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A taxonomic revision and a review of the biology of the North American seed-harvester ant genus *Veromessor* (Hymenoptera: Formicidae: Myrmicinae)

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ROBERT A. JOHNSON, MAREK L. BOROWIEC, ROY R. SNELLING & ARTHUR C. COLE
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Abstract

This paper provides a taxonomic revision and a review of the biology for the 10 species of North American seed-harvester ants in the genus *Veromessor*. Two new synonymies are proposed: *V. julianus* subsp. *clarior* W.M. Wheeler and Creighton 1934 **new synonym** and *V. julianus* subsp. *manni* W.M. Wheeler and Creighton 1934 **new synonym** are synonymized under *V. julianus* (Pergande, 1894). One new species is described: *V. pseudolariversi* **new species** (worker, queen, male), as a result of splitting *V. lariversi* Smith into two species based on morphological and genetic differences. We also diagnose previously undescribed queens and males for the following species: *V. andrei* (male), *V. chamberlini* (queen, male), *V. chicoensis* (queen, male), *V. julianus* (queen, male), and *V. stoddardi* (queen, male). Information on biology of each species is summarized, along with distribution maps and keys to workers, queens, and males. We then discuss the biology for species of *Veromessor*, focusing on several morphological and ecological traits that display strong variation across the relatively low number of species (10) in the genus. Morphological traits include degree of psammophore development, propodeal spine length, eye size and structure, and worker polymorphism and worker body size, while ecological traits include colony size and foraging method, seasonality of mating flights, mating frequency, and queen size and colony founding strategy.

Key words: ant biology, granivory, seed-harvesting ants, North America, species key, taxonomy, *Veromessor*

Preface

The senior author received a copy of an unfinished manuscript by Roy R. Snelling and Arthur C. Cole, Jr. during a

visit to the Los Angeles County Museum of Natural History in 1992. We have greatly expanded the original version of the manuscript, and we are happy to publish another one of Roy's unfinished contributions to Hymenoptera systematics.

Introduction

The ant genus *Veromessor* (subfamily Myrmicinae, tribe Stenammini) consists of 10 species that are restricted to arid and semiarid habitats in the western United States and northwestern Mexico, with the exception of one species (*V. lobognathus*) that extends into the northcentral United States (Bennett, 2000; Bolton, 2020; Johnson, 2000b). All species are granivorous such that they collect a large variety and number of seeds and impact plant communities (Brown & Human, 1997; Davidson, 1977, 1978; Gordon, 1978; Rissing, 1988). Species of *Veromessor* have received considerable attention from ecologists and behaviorists because of their seed gathering activities combined with the fact that workers are docile and unable to sting. These studies mostly have focused on *V. andrei* and especially *V. pergandei* (Brown, 1999a, 1999b; Johnson, 1992, 2021; Muscedere, Helms Cahan, Helms, & Traniello, 2016; Rissing, 1987; Rissing & Pollock, 1987; Rytí & Case, 1988a), while biology is poorly known for other congeners, especially those with small colonies.

Veromessor has been the subject of two reviews that included descriptions of species and subspecies along with natural history observations (Creighton, 1953; Wheeler & Creighton, 1934). The only other substantive taxonomic work was reconstructing a phylogeny of *Veromessor* and related genera using morphology of workers and sexual castes (Bennett, 2000). However, Bennett (2000) did not diagnose or describe sexual castes or review biology of the species. This revision describes one new species, synonymizes two infraspecific forms, provides a diagnosis for workers and sexual castes of all species, and reviews biology of each species in orders to facilitate research on the rich and interesting ecology, life history, and evolution of this genus. From an evolutionary perspective, *Veromessor* is interesting because several morphological and ecological traits vary across species despite the relatively few species in the genus and a recent divergence time, about 11 mya (Branstetter, Longino, Reyes-López, Brady & Schultz, 2022). Variable morphological traits include degree of psammophore development, propodeal spine length, eye size and structure, and worker polymorphism and worker body size, while variable ecological traits include colony size and foraging method, seasonality of mating flights and mating frequency, and queen size and colony founding strategy (see Bennett, 2000; Johnson, 2000a, 2000b, 2021). We discuss these traits across species to provide a framework to examine evolution of these traits in a companion paper.

Here we provide a taxonomic revision of the genus including identification keys to all castes. We re-evaluate previously proposed infraspecific forms and describe a new species, recognizing a total of 10 valid *Veromessor* species, and we summarize the known biology for each species. Our taxonomic actions are based on examination of morphology and preliminary phylogenetic data using Ultraconserved Elements (UCEs) (M.L. Borowiec, unpub. data, Faircloth, McCormack, Crawford, Harvey, Brumfield & Glenn, 2012).

Historical resume

The generic status of *Veromessor* has been problematic for most of its history as the species currently constituting it have been placed in five genera (*Aphaenogaster*, *Messor*, *Novomessor*, *Stenamma*, *Veromessor*), all of which are now within the tribe Stenammini (Ward, Brady, Fisher, & Schultz, 2015). Mayr (1886) described the first two species as *Aphaenogaster* (*A. andrei* and *A. pergandei*), which was followed by the description of *A. juliana* (Pergande, 1894). Soon thereafter, Emery (1895) described *Stenamma stoddardi* within the new subgenus *Messor*, and he also moved *A. andrei*, *A. julianus*, and *A. pergandei* to this subgenus.

Generic status changed several more times from 1915 to 1922. Wheeler (1915) described *Messor chamberlini* and elevated *Messor* to generic status. Two years later, Forel (1917) created *Veromessor* as a subgenus of *Novomessor*, and Emery (1921) designated *V. andrei* as the type species of the genus while it was still a subgenus of *Novomessor*. In his key to genera and subgenera of African ants, Wheeler (1922) separated *Veromessor* from *Messor* and raised *Veromessor* to generic status for the first time. His separation of the two genera was based on wing venation of sexuals, noting that species of *Veromessor* had forewings with one cubital cell, while species of *Messor* had forewings with two closed cubital cells. Wheeler and Creighton (1934) revised the genus that then comprised

seven species, and added two new subspecies to *V. andrei*, two new subspecies to *V. julianus*, and transferred the Haitian species *Aphaenogaster relictus* to *Veromessor*. This latter species was unique within *Veromessor* for three reasons: (1) it was the first time that a non-xerophilic ant was placed in *Veromessor*, (2) it was the only species of *Veromessor* that occurred outside of western North America, and (3) it is the only species assigned to *Veromessor* that does not belong there because it better fitted the diagnostic characters for *Aphaenogaster*, to where it was later transferred (Bolton, 1982). *Veromessor* was later synonymized as a subgenus of *Novomessor* (Donisthorpe, 1943). This was followed by Enzmann (1947) placing *Lobognathus* as a subgenus to *Novomessor* in a key. This label reading “*lobognathus* new subspecies” and *Lobognathus* was soon synonymized with *Veromessor* (Brown, 1949).

In his “Ants of North America”, Creighton (1950) again elevated *Veromessor* to generic status, but treated only species in the United States, i.e., all but *V. julianus* and *V. relictus*, and provided a key to species in the United States. Smith (1951) described *V. lariversi* from Nevada and *V. stoddardi chicoensis* from northern California (Smith, 1956), with the latter paper providing another key to workers in the United States. *Veromessor smithi* was the last species to be described (Cole, 1963).

Veromessor retained generic status for another two decades, when Bolton (1982) synonymized *Veromessor* with the Old World genus *Messor*; he also moved *V. relictus* to *Aphaenogaster*. Interestingly, the synonymy by Bolton (1982) was based on patterns of wing venation, which was the same character that Wheeler (1922) used to separate the two genera. However, with more material available, Bolton (1982) found a sequence of venation patterns that occurred in both *Veromessor* and *Messor*—hence, demonstrating that wing venation had no significance in discriminating between these two genera. Consequently, Bolton (1982) synonymized *Veromessor* under *Messor*. Most recently, a molecular phylogeny demonstrated that North American *Messor* were distantly related to Old World *Messor*, but that both genera belonged to the Stenammmini clade, resulting in resurrecting the genus *Veromessor* and its nine species (Ward *et al.*, 2015). Molecular data also demonstrated that *Veromessor* is most closely related to *Novomessor* (Branstetter *et al.*, 2016; Ward *et al.*, 2015), with the latter genus also recently resurrected from synonymy with *Aphaenogaster* (Demarco & Cognato, 2015).

Overall, the most substantial and influential studies on *Veromessor* were made by several taxonomists that also studied natural history of *Veromessor*. These people included William Morton Wheeler (Wheeler & Creighton, 1934), George and Jeanette Wheeler (Wheeler & Wheeler, 1986; Wheeler & Rissing, 1975a; Wheeler & Rissing, 1975b), William Steele Creighton (Creighton, 1950, 1953), Arthur Cole (Cole, 1955, 1963, 1966), and Roy Snelling (Snelling & George, 1979).

Methods

Measurements and indices

Consistent with recent literature on ant morphology (e.g., Boudinot, Moosdorf, Beutel, & Richter, 2021; Keller, 2011), we consider ants to be prognathous. Consequently, we describe the orientation of structures and surfaces on the head capsule as anterior when close to the mandibles, dorsal when facing the observer in full-face view, posterior when close to the occipital margin (= posterior margin), and ventral when observing the underside of the head. The exception to this is eyes, where directionality is considered in full-face view, meaning that lower margin refers to the margin closer to the mandibles. Morphological characters were photographed using a Spot Insight QE camera attached to a Leica MZ 12₅ microscope. Images were then projected onto a video monitor, and characters were measured using ImageJ (available at <http://rsb.info.nih.gov/nih-image/>). Measurements were calibrated using photographs of an ocular micrometer scaled in 0.1 mm increments. All measurements are given in mm (minimum–maximum). The following 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 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 view.
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).

MR	Malar Ratio: (OMD/MOD).
AOD	Anterior Ocellar Diameter (male only): transverse diameter of the anterior ocellus.
IOD	Interocellar Distance (male only): minimum distance between inner margins of the posterior ocelli.
OOD	Ocello Ocular Distance (male only): minimum distance between the outer margin of posterior ocellus and the adjacent inner margin of the compound eye.
SL	Scape Length: maximum straight line length of the antennal scape from apex to base.
SI	Scape Index: (SL/HW) \times 100.
PNW	Pronotal Width (worker only): maximum width of pronotum, in dorsal view, 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 the most distal tip of the femur.
HFI	Hind Femur Index: (HFL/HW) \times 100.
ML	Mesosoma Length: diagonal length of the mesosoma in profile from the point at which the pronotum meets the cervical shield to the posterior base of the metapleural lobe. In queens and males, diagonal length from juncture of mesoscutellum and pronotum to the posterior base of the metapleural lobe.
PW	Petiole Width: maximum width of petiolar node, as seen in dorsal view, at a right angle to the longitudinal axis of the mesosoma.
PPW	Postpetiole Width: maximum width of postpetiole, as seen in dorsal view, at a right angle to the longitudinal axis of the mesosoma.

Note that the pronotum was not measured on queens because the mesoscutum typically extends to or over most of the segment, such that margins of the pronotum were rarely visible.

We use several consistent characters to diagnose castes of each species. These characters are presented in a numerical format that allows rapid comparison between species. Characters for workers and queens are: (1) color, (2) clypeal structure, (3) number of mandibular teeth, (4) scape, (5) eye size, (6) cephalic structure, (7) psammophore, (8) mesosomal sculpture, (9) propodeum, and (10) metasternal process. Characters for males are: (11) color, (12) clypeal structure, (13) mandible, (14) ocelli, (15) mesopleural sculpture, (16) propodeum, (17) metasternal process, and (18) subpetiolar process. Detailed redescrptions of *V. andrei*, *V. julianus*, *V. lobognathus*, *V. pergandei*, and *V. stoddardi* are given in Wheeler and Creighton (1934). All other species were described thereafter or herein.

Collections are referred to by the following acronyms:

CASC	California Academy of Sciences, San Francisco, California, USA
CIDA	College of Idaho, Caldwell, Idaho, USA
JTLC	Jack Longino collection, Salt Lake City, Utah, USA
LACM	Los Angeles County Museum of Natural History, Los Angeles, California, USA
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
MLBC	Marek L. Borowiec collection, Colorado State University, Fort Collins, Colorado, USA
MMPC	Matt M. Prebus collection, Tempe, Arizona, USA
NHMW	Naturhistorisches Museum, Vienna, Austria
RAJC	Robert A. Johnson collection, Tempe, Arizona, USA
UAIC	University of Arizona, Tucson, Arizona, USA
UCDC	University of California, Davis, California, USA
UCRC	University of California, Riverside, California, USA
USNM	National Museum of Natural History, Smithsonian Institution, Washington DC, USA

Roy Snelling provided the senior author with numerous locale records for *Veromessor* that were collected in Nevada by G.C. and J. Wheeler (Wheeler & Wheeler, 1986). A number of these series were not in loans that we examined, but we include their locale records in additional material examined with the source of the locale data. However, we excluded locale data on unexamined series of *V. lariversi* because of uncertainty regarding identity of these specimens (see below). In total, we examined approximately 1325 series of *Veromessor* for this revision.

Latitude and longitude data rarely were available from older collections. To create distribution maps, these locales were approximated using Google Earth (<https://www.google.com/earth/>) and Ge names (<http://www>.

geonames.org/). The known geographical distribution of each species is also discussed relative to ecoregions of occurrence as defined by Olson *et al.* (2001). High resolution photographs of holotypes, lectotypes, paralectotypes, and non-type specimens are available at <http://www.antweb.org> and <https://www.asu.edu/clas/sirgtools/veromessor/Veromessor%20North%20America.htm>. Both web sites also display high-resolution photographs for wings of queens and for wings and genitalia of males. Collection data for specimens examined in this study are available at <https://doi.org/10.5281/zenodo.6407308>.

Results

Diagnosis of genus. With the characteristics of subfamily Myrmicinae. Worker monomorphic to strongly polymorphic, psammophore poorly to well developed, head quadrate, base of antennal scape lobate, strongly flattened, or otherwise modified; metanotal suture strongly impressed across dorsum; propodeal spines short to long.

The forewing is of typical reduced venation pheidoline form with one submarginal cell, an open marginal cell, and one discoidal cell. Queens and males both lack the cross vein r-m; Rs + M separates before, at, and after 2r, depending on the species (Bennett, 2000). Sporadic minor variations occur, especially in males, including partial to complete loss of the m-cu vein in the forewing (see also Bolton, 1982; Cantone, 2017).

Description of worker. Head quadrate, slightly longer than broad to slightly broader than long; in full-face view, head not noticeably narrowed above eyes. Mandibles broad, triangular, usually with seven or eight teeth, apical tooth large, slender or stout, apex usually acute; subapical tooth large, apex usually acute, sometimes partially fused to apical tooth; sub-basal teeth much smaller, size and spacing irregular; basal tooth large, broad. Maxillary palps six-segmented; labial palps four-segmented. Apical margin of clypeus thick; medial clypeal lobe often with shallow longitudinal groove or with preapical process; lateral clypeal lobes narrow, often forming shelf below antennal fossa. Lateral margins of frontal lobes convex, somewhat elevated, usually not extending much above level of lower eye margin. Antenna 12-segmented; apex of scape extending barely, if at all, beyond posterior corners; base of scape usually modified, varying from flared and trumpet-shaped (*V. andrei*) to slightly to strongly flattened (other congeners); apical flagellar segments not forming distinct club. Eye usually small, ovoid (somewhat pointed below in *V. pergandei*). Ocelli absent. Psammophore poorly to well developed.

Mesosoma slender, in dorsal view maximum length greater than twice the maximum width. Promesonotal suture present across dorsum in large workers, often obsolete in small workers. In profile, mesonotum weakly to strongly convex, elevated well above metanotal area. Metanotum rarely differentiated except as “saddle” between mesonotum and propodeum; propodeal spiracles small, obscure; metasternal process prominent. In profile, propodeum with distinct, more or less horizontal basal surface and oblique to vertical posterior surface; angle of juncture with short to long spines.

Legs slender; protibia with one stout preapical spine laterad of apical spur; meso- and metatibia each with two apical spurs, inner spur shorter and more slender than outer spur; tarsal claws simple.

Peduncle of petiole short, broad, merging into anterior surface of petiolar node; spiracle anterior to base of node; in profile, petiolar node broadly cuneate, sometimes with dorsum truncate or nearly so; subpetiolar process small, simple. In profile, dorsum of postpetiole weakly to moderately convex, lacking defined anterior or posterior peduncles; in dorsal view, postpetiole broader than petiolar node, usually longer than broad, sides straight or weakly curved, diverging posterad; spiracle at or slightly before mid-length of side; subpostpetiolar process absent to weakly developed.

Gaster broadly ovoid, dorsum principally consisting of first segment; sting vestigial.

Queen. Cephalic characters similar to those described for worker, except for head, in frontal view, more quadrate (i.e., posterior corners more pronounced). Ocelli present; IOD shorter than OOD. Eyes usually proportionately larger than in corresponding worker, MOD usually greater than OMD.

Mesosoma robust, ML about 1.3× depth. Anterior margin of mesoscutum not protruding over pronotum, dorsal surface flat; notauli weak; parapsidal lines strong, curved laterad anteriorly. Axillae broad, completely separating mesoscutum from mesoscutellum. Mesoscutellum with distinct dorsal, horizontal, and posterior sloping surfaces. Metanotum narrow. Propodeum without clearly defined horizontal basal area; in profile, propodeum weakly to moderately curved; propodeal spines present.

Legs slender; protibia with one stout preapical spine laterad of apical spur; meso- and metatibia each with two apical spurs, inner spur shorter and more slender than outer spur; tarsal claws simple.

Forewings large; marginal cell open at apex, rarely nearly closed; one submarginal cell, one discoidal cell; cross vein r-m absent; Rs + M separate at or after 2r in *V. chamberlini*, *V. lobognathus*, and *V. pergandei*, and after 2r in all other species (Bennett, 2000).

Peduncle of petiole short, broad, merging into anterior surface of petiolar node; spiracle anterior to base of node; in profile, petiolar node broadly cuneate, sometimes with dorsum truncate or nearly so; subpetiolar process small, simple. In profile, dorsum of postpetiole weakly to moderately convex, lacking defined anterior or posterior peduncles; in dorsal view, postpetiole broader than petiolar node, usually longer than broad, sides straight or weakly curved, diverging posterad; spiracle at or slightly before mid-length of side; subpostpetiolar process absent to weakly developed.

Gaster broadly ovoid, dorsum principally consisting of first segment; sting vestigial.

Male. Head about as broad as long; posterior corners broadly rounded. Mandible broadly triangular; apical and preapical teeth large, acute; 2–4 minute, acute, often crowded, subbasal teeth; basal tooth sometimes a little broader, its upper margin coincident with upper margin of blade. Clypeus short, medial lobe somewhat elevated, usually with medioapical impression. Frontal carinae short, elevated, not extending above level of mid-length of eye. Lower margin of antennal socket at or below level of lower eye margin. Ocelli well below posterior margin, anterior ocellus at or above level of summit of eyes; IOD less than OOD. In profile, eye large, oblique, much nearer mandibular base than posterior margin; strongly convex in frontal view. Antenna 13-segmented, without differentiated apical club; scape short, not extending beyond posterior ocelli.

Mesosoma stout, ML only slightly greater than depth. In profile, anterior portion of mesocutum moderately enlarged and slightly overhanging anterior margin of pronotum; posterior 0.75, approximately, flat in profile; notauli very weak to moderately strong; parapsidal lines strong; Mayrian furrows present. Axillae completely separate mesoscutum and mesoscutellum. In profile, mesoscutellum strongly convex. Metanotum short, vertical. In profile, propodeum with long, sloping basal surface which merges gradually to abruptly with short declivitous surface; spines or teeth present or absent. Metasternal process usually prominent (Figure 1). Two metatibial spurs present but hidden among superficially similar setae, inner spur very short; tarsal claws simple.

Wings as in female. Additional information on male wing structure is given in Cantone (2017).

In profile, petiolar node stout; anterior surface sloping to insertion with little or no interruption; in profile, petiolar node low, thick, cuneate to subtruncate; subpetiolar process present. In profile, postpetiole low, barely to moderately convex; in dorsal view, broader than petiolar node, sides diverging posterad.

Gaster large, robust, usually about as broad as long. Volsella with two lobes distally, one issuing from base of digitus and the other bearing the distal end of a line of setae which extends longitudinally along the ventral surface of the volsella. Dorsal and ventral volsellar process absent, digitus elongate and curved, line of setae along longitudinal axis of arm of volsella distally borne by a process, and with an extra lobe next to digitus. Cuspis broad in most species, but narrow in *V. lobognathus* and *V. smithi* (see also Bennett, 2000; Boudinot, 2013).

Synonymic list of species of *Veromessor*

V. andrei (Mayr, 1886): 448 (w.q.m.l.k*). Mexico (Baja California), United States (California, Oregon).

V. chamberlini (Wheeler, 1915): 410 (w.q.m.l). United States (California).

V. chicoensis Smith, 1956: 37 (w.q.m). United States (California).

V. julianus (Pergande, 1894): 164 (w.q.m). Mexico (Baja California, Baja California Sur).

V. lariversi Smith, 1951: 94 (w.q.m). United States (California, Nevada).

V. lobognathus (Andrews, 1916): 82 (w.q.m). United States (Arizona, Colorado, Idaho, Montana, Nevada, North Dakota, Oregon, South Dakota, Utah).

V. pergandei (Mayr, 1886): 448 (w.q.m). Mexico (Baja California, Baja California Sur, Sonora), United States (Arizona, California, Nevada).

