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A New Species of Seed-harvester Ant, *Pogonomyrmex hoelldobleri* (Hymenoptera: Formicidae), from the Mohave and Sonoran Deserts of North America

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Abstract

Pogonomyrmex magnacanthus Cole was described as a distinct species; unusually large eyes and a high ocular index (maximum eye diameter/head width) were listed as diagnostic characters. However, examination of numerous series of *P. magnacanthus* revealed that both characters were highly variable, and that these series consisted of *P. magnacanthus* plus an undescribed species, *Pogonomyrmex hoelldobleri* Johnson, Overson & Moreau sp. nov. This paper describes all three castes of *P. hoelldobleri* as well as the alate queen of *P. mohavensis*, which is very similar to that of *P. hoelldobleri*. A molecular phylogeny that consisted of 3,703 bp from one mitochondrial and five nuclear gene fragments supported the monophyly of *P. hoelldobleri*, *P. magnacanthus*, and *P. mohavensis*. *Pogonomyrmex magnacanthus* can be separated from other *P. californicus* group species based on: (1) its unusually large eyes, (2) a high ocular index, and (3) a malar ratio that is typically ≤ 1.0. *Pogonomyrmex hoelldobleri* can be separated from other *P. californicus* group species based on the combination of: (1) eyes not unusually large, (2) cephalic rugae not forming circumocular whorls, but rather converging posterior to the eyes, usually near the vertex, (3) mandible with seven teeth, and (4) interrugal spaces on pronotal sides moderately to strongly granulate, dull to weakly shining. *Pogonomyrmex mohavensis* can be separated from other *P. californicus* group species based on the combination of: (1) eyes not unusually large, (2) cephalic rugae not forming circum-ocular whorls, but rather extending more or less directly to the vertex or converging only slightly near the vertex, (3) mandible with six teeth (a seventh sometimes occurs as a denticle between the basal and sub-basal teeth), and (4) interrugal spaces on pronotal sides smooth and shining to weakly punctate and moderately shining. We also provide field observations and distribution maps for *P. magnacanthus*, *P. hoelldobleri*, and *P. mohavensis*, and an updated key to *P. californicus* group species that occur in central and western North America.

Key words: DNA phylogeny, Mohave Desert, new species, *Pogonomyrmex*, *P. californicus* group, Sonoran Desert

Introduction

The seed-harvester ant genus *Pogonomyrmex* Mayr, 1868 is a New World group that consists of approximately 67 described species (Bolton, 2012) that occur throughout most of North and South America, and also on the island of Hispaniola. Throughout much of the American West, Mexico, and southern South America, these are ecologically dominant ants, especially in arid habitats. Modern study of the genus began with Cole's (1968) revision of North American species, which stabilized the taxonomy of the genus and set the stage for studies of ecology, biogeography, territoriality, mating behavior, communication, caste determination, and foraging behavior that have greatly facilitated our understanding of ant biology (Anderson *et al.*, 2006; Cole & Wiernasz, 1999; Gordon, 1995; Johnson, 2000, 2001; Taber, 1998; Wiernasz *et al.*, 2001). Influential research on *Pogonomyrmex* also was conducted by Dr. Bert Hölldobler, whose numerous pioneering studies on this genus were likely responsible for *Pogonomyrmex* becoming one of the best studied and most well understood genus of ants (Gadau *et al.*, 2003;

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Hölldobler, 1971, 1974, 1976a, 1976b; 1989; Hölldobler *et al.*, 2001; Hölldobler *et al.*, 2004; Hölldobler & Wilson, 1970; Markl *et al.*, 1977; Regnier *et al.*, 1973).

Numerous North American species of *Pogonomyrmex* continue to be studied intensely in areas such as foraging behavior, colony founding strategies, reproductive physiology, phenotypic variation in workers and queens, and genetic caste determination (Anderson *et al.*, 2008; Dolezal *et al.*, 2009; Gordon & Kulig, 1996; Johnson, 2006, 2010; Johnson *et al.*, 2007; Oettler & Johnson, 2009; Sirviö *et al.*, 2011; Smith *et al.*, 2008; Wiernasz *et al.*, 2008). Such intense study on this genus necessitates that taxonomic updates appear in a timely fashion. The taxonomy of North American species is stable, such that species descriptions and new keys can provide these updates. This paper describes all three castes of a new species of *Pogonomyrmex* from the Sonoran and Mohave Deserts of the southwestern United States and northwestern Mexico. We also describe the alate queen of *P. mohavensis*, which is similar to that of *P. hoelldobleri*.

Measurements and indices

Morphological characters for *P. magnacanthus*, *P. hoelldobleri*, and *P. mohavensis* were photographed using a Spot Insight QE camera attached to a Leica MZ 125 microscope. Measurements *for P. magnacanthus* were taken for 63 workers; the HOLOTYPE, 25 PARATYPE workers from the type locality (Palm Springs, California), and 37 non-type workers. Characters for *P. hoelldobleri* were measured for 75 workers; the HOLOTYPE, 15 PARATYPES, 16 workers that A.C. Cole had identified as PARATYPES of *P. magnacanthus* that were not conspecific with the holotype, and 43 non-type workers. Measurements for *P. mohavensis* were taken for 25 workers; the HOLOTYPE, 12 PARATYPE workers (see Johnson & Overson, 2009), and 12 non-type workers. Non-type workers were selected to represent the geographic range of each species. Images were 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. The following standard measurements are used:

HL — **Head Length**: length of the head capsule excluding mandibles, in full-face view, from the midpoint of the anterior clypeal margin to the midpoint of the posterior margin.

HW — **Head Width**: maximum width of the head immediately behind the eyes, measured in full-face view.

CI — **Cephalic Index**: (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. Note that Cole (1968) calculated OI as (MOD/HL) × 100, such that values in this paper differ from those in his monograph.

OMD — **Oculo-Mandibular Distance**: minimum distance from the anterior eye margin to the nearest point of the malar area (base of mandible).

MR — **Malar Ratio**: (OMD/MOD).

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 petiole, 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.

Abbreviations of depositories

CASC	California Academy of Sciences, San Francisco, California, USA
LACM	Los Angeles County Museum of Natural History, Los Angeles, California, USA
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
RAJC	Robert A. Johnson collection, Tempe, Arizona, USA
UCDC	Bohart Museum of Entomology, University of California, Davis, California, USA
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
WPMC	William P. MacKay collection, El Paso, Texas, USA

Molecular analyses and phylogenetic inferences

Twenty-nine specimens of *Pogonomyrmex* (Hymenoptera: Formicidae) from seven species in the *P. californicus* group were sampled to test the monophyly of *P. hoelldobleri*. The phylogeny included samples from one locale (18.4 km east of Puerto Peñasco, Sonora, MEXICO) at which *P. californicus, P. hoelldobleri*, and *P. magnacanthus* occurred in sympatry. We also included samples from the other four species in the *P. californicus* group, and one sample of *P. anzensis*, whose placement is unclear because it has been suggested to belong to both the *P. occidentalis* group (Cole, 1968) and the *P. californicus* group (Parker & Rissing, 2002); three samples of *P. occidentalis* (*P. occidentalis* group) were included as an outgroup (Table 1). All sequences are deposited in Genbank: JX908144-JX908298.

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

Six gene fragments were amplified via PCR (Mullis et al. 1987; Saiki et al. 1988) using specific primers for each gene region following the protocols of Moreau et al. (2006), Moreau (2008), and Ward, et al. (2010). These six gene fragments included: (1) *cytochrome oxidase* I (COI) protein encoding mitochondrial marker (1059 base pairs [bp]), (2) *long-wavelength rhodopsin* (LR) protein encoding nuclear marker (594 bp), (3) *elongation factor 1α F1* (EF1α-F1) protein encoding nuclear marker (357 bp), (4) *elongation factor 1α F2* (EF1α-F2) protein encoding nuclear marker (517 bp), (5) w*ingless* (Wg) protein encoding nuclear marker (409 bp), and (6) *rudimentary* (CAD) protein encoding nuclear marker (767 bp) for a total of 3,703 bp of aligned sequence. Specimens were sequenced for all six genes with the following exceptions: COI missing for three taxa (GS98_052, RAJ2663, RAJ4218); EF1α-F1 missing for three taxa (GS98_052, JDP195B, RAJ4281); EF1α-F2 missing for one taxon (RAJ4270); Wg missing for four taxa (GS98_052, JDP195B, RAJ2663, RAJ4279); CAD missing for eight taxa (GS98_052, JDP195B, RAJ1005, RAJ2663, RAJ2908, RAJ4223, RAJ4279, RAJ4281).

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

To infer relationships among species, several model based phylogenetic analyses were performed on the CIPRES Science Gateway (Miller *et al*., 2010) using RAxML v7.3.2 (Stamatakis *et al*., 2005) and MrBayes v3.1.2 (Huelsenbeck & Ronquist, 2001). We evaluated fit of the data by conducting likelihood analyses using the complete concatenated data set (single) and the data partitioned by individual genes (partitioned). Modeltest 3.06 (Posada & Crandall, 2001) was used to determine the most appropriate nucleotide substitution model for all analyses and partitions (GTR+Γ+I). Two maximum likelihood searches were implemented in RAxML: (1) a single

GTR+Γ+I model of sequence evolution was assumed to underlie all genes (single) with 500 bootstrap pseudoreplicates, and (2) one that allowed each gene region to have a separate GTR+Γ+I model with parameters unlinked (partitioned) with 500 bootstrap pseudoreplicates.

TABLE 1. Locale data (state: county, locale) for specimens in the genus *Pogonomyrmex* that were used to reconstruct the DNA phylogeny (Figure 10). All locales are in the United States, except as noted. Taxonomy follows Bolton (2012).

Taxon and locality	Latitude	Longitude	Elevation (m)	Collector and accession number
P. anzensis **Cole**				
CA: San Diego, Anza Borrego State Park, Split Mountain	33º 01'N	116º 07'W	260	SP Cover #4807
P. californicus **(Buckley)**				
AZ: Maricopa, Salt River Recreation Area at Coon Bluff	33º 33'N	111º 39'W	405	RA Johnson #4246
AZ: La Paz, Mohawk Dunes at 15.5 km E Tacna	32º 42'N	113º 47'W	140	RA Johnson #2223
CA: Inyo, Alabama Hills at 7.5 km W Lone Pine	36º 36'N	118º 09'W	1540	RA Johnson #4128
MEXICO: Sonora, 18.4 km E Puerto Peñasco*	31º 20'N	113º 21'W	15	RA Johnson #4279
P. comanche **Wheeler**				
TX: Tarrant, Ft Worth Wildlife Refuge	32º 51'N	97º 28'W	180	AB Mayo #3985
TX: Bastrop, Camp Swift	30º 17'N	97º 19'W	135	JL Cook #4198
P. hoelldobleri **Johnson, Overson & Moreau**				
AZ: Yuma, 0.2 km S Tacna (**Paratype**)	32º 42'N	113º 57'W	110	RA Johnson #4255
NV: Clark, 5.0 km E Jean	35º 46'N	115º 16'W	840	RA Johnson #4223
NV: Nye, Hwy 95 at 6.4 km NW Lathrop Wells	36º 40'N	116º 28'W	790	RA Johnson #4217
MEXICO: Sonora, 18.4 km E Puerto Peñasco*	31º 20'N	113º 21'W	15	RA Johnson #4281
P. magnacanthus **Cole**				
AZ: La Paz, Mohawk Dunes at 15.5 km E Tacna	32º 42'N	113º 47'W	140	RA Johnson #4250
CA: Riverside, Palm Desert at Jct Bob Hope & Gerald Ford Dr	33º 47'N	116º 24'W	75	RA Johnson #1005
CA: San Diego, Anza Borrego, 8.0 km S Split Mountain	32º 59'N	116º 09'W	260	GC Snelling #98-052
MEXICO: Sonora, 18.4 km E Puerto Peñasco*	31º 20'N	113º 21'W	15	RA Johnson #4277
P. maricopa **Wheeler**				
AZ: Cochise, 1.4 km N Jct State Line & Portal Rds	31º 53'N	109º 03'W	1255	RA Johnson #4270
AZ: Gila, Hwy 288 at 23.7 km N Salt River	33º 47'N	110º 58'W	1440	RA Johnson #2140
NM: Hidalgo, 9.7 km ESE Portal	31˚ 52'N	109˚02'W	1240	CS Moreau #0225, 0258
MEXICO: Sonora, Rancho Agua Caliente	30º 39'N	109º 26'W	920	RA Johnson #3357

...... *continued on the next page*

TABLE 1. (Continued)

Taxon and locality	Latitude	Longitude	Elevation (m)	Collector and accession number
P. mohavensis **Johnson**				
CA: Inyo, Alabama Hills at 7.5 km W Lone Pine	36º 36'N	118º 09'W	1540	RA Johnson #4129
CA: Inyo, Alabama Hills, 1.3 km S Jct Horseshoe Meadows & Whitney Portal Rds	36º 35'N	118º 07'W	1450	RA Johnson #4145
NV: Nye, Highway 374 at Rhyolite	36º 53'N	116º 49'W	1090	RA Johnson #4218
P. occidentalis **(Cresson)**				
AZ: Cochise, Chiricahua Mtns, Rucker Canyon	31º 46'N	109º 22'W	1680	RA Johnson #2908
AZ: Cochise, Chiricahua Mtns at 8.0 km W Portal	31º 53'N	109º 12'W	1645	CS Moreau #0171
CO: Boulder, 0.8 km E Boulder	40º 01'N	105º 15'W	1590	JD Parker #195B
P. snellingi **Taber**				
MEXICO: Baja California, 9.6 km N Guerrero Negro	28º 04'N	114º 01'W	5	RA Johnson #2663
MEXICO: Baja California Sur, Vizcaino Desert	27º 47'N	113º 34'W	65	RA Johnson #3032, 3027

***** *Pogonomyrmex californicus*, *P. hoelldobleri*, and *P. magnacanthus* were sympatric at this locale.

Bayesian inference analyses were performed using MrBayes, with model parameters estimated during the run, and using the default value of four Markov chains. A "temperature" parameter of 0.2 was implemented to produce incremental heating of each chain. The Markov chain Monte Carlo length was 30,000,000 generations, with the chain sampled every 1000 generations. Bayesian posterior probabilities (BPP) were estimated as the proportion of trees sampled after 10% burn-in that contained each of the observed bipartitions (Larget & Simon, 1999; Rannala & Yang, 1996). Again two analyses were preformed: (1) a single GTR+Γ+I model of sequence evolution was assumed to underlie all gene regions (single), and (2) one that allowed each gene region to have a separate GTR+Γ+I model with parameters unlinked (partitioned). Independence of runs was ensured by only accepting analyses where the average standard deviation of split frequencies was below 0.01.

