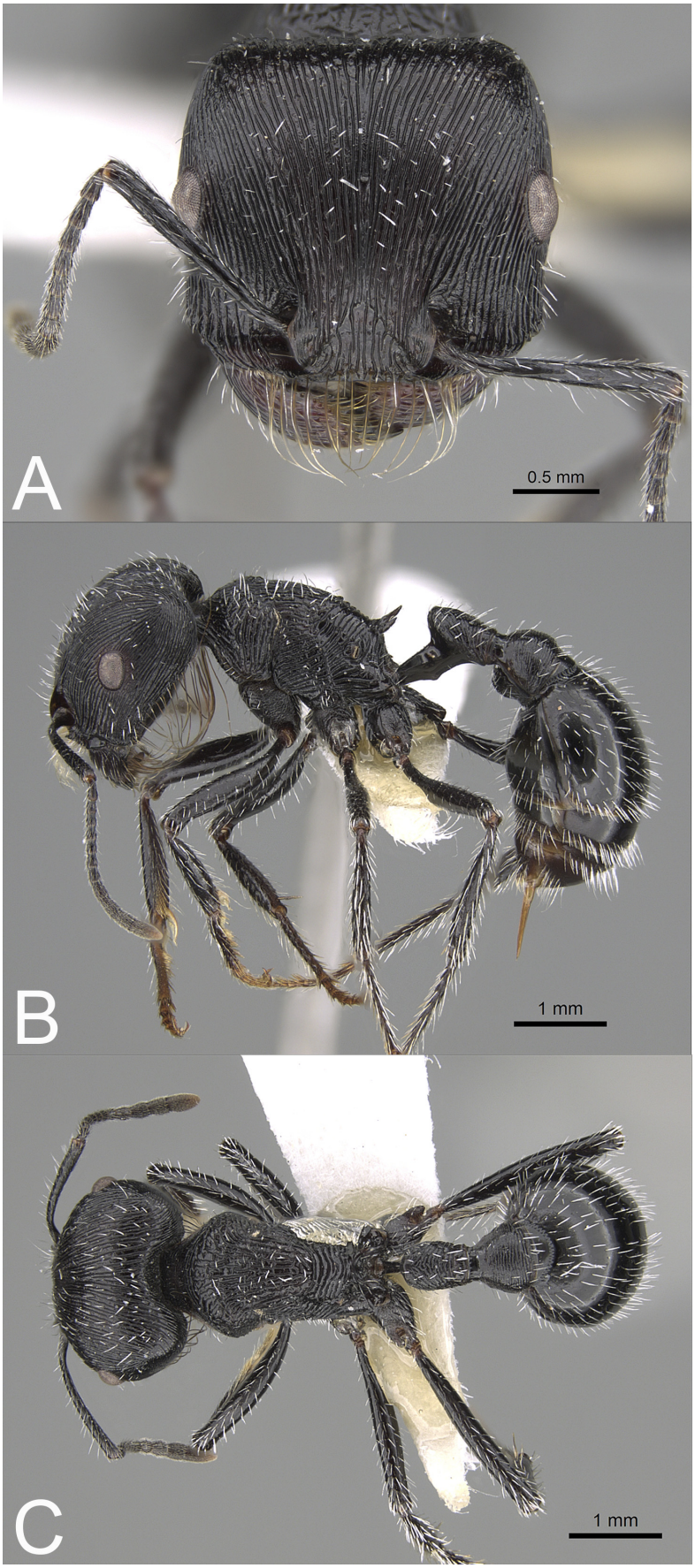

FIGURE 47. Photograph of *Pogonomyrmex tinogasta* Johnson holotype worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0914133). Photographs by Michele Esposito from www.AntWeb.org.

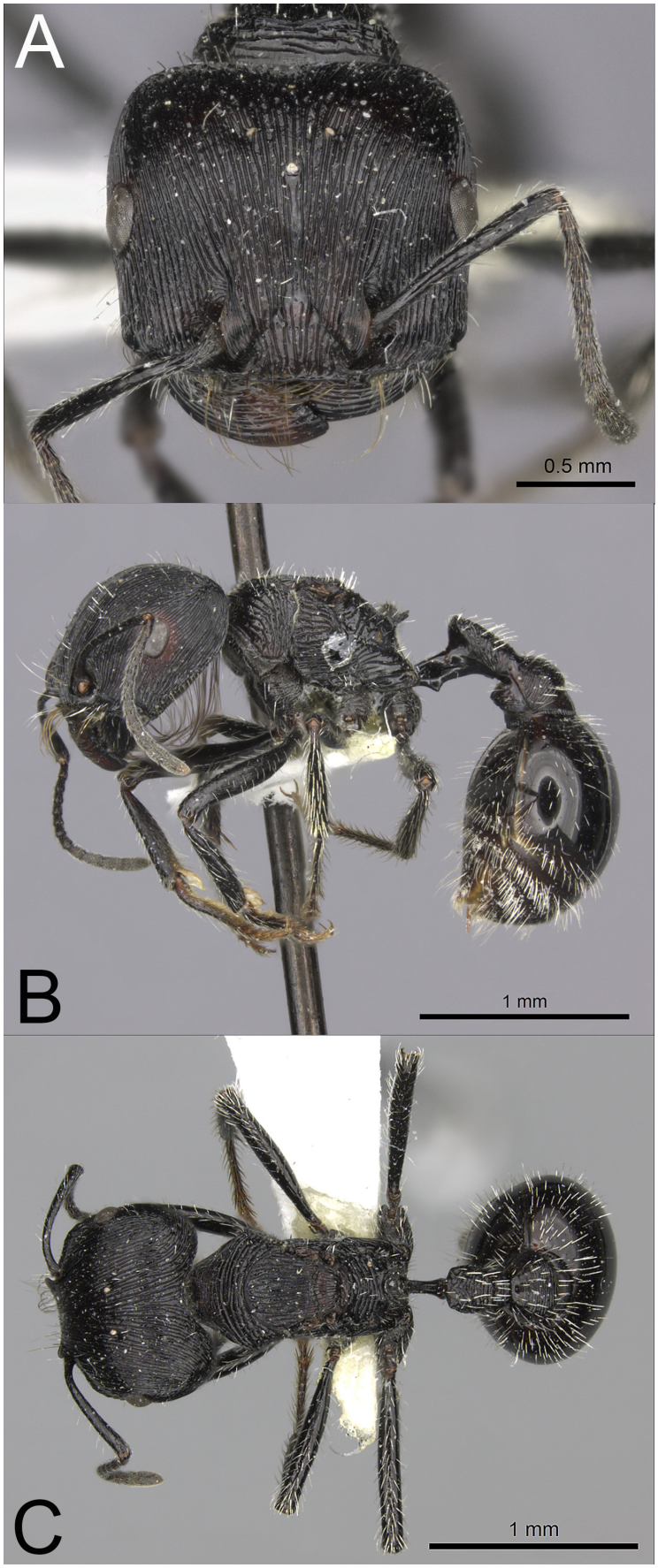

FIGURE 48. Photograph of *Pogonomyrmex tinogasta* Johnson dealate brachypterous queen: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0235287). Photographs by Will Ericson from www.AntWeb.org**.**

Dealate (brachypterous) queen. Diagnosis. This caste is diagnosed by: (1) brachypterous with ocelli on head, (2) in dorsal view, mesoscutum poorly-developed, anterior margin barely surpassing humeral shoulders of pronotum, (3) pronotum well-developed, (4) in profile, the pronotum rises at an approximately 45° angle to meet the mesoscutum, and (5) body concolorous black, often with lighter reddish-black band that encircles eyes (**Figure 48**).

Measurements—(*n* = 12). HL 2.19–2.38; HW 2.44–2.64; MOD 0.47–.59; OMD 0.57–0.61; SL 1.55–1.73; PNW 1.56–1.65; HFL 2.20–2.41; ML 2.68–3.02; PW 0.60–0.67; PPW 0.97–1.09. Indices: SI 61.00–68.03; CI 105.96–117.65; OI 18.43–22.78; HFI 84.94–96.72.

Description. Brachypterous, with caste-specific morphology of the mesosoma related to wing-bearing and presence of small ocelli on head. In full-face view, head wider than long (CI = 105.96–117.65), posterior margin weakly concave medially. Longitudinal rugae on cephalic dorsum prominent, weakly wavy; in full-face view, medial rugae diverging weakly toward posterior corners of head, interrugae weakly coriarious, weakly shining to smooth and shining; vertex rugose, interrugae smooth, shining. Mandible with six teeth, dorsal surface coarsely rugose. Psammophore well-developed.

All mesosomal surfaces with subparallel, regular to wavy rugae; interrugae weakly coriarious, weakly shining to smooth and shining. In profile, the pronotum rises at an approximately 45° angle to meet the mesoscutum. Superior propodeal spines short to medium-length; inferior spines absent to very poorly-developed. Peduncle of petiole about 0.8x as long as petiolar node, anteroventral margin with acute triangular process. In profile, petiolar node asymmetrical with anterior surface notably shorter than posterior surface, apex weakly angulate to rounded. Postpetiole wider than long. Posterior surface of petiolar node with transverse or oblique, regular to irregular rugae; dorsum of postpetiole with weaker, denser, transverse rugae; interrugae on posterior surface of petiolar node and dorsum of postpetiole weakly coriarious, weakly shining to smooth and shining. Gastral terga weakly coriarious, shining. Most body surfaces with moderately abundant suberect to erect, short to medium-length white setae. Body concolorous black, often with reddish tinge except for lighter reddish-black band that encircles eyes (**Figure 48**).

Male. Unknown.

Additional material examined. ARGENTINA: ***Catamarca***: Rt 11 at 4.8 km S Tinogasta, 3990', Jan 17, 2010 (RAJC); Rt 60 at 20.5 km W Cordobita, 3630', Jan 5, 2006 (RAJC); Rt 60 at 24.8 km NW Cordobita, 3670', Jan 5, 2006 (RAJC) (**Figure 42C**).

Etymology. The specific epithet, *tinogasta,* is a noun in apposition and invariant in form. The name is derived from a small, localized group of Native Americans that lived in a pueblo of the same name.

Discussion. *Pogonomyrmex tinogasta* is not known to co-occur with *P. laticeps* or *P. mendozanus*. *Pogonomyrmex tinogasta* can be distinguished from *P. mendozanus* by the coarse, irregular rugae on the head and mesosoma, whereas rugae on the head and mesosoma of *P. mendozanus* are fine, incised, and very regular. *Pogonomyrmex tinogasta* can be distinguished from *P. laticeps* based on the following characters: (1) body concolorous black except for dark reddish band encircling eye, (2) promesonotal rugae longitudinal, usually regular, and (3) medial rugae along posterior margin of head longitudinal, rarely rugoreticulate. In *P. laticeps*: (1) the head and mesosoma are dark reddish-black, gaster black, (2) rugae on the promesonotum are transverse, oblique, or irregular, rarely longitudinal, and (3) medial rugae along the posterior margin of the head are usually partly rugoreticulate.

Biology. *Pogonomyrmex tinogasta* is a solitary forager that harvests the seeds of various species. Most nests have an external seed chaff midden, the contents of which suggest that grass seeds are one of the primary items harvested. Nests have a tumulus that ranges from 15–25 cm in diameter. Colonies of *P. tinogasta* probably contain 300–500 workers.

Nothing is known about the reproductive biology of *P. tinogasta*, but the queens are unusual. Several dealate queens of *P. tinogasta* were collected near the surface of a nest excavated on 5 January, and several additional queens were collected foraging outside the nest. Several ant species have queens that apparently sometimes forego mating and later perform tasks such as foraging and nest maintenance (Peeters, 1997), and this behavior also appears to occur in *P. tinogasta*. Reproductive status was not determined for these queens, but they are assumed to have been unmated given that foraging queens (both ergatoid and dealate) are unmated in *P. pima*, which is the only species in which such queens have been dissected (Johnson *et al.*, 2007). These observations add another *Pogonomymex* to the list of species in which queens forage outside the nest (Johnson *et al.*, 2007).

All queens collected by the author were dealate, but close examination of morphology suggested that these queens were brachypterous—these morphological features included: (1) faint ocelli, (2) enlarged pronotum and much reduced mesoscutum, and (3) the slope at which the pronotum raises to meet the mesoscutum is less steep; it is fully vertical in normal alate queens (**Figures 33B & 36B**), while it rises at an approximately 45° angle in brachypterous queens (**Figure 48B**) and ergatoid queens (**Figure 39B**). That these queens were brachypterous was verified via dissections in which one queen was found to lack direct flight muscles and any trace of internal phragmata; the latter are cuticular projections present in all flying insects that function to support the longitudinal wing muscles.

Pogonomyrmex tinogasta inhabits sites at elevations from 1100–1330 m. This species is restricted to central portions of the High Monte Desert ecoregion as defined by Olson *et al*. (2001), and it is only known from the Tinogasta Department of Catamarca Province (**Figure 42C**). Nests are located in sand dunes and sandy soils with a rocky substrate in the Monte Desert woodland with dominant plant species including *Larrea* sp., *Parkinsonia* spp., *Prosopis* spp., *Bulnesia* sp., and *Acacia* sp.

Pogonomyrmex mayri-group

Pogonomyrmex mayri is a monotypic species-group in which all three castes are easily diagnosed. Workers are diagnosed by: (1) striae on first gastral tergum, (2) psammophore poorly-developed, consisting of numerous short hairs scattered across ventral side of head, (3) deeply incised sculpturing on head and mesosoma, (4) antennal scapes densely granulate-punctate with strongly flattened base, (5) superior and inferior propodeal spines long, acuminate, (6) posterior surface of petiolar node flattened, and (7) anterior margin of clypeus concave with a small medial tooth (**Figure 49**). Queens are diagnosed by: (1) ergatoid, with ocelli not visible or absent, (2) striae on first gastral tergum, (3) postpetiole enlarged (PPW > 1.20 mm), wider than long, (4) anterior clypeal margin with medial tooth, and (5) anterior surface of petiolar node striate (**Figure 50**).

Pogonomyrmex mayri
(Figures 49–51)

Pogonomyrmex (*Janetia*) *mayri* Forel, 1899a: 61 (worker, male, in footnote). Syntypes examined: 2 workers [AMNH], 2 workers, 1 male [NMW], 3 workers [USNM], 3 workers [ZSM], COLOMBIA, Magdalena: Ciénega; Wheeler & Wheeler, 1953: 112 (larvae); Kugler, 1979: 170, figs. 1–8 (queen). NMW worker here designated **LECTOTYPE** [CASENT0173358].

Pogonomyrmex (*Forelomyrmex*) *mayri* Forel: Wheeler, 1913: 80 (first combination in *Forelomyrmex*).

Pogonomyrmex mayri Forel: Brown, 1973: 180 (*Forelomyrmex* synonomized under *Pogonomyrmex* [provisional]); Snelling, 1981: 395 (*Forelomyrmex* synonomized under *Pogonomyrmex*).

Worker. Diagnosis. See above.

Measurements—lectotype (*n* = 12). HL 2.12 (1.78–2.19); HW 1.90 (1.63–1.94); MOD 0.31 (0.26–0.30); OMD 0.47 (0.45–0.55); SL 1.63 (1.50–1.74); PNW 1.47 (1.13–1.34); HFL 2.60 (2.03–2.71); ML 2.55 (2.13–2.49); PW 0.37 (0.34–0.43); PPW 0.69 (0.54–0.70). Indices: SI 85.79 (77.72–104.82); CI 89.62 (87.69–96.63); OI 16.32 (14.51–16.96); HFI 136.84 (121.56–140.41). See also Kugler (1979).

Redescription. Head weakly elongate to elongate (CI = 87.69–96.63), widest just posterior to eyes, narrowing to vertex; posterior margin strongly concave medially, broadly V-shaped. Cephalic dorsum, sides, and vertex rugose, rugae variable in height; in full-face view, medial rugae not diverging toward posterior corners of head. Cephalic rugae deeply incised, interrugae strongly granulate, dull. Anterior margin of clypeus convex with medial triangular tooth, dorsum of clypeus with numerous subparallel, wavy, longitudinal rugae similar to those on cephalic dorsum. Mandible with six teeth; mandibular dorsum coarsely rugose. Up to several moderately long, curved, bristle-like, amber to brownish hairs project from anterior margin of clypeus and basolateral margin of mandibles. Eyes small, MOD = 0.13–0.17x HL. In profile, eyes situated anterior to middle of head, OMD = 1.52–2.00x MOD; no hairs project from between ommatidia. Antennal scapes long (SI = 77.72–104.82), reaching to surpassing vertex by less than length of basal funicular segment; entire scape with weak longitudinal striae,

interstriae strongly granulate, dull. Basal flange of scape well-developed with recurved, carinate margin. Psammophore poorly-developed, consisting of numerous short hairs scattered across ventral side of head.

Mesosomal profile strongly convex; all mesosomal surfaces with wavy, deeply incised rugae that vary in height. Transverse rugae on pronotal sides curving dorsally, anteriorly, and posteriorly, transverse rugae on pronotal collar; dorsum of propodeum with transverse rugae that traverse to propodeal spiracle then angle posterad over metapleural lobe. Superior propodeal spines long, acuminate, bases connected by well-defined keel, spines longer than distance between their bases; inferior propodeal spines well-developed, acuminate, length approximately 0.3–0.5x that of superior spines; declivitous surface of propodeum transversely rugose. Propodeal spiracles narrowly ovate facing posterad. Rugae and interrugae on mesosoma strongly granulate, dull. Legs strongly granulate, dull.

Peduncle of petiole about 0.5x as long as petiolar node, anteroventral margin varying from broad translucent process to triangular acuminate spine. In profile, petiolar node asymmetrical with anterior surface approximately one-half as long as posterior surface, apex angulate, posterior surface flattened; all surfaces rugose. In dorsal view, petiolar node elongate, approximately twice as long as wide, lateral margins weakly convex posteriorly, nearly vertical medially, concave anteriorly, anterior one-third narrowing to acuminate tip; anterior portion of posterior surface weakly depressed below margins. Dorsum of postpetiole convex in profile, anterior margin narrowing to helcium; robust in dorsal view, longer than wide; widest near posterior margin, narrowing to truncate anterior margin; dorsum and sides coarsely rugose; ventral process strongly granulate, dull. Rugae and interrugae on posterior surface of petiolar node and dorsum of postpetiole strongly granulate, dull. First gastral tergum with fine longitudinal striae, dull.

Short to long, erect, amber to brownish hairs abundant on head, longest >MOD; mostly medium-length hairs abundant on mesosoma, petiole node, postpetiole, and gastral terga, longest approaching MOD. Scape with abundant medium-length, suberect hairs; abundant subdecumbent hairs on funicular segments. Legs with moderately abundant, short to medium-length, suberect setae. Body concolorous dark reddish-brown to dark brownish-black, or with postpetiole, gaster, legs slightly lighter reddish-brown (**Figure 49**).

Ergatoid Queen. Diagnosis. See above.

Measurements—(*n* = 2). HL 1.50–1.51; HW 1.44–1.52; MOD 0.27–0.28; OMD 0.43–0.47; SL 1.03–1.14; PNW 1.14–1.18; HFL 1.64–1.65; ML 1.99–2.02; PW 0.70–0.74; PPW 1.20–1.25. Indices: SI 71.53–75.00; CI 96.00–100.66; OI 18.42–18.75; HFI 108.55–113.89. See also Kugler (1979) (**Figure 50**).

Male. Diagnosis. This caste is diagnosed by: (1) CI < 75.0, (2) neck elongate, flattened dorsally (3) in dorsal view, postpetiole >1.5x as long as wide, (4) in dorsal view, petiolar node elongate (>2x as long as wide), (5) funiculi with numerous suberect hairs, and (6) notauli absent, presence indicated only by short black lines that indicate underlying apophyses (**Figure 51**).

Measurements—(*n* = 10). HL 1.49–1.72; HW 1.06–1.23; MOD 0.30–0.36; OMD 0.15–0.19; SL 0.22–0.37; HFL 1.47–2.03; ML 1.96–2.41; PW 0.28–0.36; PPW 0.50–0.65. Indices: SI 20.18–34.91; CI 66.25–74.52; OI 27.52–32.08; HFI 134.51–178.30. See also Kugler (1979).

Additional material examined. COLOMBIA: ***Atlantico***: Puerto Colombia, 1970 (USNM). ***Bolívar***: Santa Marta Mountains, Jul 7, 1920 & 1954 (LACM; MCZ; USNM). ***Cesar***: Santa Marta Mountains, Valledupar, Jul 4, 1920 (LACM). ***Magdalena***: Mamatoco, Jun 16, 1976 (LACM; MCZ); Río Frio, Feb 1924 & Mar 20, 1928 (LACM; MCZ; USNM); 5 km SE Río Frio, 50–200 m, Aug 15, 1985 (LACM); 2 km E Orihueca, 20 m, Aug 17, 1985 (LACM); Parque Nacional Tayrona, Guairaca, Mar 11, 1977 (LACM); Parque Nacional Tayrona, near Neguanje, 60 m, Jun 30, 1976 (MCZ); Santa Ana, Feb 1924 (USNM); Manantial, May 29, 1976 (MCZ); Cienega, no date (MZUSP; USNM); Digrera, base of mountains near Santa Marta, 100 m, Aug 23, 1976 (LACM; MCZ). ***Prov. Unknown***: Santa Marta Mountains, Jul 31, 1920 (MCZ)**.** ***Questionable locales***: **VENEZUELA:** no loc, no date (FML; MCZ). Taber (1998) indicated that he had examined a specimen from Guyana (MCZ), but these specimens were unavailable to examine (**Figure 52**).

Etymology. This species was named to honor Dr. Gustav Mayr, who erected the genus *Pogonomyrmex* in 1868.

Discussion. *Pogonomyrmex mayri* is a distinctive species that is easily diagnosed by the above characters. *Pogonomyrmex naegelii* is the only congener known to occur in Colombia.

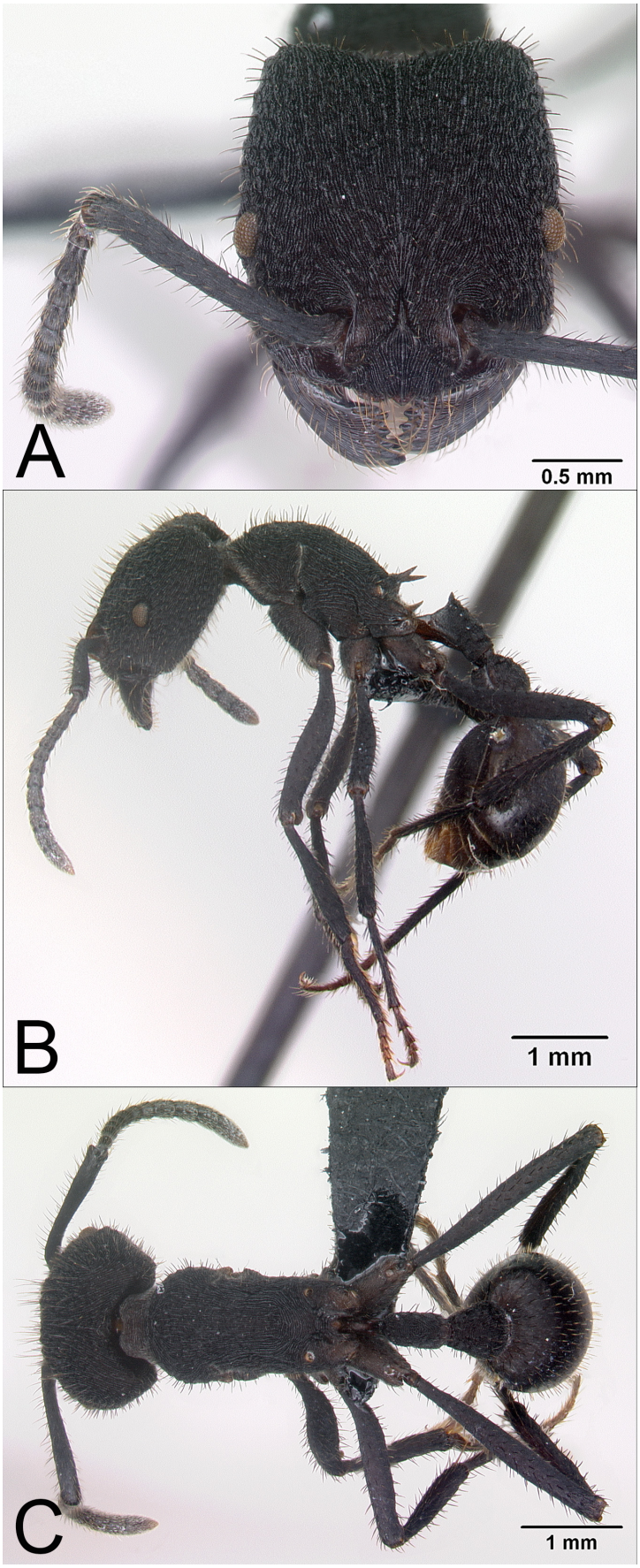

FIGURE 49. Photograph of *Pogonomyrmex mayri* Forel worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0218756). Photographs by Erin Prado from www.AntWeb.org**.**