V. pseudolariversi Johnson, Borowiec, Snelling & Cole (w.q.m). United States (California, Nevada). **NEW SPECIES**

V. smithi Cole, 1963: 678 (w.q.m). United States (Arizona, California, Colorado, Nevada, New Mexico, Oregon).

V. stoddardi (Emery, 1895): 307 (w.q.m). Mexico (Baja California), United States (California).

* w = worker, q = queen, m = male, l = larva, k = karyotype

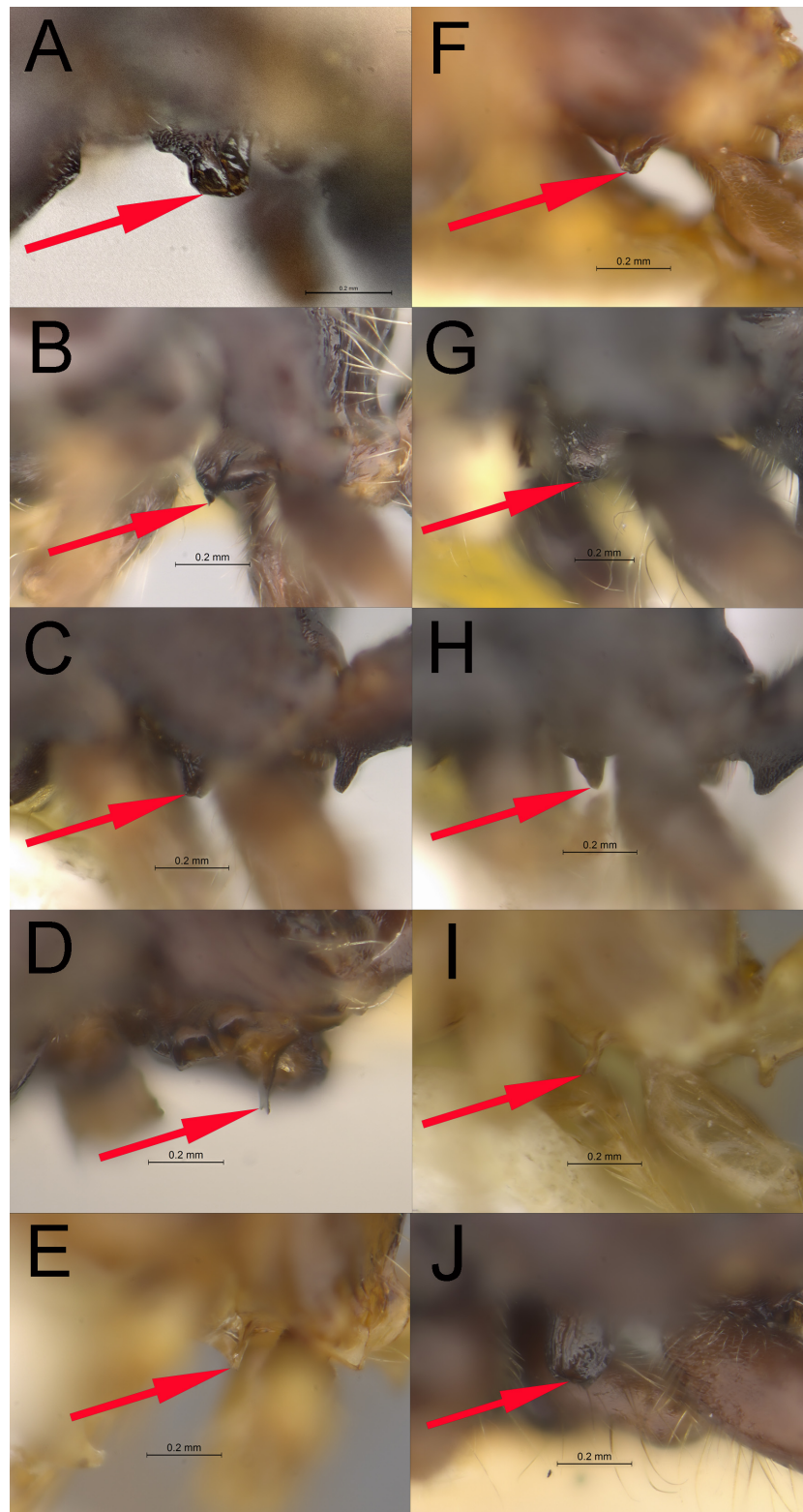


FIGURE 1. Photographs of the metasternal process on males of *Veromessor*: (A) *V. andrei* (CASENT4010823), (B) *V. chamberlini* (UCRC_ENT00500152), (C) *V. chicoensis* (CASENT0869853), (D) *V. julianus* (LACMENT359792), (E) *V. lariversi* (CASENT0761204), (F) *V. lobognathus* (LACMENT363986), (G) *V. pergandei* (CASENT0869850), (H) *V. pseudolariversi* (CASENT0869851), (I) *V. smithi* (LACMENT364071), and (J) *V. stoddardi* (LACMENT364102). Photographs by Robert Johnson from www.AntWeb.org.

Key to workers for species of *Veromessor*

- 1 Psammophore well developed, consisting of numerous, long, J-shaped hairs arranged in a distinct row along lateroventral margin of head (**Figure 6E**) 2
- Psammophore poorly developed, consisting of numerous, short to medium length hairs scattered across ventral surface of head; long J-shaped hairs lacking, or if present J-shaped hairs arranged in a V-shaped row not reaching posterior part of the lateroventral margin of head capsule, usually mixed with straight or evenly curved hairs (**Figures 6A–D**) 8
- 2 Anteromedial margin of clypeus with a small, blunt tooth or projection; in profile, eye narrowed below with a distinct ventral angle; body dark brownish-black to black *pergandei*
- Anteromedial margin of clypeus entire or concave, but lacking a small medial tooth or projection; in profile, eye rounded below; body usually concolorous yellowish or orangish-brown to rust colored, but never dark brownish-black to black 3
- 3 Propodeal spines short, length $< 0.5 \times$ maximum diameter of the eye (MOD) 4
- Propodeal spines long, length $\geq 1.0 \times$ MOD 6
- 4 Larger (HW = 1.33–1.61 mm); maximum basal width of scape greater than maximum preapical width; body concolorous dark yellowish-orange or orangish-brown to rust colored; mandible with 8 teeth, rarely 9 *smithi*
- Smaller (HW = 0.93–1.37 mm); maximum basal width of scape less than maximum preapical width; body light yellowish to yellowish-orange or yellowish-red, gaster often slightly darker; mandibles with 7 teeth 5
- 5 Anteroventral margin of postpetiole interrupted by a transverse ridge, in profile appearing as a minute process, margin weakly concave anterior to process; in dorsal view, pronotum with weak, discontinuous to continuous, wavy to irregular transverse rugae; dorsum of mesonotum with one to few weak, wavy to irregular, usually discontinuous longitudinal rugae *pseudolariversi*
- Anteroventral margin of postpetiole continuous, in profile lacking a minute process; in dorsal view, pronotum and mesonotum arugose, weakly to strongly coriarius to punctulate-granulate *lariversi*
- 6 Base of scape weakly widened; maximum basal width of scape less than maximum preapical width; cephalic dorsum with fine, closely spaced, regular to weakly wavy, longitudinal rugae, interrugae moderately to strongly shining; metasternal process about twice as long as high, apex nearly flat *julianus*
- Base of scape distinctly widened; maximum basal width of scape greater than maximum preapical width; cephalic dorsum with prominent widely spaced, mostly regular longitudinal rugae, interrugae shining or if rugae closely spaced, then rugae strongly irregular to nearly rugoreticulate, interrugae strongly granulate, dull; metasternal process as long as to slightly longer than high, apex bluntly rounded 7
- 7 Propodeal spines longer, length about $2.0 \times$ the distance between their bases; cephalic dorsum with prominent, widely spaced, mostly regular longitudinal rugae, interrugae shining; sides of pronotum with wavy to regular rugae, interrugae smooth and strongly shining; posterior margin of frontal lobes notably constricted; in frontal view, base of scape asymmetrical with ventral portion of anterior edge greatly expanded compared to dorsal edge (**Figure 12A**) *chamberlini*
- Propodeal spines shorter, length only slightly greater than to rarely $1.5 \times$ the distance between their bases; cephalic dorsum with closely spaced, strongly irregular rugae to nearly rugoreticulate, interrugae strongly granulate, dull; sides of pronotum with weakly to strongly irregular rugae to weakly rugoreticulate, interrugae moderately to strongly granulate, dull to weakly shining; posterior margin of frontal lobes not constricted; in frontal view, base of scape mostly symmetrical with ventral and dorsal portions of anterior edge similar in size or with dorsal edge expanded more than ventral edge (**Figure 12B**) *lobognathus*
- 8 Propodeal spines long, in dorsal view, length $\geq 2.5 \times$ as long as distance between their bases and $\geq 2.5 \times$ MOD; hairs on scape variable in length, suberect to erect, longest hairs about $0.3\text{--}0.4 \times$ MOD; anterodorsal margin of pronotum with one to several coarse, irregular, transverse rugae; workers mostly monomorphic *andrei*
- Propodeal spines short, in dorsal view, length less than to about as long as distance between their bases and less than to about as long as MOD; hairs on scape mostly uniform in length, subdecumbent to suberect, longest hairs about $0.1\text{--}0.2 \times$ MOD; anterodorsal margin of pronotum with weak, wavy to regular longitudinal or oblique rugae, rugae rarely transverse; workers polymorphic 9
- 9 In dorsal view, rugae on mesonotum similar to those on pronotum, interrugae weakly dull to shining; antennal scape narrowest near midlength *chicoensis*
- In dorsal view, rugae on mesonotum distinctly weaker than those on pronotum, interrugae shining; antennal scape narrowest immediately distad of basal bend *stoddardi*

Key to queens for species of *Veromessor*

- 1 Psammophore well developed, consisting of numerous, long, J-shaped hairs arranged in a distinct row along lateroventral margin of head 2
- Psammophore poorly developed, consisting of numerous, short to medium length hairs scattered across ventral surface of head; long J-shaped hairs sparse or lacking 8
- 2 Anteromedial margin of clypeus with a small, blunt tooth or projection; in posterodorsal view, medial and posteromedial surface of petiolar node usually weakly to moderately depressed or concave; concolorous blackish to black; propodeal spines short and triangular, length much less than width at base and length less than distance between their bases *pergandei*
- Anterior margin of clypeus entire, lacking a small medial tooth or projection; in posterodorsal view, medial and posteromedial

	portion of petiolar node usually evenly rounded; concolorous orangish or orangish-brown to reddish-brown or bicolored with head and mesosoma orange and gaster blackish <u>or</u> if concolorous dark brownish-black, then propodeal spines elongate, length greater than width at base and length similar to distance between their bases	3
3	Maximum basal width of scape greater than maximum preapical width	4
-	Maximum basal width of scape less than to similar to maximum preapical width	6
4	Rugae on cephalic dorsum becoming faint to disappearing above level of ocelli, lacking on posterior margin; in profile, rugae absent posterior to eyes	<i>smithi</i>
-	Rugae on cephalic dorsum continuing to posterior margin; in profile, rugae present posterior to eyes	5
5	Posterior margin of frontal lobes notably constricted; in frontal view, base of scape asymmetrical with ventral portion of anterior edge greatly expanded compared to dorsal edge	<i>chamberlini</i>
-	Posterior margin of frontal lobes not notably constricted; in frontal view, base of scape mostly symmetrical with ventral and dorsal portions of anterior edge similar in size or with dorsal edge expanded more than ventral edge	<i>lobognathus</i>
6	Rugae on cephalic dorsum continue onto posterior margin; propodeal spines elongate, length greater than width at base and length similar to distance between their bases; restricted to the Baja California peninsula of Mexico	<i>julianus</i>
-	Rugae on cephalic dorsum fade and disappear posterad, posterior margins smooth and shining; propodeal spines triangular, length less than width at base and length much less than distance between their bases; only known from California and Nevada	7
7	In profile, anteroventral margin of postpetiole interrupted by a minute process, margin weakly concave anterior to process; smaller (HW = 1.21–1.36 mm; ML = 1.95–2.04 mm); longitudinal rugae present over most to all of katapisternum	<i>pseudolariversi</i>
-	In profile, anteroventral margin of postpetiole continuous, lacking a minute process; larger (HW = 1.53–1.62 mm; ML = 2.78–2.98 mm); longitudinal rugae present on anterior and posterior portion of katapisternum, central portion lacking rugae	<i>lariversi</i>
8	Dorsal base of scape with a well developed, horizontal flange; mesoscutellum with numerous longitudinal rugae; medial lobe of clypeus with several coarse longitudinal rugae; hairs on scape variable in length, longest hairs suberect to erect	<i>andrei</i>
-	Dorsal base of scape may be broadened but lacking a horizontal flange; mesoscutellum arugose, smooth and shining; medial lobe of clypeus smooth and shining, lacking rugae, or rugae occasionally near anterior margin; hairs on scape similar in length, all hairs decumbent	9
9	Smaller (HW 1.39–1.58 mm; ML = 2.10–2.26 mm); katapisternum with longitudinal rugae; hairs on first gastral tergum longer, length of longest hairs approaching to equaling MOD; rugae on cephalic dorsum continue onto posterior margin	<i>chicoensis</i>
-	Larger (HW = 1.61–1.75 mm; ML = 2.77–2.97 mm); katapisternum mostly smooth and shining; hairs on first gastral tergum shorter, length of longest hairs < 0.4–0.5× MOD; rugae on cephalic dorsum fade to disappear on posterior margin	<i>stoddardi</i>

Key to males for species of *Veromessor*

1	Dorsum of mesoscutum smooth and shining, rugae and/or striae lacking	2
-	Rugae and/or striae cover some to most of dorsum of mesoscutum	3
2	Mandibles with 2–3 teeth basad of preapical tooth; in profile; metasternal process triangular, acuminate (Figure 1E)	<i>lariversi</i>
-	Mandibles with 1–2 minute denticles or teeth basad of preapical tooth; metasternal process elongate, slender, with a withered look (Figure 1I)	<i>smithi</i>
3	Psammophore consists of numerous, long, J-shaped hairs along lateroventral margin of head <u>and</u> larger (HW = 1.23–1.46 mm; PPW = 0.98–1.29 mm; EL = 0.50–0.59)	<i>pergandei</i>
-	Psammophore consists of numerous hairs scattered across ventral surface of head <u>and/or</u> smaller (HW = 0.68–1.00 mm; PPW = 0.37–0.70 mm; EL = 0.33–0.41 mm)	4
4	Occurring east of the Sierra Nevada and north of San Gabriel Mountains of California and east into Nevada, Arizona, and further east	5
-	Occurring in southwestern Oregon, California west of the Sierra Nevada, southwestern California, and the Baja California peninsula, Mexico	6
5	Body blackish to black; in profile, anteroventral margin of postpetiole interrupted by small transverse ridge that appears as a minute process; anepisternum and katapisternum rugose	<i>pseudolariversi</i>
-	Body light brown to brown; in profile, anteroventral margin of postpetiole continuous, lacking a minute process; anepisternum and katapisternum mostly smooth and shining to coriarius	<i>lobognathus</i>
6	In profile, propodeum evenly rounded, lacking tubercles, denticles, or enlarged rugae	7
-	In profile, propodeum not evenly rounded, profile interrupted by denticles, tubercles, or enlarged rugae	8
7	Restricted to the Baja California peninsula of Mexico	<i>julianus</i>
-	Restricted to California south and west of San Gabriel Mountains	<i>chamberlini</i>
8	Anepisternum rugose	<i>andrei</i>
-	Anepisternum contiguously punctate-granulate to mostly smooth to roughened or with faint rugae	9
9	Anepisternum and katapisternum contiguously punctulate-granulate, anepisternum occasionally with scattered rugae; sides of	

- propodeum contiguously punctulate-granulate with scattered, weak longitudinal rugae; in profile, area posterior to eyes and posterior corners strongly punctulate-granulate with several weak longitudinal rugae *chicoensis*
- Anepisternum mostly smooth to roughened or with faint rugae; katapisternum roughened or coriarius; in profile, area posterior to eyes and posterior corners with prominent longitudinal rugae, interrugae moderately punctulate-granulate *stoddardi*

Species accounts

Veromessor andrei

(Figures 1A, 2–5 6B, 7–9)

Distribution—Figure 10A

Aphaenogaster andrei Mayr, 1886: 448 (worker). Syntypes examined: 8 workers [NHMW], UNITED STATES, California: no location, April 1884; 1 worker [NHMW], California: San Mateo; 1 worker [NHMW], 12 workers [USNM], California, San Benito County, Tres Pinos; Emery, 1895: 306 (queen); Wheeler and Wheeler, 1972: 240, fig. 7 (larvae); Taber and Colkendorpher, 1988: 95, fig. 1b (karyotype). See also Wheeler and Creighton, 1934: 362, plate II, fig. 2. NHMW worker from Tres Pinos, California, here designated **LECTOTYPE** [CASENT0923122].

Stenamma (Messor) andrei (Mayr); Emery, 1895: 306 (first combination in *Stenamma* [*Messor*]).

Novomessor andrei (Mayr); Emery, 1915: 73 (first combination in *Novomessor*).

Novomessor (Veromessor) andrei (Mayr); Forel, 1917: 235 (first combination in *Novomessor* [*Veromessor*]); Emery, 1921: 67 (*andrei* designated as type species of *Novomessor* [*Veromessor*]).

Veromessor andrei (Mayr); Wheeler and Creighton, 1934: 362 (first combination in *Veromessor*).

Novomessor (Veromessor) andrei (Mayr); Enzmann, 1947: 152 (revived combination in *Novomessor* [*Veromessor*], in key).

Messor andrei (Mayr); Bolton, 1982: 341 (revived combination in *Messor*).

Veromessor andrei (Mayr); Ward, Brady, Fisher, and Schultz: 2015: 13 (revived combination in *Veromessor*).

Veromessor andrei subsp. *flavus* Wheeler and Creighton, 1934: 366 (worker). Syntypes examined: 3 workers [USNM], UNITED STATES, California: San Diego County, Jacumba (W.M. Wheeler leg., 13 August 1917). Creighton, 1950: 159 (synonymy under *andrei* subsp. *castaneus*; here confirmed). USNM worker here designated **LECTOTYPE** [USNMMENT00529212].

Veromessor andrei subsp. *castaneus* Wheeler and Creighton, 1934: 365 (worker). Syntypes examined: 5 workers [LACM], 4 workers [USNM], UNITED STATES, California: San Diego County, Jacumba (W.M. Wheeler leg., 13 August 1917). Creighton 1953: 3 (synonymy under *andrei*; here confirmed). USNM worker here designated **LECTOTYPE** [USNMMENT00529071].

Worker diagnosis. This species is uniquely characterized by the following combination of features: (1) usually dark reddish-brown to dark brownish, gaster usually darker; some populations in southern California and Baja California light yellowish-orange to ferruginous orange to rust colored; some populations in the Central Valley of California and Monterey area blackish to black, (2) medial lobe of clypeus with 2–3 coarse, lateral longitudinal rugae, medial lobe not thick and protuberant in profile, not elevated above lateral lobes in frontal view, (3) mandibles with 8 teeth, (4) entire circumference of base of scape with a strongly developed and flattened, flared and trumpet-like flange; maximum basal width of scape slightly greater than maximum preapical width, (5) MOD less than OMD, $OI < 23.5$, (6) cephalic dorsum with coarse, wavy to irregular, longitudinal rugae that usually have short lateral branches posterior to eyes; medial rugae not diverging to weakly diverging toward posterior corners; cephalic interrugae weakly punctulate, weakly shining, (7) psammophore poorly developed; ventral surface of head capsule with both J-shaped hairs and straight or evenly curved hairs, J-shaped hairs not arranged in a distinct row, (8) in dorsal view, anterior margin of pronotum with one to few irregular transverse rugae, remainder usually with strongly irregular, longitudinal rugae to rugoreticulate; sides of pronotum with wavy to strongly irregular rugae that traverse longitudinally to posterodorsally to rugoreticulate; mesosoma with coarse, strongly irregular longitudinal rugae; mesopleura with mostly longitudinal rugae or rugae angle posterodorsally, rugae (especially on dorsal one-half) often with lateral branches to rugoreticulate; interrugae on mesosoma weakly punctulate, weakly shining, (9) propodeal spines very slender, acuminate, not curved in profile or in dorsal view; length $\geq 3.0\times$ the distance between their bases, infraspinal facet and propodeal declivity weakly coriarius or with weak irregular, transverse rugae, moderately to strongly shining, and (10) metasternal process large, higher than long, apex very broadly rounded to nearly flat, partly translucent (Figures 2–5, 6B).

Measurements. lectotype ($n = 34$). HL 1.77 (1.40–1.82); HW 1.70 (1.26–1.81); MOD 0.33 (0.26–0.36); OMD 0.44 (0.28–0.49); SL 1.44 (1.09–1.60); PNW 1.09 (0.84–1.13); HFL 1.89 (1.53–2.29); ML 2.03 (1.82–2.50); PW 0.34 (0.27–0.39); PPW 0.51 (0.40–0.60). Indices: SI 84.71 (79.56–104.69); CI 96.05 (87.07–100.57); OI 19.41 (17.13–23.02); HFI 111.18 (107.75–152.34).

Queen diagnosis. This caste is diagnosed by the following combination of features: (1) usually dark reddish-brown to dark brown with gaster usually darker; some populations in southern California and Baja California light yellowish-orange to ferruginous orange to rust colored; some populations in the Central Valley of California and Monterey area blackish to black, (2) medial lobe of clypeus with 2–3 coarse, lateral longitudinal rugae, medial lobe not thick and protuberant in profile, not elevated above lateral lobes in frontal view, (3) mandibles with 8 teeth, (4) entire circumference of base of scape with a strongly developed and flattened, flared and trumpet-like flange; maximum basal width of scape slightly greater than maximum preapical width, (5) MOD slightly less than to slightly greater than OMD, (6) cephalic dorsum with coarse, wavy to irregular, longitudinal rugae; medial rugae not diverging to weakly diverging toward posterior corners; cephalic interrugae weakly to moderately punctulate, weakly shining, (7) psammophore poorly developed, (8) sides of pronotum with irregular longitudinal rugae that often have short lateral branches; mesoscutum with fine, longitudinal rugae, moderately shining; mesoscutellum with longitudinal, oblique, or transverse rugae; anepisternum with longitudinal rugae, katepisternum with longitudinal rugae except for smooth and shining anteroventral margin; interrugae weakly to moderately coriaceous, moderately shining, (9) sides of propodeum with longitudinal and oblique rugae; propodeal spines elongate-triangular, length about 1.0× the distance between their bases; infraspinal facet with transverse rugae, propodeal declivity smooth and shining, and (10) metasternal process large, higher than long, apex very broadly rounded to nearly flat, partly translucent (Figures 7–8).