RESULTS

Pogonomyrmex magnacanthus Cole
(Figures 1–2, 4–5)

Pogonomyrmex (*Pogonomyrmex*) *magnacanthus* Cole, 1968 [part]: 133, pl. 2, fig. 5; pl. 3, fig. 12; pl. 4, fig. 10; pl. 6, fig. 9; pl. 7, fig. 16; pl. 8, fig. 10; pl. 11, fig. 10 (worker, queen, male). Holotype examined [LACM, Cole No. Cal-378]; Palm Springs, California, USA (by A.C. Cole, Jr., on 8 August, 1960); Taber, Cokendolpher & Francke, 1988: 51 (karyotype) (2*n* = 32). See also Ward (2005).

Worker

Diagnosis. *Pogonomyrmex magnacanthus* is a small species (HW = 1.15–1.80 mm) that is identified by: (1) its unusually large eyes (MOD = 0.33–0.49 mm; OI = 27.22–33.61; malar ratio (MOD/OMD) usually $\leq$ 1.0) (see Figures 1–3). OI is the most reliable character to identify *P. magnacanthus* given that MOD is positively associated with HW such that it sometimes overlaps with that of other species (see Figure 3). Cole (1968) also listed an unusually large eye and a high ocular index as diagnostic characters for *P. magnacanthus*. Interestingly, the holotype that Cole selected was somewhat of an outlier for both characters because the eye was relatively small and the OI was lower than that of other paratype workers (see below and Cole, 1968).

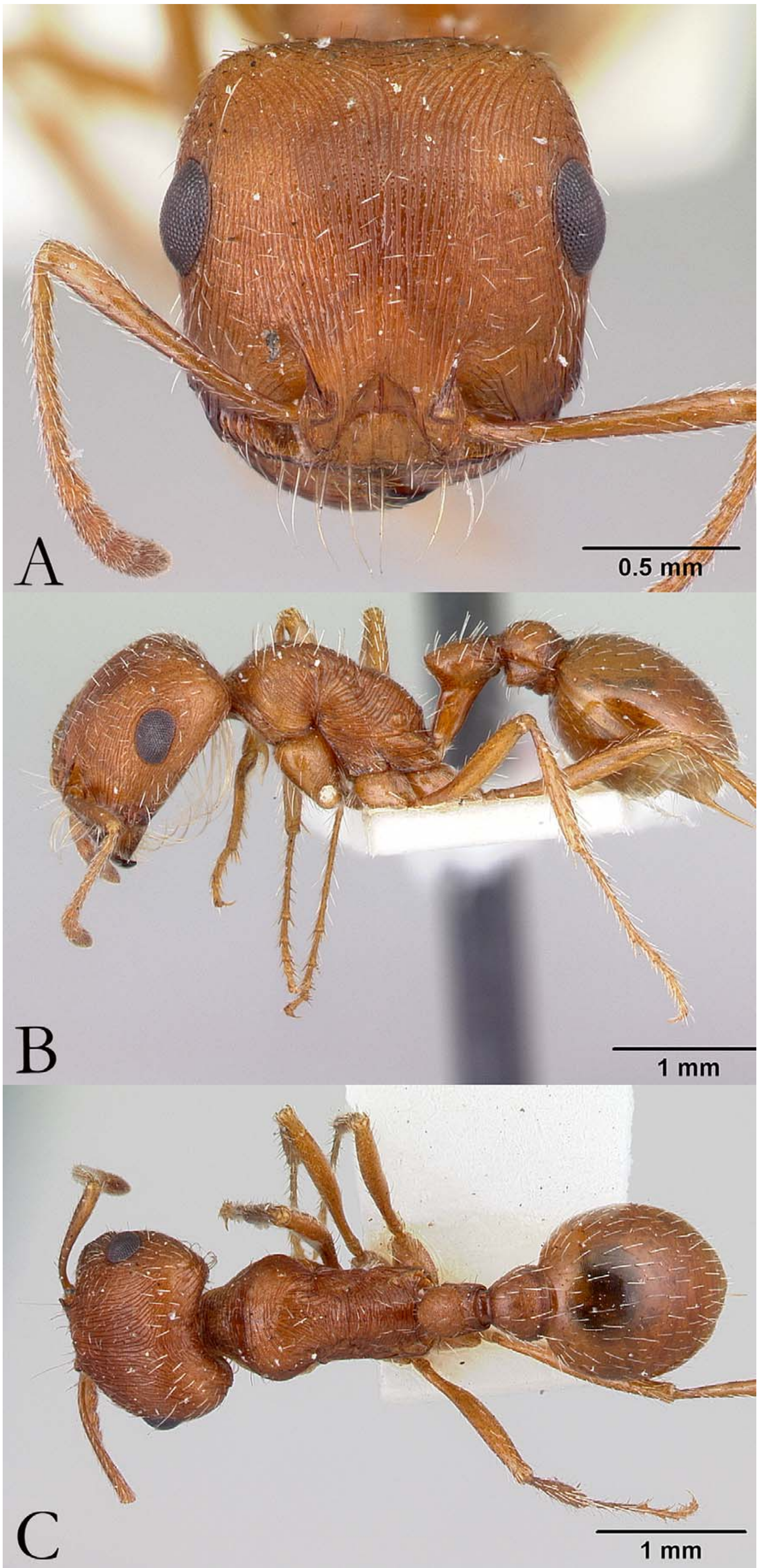

FIGURE 1. Photograph of *Pogonomyrmex magnacanthus* Cole—HOLOTYPE worker: **(A)** frontal view of head, **(B)** lateral view of body, and **(C)** dorsal view of body.

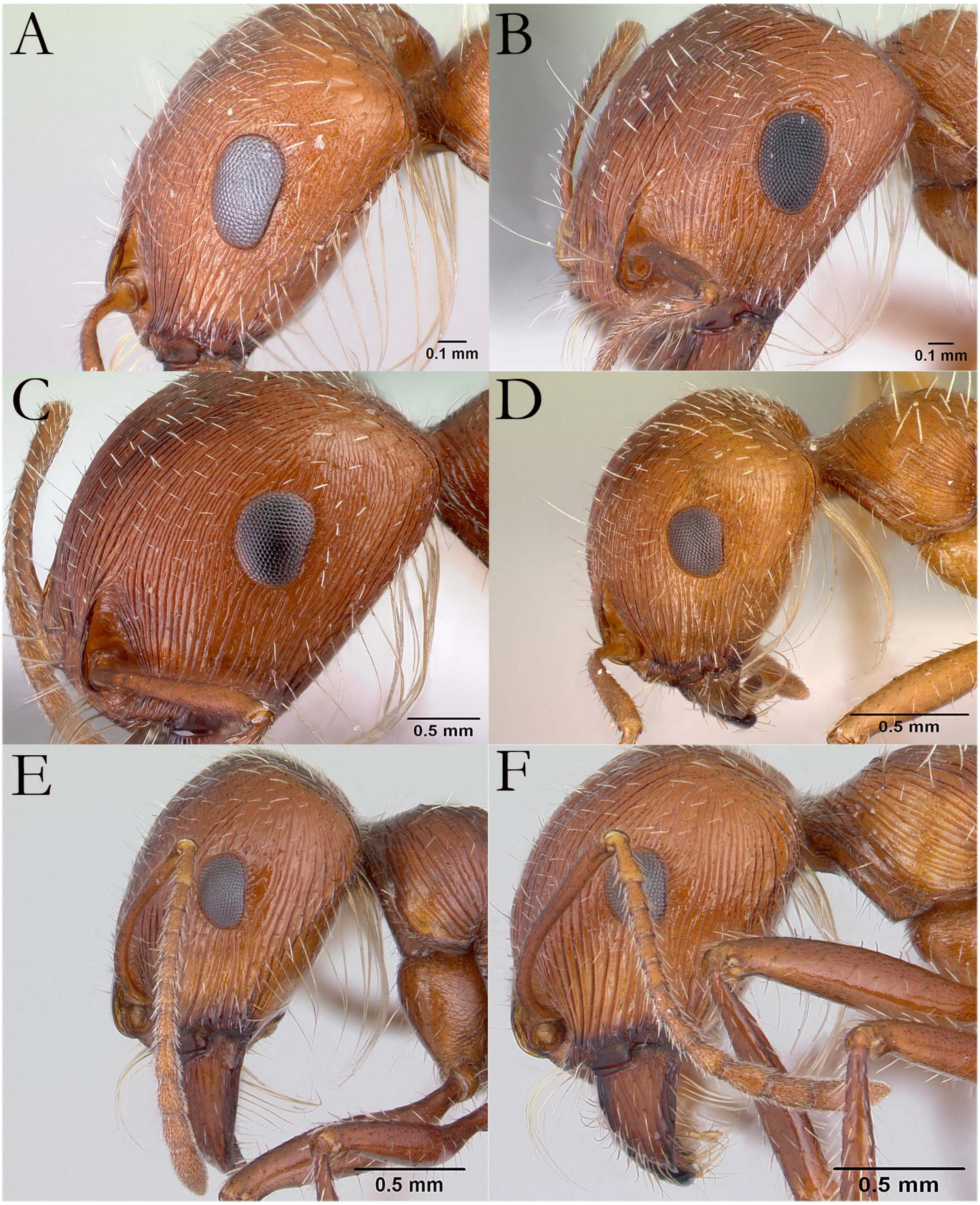

FIGURE 2. Photographs of diagnostic characters to distinguish between workers of *P. magnacanthus* Cole and those of *P. hoelldobleri* Johnson, Overson & Moreau and *P. mohavensis* Johnson. Photograph of *P. magnacanthus* PARATYPE worker: (**A**) eye and malar area (MOD = 0.44, OI = 29.5, MR = 0.98), and circumocular whorls indistinct to absent, moderately granulate toward vertex, and (**B**) circumocular whorls present. Photograph of *P. hoelldobleri* worker: (**C**) eye and malar area for HOLOTYPE worker (MOD = 0.36, OI = 23.2, MR = 1.17), and absence of circumocular whorls—rugae converging near vertex, and (**D**) absence of circumocular whorls—area posterior to eyes with faint rugae. Photograph of *P. mohavensis* worker: (**E**) eye and malar area for PARATYPE worker (MOD = 0.33, OI = 21.7, MR = 1.36), and absence of circumocular whorls—rugae extending to vertex, with rugae becoming weak to absent on/near vertex, and (**F**) absence of circumocular whorls—rugae extending to vertex; vertex rugose.