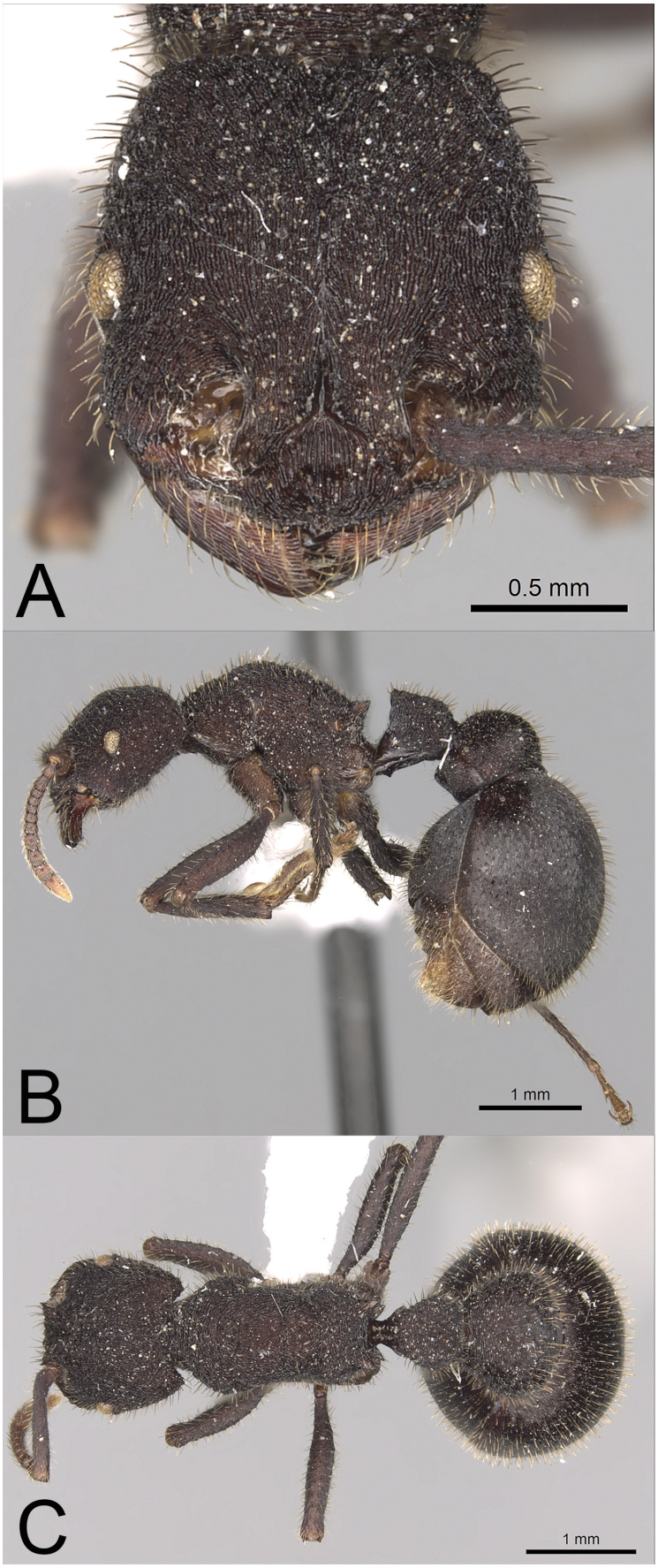

FIGURE 50. Photograph of *Pogonomyrmex mayri* Forel ergatoid queen: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0281109). Photographs by Shannon Hartman from www.AntWeb.org**.**

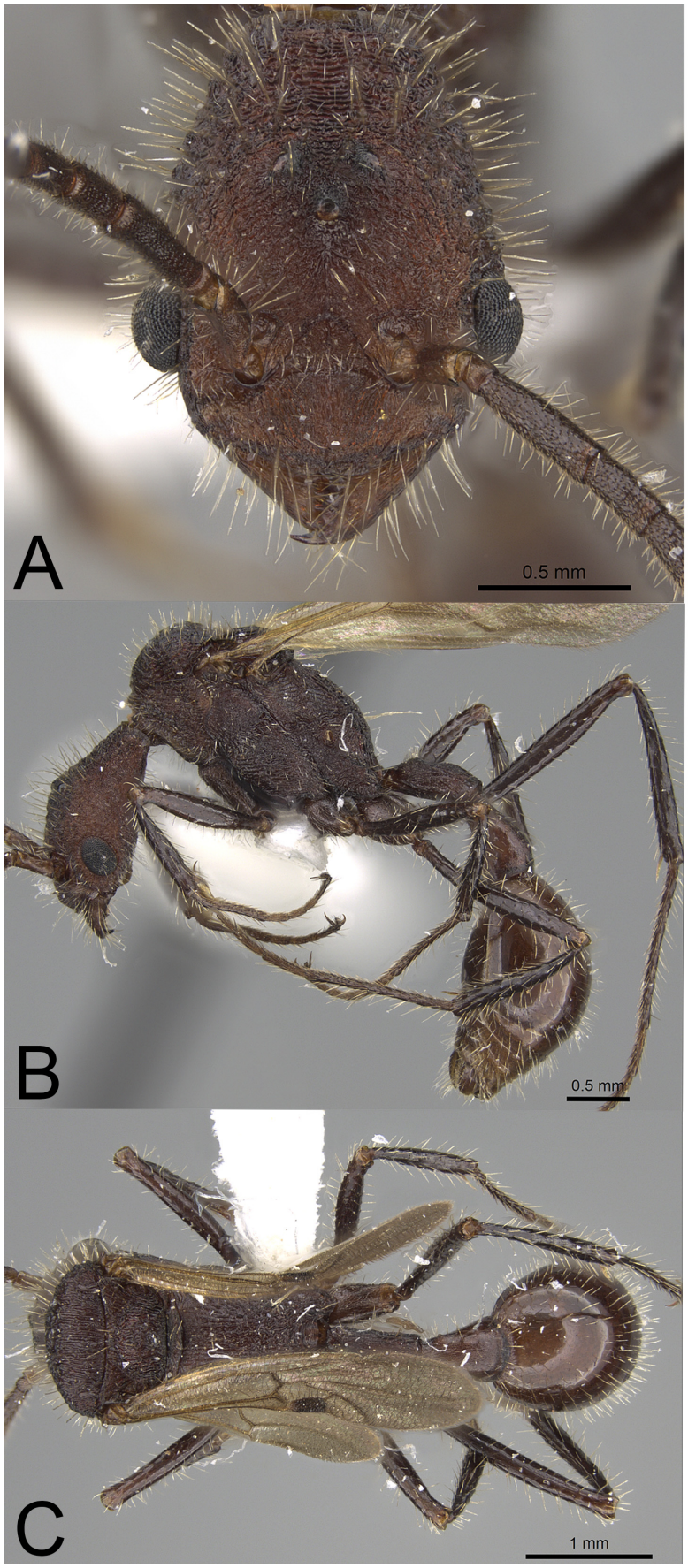

FIGURE 51. Photograph of *Pogonomyrmex mayri* Forel male: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0914119). Photographs by Michele Esposito from www.AntWeb.org.

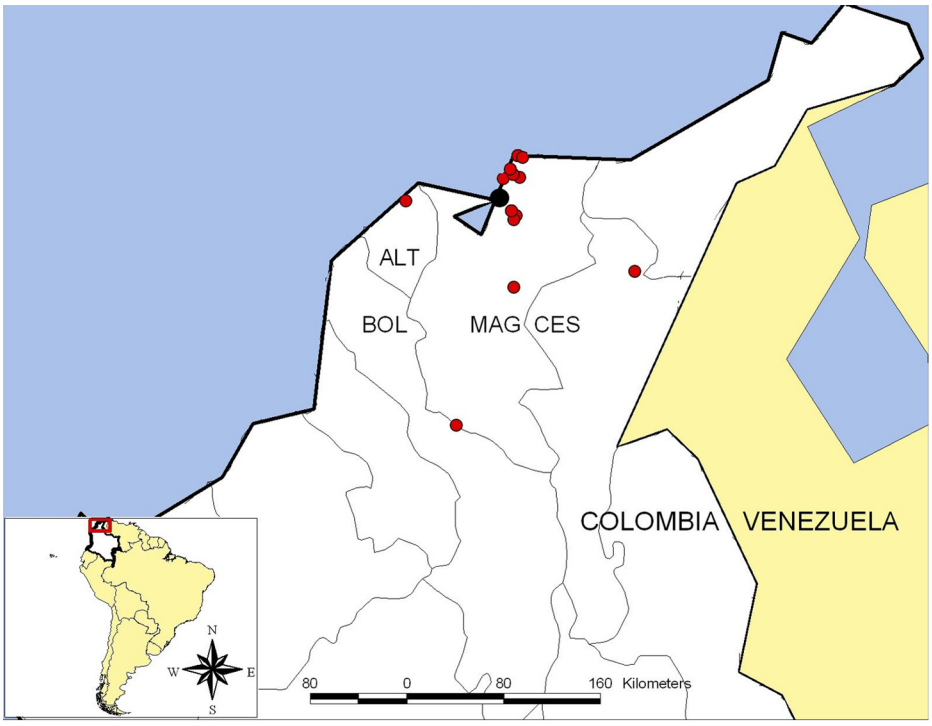

FIGURE 52. Geographic distribution of *Pogonomyrmex mayri* Forel. The larger black circle denotes the type locality.

Biology. *Pogonomyrmex mayri* is one of the more well-studied South American species of *Pogonomyrmex*. This is a phylogenetically basal species in the genus that is most closely related to *P. sylvestris*-group species (C.S. Moreau & R.A. Johnson, unpub. data).

Nests are typically located in soil at the base of trees or shrubs, or occasionally in cracks at the base of rocky outcrops or high on sandy beaches. Nests have one large (1–3 cm diameter), irregularly-shaped entrance, and the nest is normally covered by dry leaves, a log, or a stone; the nest lacks a crater, mound, or tumulus. Nests contain two to three chambers and range from 15–22 cm deep. Nest density ranges from approximately 50–150/ha; density decreases at elevations >100 m (Kugler & Hincapie, 1983).

Workers of *P. mayri* are diurnal scavengers that forage on the surface of the leaf litter or bare soil. Diet varies seasonally; more insects (especially termites and isopods) are harvested during the wet season (probably because of increased availability), while flower and leaf fragments are more commonly harvested during the dry season. Dead and dry arthropods comprise >50% of the harvested items in both seasons, but larger insects that struggle are avoided; seeds account for a small portion of the diet (ca. 10%) regardless of season. Colonies are small and consist of from 200–900 workers plus 25–270 larvae and pupae, and up to 28 males. Thus, overall colony size ranges from 284–1020 individuals (Kugler, 1984; Kugler & Hincapie, 1983).

No information is available on timing or location of mating flights or method of colony founding. However, males are relatively common in nest excavations, and they have been collected on vegetation outside the nest in March, April, June, September, October, and November; this suggests that *P. mayri* has a very different type of mating flight and mating behavior than is known for all congeners. Colonies have one ergatoid queen (known from 2 of 10 excavated colonies). Nothing is known about production of ergatoid queens (Kugler & Hincapie, 1983). Interestingly, ocelli were not visible on either of two examined ergatoid queens indicating that the ocelli are vestigial or absent, and Kugler (1979) did not mention ocelli in his description of the ergatoid queen.

The geographic range of *P. mayri* appears to be restricted to desert and dry deciduous forest habitats, mostly below 200 m, on the northwestern, western, and possibly southern end of the Sierra Nevada de Santa Marta, but it is also known to occur in more mesic habitats at elevations up to 835 m (Guerrero & Sarmiento, 2010; Kugler, 1979, 1984; Kugler & Hincapie, 1983). *Pogonomyrmex mayri* is only known to occur in northeastern Colombia in

the Guajira-Barranquilla Xeric Scrub and Sinú Valley Dry Forest ecoregions as defined by Olson *et al*. (2001), with one additional record from the Magdalena-Urabá Moist Forests ecoregion (**Figure 52**).

I have also examined workers labelled as having been collected in Venezuela (FML; MCZ); no further locality information was listed on either pin. Additionally, Taber (1998: 97) indicated that he had examined workers from Guyana (MCZ). Both records are considered dubious without further verification, especially given that *P. mayri* has not been collected from potential habitats in western Venezuela (J. Lattke, pers. comm.).

Pogonomyrmex naegelii-group

Workers in the *P. naegelii*-group are diagnosed by the following characters: (1) first gastral tergum lacking striae or striae restricted to base or rarely extending beyond the base, (2) small (HW = 1.06–1.33 mm), (3) psammphore poorly-developed, consisting of short to medium-length hairs scattered across ventral side of head, (4) superior and inferior propodeal spines well-developed, inferior spines ≥0.5–1.0x length of superior spines, (5) in profile, ventral process of postpetiole large and bulbous, its height much greater than its length, and (6) concolorous tannish-brown, occasionally with blackish gaster. Queens in the *P. naegelii*-group are diagnosed by: (1) first gastral tergum lacking striae or with faint to moderately strong longitudinal striae near base that sometimes extend over anterior one-half of tergum, (2) small (HW < 1.30 mm), (3) psammophore poorly-developed, consisting of short to medium-length hairs scattered across ventral side of head, (4) inferior propodeal spines triangular, moderately to well-developed, (5) in profile, ventral process of postpetiole large and bulbous, its height much greater than its length (for only alate queens), (6) concolorous tannish-brown, occasionally with blackish gaster, and (7) anterior margin of clypeus flat.

Pogonomyrmex abdominalis

(Figures 53–55)

Pogonomyrmex (*Ephebomyrmex*) *naegelii* st. *abdominalis* Santschi, 1929: 278 (worker, queen). Syntypes examined: 8 workers, 4 queens [MACN], ARGENTINA, Córdoba: Sierras de Córdoba, Alta Gracia La Granja, #1710 (Charles Bruch leg.). See also Gallardo, 1932: 112, figs. 6, 7. MACN worker here designated **LECTOTYPE** [CASENT0235285].
Pogonomyrmex (*Ephebomyrmex*) *abdominalis* Santschi: Kusnezov, 1951: 250, raised to species.
Ephebomyrmex abdominalis (Santschi): Kempf, 1972: 106, first combination in *Ephebomyrmex*.
Pogonomyrmex abdominalis Santschi: Bolton, 1995: 339, revived combination in *Pogonomyrmex.*

Worker. Diagnosis. Within the *P. naegelii*-group, the combination of: (1) approximately 8–10 coarse, longitudinal rugae between frontal lobes, (2) lacking small lobe that projects dorsally from anterior margin of antennal fossa, (3) peduncle of petiole and anterior surface of petiolar node meet at or near a right angle, (4) in dorsal view, posterior surface of petiolar node distinctly wider than distance between tips of superior propodeal spines, and (5) longest hairs on mesosoma approaching to slightly >MOD uniquely characterize this species (**Figures 53–54**).

Measurements—lectotype (*n* = 31). HL 1.25 (1.17–1.41); HW 1.26 (1.14–1.33); MOD 0.26 (0.25–0.30); OMD 0.28 (0.24–0.33); SL 0.84 (0.87–0.99); PNW 0.82 (0.75–0.92); HFL 1.09 (1.03–1.27); ML 1.38 (1.33–1.55); PW 0.38 (0.34–0.43); PPW 0.49 (0.46–0.54). Indices: SI 66.67 (70.08–85.09); CI 100.80 (92.37–105.69); OI 20.63 (20.49–24.56); HFI 86.51 (83.46–103.31).

Redescription. Head subquadrate to quadrate (CI = 92.37–105.69), widest just posterior to eye; posterior margin flat to weakly concave. Longitudinal rugae on cephalic dorsum prominent, occasionally weakly rugoreticulate especially near posterior margin; approximately 8–10 coarse, longitudinal rugae between frontal lobes; in full-face view, medial rugae not diverging toward posterior corners of head. In profile, area posterior to eyes rugose to moderately rugoreticulate, rugae not converging toward vertex. Cephalic interrugae moderately to strongly granulate, dull to weakly shining; vertex rugose. Anterior margin of clypeus moderately to strongly concave, dorsal surface with numerous subparallel, longitudinal rugae; lacking small lobe that projects dorsally from anterior margin of antennal fossa. Mandible with six teeth; mandibular dorsum coarsely rugose. Up to several moderately long, curved, bristle-like, yellow-brown to brownish hairs project from anterior margin of clypeus and basolateral margin of mandibles. MOD ranging from 0.20–0.25x HL. In profile, eyes situated anterior to middle of

head, OMD = 0.80–1.19x MOD. Antennal scapes moderately long (SI = 66.67–85.09), failing to reach vertex by 1.0–1.5x length of basal funicular segment; entire scape with strong longitudinal striae, dull to weakly shining; basal flange of scape flattened and well-developed with carinate margin. Psammophore poorly-developed, consisting of short to medium-length hairs scattered across ventral side of head.

Mesosomal profile convex; all mesosomal surfaces with highly irregular rugae, rugoreticulate, or vermiculate. Mesoepinotal sulcus not impressed. Dorsum of promesonotum and sides of pronotum rugoreticulate to vermiculate. Mesopleura with irregular rugae angling posterodorsally to rugoreticulate. Dorsum of propodeum with wavy to irregular transverse rugae that traverse anteroventrally, becoming more irregular on sides. Superior propodeal spines moderately long, acuminate, connected by well-defined keel; spine length approximately 0.7–0.8x distance between their bases. Inferior propodeal spines well-developed, acuminate, length approximately 0.5–1.0x that of superior spines, base wider than length of superior spines; inferior and superior spines connected by weak crest. Propodeal spiracles ovoid to circular facing posterad. Interrugae on mesosoma moderately granulate, weakly shining to smooth and strongly shining. Legs moderately coriarious, weakly shining.

Peduncle of petiole about as long as petiolar node, anteroventral margin with a weakly to strongly-developed triangular process. In profile, petiolar node asymmetrical with anterior surface shorter than posterior surface; apex weakly rounded to subangulate; anterior surface meeting peduncle at or near a right angle. In dorsal view, petiolar node longer than wide, widest near middle, narrowing to spatulate to rounded anterior margin; maximal width of posterior surface greater than distance between tips of superior propodeal spines; dorsum and sides strongly rugoreticulate to vermiculate, interrugae granulate, dull to weakly shining. Dorsum of postpetiole convex in profile; in dorsal view, postpetiole robust, widest at or near posterior margin, narrowing from near middle to weakly truncate anterior margin; maximal width slightly greater than length; dorsum and sides weakly to moderately rugoreticulate or with several irregular longitudinal to oblique rugae, interrugae moderately to strongly granulate, dull to weakly shining. Ventral process of postpetiole large, bulbous, height similar to dorsal portion of postpetiole. First gastral tergum weakly to strongly coriarious, dull to weakly shining to smooth and strongly shining; anterior margin sometimes with weak longitudinal striae.

Erect yellow-brown to brownish pilosity moderately abundant on head, variable in length, mostly short to medium-length, often with one or more longer hairs that approximate MOD. Moderately abundant suberect to semidecumbent pilosity on scape, abundant decumbent hairs on funicular segments. Legs with moderately abundant semidecumbent brownish setae. Mesosoma, petiolar node, postpetiole, gastral terga with moderately dense, erect setae, mostly similar in length, longest approaching to slightly >MOD; hairs on propodeum less dense. Concolorous tan to tannish-brown with darker gaster (**Figures 53–54**).

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) small (HW < 1.35 mm), (3) petiolar node and postpetiole wide (petiolar node > 0.50 mm, postpetiole > 0.70 mm), (4) posterior surface of petiolar node granulate-punctate, and (5) longitudinal rugae on mesoscutum and mesoscutellum (**Figure 55**).

Measurements—(*n* = 4). HL 1.19–1.35; HW 1.24–1.30; MOD 0.30–0.32; OMD 0.27–0.31; SL 0.69–0.75; PNW 1.00–1.03; HFL 0.92–0.95; ML 1.56–1.65; PW0.54–0.57; PPW 0.71–0.76. Indices: SI 54.33–57.69; CI 95.38–106.72; OI 23.08–25.20; HFI 72.44–76.61.

Male. Unknown.

Additional material examined. ARGENTINA: ***Córdoba***: Alta Gracia la Granja, Sierras de Córdoba, no date (MACN); Estancia Santo Domingo, 24 Feb, 2009 (RAJC; RGPC). ***Entre Ríos***: Parque Nacional El Palmar, Jan 5–6, 2006 (RGPC); El Palmar, 25 m, Feb 7, 1999 (RAJC); Victoria, 80', Jan 6, 2008 & Jan 12, 2011 (FML; MCZ; RAJC). ***Misiones***: Loreto, no date (MACN); Estación Experimental Loreto, no date (FML). **BOLIVIA:** ***Beni***: Reyes, Nov 22, 1921 (USNM). ***Dpto. Unknown***: San Antonio, Nov 22, 1921 (USNM). **BRAZIL:** ***Mato Grosso***: Belo Horizonte, Nov 4, no year (CASC; MCZ). ***Minas Gerais***: 6 km E Mariana Mtns, 1000 m, May 16, 1971 (MCZ). ***Río Grande do Sul***: Porto Alegre, Mar 24, 1971 (MZUSP). ***São Paulo***: Fazanda Itaquera, Nova Europa, no date (MZUSP); Pindamonhangaba, Aug 25, 1961 (MZUSP). ***Estado Unknown***: Pirafron?, no date (MZUSP) (**Figure 56A**).

Etymology. The specific epithet, *abdominalis* (from Latin, *abdomen-* = abdomen), appears to be derived from the enlarged postpetiole on this species, which Santschi described as wider than long for the worker and even larger and more pronounced in the queen.

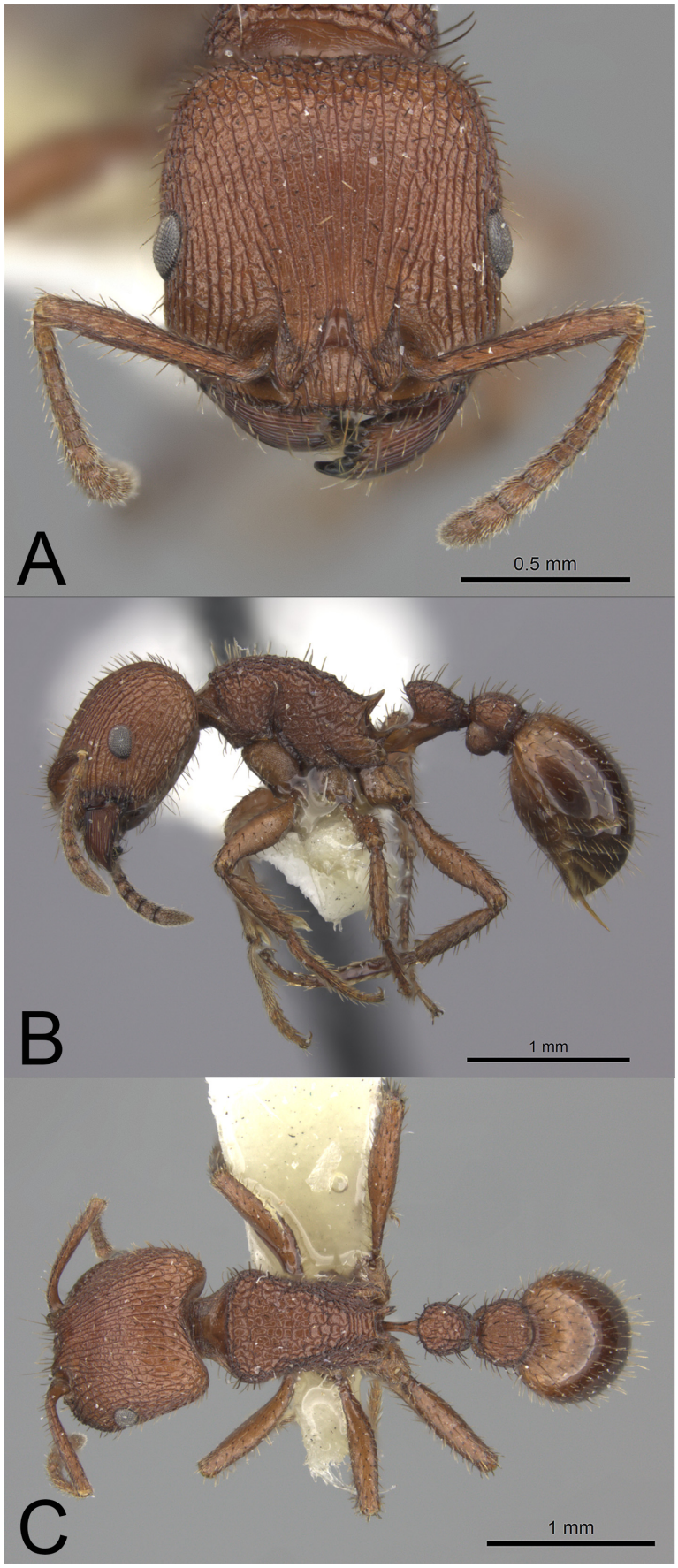

FIGURE 53. Photograph of *Pogonomyrmex abdominalis* Santschi worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0235283). Photographs by Will Ericson from www.AntWeb.org.