Measurements. ($n = 12$). HL 1.71–1.89; HW 1.73–1.89; MOD 0.39–0.47; OMD 0.37–0.45; SL 1.41–1.58; HFL 2.03–2.24; ML 2.99–3.38; PW 0.45–0.55; PPW 0.76–0.88. Indices: SI 76.63–88.51; CI 95.60–103.287; OI 22.04–24.87; HFI 115.25–124.28.

Male diagnosis. This caste is diagnosed by the following combination of features: (11) dark brown to blackish, (12) medial lobe of clypeus moderately convex with several irregular, mostly longitudinal rugae, (13) mandibles with 3, rarely 4, small teeth basad of preapical tooth, (14) in frontal view, anterior ocellus above level of top of eyes, (15) mesopleura dull to moderately shining; anepisternum densely punctate, usually with fine longitudinal rugae; katepisternum densely punctate, usually with weak, widely scattered longitudinal or oblique rugae, (16) propodeum rugose to rugoreticulate, interrugae densely punctate; propodeal spines cariniform or with acuminate denticles to small teeth, (17) metasternal process as long as high, tapering to a subangulate to broadly rounded apex, and (18) anterior angle of subpetiolar process subacute to acute (Figures 1A, 9).

Measurements. ($n = 12$). HL 0.87–1.15; HW 0.79–1.07; MOD 0.34–0.47; OMD 0.10–0.15; SL 0.32–0.43; HFL 1.60–2.27; ML 2.25–2.95; PW 0.30–0.46; PPW 0.53–0.80; AOD 0.11–0.15; IOD 0.28–0.37; OOD 0.30–0.35. Indices: SI 35.42–44.81; CI 84.38–95.54; OI 39.25–47.25; HFI 197.53–233.73.

Additional material examined. MEXICO: Baja California: South Coronado Island, no date (USNM); Coronado Island, no date & Dec 1915 (LACM; USNM); 20 mi N Ensenada, Apr 1, 1931 (USNM); 20 km E Ensenada, 650 m, Apr 27, 1998 (UCDC); 2.5 mi SW Mike's Sky Ranch, 4700', May 11, 1998 (RAJC; UCDC); 0.5 mi N El Molino, Bahía San Quintín, Mar 29, 1970 (LACM); Río Amargo (=Arroyo Amargo?), Sep 1, 1961 (LACM); 18 km E Tecate, 850 m, Apr 27, 1998 (UCDC). **UNITED STATES: California:** Alameda Co.: Livermore, Mar 14, 1937 (LACM; USNM); Hayward, Oct 2, 1910 (USNM); Berkeley, Jun 18, 1917 (LACM); Mills College, no date (LACM); Niles Canyon, Apr 15, 1922 (LACM). Amador Co.: 9 km WNW Plymouth, 200 m, Mar 20, 1994 & Aug 11, 1994 (UCDC); 3 mi SSE Ione, 120 m, Jun 4, 1988 (UCDC). Butte Co.: Bidwell Park, Apr 26, 1975 (LACM); Neal Rd at 6.1 mi NE Jct Hwy 99, 1000', Jun 23, 1979 (LACM); Pentz, May 1993 (UCDC); North Table Mtn at 9 km N Oroville, 360 m, Apr 18, 1982 & Mar 28, 1993 (UCDC). Colusa Co.: Wilbur Springs, 510 m, Jun 7, 1989 (UCDC); Fout Springs, Jun 27, 1995 (UCDC); 1 km W Fouts Springs, 600 m, May 14, 1983 (UCDC). Contra Costa Co.: Russell Reservation, Aug 29, 1970 (LACM); Mt Diablo State Park, 490 m, Mar 14, 1982 (UCDC); Moraga, Jan 25, 1936 (UCDC); Black Diamond Mines Regional Preserve, 360 m, Apr 10, 1999 (UCDC). El Dorado Co.: 2 km WNW Somerset, 500 m, Aug 16, 1987 (UCDC); Shingle Springs, Nov 1, 1980 (UCDC). Fresno Co.: 12 mi SW Coalinga, Nov 12, 1959 (LACM); Fresno, Aug 1, 1991 (UCDC); Joaquin Ridge at 2 km E Wright Mtn, 1240 m, Apr 17, 1999 (UCDC); 2 km SW Marshall Station, 250 m, May 8, 1999 (UCDC). Humboldt Co.: Bair's Ranch at Redwood Creek, no date (USNM); Etters Cabin, King Ranch Conservancy Area, 10 m, May 24, 1987 (UCDC). Kern Co.: Rancheria Creek on Piute Mtn Rd (T29S, R33E, Section 23), 4350', Jun 13, 1971 (LACM); Tehachapi, 3950', Apr 30, 2018 (RAJC). Kings Co.: Kansas Ave (= Ave 232) at 14.0 mi W Hwy 99, 180', Oct 2, 2018 (RAJC). Lake Co.: 14 km ENE Lower Lake, 290 m, Jun 18, 1995 (UCDC); McLaughlin Reserve, 19 km ESE Lower Lake, 210–700 m, Oct 29, 2010 & Apr 25, 2015 (MLBC); no loc, Apr 18, 1972 (UCDC). Los Angeles Co.: Claremont,

Aug 9, 1895 & Nov 16, 1945 & no date (USNM); 3 mi N Claremont, Nov 28, 1969 (LACM); Santa Catalina Island, no date (LACM; USNM); Avalon, no date (USNM); 1 km WNW Catalina Airport, Catalina Island, 410 m, Apr 15, 2002 (UCDC); Los Angeles, Sept 15, 1886 & no date (USNM); 5 mi S Palmdale, Jun 22, 1931 (USNM); Pasadena, Mar 1, 1919 (USNM); Culver City, no date, 1937 (USNM); Tejon Pass, Aug 19, 1917 (LACM); San Gabriel Mtns at Vasquez Rocks, Jul 17, 1984 (LACM); Westwood Hills, May 12, 1936 (LACM); Pomona, Mar 23, 1927 (LACM); Mt Baldy Rd, 3850', Aug 14, 2004 (UCDC); I-14 at Red Rover Mine Rd, 3040', Apr 30, 2018 (RAJC). *Madera Co.*: Patterson, Apr 3, 1954 (UCDC). *Marin Co.*: San Rafael, Jul 16, 1922 & Jun 26, 1932 (LACM; USNM); Laguna Lakes, Jan 5, 1929 (USNM); Tamalpais, Nov 12, 1922 (LACM); Copper Mines (=Copper Mine Gulch?), Jan 18, 1958 (LACM). *Mariposa Co.*: 1.6 mi W Mt Bulliam, 2000', May 6, 1970 (LACM); 4 km SSE Coulterville, 650 m, Mar 25, 2000 (UCDC). *Mendocino Co.*: Hopland Field Station, 240 m, Apr 29–30, 1977 & Jul 25, 1982 (UCDC). *Merced Co.*: Snelling, Jun 18, 1951 (LACM); Great Valley Grassland State Park, Jul 25, 1995 (UCDC). *Monterey Co.*: Hastings Reservation, Jul 2, 1944 (USNM); South Hastings Natural History Reservation, Apr 21, 1941 (USNM); Hastings Natural History Reservation, Apr 21, 1941 (USNM); Monterey, May 31, 1943 (USNM); Monterey at School Hill, May 1, 1943 (USNM); Monterey at Lane-Long Field, June 1, 1943 (USNM); Monterey at Forsman Road, Apr 29, 1943 (USNM); Monterey at King City Road, Apr 27, 1943 (USNM); Salinas, Aug 15, 1988 (UCDC); Mission San Antonio de Padua, 340 m, Jun 6, 1998 (UCDC). *Napa Co.*: Twin Peaks at 4 km W Aetna Springs, 660 m, May 28, 1988 (UCDC); 5 km ENE Rutherford, 120 m, Apr 23, 1988 (UCDC); 5 mi S Pope Valley, Apr 28, 1973 (UCDC); 5 km NNE Calistoga, Oat Mine Hill Trail, 555–645 m, Nov 26, 2010 (MLBC). *Nevada Co.*: 7 km SW Grass Valley, 700 m, May 30, 1998 (UCDC). *Orange Co.*: Modjeska Canyon, Jun 2, 1968 (LACM); Laguna Ranch (=Laguna Beach?), no date (LACM); Santa Ana Canyon, May 13, 1934 (LACM); Pleasants Peak in Santa Ana Mtns, 1140 m, Apr 16, 2002 (UCDC); Limestone Canyon at El Toro Rd, 1.8 mi E Cooks Corner, Jul 11, 1996 (UCDC); 6 km N Lake Wildwood, 200 m, May 31, 2013 (MMPC). *Placer Co.*: Roseville near PFE & Walerga Rds, 110', Jul 21, 1992 (RAJC); Roseville at 0.5 mi N Jct I-80 & Douglas Blvd, 180', Jul 21, 1992 (RAJC); Roseville at Jct I-80 & Douglas Blvd, 170', Jul 21, 1992 (RAJC). *Riverside Co.*: San Jacinto, Aug, no year & Nov, no year (LACM); Nightingale, 4000', Sep 2, 1969 & Apr 18, 1971 (NHMW; RAJC); Reche Canyon at 5 mi S Riverside, 1500', Jun 1, 1966 (LACM); Joshua Tree National Monument at Queen Valley, 5000', Jul 1969 (LACM); Joshua Tree National Monument at Lower Covington Flat, no date (LACM); Beaumont, Jan 29, 1956 (LACM); 8 mi N Temecula, Jul 19, 1956 (LACM); 15.5 km NE Temecula, 470 m, May 2, 2016 (MMPC); Lake Skinner, 462 m, Mar 29, 1996 (UCDC). *Sacramento Co.*: Sacramento, Jul 1931 & Jun 17, 1938 & Jun 18, 1941 (LACM; UCDC; USNM); Antelope Pass, May 19, 1932 (LACM); Orangevale, May 24, 1930 (LACM; UCDC); Rancho Cordova, Apr 16, 1984 (UCDC); Folsom, July 18, 1985 (USNM). *San Benito Co.*: 5 km S Panoche, 425 m, Aug 17, 1988 (UCDC); Hollister, May 30, 1947 (UCDC). *San Bernardino Co.*: Bighorn Mtns at Rattlesnake Canyon, 3720', May 24, 2008 (RAJC); Rialto at Jct Riverside & Sierra Ave, 1950', May 11, 2018 (RAJC). *San Diego Co.*: Green Valley Falls, 1300 m, Apr 4, 1993 (CASC); Santa Ysabel Valley, no date (USNM); Santa Ysabel, Jul 21, 1895 (USNM); Carlsbad, no date (USNM); Ramona, no date, 1928 (USNM); Descanso, no date (USNM); East Lake, May 25, 1888 (USNM); 1 mi S Jct La Posta Rd & I-8, 3500', Jul 15, 2000 (RAJC); 1 mi SE Boulder Oaks, 3300', Jun 30, 1993 (RAJC); 0.2 mi N Cameron Fire Station, 3300', Jun 28, 1992 & May 13, 2018 (CIDA; RAJC); I-8 at Buck Springs Rest Stop, 3270', Jul 17, 1992 (RAJC); San Isidro, 200', Jul 9, 1952 (LACM); Encinitas, Jul 19, 1956 (LACM; UAIC); Indian Flats, 3800', Apr 12, 1969 (LACM); Escondido, Jul 14, 1956 (LACM); Point Lorma (=Point Loma?), no date (LACM); Carmel Mountain, 124 m, Nov 5, 1993 (UCDC); Chula Vista (CV2), 160 m, Mar 9, 1996 & May 26, 1996 (UCDC); Chula Vista (Home Depot), 70 m, Oct 27, 1995 & Feb 22, 1996 (UCDC); E end Chula Vista, 160 m, Mar 8, 1996 (UCDC); Chula Vista (Paseo del Rey), 178 m, Oct 23, 1995 & Mar 26, 1996 (UCDC); Chula Vista (Terranova), 78 m, Oct 27, 1995 & Jun 5, 1996 (UCDC); Los Peñasquitos Creek, 25 m, Jul 24–29, 2002 (UCDC); Carney Canyon, 455 m, May 9, 2004 (UCDC); Julian, Jun 19, 1962 & Jul 4, 1962 (UCDC); La Jolla, 113 m, Jul 18, 1963 & May 13, 1987 & Jun 26–Aug 1, 1994 (UCDC); Granite Springs at Rancho Cuyamaca, 4800', Nov 28, 2003 (UCDC); Kate Sessions Park, 92 m, Dec 16, 1995 (UCDC); Hwy 79 at Oak Grove Fire Station, 2760', May 12, 2018 (RAJC); no loc, no date & Jun 10, no year (LACM; USNM); Pacific Beach, no date (LACM). *San Luis Obispo Co.*: 5 mi NE Santa Margarita, Jun 24, 1963 (LACM); Cholame, Mar 23, 1947 (LACM); Paso Robles, Apr 5, 1988 (UCDC); E of Paso Robles, Jul 11–17, 1999 (UCDC); W side Soda Lake in Carrizo Plains National Monument, 580 m, May 24, 2003 (UCDC); 20 km ESE California Valley, Carrizo Plain Natural Area, 800 m, Apr 19, 1997 (UCDC). *San Mateo Co.*: Jasper Ridge, 150 m, Apr 27, 2003 (UCDC); San Bruno Mtn, 100 m, Apr 5, 1997 (UCDC). *Santa Barbara Co.*: N end of Sedgewick Ranch, 610 m, Mar 2, 1996 (UCDC). *Santa Clara Co.*: Palo Alto, no date

(LACM; USNM); Stanford University, Sep 26, 1906 (LACM); Mt Hamilton, May 13, 1914 (LACM); Blue Oak Ranch Reserve, 720 m, Nov 21, 2009 (UCDC); no loc, no date (LACM). *Santa Cruz Co.*: Santa Cruz, Aug 16, 1968 (UCDC); Castle Rock State Park, 880 m, Apr 18, 2010 (MLBC). *Shasta Co.*: Enterprise, 175 m, Jul 8, 2001 (UCDC). *Solano Co.*: Cold Canyon, 120 m, no date & Aug 16, 1981 & Apr 6–Jul 9, 1983 & Aug 19–21, 1984 & Mar 27, 1986 (UCDC); Cold Canyon at 19 km NNW Vacaville, 120 m, Jul 9, 1983 & Sep 30–Oct 21, 1987 & Oct 21–Nov 11, 1997 & Jun 29–Jul 20, 1988 & May 31, 1989 & Sep 25, 1991 & Sep 18, 2010 (MLBC; UCDC); 9 mi W Winters at GL Stebbins Cold Canyon Reserve, May 30, 1992 (UCDC); 11 km W Winters, 120 m, Jun 1, 2013 (MMPC); nr Dozier at 11 mi S Dixon, May 4, 1973 & Apr 4–13, 1975 & Sep 11, 1975 & Apr 8–29, 1977 & May 20, 1977 & Apr 11–27, 1979 & Apr 8, 1983 (UCDC); WL Jepson Prairie Preserve TNC at 13 mi S Dixon, Apr 19, 1971 & Apr 19, 1985 (UCDC); Jepson Prairie at 18 km S Dixon, 10 m, Feb 13, 1983 & Jan 29, 1984 & Apr 4, 1993 (UCDC); Fairfield, Oct 19, 1962 (UCDC); Pleasants Ridge, 530 m, Oct 24, 1982 (UCDC); Gates Canyon road at 9 km WNW Vacaville, 480 m, Mar 22, 2014 (MLBC). *Stanislaus Co.*: 10 mi SW Turlock, May 12, 1952 (LACM); Del Puerto Canyon at 18 km WSW Patterson, 300 m, May 9, 1997 (UCDC); 20 km WSW Patterson, 310 m, May 4, 2013 (MMPC); Del Puerto Canyon, 300 m, May 29, 1971 & May 7, 2005 (UCDC). *Sutter Co.*: 7 km NNW Sutter, 360 m, May 14, 1988 (UCDC); 1 km W North Butte, Sutter Buttes, 2000 m, May 28, 2007 (UCDC). *Tehama Co.*: Proberta, Jul 11, 1962 (LACM); 6 km E Paynes Creek, 1360 m, May 24, 1981 (UCDC). *Trinity Co.*: Weaverville, Aug 15, 1937 (LACM). *Tulare Co.*: Sequoia National Park, Jul 17, 1931 (LACM; USNM); Goshen, Jul 6, 1988, (UCDC); Tulare, Apr 26, 1937 (UCDC); Pixley National Wildlife Refuge at 0.2 mi W of entrance, 170', May 1, 2018 & Oct 2, 2018 (RAJC). *Tuolumne Co.*: 4 mi N Columbia, Apr 26, 1952 (LACM); 5 mi S Columbia, Apr 29, 1952 (LACM); 3 mi N Chinese Camp, 1300', Apr 18, 1966 (LACM); 14 km SSW Jamestown, 400 m, Jun 4, 1988 (UCDC). *Ventura Co.*: Simi Hills, 240 m, Oct 2002 (UCDC); 29 km WNW Stauffer, 1460 m, Apr 20, 1997 (UCDC). *Yolo Co.*: Hwy 128 W of Winters, May 13, 2001 (UCDC); 6 km SW Winters, 45 m, Apr 13, 1984 & May–Jul 1995 (UCDC); 6 km W Winters, 50 m, Apr 13, 1984 (UCDC); Cold Canyon Reserve at 11 km W Winters, Jun 20–Jul 4, 1990 & Feb 5, 2012 & Apr 8, 2012 (MMPC; UCDC); Putah Canyon, Aug 10, 1970 (UCDC); Brooks, Apr 23, 1986 (UCDC); 13 km W Rumsey, 525 m, Apr 24–May 15, 1993 (UCDC); Grassland Regional Park at 8 km SE Davis, 10 m, May 21, 1997 (UCDC); Elkhorn Ferry, Apr 16, 1952 (UCDC); 6 km WNW Rumsey, 270 m, Apr 15, 2012 (MMPC). *Yuba Co.*: Sierra Foothill Range at 18 mi NE Marysville, May 7, 1977 & May 1, 1983 (UCDC). *No county*: no loc, no date & no loc, Jun 1884 (LACM; USNM); Mohave Desert, Jul 1931 (LACM). **Oregon**: *Jackson Co.*: Siskiyou Mtns at 6 mi W of Jacksonville, 1500', Jul 22, 1952 (USNM). **Questionable locales (appear to be or are outside of geographical range)**: **UNITED STATES**: *Missouri*: *Barton Co.*: no loc, May 1920 (LACM). *Nevada*: *Ormsby Co.*: no further data (not examined, see Wheeler & Creighton, 1934) (Figure 10A).

Etymology. The specific epithet, *andrei*, honored Jacques Ernest Edmond André, an eminent French hymenopterist.

Discussion. *Veromessor andrei* is not likely to be confused with any congener. This species is easily diagnosed by its poorly developed psammophore combined with long propodeal spines ($\geq 3\times$ as long as the distance between their bases), mostly monomorphic workers, and coarse, irregular rugae to rugoreticulate on the cephalic dorsum posterior to eyes and dorsum and sides of pronotum. This species is recognized in the field based on colonies that consist of tens of thousands of workers that forage in columns, usually near dusk and dawn, and it usually occurs in grasslands or similar open habitats (Brown & Gordon, 2000; Creighton, 1953; Wheeler & Creighton, 1934). *Veromessor chicoensis* and *V. stoddardi* are the only sympatric species that have a poorly developed psammophore, but both species have short propodeal spines (length less than distance between their bases), strongly polymorphic workers, and cephalic dorsum posterior to eyes and dorsum of pronotum with weak, regular rugae.

Wheeler and Creighton (1934) described two subspecies of *V. andrei* (*flavus* and *castaneus*) from the same locality (Jacumba, California). *Veromessor andrei* subsp. *flavus* was described based on its lighter yellow coloration combined with morphological differences that included: (1) narrower head (especially in the posterior one-half) with a nearly flat posterior margin, (2) longer antennal scapes that slightly surpassed the posterior margin as in subspecies *castaneus*, (3) smaller, narrower petiolar node, and (4) more feeble sculpturing, especially on the mesosoma.

Wheeler and Creighton (1934) also described *V. andrei* subsp. *castaneus* largely based on its lighter uniform castaneous brown coloration. Other differences included: (1) less polymorphic with the largest workers only 5.2 mm in length (7.0 mm in typical *andrei*), (2) longer antennal scapes that slightly surpassed the posterior margin, (3) tooth and lamella on anteroventral surface of petiolar peduncle reduced or lacking so that the ventral surface appears sinuate, and (4) less deeply impressed propodeal suture.

Creighton (1950) synonymized *flavus* under *castaneus* without discussion, except to say that *flavus* and *castaneus* cannot both be considered valid subspecies as both occur in the same area of southern California. Creighton (1953) synonymized subsp. *castaneus* under *andrei* after examining large series from Cameron Valley, about 20 miles east of Jacumba (type locality). Creighton noted that none of the characters separating these two subspecies (except possibly for color) held up after examining adequate material. He also indicated that differences used to separate these two forms resulted from comparing the smaller workers of *castaneus* with the larger workers of *andrei*, and that all morphological differences disappeared when comparing same-sized workers. The only remaining difference was the uniformly light color of *castaneus*, but Creighton noted considerable intranidal variation in color, such that the light *castaneus* workers sometimes occurred in the same colony as dark *andrei* workers. We agree with Creighton (1950) and Creighton (1953) in their synonymizing both subspecies under *V. andrei*.

As mentioned above, *V. andrei* displays wide variation in color. Wheeler and Creighton (1934) described *V. andrei* as “Color variable. In some specimens the entire insect is reddish black, except for the nodes of the petiole which are reddish. In other specimens, only the posterior part of the gaster is black, the first gastric segment castaneous and the remainder of the insect clear, deep red. Not infrequently both the head and gaster are infuscated, leaving only the thorax and nodes of the petiole red.” We also have examined numerous color variants that include concolorous orangish, concolorous dark brownish-red, brown, and black, as well as color combinations that include reddish-orange head and mesosoma with a black gaster, orangish-red head and mesosoma with a orangish-black gaster, and head and gaster black with a reddish mesosoma infused with black (Figures 2–5; see also <https://www.antweb.org/> and <https://www.asu.edu/clas/sirgtools/veromessor/V%20andrei%20second%20layer.htm>).