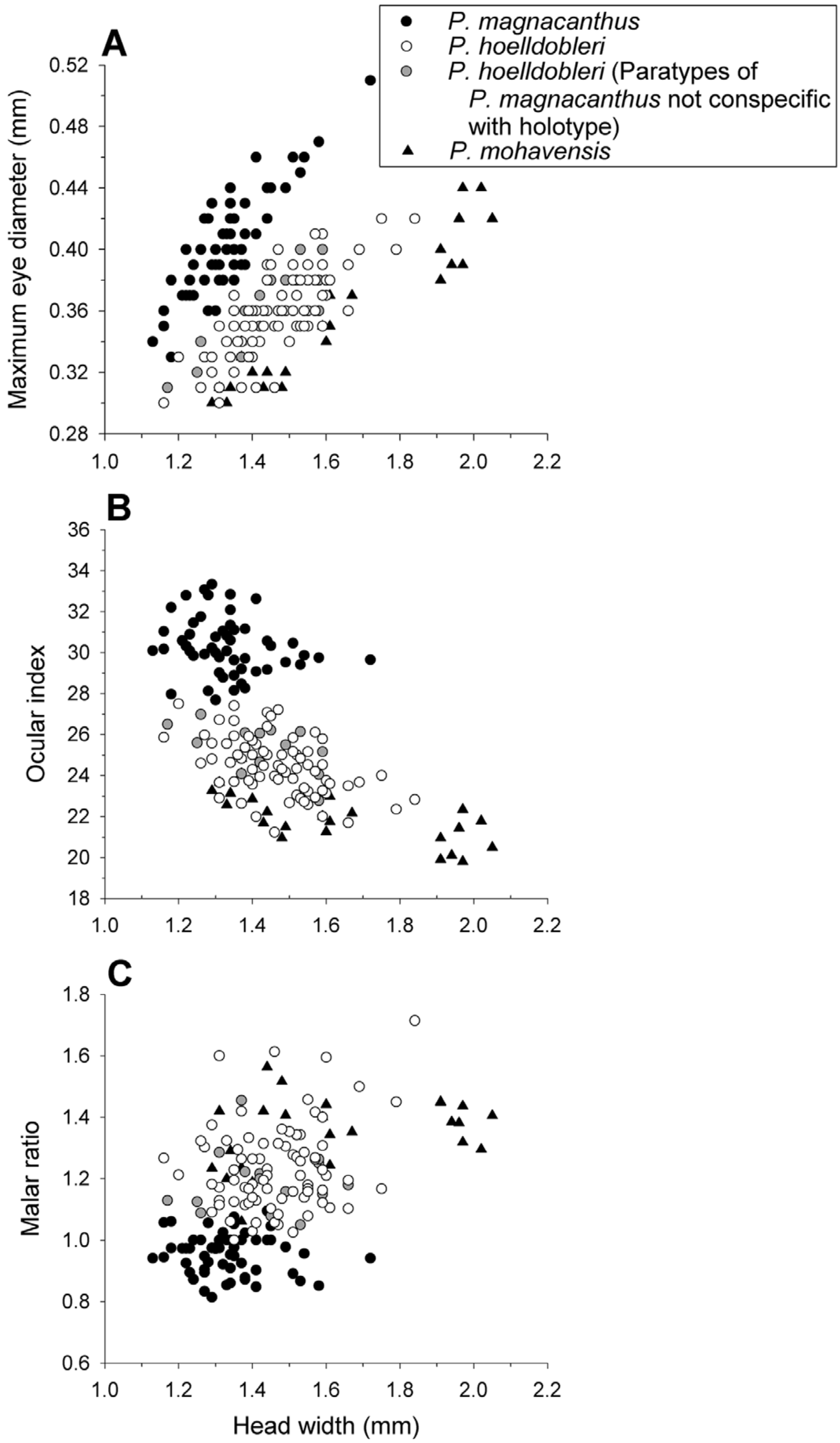

FIGURE 3. Bivariate plots for workers: (**A**) maximum eye diameter versus head width, (**B**) ocular index versus head width, and (**C**) malar ratio versus head width (n = 63 for *P. magnacanthus* Cole, n = 59 for *P. hoelldobleri* Johnson, Overson & Moreau, plus 16 PARATYPE workers of *P. magnacanthus* that do not belong to the latter species [see text], n = 25 for *P. mohavensis* Johnson). Non-type workers were selected to represent the geographic range of each species.

Measurements (mm)—holotype (*n* = 25 paratypes, all from the type locality at Palm Springs, California [CAL-356, CAL-374, CAL-378, CAL-380, CAL-381, CAL-382], plus 37 non-type workers). HL 1.37 (1.17–1.65); HW 1.38 (1.15–1.80); MOD 0.39 (0.33–0.49); OMD 0.39 (0.31–0.46); SL 1.02 (0.86–1.15); PNW 0.88 (0.73–1.08); HFL 1.38 (1.08–1.74); ML 1.67 (1.28–1.91); PW 0.36 (0.28–0.45); PPW 0.54 (0.40–0.60). Indices: SI 74.45 (63.89–81.67); CI 99.28 (92.54–112.21); OI 28.47 (27.22–33.61); HFI 100.73 (88.00–112.50).

*Description***.** Head subquadrate to quadrate (CI = 92.54–112.21), broadest just posterior to eye; posterior margin flat in full-face view. Longitudinal cephalic rugae prominent, in full-face view median rugae diverging toward posterior corners near posterior margin of head. In side view, rugae converging immediately posterior to eyes to form indistinct to well defined circumocular whorls that often weaken toward vertex, or rugae converging toward vertex, or circumocular whorls and rugae mostly absent posterior to eye and weakly to densely granulate-punctate, dull to sub-shining, especially toward vertex. Vertex rugose, densely granulate, or occasionally smooth to weakly striated, dull to shining. Cephalic interrugal spaces weakly to moderately granulate-punctate on anterior portion of head, often becoming more strongly granulate-punctate on posterior half of head, sub-shining to shining. Anterior margin of clypeus flat to weakly concave. Mandible with seven teeth; mandibular dorsum coarsely striate. In profile, eyes large, MOD ranging from 0.27–0.32x HL, OI = 27.22–33.61, MR usually $\leq$ 1.0; eye situated near middle of head. Antennal scapes moderately long (SI = 63.89–81.67), failing to reach vertex by length of basal funicular segment. Basal flange of antennal scape flattened and well developed, margin weakly carinate. Psammophore well developed.

Mesosomal profile convex. All mesosomal surfaces with prominent parallel/subparallel rugae. Dorsum of promesonotum with transverse rugae that curve obliquely to posterior, often becoming indistinct on pronotal sides. Mesopleura with subparallel rugae angling posterodorsally. Propodeum lacking spines or teeth, occasionally with minute denticles; in side view, juncture of propodeum and propodeal declivity evenly convex to weakly angulate; rugae on dorsum of propodeum transverse, declivitous face often with one or two discontinuous to continuous transverse rugae, interrugal spaces smooth and shining. Propodeal spiracles narrowly ovate. Interrugal spaces on mesosoma moderately granulate-punctate, sub-shining to smooth and shining; interrugal spaces on pronotal sides moderately to densely granulate, dull. Legs moderately to strongly shining.

Petiolar peduncle long, ventral margin straight. In side view, posterior face of petiole weakly convex; petiolar node asymmetrical with anterior surface shorter than posterior surface. Apex of node weakly to moderately angulate. In dorsal view, petiolar node longer than broad, sides subparallel or diverging slightly toward the smoothly rounded to weakly angulate anterior margin. Sides and dorsum of petiolar node moderately to strongly granulate-punctate, dull to sub-shining, occasionally with several longitudinal to oblique rugae that are restricted to posterior one-third of petiole. 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, moderately granulate-punctate, dull to sub-shining. Gaster smooth and strongly shining.

Erect to suberect white pilosity moderately abundant on head, short to medium in length, often with one to few longer hairs, none exceeding MOD. Moderately abundant semidecumbent to decumbent pilosity on scape with occasional suberect hairs, abundant semidecumbent to decumbent hairs on funicular segments. Legs with moderately abundant suberect to semidecumbent white setae. Mesosoma, petiole, and postpetiole with a lower density of mostly long, flexuous hairs mostly concentrated on dorsal surfaces, longest distinctly shorter than MOD; gastric tergites with moderately abundant, medium length suberect hairs. Entire body concolorous light to dark ferruginous orange (Figure 1).

Queen

*Diagnosis***.** As in worker diagnosis, but with caste-specific morphology of the mesosoma related to wing-bearing, presence of small ocelli on the head, and as illustrated in Figure 4. Mandible with seven teeth; cephalic rugae forming circumocular whorls. Eyes large (OI = 29.35–35.29), MR $\leq$ 1.00, MOD ranging from 0.30–0.35x HL. All mesosomal surfaces with prominent rugae.

Measurements (mm)—(*n* = 3). HL 1.79–1.88; HW 1.84–1.95; MOD 0.54–0.66; OMD 0.40–0.58; SL 1.22–1.26; PNW 1.40–1.45; HFL 1.73–1.90; ML 2.61–2.75; PW 0.56–0.62; PPW 0.82–0.93. Indices: SI 64.62–66.30; CI 99.47–107.73; OI 29.35–35.29; HFI 94.02–100.00.

Description. As in worker diagnosis, but with caste-specific structures related to wing-bearing, presence of small ocelli on head, and as illustrated in Figure 4. Small, only slightly larger than conspecific workers. In full-face view, head quadrate to slightly broader than long, posterior margin flat, median rugae diverging toward posterior corners near posterior margin of head. Dorsum and sides of head conspicuously rugose, in side view rugae forming circumocular whorls posterior to eyes, interrugal spaces mostly smooth and shining. Mandible with seven teeth, dorsal surface coarsely rugose, strongly shining. Eyes large (OI = 29.35–35.29), MR ≤ 1.00, MOD ranging from 0.30–0.35x HL. Base of scape not flattened; superior and inferior lobes poorly developed, no wider than width of base of scape.

All mesosomal surfaces with prominent subparallel/parallel rugae, those on mesoscutum and mesoscutellum fine, parallel, and longitudinal; interrugal spaces smooth and shining. In side view, propodeum unarmed, juncture of propodeum and propodeal declivity slightly angulate, sides and dorsal surface transversely or obliquely rugose, declivitous surface smooth and strongly shining. Petiolar peduncle long, ventral margin straight. In side view, petiolar node asymmetrical with anterior surface shorter than posterior surface. Apex of node rounded. In dorsal view, petiole length and width similar to slightly longer than wide; posterior face finely rugose, interrugal spaces weakly coriarious, sub-shining. Postpetiole broader than long; posterior portion finely rugose, interrugal spaces weakly coriarious, sub-shining; anterior portion granulate-punctate. Gastric tergites weakly coriarious and sub-shining to smooth and shining. Most body surfaces with moderately abundant coarse suberect to erect setae. Entire body concolorous light to dark ferruginous orange.

Male

Diagnosis. Mandible with four teeth on suboblique cutting margin. Mandibular dorsum with faint rugae/striae, mostly sub-shining. Anterior margin of clypeus moderately concave, lateral lobes distinct, broadly rounded; antennal scapes with faint rugae/striae, sub-shining, or lacking sculpture, smooth and shining. Eye unusually large (MOD ≥ 0.53, OI > 42.5, MR ≤ 0.34) (Figure 5).

Measurements (mm)—(*n* = 4). HL 1.09–1.29; HW 1.20–1.36; MOD 0.53–0.59; OMD 0.15–0.19; SL 0.43–0.57; HFL 1.53–1.66; ML 2.29–2.54; PW 0.52–0.61; PPW 0.70–0.82. Indices: SI 32.09–41.91; CI 104.69–111.82; OI 42.54–44.17; HFI 120.59–130.08.

Description. Mandible with four teeth on suboblique cutting margin; basal tooth sometimes weakly bifid; basal tooth not offset; mandibular dorsum as described above. Clypeus lacking sculpture, mostly smooth and shining except for scattered punctures, anterior margin moderately concave, lateral lobes distinct, broadly rounded. Antennal scapes reaching to or near posterior margin of eye, mostly smooth and shining to faintly striate. Parallel/subparallel cephalic rugae fine and close, slightly wavy, interrugae weakly punctate, sub-shining.

In profile, anterior face of mesonotum forming a mostly straight line with pronotum, slightly less than one-half as long as dorsal surface. In side view, juncture between propodeum and propodeal declivity subangulate, without spines or denticles. Sides of pronotal collar smooth and shining; katepisternum mostly smooth and shining with scattered foveae, posterior margin often faintly striate, shining. Mesonotum shiny with piligerous punctures, notauli very weakly impressed. Propodeum smooth and shining. Ventral margin of petiolar peduncle straight. In side view, petiolar node broadly rounded, anterior surface longer than posterior surface, forming a mostly straight continuous to slightly curved profile with dorsal margin of petiolar peduncle. Dorsal surface of petiole smooth and shining with scattered punctures to microrugoreticulate, sub-shining. Postpetiole broader than long, dorsal surface mostly smooth, sub-shining to shining. Head, mesosoma, petiole, and postpetiole with moderately abundant flexuous white hairs, often similar in length to MOD. Gastric tergites smooth and shining, hairs shorter and less dense than on rest of body. Entire body a concolorous ferruginous orange to brownish-orange (Figure 5).

Additional material examined. **UNITED STATES:** ***Arizona***: *La Paz Co.*: 3.5 mi SE Parker on Hwy 95, 460', Apr 4, 1997, SP Cover SPC#4830 (6w, MCZ), SPC#4834 (8w, MCZ). *Maricopa Co.*: Sentinel, Jul 9, 1956, AC Cole AZ-404 (9w PARATYPES, LACM), AZ-405 (9w PARATYPES, LACM), AZ-406 (9w PARATYPES, LACM). *Yuma Co.*: Blaisdell, 200', Oct 26, 1952, #406 (6w, LACM); Dateland, Apr 21, 1994, RA Johnson RAJ#481 (4w, RAJC), RAJ#482 (6w, RAJC); 0.5 mi S Dateland, Sep 18, 1992, RA Johnson RAJ#103-1 (2w, RAJC); Mohawk Dunes at 9.7 mi E Tacna, Mar 21, 2001, RA Johnson RAJ#2235 (3w, RAJC); NE end of Mohawk Dunes, 460', Jun 24, 2009, RA Johnson RAJ#4248 (6w, RAJC), RAJ#4249 (3w, RAJC), RAJ#4250 (9w, RAJC); I-8 at 1.0 mi E Dome Valley, 250', Apr 26, 2012, RA Johnson RAJ#4920 (3w, RAJC); Hwy 95 at Yuma Proving Grounds, 250', Apr 27, 2012, RA Johnson RAJ#4922 (3w RAJC). ***California***: *Imperial Co.*: 15 mi E Holtville, Jul 27, 1961, AC Cole CAL-395 (16w, LACM); 13.5 mi E Holtville, Jul 31, 1960, AC Cole CAL-359 (12w PARATYPES, LACM); CAL-360 (15w PARATYPES, LACM); 19 mi W Winterhaven, Jul 28, 1959, AC Cole CAL-336 (8w PARATYPES, LACM), CAL-335 (11w PARATYPES, LACM); 7 mi W Winterhaven, Jul 28,