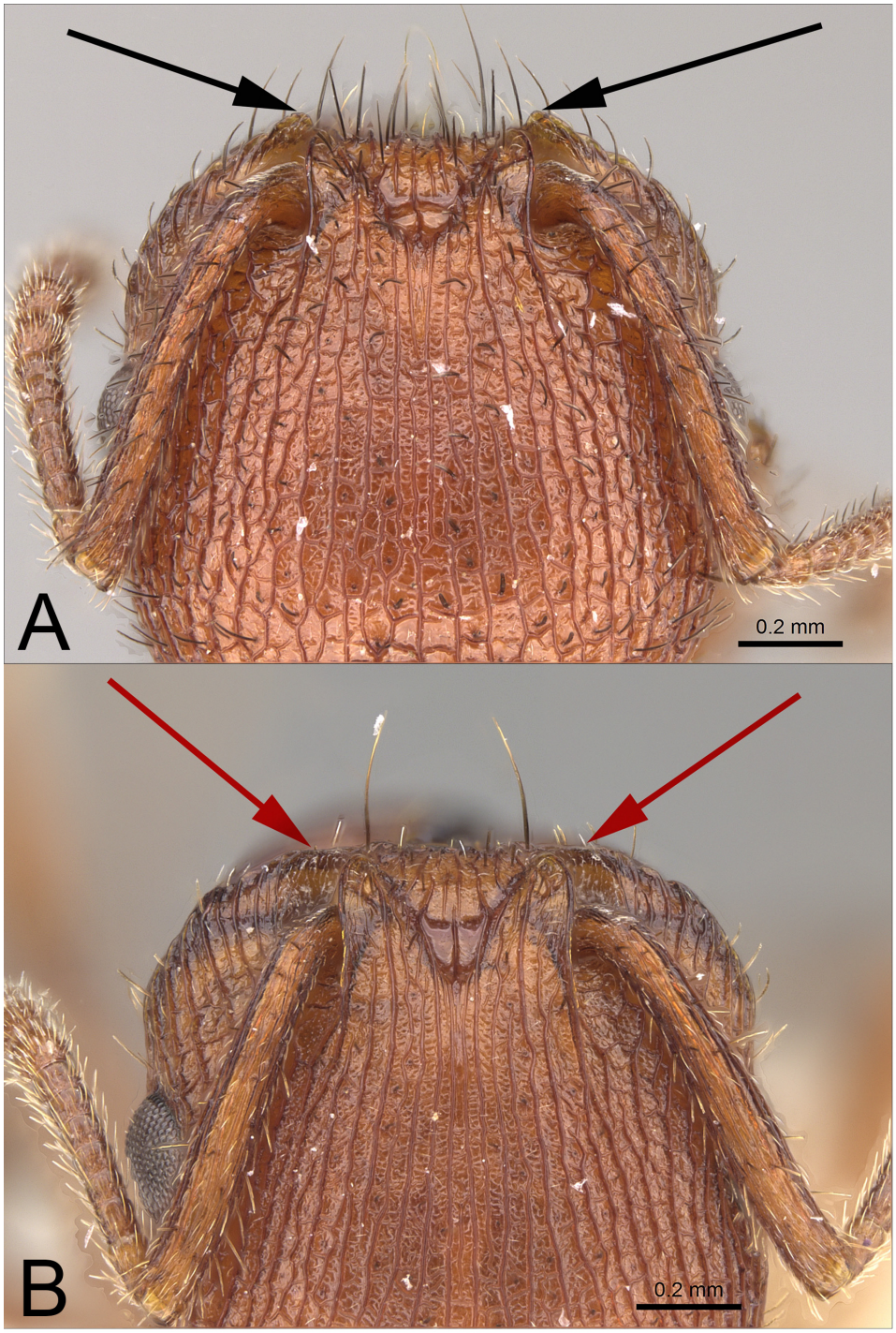

FIGURE 54. Photograph from posterior margin of head looking down onto lateral clypeal lobes: (A) *Pogonomyrmex naegelii* Forel—black arrows show small lobe that projects dorsally from anterior margin of antennal fossa (CASENT0914811), and (B) *Pogonomyrmex abdominalis* Santschi—red arrows show absence of small lobe on anterior margin of antennal fossa (CASENT0914813). Photographs by Michele Esposito from www.AntWeb.org.

Discussion. *Pogonomyrmex abdominalis* co-occurs with the other two *P. naegelii*-group species. *Pogonomyrmex abdominalis* can be distinguished from *P. tenuipubens* based on the following characters: (1) hairs on the mesosoma and psammophore are coarse and much longer than width of cephalic interrugae, and (2) approximately 8–10 coarse rugae between frontal lobes. In *P. tenuipubens*: (1) the abundant hairs on the mesosoma and psammophore are thin and delicate, their maximal length is similar to the width of cephalic interrugae, and (2) more than 15 fine rugae are present between the frontal lobes. *Pogonomyrmex abdominalis* is distinguished from *P. naegelii* based on the following characters: (1) usually larger (HW = 1.14–1.33 mm; **Figure 57**), (2) lacking small

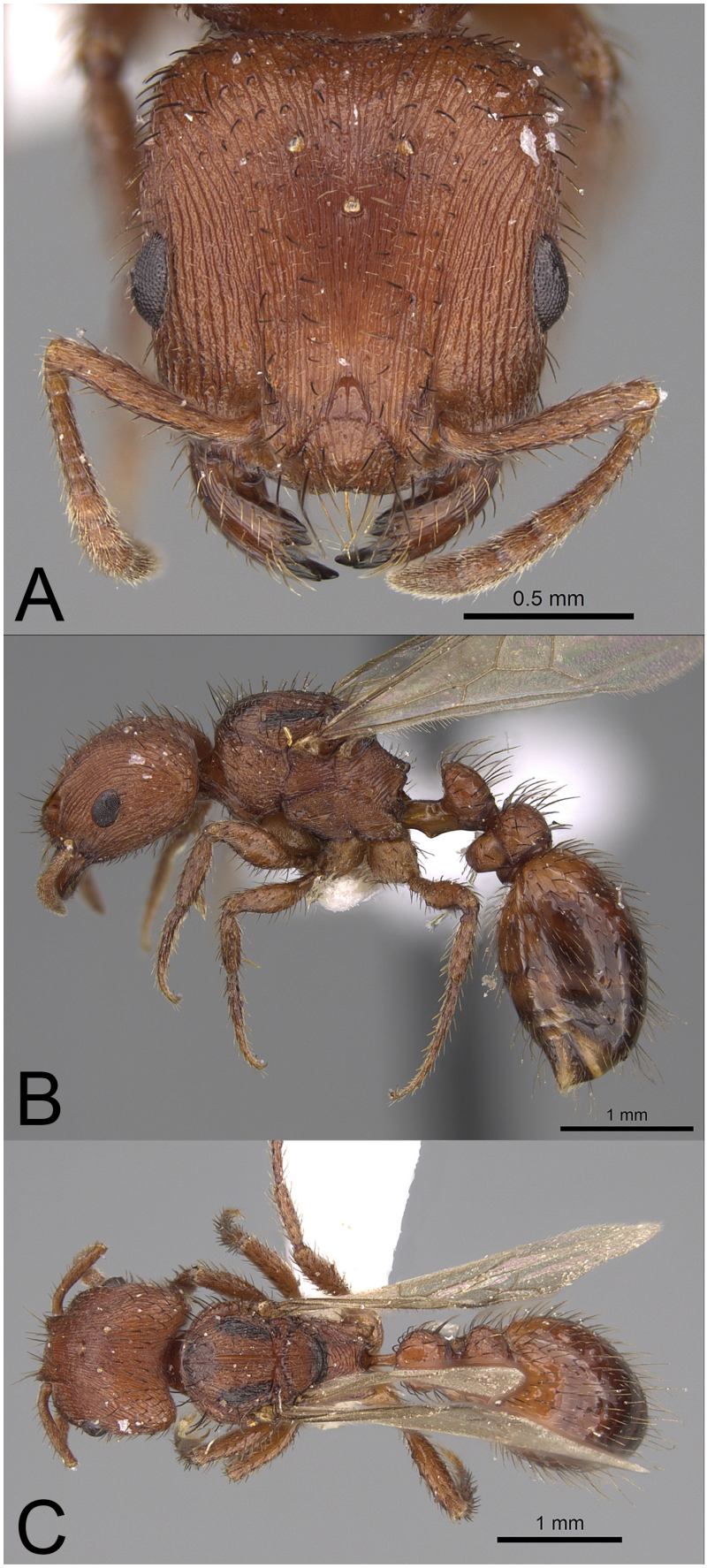

FIGURE 55. Photograph of *Pogonomyrmex abdominalis* Santschi alate queen: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0914378). Photographs by Michele Esposito from www.AntWeb.org.

FIGURE 56. Geographic distribution of: (**A**) *Pogonomyrmex abdominalis* Santschi, (**B**) *Pogonomyrmex naegelii* Forel, and (**C**) *Pogonomyrmex tenuipubens* Santschi. The larger black circle in each panel (when present) denotes the type locality. For *P. naegelii*, Argentina province borders are in blue, Brazil state borders are in green.

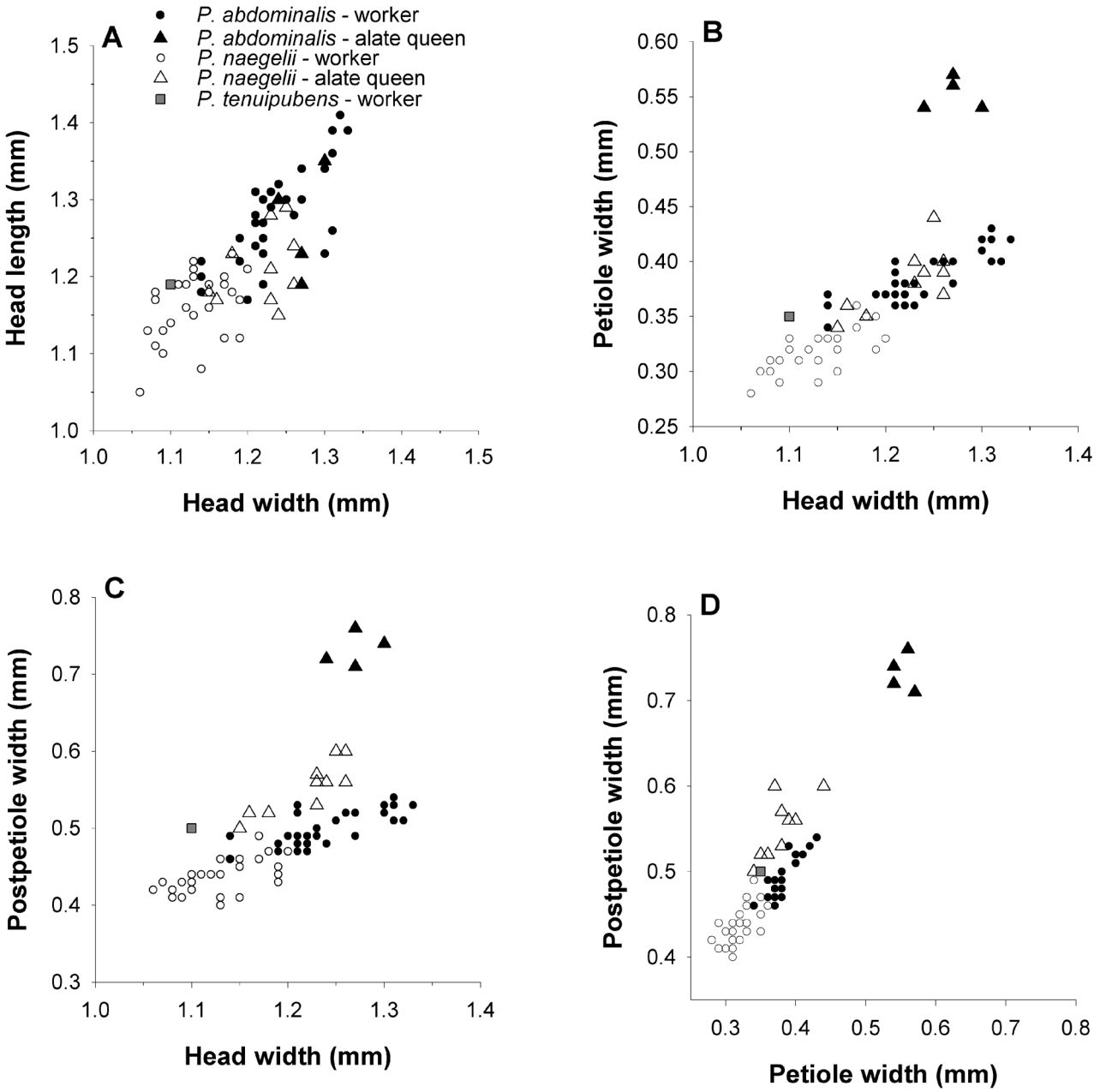

FIGURE 57. Bivariate plots for morphological comparisons of *Pogonomyrmex abdominalis* Santschi, *P. naegelii* Forel, and *P. tenuipubens* Santschi: (**A**) head width versus head length, (**B**) head width versus petiolar node width, (**C**) head width versus postpetiole width, and (**D**) petiolar node width versus postpetiole width.

lobe that projects dorsally from anterior margin of antennal fossa, (3) peduncle of petiole and anterior surface of petiolar node meet at or near a right angle, and (4) the posterior surface of petiolar node wider than distance between tips of superior propodeal spines. In *P. naegelii*: (1) the body is usually smaller (HW = 1.05–1.23 mm), (2) a small lobe projects dorsally from the anterior margin of the antennal fossa (**Figure 54**), (3) the peduncle of petiole and anterior surface of petiolar node meet at an obtuse angle, and (4) the width of the posterior surface of petiolar node is similar to or slightly greater than the distance between the tips of the superior propodeal spines.

In his description, Santschi listed Alta Gracia, Córdoba, as the type locality for *P. abdominalis*, as did all subsequent authors (see Gallardo, 1932; Kempf, 1972; Kusnezov, 1951). However, labels on all syntypes say, "Alta Gracia La Granja, Sierras de Córdoba". Alta Gracia and La Granja are two small towns that are located approximately 75 km apart along the eastern side of the Sierras de Córdoba. Thus, the labels suggest that the type locality was somewhere between these two towns.

Biology. *Pogonomyrmex abdominalis* is a solitary forager. Nests usually have a tumulus that is up to 15 cm in diameter. All series collected by the author were in open, grassy, park-like habitats. Colonies probably contain up to about 500 workers.

Pogonomyrmex abdominalis appears to be a relatively uncommon species that has a wide geographic distribution. Little is known about the biology of *P. abdominalis* but it is probably similar to that of *P. naegelii.* Alate queens were collected as part of the type series (no date) and on 24 February, suggesting that mating flights occur during the austral summer. Additional queens need to be collected to determine if *P. abdominalis* also produces ergatoid queens, as occurs in *P. naegelii* and related North American species (Heinze, Hölldobler, & Cover, 1992; Johnson *et al.*, 2007).

Pogonomyrmex abdominalis appears to be a lowland species that inhabits sites at elevations from 10–1000 m. This species occurs in the Dry Chaco, Humid Pampas, Uruguayan Savanna, Alto Paraná Atlantic Forest, Cerrado, Bahia Interior Forests, and Beni Savanna ecoregions as defined by Olson *et al*. (2001) (**Figure 56A**). It is likely that *P. abdominalis* occurs in several additional ecoregions given the few records that are scattered over a very large geographic area.

Pogonomyrmex naegelii

(Figures 54, 58–61)

Pogonomyrmex naegelii Forel, in Emery, 1878: X (worker, name made available); Forel 1886: XLI (worker description). Syntypes examined: 1 worker [MCZ], 2 workers [MSNG], 1 worker [USNM], BRAZIL, Rio de Janeiro (Carlos Naegeli leg.); Mayr, 1887: 612 (queen, male); Wheeler and Wheeler, 1972: 237 (larvae). See also Gallardo, 1932: 109, figs. 4, 5. MSNG worker here designated **LECTOTYPE** [CASENT0280989].

Pogonomyrmex (*Ephebomyrmex*) *naegelii* Forel: Wheeler, 1902: 390, first combination in subgenus *Ephebomyrmex*.

Ephebomyrmex naegelii (Forel): Kempf, 1972: 106, first combination in *Ephebomyrmex.*

Pogonomyrmex naegelii Forel: Bolton, 1995: 341, revived combination in *Pogonomyrmex*.

Pogonomyrmex (*Ephebomyrmex*) *venezuelensis* Weber, 1943: 69, fig. 2 (incorrectly captioned as *Leptothorax anduzei*) (worker). Syntypes examined: 4 workers [MCZ], VENEZUELA, Anzoátegui: from the llanos about 15 km north of Soledad, across from Ciudad Bolívar (Neal A. Weber leg., 27 January 1935). Kempf, 1960: 428 (synonomy under *naegelii*: here confirmed). MCZ worker here designated **LECTOTYPE** [CASENT0914121].

Pogonomyrmex (*Ephebomyrmex*) *venezuelensis* ssp. *rupununi* Weber, 1943: 71 (worker). Holotype worker [MCZ, MCZ-ENT00035809], BRITISH GUIANA, Upper Takutu-Upper Essequibo: in the southern Rupununi Savannah, #5606 (Dr. J.G. Myers leg., 11 November 1935). Kempf, 1960: 428 (synonomy under *naegelii*: here confirmed).

Worker. Diagnosis. Within the *P. naegelii*-group, the combination of: (1) approximately 8–10 coarse, longitudinal rugae between frontal lobes, (2) small lobe projecting dorsally from anterior margin of antennal fossa, (3) peduncle of petiole and anterior surface of petiolar node meet at an obtuse angle, (4) in dorsal view, posterior surface of petiolar node narrow, width similar to or slightly greater than distance between tips of superior propodeal spines, and (5) longest hairs on mesosoma rarely >0.7–0.8x MOD uniquely characterize this species (**Figures 54 & 58**).

Measurements—lectotype (n = 31 + 1 paralectotype). HL 1.15 (1.05–1.23); HW 1.15 (1.06–1.20); MOD 0.24 (0.22–0.28); OMD 0.28 (0.21–0.31); SL 0.84 (0.80–0.94); PNW 0.78 (0.69–0.84); HFL 1.15 (0.95–1.20); ML 1.34 (1.20–1.46); PW 0.30 (0.28–0.36); PPW 0.45 (0.40–0.49). Indices: SI 73.04 (68.97–85.45); CI 100.00 (91.53–106.25); OI 20.87 (20.17–24.30); HFI 100.00 (84.82–103.64).

Redescription. Head subquadrate to quadrate (CI = 91.53–106.25), widest just posterior to eye; posterior margin flat to weakly concave. Longitudinal rugae on cephalic dorsum prominent, usually moderately to coarsely rugoreticulate especially medial to eyes and near posterior margin; approximately 8–10 coarse longitudinal rugae between frontal lobes; in full-face view, medial rugae not diverging toward posterior corners of head. In profile, area posterior to eyes moderately to strongly rugoreticulate. Cephalic interrugae moderately to strongly granulate, dull to weakly shining; vertex rugose to rugoreticulate. Anterior margin of clypeus flat to weakly concave, dorsal surface with numerous subparallel, longitudinal rugae; small lobe projects dorsally from anterior margin of antennal fossa. Mandible with six teeth; mandibular dorsum coarsely rugose. Up to several moderately long, curved, bristle-like, yellow-brown to brownish hairs project from anterior margin of clypeus and basolateral margin of mandibles. MOD ranging from 0.19–0.25x HL. In profile, eyes situated anterior to middle of head, OMD = 0.84–1.25x MOD. Antennal scapes moderately long (SI = 70.83–85.45), failing to reach vertex by 1.0–1.5x length

of basal funicular segment; entire scape with strong longitudinal striae, dull to weakly shining. Basal flange of scape flattened, well-developed with carinate margin. Psammophore poorly-developed, consisting of short to medium-length hairs scattered across ventral side of head.

Mesosomal profile convex; all mesosomal surfaces rugoreticulate to vermiculate. Mesoepinotal sulcus sometimes weakly to moderately impressed. Dorsum of promesonotum and sides of pronotum rugoreticulate to vermiculate. Mesopleura with highly irregular rugae angling posterodorsally to rugoreticulate-vermiculate. Dorsum and sides of propodeum with irregular to very irregular, transverse rugae to occasionally rugoreticulate-vermiculate. Superior propodeal spines moderately long, acuminate, connected by well-defined keel; spine length approximately 0.7–0.8x distance between their bases. Inferior propodeal spines well-developed, acuminate, length approximately 0.5–1.0x that of superior spines, base wider than length of superior spines; inferior and superior spines connected by crest that defines the propodeal declivity. Propodeal spiracles ovoid to circular facing posterad. Interrugae on mesosoma weakly to strongly granulate, dull to weakly shining to smooth and strongly shining. Legs moderately coriarious, weakly shining.

Peduncle of petiole about as long as petiolar node, anteroventral margin with weakly to strongly-developed triangular process. In profile, petiolar node asymmetrical with anterior surface shorter than posterior surface; apex weakly rounded to subangulate; anterior surface meeting peduncle of petiole at an obtuse angle. In dorsal view, petiolar node longer than wide, widest near middle, narrowing to spatulate to subangulate anterior margin; maximal width of posterior surface similar to slightly greater than distance between tips of superior propodeal spines; posterior surface and sides strongly rugoreticulate-vermiculate, interrugae weakly to moderately granulate, weakly shining. Dorsum of postpetiole convex in profile; in dorsal view, postpetiole widest at or near posterior margin, narrowing near middle to convex anterolateral margin; maximal width about equal to length; dorsum and sides moderately to coarsely rugoreticulate or with several irregular, longitudinal to oblique rugae, interrugae moderately to strongly granulate, dull to weakly shining. Ventral process of postpetiole large, bulbous, height similar to dorsal portion of postpetiole. First gastral tergum moderately to strongly coriarious, weakly shining, to smooth and strongly shining; anterior margin to anterior one-half often with weak to moderately strong longitudinal striae.

Erect yellow-brown to brownish pilosity moderately abundant on head, similar in length, mostly short, often with one or more longer hairs that approximate MOD. Moderately abundant suberect to semidecumbent pilosity on scape, abundant decumbent hairs on funicular segments. Legs with moderately abundant semidecumbent, brownish setae. Mesosoma, petiolar node, postpetiole, gastral terga with moderately dense, erect setae, mostly similar in length, longest approximately 0.7–0.8x MOD; hairs on propodeum less dense. Concolorous tan to tannish-brown with darker to blackish gaster (**Figures 54 & 58**).

Alate 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) small size (HW < 1.35 mm), (3) petiolar node and postpetiole relatively narrow (petiolar node < 0.45 mm, postpetiole < 0.60 mm), (4) posterior surface of petiolar node rugoreticulate to vermiculate, and (5) mesoscutum and mesoscutellum rugoreticulate-vermiculate (**Figure 59**).

Measurements—(*n* = 11). HL 1.15–1.29; HW 1.15–1.26; MOD 0.24–0.32; OMD 0.23–0.30; SL 0.85–0.98; PNW 0.87–1.01; HFL 1.09–1.30; ML 1.56–1.75; PW 0.34–0.44; PPW 0.50–0.60. Indices: SI 73.91–78.86; CI 95.93–107.83; OI 20.69–25.40; HFI 87.90–108.47.

Ergatoid queen. Diagnosis. This caste is diagnosed by: (1) ergatoid, with small ocelli on head, (2) small species (HW < 1.30 mm), (3) mesoscutum, mesoscutellum, and posterior surface of petiolar node rugoreticulate, (4) in profile, mesosomal outline discontinuous with a break between mesoscutellum and metanotum and between metanotum and propodeum (**Figure 60**).

Measurements—(*n* = 6). HL 1.12–1.27; HW 1.17–1.27; MOD 0.23–0.29; OMD 0.23–0.28; SL 0.83–0.94; PNW 0.89–0.99; HFL 1.09–1.22; ML 1.45–1.60; PW 0.39–0.41; PPW 0.56–0.63. Indices: SI 65.35–77.78; CI 94.49–110.71; OI 18.55–23.93; HFI 89.76–99.19.

Description. Ergatoid; small species (HW = 1.17–1.27 mm), head subquadrate to wider than long (CI = 94.49–110.71), posterior margin flat to weakly concave. Longitudinal rugae on cephalic dorsum prominent medially, becoming rugoreticulate laterally; interrugae weakly to moderately coriarious, weakly shining. Mandible with six teeth, dorsal surface coarsely rugose. Psammophore poorly-developed, consisting of numerous short hairs scattered across ventral side of head.

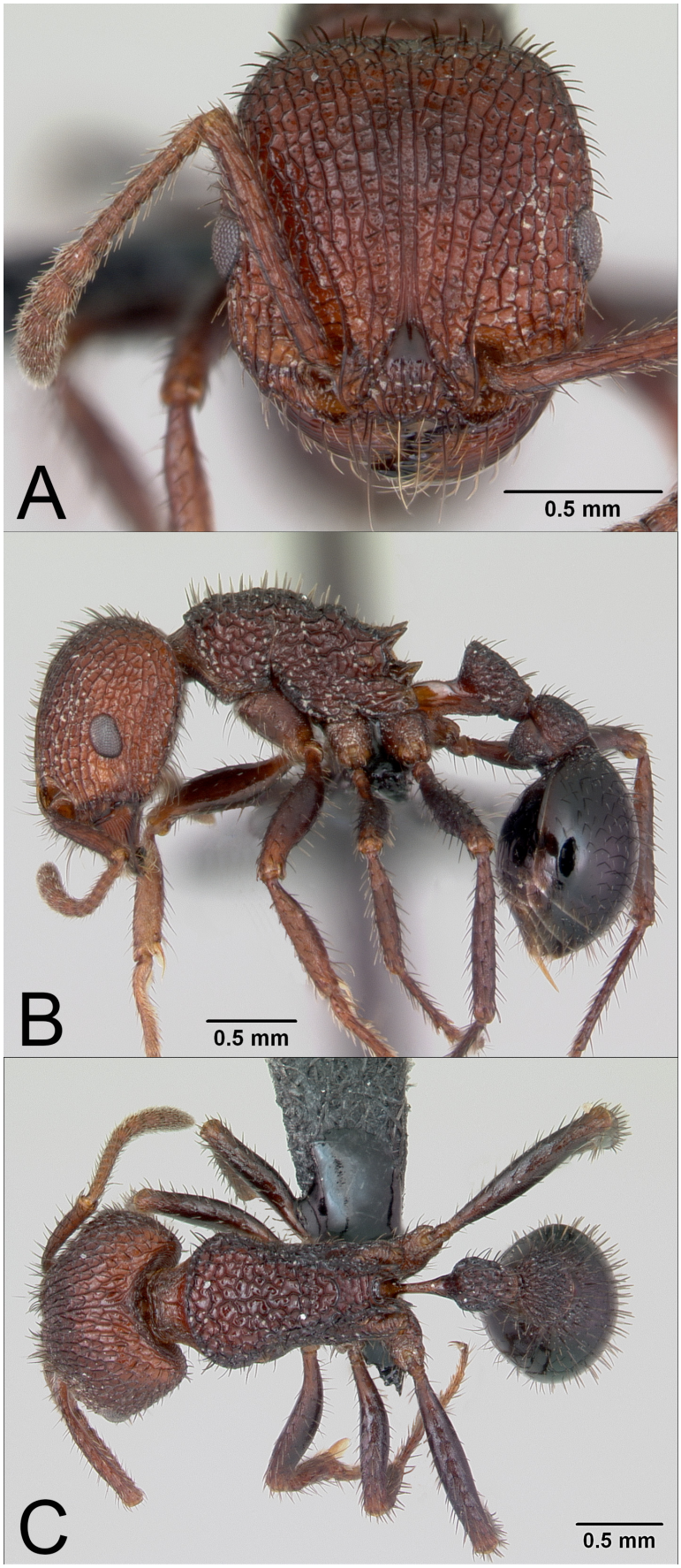

FIGURE 58. Photograph of *Pogonomyrmex naegelii* Santschi worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0172677). Photographs by April Nobile from www.AntWeb.org.