Color does not correlate with geography except that concolorous orangish workers occur only in southern California and northern Baja California, Mexico. Moreover, several morphological traits are stable in *V. andrei*, while color varies greatly, such that color cannot be used as a taxonomic character. A molecular phylogeny based on UCEs does not show color morphs clustering and indicates an average amount of genetic variation within *V. andrei* compared to other species, proving color to be of little taxonomic significance in this species (M.L. Borowiec, unpub. data).

Mayr (1886) described *V. andrei* listing the type locality as “California”. We examined 10 syntype workers, each on a separate pin (NHMW), finding several localities on the labels. The label on eight pins was “California”, one label was “Tres Pinos, California”, and one label was “San Mateo, California”. Moreover, it appears that Mayr examined syntype workers from several localities, but he chose the type locality as “from California”, perhaps because all 10 syntype workers were from California. We chose the syntype from Tres Pinos, California, as the lectotype so as to define the type locality. Twelve workers from USNM also had a label that read “Tres Pinos, California, Jun, 1884”. We consider these 12 workers to be part of the Tres Pinos syntype series, and we placed syntype and paralectotype labels on all 12 workers.

Biology. Nests of *V. andrei* occur in open sites in most soil types and consist of one to multiple entrances with irregularly-shaped entrances up to 5 cm in diameter. Nest entrances usually are surrounded by an irregular gravel mound of excavated soil and chaff that ranges up to 60 cm in diameter (Boulton, Jaffee, & Scow, 2003; Creighton, 1953; Snelling & George, 1979; Wheeler & Creighton, 1934). Workers of *V. andrei* are mostly monomorphic (Wheeler & Creighton, 1934).

Colonies of *V. andrei* have not been censused, but observations indicate that they contain tens of thousands of workers that form foraging columns up to 20 m long, with workers fanning out to forage at the distal end of the column (Brown & Gordon, 2000; Creighton, 1953; Wheeler & Creighton, 1934); vegetation and debris are removed to construct trails when necessary. Colonies sometimes have more than one foraging column. Colonies forage most days during the foraging season, which typically lasts from late March to late October or early November. Foraging time varies seasonally with changes in temperature: colonies forage during the day when days are cool, they become crepuscular-matinal as temperatures increase, and they forage nocturnally when nights are warm (Brown & Gordon, 2000; Hobbs, 1985). Foraging columns can revisit the same location for multiple days or they can change direction on successive days such that colonies visit the entire area surrounding their nests (Brown & Gordon, 2000; Hobbs, 1985). Neighbors also affect foraging direction because encounters with neighbors on one day increasing the probability of revisiting that area the following day; encounters with neighbors resulted in fighting that typically involve relatively few pairs of ants (Brown & Gordon, 2000). This behavior contrasts with that of *V. pergandei*, in which foraging columns avoid nearest neighbors (Ryti & Case, 1988a).

Foraging patterns of *V. andrei* result from chemicals released by several glands. Secretions from the pygidial

gland (primarily n-tridecane) appear to initiate the foraging column (Hölldobler *et al.*, 2013), while a trail pheromone (primarily 1-phenylethanol) released from the poison gland maintains recruitment to the foraging fan (Plowes, Colella, Johnson, & Hölldobler, 2014). The recruitment effect from the poison gland is enhanced when adding pygidial gland secretions (Plowes, Colella, *et al.*, 2014). Like other large-colony congeners, workers of *V. andrei* have a large pygidial gland reservoir with a textured tergal cuticle (Hölldobler *et al.*, 2013).

Mating flights of *V. andrei* occur in post-dawn hours over an up to several week period from mid-June through July, usually with relatively few sexuals released per day (Brown, 1999b; McCluskey, 1963; Snelling & George, 1979; R.A. Johnson, pers. obs.). Flights are synchronized across colonies, apparently in response to a circadian rhythm in which activity of males increases drastically during early morning hours (McCluskey, 1958, 1963). That photoperiod triggers mating flights is based on observations that males exhibit sharp daily activity peaks under controlled light cycles and that these cycles appear to be under endogenous control. Sexuals fly from the nest and mate in the air (Brown, 1999b; R.A. Johnson, pers. obs.).

Mating frequency for queens of *V. andrei* is unknown. Dry mass of alate queens averages 7.5 ± 0.3 mg. Alate queens contain an average of 44.0 ± 1.9 ($n = 5$) ovarioles, and mated queens contain an average of 1.52 ± 0.11 ($n = 5$) million sperm. Dry mass for virgin males averages 2.1 ± 0.1 mg, and they contain an average of 9.15 ± 0.64 ($n = 3$) million sperm (R.A. Johnson, unpub. data).

Little is known about colony founding, but Brown (1999b) observed that founding queens are semi-claustral, i.e., they leave the nest to forage. Brown (1999b) also reported that queens of *V. andrei* lack storage proteins, inferring that they are obligate foragers, i.e., they cannot rear their first brood of minors without an external food source. Laboratory experiments should examine the founding strategy of *V. andrei* queens in more detail (e.g., Johnson, 2002, 2006).

Queens of *V. andrei* also are unusual because dealate queens sometimes occur in foraging columns. Creighton (1953) observed this behavior and suggested that these dealate queens were taken into established nests after mating. These observations were studied by Brown (1999b), who documented that dealate queens occur in foraging columns for about one month, and that all of these dealate queens were uninseminated. The mechanism that causes queens to forego mating and to perform worker-like tasks is unknown, especially in *V. andrei*, where this behavior cannot be attributed to lack of rains that trigger mating flights. The only other study to examine this behavior in detail found that dealate foraging queens of *Pogonomyrmex pima* also were uninseminated (Johnson, Holbrook, Strehl, & Gadau, 2007). Dealate queens from mature colonies in several other ant genera also leave the nest to forage (Johnson, 2015; Peeters, 1997).

Most colonies of *V. andrei* relocate their nest every year, with some colonies relocating nests up to 10 times per year. Relocation was not caused by encounters with their nearest neighbor even though the new nest site was typically more distant from that nearest neighbor. Predation, disease, microclimate, and local resource depletion were suggested as other possible causes of nest relocation (Brown, 1999a). Patterns of relocation were consistent within this population, but differed from patterns at a distant site (Pinter-Wollman & Brown, 2015). *Veromessor andrei* also affects local abundance and distribution of plants through their seed-harvesting and nest building activities. Workers typically display strong preferences for the seeds of some plant species, which results in changing the density and composition of plant species in areas that foragers visit (Hobbs, 1985; Peters, Chiariello, Mooney, Levin, & Hartley, 2005; but see Brown & Human, 1997). The nest mound itself also consists of a localized microsite that is affected by *V. andrei* because nest mounds contain higher concentrations of nutrients, a higher abundance and diversity of soil organisms (e.g., fungi, nematodes, microarthropods), and different plant species compared to adjacent non-mound soils (Boulton *et al.*, 2003; Hobbs, 1985; Peters *et al.*, 2005).

Veromessor andrei occurs in most open habitats from seaside to mountain valleys throughout the California coastal range from southern Oregon to northern Baja California, Mexico, at elevations from 0–2,000 m (Creighton, 1953; Wheeler & Wheeler, 1973). This species occurs in the Baja California desert, California coastal sage and chaparral, California montane chaparral and woodlands, California interior chaparral and woodlands, California Central Valley grasslands, Northern California coastal forests, and Klamath-Siskiyou forests ecoregions, as defined by Olson *et al.* (2001). There also are several records from higher elevations ($> 1,120$ m) in the Mohave Desert ecoregion in San Bernardino and Riverside Counties (Figure 10A). We regard the literature record of *V. andrei* from Ormsby County, Nevada, to be spurious (Wheeler & Creighton, 1934) until it is reverified.

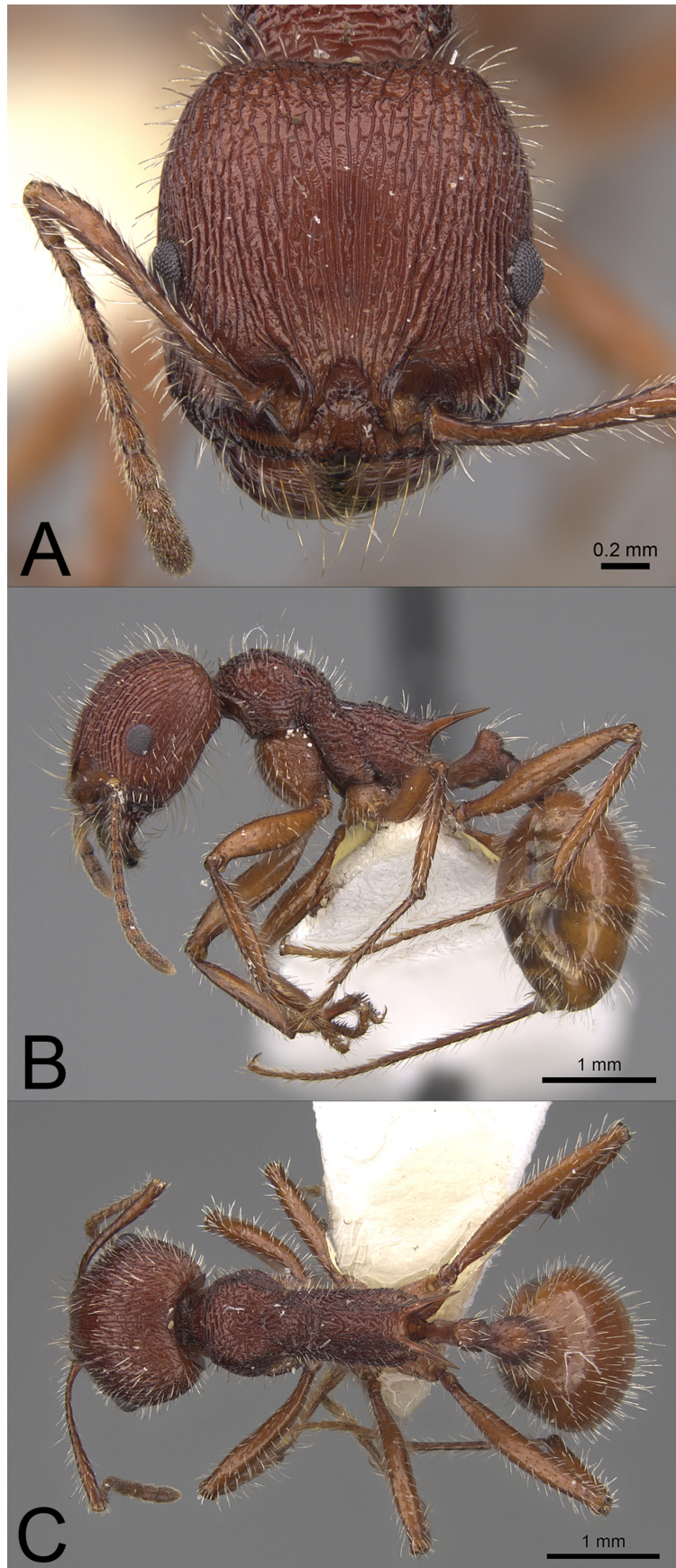


FIGURE 2. Photograph of *Veromessor andrei* worker (orange form): (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0923137). Photographs by Wade Lee from www.AntWeb.org.

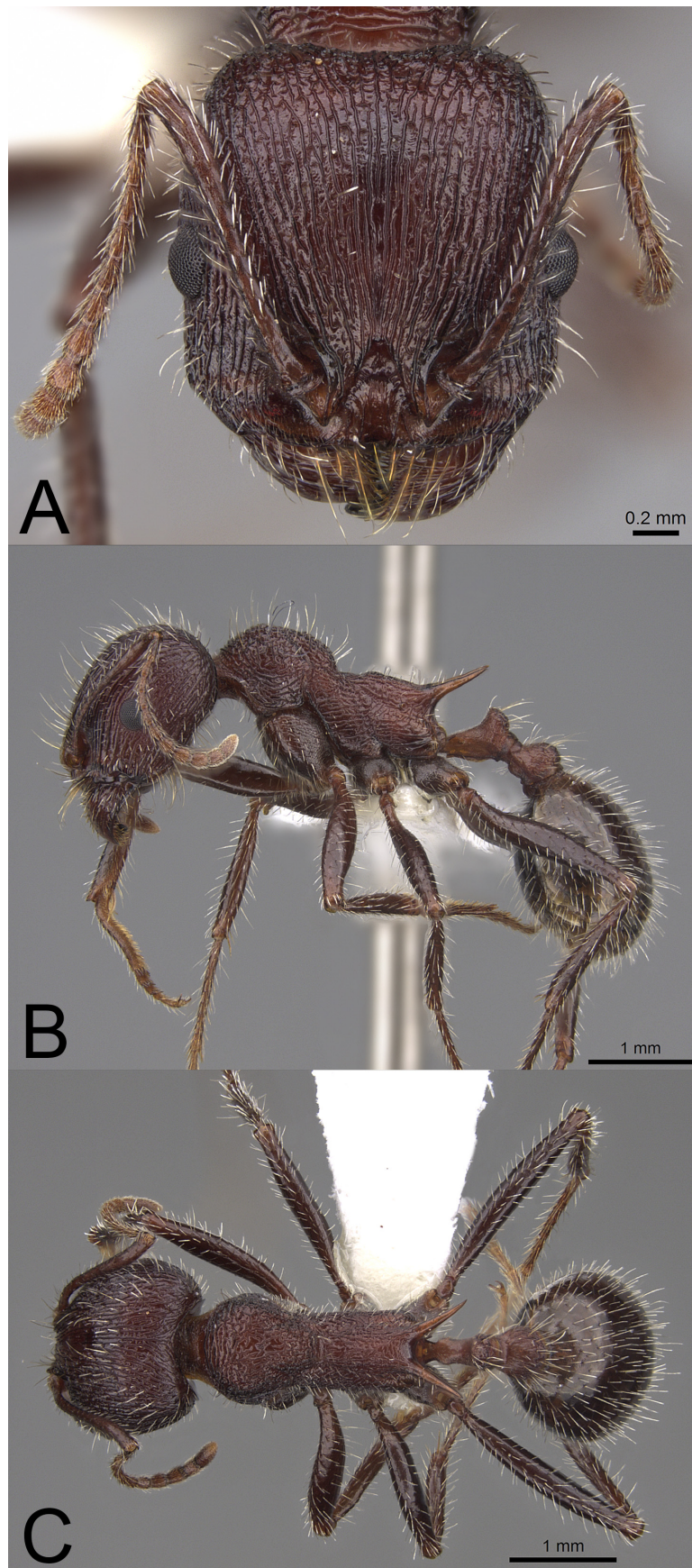


FIGURE 3. Photograph of *Veromessor andrei* worker (red form): (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0923139). Photographs by Wade Lee from www.AntWeb.org.

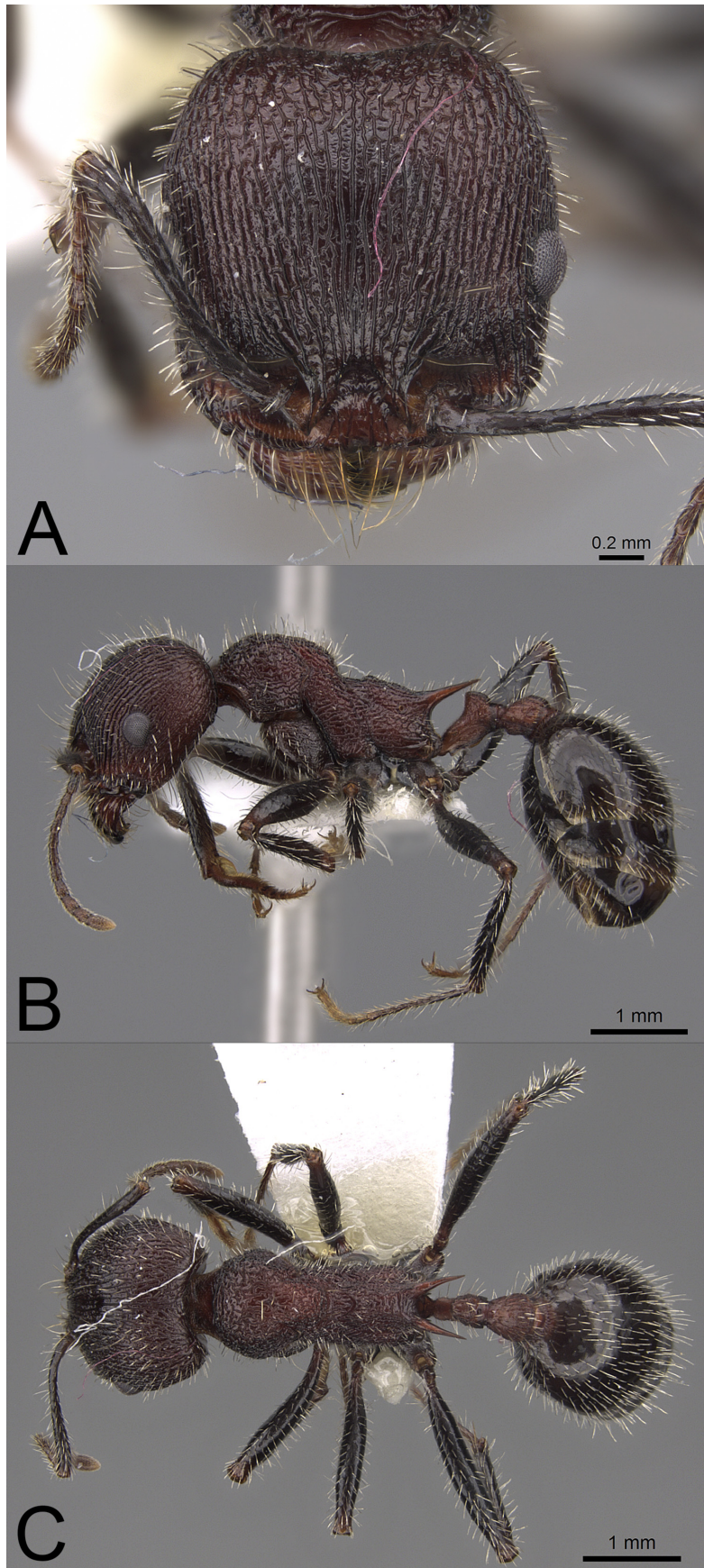


FIGURE 4. Photograph of *Veromessor andrei* worker (bicolored form): (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0923133). Photographs by Wade Lee from www.AntWeb.org.

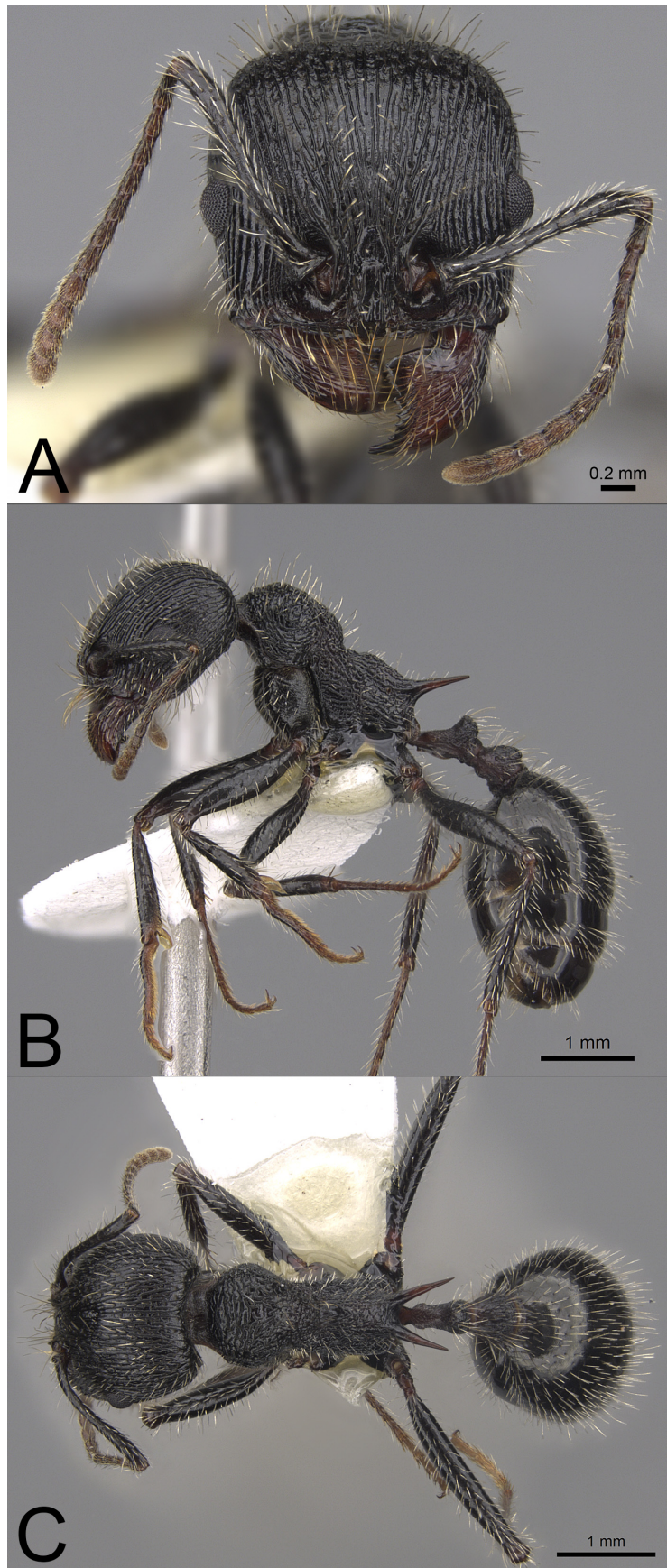


FIGURE 5. Photograph of *Veromessor andrei* worker (black form): (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0923138). Photographs by Wade Lee from www.AntWeb.org.