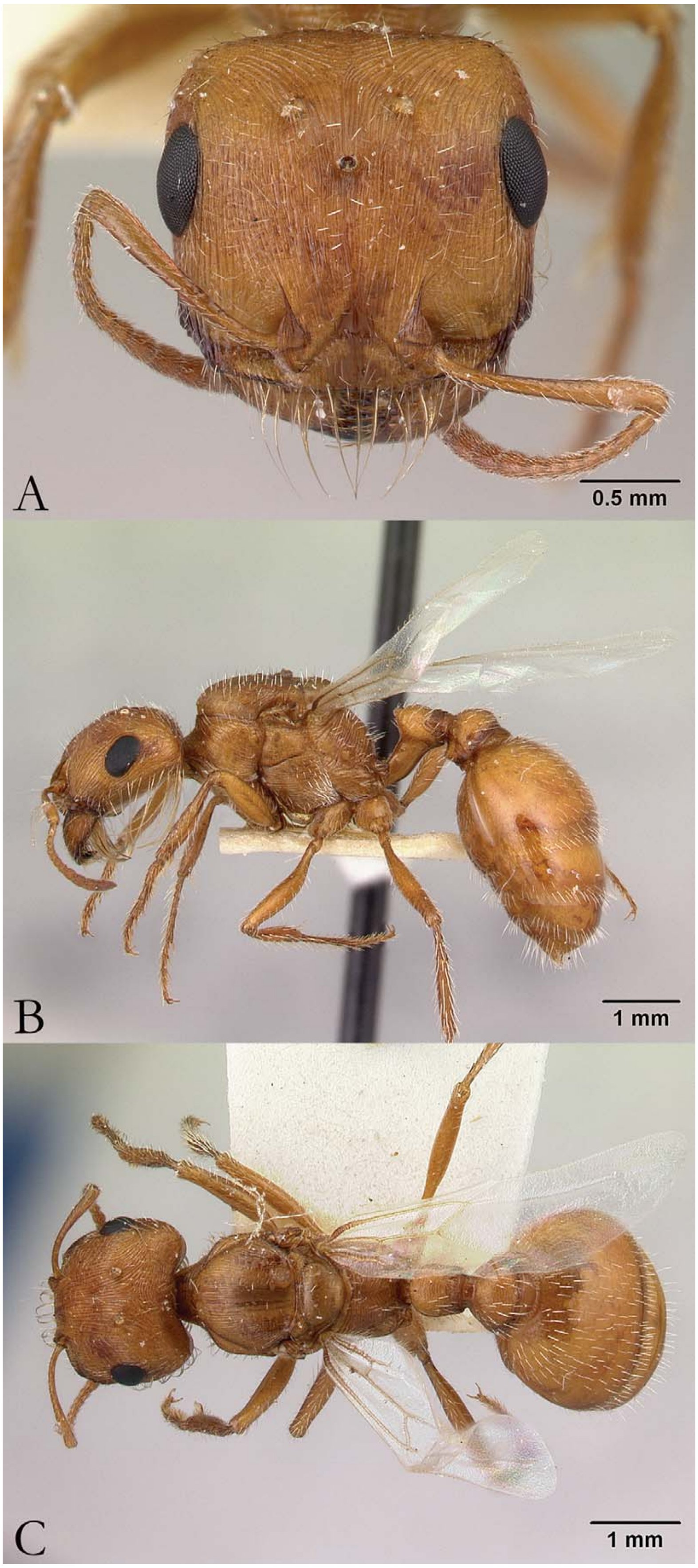

FIGURE 4. Photograph of *Pogonomyrmex magnacanthus* Cole alate queen: **(A)** frontal view of head, **(B)** lateral view of body, and **(C)** dorsal view of body.

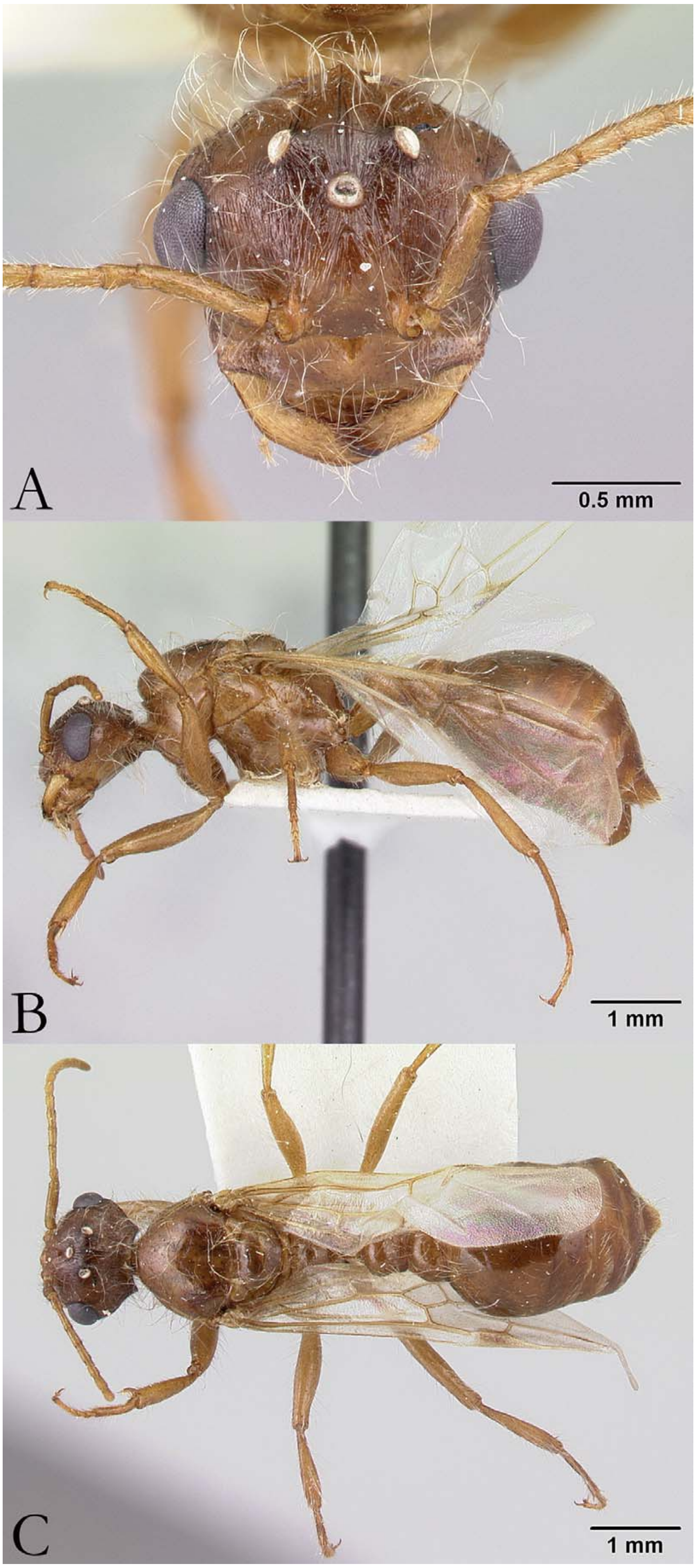

FIGURE 5. Photograph of *Pogonomyrmex magnacanthus* Cole male: **(A)** frontal view of head, **(B)** lateral view of body, and **(C)** dorsal view of body.

1959, AC Cole CAL-333 (13w PARATYPES, LACM); Glamis, Mar 28, 1964, Saul Frommer (2w, LACM); Algodones Dunes at 15.5 mi NNW Glamis, 180', Mar 31, 1997, RA Johnson #945 (6w, RAJC). *Riverside Co.*: 14.5 mi N Midland (site) ca 34º 02.5'N 114º 52'W, sand dunes, Apr 9, 1994, RR Snelling #94-12b (2w, LACM); Palm Springs, Jun 16, 1963, AC Cole CAL-424 (4w, 2aq PARATYPES, LACM), CAL-425 (1w, 1aq, 1m PARATYPES, LACM); Aug 8, 1960, CAL-356 (51w PARATYPES, LACM), CAL-374 (9w PARATYPES, LACM), CAL-375 (6w PARATYPES, LACM), CAL-376 (29w PARATYPES, LACM), CAL-377 (9w PARATYPES, LACM), CAL-378 (30w PARATYPES, LACM), CAL-379 (6w PARATYPES, LACM), CAL-380 (9w PARATYPES, LACM), CAL-381 (9w PARATYPES, LACM), CAL-382 (21w PARATYPES, LACM); 7.5 mi NE Desert Center (33.79'N, 115.30'W), Apr 11, 2004, RR Snelling #04-002 (8w, LACM); Palm Desert, Bob Hope & Gerald Ford Dr, May 15, 1997, RA Johnson RAJ#1005 (3w, RAJC), RAJ#1006 (12w, RAJC); 20 mi W Blythe, May 5, 1963, RR Snelling (3w, LACM); 3 mi E Mecca, 100', Mar 26, 1986, RR Snelling (10w, 2m, LACM). *San Bernardino Co.*: 3 mi SSW Rice (34.04'N, 114.87'W), Apr 11, 2004, RR Snelling #04-004 (7w, LACM); 2 mi W Rice, 1000', Oct 12, 1963, RR Snelling (6w, LACM); Cadiz Dunes, Apr 25, 1978, AR Hardy & FG Andrews (2w, 1m, LACM); 29 Palms, 2000', Nov 6, 1967, RR Snelling #67-290 (3w, LACM); Johnson Valley, May 15, 2008, RA Johnson RAJ#4126 (6w, RAJC); 4 km S Kelso, 670 m, Mar 29, 2004, PS Ward PSW#15179 (3w, MCZ); 2.8 mi NW Pisgah Crater, 2110', Apr 5, 2010, RA Johnson RAJ#4483 (6w, RAJC), RAJ#4484 (6w, RAJC), RAJ#4485 (6w, RAJC). *San Diego Co.*: Anza Borrego State Park, 5.0 mi S Split Mountain, 850', Apr 2, 1997, GC Snelling #98-052 (6w, RAJC), RA Johnson RAJ#955-1 (12w, RAJC), RAJ#951 (6w, RAJC), SP Cover SPC#4811 (6w, MCZ), SPC#4812 (6w, MCZ). **MEXICO**: ***Baja California***: Hwy 5 at 1 mi S Laguna Salada, May 10, 1998, RA Johnson RAJ#BC-1373 (9w, RAJC), RAJ#BC-1374 (8w, RAJC; 3w UCDC); Hwy 5 at 17.5 mi SE San Felipe, Feb 27, 1992, RA Johnson RAJ#BC-43 (6w, RAJC). ***Sonora***: 11.5 mi E Puerto Peñasco, 50', Jul 17, 2009, RA Johnson RAJ#4275 (6w, RAJC), RAJ#4276 (9w, RAJC), RAJ#4277 (6w, RAJC), RAJ#4280 (9w, RAJC); 16 mi E Puerto Peñasco, 30', Jul 16, 2009, RA Johnson RAJ#4272 (6w, RAJC).

Etymology. The specific epithet, *magnacanthus* (from Latin, *magna* for great or large, and Greek, *kanthos*, for corner of the eye), likely refers to the greatly enlarged corner of the eye in this species. In describing this species, Cole discussed the unusually large eyes but made no mention in regard to the corners of the eyes.

Discussion. *Pogonomyrmex magnacanthus* is most likely to be confused with *P. hoelldobleri*, as evidenced by the numerous series of the latter species (including several paratype series) that A.C. Cole misidentified as *P. magnacanthus*. The significantly larger eye (MOD and OI) separates *P. magnacanthus* from *P. hoelldobleri* (Figures 2–3), but OI is the more diagnostic character because it is consistently higher for *P. magnacanthus* (OI = 27.22–33.61) than for *P. hoelldobleri* (OI usually $\leq$ 27.50)(Figure 3). Additionally, the malar ratio is usually $\leq$ 1.0 for *P. magnacanthus*, while this ratio is usually > 1.05 for *P. hoelldobleri* (Figure 3).

Pogonomyrmex magnacanthus occurs sympatrically with *P. californicus*, but it has a low likelihood of co-occurring with *P. maricopa* and *P. mohavensis*. Two other *P. californicus* group species (*P. anzensis* and *P. snellingi*) also occur in the Sonoran Desert, but it is doubtful that *P. magnacanthus* occurs sympatrically with either species; *P. anzensis* inhabits unproductive, rocky hillsides that are unlike any sites known to be occupied by *P. magnacanthus*, while *P. snellingi* is well removed from the probable geographic distribution of *P. magnacanthus*. *Pogonomyrmex magnacanthus* can be distinguished from all of these species using the characters described above.

Pogonomyrmex hoelldobleri **Johnson, Overson & Moreau, NEW SPECIES**
(Figures 2, 6–8)

Pogonomyrmex magnacanthus Cole, 1968: 133 [part].

Worker

Diagnosis. Pogonomyrmex hoelldobleri is characterized by: (1) eye not unusually large (MOD usually $\leq$ 0.42, OI usually $\leq$ 27.50, MR usually $\geq$ 1.05 (Figure 3), (2) mandible with seven teeth, (3) cephalic rugae converge posterior to eyes, usually near vertex, but not forming circumocular whorls, (4) interrugal spaces on pronotal sides moderately to strongly granulate, dull to weakly shining (see Figures 2, 6), and (5) gaster concolorous with head and mesosoma.