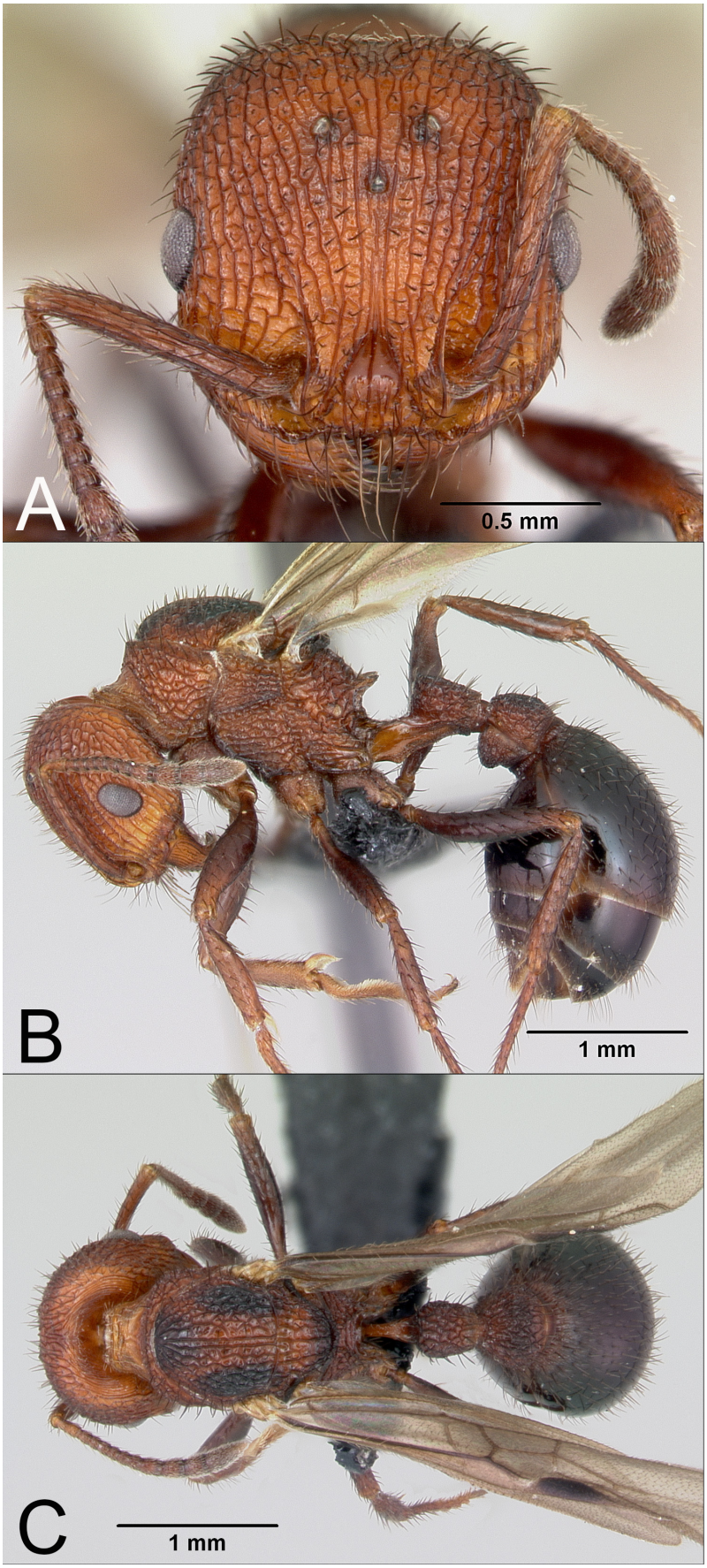

FIGURE 59. Photograph of *Pogonomyrmex naegelii* Santschi alate queen: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0172678). Photographs by April Nobile from www.AntWeb.org.

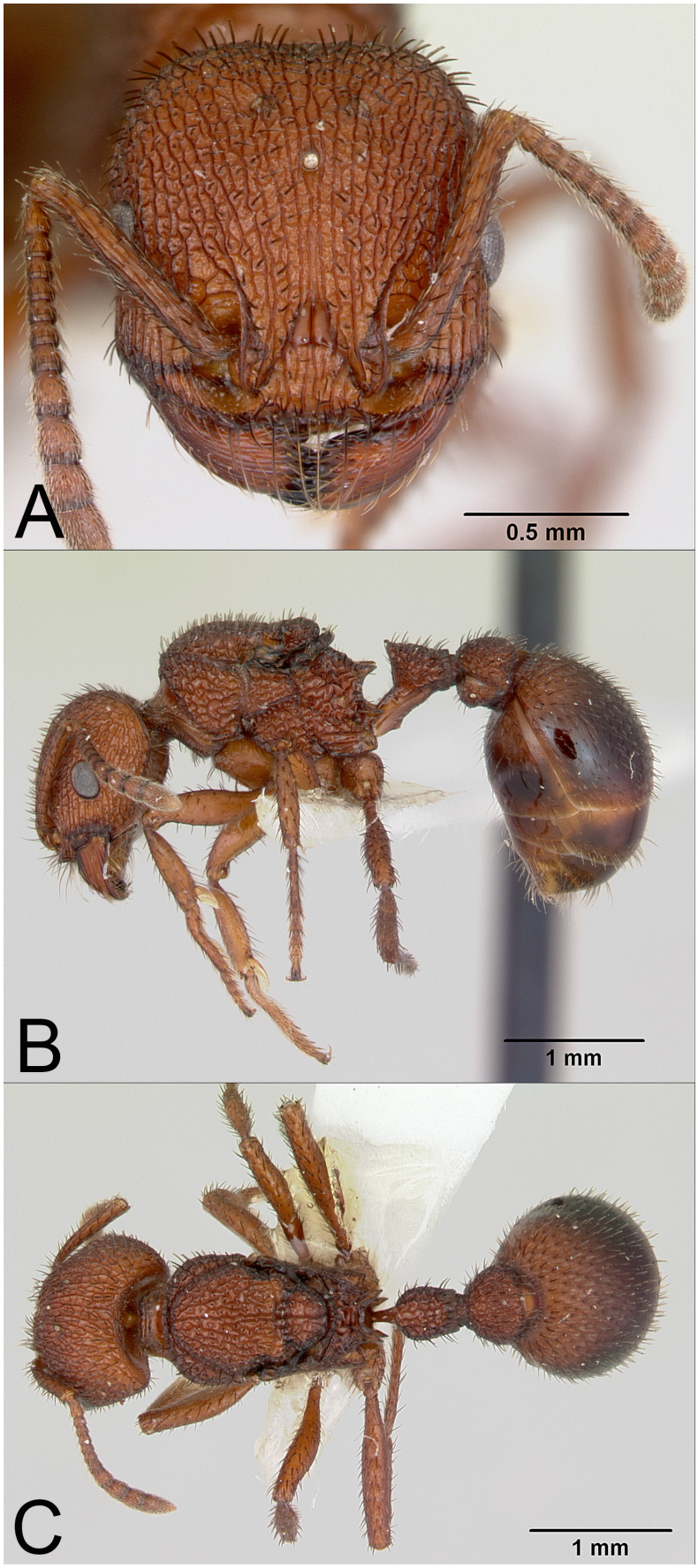

FIGURE 60. Photograph of *Pogonomyrmex naegelii* Santschi ergatoid queen: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0173110). Photographs by April Nobile from www.AntWeb.org.

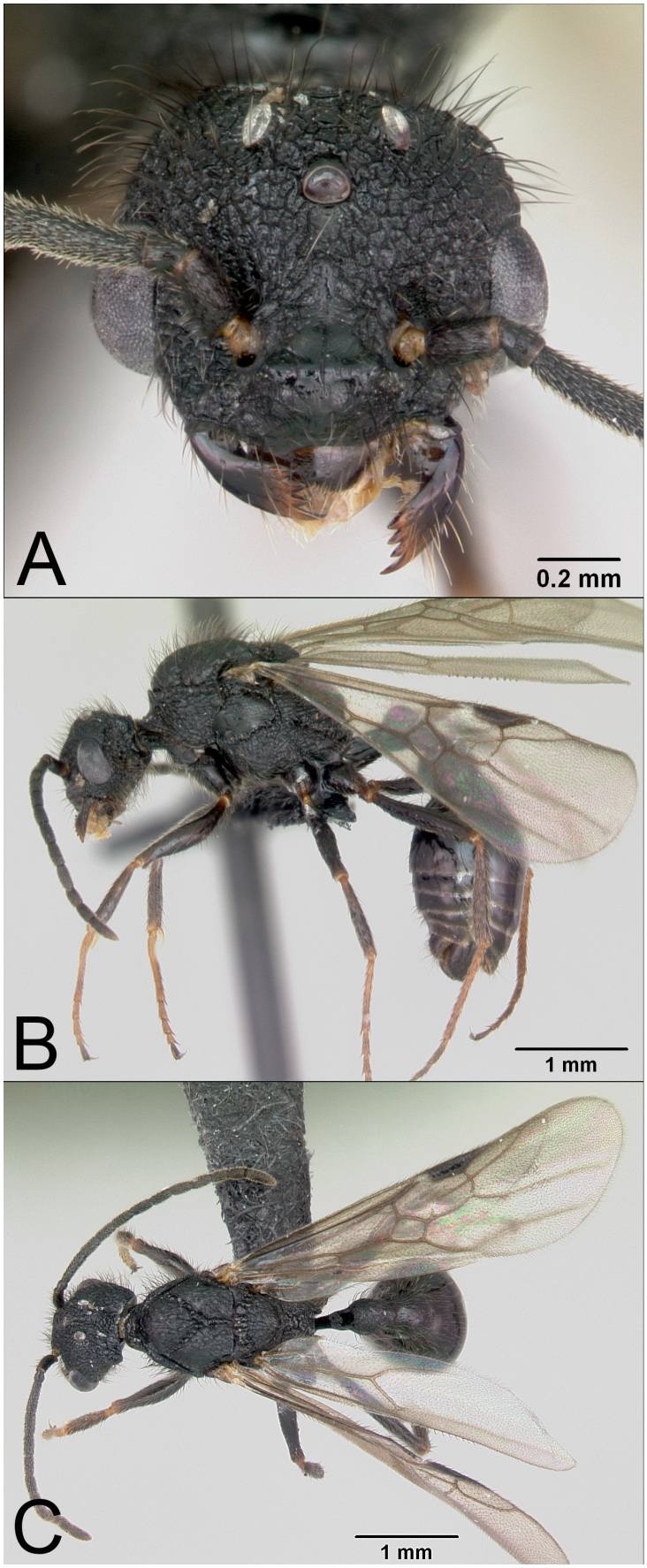

FIGURE 61. Photograph of *Pogonomyrmex naegelii* Santschi male: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0172688). Photographs by April Nobile from www.AntWeb.org.

All mesosomal surfaces rugoreticulate. In profile, mesoscutum and mesoscutellum flattened, mesoscutellum angled upward posterad; metanotum discontinuously connected to mesoscutellum and propodeum. Superior and inferior propodeal spines moderately well-developed, similar in length. Peduncle of petiole long, anteroventral margin with small to moderately well-developed acuminate triangular process. In profile, petiolar node asymmetrical with anterior surface notably shorter than posterior surface, apex angulate. Postpetiole slightly wider than long. Posterior surface of petiolar node coarsely rugoreticulate, dorsum of postpetiole finely rugoreticulate; interrugae weakly to moderately punctate, weakly shining. First gastral tergum weakly to strongly coriarious, dull to weakly shining with faint to moderately strong longitudinal striae near base that sometimes extend over anterior one-half of tergum. Most body surfaces with abundant suberect to erect, brownish hairs that are similar in length, longest approximately 0.5–0.7x MOD. Body concolorous tannish-brown to orangish-brown, posterior gastral terga often darker (**Figure 60**).

Male. Diagnosis. This caste is diagnosed by: (1) first gastral tergum lacking striae, (2) small (HW < 1.10 mm; ML < 2.00 mm), (3) in dorsal view, posterior surface of petiolar node rugoreticulate, (4) in profile, petiolar node rounded, (5) pronotal sides rugoreticulate, (6) in profile, inferior propodeal spines moderately well-developed, broadly rounded, and (7) notauli present (**Figure 61**). Note that males are unknown for *P. abdominalis* and *P. tenuipubens*.

Measurements—(*n* = 12). HL 0.89–1.10; HW 0.84–1.08; MOD 0.32–0.42; OMD 0.06–0.18; SL 0.14–0.23; HFL 1.03–1.40; ML 1.51–1.95; PW 0.33–0.43; PPW 0.44–0.58. Indices: SI 14.00–22.12; CI 94.38–109.18; OI 33.98–42.00; HFI 106.80–136.00.

Additional material examined. ARGENTINA: ***Buenos Aires***: Campana, 10 m, Oct 31, 2002 (ALWC; MLPA); 10 km SE Campana, Dec 1, 2005 (CSC); Hwy 12 at 9 km N Zárate, 30', Dec 3, 2003 (RAJC); Reserva Otamendi, 50', Dec 3, 2003 (RAJC); Buenos Aires Zoo, 10', Jan 10, 2011 (RAJC); Bella Vista, no date (MCZ); San Fernando, Aug 1963 (USNM); Rosas, Aug 1963 (USNM); Rt 12 at Rivadavia, 340', Jan 20, 2011 (RAJC); Argerich, Feb 2, 1950 (FML). ***Chaco***: Presidente Roque Sáenz Peña, Feb 7–9 & 19, 1933 (FML). ***Córdoba***: Estancia Santo Domingo, Feb 24, 2009 (RGPC); Los Aromos, Sept 16, 2008 & Dec 14, 2008 (RGPC); Nono, 2940', Jan 17, 2008 (RAJC); Rt 20 at 1.0 km N Nono, 2920', Jan 23, 2006 (RAJC); 2.6 km N Nono, Dec 17, 2006 (CSC); Alta Gracia La Granja, Sierras de Córdoba, Jan 1922 (USNM); Rt 5 at 2.4 km N Alta Gracia, 1980', Jan 24, 2006 (RAJC); Rt 5 at 3.4 km S Alta Gracia, 1830', Jan 23, 2006' (RAJC); 6 km SW Alta Gracia, 600 m, Jan 27, 1995 (MCZ); 22 km WSW Alta Gracia, Jan 28, 1995 (MCZ); Rt 9 at 6.5 mi E Bell Ville, 390', Dec 21, 2005 (RAJC); Sierra Chica, 3670', Jan 23, 2006 (RAJC); La Cruz, 1860', Jan 16, 2008 (RAJC); Rt 9 at 3.5 km E Marcos Juárez, 330', Jan 14, 2010 (RAJC); Unguillo, no date (MLPA); Río Calera (=El Calera), Apr 25, 1948 (FML). ***Corrientes***: Rt 12 at Scorze Cue, 180', Jan 18, 2011 (RAJC). ***Entre Ríos***: Parque Nacional El Palmar, Feb 24, 2009 (RGPC); 34.7 km N Jct Rts 14 & 130, 70', Dec 18, 2005 (RAJC); Jct Rts 14 & 22, 70', Dec 18, 2005 (RAJC); 1.4 km W Pueblo Liebig, 70', Feb 13, 2010 (RAJC). ***La Pampa***: 51 km E Río Colorado, Nov 20, 2005 (CSC); General Pico, Jan 14, 1950 (FML). ***Mendoza***: Rt 188 at 20 km W Río Salado, 1250', Dec 4, 2003 (MCZ; RAJC); Rt 188 at 11.8 km W Canalejas, 1260', Jan 27, 2008 (RAJC). ***Misiones***: Esperanza, no date (MHNG); Loreto, no date (LACM; MZUSP); Loreto, 210', Jan 13, 2011 (RAJC); Parque Nacional Iguazú at Puerto Canoas, 191 m, Mar 29, 2003 (USNM); 2 km E Bonpland, 460', Jan 14, 2011 (RAJC); Corpus, 490', Jan 15, 2011 (RAJC); Rt 12 at El Dorado, 730', Jan 15, 2011 (RAJC); Rt 12 at Puerto Rico, 700', Jan 15, 2011 (RAJC). ***Salta***: Campo Quijano, Jan 20, 1948 (FML); Horcones, Jan 18, 1948 (FML). ***Santa Fe***: Esperanza, Aug 3, 1949 (FML); 10 km E Santa Fe, 30 m, Oct 18, 2002 (ALWC); Rt 34 at Cañada Rosquín, 230', Dec 21, 2005 (RAJC); Rt 65 at 4.2 mi SE Las Rosas, 310', Dec 21, 2005 (RAJC); Rt 65 at 5.0 mi W Las Rosas, 330', Dec 21, 2005 (RAJC); Rt 65 at Bouquet, 350', Dec 21, 2005 (RAJC); Fives Lille, no date (MACN); Nare, Oct 1957 (FML). ***San Luis***: 10 km E Jct Rts 148 & 188, 850', Dec 4, 2003 (CASC; RAJC); Rt 188 at 32.0 km W Unión, 1360', Jan 27, 2008 (RAJC); Villa Mercedes, 1700', Dec 25, 2005 (RAJC); Rt 7 at Alto Pencoso, 2330', Dec 27, 2005 (RAJC); Rt 7 at Balde, 1690', Dec 27, 2005 (RAJC); Rt 20 at 1 km NE Luján, 1940', Dec 26, 2005 (RAJC); Rt 20 at 38.8 km W Luján, 2030', Dec 27, 2005 (RAJC); Potrero de los Funes, 3130', Dec 25, 2005 (CASC; RAJC); La Florida, 3310', Dec 25, 2005 (RAJC); 2.0 km S El Trapiche, 3350', Dec 25, 2005 (RAJC); Rt 7 at 25 km SE San Luis, 2870', Dec 12, 2003 (RAJC). ***Tucumán***: Vipos, Rt 39, N 9, Dec 11, 1947 (FML); Villa Padre Monti, Jan 17–Feb 7, 1948 (FML). ***Prov. Unknown***: no loc, no date (USNM). **BOLIVIA:** ***Asunción***: Asunción, Oct 2, 1948 (FML). ***Beni***: Ivón, Feb 1922 (USNM); Cavinas, no date (USNM); Reyes, Nov 1921 (USNM); Riberalta, Jan 1922 (USNM); Cachuela Esperanza, Mar 1922 (USNM); Rosario, no date (USNM); Guayaramerín, no date (FML). ***La Paz***: Ixiamas, Dec

1921 (USNM). ***Tarija***: Tarija, no date (FML). **BRAZIL:** ***Acre***: Río Branco, Parque Zoologica, Nov 28, 1987 (MZUSP). ***Bahia***: Anagé, Nov 2, 1990 (MZUSP); Fazenda Maria Inácia, Maracás, Nov 29, 1990 (MZUSP); Salvador, no date (MZUSP). ***Espírito Santo***: Santa Teresa, 700 m, Feb 23, 1967 (MCZ); Pedro Canário, Oct 1972 (MZUSP). ***Goiás***: Colinas do Sul, Serra da Mesa, Dec 2–15, 1995 (MZUSP); Anápolis, Dec 28, 1953 (MZUSP); Municipio de Anápolis at km 46 on road to Goiâna, May 10–12, 1971 (MCZ); Niquelândia, Sep 24—Oct 6, 1995 (MZUSP); Parque Nacional das Emas, Sep 6, 1996 (MZUSP). ***Maranhão***: Balsas, Gerais de Basa, Río Mandacaru, Nov 4, 1999 (MZUSP). ***Mato Grosso***: Municipio Diamantino, Fazanda Junquiera Vilela, Jul 17–18, 1973 (MCZ); 18 km SSW Pocone, 110 m, Nov 1, 1995 (MCZ); Várzea Grande, Jan 25, 1985 (MZUSP); Rondónopolis, Jun 11, 1972 (MZUSP); Salto de Céu, Nov 11, 1986 (MZUSP); no loc, no date (MSNG). ***Minas Gerais***: Serra Caraca, 1380 m, Nov 1961 (MZUSP). ***Paraná***: Iguazú Falls, Apr 12, 1989 (LACM); Rolândia, Nov 1–15, 1989 (LACM). ***Río de Janeiro***: no loc, no date (AMNH; LACM; MCZ; USNM); Ilha Grande, Feb 7–8, 1999 (ALWC); Petrópolis, no date (AMNH); Mendes, Sep 11, 1933 (LACM); A Guanabara, Sep 8, 1941 (USNM). ***Río Grande do Sul***: Tramandai, 1 m, Dec 20, 2008 (RAJC); São Leopoldo, no date (USNM); Campinas do Sul, Dec 1954 (USNM); no loc, 1954 (MSNG; USNM). ***Roraima***: Ilha de Maracá, Sep 26, 1987 (MZUSP). ***Santa Catarina***: Blumenau, Jan 19, 1972 (LACM; MCZ; MZUSP; USNM; ZSM); Nova Teutonia, Jul 1936 (LACM); no loc, no date (MCZ). ***São Paulo***: Pindamonhangaba, Aug 25, 1961 (MZUSP); Agudos, Mar 1952 & Oct 12, 1952 (LACM; MCZ; USNM); Campos de Jordão, Oct 16, 1956 (LACM); Municipio Piracununga, Cachoeira de Emas, Feb 1967 (MCZ); Palestina, Sep 27, 1974 (MZUSP); Botucatu, Nov 15, 1953 (MZUSP); Jardim de Botânico, Agua Funda, Feb 1967 (MCZ); São Sebastião, Jan 30, 1955 & Dec 24, 1993 (LACM; MZUSP); Ilhabela, Dec 24, 1993 (MZUSP); Mirassol, Sep 27, 1970 (USNM); Barueri, Oct 25, 1958 (LACM; MZUSP); Mogy (=Mogi das Cruzes?), no date (USNM). ***Tocantins***: Pedro Afonso, Nov 12, 1998 (MZUSP). ***Estado Unknown***: no loc, no date (MCZ; USNM). **COLOMBIA:** ***Meta***: Carimagua, May 15, 1996 (USNM). **PARAGUAY:** no loc, no date (MSNG). ***Amambay***: Parque Nacional Cerro Corá, May 13, 1997 (ALWC); Pedro Juan Caballero, Aug 20, 1998 (ALWC). ***Boquerón***: Mister Long, 460', Sep 17–18, 2003 (RAJC; RBINS); General Eugenio Alejandrino Garay, Jun 3, 1995 (ALWC). ***Caaguazú***: Pastoreo, Sep 29, 1974 (MZUSP); San Antonio, Feb 12, 1998 (ALWC). ***Canindeyú***: Reserva Natural del Bosque Mbaracayú, Jejuimi, Jun 11, 1996 (ALWC; LACM; MCZ); Reserva Natural del Bosque Mbaracayú, Lagunita, Jun 11 & 16, 1996 (ALWC; LACM); 6 km N Ygatimi, Sep 30, 1996 (ALWC); 2 km W Arroyo Bandera, Feb 4, 1997 (ALWC); Camino a Mboi Jaguá, Apr 18, 1997 (ALWC). ***Central***: Aregua, Oct 1, 1995 (ALWC; LACM); Guarambaré, Apr 25, 1997 (ALWC), no loc, Feb 20, 1940 (FML). ***Cordillera***: Caacupé, Dec 1992 (ALWC). ***Guairá***: Colonia Independencia, Feb 11, 1998 (ALWC). ***Parguari***: Paraguari, no date (MCZ). ***President Hayes***: Trans Chaco Hwy at km 140, Dec 3, 1993 (ALWC). ***San Pedro***: Liberación, Jan 3, 1994 (ALWC); Naranjito, Dec 31—Jan 2, 1996 (ALWC). **PERU:** ***Huánuco***: Huánuco, Oct 16, 1954 (CASC). ***Junín***: El Campamiento Perené, Jul 1, 1920 (AMNH; LACM; MCZ); La Merced, Río Chanchamayo, Jun 20, 1920 (MCZ). ***Madre de Dios***: Puerto Maldonado, 202 m, Nov 14, 2010 (RAJC); ***Pasco***: Oxapampa, 1600 m, 1940 (MCZ). **URUGUAY:** ***Colonia***: Carmelo, Río Uruguay, no date (MACN). **VENEZUELA:** ***Aragua***: Corte Fuego de Mata Seca, Sendero de Mata Seca, Maracay, 516 m, Aug 28, 2003 (RAJC). ***Bolívar***: Ciudad Bolívar, Jan 27, 1935 (MCZ). ***Delta Amacuro***: Orinoco Delta, Jan 27, 1935 (MCZ). ***Guarico***: Estación Biológica Llanos at 10 km S Calabozo, Jul 1–2, 1971 (MCZ). ***Locations not found.*** **ARGENTINA:** ***Tucumán*?**: Reserva Forestal, Rt 9 at km 1326, Mar 24, 1948 (FML); Rt 9 at km 1398, Dec 13, 1947 (FML). ***Questionable locales*** **(appear to be outside geographic range): ARGENTINA:** ***Neuquén***: Hua-Hum, Jan 1, 1949 (USNM). ***Salta***: no loc, Aug 19, 1898? (MSNG) (**Figure 56B**).

Etymology. The specific epithet, *naegelii* (Latinization of *Naegeli*), is derived from Carlos Naegeli, who collected the syntype workers.