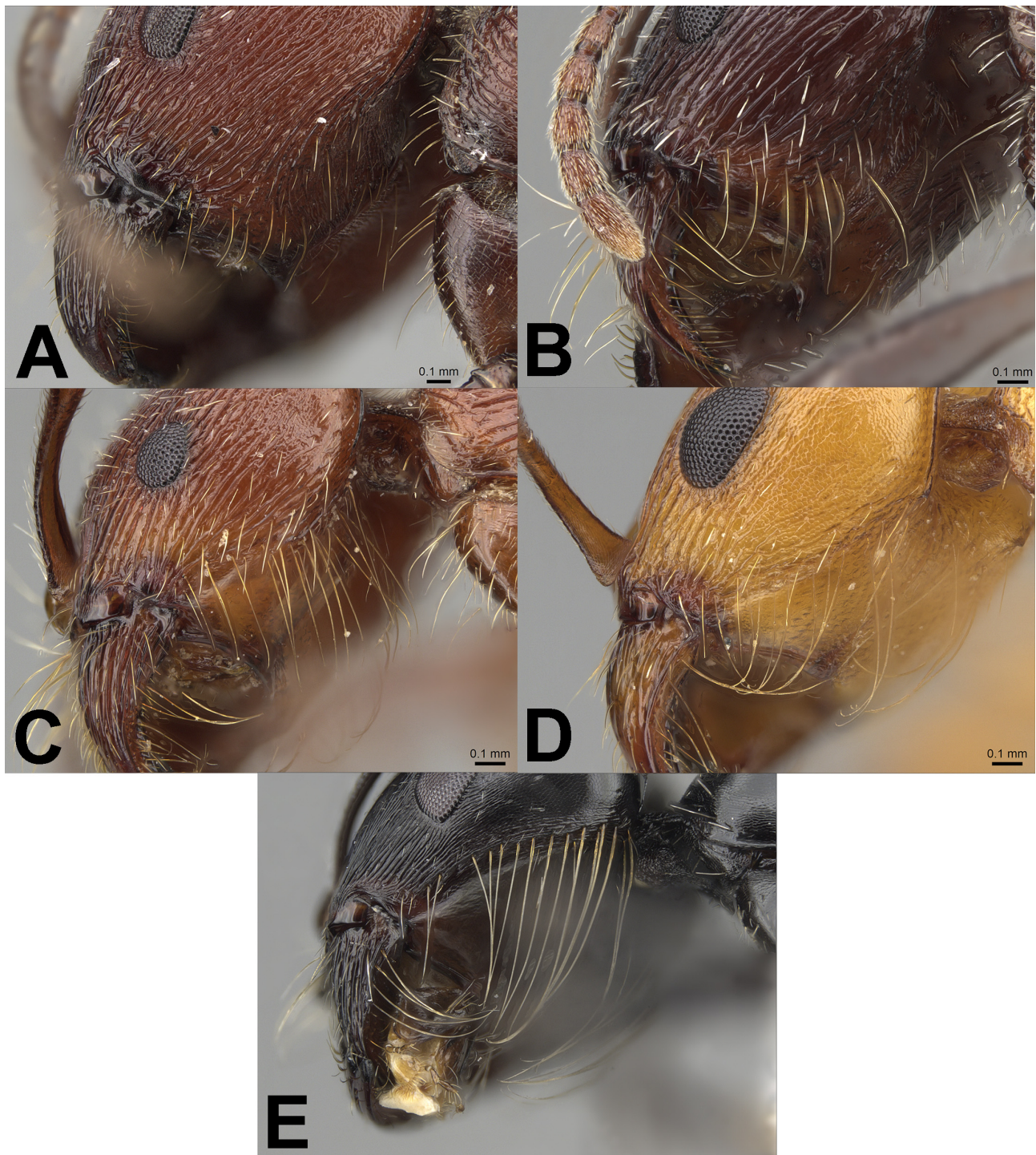


FIGURE 6. Photographs of the four categories of increasing psammophore development for species of *Veromessor* based on number and distribution of long J-shaped hairs on the ventral surface of the head capsule (= hypostomal region) (see text). Photograph of: (A) *V. chicoensis* (CASENT0923125)—J-shaped hairs mostly absent with scattered straight or evenly curved hairs, (B) *V. andrei* (CASENT0923140)—J-shaped hairs present but not arranged in a distinct row, usually mixed with straight or evenly curved hairs, (C) *V. chamberlini* (CASENT0761101) and (D) *V. smithi* (CASENT0923131)—J-shaped hairs present, arranged in a V-shaped row which does not reach the posterior part of the lateroventral margin of head capsule, usually mixed with straight or evenly curved hairs, and (E) *V. pergandei* (CASENT0923124)—J-shaped hairs present, many long J-shaped hairs arranged in a distinct row around the outer margin of the ventral region of the head capsule. Photographs by Wade Lee from www.AntWeb.org.

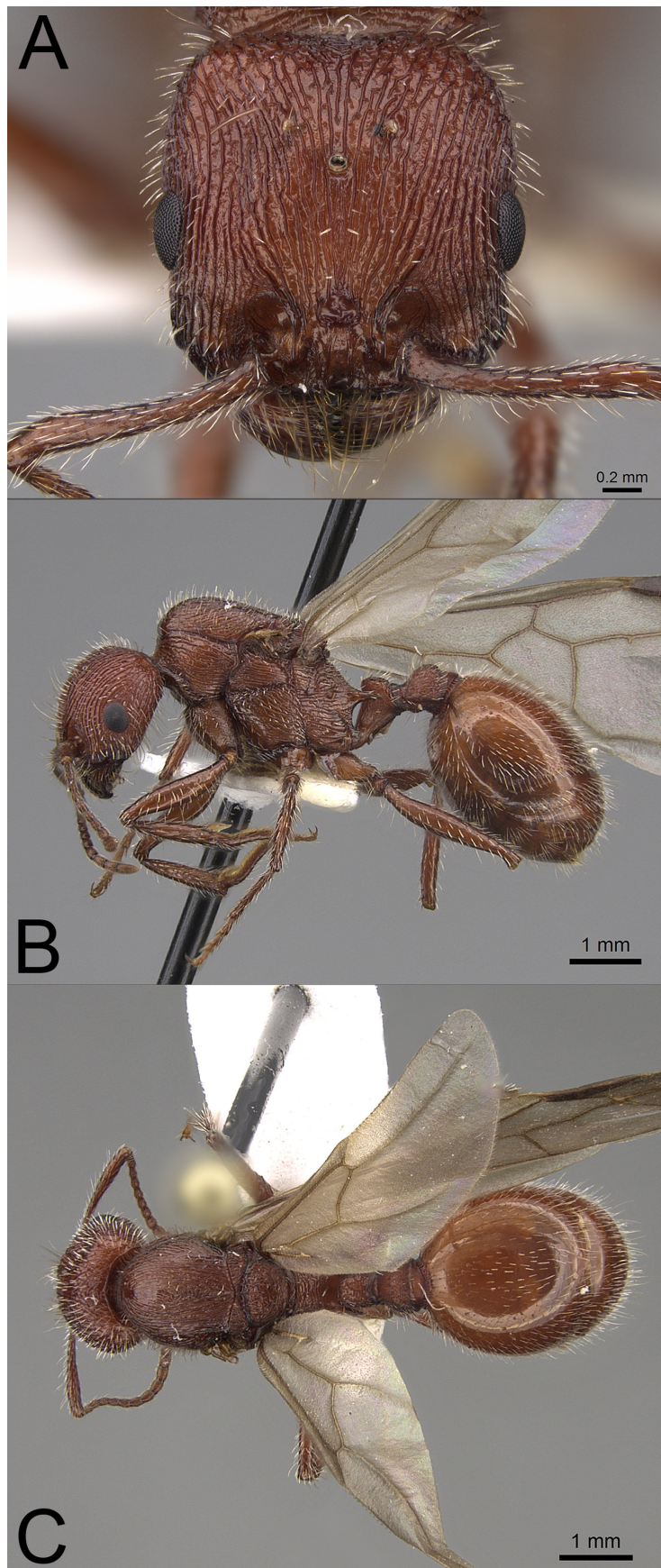


FIGURE 7. Photograph of *Veromessor andrei* alate queen (orange form): (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0923142). Photographs by Wade Lee from www.AntWeb.org.

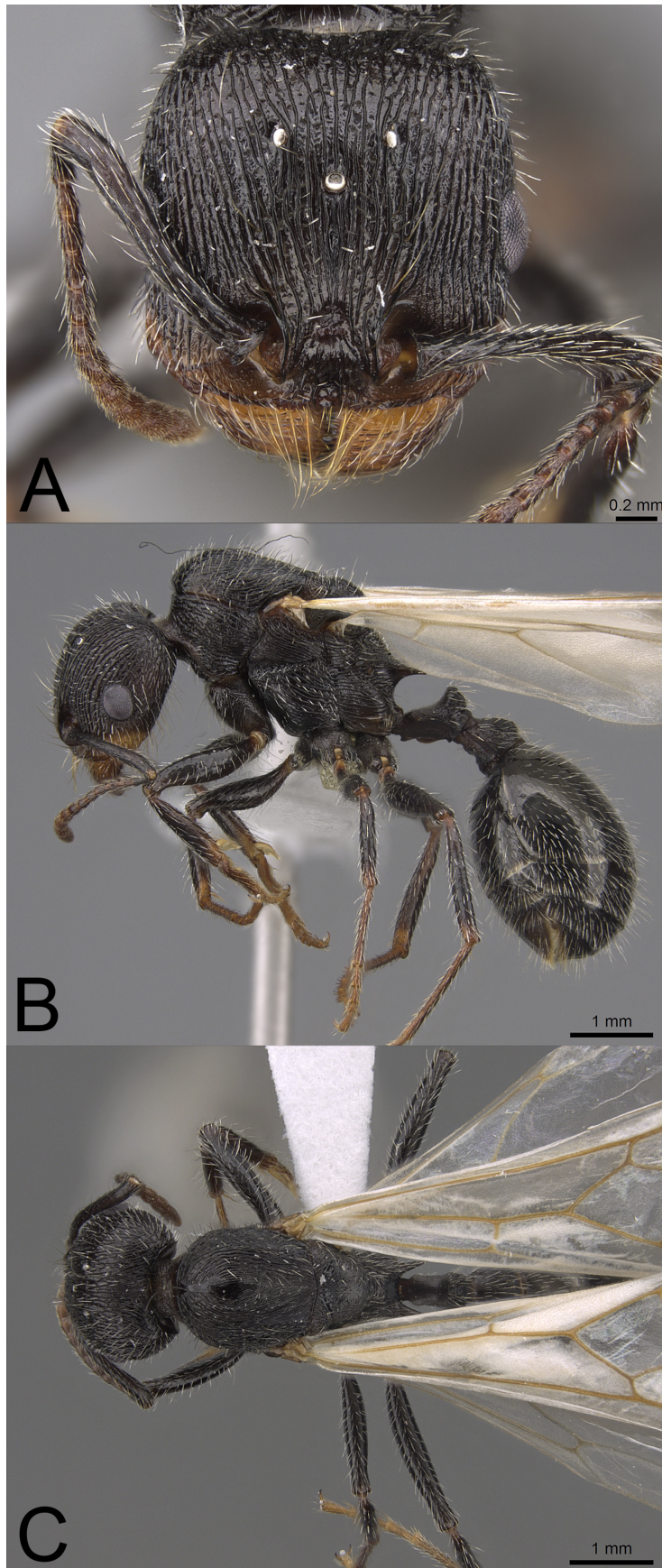


FIGURE 8. Photograph of *Veromessor andrei* alate queen (black form): (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0923141). Photographs by Wade Lee from www.AntWeb.org.

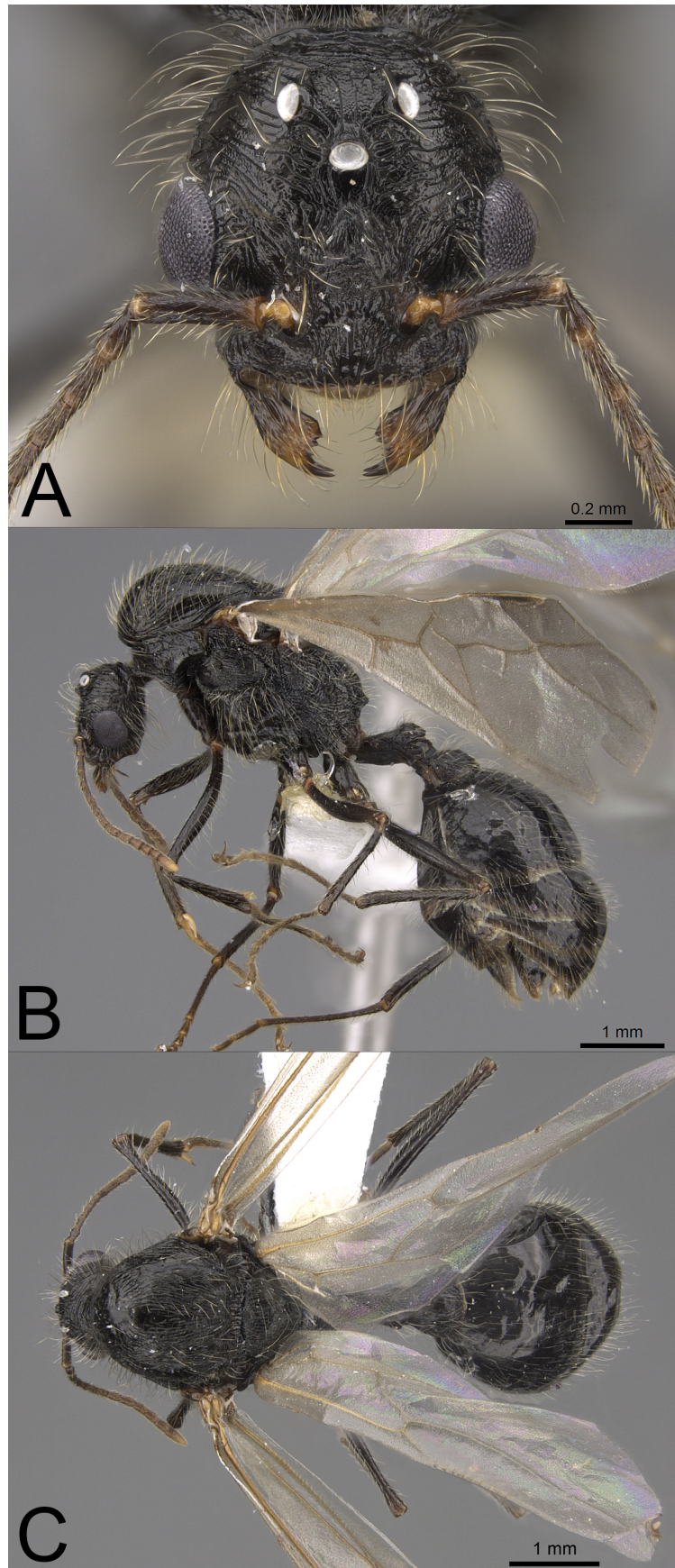


FIGURE 9. Photograph of *Veromessor andrei* male: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0923143). Photographs by Wade Lee from www.AntWeb.org.

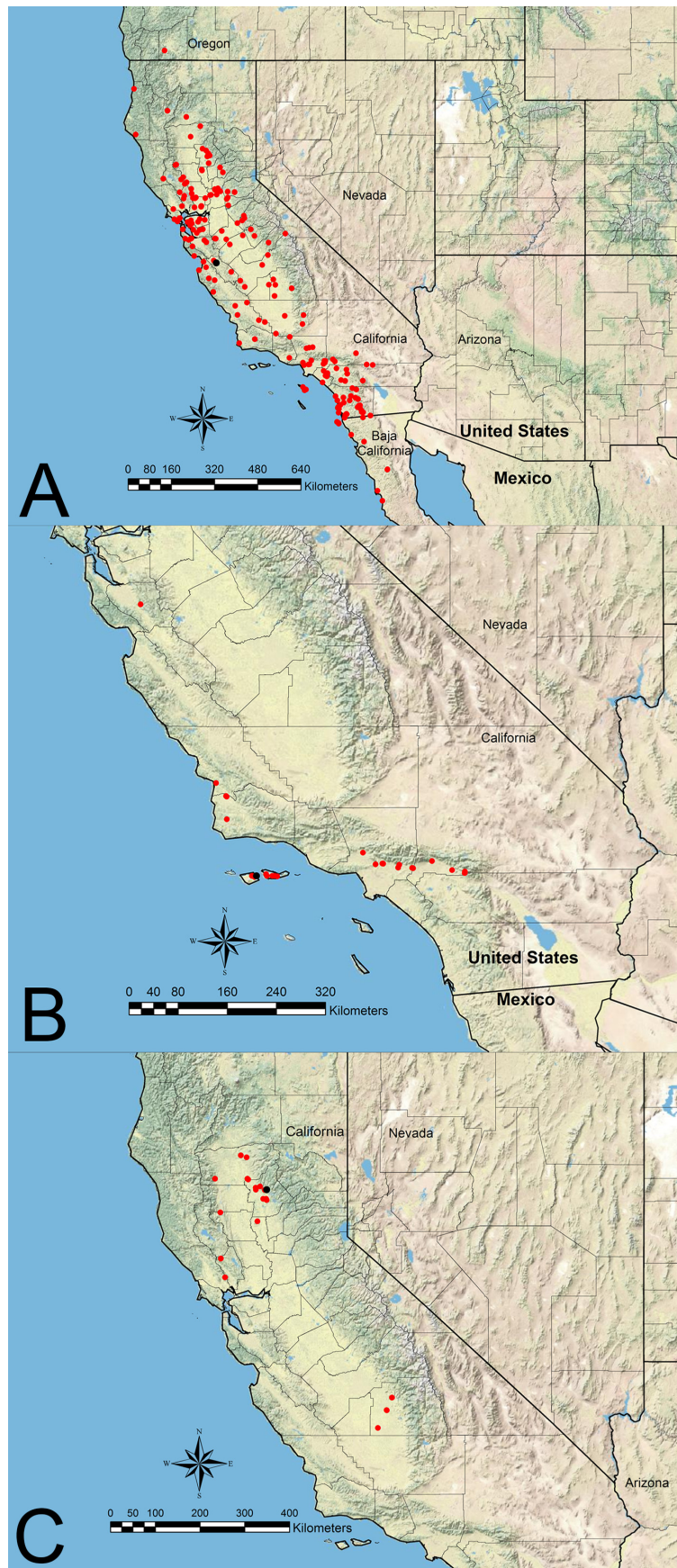


FIGURE 10. Geographic distribution of: (A) *Veromessor andrei*, (B) *V. chamberlini*, and (C) *V. chicoensis*. The larger black circle in each panel denotes the type locality. The northernmost locale for *V. chamberlini* was given only as Santa Clara County, and we have placed this locale near the center of the county.

Veromessor chamberlini

(Figures 1B, 6C, 11, 12A, 13–14)

Distribution—Figure 10B

Messor chamberlini Wheeler, 1915: 410 (worker). Syntypes examined: 3 workers [LACM], 6 workers [MCZC], 3 workers [USNM], UNITED STATES, California, Santa Barbara County, Santa Cruz Island, no date (Dr. R. V. Chamberlin); Wheeler and Wheeler, 1972: 240 (larvae); Enzmann, 1947: 152 (as subspecies of *Veromessor andrei*); Creighton, 1950: 159 (revived status as full species). See also Wheeler and Creighton, 1934: 366, plate II, fig. 5. USNM worker here designated **LECTOTYPE** [USNMMENT00529080].

Novomessor (Veromessor) chamberlini (Wheeler); Emery, 1921: 67 (first combination in *Novomessor [Veromessor]*).

Veromessor chamberlini (Wheeler); Wheeler and Creighton, 1934: 366 (first combination in *Veromessor*).

Novomessor (Veromessor) andrei subsp. *chamberlini* (Wheeler); Enzmann, 1947: 152 (revived combination as subgenus of *Novomessor* and first combination as subspecies of *andrei*).

Veromessor chamberlini (Wheeler); Creighton, 1950: 157 (revived combination in *Veromessor*; re-elevated to specific status).

Messor chamberlini Wheeler; Bolton, 1982: 341 (revived combination in *Messor*).

Veromessor chamberlini (Wheeler); Ward, Brady, Fisher & Schultz, 2015: 13 (revived combination in *Veromessor*).

Worker diagnosis. This species is uniquely characterized by the following combination of features: (1) yellowish-red to dark orangish-red, (2) medial lobe of clypeus with two strong submedial rugae, sometimes with one to two weaker sublateral rugae, medial lobe not thick and protuberant in profile, not elevated above lateral lobes in frontal view, (3) mandibles with 8 teeth, (4) dorsal base of scape flattened and widened; maximum basal width of scape distinctly greater than maximal preapical width; in frontal view, base of scape asymmetrical with ventral portion of anterior edge greatly expanded compared to dorsal edge, (5) MOD less (usually much less) than OMD, $OI < 22.0$, (6) cephalic dorsum with prominent wavy to weakly irregular rugae, medial rugae diverging toward posterior corners; rugae along posterior margin strongly irregular to weakly rugoreticulate; cephalic interrugae weakly to moderately coriarius, moderately shining, (7) psammophore moderately well developed; ventral surface of head capsule with J-shaped hairs arranged in a V-shaped row which does not reach the posterior part of lateroventral margin of head capsule, usually mixed with straight or evenly curved hairs, (8) dorsum of pronotum with weakly to strongly irregular rugae; sides of pronotum with widely spaced, regular to wavy, longitudinal rugae; mesonotum with irregular longitudinal rugae; mesopleura with regular to wavy rugae that traverse longitudinally to posterodorsally; interrugae on mesosoma weakly coriarius, shining, (9) propodeal spines slender, acuminate, weakly curved posterad in profile and weakly curved inward in dorsal view; length $\geq 3.0 \times$ the distance between their bases and length $\geq 1.0 \times$ MOD; infraspinal facet and propodeal declivity weakly coriarius to weakly rugose, strongly shining, and (10) metasternal process moderately large, longer than high, apex broadly rounded, margin irregular and translucent (Figures 6C, 11, 12A).