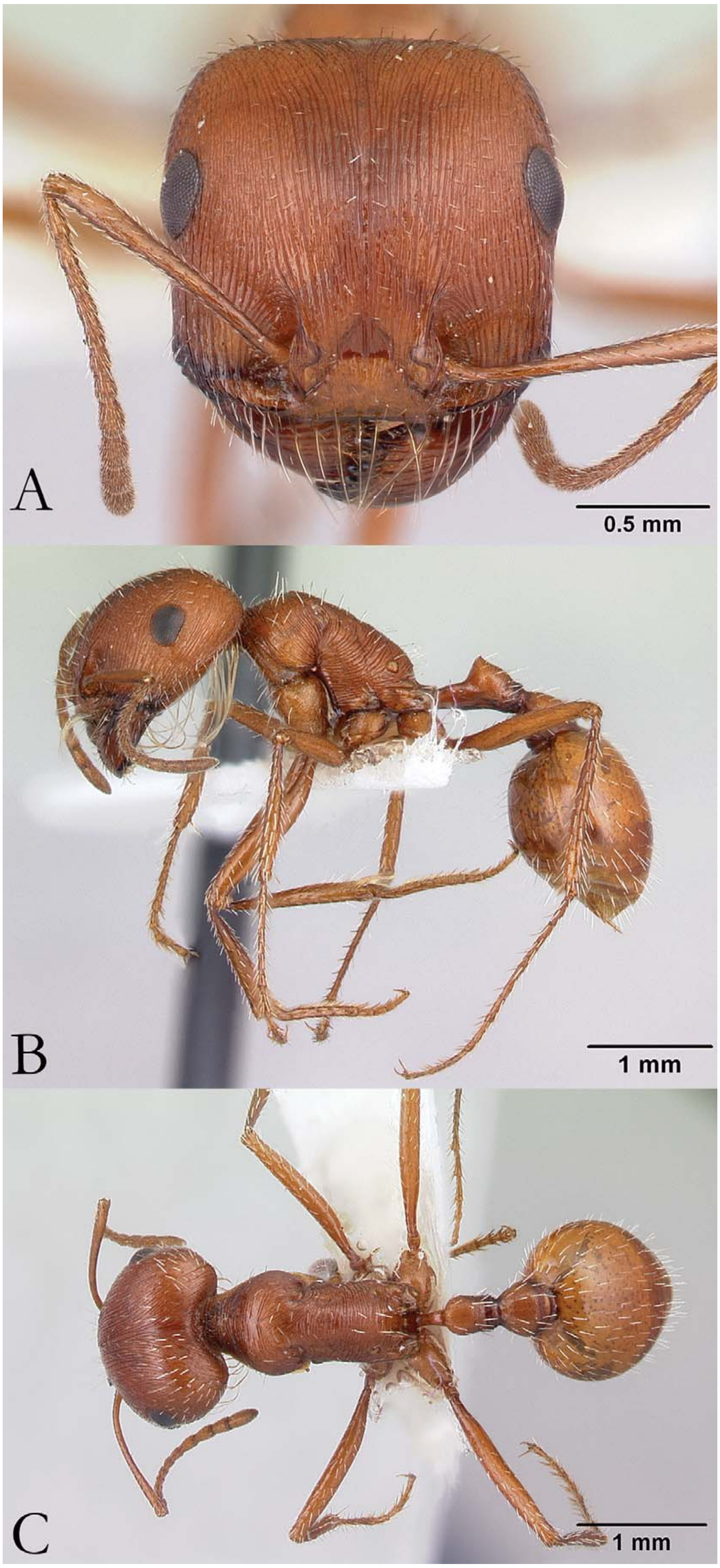

FIGURE 6. Photograph of *Pogonomyrmex hoelldobleri* Johnson, Overson & Moreau—HOLOTYPE worker: **(A)** frontal view of head, **(B)** lateral view of body, and **(C)** dorsal view of body.

Measurements (mm)—holotype (*n* = 75 [15 paratypes, 43 non-types, 16 *P. magnacanthus* Paratypes]). HL 1.57 (1.24–1.76); HW 1.55 (1.17–1.84); MOD 0.36 (0.30–0.42); OMD 0.42 (0.35–0.72); SL 1.20 (0.94–1.34); PNW 0.91 (0.77–1.11); HF 1.67 (1.19–1.89); ML 1.84 (1.35–2.03); PW 0.34 (0.27–0.46): PPW 0.51 (0.38–0.59). Indices: SI 77.42 (66.25–87.18); CI 98.73 (93.98–115.79); OI 23.23 (21.12–29.01); HFI 107.74 (84.97–117.93).

Description. Head subquadrate to quadrate (CI = 93.98–115.79), broadest just posterior to eye; posterior margin flat in full-face view. Longitudinal cephalic rugae prominent, in full-face view median rugae usually diverging toward posterior corners near posterior margin of head. In side view, rugae converging slightly near vertex, occasionally becoming faint between posterior margin of eye and vertex. Vertex faintly to strongly rugose, occasionally mostly smooth to weakly granulate, sub-shining to shining. Cephalic interrugal spaces moderately punctate, sub-shining to smooth and shining. Anterior margin of clypeus slightly concave. Mandible with seven teeth; mandibular dorsum coarsely striate. In profile, eyes not unusually large, MOD ranging from 0.22–0.29x HL, OI = 21.12–29.01, MR usually > 1.05; eye situated near middle of head. Antennal scapes moderately long (SI = 66.25–87.18), failing to reach vertex by less than length of basal funicular segment. Basal flange of antennal scape flattened and well developed, margin weakly carinate. Psammophore well developed.

Mesosomal profile convex. All mesosomal surfaces with prominent parallel/subparallel rugae. Dorsum of promesonotum with transverse rugae that curve obliquely to posterior on pronotal sides, rugae on pronotal sides often slightly less distinct than on other portions of mesosoma; rugae usually oblique to longitudinal on anterior portion of mesonotum. Mesopleura with subparallel rugae angling posterodorsally. Propodeum lacking spines or teeth; in side view, juncture of propodeum and propodeal declivity evenly convex to weakly angulate; rugae on propodeal dorsum transverse, declivitous face smooth and shining. Propodeal spiracles narrowly ovate. Interrugal spaces on mesosoma moderately granulate-punctate, sub-shining to smooth and shining; interrugal spaces on pronotal sides usually more densely granulate than other portions of mesosoma. Legs moderately to strongly shining.

Petiolar peduncle long, ventral margin straight. In side view, posterior face of petiole slightly convex; petiolar node asymmetrical with anterior surface slightly shorter than posterior surface. Apex of node weakly to strongly angulate, posterior surface sometimes curved upward near anterior margin. In dorsal view, petiolar node longer than broad, sides subparallel or diverging slightly toward the smoothly rounded to weakly angulate anterior margin. Sides and dorsum of petiolar node strongly granulate-punctate, dull to sub-shining to smooth and shining, occasionally with several longitudinal to oblique rugae that are restricted to posterior one-third of petiole. 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 moderately granulate, dull to sub-shining. Gaster smooth and strongly shining.

Erect to suberect white pilosity moderately abundant on head, short to medium in length, often with one to few longer hairs, none exceeding MOD. Moderately abundant semidecumbent to decumbent pilosity on scape, abundant semidecumbent to decumbent hairs on funicular segments. Legs with moderately abundant suberect to semidecumbent white setae. Mesosoma, petiole, and postpetiole with a lower density of mostly longer, flexuous hairs mostly concentrated on dorsal surface, longest distinctly shorter than MOD; gastric tergites with moderately abundant, medium length suberect hairs. Entire body concolorous light to dark ferruginous orange, posterior portion of gaster sometimes slightly darker (Figure 6).

Queen

Diagnosis. As in worker diagnosis, but with caste-specific structures related to wing-bearing and presence of small ocelli on head. Mandible with seven teeth. Eye not unusually large (MOD ≤ 0.45, OI < 28.50, MR usually ≥ 1.05). All mesosomal surfaces except for mesoscutum and mesoscutellum with prominent rugae; sculpturing absent on mesoscutum and mesoscutellum except for scattered punctures and occasional faint longitudinal striae (Figure 7). Posterior face of petiole and dorsum of postpetiole weakly to moderately granulate or with weak tranverse rugae. Base of scape rounded; superior and inferior lobes poorly developed, no wider than width of scape base.

Measurements (mm)—(*n* = 8). HL 1.36–1.66; HW 1.44–1.79; MOD 0.40–0.45; OMD 0.40–0.50; SL 0.97–1.23; PNW 1.24–1.54; HFL 1.38–1.67; ML 2.18–2.62; PW 0.45–0.57; PPW 0.61–0.73. Indices: SI 65.52–72.12; CI 100.00–114.10; OI 22.47–28.47; HFI 83.64–109.03.

Description. As in worker diagnosis, but with caste-specific structures related to wing-bearing, presence of small ocelli on head, and as illustrated in Figure 7. Small, only slightly larger than conspecific workers. In full-face view, head quadrate to broader than long, posterior margin flat. Dorsum and sides of head conspicuously rugose, in side view rugae forming circumocular whorls posterior to eyes or rugae converging near vertex, interrugal spaces smooth and strongly shining. Mandible with seven teeth, dorsal surface coarsely rugose, strongly shining. Eyes not large (OI = 22.47–28.47), MR usually ≥ 1.05, MOD ranging from 0.25–0.30x HL. Base of scape not flattened; superior and inferior lobes poorly developed, no wider than width of base of scape.

Mesosoma as described above, propodeum unarmed; in side view, juncture of propodeum and propodeal declivity rounded to subangulate, sides and dorsal surface rugose or rugae absent near mid-line, shining, posterior surface smooth and strongly shining. Petiolar peduncle long, ventral margin straight. In side view, petiolar node asymmetrical with anterior surface shorter than posterior surface. Apex of node moderately to strongly angulate, anterior edge of posterior face sometimes curved upward forming a crest. Postpetiole broader than long. Posterior face of petiole and dorsum of postpetiole weakly to moderately granulate or with weak transverse rugae, sub-shining to shining. Gastric tergites smooth and shining. Most body surfaces with moderately abundant coarse suberect to erect setae. Entire body concolorous light to dark ferruginous orange, except for incomplete to complete darker transverse bands on one or more gastric tergites.

Male

Diagnosis. Mandible with four teeth on suboblique cutting margin. Mandibular dorsum, clypeus, and antennal scapes lacking sculpture (mandibular dorsum occasionally with faint striae), mostly smooth and shining except for scattered punctures; anterior margin of clypeus weakly concave, lateral lobes indistinct. Eye not unusually large (MOD ≤ 0.50, OI ≤ 39.4, MR ≥ 0.38) (Figure 8).

Measurements (mm)—(*n* = 2). HL 1.15–1.25; HW 1.27–1.30; MOD 0.49–0.50; OMD 0.19–0.20; SL 0.54–0.56; HFL 1.43–1.56; ML 2.08–2.26; PW 0.54–0.58; PPW 0.65–0.73. Indices: SI 42.52–43.08; CI 104.00–110.43; OI 37.69–39.37; HFI 112.60–120.00.

Description. Mandible with four teeth on suboblique cutting margin; tip of sub-apical tooth sometimes weakly bifid; basal tooth not offset; mandibular dorsum as described above. Anterior margin of clypeus broadly and shallowly concave, mostly smooth and shining except for scattered punctures, lateral lobes indistinct. Antennal scapes reaching to or near posterior margin of eye, mostly smooth and shining. Cephalic rugae fine and close, slightly wavy to irregular, interrugae weakly punctate, moderately shining.

In profile, anterior face of mesonotum forming a mostly straight line with pronotum, slightly less than one-half as long as dorsal surface. In side view, juncture between propodeum and propodeal declivity subangulate, without spines or denticles. Sides of pronotal collar superficially rugoreticulate to punctate-granulate; katepisternum partially to largely covered by very fine wavy to irregular longitudinal striae, sub-shining to shining. Mesonotum shiny with piligerous punctures, notauli weakly impressed. Propodeum mostly smooth and shining to microrugoreticulate, granulate, sub-shining. Ventral margin of petiolar peduncle straight. In side view, petiolar node broadly rounded, anterior surface longer than posterior surface, forming a mostly straight continuous to slightly curved profile with dorsal surface of petiolar peduncle. Dorsal surface of petiole smooth and shining with scattered punctures to microrugoreticulate, sub-shining. Postpetiole broader than long, dorsal surface mostly smooth, sub-shining to shining. Head, mesosoma, petiole, and postpetiole with moderately abundant flexuous white hairs, often similar in length to MOD. Gastric tergites smooth and shining, hairs shorter and less dense than on rest of body. Head and mesosoma brownish-orange, gaster a lighter ferruginous orange (Figure 8).

Type material: Holotype (worker) plus 27 paratypes. **UNITED STATES: *Arizona***: *Yuma Co*.: 0.2 km S Tacna, 125 m (22° 6.4'S 65° 36.8'W), May 14, 2010, leg. R.A. Johnson #4500. Nests were in Sonoran Desert habitat that was dominated by scattered individuals of *Larrea tridentata* and *Ambrosia dumosa*. The holotype is deposited in the MCZ. Paratypes (*n* = 27 workers) all from the same locality and date as the holotype and leg. R.A. Johnson #4500 are distributed as follows: MCZ (6w), LACM (3w), UCDC (3w), USNM (6w), WPMC (3w), RAJC (6w). Additional paratype series (RAJC), collected on June 24, 2009, include RAJ #4253 (6w) and RAJ#4255 (9w): all series have additional workers in ethanol.