Discussion. *Pogonomyrmex naegelii* co-occurs with the other two *P. naegelii*-group species. *Pogonomyrmex naegelii* can be distinguished from *P. tenuipubens* by: (1) the approximately 8–10 coarse longitudinal rugae between the frontal lobes, (2) a small lobe that project dorsally from the anterior margin of the antennal fossa, and (3) the longest hairs on the psammophore and mesosoma are coarse, their length ≥0.5x MOD. In *P. tenuipubens*: (1) there are 16–20 fine, weak, longitudinal rugae between the frontal lobes, (2) the anterior margin of the antenna fossa lacks a lobe-like projection, and (3) the psammophore and abundant hairs on the mesosoma are very short, delicate, length <0.2x MOD, except for one to few long, coarse hairs that are sometimes present on the posterior margin of head and pronotum. *Pogonomyrmex naegelii* can be distinguished from *P. abdominalis* by: (1) usually smaller (HW = 1.05–1.23 mm), (2) a small lobe that projects dorsally from anterior margin of antennal fossa, (3)

peduncle of petiole and anterior surface of petiolar node meet at an obtuse angle, and (4) width of posterior surface of petiolar node is similar to or slightly greater than distance between tips of superior propodeal spines. In *P. abdominalis*: (1) the body is usually larger (HW = 1.14–1.33 mm; **Figure 57**), (2) no small lobe projects dorsally from anterior margin of antennal fossa, (3) the peduncle of petiole and anterior surface of petiolar node meet at or near a right angle, and (4) the posterior surface of petiolar node is distinctly wider than distance between tips of superior propodeal spines.

Weber's (1943) description of *P.* (*E.*) *venezuelensis* and *P.* (*E.*) *venzuelensis* subsp. *rupununi* appear to have been driven by geography rather than morphology as he notes that his records from Venezuela and British Guiana (= Guyana) bridge the considerable distribution gap between records in North America and South America. At that time, the southern most records for North American species were in Guatemala, and the northernmost record for South American species were in southern Brazil, Bolivia, and Chile. Moreover, it appears that Weber was unaware of or ignored comparing his specimens with those of *P. abdominalis* and *P. naegelii* because his paper did not mention either species. His only comment on *P. venezuelensis* var. *rupunini* was that it was larger and darker, and the gaster more heavily sculptured, being shallowly reticulate-punctate at the base compared to *P. venezuelensis* (Weber, 1943).

Kempf (1960) synonomized *P. venezuelensis* and *P. venezuelensis* var. *rupunini* under *P. naegelii* indicating that the description and figure of *P. venezuelensis* matched that of *P. naegelii*. He also noted that Dr. Weber failed to differentiate *P. venezuelensis* from other known species in the group. Kempf subsequently synonomized *P. venezuelensis* under *P. naegelii*, noting that Dr. Brown at the MCZ found no differences between the two forms when comparing a syntype of *P. venezuelensis* with *P. naegelii* from several locations. Kempf indicated that the same applied to *P. venezuelensis* ssp. *rupunini*, even though Kempf had not examined syntypes of this form.

I have examined syntypes of *P. venezuelensis* and *P. venezuelensis* subsp. *rupununi*, and both taxa fall within the range of morphological variation displayed within a nest series of *P. naegelii*. No consistent differences were observed between *P. naegelii*, *P. venezuelensis*, and *P. venzuelensis* subsp. *rupununi*, and the two latter forms are maintained as junior synonyms of *P. naegelii*. Also note that the types of *P. venezuelensis* ssp. *rupununi* are labeled as *P. venezuelensis myersi* (after Myers, who collected the type series); Weber apparently changed his mind about naming this form while writing the description.

Biology. *Pogonomyrmex naegelii* is a solitary forager that has a generalist and season-dependent diet that consists of grass seeds, and to a lesser extent nongrass species, various plant parts, and insects; ants and termites are the primary animal prey. The diet is primarily granivorous during the dry/cold season, whereas arthropods are collected to a greater extent during the warm/wet season (Belchior, Del-Claro, & Oliveira, 2012). Nests range from a cryptic entrance to a 10 cm tumulus, and they sometimes have a secondary entrance. Nests in the cerrado savanna of Brazil are relatively shallow, reaching about 70 cm below the soil surface and have 5–10 chambers (Belchior *et al.*, 2012). Colonies are relatively small, ranging from 166–580 workers (n = 3 nests) (Belchior *et al.*, 2012). Nests had one queen (n = 3) (Belchior *et al.*, 2012), and the author has found multiple dealate queens in several nests. In the latter case, it is unknown if these queens were reproductive, especially given that colonies of the related North American species *P. pima* sometimes have numerous unmated dealate queens that forage (see Johnson *et al.*, 2007).

Collection dates for sexuals range from 3–25 December. Mating flights have not been observed, but they likely occur during austral summer based on dates on which sexuals have been collected. *Pogonomyrmex naegelii* has both alate and ergatoid queens. From collections to date, the author has not seen any series in which both queen phenotypes were collected in the same colony, similar to observations for *P. pima* (Johnson *et al.*, 2007). One alate queen had eight ovarioles (unpub. data).

Pogonomyrmex naegelii inhabits sites at elevations from 0–1115 m, and it is the most widespread and commonly collected *Pogonomyrmex* in South America. It is known from all countries except Chile, Ecuador, Suriname, and French Guiana (**Figure 56B**). *Pogonomyrmex naegelii* occurs in numerous ecoregions, but appears to be absent from deserts, rainforests, and high-elevation areas.

Pogonomyrmex tenuipubens

(Figure 62)

Pogonomyrmex (*Ephebomyrmex*) *tenuipubens* Santschi, 1936: 403, fig. 4 (worker). Syntypes examined: 1 worker [FML], 1

worker [NHMB], ARGENTINA, Misiones: Loreto, #2055 (Dr. A. Ogloblin, 19 September 1933). NHMB worker here designated **LECTOTYPE** [CASENT0281113].

Ephebomyrmex tenuipubens (Santschi): Kempf, 1972: 106, first combination in *Ephebomyrmex.*

Pogonomyrmex tenuipubens Santschi: Bolton, 1995: 341, revived combination in *Pogonomyrmex*.

Worker. Diagnosis. Within the *P. naegelii*-group, the combination of: (1) approximately 16–20 fine, weak, longitudinal rugae between frontal lobes, (2) abundant, very short, delicate hairs on head (including psammophore) and mesosoma, maximal length similar to width of cephalic interrugae uniquely characterize this species (**Figure 62**).

Measurements—lectotype (*n* = 1 paralectotype). HL 1.19 (1.23); HW 1.10 (1.16); MOD 0.27 (0.28); OMD 0.27 (0.27); SL 0.78 (0.75); PNW 0.77 (0.80); HFL 1.07 (1.15); ML 1.37 (1.38); PW 0.35 (0.37); PPW 0.50 (0.50). Indices: SI 70.91 (64.66); CI 92.44 (94.31); OI 24.55 (24.14); HFI 97.27 (99.14).

Redescription. Head elongate (CI = 92.44–94.31), widest just posterior to eye; posterior margin flat. Longitudinal rugae on cephalic dorsum fine and dense, slightly wavy; approximately 16–20 fine, longitudinal rugae between frontal lobes; in full-face view, medial rugae not diverging toward posterior corners of head. In profile, area posterior to eyes rugose, rugae converging between posterior margin of eye and vertex. Cephalic interrugae moderately granulate, weakly shining; vertex rugose. Anterior margin of clypeus moderately concave, dorsal surface with numerous fine, subparallel, longitudinal rugae; lateral lobe of clypeus lacking small lobe that projects from anterior margin of antennal fossa. Mandible with five teeth; mandibular dorsum coarsely rugose. Up to several moderately long, curved, bristle-like, yellow-brown to brownish hairs project from anterior margin of clypeus. MOD = 0.23x HL. In profile, eyes situated anterior to middle of head, OMD = 0.96–1.00x MOD. Antennal scapes moderately long (SI = 64.66–70.91), failing to reach vertex by approximately 2.0x length of basal funicular segment; entire scape strongly striate, dull. Basal flange of scape flattened, moderately well-developed with carinate margin. Psammophore poorly-developed, consisting of numerous very short hairs scattered across ventral side of head.

Mesosomal profile weakly convex; all mesosomal surfaces with weak, wavy to irregular rugae or rugoreticulate. Mesoepinotal sulcus not impressed. Dorsum and sides of pronotum with irregular rugae to rugoreticulate. Dorsum of mesonotum with irregular transverse rugae, mesopleura with irregular rugae angling posterodorsally; dorsum of propodeum with wavy, transverse rugae that traverse anteroventrally. Propodeum with moderately long, bluntly tipped spines connected by well-defined keel; spine length approximately 0.5-0.6x distance between their bases. Inferior propodeal spines well-developed, acuminate, length approximately 0.6x that of superior spines, width at base greater than length of superior spines; inferior and superior spines connected by a weak ruga. Propodeal spiracles ovoid to circular facing posterad. Interrugae on mesosoma moderately granulate, weakly shining. Legs weakly coriarious, weakly shining.

Peduncle of petiole about 0.7x as long as petiolar node, anteroventral margin weakly convex but lacking triangular process. In profile, petiolar node asymmetrical with anterior surface shorter than posterior surface, apex weakly rounded, anterior surface meeting peduncle at a right angle. In dorsal view, petiolar node longer than wide, widest near middle, narrowing to rounded anterior margin; maximal width of posterior surface slightly greater than distance between tips of superior propodeal spines; posterior surface and sides with weak transverse to oblique rugae, interrugae moderately granulate, weakly shining. Dorsum of postpetiole convex in profile; robust in dorsal view, widest at or near posterior margin, margins of posterior one-half mostly parallel, anterior one-half narrowing to broadly rounded anterior margin, maximal width greater than length, dorsum and sides moderately to strongly granulate-punctate, dull. Ventral process of postpetiole large, bulbous, height similar to dorsal portion of postpetiole. First gastral tergum smooth and strongly shining.

Short, thin, delicate, suberect, whitish pilosity moderately abundant on head, mesosoma, petiolar node, and postpetiole, hairs rarely longer than width of cephalic interrugae; one very long hair on each frontal lobe, length >MOD, and one to several long, coarse hairs occasionally present on posterior margin of head and pronotum. Moderately abundant short, appressed pilosity on scape plus several longer suberect hairs; abundant decumbent hairs on funicular segments. Legs with moderately abundant appressed setae; gastral terga with sparse, appressed, thin, delicate hairs that are longer than those on rest of body; posterior margin of second gastral tergum with several long erect hairs $\geq$MOD. Concolorous tan to tannish-brown with darker brownish gaster (**Figure 62**).

Queen. Unknown.

Male. Unknown.

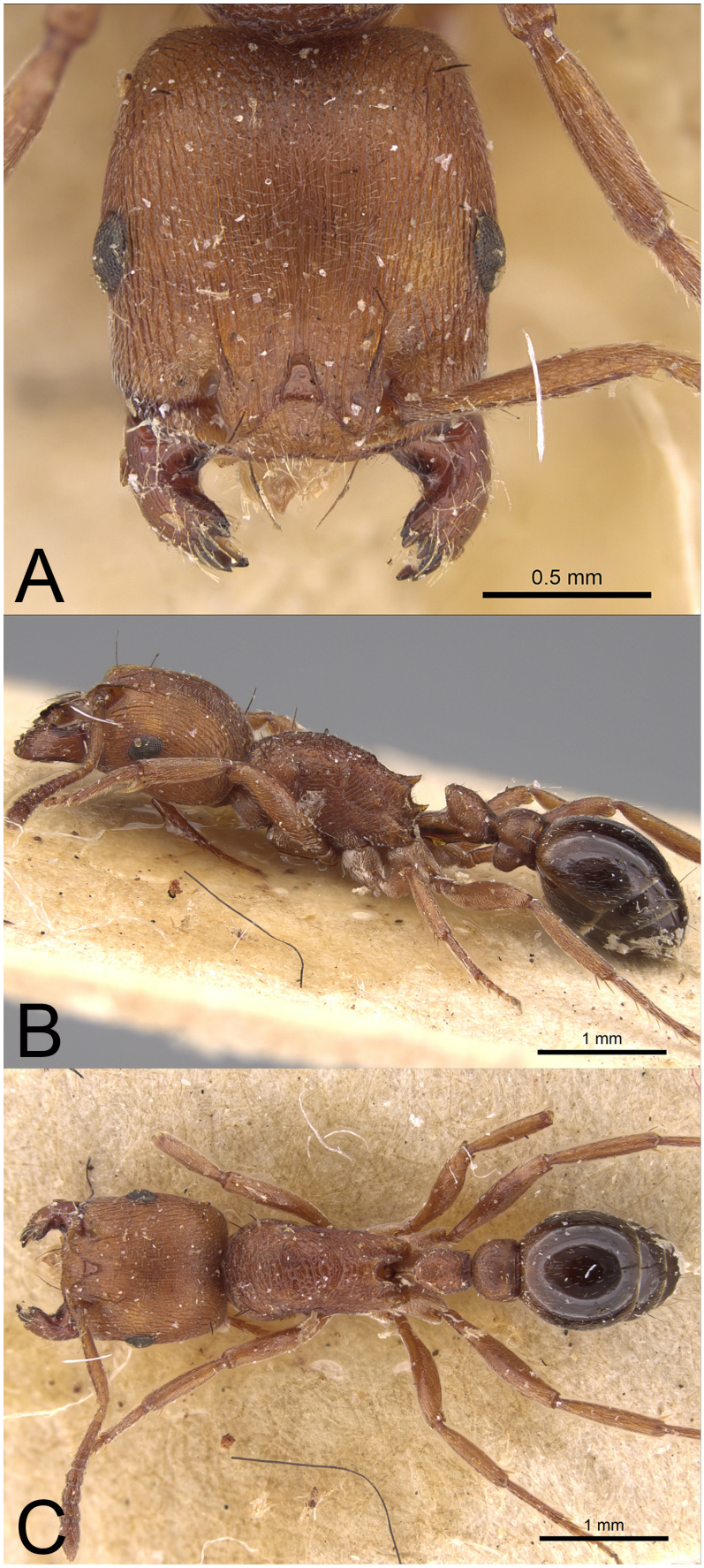

FIGURE 62. Photograph of *Pogonomyrmex tenuipubens* Santschi paralectotype worker: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0914377). Photographs by Michele Esposito from www.AntWeb.org.

Additional material examined. PARAGUAY: ***Caaguazú***: Pastoreo (see Fowler, 1981; not examined) (**Figure 56C**).

Etymology. Santschi named this species (Latin, *tenui-* = thin, narrow, or slender plus *pubens* = hair of an adolescent) for the fairly abundant, extremely short, fine pubescence over most of the body.

Discussion. *Pogonomyrmex tenuipubens* co-occurs with both *P. abdominalis* and *P. naegelii*. *Pogonomyrmex tenuipubens* can be distinguished from these two species based on the following characters: (1) *P. tenuipubens* has approximately 16–20 fine, weak, longitudinal rugae between the frontal lobes, and (2) very short, thin, delicate hairs on head (including psammophore) and mesosoma, their maximal length similar to width of cephalic interrugae. Both *P. abdominalis* and *P. naegelii* have: (1) approximately 8–10 coarse longitudinal rugae between frontal lobes, and (2) hairs on head (including psammophore) and mesosoma longer and coarse, their maximal length much longer than width of cephalic interrugae.

Biology. *Pogonomyrmex tenuipubens* appears to be uncommon given the very few times that it has been collected. Kusnezov (1951) and the author searched the type locality for this species: both found numerous colonies of *P. naegelii* but none of *P. tenuipubens*. Little is known about the biology of *P. tenuipubens*, but it is probably similar to that of *P. naegelii*.

Pogonomyrmex tenuipubens appears to inhabit low elevation sites (the type locality is at an elevation of about 65 m), and it is only known from the Alto Paraná Atlantic Forest ecoregion as defined by Olson *et al*. (2001) (**Figure 56C**).

Pogonomyrmex sylvestris-group

Workers in the *P. sylvestris*-group are diagnosed by the following characters: (1) first gastral tergum lacking striae, (1) anteroventral margin of peduncle of petiole with acuminate spine, (2) in dorsal view, postpetiole triangular, longer than wide, (3) superior and inferior propodeal spines long, (4) in dorsal view, petiolar node elongate; in profile, petiolar node flattened with crest at anterior margin that is elevated above posterior surface, (5) eyes small, situated anterior to middle of head, (6) psammophore poorly-developed, consisting of numerous short hairs scattered across ventral side of head, (7) mesosoma with several or more long, flexuous hairs, (8) propodeal spiracles circular, and (9) anterior margin of clypeus with medial tooth, sometimes very small, indistinct. Queens are unknown for all species; males are known for only *P. stefani*.

Pogonomyrmex stefani

(Figures 63–64)

Pogonomyrmex stefani Lattke, 2006: 53, figs. 1–4 (worker, male). Holotype worker [MIZA] (not examined). VENEZUELA, Bolívar: Fundo San Rafael, Río Víllacoa, 165 m, 6º25'N, 67º01'W, 6 December 2004 (J.E. Lattke leg. #2964). Paratypes examined—same data as holotype: 1 worker [MCZ], 1 worker, 1 male [MIZA].

Worker. Diagnosis. Within the *P. sylvestris*-group, the combination of: (1) six mandibular teeth, (2) eyes with hairs between ommatidia, (3) in profile, anterior margin of postpetiole not meeting helcium at a smooth, continuous angle, (4) in profile, procoxae transversely striate, (5) femur and tibiae smooth to weakly coriarious, weakly to moderately shining, and (6) medial clypeal region between antennal insertions with 9–12 fine, closely-spaced, longitudinal rugae, interrugae dull to weakly shining uniquely characterize this species (**Figure 63**).

Measurements—(*n* = 1 paratype). HL 1.29; HW 1.29; MOD 0.23; OMD 0.25; SL 1.02; PNW 0.89; HFL 1.38; ML 1.39; PW 0.29; PPW 0.42. Indices: SI 79.07; CI 100.00; OI 17.83; HFI 106.98. See also Lattke (2006).

Redescription. Head quadrate (CI = 100.00), widest just posterior to eye; posterior margin weakly concave. Longitudinal rugae on cephalic dorsum coarse, wavy to irregular medially, becoming more irregular to rugoreticulate laterally. Cephalic interrugae moderately granulate-punctate, weakly shining. Anterior margin of clypeus weakly convex with very small medial tooth; dorsum between antennal insertions with 9-12 fine, closely-spaced, longitudinal rugae, interrugae dull to weakly shining. Mandible with six teeth; mandibular dorsum coarsely rugose. Up to several moderately long, curved, bristle-like, yellowish hairs project from anterior margin of clypeus. Eyes small, MOD = 0.18x HL. In profile, eyes situated anterior to middle of head, OMD = 1.09x MOD; several

hairs project from between ommatidia. Antennal scapes long (SI = 79.07), surpassing vertex by less than width of basal funicular segment; entire scape with moderately coarse, longitudinal striae, dull to weakly shining. Basal flange of scape well-developed with carinate margin. Psammophore poorly-developed, consisting of numerous medium to long hairs scattered across ventral side of head.

Mesosomal profile strongly convex; all mesosomal surfaces with prominent rugae. Promesonotum with irregular longitudinal rugae medially, dorsum of propodeum with irregular transverse rugae, all other mesosomal surfaces rugoreticulate to vermiculate. Superior propodeal spines long, acuminate, bases connected by poorly-defined keel, spine length greater than distance between their bases. Inferior propodeal spines well-developed with broad triangular base, length less than 0.5x that of superior spines. Propodeal spiracles circular facing posterad. Interrugae on mesosoma weakly shining. In profile, procoxae with fine, subparallel, transverse striae. Legs smooth and shining to weakly coriarious, weakly shining.

Peduncle of petiole about 0.7x length of petiolar node; anteroventral margin with acuminate spine. In profile, posterior surface of petiolar node weakly convex; in profile, petiolar node asymmetrical with anterior surface slightly less than one-half the length of posterior surface, apex forming a bluntly tipped crest or tooth elevated above posterior surface; sides with wavy to irregular longitudinal rugae, posterior surface weakly rugoreticulate. In dorsal view, petiolar node elongate (length >1.90x width), sides subparallel, anterior portion narrowing to subangulate tip; interrugae with weaker secondary rugae, weakly shining. Dorsum of postpetiole convex in profile, anterior margin truncate, not meeting helcium at a smooth, continuous angle; robust in dorsal view, trapezoidal, widest near posterior margin, narrowing to rounded anterior margin; lateral margins wider ventrally at posterior margin; dorsum smooth and strongly shining to very weakly coriarious, shining. First gastral tergum smooth and strongly shining to weakly coriarious, shining.

Long, flexuous, yellowish to golden hairs abundant on head; medium to long hairs abundant on mesosoma, petiolar node, postpetiole, and gastral terga; longest hairs on head and mesosoma >MOD. Scape with abundant medium to long, suberect hairs; abundant decumbent hairs on funicular segments. Legs with moderately abundant, long, suberect to semidecumbent setae. Head, antennae, mesosoma, petiolar node, and postpetiole dark brown; mandibles, legs, and gaster brown (**Figure 63**).

Queen. Unknown.

Male. Diagnosis. This caste is diagnosed by: (1) first gastral tergum lacking striae, (2) small (HW < 1.10 mm; ML < 2.00 mm), (3) in dorsal view, posterior surface of petiolar node strongly coriarious, (4) in profile, petiolar node angulate, (5) pronotal sides granulate with a beaded appearance, (6) in profile, inferior propodeal spines broad, well-developed, acuminate or nearly so, and (7) notauli present (**Figure 64**). Note that males are unknown for *P. striatinodis* and *P. sylvestris*.

Measurements—(n = 1). HL 1.04; HW 1.01; MOD 0.43; OMD 0.14; SL 0.24; HFL 1.27; ML 1.88; PW 0.31; PPW 0.51. Indices: SI 23.76; CI 97.12; OI 42.57; HFI 125.74. See also Lattke (2006).

Additional material. VENEZUELA: *Bolívar*: c. Amarawai Tepui, 470 m, May 2, 1986 (5º55'N, 62º15'W) (not examined, locale record from J. Lattke) (**Figure 65A**).

Etymology. This species was named in honor of Dr. Stefan Schödl, who occupied the post of Curator of Hymenoptera in the Naturhistoriches Museum of Vienna until his death in April 2005.

Discussion. *Pogonomyrmex stefani* is the only *P. sylvestris*-group species known to occur in mesic lowland forests. The prominent transverse striae on the procoxae separate *P. stefani* from both *P. striatinodis* (procoxae sometimes very weakly striate, mostly smooth and shining) and *P. sylvestris* (procoxae imbricate, dull).

Pogonomyrmex naegelii is the only congener that might occur sympatrically with *P. stefani*, but the former species would occur in open, drier habitats than those occupied *P. stefani*. *Pogonomyrmex stefani* is distinguished from *P. naegelii* by: (1) hairs project from between the ommatidia, (2) an elongate, triangular postpetiole, and (3) in profile, the petiolar node is flattened to weakly convex with a crest or tooth on the anterior margin that is elevated above the posterior surface. *Pogonomyrmex naegelii*: (1) lacks hairs between the ommatidia, (2) the postpetiole is nearly globular with width and length similar, and (3) in profile, the petiolar node is convex and lacks a crest or tooth on the anterior margin.

Biology. Very little is known about the biology of *P. sylvestris*-group species. All three species are discussed together because they likely share a similar biology. Stray foragers comprise most collections for these three species. Few nests have been located: nests of *P. stefani* consisted of a small exposed entrance (Lattke, 2006), one nest of *P. sylvestris* was in a rotten log (Lattke, 2006), and nests of *P. striatinodis* are unknown. Diet and the sexual castes are unknown (except for the male of *P. stefani*) for all three species.