Measurements. lectotype ($n = 32 + 1$ paralectotype). HL 1.32 (1.11–1.45); HW 1.33 (1.06–1.42); MOD 0.24 (0.21–0.27); OMD 0.34 (0.23–0.39); SL 1.06 (0.92–1.15); PNW 0.83 (0.67–0.90); HFL 1.39 (1.14–1.53); ML 1.68 (1.33–1.88); PW 0.28 (0.20–0.29); PPW 0.43 (0.34–0.46). Indices: SI 79.70 (73.23–87.74); CI 100.76 (94.12–104.17); OI 18.05 (16.30–21.70); HFI 104.51 (93.60–110.16).

Queen diagnosis. This caste is diagnosed by the following combination of features: (1) orangish to orangish-brown, (2) medial lobe of clypeus with two strong submedial rugae, sometimes with one to two weaker sublateral rugae, medial lobe not thick and protuberant in profile, not elevated above lateral lobes in frontal view, (3) mandibles with 8 teeth, (4) dorsal base of scape flattened and widened; maximum basal width of scape distinctly greater than maximal preapical width; in frontal view, base of scape asymmetrical with ventral portion of anterior edge greatly expanded compared to dorsal edge, (5) MOD similar to OMD, (6) cephalic dorsum with prominent wavy to weakly irregular rugae, medial rugae diverging toward posterior corners; rugae along posterior margin weakly irregular to weakly rugoreticulate; interrugae on cephalic dorsum weakly to moderately coriarius, weakly shining, (7) psammophore moderately well developed, (8) mesoscutum shining with fine longitudinal rugae, midline broadly smooth and shining between fine longitudinal rugae, (9) propodeal spines shorter than distance between their bases; infraspinal facet smooth and shining, and (10) metasternal process moderately large, longer than high, apex broadly rounded, margin irregular and translucent (Figure 13).

Measurements. ($n = 4$). HL 1.42–1.47; HW 1.44–1.50; MOD 0.33–0.36; OMD 0.35–0.36; SL 1.12–1.25; HFL 1.52–1.61; ML 2.30–2.49; PW 0.37–0.41; PPW 0.58–0.61. Indices: SI 77.24–83.33; CI 99.31–103.52; OI 22.76–24.49; HFI 101.33–111.81.

Male diagnosis. This caste is diagnosed by the following combination of features: (11) blackish brown, (12) *, (13) *, (14) *, (15) anepisternum densely lineopunctate; katapisternum strongly coriarius, anterior one-half of katapisternum with scattered, long, flexuous hairs, posterior one-half lacking long flexuous hairs except for a row of short hairs along posterior border, (16) propodeum with widely spaced longitudinal rugae, interrugae densely punctate, dull; spines absent, (17) metasternal process triangular, acute, with lamella extending on each side, portion posterior to lamella longer than portion anterior to lamella, and (18) subpetiolar process bluntly triangular, apex acute (Figures 1B, 14). * = head missing.

Measurements. ($n = 1$). HL *; HW *; MOD *; OMD *; SL * HFL 1.68; ML 2.09; PW 0.27; PPW 0.48; AOD *; IOD *; OOD *. Indices: SI *; CI *; OI *; HFI *. * = head missing.

Additional material examined. **UNITED STATES: California:** *Los Angeles Co.:* Pasadena, Nov 11, 1922 & May 13, 1946 & June 13, 1946 (LACM; UCDC; USNM); San Gabriel River at Irwindale, Feb 17, 1963 & May 9, 1963 & Jun 19, 1963 & Feb 22, 1965 (CASC; LACM; RAJC; UAIC; UCDC; USNM); Azusa, Dec 5, 1928 & Jun 14, 1931 (USNM); Claremont, Nov 16, 1945 (UCDC; USNM); 2 mi E San Fernando, May 7, 1931 (USNM); Glendale, July 1941 (UCDC). *San Bernardino Co.:* Mentone, Aug 22, 1965 (LACM); Oak Glen, 1500 m, Sep 23, 1982 & May 2, 1983 & Jul 26–Aug 2, 1983 & Jul 1–14, 1985 & Aug 1, 1985 (CASC; LACM; UCRC); Rialto at Riverside & Sierra Avenues, 1870', Jul 20, 1992 (RAJC). *San Luis Obispo Co.:* Arroyo Grande, Aug 2–3, 1988 (UCDC). *Santa Barbara Co.:* Santa Maria (as San Maria on one label), Jun 8, 1957 & Aug 6, 1957 & Aug 29, 1957 (LACM; USNM); Santa Cruz Island at E end of central valley, May 23, 2013 (RAJC); Santa Cruz Island at Field Station, 70 m, Jun 26, 1993 & Jul 4, 2003 & Aug 4, 2003 (NHMW; RAJC; UCDC); Santa Cruz Island at South Ridge, 430 m, Jun 27, 1993 (RAJC); Santa Rosa Island at Cherry Canyon, 45 m, Apr 12, 2014 (MLBC; UCDC); Santa Rosa Island at Windmill Canyon, 45 & 85 m, Apr 12–14, 2014 (UCDC); Santa Cruz Island, Apr 18, 1936 (USNM); Santa Cruz Island at El Tigre Ridge, May 4, 2000 (UCDC); Santa Cruz Island at Torrey Pines, 30 m, Apr 13, 2014 (MMPC; UCDC); La Purisima Mission in NE Lompoc, 60 m, May 25, 1985 (JTLC); La Purisima at 5 km NE Lompoc, 125 m, Jun 12, 1994 (record from M. Bennett, pers. comm.). *Santa Clara Co.:* no loc, no date (LACM). **Questionable locales (appear to be or are outside of geographical range):** **UNITED STATES: Missouri: Barton Co.:** no loc, no date (MCZC) (Figure 10B).

Etymology. This species was named to honor Dr. D.V. Chamberlin, who collected the type series on Santa Cruz Island.

Discussion. *Veromessor chamberlini* appears to have a relatively small geographic range, such that it might be sympatric only with *V. andrei* and *V. stoddardi*. Workers of *V. chamberlini* are separated from both species based on: (1) moderately well developed psammophore, and (2) posterior margin of frontal lobes notably constricted. Both *V. andrei* and *V. stoddardi* have: (1) poorly developed psammophore, and (2) posterior margin of frontal lobes lacking a constriction.

A molecular phylogeny that used UCEs shows *V. chamberlini* and *V. andrei* are sister lineages (M.L. Borowiec, unpub. data).

Biology. Little is known about the biology of *V. chamberlini*. Workers are diurnal and forage in a column (M. Bennett, pers. comm.). Colonies are small with a maximum of 627 workers (M. Bennett, pers. comm.). Workers are monomorphic.

Gland chemistry has not been examined in *V. chamberlini*. Like other small-colony congeners, workers of *V. chamberlini* have a small pygidial gland reservoir and lack a textured tergal cuticle (Hölldobler *et al.*, 2013).

Mating flights have not been observed, but sexuals have been collected in Malaise traps from July 1 through Aug 2, indicating that mating flights occur during summer.

The geographic range of *V. chamberlini* appears to be restricted to coastal islands and adjacent mainland coastal areas of southern California and extending inland along the southern base of the San Gabriel Mountains. Most potential habitat south of the San Gabriel Mountains has been developed. There also is one disjunct record from Santa Clara County that did not indicate a collector, locale, or date. The veracity of this record is unknown, but it seems likely that the historical range of *V. chamberlini* extended along coastal areas north to or near the San Francisco Bay area. Efforts should be made to reverify this northern record. This species occurs at elevations from 30–1,500 m in the California interior chaparral and woodlands, California coastal sage and chaparral, and California montane chaparral and woodlands ecoregions, as defined by Olson *et al.* (2001) (Figure 10B).

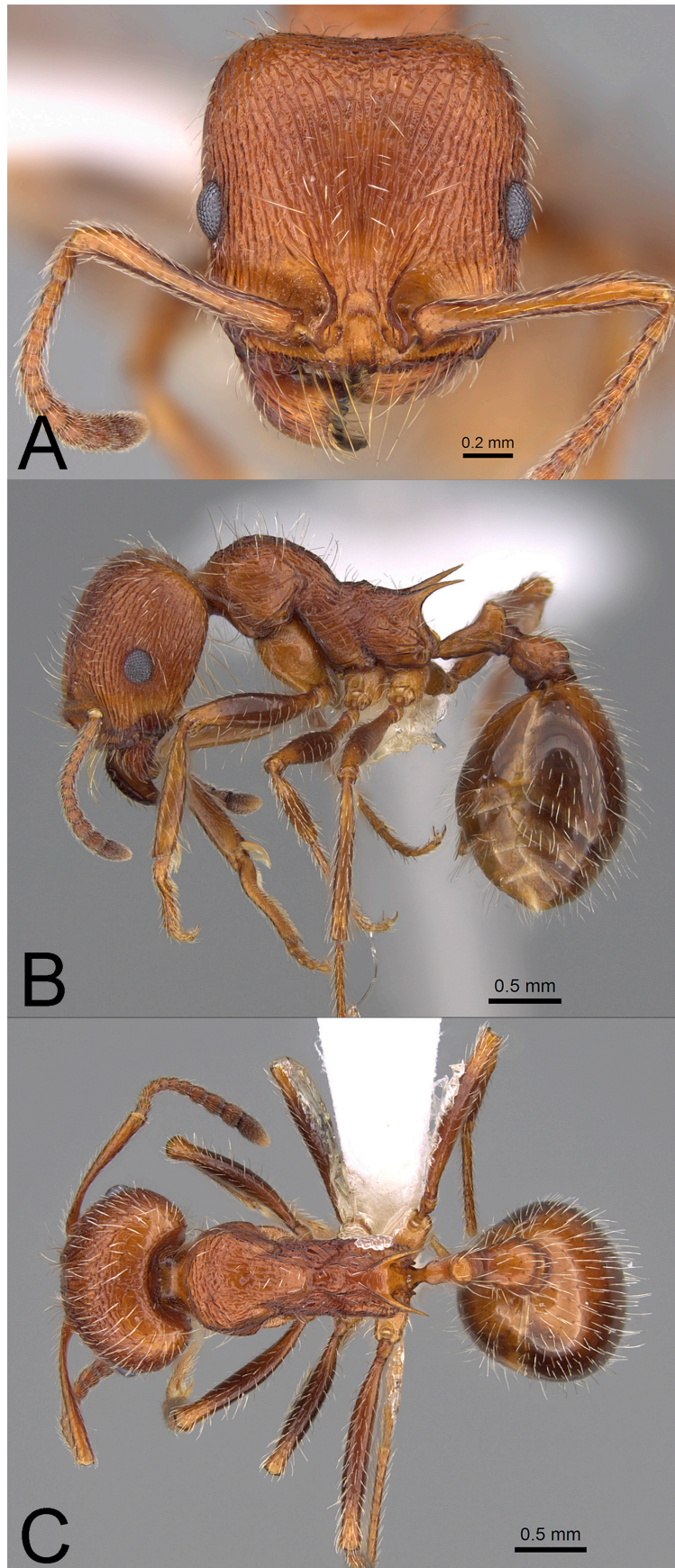


FIGURE 11. Photograph of *Veromessor chamberlini* worker: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0922840). Photographs by Michele Esposito from www.AntWeb.org.

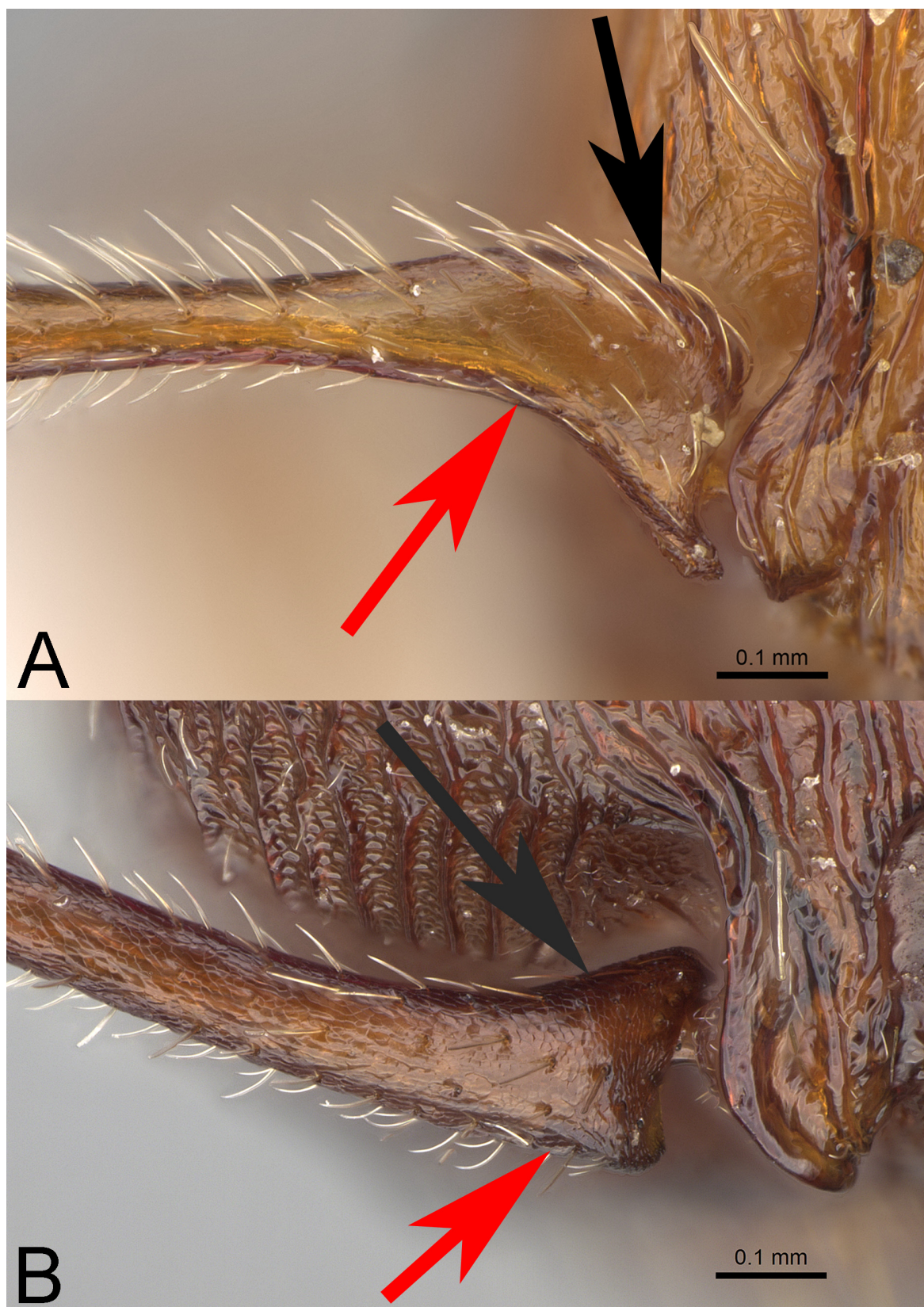


FIGURE 12. Photographs of dorsal surface of scape: (A) *Veromessor chamberlini* (LACMENT359743)—anterior edge of scape curving inward distad of base (red arrow), posterior edge of scape flat to weakly convex at base (black arrow), narrowing distad of base; widened area at base of scape much longer than width at base, and (B) *V. lobognathus* (LACMENT363932)—anterior edge of scape flat at base (red arrow), posterior edge of scape narrowing from base (black arrow); widened area at base of scape shorter than width at base. Photographs by Michele Esposito from www.AntWeb.org.

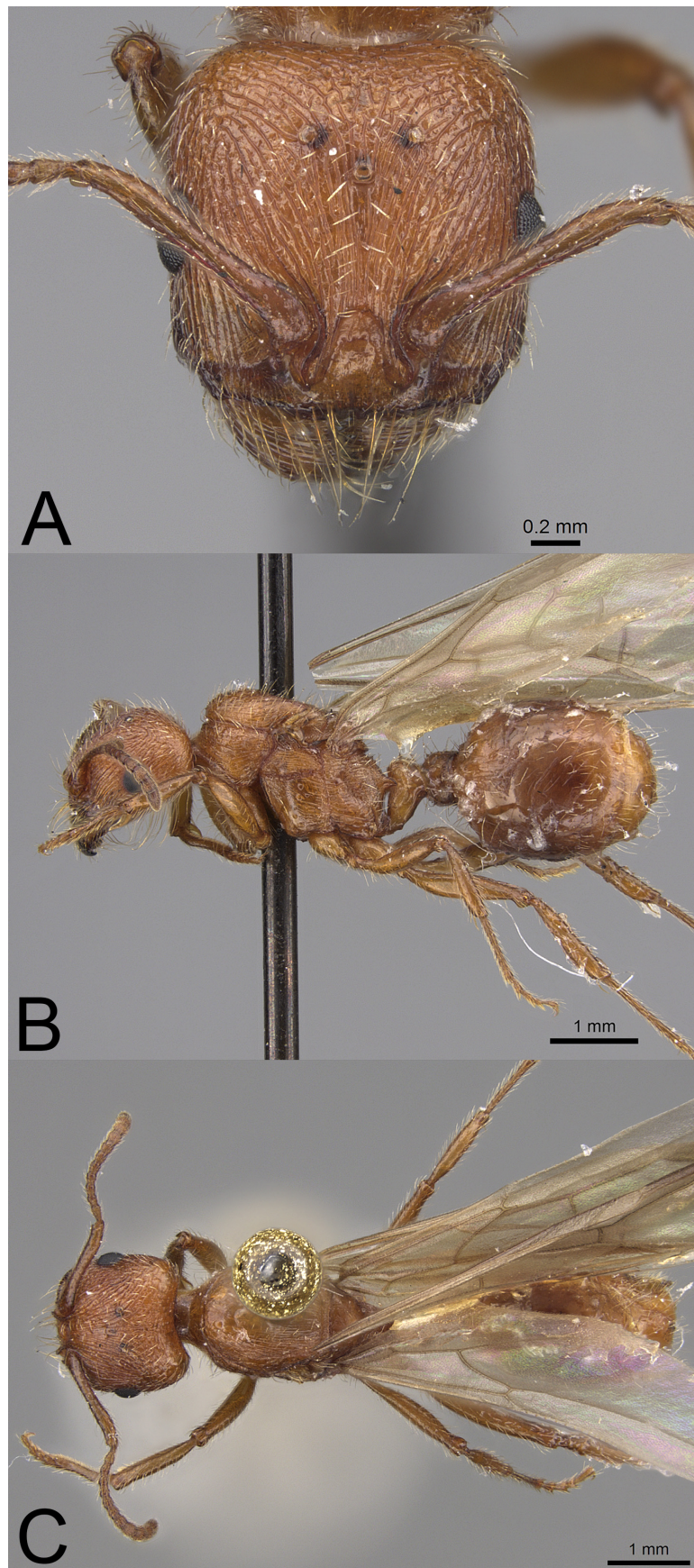


FIGURE 13. Photograph of *Veromessor chamberlini* alate queen: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (UCRCENT00500153). Photographs by Wade Lee from www.AntWeb.org.

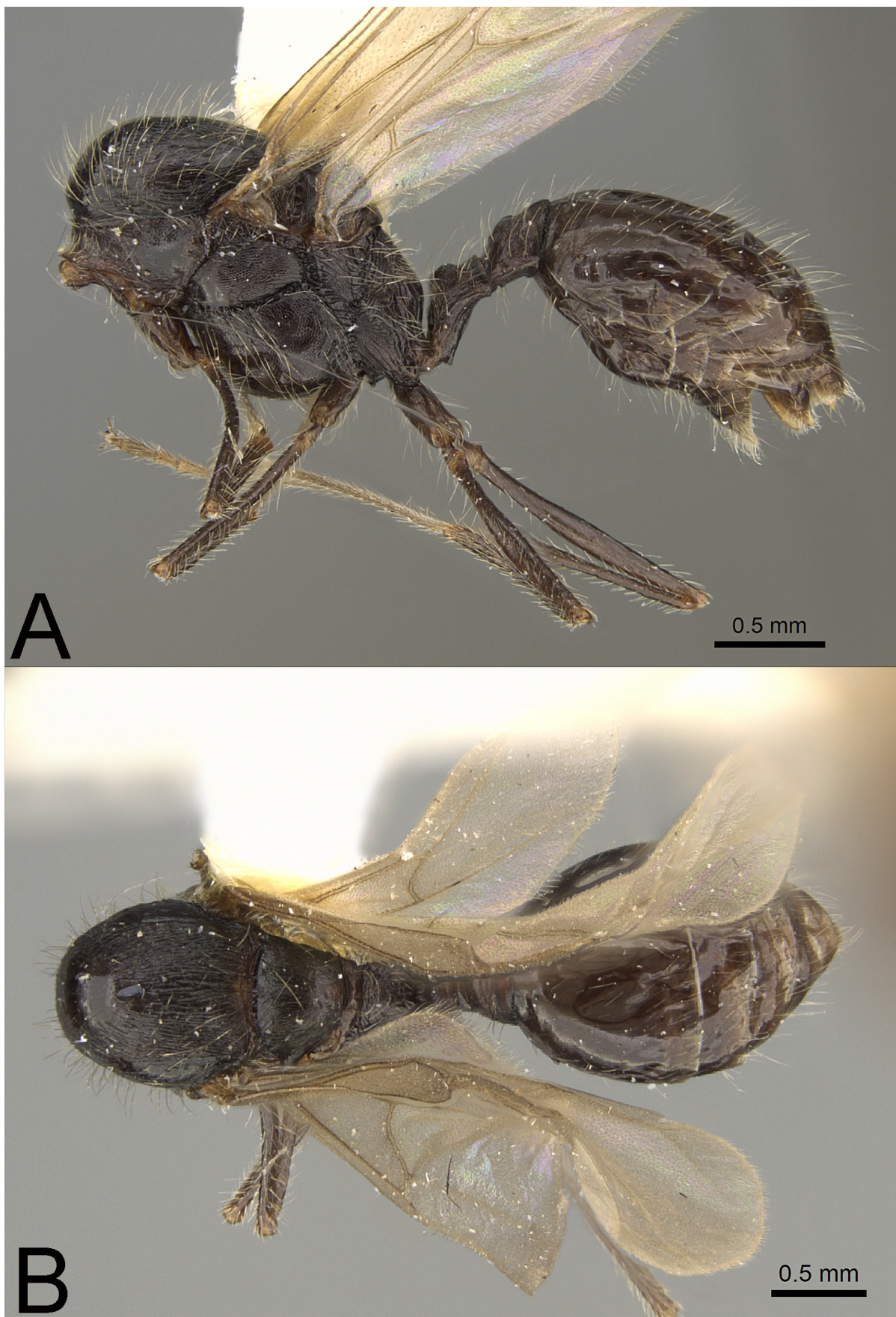


FIGURE 14. Photograph of *Veromessor chamberlini* male: (A) lateral view of body, and (B) dorsal view of body (UCRCENT00500152). The head is missing. Photographs by Michele Esposito from www.AntWeb.org.