Additional material examined*. UNITED STATES: *Arizona*:** *Maricopa Co.:** 12 mi E Sentinel, Jul 30, 1960, AC Cole AZ-519 (26w PARATYPES of *P. magnacanthus,* LACM). *Mohave Co.***:** Golden Shores, Sep 5, 1995, RA Johnson RAJ#691 (8w, RAJC); 0.3 mi W Golden Shores, May 18, 2010, 620', RA Johnson RAJ#4490 (6w, RAJC). *Yuma Co.***:** I-8 at Aztec Road, 490', Apr 26, 2012, RA Johnson #4919 (6w, RAJC). ***California*:** *Imperial Co*.: Coyote Wells, Jul 29, 1957, AC Cole CAL-305 (17w, LACM); El Centro to Jacumba, Jul 10, 1956, AC Cole

CAL-11 (3w PARATYPES of *P. magnacanthus*, LACM), CAL-12 (3w PARATYPES of *P. magnacanthus*, LACM); 14 mi W Winterhaven, Jul 28, 1959, AC Cole CAL-334A (6w PARATYPES of *P. magnacanthus*, LACM); 15 mi E Holtville, Jul 27, 1961, AC Cole CAL-394 (24w PARATYPES of *P. magnacanthus*, LACM). *Inyo Co.*: Death Valley National Monument at Ashford Mill, 0', Apr 28, 1952, WS Creighton no number (16w, 5aq, LACM), CR-226 (10w, 1aq, 1m, LACM), CR-417 (11w, 1aq, LACM), CR-618 (15w, 1aq, 1m, LACM); Death Valley National Park, Spring 2000, KE Anderson KEA#550 (3w, RAJC); 9.05 km W Panamint Springs, 4450', May 30, 2006, RR Snelling #06-006 (1w, RAJC); *Riverside Co.*: 21 mi E Indio, 1600', Apr 8, 1952, WS Creighton CR-324 (19w PARATYPES of *P. magnacanthus*, LACM). *San Bernardino Co.*: Needles, May 1905, WM Wheeler (3w, LACM); 3.5 mi N Pisgah Crater, 2270', May 11, 2010, RA Johnson RAJ#4488 (6w, RAJC), RAJ#4489 (6w, RAJC); 5.5 mi NW Pisgah Crater, 1890', May 4, 2010, RA Johnson RAJ#4493 (3w, RAJC), RAJ#4494 (5w, 1aq, RAJC); I-40 at Goffs Road, 2040', Sep 16, 2011, RA Johnson RAJ#4808 (6w, RAJC). *San Diego Co.*: Anza Borrego State Park, Palm Canyon, Apr 17, 1952, WS Creighton CR-559 (6w, LACM); Ocotillo Well, Aug 8, 1960, AC Cole CAL-366 (4w PARATYPES of *P. magnacanthus*, LACM). ***Nevada***: *Clark Co.*: 7 mi W Echo Bay, 1800', Apr 5, 1976, G & J Wheeler NEV-725 (3w, LACM); 4 mi SW Riverside, 1500', Apr 2, 1970, G & J Wheeler NEV#707 (3w, LACM); 5 km E Jean, Apr 26, 2009, 2780', RA Johnson RAJ#4222 (3w, RAJC), RAJ#4223 (3w, RAJC); Valley of Fire, 2100', Mar 14, 1970, G & J Wheeler NEV#640 (3w, LACM), NEV#631 (3w, LACM); Valley of Fire, 2000', NEV#645 (2w, LACM); W base of Mormon Mesa, 1500', Apr 3, 1970, G & J Wheeler NEV#720 (3w, LACM), NEV#716 (3w, LACM); 3 mi W Cottonwood Cove, 1200', Dec 10, 1970, G & J Wheeler NEV-1498 (3w, LACM). *Nye Co.*: Mercury, Jul 11, 1961, #5AA1C (1w, LACM), May 24, 1961, #5EA7C (1w, LACM); Pahrump, spring 2000, KE Anderson KEA#532 (3w, RAJC); 2 mi N Pahrump, 2700', Apr 4, 1970, G & J Wheeler NEV-740 (2w, LACM); Beatty, Jul 17, 1954, AC Cole, NEV-374 (6w, LACM), NEV-375 (4w, LACM), NEV-376 (6w, LACM), NEV-377 (22w, LACM), NEV-380 (2w, LACM); Hwy 95 at 4.0 mi NW Lathrop Wells, 2610', Apr 17, 2009, RA Johnson RAJ#4216 (6w, RAJC), RAJ#4217 (9w, RAJC); Rock Valley, 9 mi ENE Lathrop Wells, Apr 14, 1970, G & J Wheeler, NEV-781 (9w, LACM). **MEXICO**: ***Baja California***: Valle San Felipe, May 10, 1998, RA Johnson RAJ#BC 1376 (9w, RAJC), RAJ#BC 1377 (9w, RAJC). ***Sonora***: Pinacate Desert, no date, 1982, IR López Moreno #F-11 (2w, LACM), #F-16 (8w, LACM); Puerto Peñasco, 50', Jul 15, 1950, WS Creighton #308 (30w, LACM), #304 (3w, LACM); 11.5 mi E Puerto Peñasco, July 17, 2009, RA Johnson RAJ#4274 (9w, RAJC), RAJ#4278 (3w, RAJC), RAJ#4281 (9w, RAJC).

Etymology. The specific epithet honors Prof. Dr. Bert Hölldobler, who was an "ant god" during the tenure of RAJ in graduate school and beyond—and who now is a good friend, colleague, collaborator, and supporter who is dedicated to understanding all aspects of ant biology. His continued child-like enthusiasm for learning about ants and his earnest interest in helping students invigorate all of those around him.

Discussion. *Pogonomyrmex hoelldobleri* is most likely to be confused with *P. magnacanthus*, especially given the large number of series that A.C. Cole erroneously identified as *P. magnacanthus*. The two species occur sympatrically in several locales. The significantly larger eye (MOD and OI) separates *P. magnacanthus* from *P. hoelldobleri* (Figures 2-3). OI is the best character to separate the two species because it is consistently higher for *P. magnacanthus* (OI = 27.22-33.61) than for *P. hoelldobleri* (OI rarely $\geq$ 27.50)(Figure 3). The malar ratio is usually $\leq$ 1.0 for *P. magnacanthus*, while this ratio is usually > 1.05 for *P. hoelldobleri* (Figure 3).

Pogonomyrmex hoelldobleri also occurs in sympatry with *P. californicus* and is likely to occur in sympatry with *P. mohavensis*, but it has a low likelihood of co-occurring with *P. maricopa*. *Pogonomyrmex hoelldobleri* can be distinguished from *P. mohavensis* based on the following characters: (1) *P. hoelldobleri* has seven teeth, (2) the interrugal spaces on the pronotal shoulders are weakly to strongly punctate/granulate, dull to sub-shining, and (3) the cephalic rugae typically converge near the vertex. In *P. mohavensis*, the mandible has six teeth (a seventh sometimes occurs as a denticle between the basal and sub-basal teeth), interrugal spaces on the pronotal shoulders are smooth and shining, and the cephalic rugae extend more or less directly to the vertex or converge only slightly near the vertex. Two other *P. californicus* group species (*P. anzensis* and *P. snellingi*) also occur in the Sonoran and Mohave Deserts, but it is doubtful that *P. hoelldobleri* occurs sympatrically with either species; *P. anzensis* occurs in unproductive, rocky hillside habitats unlike any sites that are known to be occupied by *P. hoelldobleri*, while *P. snellingi* is well removed from the probable geographic distribution of *P. hoelldobleri*. Regardless, the absence of circumocular whorls separates *P. hoelldobleri* from both species.

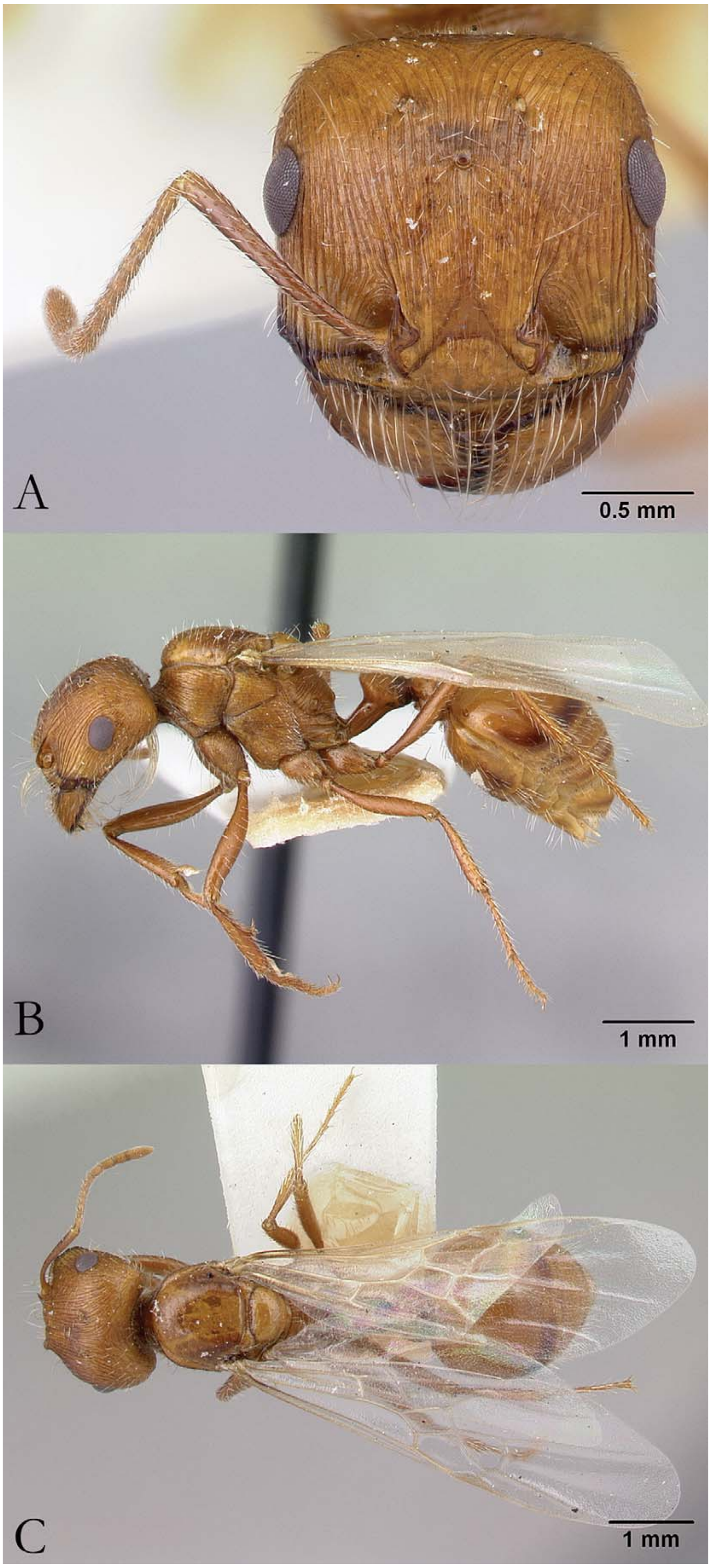

FIGURE 7. Photograph of *Pogonomyrmex hoelldobleri* Johnson, Overson & Moreau alate queen: **(A)** frontal view of head, **(B)** lateral view of body, and **(C)** dorsal view of body.

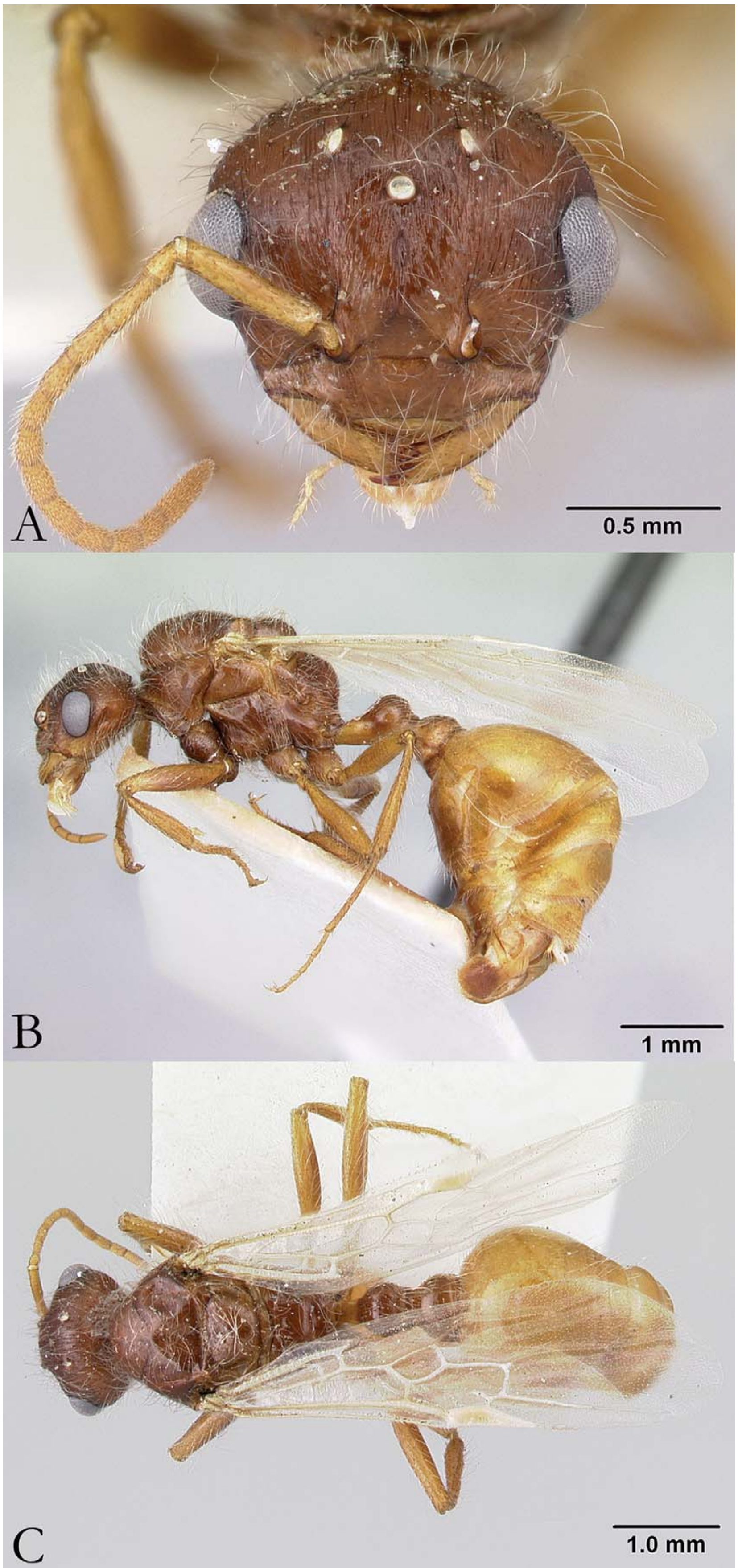

FIGURE 8. Photograph of *Pogonomyrmex hoelldobleri* Johnson, Overson & Moreau male: **(A)** frontal view of head, **(B)** lateral view of body, and **(C)** dorsal view of body.