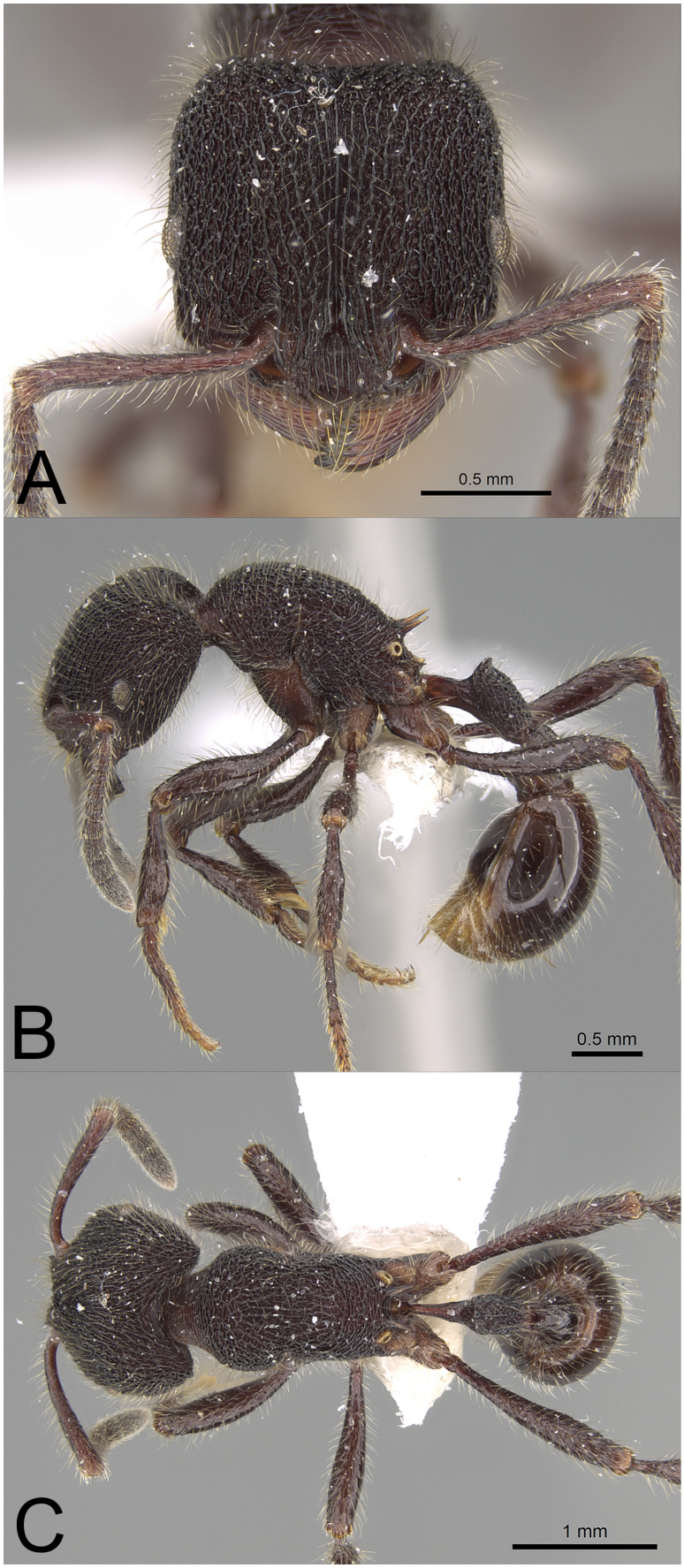

FIGURE 63. Photograph of *Pogonomyrmex stefani* Lattke paratype worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0914135). Photographs by Michele Esposito from www.AntWeb.org**.**

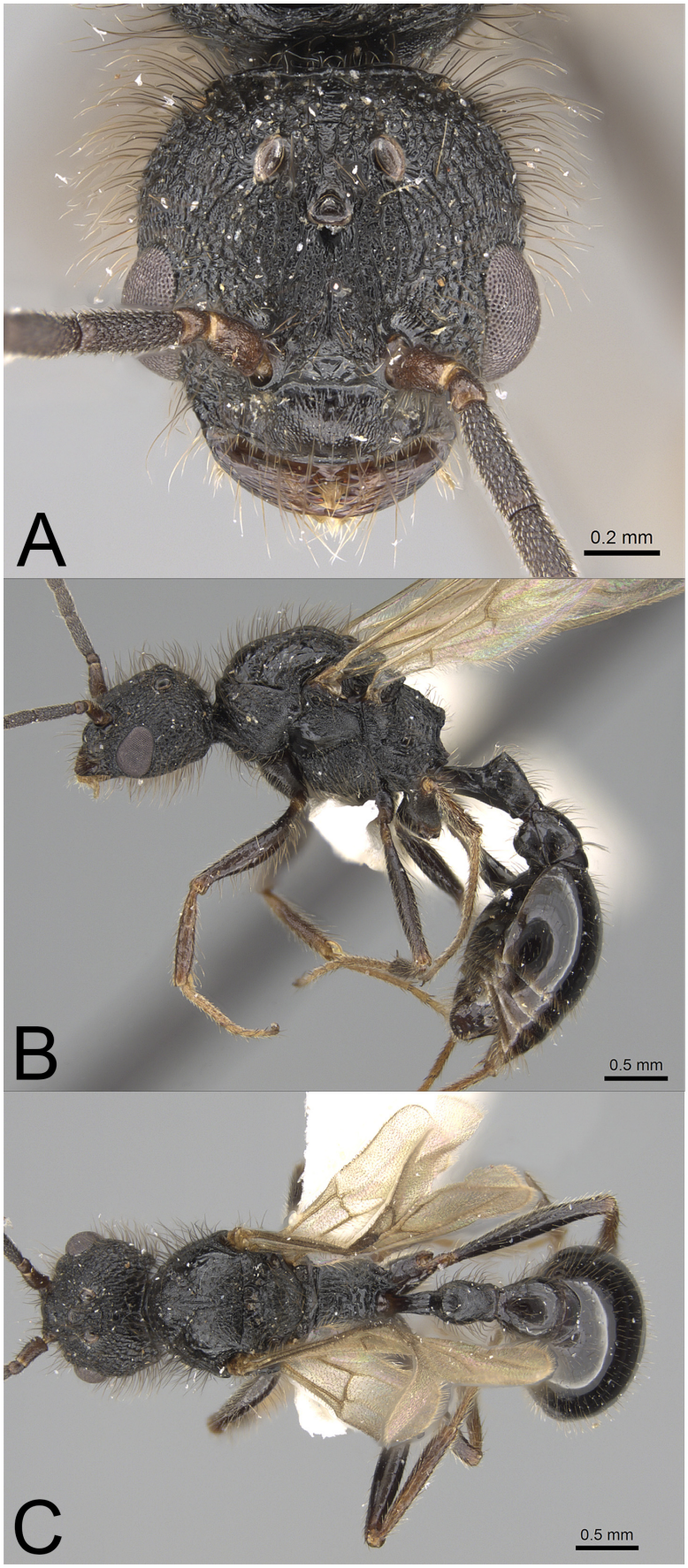

FIGURE 64. Photograph of *Pogonomyrmex stefani* Lattke male: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0914136). Photographs by Michele Esposito from www.AntWeb.org.

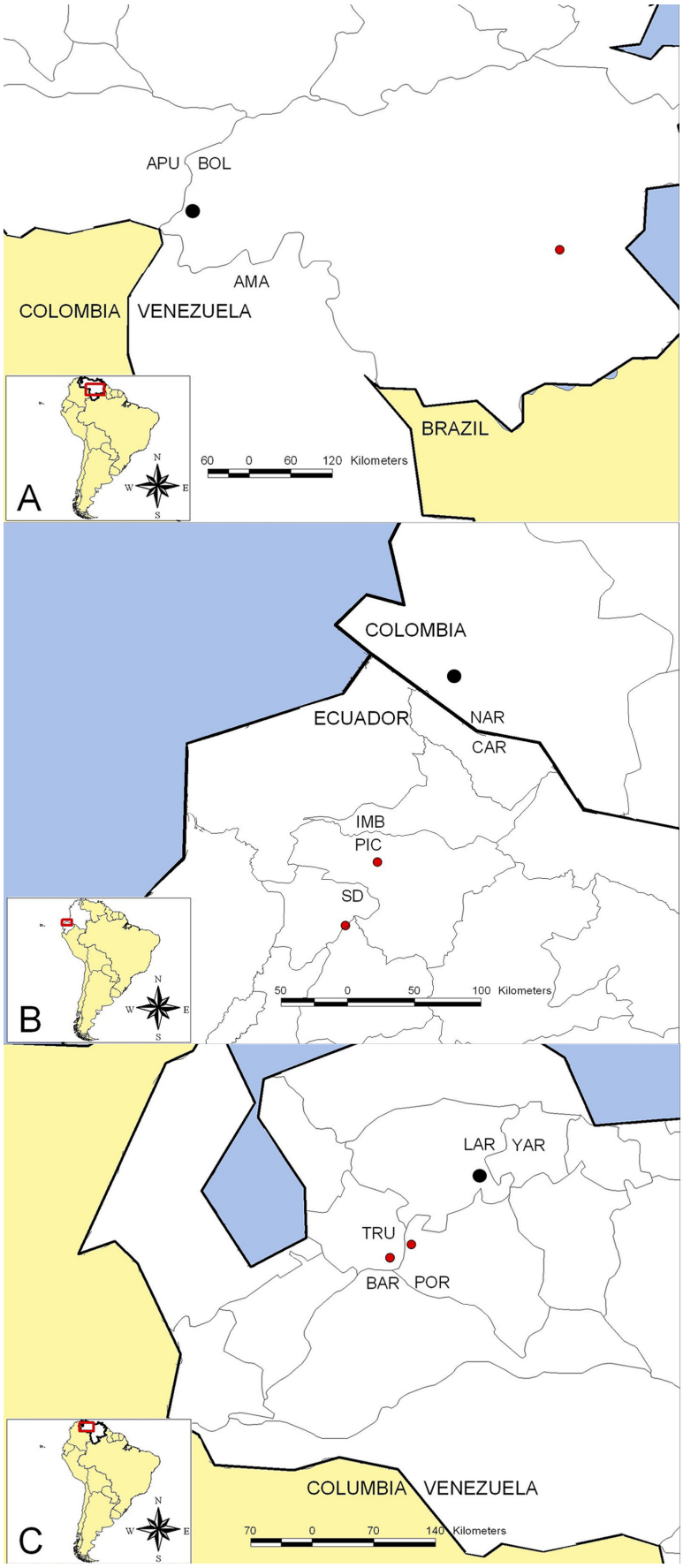

FIGURE 65. Geographic distribution of: (**A**) *Pogonomyrmex stefani* Lattke, (**B**) *Pogonomyrmex striatinodis* Fernández & Palacio, and (**C**) *Pogonomyrmex sylvestris* Lattke. The larger black circle in each panel denotes the type locality.

The *P. sylvestris*-group and *P. mayri*-group are sister groups that together form a clade that is sister to all other *Pogonomyrmex* (C.S. Moreau & the author, unpub. data). Consequently, obtaining information on the biology of *P. sylvestris*-group species (including diet, colony size and structure, phenotype of males and especially queens) would facilitate understanding the early evolution of the genus; queens would be especially interesting to collect given that *P. mayri* has ergatoid queens. It is predicted that biology of these species is similar to that of *P. mayri*, which suggests that colonies are small (no more than several hundred workers) and that their diet consists of mostly dead arthropods and plant parts, but relatively few seeds (Kugler, 1979, 1984; Kugler & Hincapie, 1983).

All three species are known to occur only in northern South America (Venezuela, Colombia, and Ecuador), and they comprise the small group of South American congeners that inhabit mesophilic forests. *Pogonomyrmex sylvestris* and *P. striatinodis* are mid-elevation species—*P. sylvestris* has been collected only in premontane cloud forest habitats of Venezuela at elevations from 1000–1300 m, and *P. striatinodis* is only known from mesic forests at elevations from 1000–1525 m. *Pogonomyrmex sylvestris* occurs in the La Costa Xeric Shrublands and Venezuelan Andes Montane Forest ecoregions, and *P. striatinodis* occurs in Northwestern Andean Montane Forest ecoregion as defined by Olson *et al*. (2001). Alternatively, *P. stefani* is only known from two locations in the mesic lowland forests at elevations from 165–470 m, and its geographic distribution may be restricted to the Orinoco watershed of Venezuela (Lattke 2006); it occurs in the Llanos and Pantepui ecoregions as defined by Olson *et al*. (2001). None of these three species are known to occur proximate to one another (**Figure 65**).

Pogonomyrmex striatinodis
(Figure 66)

Pogonomyrmex striatinodis Fernández & Palacio, 1998: 1650, figs. 1–8 (worker). Holotype worker [UNCB] (not examined). COLOMBIA, Nariño: Municipio de Barbacoas, Corregimiento de Altaquer, Reserva Natural Privada Río Ñambí, 1200–1400 m (Carlos Sarmiento leg., 14 July 1995). Paratypes examined, same data as holotype: 1 worker [FML], 1 worker, [LACM], 1 worker [NMW], 2 workers [USNM].

Worker. Diagnosis. Within the *P. sylvestris*-group, the combination of: (1) seven mandibular teeth, (2) eyes lacking hairs between ommatidia, (3) clypeus with prominent medial carina, and (4) in profile, anterior margin of postpetiole meeting helcium at a smooth continuous angle uniquely characterize this species (**Figure 66**).

Measurements—(*n* = 2 + 3 paratypes). HL 1.75–1.91; HW 1.58–1.68; MOD 0.28–0.32; OMD 0.37–0.42; SL 1.40–1.71; PNW 1.06–1.17; HFL 2.08–2.59; ML 2.20–2.34; PW 0.29–0.31; PPW 0.53–0.55. Indices: SI 88.05–103.01; CI 85.48–90.32; OI 16.67–19.28; HFI 130.82–156.97. See also Fernández and Palacio (1998).

Redescription. Head elongate (CI = 85.48–90.32), widest just posterior to eye; posterior margin weakly concave. Cephalic dorsum, sides, and vertex rugoreticulate. Cephalic interrugae smooth, shining to strongly shining. Anterior margin of clypeus weakly convex with medial tooth that continues as a medial carina on dorsum of clypeus, dorsal surface with several subparallel, longitudinal rugae. Mandible with seven teeth; mandibular dorsum coarsely rugose. Up to several moderately long, curved, bristle-like, yellowish hairs project from anterior margin of clypeus. Eyes small, MOD = 0.15–0.17x HL. In profile, eyes situated anterior to middle of head, OMD = 1.19–1.45x MOD; no hairs project from between ommatidia. Antennal scapes long (SI = 88.05–103.01), surpassing vertex by slightly less than length of basal funicular segment; entire scape with moderately coarse, longitudinal striae, dull. Basal flange of scape well-developed with carinate margin. Psammophore poorly-developed, consisting of numerous short to moderately long hairs (similar in length to slightly shorter than those on cephalic dorsum) scattered across ventral side of head.

Mesosomal profile strongly convex; all mesosomal surfaces rugoreticulate to vermiculate. Superior propodeal spines long, acuminate, bases not connected by well-defined keel, spines about the same length as distance between their bases. Inferior propodeal spines well-developed, acuminate, length similar to that of superior spines but with a wider base. Interrugae on mesosoma smooth, shining. Propodeal spiracles circular facing posterad. In profile, procoxae with very weak, irregular to discontinuous transverse rugae, weakly shining. Legs moderately coriarious, weakly shining.

Peduncle of petiole about 0.4x length of petiolar node, anteroventral margin with acuminate spine. In profile, petiolar node asymmetrical with anterior surface approximately one-third the length of posterior surface, apex forming acutely tipped crest or tooth elevated above posterior surface; posterior surface flattened; anterior surface

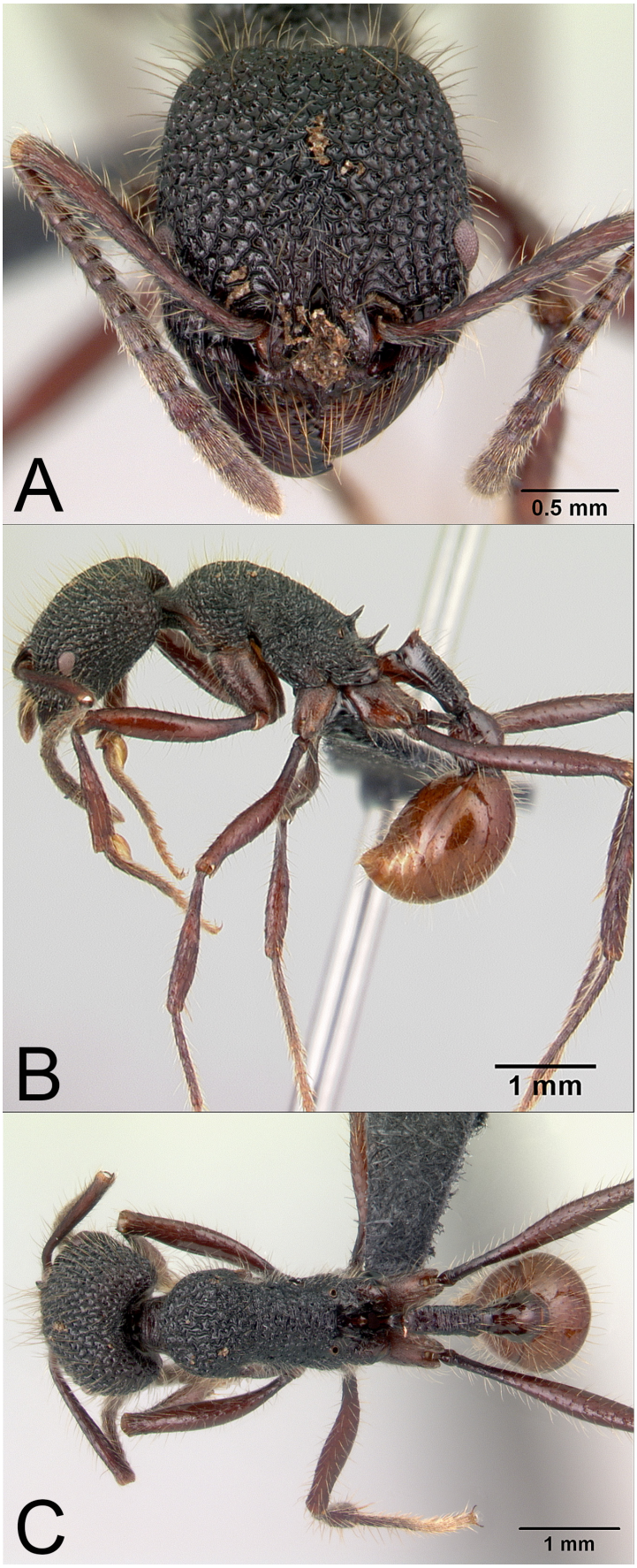

FIGURE 66. Photograph of *Pogonomyrmex striatinodis* Fernández & Palacio worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0179592). Photographs by Erin Prado from www.AntWeb.org.

smooth and shining to moderately coriarious, weakly shining; lateral surface smooth and shining anterad, posterior one-half to two-thirds with coarse vertical rugae. In dorsal view, petiolar node elongate (length >2.70x width), weakly convex posterad, nearly vertical near center, and concave anterad, anterior one-third narrowing to subangulate tip; posterior surface with moderately coarse transverse rugae, interrugae weakly to moderately granulate-punctate, weakly shining. Dorsum of postpetiole convex in profile, anterior margin curving gradually to meet helcium at a smooth, continuous angle; in dorsal view, nearly triangular, widest near posterior margin, narrowing to nearly straight anterior margin; dorsum weakly coriarious, shining to smooth and strongly shining. First gastral tergum weakly coriarious, shining to smooth and strongly shining.

Short to long, flexuous, yellowish hairs abundant on head; medium to long hairs abundant on mesosoma, petiolar node, postpetiole, and gastral terga; longest hairs on head and mesosoma >MOD. Scape with abundant medium to long suberect hairs; abundant decumbent hairs on funicular segments. Legs with moderately abundant, long, suberect setae. Head and mesosoma dark reddish-brown to dark brown; petiolar node, postpetiole, legs, gaster slightly lighter orangish-brown (**Figure 66**).

Queen. Unknown.

Male. Unknown.

Additional material examined. ECUADOR: ***Pichincha***: Mindo, 1525 m, Nov 6, 2004 & Aug 27, 2005 (ALWC; RAJC); ***Santo Domingo***: Reserva Otonga, Alluriquin-Las Damas Rd, 1209 m, Jun 5–10, 2014 (CISEC; RAJC; RIBNS) (**Figure 65B**).

Etymology. The specific epithet, *striatinodis (*from Latin—*striãre* = striate*,* and *nõdus* = node*)* refers to the transverse striae on the dorsolateral surfaces of the petiolar node.

Discussion. *Pogonomyrmex striatinodis* and *P. sylvestris* are the only congeners known to inhabit mid-elevation mesic forests. *Pogonomyrmex striatinodis* is diagnosed by: (1) lack of hairs between ommatidia, (2) seven mandibular teeth, and (3) in profile, anterior margin of postpetiole meeting helcium at a smooth, continuous angle; *P. stefani* has: (1) several hairs between ommatidia, (2) six mandibular teeth, and (3) in profile, the anterior margin of the postpetiole is truncate and does not meet the helcium at a smooth, continuous angle. *Pogonomyrmex striatinodis* is separated from *P. stefani* by its sometimes weakly striate procoxae and absence of hairs between ommatidia; in *P. stefani*, the procoxae have prominent transverse striae and hairs are present between the ommatidia.

Pogonomyrmex naegelii might occur in open, drier habitats proximate to areas occupied *P. striatinodis*. *Pogonomyrmex striatinodis* is distinguished from *P. naegelii* by: (1) an elongate, triangular postpetiole, (2) in profile, the petiolar node is flattened with a crest or tooth on the anterior margin that is elevated above the posterior surface, and (3) head and mesosoma with numerous, long, flexuous hairs (longest hairs >MOD). In *P. naegelii*: (1) the postpetiole is nearly globular with length and width similar, (2) in profile, the petiolar node is convex and lacks a crest or tooth on the anterior margin, and (3) head and mesosoma have numerous short, relatively stiff hairs (longest hairs shorter than MOD). *Pogonomyrmex striatinodis* might also occur in areas proximate to *P. theresiae*; *P. striatinodis* lacks a well-developed psammophore and has long superior and inferior propodeal spines, whereas *P. theresiae* has a well-developed psammophore and lacks superior and inferior propodeal spines.

Biology. See discussion under *P. stefani*.

Pogonomyrmex sylvestris

(Figure 67)

Pogonomyrmex sylvestris Lattke, 1991: 305, figs. 1, 2 (worker). Holotype worker [MCZ] (not examined), VENEZUELA, Lara: 10 km SSE Barquisimeto (9º58'N 69º17'W), Parque Nacional Terepaima, 1100 m (J. Lattke leg., 13 September 1983).

Worker. Diangosis. Within the *P. sylvestris*-group, the combination of: (1) six mandibular teeth, (2) eyes with hairs between ommatidia, (3) in profile, anterior margin of postpetiole not meeting helcium at a smooth, continuous angle, (4) in profile, procoxae finely imbricate, (5) femur and tibiae strongly coriarious, dull, and (6) medial clypeal region between antennal insertions with 4–8 coarse, sometimes wavy, longitudinal rugae, interrugae more or less shining uniquely characterize this species (**Figure 67**).

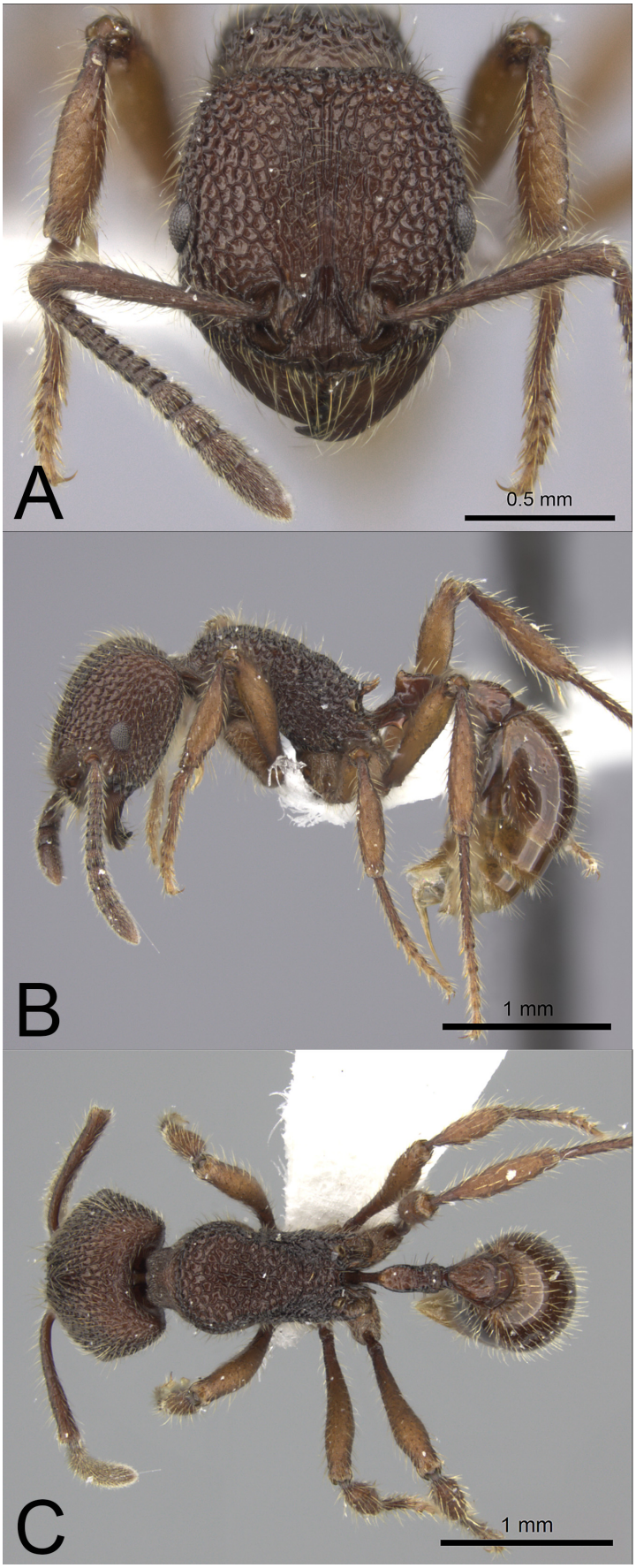

FIGURE 67. Photograph of *Pogonomyrmex sylvestris* Lattke worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (LACMENT273795). Photographs by Will Ericson from www.AntWeb.org**.**

Measurements—(*n* = 4). HL 1.24–1.32; HW 1.16–1.20; MOD 0.20–0.21; OMD 0.30–0.32; SL 0.88–1.03; PNW 0.81–0.84; HFL 1.13–1.34; ML 1.51–1.61; PW 0.21–0.21; PPW 0.42–0.46. Indices: SI 73.95–86.44; CI 90.91–94.40; OI 16.67–17.80; HFI 94.17–113.56. See also Lattke (1991).

Redescription. Head elongate (CI = 90.91–93.55), widest just posterior to eye; posterior margin weakly concave. Cephalic dorsum rugoreticulate except for several irregular, medial, longitudinal rugae that become rugoreticulate near posterior margin. Cephalic interrugae smooth, shining; vertex rugoreticulate. Anterior margin of clypeus weakly convex with small medial tooth, dorsal surface between antennal insertions with 4–8 coarse, sometimes wavy, longitudinal rugae, interrugae more or less shining. Mandible with six teeth; mandibular dorsum coarsely rugose. Up to several moderately long, curved, bristle-like, yellowish hairs project from anterior margin of clypeus. Eyes small, MOD = 0.15–0.16x HL. In profile, eyes situated anterior to middle of head, OMD = 1.50–1.55x MOD; several short, delicate hairs project from between ommatidia. Antennal scapes moderately long (SI = 82.76–83.74), failing to reach vertex by less than length of basal funicular segment; entire scape with scattered, weak, longitudinal striae, strongly granulate-punctate, dull. Basal flange of scape well-developed with carinate margin. Psammophore poorly-developed, consisting of numerous short hairs (length similar to those on cephalic dorsum) scattered across ventral side of head.

Mesosomal profile strongly convex; all mesosomal surfaces rugoreticulate to vermiculate. Superior propodeal spines long, acuminate, bases not connected by well-defined keel, spines slightly shorter than distance between their bases. Inferior propodeal spines well-developed, acuminate, length similar to that of superior spines but with wider base. Interrugae on mesosoma moderately granulate, weakly shining to smooth, shining. Propodeal spiracles circular facing posterad. In profile, procoxae finely imbricate, dull. Legs strongly granulate-punctate, dull.