Veromessor chicoensis

(Figures 1C, 6A, 15–18)

Distribution—Figure 10C

Veromessor stoddardi subsp. *chicoensis* Smith, 1956: 37 (worker). Types examined: holotype worker [USNM: USNMMENT00529087], USNM#62959, 8 paratype workers [USNM], 6 paratype workers [LACM], UNITED STATES, California: Butte County, Chico (T22N, R2E, Section 17), 450', 2 March 1954 (Adrian Wenner).

Messor stoddardi subsp. *chicoensis* (Smith); Bolton, 1995: 253 (first combination in *Messor*).

Messor chicoensis Smith; Johnson, 2000: 96 (raised to species, in list); see also Ward, 2005: 13 (in list).

Veromessor chicoensis Smith; Ward, Brady, Fisher, and Schultz, 2015: 13 (revived combination in *Veromessor*).

Worker diagnosis. This species is uniquely characterized by the following combination of features: (1) head and mesosoma orangish-red or orangish-brown to reddish-brown, gaster blackish-orange to blackish, (2) medial lobe of clypeus lacking medial groove but with several lateral longitudinal rugae, medial lobe not thick and protuberant in profile, not elevated above lateral lobes in frontal view, (3) mandibles with 8 teeth, (4) scape narrowest near midlength, (5) MOD distinctly less than OMD, $OI < 23.0$, (6) cephalic dorsum weakly shining between fine longitudinal rugae, usually becoming somewhat reticulate on posterior margin; antennal fossa sometimes with several concentric rugae, (7) psammophore poorly developed; ventral surface of head capsule with scattered straight or evenly curved hairs, but J-shaped hairs mostly absent, (8) pronotum with fine, wavy to irregular, longitudinal rugae; sides of pronotum with longitudinal rugae that sometimes fade to disappear posterad, becoming granulate posterad; mesonotum with wavy to weakly irregular longitudinal rugae; mesopleura with wavy to irregular rugae that traverse longitudinally to posterodorsally, rugae sometimes with lateral branches, interrugae moderately to strongly granulate, (9) propodeal spines short, acuminate, length less than distance between their bases; infraspinal facet and propodeal declivity strongly coriaceous or rugose, weakly dull to weakly shining, and (10) metasternal process large, higher than long with broadly rounded apex; anterior and posterior surfaces decline steeply; weakly translucent in profile (Figures 6A, 15–16).

Measurements. holotype ($n = 64$). HL 1.63 (1.16–1.81); HW 1.66 (1.02–1.94); MOD 0.30 (0.21–0.34); OMD 0.39 (0.24–0.49); SL 1.25 (0.87–1.37); PNW 0.98 (0.69–1.19); HFL 1.51 (1.06–1.73); ML 2.01 (1.43–2.16); PW 0.30 (0.17–0.36); PPW 0.43 (0.27–0.52). Indices: SI 75.30 (67.03–94.58); CI 101.84 (80.56–119.5); OI 18.07 (16.4–22.66); HFI 90.96 (75.46–117.24).

Queen diagnosis. This caste is diagnosed by the following combination of features: (1) head and mesosoma dark orangish to orangish-brown with parts of mesopleura and mesoscutum blackish-orange to blackish; gaster blackish-orange, (2) medial lobe of clypeus with strong submedial and sublateral rugae, (3) mandibles with 8 teeth, (4) dorsal base of scape weakly flattened; maximum basal width of scape greater than maximum preapical width, (5) MOD less than to greater than OMD, (6) cephalic dorsum weakly shining between fine, wavy to irregular, longitudinal rugae; medial rugae diverging toward posterior corners, rugae becoming strongly irregular to weakly rugoreticulate along posterior margin, (7) psammophore poorly developed, (8) sides of pronotum weakly shining between fine, longitudinal rugae; mesoscutum with fine, longitudinal rugae; mesoscutellum smooth and shining; anepisternum weakly shining between fine longitudinal rugae; katepisternum moderately shining between slightly more widely spaced rugae, (9) sides of propodeum weakly shining and densely punctate-granulate between longitudinal and oblique rugae; propodeal spines triangular, acuminate, length less than distance between their bases; infraspinal facet and propodeal declivity with fine transverse rugae, interrugae weakly dull to weakly shining, and (10) metasternal process large, higher than long with broadly rounded apex; anterior and posterior surfaces decline steeply; weakly translucent in profile (Figure 17).

Measurements. ($n = 5$). HL 1.44–1.61; HW 1.39–1.58; MOD 0.32–0.35; OMD 0.28–0.36; SL 1.08–1.12; HFL 1.34–1.50; ML 2.10–2.26; PW 0.35–0.39; PPW 0.49–0.55. Indices: SI 68.35–79.14; CI 94.74–98.14; OI 22.22–26.58; HFI 94.44–100.00.

Male diagnosis. This caste is diagnosed by the following combination of features: (11) head and mesosoma dark brown to dark blackish-brown; gaster a lighter medium brown, (12) clypeus weakly convex in profile; anteromedial margin weakly concave, with a weak medial longitudinal carina, (13) mandibles with 1–3 teeth basad of preapical tooth, (14) anterior ocellus well above level of top of eyes, (15) mesopleura weakly shining, moderately to strongly lineopunctulate-lineogranulate, sometimes with rugae along posterior margin, (16) propodeum contiguously punctate-granulate and with scattered, irregular, fine rugae; propodeal spines cariniform to knoblike and inconspicuous, (17)

metasternal process prominent and acute to elongate and narrowly rounded, and (18) subpetiolar process short, elongate-triangular to spiniform, apex acuminate to rounded (Figures 1C, 18).

Measurements. ($n = 10$). HL 0.84–1.01; HW 0.80–1.00; MOD 0.34–0.40; OMD 0.09–0.13; SL 0.34–0.49; HFL 1.43–1.90; ML 2.12–2.59; PW 0.28–0.39; PPW 0.46–0.55; AOD 0.09–0.13; IOD 0.26–0.34; OOD 0.26–0.35. Indices: SI 40.70–61.25; CI 80.00–114.94; OI 34.00–46.25; HFI 159.00–235.00.

Additional material examined. UNITED STATES: California: *Butte Co.*: Chico, 300', May 18–19, 1956 & Aug 23, 1968 & no date (LACM; USNM); Neal Rd at 6.1 mi NE Jct Hwy 99, 1000', Jun 23, 1979 (CASC; LACM); Hwy 99 at 15 mi S Chico, Apr 28, 1967 (LACM; UAIC; USNM); 9 km N Oroville, 360 m, Apr 18, 1992 (UCDC). *Colusa Co.*: Fouts Springs, 500 m, Apr 12, 1986 & May 28, 1995 (UCDC); Stonyford, 355 m, Apr 12, 1986 & Jun 19, 1988 (UCDC). *Napa Co.*: Twin Peaks at 4 km W Aetna Springs, 660 m, May 28, 1988 (UCDC). *Sonoma Co.*: 6 km N Sonoma, 300 m, Apr 13, 1997 (UCDC). *Sutter Co.*: 1 km W North Butte, Sutter Buttes, 200 m, May 28, 2007 (UCDC). *Tehama Co.*: Hwy 36 at 5.8 Rd mi E Jct Hwy 99, 550', Jun 22, 1979 (CASC; LACM; USNM); Vina Plains Nature Preserve at 16 km E Corning, 60 m, Oct 10, 1992 & Mar 28, 1993 (UCDC); Dye Creek at 18 km SE Red Bluff, 335 m, Jun 30–Jul 2, 2002 (CASC). *Tulare Co.*: Woodlake (on label as “Wood L.”), May 14, 1947 (LACM); James K. Herbert Wetland Prairie Preserve, 310', no date, 2004 (not examined, see Hamm & Kamansky, 2009) & Oct 2, 2018 (LACM; NHMW; RAJC; UCDC); Pixley National Wildlife Refuge, 200', no date, 2004 (not examined, see Hamm & Kamansky, 2009) (Figure 10C).

Etymology. This species was named based on the type locality at Chico, California.

Discussion. The poorly developed psammophore and short propodeal spines distinguish workers of *V. chicoensis* from all congeners except the closely related *V. stoddardi*. *Veromessor chicoensis* is distinguished by: (1) antennal scape narrowest near mid-length; maximum basal width of scape greater than maximum preapical width, and (2) in dorsal view, rugae on mesonotum similar to those on pronotum, interrugae weakly dull. In *V. stoddardi*: (1) antennal scape narrowest immediately distad of basal bend; maximum basal width of scape about equal to maximum preapical width, and (2) in dorsal view, the mesonotum usually smooth and shining, rugae distinctly weaker than those on pronotum.

Smith (1956) described *V. stoddardi chicoensis* from a holotype and 20 paratype workers and indicated specimens were deposited at USNM. We examined nine type workers (on three pins) from USNM. All nine had type labels USNM #62959, but none of these specimens had a holotype label. Two pins had a USNM Paratype No. 62959 label, and one pin had a USNM Type No. 62959 label; the latter pin also had a black dot on the uppermost triangle, and this specimen is presumed to be the holotype. Consequently, we placed a holotype label on this worker.

Veromessor chicoensis was described as a subspecies of *V. stoddardi* because of the similarity between workers of the two species. The two species are allopatric and workers of the two species display few consistent morphological differences, but queens and males differ in both morphology and size. Worker allometry is similar for both species (see above), but queens and males of *V. chicoensis* are distinctly smaller than those of *V. stoddardi* (Figure 19). A molecular phylogeny that used UCEs shows *V. chicoensis* and *V. stoddardi* to be sister lineages, but well-separated and reciprocally monophyletic (M.L. Borowiec, unpub. data).

As discussed by Hamm and Kamansky (2009), workers from an apparently disjunct population in Tulare County, California (see Figure 10C and below), differed slightly from those in northern populations with rugae on the head and mesosoma less pronounced with the interrugae more shining. A molecular phylogeny based on UCEs shows that these populations show little divergence compared to interspecific genetic distances in the genus (M.L. Borowiec, unpub. data). Specimens referred to in Hamm and Kamansky (2009) were deposited in LACM, but could not be located, and they are presumed lost.

Biology. Little is known about the biology of *V. chicoensis*. Workers are diurnal foragers during spring and summer months, but shift to crepuscular foraging at temperatures of about 30° C and forage nocturnally at temperatures of 35° C (Hamm & Kamansky, 2009). Previous indications were that *V. chicoensis* workers were solitary foragers based on “no conspicuous foraging trail was observed” (M. Bennett, pers. comm.). However, the senior author observed two colonies in Tulare County in early October 2018 that were foraging in a narrow 5–10 m long column during mid-morning. Colonies appeared to contain about 1,000–2,000 workers (R.A. Johnson, pers. obs). Workers are polymorphic (Figure 19). Nests are placed in hard clay soils. *Veromessor chicoensis* is sometimes sympatric with *V. andrei*, whereas it appears to occur without *V. andrei* at other locations, especially those with marginal, thin soil habitats (P.S. Ward, pers. comm.).

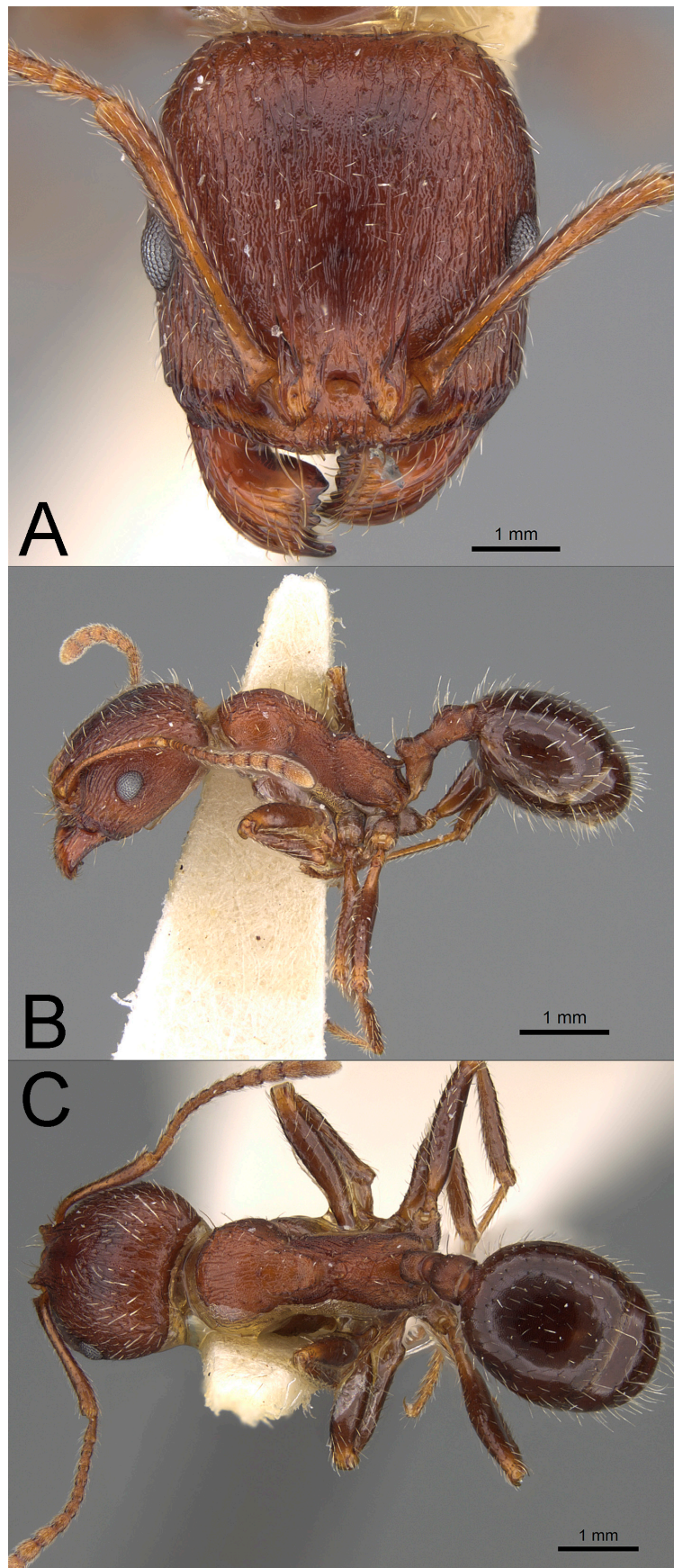


FIGURE 15. Photograph of *Veromessor chicoensis* minor worker: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (LACMENT359751). Photographs by Michele Esposito from www.AntWeb.org.

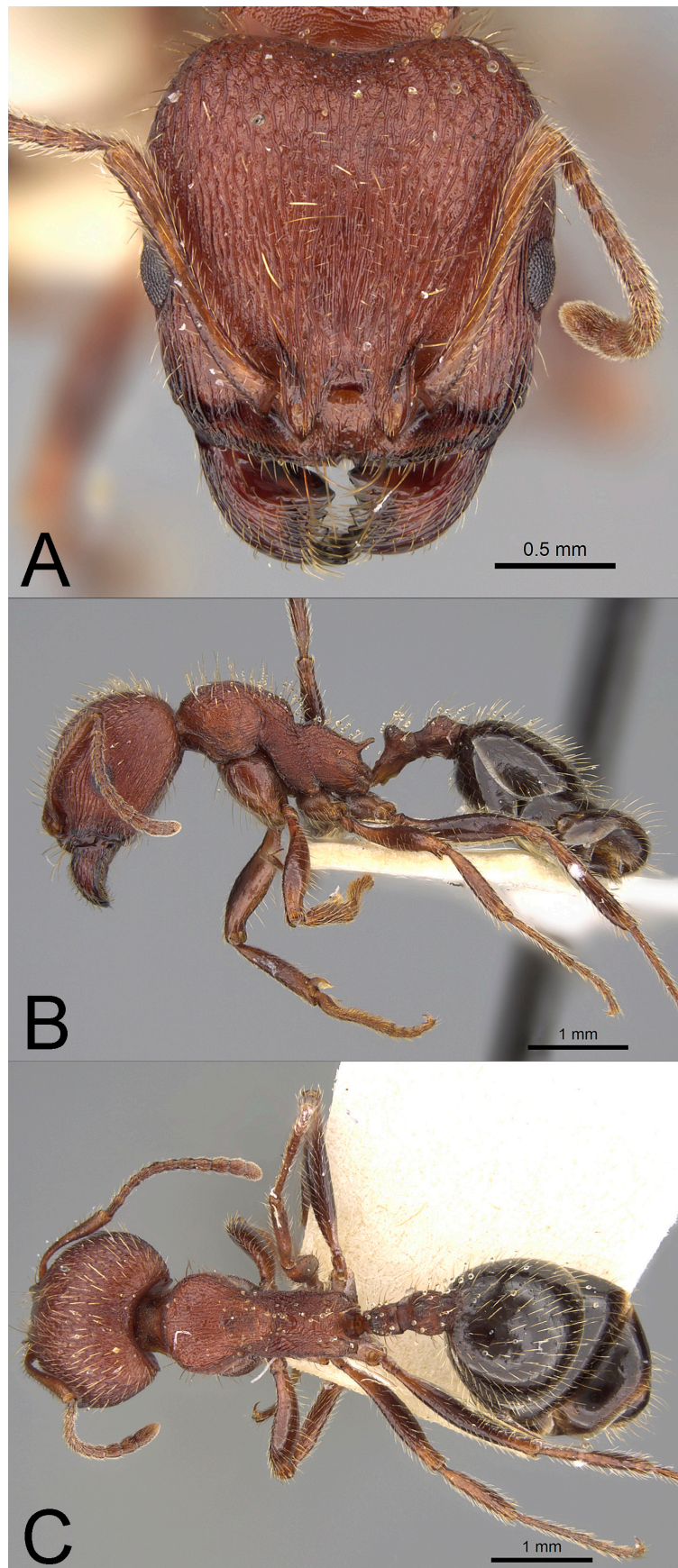


FIGURE 16. Photograph of *Veromessor chicoensis* major worker: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (LACMENT359767). Photographs by Michele Esposito from www.AntWeb.org.

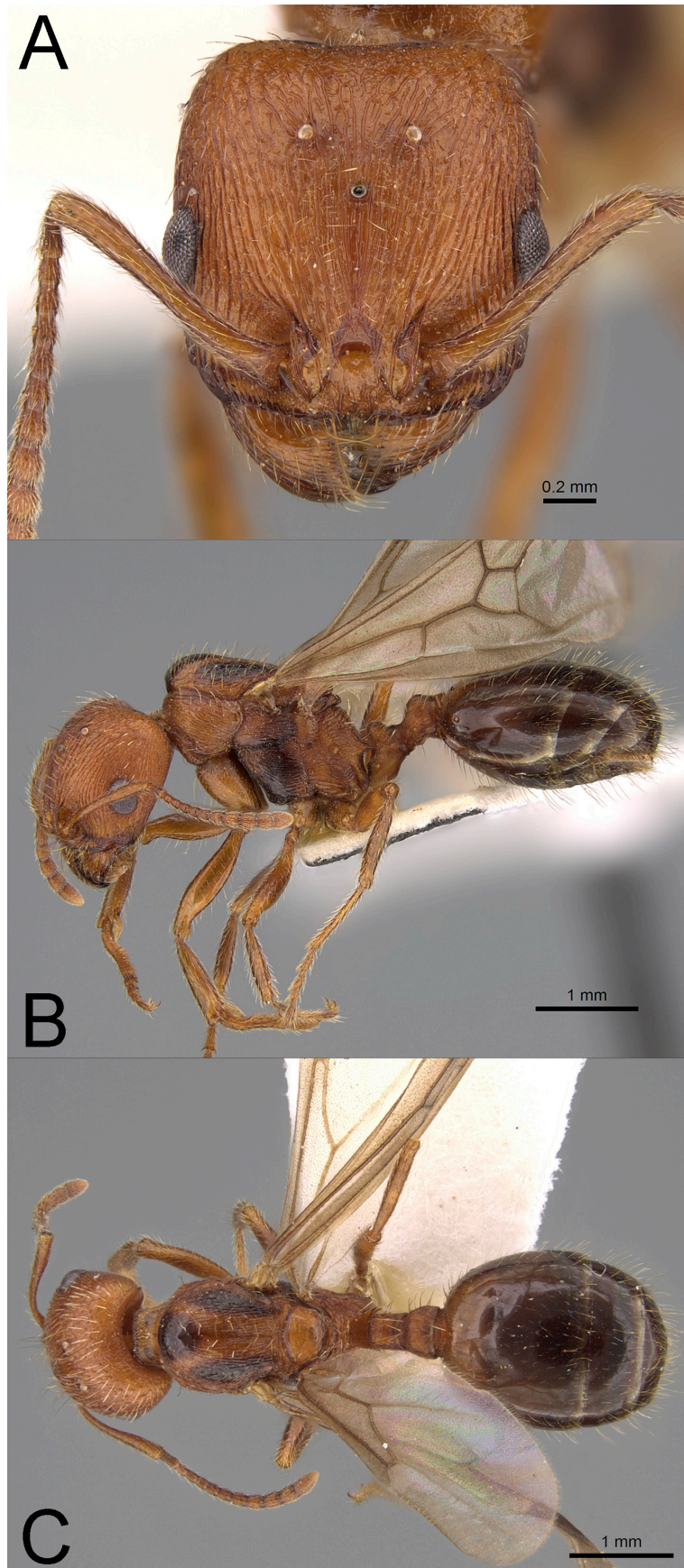


FIGURE 17. Photograph of *Veromessor chicoensis* alate queen: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0922823). Photographs by Michele Esposito from www.AntWeb.org.