Pogonomyrmex mohavensis **Johnson**
(Figures 2, 9)

Pogonomyrmex mohavensis was described from workers at several locations in California and Nevada (Johnson & Overson, 2009). Alate queens were recently collected from a nest in California: Kern County, Hwy 43 at 17.6 km N Wasco, Sept 15, 2011; 35º45.0'N 119º20.7'W, 80 m (RAJ #4805; specimens in RAJC), and they are described herein. The nest was in disturbed roadside habitat surrounded by agricultural fields. Workers in this nest were significantly larger than those collected at previous locations; HW ranged from 1.31–1.67 mm in the description of the species, while those at the present location ranged from 1.91–2.05 mm (*n* = 9).

Worker.
Diagnosis. Pogonomyrmex mohavensis is characterized by: (1) cephalic rugae not forming circumocular whorls, but rather extending more or less directly to the vertex or converging only slightly near the vertex, (2) mandible with six teeth (a seventh sometimes occurs as a denticle between the basal and sub-basal teeth), and (3) interrugal spaces on pronotal sides smooth and shining to slightly punctate and moderately shining.

Queen
Diagnosis. As in worker diagnosis, but with caste-specific structures related to wing-bearing, presence of small ocelli on head, and as illustrated in Figure 9. Mandible with six teeth or with a seventh tooth that occurs as a denticle between the basal and sub-basal teeth. All mesosomal surfaces except for mesoscutum and mesoscutellum with prominent rugae; sculpturing absent on mesoscutum and mesoscutellum except for scattered punctures or with faint longitudinal striae. Posterior face of petiole with coarse transverse, oblique, or longitudinal rugae, dorsum of postpetiole with weaker transverse rugae. Base of scape noticeably flattened; superior and inferior lobes very well developed, wider than width of scape base.

Measurements (mm)—(*n* = 2). HL 1.91–1.95; HW 2.01–2.08; MOD 0.43–0.43; OMD 0.49–0.57; SL 1.36–1.38; PNW 1.52–1.62; HFL 1.91–2.00; ML 2.60–2.70; PW 0.74–0.74; PPW 0.89–0.90. Indices: SI 66.35–67.66; CI 105.24–106.67; OI 20.67–21.39; HFI 95.02–96.15.

Description. As in worker diagnosis, but with caste-specific structures related to wing-bearing, presence of small ocelli on head, and as illustrated in Figure 9. Dorsum and sides of head with strong, widely spaced rugae, in side view rugae converging near or slightly anterior to vertex, interrugal spaces smooth and strongly shining. In full-face view, head slightly broader than long, posterior margin flat. Mandible with six teeth on one queen, the other with a seventh tooth that occurred as a denticle between the basal and sub-basal teeth (Figure 9), dorsal surface coarsely rugose, strongly shining. Eye not large (OI = 20.67–21.39), MOD ranging from 0.22–0.23x HL. Base of scape noticeably flattened; superior and inferior lobes very well developed, wider than width of scape base.

Mesosoma as described above, propodeum unarmed; in side view, juncture of dorsum of propodeum and propodeal declivity rounded to subangulate, sides and dorsal surface rugose, shining, posterior surface smooth and strongly shining. Petiolar peduncle long, ventral margin straight. In side view, petiolar node asymmetrical with anterior surface shorter than posterior surface. Apex of node weakly rounded. Postpetiole broader than long. Posterior face of petiole with coarse transverse, oblique, or longitudinal rugae, dorsum of postpetiole with weaker transverse rugae, interrugal spaces weakly to moderately punctate, sub-shining. Gastric tergites weakly coriarious to mostly smooth and shining. Most body surfaces with moderately abundant coarse suberect to erect white setae. Entire body concolorous light to dark ferruginous orange.

Male. Unknown.

Discussion. The queens of *P. mohavensis* and *P. hoelldobleri* are very similar. The best characters to separate queens of these two species appear to be: (1) number of teeth (seven in *P. hoelldobleri*, six or with a seventh tooth that occurs as a denticle between the basal and sub-basal teeth in *P. mohavensis*), (2) sculpturing (posterior face of petiole and dorsum of postpetiole weakly to moderately granulate or with weak tranverse rugae in *P. hoelldobleri*; posterior face of petiole with coarse transverse, oblique, or longitudinal rugae, dorsum of postpetiole with weaker transverse rugae in *P. mohavensis*), and (3) conformation of the base of the scape (base of scape rounded, superior and inferior lobes poorly developed in *P. hoelldobleri*; base of scape noticeably flattened, superior and inferior lobes well developed in *P. mohavensis*). The queens of *P. mohavensis* also were significantly larger (HW = 2.01–2.08 mm) than those of *P. hoelldobleri* (HW = 1.44–1.79 mm). However, these queens of *P. mohavensis* are likely to be significantly larger than those in other parts of their range where the workers are much smaller.

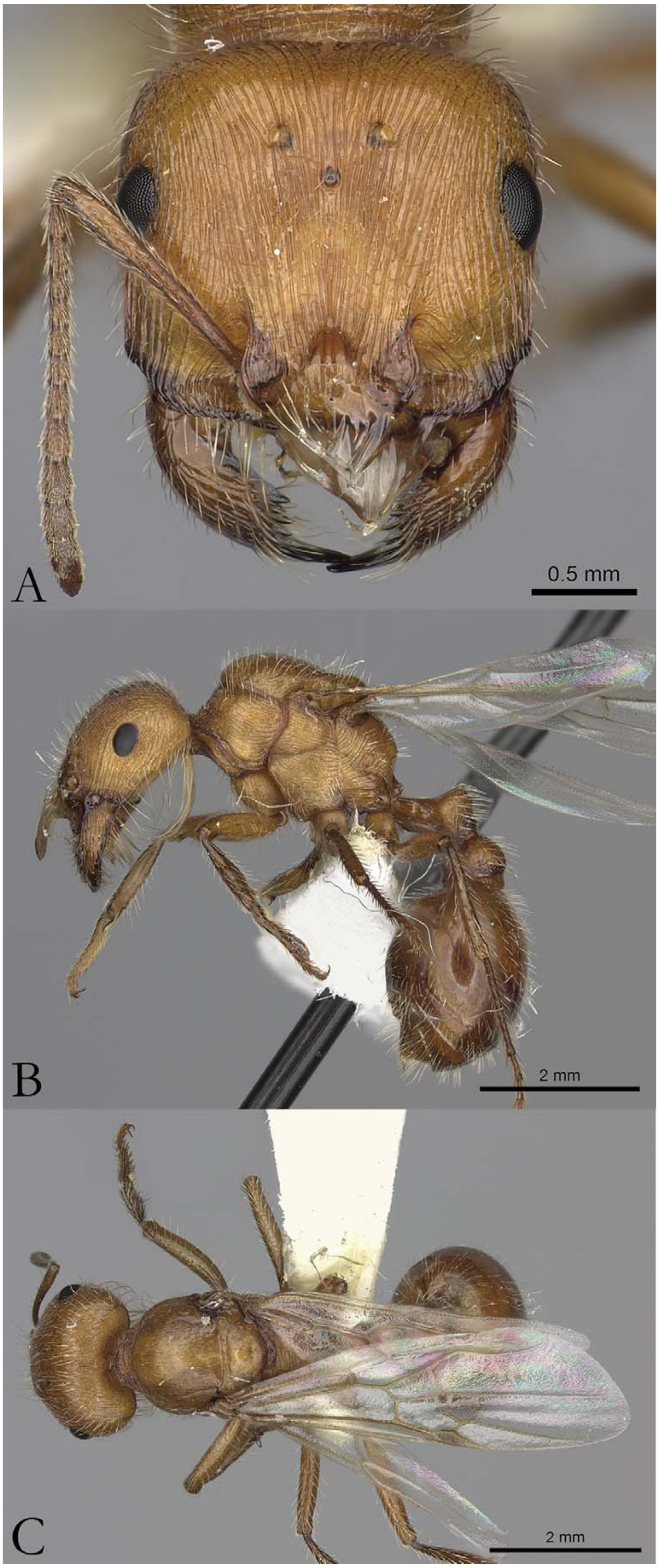

FIGURE 9. Photograph of *Pogonomyrmex mohavensis* Johnson alate queen: **(A)** frontal view of head, **(B)** lateral view of body, and **(C)** dorsal view of body.

Phylogenetic data

The aligned fragment contained 3268 constant sites (88.3%), 137 variable non-parsimoniously informative sites (3.7%) and 298 parsimoniously informative sites (10.7%). The Bayesian inference topology for the partitioned analysis is presented in Figure 10 with support values for the Bayesian posterior probabilities (BPP) and maximum likelihood bootstrap (ML BS) using both the partitioned and single analyses. All partitioning schemes in both the Bayesian analyses and maximum likelihood resulted in nearly identical topologies with only two weakly supported clades in conflict (represented on Figure 10 by "--" denoting support values below 50%). All Bayesian inference and maximum likelihood tree topologies showed strong support (1.0 BPP partitioned; 1.0 BPP single; 95% ML BS partitioned; 95% ML BS single) for the monophyly of *P. magnacanthus*, *P. mohavensis*, and the new species *P. hoelldobleri* (Figure 10).

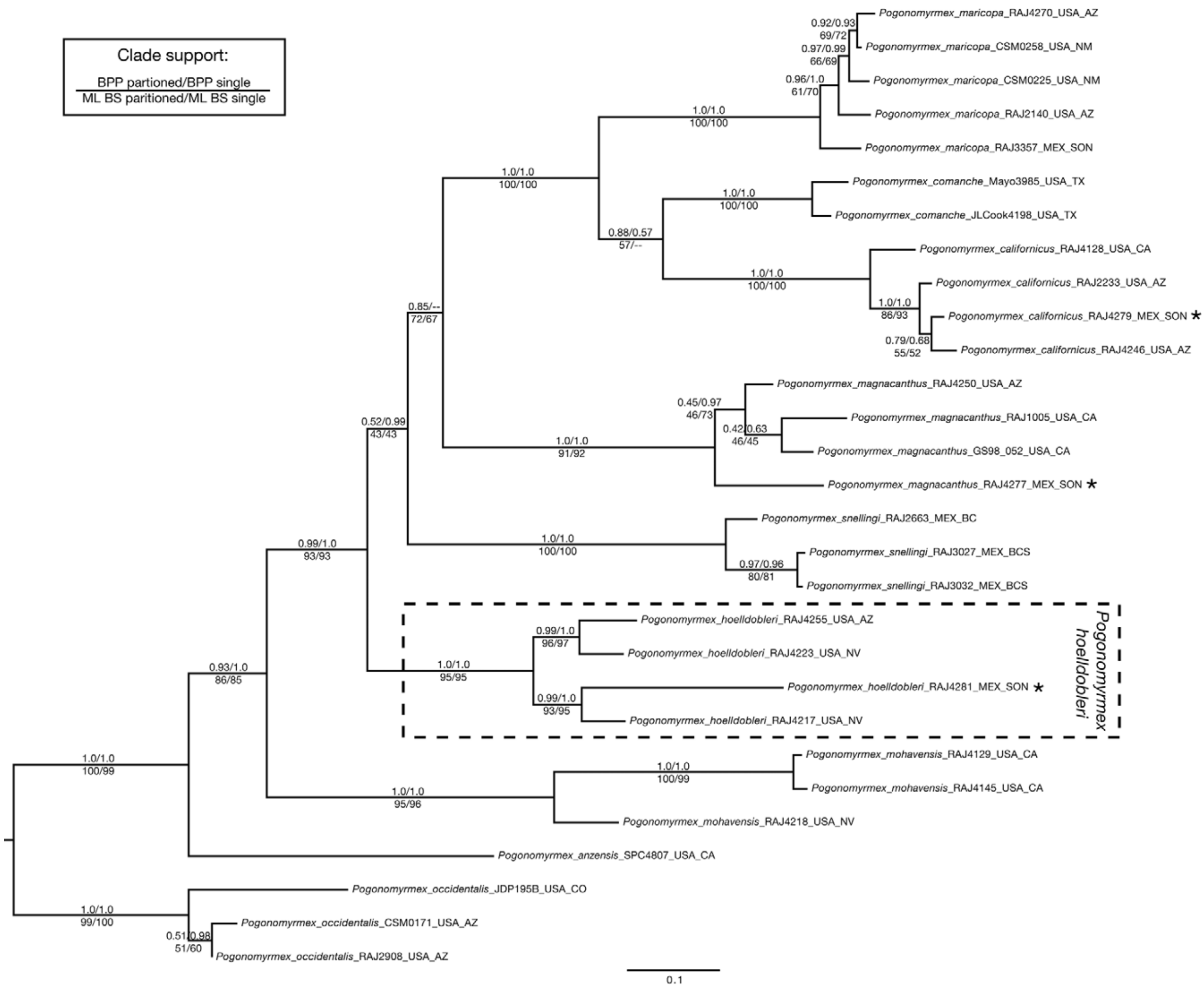

FIGURE 10. Phylogram of species in the *Pogonomyrmex californicus* group as inferred through Bayesian analysis for the partitioned dataset. Specimens of *P. hoelldobleri* are in the dashed box. Branch lengths are proportional to substitution/site as indicated by the bottom legend inset. Clade support greater than 50% is denoted on branches and in the top insert as follows: values above and below branches represent Bayesian posterior probabilities (BPP) and maximum likelihood bootstrap (ML BS), respectively, for the partitioned dataset followed by the single dataset. Clade support of "--" denotes clades not supported in an individual analysis. Numbers following each species name refer to the accession number of the series from which the individual was taken; locale data are given for each series in Table 1. *Pogonomyrmex californicus*, *P. hoelldobleri*, and *P. magnacanthus* occurred sympatrically at one site (designated by an *).