Peduncle of petiole about 0.6x as long as petiolar node, anteroventral margin with acuminate spine. In profile, petiolar node asymmetrical with anterior surface about 0.5x as long as posterior surface, apex forming a crest or tooth that is elevated above posterior surface; posterior surface flattened to weakly convex; anterior and lateral surfaces mostly smooth and shining; lateral surface nearly vertical, meeting posterior surface at or near a right angle. In dorsal view, petiolar node elongate (length >2.3x width), sides subparallel, weakly constricted near posterior margin, anterior one-third narrowing to subangulate tip; dorsum coarsely rugoreticulate, interrugae smooth and shining. Dorsum of postpetiole convex in profile, anterior margin with subangulate tip that overhangs connection to helcium; in dorsal view, nearly triangular, widest near posterior margin, narrowing to bluntly rounded anterior margin; lateral margins wider ventrally; dorsum moderately to strongly coriarious to moderately granulate, weakly shining, with several weak longitudinal rugae near anterior margin. First gastral tergum weakly coriarious, weakly shining to smooth and shining.

Short to long, flexuous, yellowish to golden hairs abundant on head; medium to long hairs abundant on mesosoma, petiolar node, postpetiole, gastral terga; longest hairs on head and mesosoma >MOD. Scape with abundant moderately long, suberect hairs; abundant decumbent hairs on funicular segments. Legs with moderately abundant, long, suberect setae. Head and mesosoma dark brown; petiolar node, postpetiole, gaster, legs slightly lighter brown to tan (**Figure 67**).

Queen. Unknown.

Male. Unknown.

Additional material examined. VENEZUELA: *Portuguesa*: 9 km S Biscucuy, 1000 m, Aug 18, 1983 [MIZA] (paratype worker, not examined). ***Trujillo***: Quebrada de los Amarillos, 14.5 km SSE Boconó, 1300 m, Apr 8, 1993 (LACM; MCZ); 14.4 km SE Boconó, Jul 1993 (not examined, J. Lattke, pers. comm.) (**Figure 65C**).

Etymology. The specific epithet, *sylvestris* (*sylva*—Latin for forest), was derived from the type series being collected in cloud forest (premontane rain) habitats in Venezuela.

Discussion. *Pogonomyrmex sylvestris* might co-occur with *P. striatinodis* and *P. naegelii*. Both of the former species occur in mesic forest habitats, while *P. naegelii* occurs in open, drier habitats. *Pogonomyrmex sylvestris* is distinguished from *P. striatinodis* by: (1) hairs between ommatidia, (2) clypeus lacks a medial carina, and (3) in profile, the anterior margin of postpetiole does not meet the helcium at smooth continuous angle. In *P. striatinodis*: (1) lacks hairs between the ommatidia, (2) the clypeus has a prominent medial carina, and (3) in profile, the anterior margin of postpetiole meets the helcium at smooth continuous angle. *Pogonomyrmex sylvestris* is distinguished from *P. naegelii* by: (1) hairs between ommatidia, (2) an elongate, triangular postpetiole, and (3) in profile, the petiolar node is flattened to weakly convex with a crest on the anterior margin that is elevated above the posterior surface. *Pogonomyrmex naegelii*: (1) lacks hairs between the ommatidia, (2) the postpetiole is nearly

globular with the width and length similar, and (3) in profile, the petiolar node is convex and the anterior margin lacks a crest.

Biology. See discussion under *P. stefani*.

Unplaced species

Pogonomyrmex theresiae

(Figure 68)

Pogonomyrmex theresiae Forel, 1899b: 303 (worker). Holotype worker [ZSM, CASENT0281108], ECUADOR, Guayas: Estero Salado near Guayaquil; Forel, 1899c: 274 (worker redescribed as new).

Worker. Diagnosis. The combination of: (1) first gastral tergum lacking striae, (2) superior propodeal spines consisting of small tubercles or denticles, and (3) transverse rugae on dorsum of postpetiole uniquely characterize this species (**Figure 68**).

Measurements—holotype. HL 1.45; HW 1.46; MOD 0.30; OMD 0.39; SL (scapes missing); PNW 1.01; HFL 1.42; ML 1.67; PW 0.36; PPW 0.52. Indices: SI (scapes missing); CI 100.69; OI 20.55; HFI 97.26.

Redescription. Head quadrate (CI = 100.69), widest just posterior to eye; posterior margin weakly convex in full-face view. Longitudinal rugae on cephalic dorsum prominent, weakly wavy; in full-face view, medial rugae diverging weakly toward posterior corners of head. In profile, cephalic rugae converging approximately midway between posterior margin of eye and vertex. Cephalic interrugae moderately granulate, weakly shining; vertex weakly to moderately rugose, interrugae smooth, strongly shining. Anterior margin of clypeus concave; dorsal surface with numerous subparallel, longitudinal rugae. Mandibles with six teeth; mandibular dorsum coarsely rugose. Numerous moderately long, curved, bristle-like, cream to light yellowish hairs project from basolateral margin of mandibles. MOD = 0.21x HL. In profile, eyes situated near middle of head, OMD = 1.30x MOD. Scapes missing; scapes not reaching vertex as per Forel (1899c). Psammophore well-developed.

Mesosomal profile moderately convex; all mesosomal surfaces with prominent rugae. In profile and dorsal views, humeral shoulders of pronotum enlarged, angulate. Dorsum of promesonotum and sides of pronotum rugoreticulate to vermiculate. Mesopleura with irregular rugae angling posterodorsally. Dorsum of propodeum with irregular rugae to rugoreticulate. Superior propodeal spines consist of small denticles or tubercles; inferior propodeal spines weakly developed, consisting of a small, broadly rounded, triangular process. Propodeal spiracles narrowly ovate facing posterad. Interrugae on mesosoma moderately granulate, dull to weakly shining. Legs weakly coriarious, weakly shining to smooth and shining.

Peduncle of petiole about as long as petiolar node, anteroventral margin with bluntly rounded triangular process. In profile, posterior surface of petiolar node weakly convex; petiolar node asymmetrical with anterior surface slightly shorter than posterior surface, apex weakly rounded to subangulate. In dorsal view, petiolar node longer than wide, narrowest at posterior margin, gradually widening to spatulate anterior margin; posterior surface with moderately strong, wavy to irregular transverse, sometimes discontinuous rugae. Dorsum of postpetiole convex in profile; in dorsal view, widest near posterior margin, narrowing to anterior margin; maximal width about equal to length; dorsum and sides with wavy transverse rugae that are finer, denser, more regular than those on posterior surface of petiolar node. Interrugae on posterior surface of petiolar node and dorsum of postpetiole weakly granulate, weakly shining to smooth and shining. Base of first gastral tergum weakly coriarious, shining, remainder smooth, strongly shining.

Short, erect, whitish pilosity sparse on head. Scapes missing; as per Forel (1899c) scapes with a few scattered oblique, short, stiff, yellowish hairs. Mesosoma, petiolar node, postpetiole, and gastral terga mostly lacking hairs except for several short, suberect hairs on legs, mesopleura, posterior declivity of propodeum, and ventral surface of postpetiole. Head ferruginous orange; mesosoma slightly darker ferruginous orange; petiolar node, postpetiole, gaster, and legs blackish-orange (**Figure 68**).

Queen. Unknown.

Male. Unknown.

Additional material examined. None.

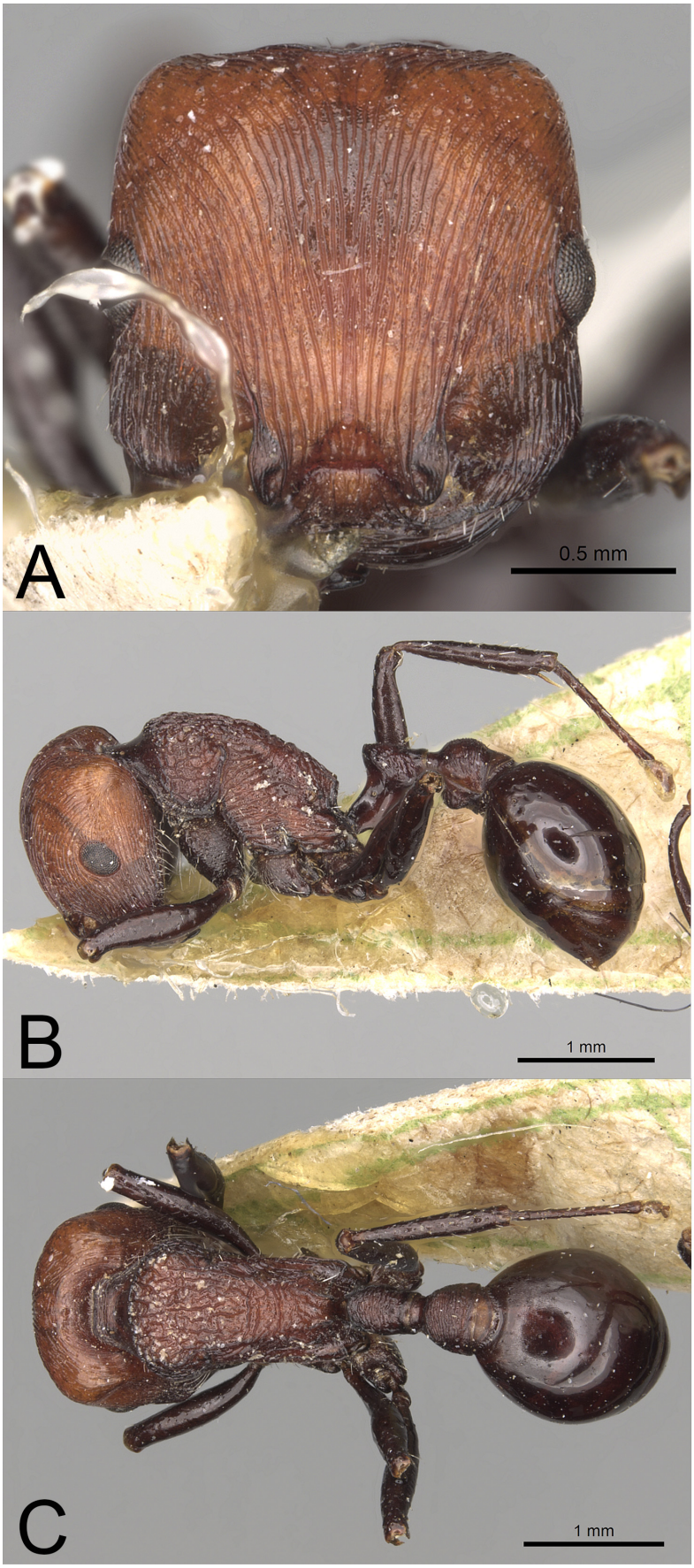

FIGURE 68. Photograph of *Pogonomyrmex theresiae* Forel holotype worker: (**A**) frontal view of head, (**B**) lateral view of body, and (**C**) dorsal view of body (CASENT0281108). Photographs by Shannon Hartman from www.AntWeb.org**.**

Etymology. Forel dedicated this interesting species to her Royal Highness Princess Therese of Bavaria, who collected this ant.

Discussion. *Pogonomyrmex striatinodis* is the only congener known to occur in Ecuador, but it is only known from mesic forests, lacks a psammophore, and has long superior and inferior propodeal spines. Alternatively, *P. theresiae* has a well-developed psammophore and lacks superior and inferior propodeal spines. *Pogonomyrmex naegelii* might also occur in Ecuador; *P. theresiae* is easily distinguished by transverse rugae on the posterior surface of the petiolar node and dorsum of the postpetiole (rugoreticulate in *P. naegelii*) and absence of superior propodeal spines (present in *P. naegelii*).

Forel described *P. theresiae* twice in the same year. The original description (Forel, 1899b) indicated that the type locality was Colombia, while the redescription gave the type locality as Estero Salado, near Guayaquil, Ecuador. The label on the holotype gives the locale as Estero Salado, verifying that the correct type locality was given in the redescription (Forel, 1899c).

Biology. Nothing is known about the biology of *P. theresiae*, which appears to be known from only one worker that was collected over 100 years ago at Estero Salado near Guayaquil, Ecuador, in the Western Ecuador Moist Forests ecoregion as defined by Olson *et al*. (2001) (**Figure 69**). Guayaquil is currently the largest and most populous city in Ecuador, such that the type locality is probably urbanized or destroyed. However, it might be productive to search for *P. theresiae* along roadsides in agricultural areas surrounding Guayaquil, as many North and South American congeners commonly occur in disturbed habitats. Other areas in which to search for *P. theresiae* would seem to be those that have a tropical savanna climate similar to that of Guayaquil, including western portions of Guayas and Manabí Provinces and the southernmost part of Esmeraldas Province (see also Lattke, 2006).

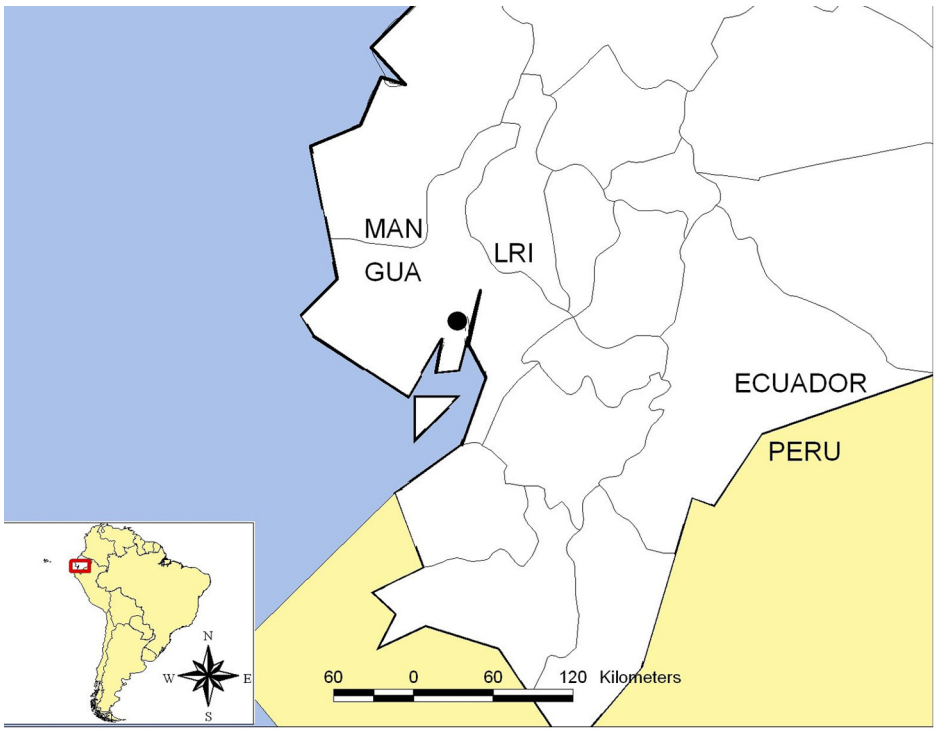

FIGURE 69. Geographic distribution of *Pogonomyrmex theresiae* Forel. The black circle denotes the type locality.

LIFE HISTORY AND PHENOTYPIC DIVERSITY

The South American species of *Pogonomyrmex* treated herein comprise a diverse group of species in terms of worker morphology, variation in queen phenotypes, and behavior.

Worker morphology

Worker polymorphism is relatively rare among ants, having evolved approximately 15–20 times in the more than 300 extant ant genera (Bolton, 2014; Brady, Schultz, Fisher, & Ward, 2006; Oster & Wilson, 1978). Despite the relative rarity of this trait, polymorphism has evolved two times within *Pogonomyrmex*, once in South America (*P. coarctatus*) and once in North America (*P. badius*), and both species produce supermajors (Cole, 1968; Kusnezov, 1951). Head width for *P. badius* ranges from 1.27–3.74 mm, while that for *P. coarctatus* ranges from 1.97–3.99 mm (**Figure 7**)**.** In addition, the size-frequency distribution is bimodal in *P. badius*, with nests containing numerous minors and few majors, with intermediate-sized workers being rare. Alternatively, the distribution is continuous in *P. coarctatus*, with nests containing numerous minors, and abundant medias and majors (Tschinkel, 1998, C. Smith, unpub. data). Majors of the two species also concentrate in different parts of the nest and appear to specialize at different tasks; *P. badius* majors occur deeper in the nest and rarely forage, leading to the suggestion that these individuals are seed-milling specialists (direct data are meager to support this hypothesis), while those of *P. coarctatus* concentrate in upper parts of the nest and appear to be foraging specialists (Tschinkel, 1998, C. Smith, unpub. data). These differences suggest that different evolutionary pressures selected for polymorphism in these two species.

The ecological release hypothesis has been suggested to explain the evolution of polymorphism in *P. badius* and other species of ants (Oster & Wilson, 1978). This hypothesis suggests that polymorphism evolved to expand dietary breadth in species that experience reduced interspecific competition (*P. badius* is the only large harvester ant in the eastern United States). However, this hypothesis was not supported for *P. badius* because workers did not display a significant correlation between worker size and seed or prey size harvested (Ferster & Traniello, 1995; Traniello & Beshers, 1991). Neither does the ecological release hypothesis apply to *P. coarctatus*, which is sympatric with two to four congeners throughout its geographic range (this study). One commonality between *P. badius* and *P. coarctatus* is that both species live in mesic, low-elevation habitats where resources appear to be abundant (pers. obs.; C. Smith, pers. comm.). Moreover, factors selecting for the evolution of polymorphism in these two species remain unknown, but mechanisms that determine caste (at least in *P. badius*) involve an interaction of nutrition, social environment, and genetics (Rheindt, Strehl, & Gadau, 2005; Smith, Anderson, Tillberg, Gadau, & Suarez, 2008).

Variation in queen phenotypes

Species of *Pogonomyrmex* display most of the wide array of queen phenotypes known among ants, including species with alate queens, brachypterous queens, and ergatoid queens. In some species queens are dimorphic, i.e., winged and ergatoid queens or brachypterous and ergatoid queens within the same species (Heinze *et al.*, 1992; Johnson *et al.*, 2007; Peeters, 2012; Peeters *et al.*, 2012). The most striking pattern related to queen phenotypes in *Pogonomyrmex* is the large number of South American species that have only ergatoid queens (five species in three species-groups; *bispinosus* [*bispinosus*-group], *mayri* [*mayri*-group], and *cunicularius*, *pencosensis*, and *serpens* [*cunicularius*-group]), whereas no species with only ergatoid queens occur in North America. The most worker-like ergatoid queen species are those in the *P. cunicularius*-group, in which queens and workers are morphologically similar (the mesosomal segments are fused as in workers), except that queens are slightly larger, possess ocelli and a spermatheca (lacking in workers), and contain more ovarioles than workers (Johnson, 2010). The ergatoid queens of *P. mayri* appear to lack ocelli. The sister genus *Hylomyrma* (Ward *et al.*, 2015) also has several species with ergatoid queens (Kempf, 1973). Ergatoid queens are absent in the *P. angustus*-group, which consists of three species that will be placed in a new genus (Ward *et al.*, 2015). Poor dispersal ability likely precluded migration to North America by species that possess only ergatoid queens.

Queen dimorphic species occur in both North and South America. Little is known about mechanisms that cause queen dimorphism, but a mitochondrial phylogeny and a comparison of microsatellite allele frequencies in the North American species *P. pima* inferred that the two queen phenotypes (alate and ergatoid) belong to the same gene pool (Johnson *et al.*, 2007). Ergatoid queens of both *P. pima* and *P. imberbiculus* (another queen dimorphic species) possess all the reproductive structures of alate queens (except for wings), and both phenotypes have a similar reproductive capacity; this same pattern is probable for *P. naegelii*, but dissections have not be done.

In another type of queen dimorphism, the South American species *P. laticeps* produces ergatoid and brachypterous queens; so far, only one queen phenotype has been found in a colony (Peeters *et al.*, 2012). Current data also suggest that ergatoid and brachypterous queens have discrete geographic ranges—ergatoid queens are

only known from southern portions of the range, whereas brachypterous queens are only known from northern portions of the range. In all queen dimorphic species, ergatoid queens are intermediate in size between that of worker and alate/ brachypterous queens (Heinze *et al.*, 1992; Johnson *et al.*, 2007; Peeters *et al.*, 2012).

Queens of *Pogonomyrmex* are also known for their dramatic variation in body size. Queen dry mass varies by approximately 20-fold across species in both North and South America, from approximately 1.5 mg dry mass (*P. pima* and *P. imberbiculus* in North America, *P. naegelii* in South America) to those that approach 30 mg dry mass (*P. wheeleri* in North America, *P. coarctatus* in South America) (unpub. data).

Mating frequency

In social insects, obligate multiple mating (effective queen mating frequency ≥2) is only known to occur in vespine wasps (Foster & Ratnieks, 2001), the leaf-cutter ant genera *Acromyrmex* and *Atta* (Villesen, Murakami, Schultz, & Boomsma, 2002), army ants (Denny, Franks, Powell, & Edwards, 2004; Kronauer, Johnson, & Boomsma, 2007), honeybees (Moritz *et al.*, 1995; Palmer & Oldroyd, 2000), the ant *Cataglyphis cursor* (Pearcy, Aron, Doums, & Keller, 2004), and harvester ants in the genus *Pogonomyrmex* (Gadau, Strehl, Oettler, & Hölldobler, 2003; Overson, 2011; Pol *et al.*, 2008; Rheindt, Gadau, Strehl, & Hölldobler, 2004; Wiernasz, Perroni, & Cole, 2004). Multiple mating is widespread in species of *Pogonomyrmex* as it has been documented in both North America (*P. barbatus*, *P. rugosus*, *P. badius*, *P. californicus*, *P. occidentalis*) and South America (*P. coarctatus*, *P. inermis*, *P. mendozanus*), suggesting that this trait evolved early in the history of the genus (Pol *et al.*, 2008). In addition, both alate and ergatoid queens of *P. pima* mate with only one male, such that *Pogonomyrmex* is the only ant genus known to contain species with both single- and multiple-mating queens (Holbrook, Strehl, Johnson, & Gadau, 2007). Consequently, *Pogonomyrmex* is an ideal genus to examine the evolution of mating frequency.

Colony founding

North American species of *Pogonomyrmex* exhibit a range of colony founding strategies (Johnson, 2002, 2004, 2006, 2010), and available data suggest that those in South America display an equally wide range of strategies (Johnson, 2010; Kusnezov, 1951). There are several species with ergatoid or brachypterous queens that are known to employ independent colony founding (e.g., *P. cunicularius, P. pencosensis, P. mendozanus*, and both ergatoid and brachypterous queens of *P. laticeps*). This is unusual because ergatoid and brachypterous queen species typically reproduce via dependent colony founding, i.e., with a group of nesmate workers (Peeters, 2012; Peeters & Molet, 2009). Dependent colony founding is associated with producing few queens, short-distance dispersal on foot, and relatively high survival rates. Alternatively, independent colony founding is associated with producing many queens, long-distance dispersal via wings, and very low survival rates.

The few data available indicate that these four ergatoid and brachypterous queen species are exceptions to these two reproductive syndromes. Haplometrotic foundresses of the ergatoid queen species *P. cunicularius* and *P. pencosensis* have been excavated (n = 1 for each species) (Johnson, 2010), and colonies typically produce >100 queens (pers. obs.). Haplometrotic foundresses have also been excavated for ergatoid (n = 1) and brachypterous queens (n = 1) of *P. laticeps*, and colonies of both queen phenotypes produce >50 queens (Peeters *et al.*, 2012). Brachypterous queens also have been observed to employ independent colony founding in *P. mendozanus*, in which colonies can also produce approximately 100 queens (pers. obs.; **Figure 46**). More data are needed to better document nest founding strategies in these and other ergatoid queen species of *Pogonomyrmex*.

These species clearly provide an opportunity to examine previously unknown tradeoffs in nest founding syndromes. All of these species probably employ queen foraging, which allows queens to adjust brood production to environmental conditions. When food is high in abundance and/or predictable in occurrence, foraging queens can produce more minim workers than fully claustral queens that have fixed energy reserves (Johnson, 2006). A granivorous diet has been proposed as one explanation—many arid and semi-arid habitats, such as those occupied by species of *Pogonomyrmex*, experience relatively predictable pulses of seed production that result from seasonal rainfall. These seeds can remain dormant in the seed bank for several or more years (Lopez, 2003; Reichman, 1984; Tevis, 1958), and have the additional advantage that they can be stored for extended periods by the ants. However, seed use may not be the only explanation because these four species have different diets and two of them, *P. pencosensis* and probably *P. cunicularius*, harvest more insects than seeds (Aranda-Rickert & Fracchia, 2011, 2012).

Future studies

Studies of North American *Pogonomyrmex* have greatly increased our understanding numerous areas of ant biology (Anderson *et al*., 2006; Cole & Wiernasz, 1999; Gordon, 1995; Hölldobler, 1971, 1974, 1976a, 1976b; Johnson, 2000, 2001; Kwapich & Tschinkel, 2013; Wiernasz, Sater, Abell, & Cole, 2001). In contrast, their South American congeners have been studied much less, yet these species appear to be even more diverse in their ecologies and natural histories. *Pogonomyrmex* evolved in northern South America (C.S. Moreau & R.A. Johnson, unpub. data), and phylogenetically basal species inhabit mesic forests and appear to have a very different biology from that typical of congeners that inhabit open, exposed, semi-arid to arid areas. South American species also provide systems to study phenotype evolution given that ergatoid, brachypterous, and dimorphic queens have evolved in several species-groups that also have species with alate queens.

Acknowledgments

The following individuals (museums) kindly provided specimens used in this study: Brian Fisher (CAS), Fabianna Cuezzo (FML), Brian Brown (LACM), Arturo Roig-Alsina (MACN), Stefan Cover (MCZ), Alberto Abrahamovich (MLPA), Bernard Landry (MHNG), Beto Brandão (MZUSP), Daniel Burkhardt (NHMB), Manuela Vizek (NMW), Phil Ward (UCDC), Ted Schultz (USNM), Stefan Schmidt (ZSM), and Thibaut Delsinne (RBINS). This project was funded partly by the Ernst Mayr Travel Grant in Animal Systematics from the Museum of Comparative Zoology at Harvard University. I thank Gary Alpert for his hospitality during visits to Harvard University, and Carolina Paris, Gabriella Pirk, Rodrigo Pol, Chris Smith, Juergen Gadau, and Andy Suarez for help with logistics, permits, and/or company in the field, and Rodrigo Pol and Chris Smith for providing unpublished data. I also thank John Lattke and Stefan Cover for testing and providing comments on keys, Brian Fisher and AntWeb for high-resolution photographs, and Carolina Paris and John Lattke for translating the abstract and keys into Spanish.

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

Aranda-Rickert, A. & Fracchia, S. (2011) *Pogonomyrmex cunicularius* as the keystone disperser of elaiosome-bearing *Jatropha excisa* seeds in semi-arid Argentina. *Entomologia Experimentalis et Applicata,* 139, 91–102. http://dx.doi.org.ezproxy1.lib.asu.edu/10.1111/j.1570-7458.2011.01111.x

Aranda-Rickert, A. & Fracchia, S. (2012) The biology of *Pogonomyrmex cunicularius pencosensis* (Hymenoptera: Formicidae) in relationship to its behaviour as disperser of elaiosome-bearing seeds in semiarid northwest Argentina. *Revista de la Sociedad Entomológica Argentina,* 71, 11–27.

Baldini, L. & Scattolin, M.C. (1993) El sitio Masao. Nota acerca de su identificación. *Revista del Museo de Historia Natural de San Rafael (Mendoza),* 12, 47–62.

Belchior, C., Del-Claro, K. & Oliveira, P.S. (2012) Seasonal patterns in the foraging ecology of the harvester ant *Pogonomyrmex naegelii* (Formicidae, Myrmicinae) in a Neotropical savanna: daily rhythms, shifts in granivory and carnivory, and home range. *Arthropod-Plant Interactions,* 6, 571–582. http://dx.doi.org/10.1007/s11829-012-9208-1

Bolton, B. (1995) *A New General Catalogue of the Ants of the World*. Harvard University Press, Cambridge, Massachusetts, 504 pp.

Bolton, B. (2014) An online catalog of the ants of the world. Available from: http://antcat.org (accessed 15 July 2015)

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

Brown, W.L.J. (1973) A comparison of the Hylean and Congo-West African rain forest ant faunas. *In:* Meggers, B.J., Ayensu, E.S. & Duckworth, W.D. (Eds.), *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*. Smithsonian Institute Press, Washington, D.C., pp. 161–185.

Bruch, C. (1916) Hormigas de la provincia de San Luis. *Revista del Museo de la Plata,* 23, 291–357.

Bruch, C. (1917) Costumbres y nidos de hormigas. *Anales de la Sociedad Científica Argentina,* 83, 302–316.

Claver, S. & Fowler, H.G. (1993) The ant fauna (Hymenoptera, Formicidae) of the Ñancuñan Biosphere Reserve. *Naturalia,*

Sao Paulo, 18, 189–193.
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
Cuezzo, F. & Claver, S. (2009) Two new species of the ant genus *Pogonomyrmex* (Hymenoptera: Formicidae) from Argentina. *Revista de la Sociedad Entomológica Argentina,* 68, 97–106.
Dalle Torre, C.G. (1893) *Catalogus Hymenopterorum, hucusque descriptorum systematicus et synonymicus. Vol. 7. Formicidae (Heterogyna)*. W. Engelmann, Leipzig, 289 pp.
Denny, A.J., Franks, N.R., Powell, S. & Edwards, K.J. (2004) Exceptionally high levels of multiple mating in an army ant. *Naturwissenschaften,* 91, 396–399. http://dx.doi.org/10.1007/s00114-004-0546-4
Donisthorpe, H. (1933) On a small collection of ants made by Dr. F.W. Edwards in Argentina. *Annals and Magazine of Natural History,* 12, 532–538.
Emery, C. (1878) Liste des fourmis de la collection de feu Camille van Volxem, avec la description d'une espèce nouvelle. *Annales de la Société Entomologique de Belgique,* 21, viii–x.
Emery, C. (1906) Studi sulle formiche della fauna Neotropica. *Bollettino della Società Entomologica Italiana,* 37, 107–194.
Fernández, F.C. & Palacio, E.E. (1998, "1997") Clave para las *Pogonomyrmex* (Hymenoptera: Formicidae) del Norte de Suramérica, con la descripción de una nueva especie. *Revista Biologica Tropical,* 45, 1649–1661.
Ferster, B. & Traniello, J.F.A. (1995) Polymorphism and foraging behavior in *Pogonomyrmex badius* (Hymenoptera: Formicidae): worker size, foraging distance, and load size associations. *Environmental Entomology,* 24, 673–678.
Forel, A. (1886) Espèces nouvelles de fourmis Américaines. *Annales de la Société Entomologique de Belgique,* 30, 37–49.
Forel, A. (1899a) Insecta. Hymenoptera (Formicidae). *Biologia Centrali-Americana,* 3, 1–169.
Forel, A. (1899b) Trois notices myrmécologiques. *Annales de la Société Entomologique de Belgique,* 43, 303–310.
Forel, A. (1899c) Von Ihrer Königl. Hoheit der Prinzessin Therese von Bayern auf einer Reise in Südamerika gesammelte Insecten. 1. Hymenoptera. a. Fourmis. *Berliner Entomologische Zeitschrift,* 44, 273–276.
Forel, A. (1912) Formicides Néotropiques. Part IV. 3me sous-famille Myrmicinae Lep (suite). *Mémoires de la Société Entomologique de Belgique,* 20, 1–32.
Forel, A. (1913) Fourmis d'Argentine, du Brésil, du Guatémala and de Cuba. Recues de M.M. Bruch, Prof. v. Ihering, Mlle Baez, M. Peper et M. Rovereto. *Bulletin de la Société Vaudoise des Sciences Naturelles,* 49, 203–250.
Forel, A. (1914) Formicides d'Afrique et d'Amérique nouveaux ou peu connus. *Bulletin de la Société Vaudoise des Sciences Naturelles,* 50, 211–288.
Foster, K.R. & Ratnieks, F.L.W. (2001) Paternity, reproduction and conflict in vespine wasps: a model system for testing kin selection predictions. *Behavioral Ecology and Sociobiology,* 50, 1–8. http://dx.doi.org/10.1007/s002650100336
Fowler, H.G. (1981) Nuevos registros de hormigas para el Paraguay (Hymenoptera Formicidae). *Neotropica,* 26, 183–186.
Gadau, J., Strehl, C.P., Oettler, J. & Hölldobler, B. (2003) Determinants of intracolonial relatedness in *Pogonomyrmex rugosus* (Hymenoptera: Formicidae): mating frequency and brood raids. *Molecular Ecology,* 12, 1931–1938. http://dx.doi.org/10.1046/j.1365-294X.2003.01853.x
Gallardo, A. (1931) Deux nouvelles espèces de *Pogonomyrmex* de la République Argentina (Hymenoptères Formicidaes). *Revista del Museo de la Plata,* 33, 185–188.
Gallardo, A. (1932) Las hormigas de la República Argentina. Subfamilia Mirmicinas, segunda sección Eumyrmicinae, tribu Myrmicini (F. Smith), género *Pogonomyrmex* Mayr. *Anales del Museo Nacional de Historia Natural "Bernardino Rivadavia",* 37, 89–170.
Gordon, D.M. (1995) The development of an ant colony's foraging range. *Animal Behaviour,* 49, 649–659. http://dx.doi.org/10.1016/0003-3472(95)80198-7
Guerrero, R.J. & Sarmiento, C.E. (2010) Distribución altidudinal de hormigas (Hymenoptera, Formicidae) en la vertiente noroccidental de la Sierra Nevada de Santa Marta (Colombia). *Acta Zoológica Mexicana,* 26, 279–302.
Heinze, J., Hölldobler, B. & Cover, S.P. (1992) Queen polymorphism in the North American harvester ant, *Ephebomyrmex imberbiculus*. *Insectes Sociaux,* 39, 267–273. http://dx.doi.org/10.1007/BF01323947
Holbrook, C.T., Strehl, C., Johnson, R.A. & Gadau, J. (2007) Single mating in the seed-harvester ant *Pogonomyrmex* (*Ephebomyrmex*) *pima*: implications for the evolution of polyandry. *Behavioral Ecology and Sociobiology,* 62, 229–236. http://dx.doi.org/10.1007/s00040-007-0916-y
Hölldobler, B. (1971) Homing in the harvester ant *Pogonomyrmex badius*. *Science,* 171, 1149–1151.
Hölldobler, B. (1974) Home range orientation and territoriality in harvesting ants. *Proceedings of the National Academy of Science,* 71, 3274–3277.
Hölldobler, B. (1976a) The behavioral ecology of mating in harvester ants (Hymenoptera: Formicidae: *Pogonomyrmex*). *Behavioral Ecology and Sociobiology,* 1, 405–423. http://dx.doi.org/10.1007/BF00299401
Hölldobler, B. (1976b) Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*.

Behavioral Ecology and Sociobiology, 1, 3–44.
Jansen, G. & Savolainen, R. (2010) Molecular phylogeny of the ant tribe Myrmicini (Hymenoptera: Formicidae). *Zoological Journal of the Linnean Society,* 160, 482–495.
http://dx.doi.org/10.1111/j.1096-3642.2009.00604.x
Johnson, R.A. (2000) Seed-harvester ants (Hymenoptera: Formicidae) of North America: an overview of ecology and biogeography. *Sociobiology,* 36, 89–122.
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. (2004) Colony founding by pleometrosis in the semi-claustral seed-harvester ant *Pogonomyrmex californicus* (Hymenoptera: Formicidae). *Animal Behaviour,* 68, 1189–1200.
http://dx.doi:10.1016/j.anbehav.2003.11.021
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. (2010) Independent colony founding by ergatoid queens in the ant genus *Pogonomyrmex*: queen foraging provides an alternative to dependent colony founding. *Insectes Sociaux,* 57, 169–176.
http://dx.doi.org/10.1007/s00040-010-0065-6
Johnson, R.A. & Cover, S.P. (2015) A taxonomic revision of the seed-harvester ant genus *Pogonomyrmex* (Hymenoptera: Formicidae) on Hispaniola. *Zootaxa,* 3972, 231–249.
Johnson, R.A., Holbrook, C.T., Strehl, C. & Gadau, J. (2007) Population and colony structure and morphometrics in the queen dimorphic harvester ant, *Pogonomyrmex pima*. *Insectes Sociaux,* 54, 77–86.
http://dx.doi.org/10.1007/s00040-007-0916-y
Kempf, W.W. (1960) Miscellaneous studies on Neotropical ants (Hym., Formicidae). *Studia Entomologica,* 3, 417–466.
Kempf, W.W. (1972) Catálogo abreviado das formigas da Região Neotropical (Hym. Formicidae). *Studia Entomologica,* 15, 3–344.
Kempf, W.W. (1973) A revision of the Neotropical myrmicine ant genus *Hylomyrma* Forel. (Hymenoptera, Formicidae). *Studia Entomologica,* 16, 225–260.
Kronauer, D.J.C., Johnson, R.A. & Boomsma, J.J. (2007) The evolution of multiple mating in army ants. *Evolution,* 61, 413–422.
http://dx.doi.org/10.1111/j.1558-5646.2007.00040.x
Kugler, C. (1979, "1978") Description of the ergatoid queen of *Pogonomyrmex mayri* with notes on the worker and male (Hym., Formicidae). *Psyche,* 85, 169–182.
Kugler, C. (1984) Ecology of the ant *Pogonomyrmex mayri*: foraging and competition. *Biotropica,* 16, 227–234.
http://dx.doi.org/10.2307/2388056
Kugler, C. & Hincapie, M.C. (1983) Ecology of the ant *Pogonomyrmex mayri*: distribution, abundance, nest structure, and diet. *Biotropica,* 15, 190–198.
http://dx.doi.org/10.2307/2387828
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. (1954) Descripción de *Pogonomyrmex marcusi* Kusnezov. *Folia Universitaria Cochabamba,* 7, 82–86.
Kwapich, C.L. & Tschinkel, W.R. (2013) Demography, demand, death, and the seasonal allocation of labor in the Florida harvester ant (*Pogonomyrmex badius*). *Behavioral Ecology and Sociobiology,* 67, 2011–2027.
http://dx.doi.org/10.1007/s00265-013-1611-9
Latreille, P.A. (1802) *Histoire naturelle générale et particulière des Crustacés et des insectes. Tome 3. Familles naturelles des genres*. F. Dufart, Paris, xii + 467 pp.
Lattke, J.E. (1991, "1990") Una nueva especie de *Pogonomyrmex* Mayr de selva húmeda tropical (Hymenoptera: Formicidae). *Revista de Biologica Tropical*, 38, 305–309.
Lattke, J.E. (2006) A new species of *Pogonomyrmex* (Hymenoptera: Formicidae) from gallery forests of the Orinoco watershed, Venezuela. *Myrmecologische Nachrichten,* 8, 53–57.
Marcus, H. (1953) Estudios mirmecologicos. *Folia Universitaria Cochabamba,* 6, 17–68.
Marcus, H. & Marcus, E.E. (1951) Los nidos y los órganos de estridulación y de equilibrio de *Pogonomyrmex marcusi* y de *Dorymyrmex emmaericaellus* (Kusn). *Folia Universitaria Cochabamba,* 5, 117–143.
Mayr, G. (1868) Formicidae novae americanae collectae a Prof. P. de Strobel. *Annuario della Società dei Naturalisti Modena,* 3, 161–178.

Mayr, G. (1870) Neue Formiciden. *Verhandlungen Zoologisch-Botanische Gesellschaft in Wein,* 20, 939–996.
Mayr, G. (1887) Südamerickanische Formiciden. *Verhandlungen der k. k. Zoologisch-Botanischen Gesellschaft in Wein,* 37, 511–632.
Medel, R.G. & Fuentes, J.E. (1995) Notes on the individual activity, diet, and abundance of the ants *Pogonomyrmex vermiculatus* and *Solenopsis gayi* (Hymenoptera: Formicidae) in a semiarid ecosystem of northern Chile. *Revista Chilena de Entomologia,* 33, 81–84.
Menozzi, C. (1935) Fauna Chilensis. II. (Nach Sammlungen von W. Goetsch). Le formiche del Cile. *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere,* 67, 319–336.
Moritz, R.F.A., Kryger, P., Koeniger, G., Koeniger, N., Estoup, A. & Tingek, S. (1995) High degree of polyandry in *Apis dorsata* queens detected by DNA microsatellite variability. *Behavioral Ecology and Sociobiology,* 37, 357–363.
Nobua-Behrmann, B.E., Lopez de Casenave, J., Milesi, F.A. & Pavan, B. (2013) Forager abundance and its relationship with colony activity level in three species of South American *Pogonomyrmex* harvester ants. *Insectes Sociaux,* 60, 243–249. http://dx.doi.org/10.1007/s00040-013-0288-4
Nobua Behrmann, B.E., Milesi, F.E., Lopez de Casenave, J., Pol, R.G. & Pavan, B. (2010) Tamaño y composición de la colonia de tres especies de hormigas del género *Pogonomyrmex* (Hymenoptera: Formicidae) en la porción central del desierto del Monte, Argentina. *Revista de la Sociedad Entomológica Argentina,* 69, 117–122.
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., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, 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
Oster, G.F. & Wilson, E.O. (1978) *Caste and Ecology in the Social Insects. Vol. 12.* Princeton University Press, Princeton, New Jersey, 352 pp.
Overson, R.P. (2011) Causes and Consequences of Queen-number Variation in the California Harvester Ant *Pogonomyrmex californicus*. Ph.D. thesis, Arizona State University, Tempe, Arizona, 113 pp.
Palmer, K.A. & Oldroyd, B.P. (2000) Evolution of multiple mating in the genus *Apis*. *Apidologie,* 31, 235–248. http://dx.doi.org/10.1051/apido:2000119
Pearcy, M., Aron, S., Doums, C. & Keller, L. (2004) Conditional use of sex and parthenogenesis for worker and queen production in ants. *Science,* 306, 1780–1783. http://dx.doi.org/10.1126/science.1105453
Peeters, C. (1997) Morphologically 'primitive' ants: comparative review of social characters, and the importance of queen-worker dimorphism. *In:* Choe, J.C. & Crespi, B.J. (Eds.), *The Evolution of Social Behavior in Insects and Arachnids*. Cambridge University Press, New York, pp. 372–391.
Peeters, C. (2012) Convergent evolution of wingless reproductives across all subfamilies of ants, and sporadic loss of winged queens (Hymenoptera: Formicidae). *Myrmecological News,* 16, 75–91.
Peeters, C., Johnson, R.A. & Keller, R.A. (2012) Selection against aerial dispersal in ants: two non-flying queen phenotypes in *Pogonomyrmex laticeps*. *PLoS ONE,* 7 (10), e47727. http://dx.doi.org/10.1371/journal.pone.0047727
Peeters, C. & Molet, M. (2009) Colonial reproduction and life histories. *In:* Lach, L., Parr, C. & Abbott, K. (Eds.), *Ant Ecology.* Oxford University Press, Oxford, pp. 161–178.
Pirk, G.I. & Lopez de Casenave, J. (2006) Diet and seed removal rates by the harvester ants *Pogonomyrmex rastratus* and *Pogonomyrmex pronotalis* in the central Monte desert, Argentina. *Insectes Sociaux,* 53, 119–125. http://dx.doi.org/10.1007/s00040-005-0845-6
Pirk, G.I. & Lopez de Casenave, J. (2010) Influence of seed size on feeding preferences and diet composition of three sympatric harvester ants in the Monte Desert, Argentina. *Ecological Research,* 25, 439–445. http://dx.doi.org/10.1007/s11284-009-0673-7
Pirk, G.I. & Lopez de Casenave, J. (2011) Seed preferences of three harvester ants of the genus *Pogonomyrmex* (Hymenoptera: Formicidae) in the Monte Desert: are they reflected in the diet? *Annals of the Entomological Society of America,* 104, 212–220. http://dx.doi.org/10.1603/AN10093
Pirk, G.I., Lopez de Casenave, J. & Marone, L. (2007) Evaluation of three techniques for the study of harvester ant (*Pogonomyrmex* spp.) diet. *Environmental Entomology,* 36, 1092–1099. http://dx.doi.org/10.1603/0046-225X(2007)36[1092:EOTTFT]2.0.CO;2
Pirk, G.I., Lopez de Casenave, J. & Pol, R.G. (2004) Asociación de las hormigas granívoras *Pogonomyrmex pronotalis*, *P. rastratus* y *P. inermis* con caminos en el Monte central. *Ecología Austral,* 14, 65–76.
Pirk, G.I., Lopez de Casenave, J., Pol, R.G., Marone, L. & Milesi, F.A. (2009) Influence of temporal fluctuations in seed abundance on the diet of harvester ants (*Pogonomyrmex* spp.) in the central Monte desert, Argentina. *Austral Ecology,* 34, 908–919.
Pol, R.G. & Lopez de Casenave, J. (2004) Activity patterns of harvester ants *Pogonomyrmex pronotalis* and *Pogonomyrmex rastratus* in the Central Monte Desert, Argentina. *Journal of Insect Behavior,* 17, 647–661. http://dx.doi.org/10.1023/B:JOIR.0000042546.20520.c8
Pol, R.G., Lopez de Casenave, J., Feldhaar, H., Milesi, F.A. & Gadau, J. (2008) Polyandry in two South American harvester ants. *Insectes Sociaux,* 55, 91–97.

http://dx.doi.org/10.1007/s00040-007-0975-0
Pol, R.G., Lopez de Casenave, J. & Milesi, F. (2015) Foraging strategies and foraging plasticity in harvester ants (*Pogonomyrmex* spp., Hymenoptera, Formicidae) of the central Monte desert, Argentina. *Myrmecological News,* 21, 1–12.
Pol, R.G., Lopez de Casenave, J. & Pirk, G.I. (2011) Influence of temporal fluctuations in seed abundance on the foraging behaviour of harvester ants (*Pogonomyrmex* spp.) in the central Monte desert, Argentina. *Austral Ecology,* 36, 320–328.
Rheindt, F.E., Gadau, J., Strehl, C.P. & Hölldobler, B. (2004) Extremely high mating frequency in the Florida harvester ant (*Pogonomyrmex badius*). *Behavioral Ecology and Sociobiology,* 56, 472–481.
http://dx.doi.org/10.1007/s00265-004-0808-3
Rheindt, F.E., Strehl, C.P. & Gadau, J. (2005) A genetic component in the determination of worker polymorphism in the Florida harvester ant *Pogonomyrmex badius*. *Insectes Sociaux,* 52, 163–168.
http://dx.doi.org/10.1007/s00040-004-0787-4
Santschi, F. (1921) Ponerinae, Dorylinae et quelques autres formicides néotropiques. *Bulletin de la Société Vaudoise des Sciences Naturelles,* 54, 81–103.
Santschi, F. (1922) Myrmicines, dolichodérines et autres formicides néotropiques. *Bulletin de la Société Vaudoise des Sciences Naturelles,* 54, 345–378.
Santschi, F. (1925) Fourmis des provinces Argentine de Santa Fe, Catamarca, Santa Cruz, Córdoba et Los Andes. *Comunicaciones del Museo Nacional de Historia Natural "Bernardino Rivadavia",* 2, 149–168.
Santschi, F. (1929) Nouvelles fourmis de la République Argentine et du Brésil. *Anales de la Sociedad Científica Argentina,* 107, 273–316.
Santschi, F. (1931) Contribution à l'étude des fourmis de l'Argentine. *Anales de la Sociedad Científica Argentina,* 112, 273–282.
Santschi, F. (1936) Fourmis nouvelles ou intéressantes de la République Argentine. *Revista de Entomologia,* 6, 402–421.
Smith, C.R., Anderson, K.E., Tillberg, C.V., Gadau, J. & Suarez, A.V. (2008) Caste determination in a polymorphic social insect: nutritional, social, and genetic factors. *American Naturalist,* 172, 497–507.
http://dx.doi.org/10.1086/590961
Snelling, R.R. (1981) Systematics of social Hymenoptera. *In:* Hermann, H.R. (Ed), *Social Insects*. Academic Press, New York, pp. 369–453.
Snelling, R.R. & Hunt, J.H. (1975) The ants of Chile (Hymenoptera: Formicidae). *Revista Chilena de Entomologia,* 9, 63–129.
Spinola, M. (1851) Insectos. Orden 7. Himenopteros. *In:* Gay, C. (Ed.), *Historia Fisica y Politica de Chile*. Maulde & Renon, Paris, pp. 153–569.
Taber, S.W. (1990) Cladistic phylogeny of the North American species complexes of *Pogonomyrmex* (Hymenoptera: Formicidae). *Annals of the Entomological Society of America,* 83, 307–316.
http://dx.doi.org/10.1093/aesa/83.3.307
Taber, S.W. (1998) *The World of the Harvester Ants*. Texas A&M University Press, College Station, Texas, 213 pp.
Torres-Contreras, H. (2001) Biological background of ants found in Chile published in national and foreign scientific journals during the XX century. *Revista Chilena de Historia Natural,* 74, 653–668.
http://dx.doi.org/10.4067/S0716-078X2001000300011
Torres-Contreras, H., Olivares-Donoso, R. & Niemeyer, H.M. (2007) Solitary foraging in the ancestral South American ant, *Pogonomyrmex vermiculatus*. Is it due to constraints in the production or perception of trail pheromones? *Journal of Chemical Ecology,* 33, 435–440.
http://dx.doi.org/10.1007/s10886-006-9240-7
Torres-Contreras, H., Olivares-Donoso, R. & Niemeyer, H.M. (2009) Fasting and chemical signals affect recruitment and foraging efficiency in the harvester ant, *Pogonomyrmex vermiculatus*. *Behaviour,* 146, 923–938.
http://dx.doi.org/10.1163/156853908X396773
Traniello, J.F.A. & Beshers, S.N. (1991) Polymorphism and size-pairing in the harvester ant *Pogonomyrmex badius*: a test of the ecological release hypothesis. *Insectes Sociaux,* 38, 121–127.
http://dx.doi.org/10.1007/BF01240962
Tschinkel, W.R. (1998) Sociometry and sociogenesis of colonies of the harvester ant, *Pogonomyrmex badius*: worker characteristics in relation to colony size and season. *Insectes Sociaux,* 45, 385–410.
http://dx.doi.org/10.1007/s000400050097
Villesen, P., Murakami, T., Schultz, T.R. & Boomsma, J.J. (2002) Identifying the transition between single and multiple mating of queens in fungus-growing ants. *Proceeding of the Royal Society of London, Series B,* 269, 1541–1548. http://dx.doi.org/10.1098/rspb.2002.2044
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
Weber, N.A. (1943) New ants from Venezuela and neighboring countries. *Boletin de Entomologia Venezolana,* 2, 67–78.
Wheeler, G.C. & Wheeler, J. (1953) The ant larvae of the myrmicine tribe Myrmicini. *Psyche,* 59, 105–125.
Wheeler, G.C. & Wheeler, J. (1960) Supplementary studies on the larvae of the Myrmicinae (Hymenoptera: Formicidae). *Proceedings of the Entomological Society of Washington,* 62, 1–32.
Wheeler, G.C. & Wheeler, J. (1972) Ant larvae of the subfamily Myrmicinae: second supplement on the tribes Myrmicini and

Pheidolini. *Journal of the Georgia Entomological Society,* 7, 233–246.
Wheeler, W.M. (1902) New agricultural ants from Texas. *Psyche,* 9, 387–393.
Wheeler, W.M. (1913) Corrections and additions to "list of type species of the genera and subgenera of Formicidae". *Annals of the New York Academy of Sciences,* 23, 77–83.
Wiernasz, D.C., Perroni, C.L. & Cole, B.J. (2004) Polyandry and fitness in the western harvester ant, *Pogonomyrmex occidentalis*. *Molecular Ecology,* 13, 1601–1606.
http://dx.doi.org/10.1111/j.1365-294X.2004.02153.x
Wiernasz, D.C., Sater, A.K., Abell, A.J. & Cole, B.J. (2001) Male size, sperm transfer, and colony fitness in the western harvester ant, *Pogonomyrmex occidentalis*. *Evolution,* 55, 324–329.
http://dx.doi.org/10.1554/0014-3820(2001)055[0324:MSSTAC]2.0.CO;2