Biology

The large series of workers and the small number of alate queens, combined with morphological data, genetic data, and collection of sympatric colonies of *P. magnacanthus* and *P. californicus* provide strong evidence that *P. hoelldobleri* is a valid species, and provides evidence to justify a formal description. *Pogonomyrmex hoelldobleri* also appears to be the undescribed species that has been known to exist for about twenty years and has been referred to by some authors as *Pogonomyrmex* sp. B (Johnson, 2000; Taber, 1990, 1998).

The biology of *P. magnacanthus and P. hoelldobleri* appear to be very similar, and are thus discussed together. In both species, the nests are variable and can range from a nest entrance that lacks a tumulus to a tumulus that ranges from 3–15 cm in diameter; the nest entrance commonly lacks a tumulus in *P. hoelldobleri*. Nests are typically placed in open exposed sites, but can be difficult to locate because of their small size or absence of an external tumulus. In such cases, nests are most easily located by baiting foragers, then following them back to the nest. Workers of both species forage solitarily during the day, harvesting seeds and related items. Colonies of *P. magnacanthus* contain relatively few workers; Cole (1968) estimated that colony size ranged from 100–225 workers, which accords with observations of the senior author. Colonies of *P. hoelldobleri* are also small and appear to contain no more than 300–400 workers (R.A. Johnson, pers. obs.).

Reproductive sexuals of *P. magnacanthus, P. hoelldobleri,* and *P. mohavensis* have been collected infrequently (a total of 3 alate queens and 4 males for *P. magnacanthus,* 8 alate queens and 2 males plus one male pupae for *P. hoelldobleri*, and 2 alate queens for *P. mohavensis*); collection dates range from 26 March to 13 June for *P. magnacanthus* and from 23 April to 5 May for *P. hoelldobleri*. Mating flights have not been observed for either species, but they are predicted to be similar to those of *P. californicus*, in which flights are triggered by cues such as photoperiod, temperature, or humidity (but not rain-triggered as in most species of *Pogonomyrmex*), and they likely take place over several weeks during late spring to early summer (Johnson, 2000). Alate queens of *P. mohavensis* were collected on 15 September; several nests of *P. californicus* in the vicinity of this collection also contained alate queens on this date, and these queens were observed outside the nest preparing for their mating flight. Thus, in the central valley area of California, mating flights for *P. californicus* and *P. mohavensis* appear to be up to several months later than those in other parts of their geographic ranges.

Both *P. magnacanthus* and *P. hoelldobleri* are restricted to hot desert habitats (Wheeler & Wheeler, 1973) in the Mohave and Sonoran Deserts of southeastern California, western Arizona, northwestern Sonora, Mexico, and the San Felipe Desert of Baja California, Mexico; the range of *P. hoelldobleri* also extends further north into southern Nevada (Figure 11). Current records indicate that the geographic range of *P. magnacanthus* is more restricted than previously believed (Figure 11), especially given that this study transferred all Nevada records (see Wheeler & Wheeler, 1986) to *P. hoelldobleri* (see below). *Pogonomyrmex magnacanthus* inhabits sites at elevations that range from approximately 5–855 m, while *P. hoelldobleri* is known from elevations that range from 0–1350 m. The two species have broadly overlapping geographic distributions and occur in sympatry at several locales (Figure 11), but preferred microhabitat differs for the two species. *Pogonomyrmex magnacanthus* is largely restricted to sand dunes, interdune habitats, and other areas with a loose sand substrate (Cole, 1968; Johnson, 2000), whereas *P. hoelldobleri* sometimes occurs in loose sandy soils, but it is most common in relatively compact sandy or gravelly alluvial soils.

Identification of workers for species in the *P. californicus* group

Identification of species in the *P. californicus* group can be challenging given the considerable degree of morphological variation, both within and among nests (see Cole, 1968; Ward, 2005). In the experience of RAJ, and as noted by Cole (1968), it is particularly important to observe these species in the field because characters such as nest structure, nest sites, microhabitat, and behavior provide valuable information to make an accurate identification. Such observations and collections are especially helpful when difficult to identify species occur in sympatry (e.g., *P. magnacanthus* and *P. hoelldobleri*, *P. mohavensis* and *P. californicus, P. hoelldobleri* and *P. californicus*, and *P. maricopa and P. californicus*).

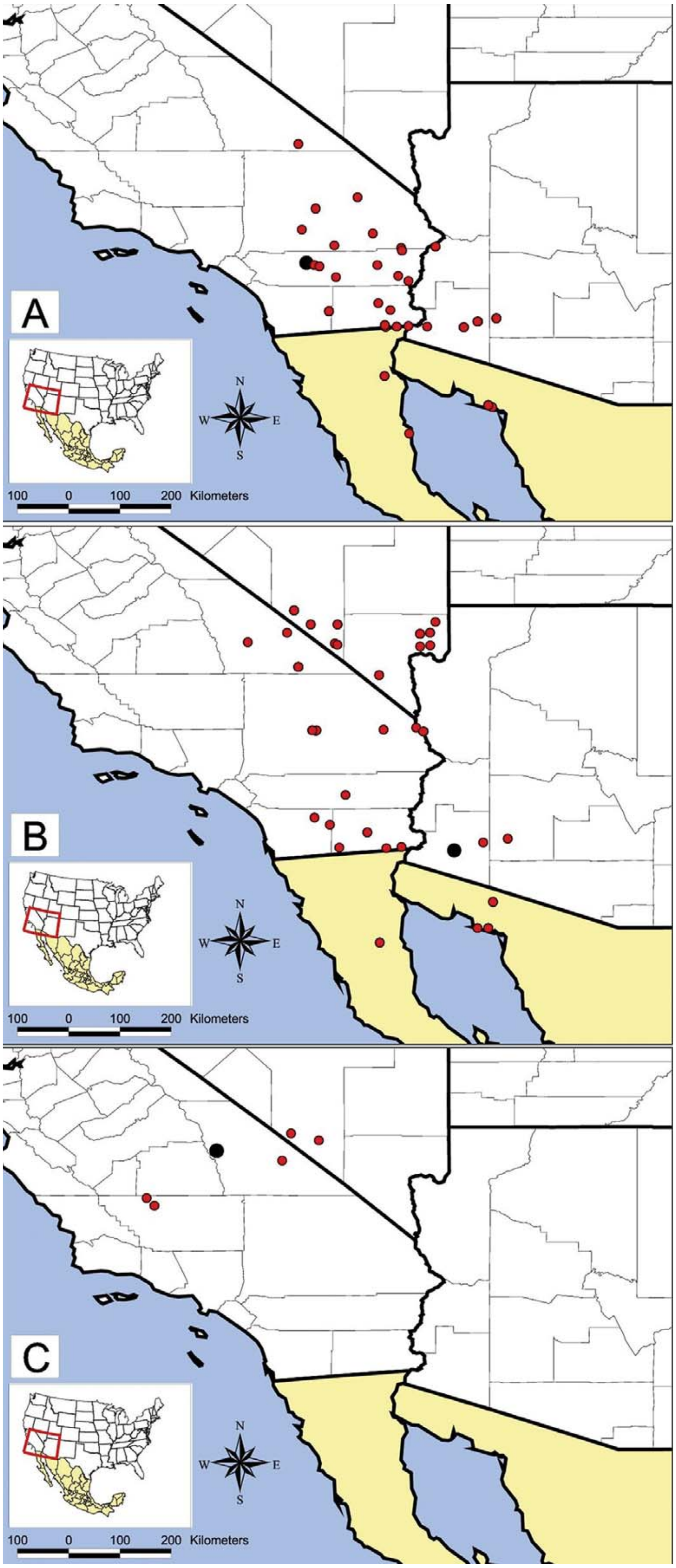

FIGURE 11. Geographic distribution of: (**A**) *Pogonomyrmex magnacanthus* Cole, (**B**) *Pogonomyrmex hoelldobleri* Johnson, Overson & Moreau, and (C) *Pogonomyrmex mohavensis* Johnson; the larger filled black circle in each panel denotes the type locality. All three maps are drawn on the same geographic area so that distribution patterns are directly comparable.

Circumocular whorls, which are generally considered to be a diagnostic character for species in the *P. californicus* group (e.g., Cole, 1968), are an especially noteworthy character that causes problems during identification. The problem relates to the fact that circumocular whorls are lacking in two species (*P. hoelldobleri* and *P. mohavensis*), and they are highly variable and sometimes lacking in other species (e.g., *P. maricopa* and *P. californicus*).

Tooth number is also an important character for separating *P. hoelldobleri* and *P. mohavensis*, but most series of *Pogonomyrmex* consist of foragers, and these older workers typically have substantial mandibular wear that might negate using this character; pinning specimens such that teeth are not easily visible presents an additional problem. Moreover, at least several workers from each nest series should be examined when attempting identification. Collectors should also locate and excavate nests so as to collect series that include non-foragers. Lastly, it is recommended that collectors search sites to locate possible sympatric congeners, which will significantly reduce problems during identification.

Key to the workers in the *Pogonomyrmex californicus* group from central and western North America

(*P. anzensis* is included, though it may not belong in this species group)

1 Basal tooth strongly offset from basal margin; diastema present between basal and sub-basal teeth, mandible sometimes with eight teeth when a very small tooth occurs in diastema . . . . ***snellingi***

\- Basal tooth not offset, lacking diastema between basal and sub-basal teeth **2**

2 Dorsum of petiolar node, viewed from side, distinctly flattened, and viewed from above, with strong widely spaced wavy, subparallel rugae and usually a distinct, broad, shallow, longitudinal depression; propodeum armed with short to long spines; cephalic interrugal punctures prominent . . . . ***comanche***

\- Dorsum of petiolar node, viewed from side, not flattened, and viewed from above, lacking strong, widely spaced, wavy, subparallel rugae and a broad, shallow longitudinal depression; propodeal armature present or absent; cephalic interrugal punctures absent to prominent **3**

3 Mandible with six teeth <u>*and*</u> circumocular whorls present; venter of postpetiole with a strong, triangular tooth. . . . . ***anzensis***

\- Mandible with seven teeth <u>*or*</u> mandible with six teeth <u>*and*</u> cephalic rugae extending to vertex in side view, not forming circumocular whorls; venter of postpetiole lacking a strong triangular tooth. **4**

4 In side view, eye unusually large, OI usually $\geq$ 28.5 and malar ratio usually $\leq$ 1.0; circumocular whorls usually present, though sometimes indistinct . . . .***magnacanthus***

\- In side view, eye not unusually large, OI < 27.5 and malar ratio usually $\geq$ 1.05; circumocular whorls present or absent **5**

5 Propodeal spines absent or with a pair of angles, denticles, or short to long spines; cephalic interrugal punctulation rather strong <u>*and*</u> interrugal punctulation of mesepisternum moderate to strong; rugae on mesepisternum often indistinct; interrugal spaces dull to weakly shining in both areas; circumocular whorls usually present; posterior declivity of propodeum with transverse rugae, not smooth and strongly shining . . . . ***maricopa***

\- Propodeal spines absent; cephalic interrugal punctulation absent to weak <u>*and*</u> interrugal punctulation of mesepisternum absent to moderately strong; rugae on mesepisternum usually distinct; interrugal spaces moderately to strongly shining in both areas; circumocular whorls present or absent; posterior declivity of propodeum lacking transverse rugae, smooth and strongly shining **6**

6 Mandibles with six teeth, a seventh small (subequal) tooth sometimes present between basal and sub-basal teeth; cephalic rugae extending more or less directly to the vertex in side view, not converging posterior to eyes or forming circumocular whorls; gaster concolorous with head and mesosoma . . . . ***mohavensis***

\- Mandibles with seven teeth; cephalic rugae forming circumocular whorls <u>*or*</u> rugae (sometimes faint) converge at or near vertex, but not forming circumocular whorls; gaster black or concolorous with head and mesosoma **7**

7 Circumocular whorls almost always present, occasional individuals with rugae converging toward vertex; area posterior to eyes always with distinct rugae; interrugal spaces on pronotal sides smooth and shining, rarely weakly granulate; gaster black or concolorous with head and mesosoma . . . . ***californicus***

\- Circumocular whorls absent, cephalic rugae converging near vertex <u>*or*</u> area posterior to eye with very faint rugae; interrugal spaces on pronotal sides moderately to strongly granulate, dull to weakly shining; gaster concolorous with head and mesosoma . . . . ***hoelldobleri***

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