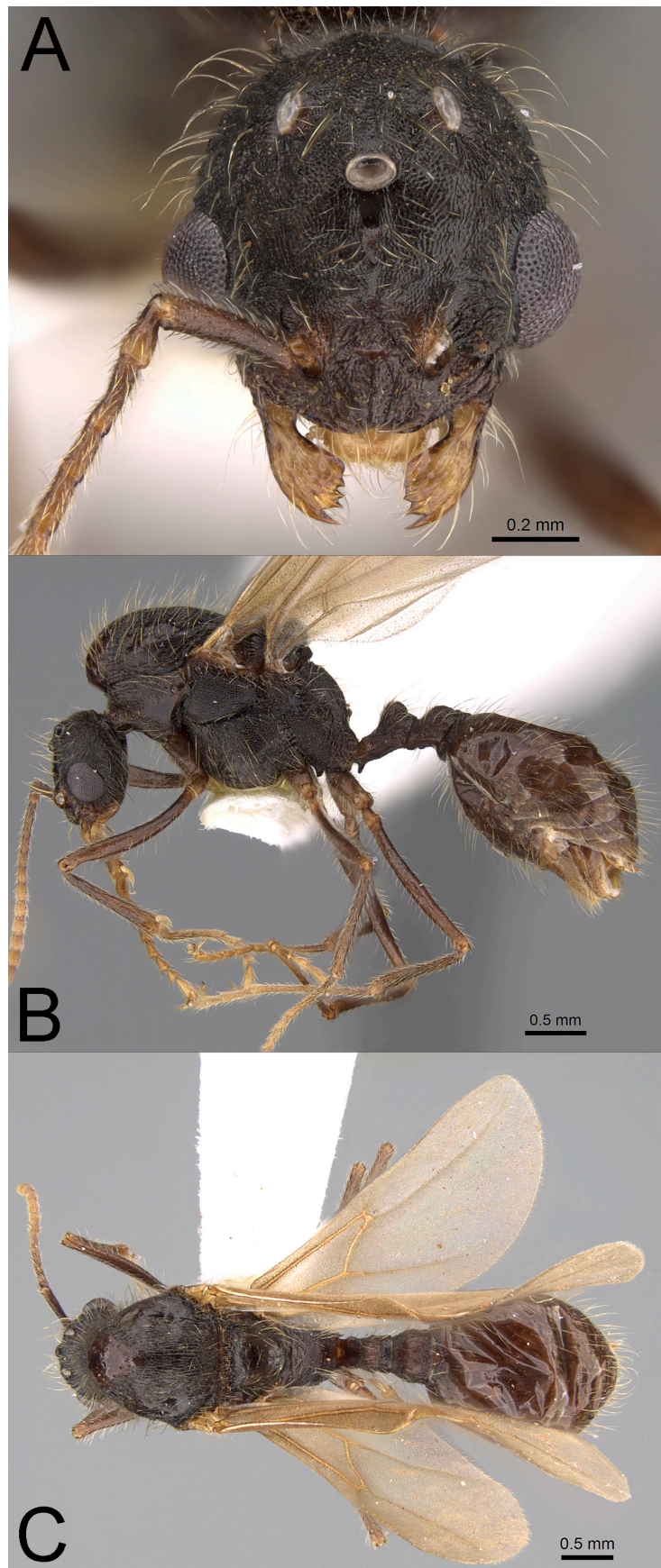


FIGURE 18. Photograph of *Veromessor chicoensis* male: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (LACMENT359769). Photographs by Michele Esposito from www.AntWeb.org.

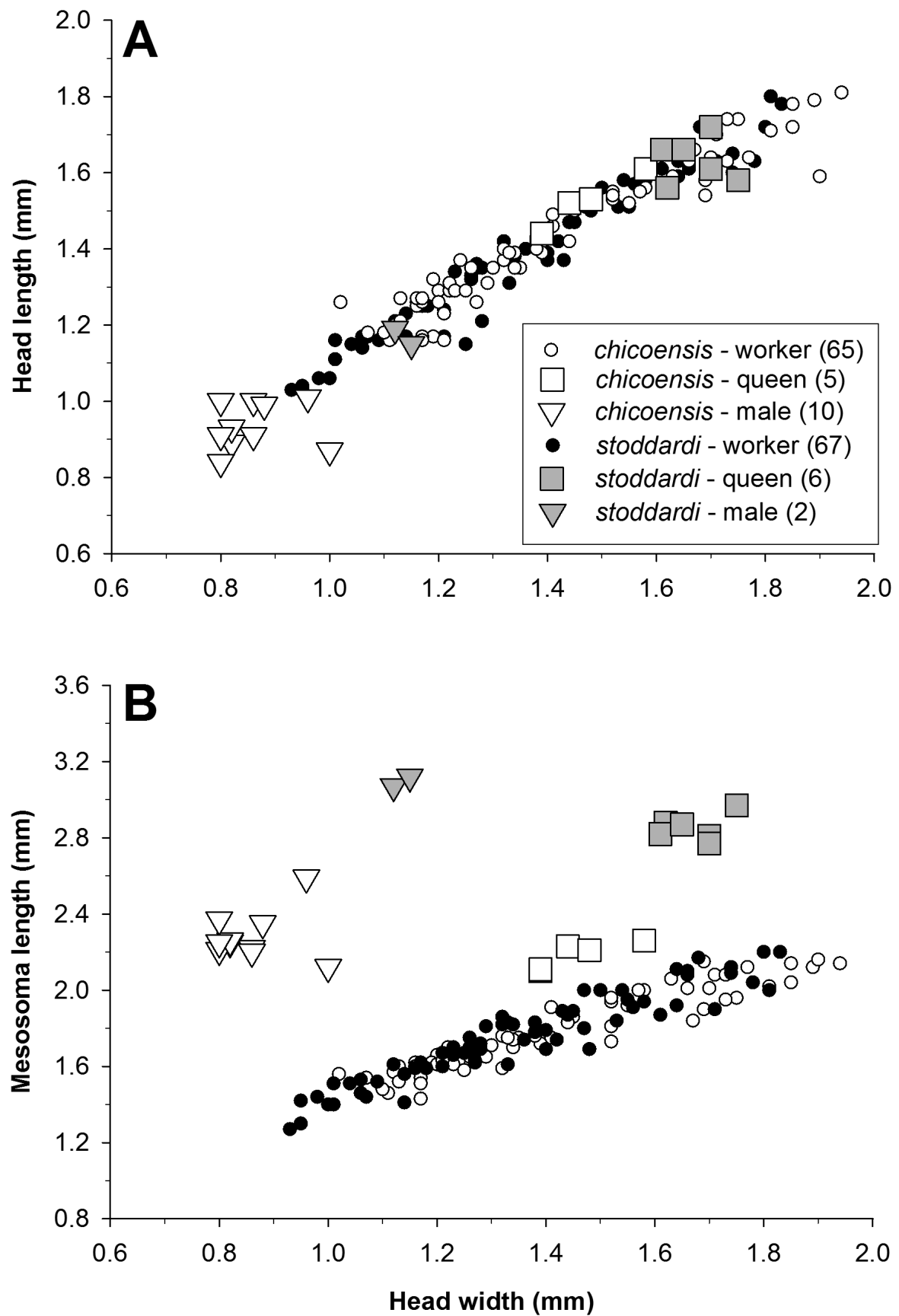


FIGURE 19. Bivariate plots for workers, queens, and males of *Veromessor chicoensis* and *V. stoddardi*: (A) head width versus head length and (B) head width versus mesosoma length. Sample size for each caste is in parentheses.

Mating flights have not been observed, but sexuals have been collected from May 14 through August 28, suggesting that mating flights start early in the summer and last for an extended period. Nothing is known about colony founding, but head width and head length of queens of *V. chicoensis* are about the same as medium-sized workers, whereas mesosoma length is greater in queens than in workers (Figure 19). Their small size infers that founding queens of *V. chicoensis* are semiclaustral, probably obligate foragers.

Veromessor chicoensis is also unusual because dealate queens sometimes occur in foraging columns (one foraging dealate queen collected by the senior author on October 2, 2018). Foraging by dealate queens is common in *V. andrei*, but this is the first such record in *V. chicoensis* (see above discussion under *V. andrei*).

Gland chemistry has not been examined in *V. chicoensis*. Like other small-colony congeners, workers of *V. chicoensis* have a small pygidial gland reservoir and lack a textured tergal cuticle (Hölldobler *et al.*, 2013).

The Pacific Coast horned lizard (*Phrynosoma cornutum*) preys upon *V. chicoensis*, and it sometimes is the main component in the diet of these lizards (Hamm & Kamansky, 2009).

Veromessor chicoensis appears to be restricted to the Sacramento and San Joaquin Valleys in northern and central California and in low mountains along the northwestern edge of the Sacramento Valley. *Veromessor chicoensis* probably occurred throughout most to all of the San Joaquin Valley historically given a 1947 record of one male from Tulare County, and more recent collections from Tulare County near vernal pools in Pixley National Wildlife Refuge and James K. Herbert Wetland Prairie Preserve (Hamm & Kamansky, 2009). The senior author collected two colonies in the James K. Herbert Wetland Prairie Preserve in October 2018, but this species was not located during a brief survey at Pixley National Wildlife Refuge at that time. Moreover, the current range of *V. chicoensis* in the San Joaquin Valley appears to be limited to isolated properties and refuges that have not been developed for agriculture (Hamm & Kamansky, 2009).

This species occurs at elevations from 60–660 m in the California interior chaparral and woodlands and California Central Valley grasslands ecoregions, as defined by Olson *et al.* (2001) (Figure 10C).

Veromessor julianus

(Figures 1D, 20–25)

Distribution—Figure 27A

Aphaenogaster juliana Pergande, 1894: 164 (worker). Syntypes examined: 1 worker [CASC], 5 workers [USNM], #4479, MEXICO, Lower California (=Baja California Sur): San Julio, no date (Dr. Gustav Eisen). See also Creighton and Wheeler, 1934: 368, plate II, fig. 7. CASC worker here designated **LECTOTYPE** [CASTYPE00619].

Stenamma (Messor) julianum (Pergande); Emery, 1895: 308 (first combination in *Stenamma [Messor]*).

Aphaenogaster (Messor) juliana Pergande; Forel, 1899: 59 (first combination in *Aphaenogaster [Messor]*).

Novomessor (Veromessor) julianus (Pergande); Forel, 1917: 235 (first combination in *Novomessor [Veromessor]*).

Veromessor julianus (Pergande); Wheeler and Creighton, 1934: 368 (first combination in *Veromessor*).

Messor julianus (Pergande); Bolton, 1982: 341 (first combination in *Messor*).

Veromessor julianus (Pergande); Ward, Brady, Fisher, and Schultz, 2015: 13 (revived combination in *Veromessor*).

Veromessor julianus subsp. clarior Wheeler and Creighton, 1934: 370 (worker). Syntypes examined: 3 workers [LACM], 6 workers [USNM], MEXICO, Baja California Sur: San José de Comondú, February 1923 (H.C. Millender). **NEW SYNONYMY**. USNM worker here designated **LECTOTYPE** [USNMMENT00529096].

Veromessor julianus subsp. manni Wheeler and Creighton, 1934: 371. Syntypes examined: 2 workers [USNM], MEXICO, Baja California Sur: Las Parras (see below), no date (Dr. W.M. Mann). **NEW SYNONYMY**. USNM worker here designated **LECTOTYPE** [CASENT0922841].

Worker diagnosis. This species is uniquely characterized by the following combination of features: (1) head and gaster light to dark brownish-orange to dark brown; mesosoma lighter orangish-brown or head, mesosoma, petiole, postpetiole dark ferruginous orange; gaster dark brown to blackish, (2) medial lobe of clypeus with 2–3 moderately coarse longitudinal rugae on either side of medial groove, medial lobe not thick and protuberant in profile, not elevated above lateral lobes in frontal view, (3) mandibles with 8 teeth, (4) dorsal base of scape weakly flattened, weakly widened; maximum basal width of scape distinctly less than maximum preapical width, (5) MOD usually much less than OMD, $OI \leq 25.0$, (6) cephalic dorsum with fine, closely spaced, wavy, longitudinal rugae; medial rugae diverging toward posterior corners; cephalic interrugae weakly to moderately punctulate, moderately shining, (7) psammophore well developed; ventral surface of head capsule with many long J-shaped hairs arranged in a distinct row around the outer margin of the ventral region of the head capsule, (8) dorsum of pronotum with mostly

transverse, weakly to strongly irregular rugae, rugae often with lateral branches and/or becoming rugoreticulate posterad; sides of pronotum variable: with irregular vertical and/or longitudinal rugae or rugae mostly confined to anterior one-half, posterior one-half strongly granulate or strongly granulate over entire surface, interrugae and granulate surfaces dull; mesonotum with irregular longitudinal rugae, rugae sometimes with short lateral branches, interrugae weakly coriarius, moderately shining to strongly granulate, dull or entire surface strongly granulate, dull; mesopleura variable: strongly granulate between irregular, longitudinal and/or oblique rugae, rugae often with short lateral branches on dorsal one-half, irregular longitudinal rugae on ventral one-half or rugae faint to mostly lacking, entire surface strongly granulate, dull, (9) propodeal spines elongate, slender, acuminate; spines straight in profile, weakly curved inward in dorsal view; length $\geq 2.0\times$ the distance between their bases and length $\geq 1.0\times$ MOD; infraspinal facet weakly coriarius to weakly rugose, moderately shining; propodeal declivity smooth and shining, and (10) metasternal process large, about twice as long as high, apex more or less flat, translucent in profile (Figures 20–22).

Measurements. lectotype ($n = 125$). HL 1.70 (1.15–1.85); HW 1.61 (1.08–1.86); MOD 0.34 (0.26–0.45); OMD 0.37 (0.32–0.53); SL 1.48 (1.02–1.63); PNW 1.06 (0.65–1.21); HFL 1.90 (1.28–2.14); ML 2.25 (1.45–2.48); PW 0.31 (0.22–0.40); PPW 0.51 (0.34–0.61). Indices: SI 91.93 (72.12–100.93); CI 94.71 (88.52–111.97); OI 21.12 (18.39–25.42); HFI 118.01 (90.51–127.34).

Queen diagnosis. This caste is diagnosed by the following combination of features: (1) color variable: mostly concolorous medium to dark brown to brownish-black, legs and gaster usually orangish-brown or mostly concolorous ferruginous orange except for brownish katapisternum and mesoscutum (mesoscutum sometimes partly orangish), gastral terga with transverse blackish band along posterior margins, (2) medial lobe of clypeus with two to three submedial and sublateral, longitudinal rugae, (3) mandibles with 8 teeth, (4) dorsal base of scape weakly flattened; maximum basal width of scape less than maximum preapical width, (5) OMD distinctly less than MOD, (6) cephalic dorsum shining between fine, longitudinal rugae, medial rugae continuing to posterior margin or medial rugae diverging toward posterior margin with fine, transverse to arcuate rugae along posterior margin; longitudinal rugae above and below eyes; (7) psammophore well developed, (8) sides of pronotum weakly to moderately punctulate between mostly longitudinal rugae; mesoscutum and mesoscutellum smooth and shining with scattered piligerous punctures, mesocutum often with faint longitudinal rugae posterad, mesoscutellum with faint rugae along anterior and/or lateral margins; anepisternum weakly to moderately punctulate, weakly shining, between fine, longitudinal rugae; katapisternum shinier, rugae weaker, rugae sometimes absent along anteroventral margin; sides of propodeum moderately punctate, weakly shining between coarser longitudinal and oblique rugae, (9) propodeal spines elongate, acuminate, weakly recurved in profile, length greater than width at base and less than the distance between their bases; infraspinal facet and posterior declivity weakly to moderately coriarius, weakly shining to shining, and (10) metasternal process large, about twice as long as high, apex more or less flat, translucent (Figures 23–24).

Measurements. ($n = 13$). HL 1.76–2.05; HW 1.80–2.03; EL 0.46–0.54; OMD 0.36–0.45; SL 1.45–1.66; HFL 1.72–2.27; ML 2.97–3.51; PW 0.34–0.53; PPW 0.67–0.79. Indices: SI 74.36–87.57; CI 97.89–107.73; OI 24.10–27.84; HFI 88.21–119.25.

Male diagnosis. This caste is diagnosed by the following combination of features: (11) blackish brown, gaster and appendages brown, (12) clypeus weakly convex in profile, anteromedial margin of medial lobe concave with a small, narrow, medial excision, (13) mandibles with 2, rarely 3, small triangular denticles or teeth basad of preapical tooth, (14) anterior ocellus above level of top of eyes, (15) anepisternum with wavy longitudinal rugae or rugae restricted to dorsad portion, interrugae weakly to moderately coriarius, dull to weakly shining, areas lacking rugae usually lineopunctate-granulate; katapisternum shinier, lacking obvious rugae, weakly to moderately coriarius with ventral margin usually less coriarius and shinier than rest of katapisternum, (16) propodeum contiguously punctate, with scattered short, irregular, fine, oblique rugae; teeth or spines absent, (17) metasternal process about twice as long as tall, apex mostly flat with anterior and posterior corners broadly rounded, and (18) subpetiolar process absent to low and obtuse (Figures 1D, 25).

Measurements. ($n = 4$). HL 0.99–1.08; HW 0.92–0.99; MOD 0.39–0.41; OMD 0.14–0.16; SL 0.35–0.43; HFL 1.79–2.01; ML 2.58–2.78; PW 0.33–0.40; PPW 0.66–0.70; AOD 0.10–0.11; IOD 0.31–0.35; OOD 0.31–0.35. Indices: SI 37.89–38.04; CI 87.04–92.93; OI 41.41–42.55; HFI 194.57–204.26.

Additional material examined. MEXICO: *Baja California*: Bahía de los Ángeles, 10', Jan 9, 1991 (RAJC); Hwy 1 at 11.65 mi W Bahía de los Ángeles, Mar 9, 1992 (RAJC); 16 km W Bahía de los Ángeles, 450 m, Mar 29, 2012 (UCDC); Hwy 1 at 2.8 mi N turn to Bahía de los Ángeles, Feb 19, 1994 (RAJC); 14 km ENE Jct Hwy 1 and

Road to Bahía de los Ángeles, 480 m, Apr 6, 1998 (UCDC); 11.5 mi S Bahía de los Ángeles, Mar 9, 1992 (RAJC); 16.5 km E Hwy 1 on turnoff road to Bahía de los Ángeles, Feb 1, 1995 (RAJC); 19.85 mi S Bahía de los Ángeles, Mar 9, 1992 (RAJC); 29.7 mi SSE Bahía de los Ángeles, 260', Feb 4, 1995 (RAJC); 48.5 mi S Bahía de los Ángeles, 250', Mar 6, 1998 (RAJC; UCDC); 4.3 mi NE Pozo Alemán, 1120', Feb 2, 1996 (RAJC); 0.5 mi E San Ignacio, 1000', Feb 2, 1995 (RAJC); 0.6 mi N El Progreso, Mar 9, 1992 (RAJC); 5 mi W El Progreso, Mar 8, 1992 (RAJC); 14.7 mi NW El Progreso, 960', Mar 9, 1992 (RAJC); 14.9 mi NE El Progreso, 700', Jan 29, 1995 (RAJC); 1.3 mi SW Campo El Faro site, 300', Jan 25, 1995 (RAJC); 10.5 mi NE El Arco, Mar 8, 1992 (RAJC); 22.25 mi NE El Arco, Mar 8, 1992 (RAJC); 6.5 mi N Las Arrastras de Arriola, 1000', Feb 9, 1994 (RAJC); Misión Calamalli (at 6.3 mi N El Arco), Mar 8, 1992 (RAJC); San Luis Wash at 8.5 mi W Misión Calamalli, Mar 8, 1992 (RAJC); Vado las Lamparas, 620', Feb 15, 1997 (RAJC); 4.2 mi W Hwy 1 on road to Santa Rosalita, Feb 29, 1992 (RAJC); 1 mi N of N end Bahía Falsa, 30', Mar 22, 2001 (RAJC; UCDC); S end Laguna Chapala, 2050', Mar 10, 2003 (RAJC; UCDC); 2.0 mi E La Chocera, 40', Mar 10, 2002 (RAJC; UCDC); Bahía San Quintin, 5', May 1, 1952 & May 21–22, 1952 (LACM; USNM); Bahía Colonet (as Collnet Bay), no date (LACM); El Consuelo, no date, 1969 & Aug 23, 1977 (LACM); 6 mi NW Rancho Santa Ynez, 1800', Jan 24, 1976 & Apr 5–12, 1977 (CIDA); S end Isla Smith (= Isla Coronado), 10 m & 30 m, Feb 10–11, 1997 (UCDC); Isla Ventana, Mar 10–May 10, 1999 (UCDC); Puerto don Juan at 11 km E Bahía de los Ángeles, 10 m, Feb 12, 1997 (UCDC); Catavina, 550 m, Feb 14, 1997 (UCDC); 14 km S Rosarito, 40 m, Apr 8–9, 1998 (UCDC); 6.2 mi E Rosarito, Jul 10, 1979 (UCDC); 38 km WNW San Ignacio, 90 m, Apr 13, 1998 (UCDC). **Baja California Sur:** Hwy 18 at 7.9 mi SE El Arco, 440', Jan 28, 1995 (RAJC); 21.4 mi S San Ignacio, Mar 7, 1992 (RAJC); 15 mi N San Ignacio, May 24, 1938 (LACM; USNM); 50 km SSW San Ignacio, 5 m, Jan 4, 1990 (UCDC); nr Rancho Esperanza, 8.8 mi S San Ignacio, 4.3 km N KP 59.5, Sep 7, 1985 (LACM); 45 mi N San Ignacio, Jul 27, 1938 (USNM); Hwy 1 at 7.8 mi S Santa Rosalía, Feb 29, 1992 (RAJC); 17 mi W Santa Rosalía, Jun 18, 1967 (LACM); 10 km S Santa Rosalía, 1800', Oct 4, 1975 (LACM; UAIC); Boca Magdalena (Hwy 1 at 21.7 mi S Santa Rosalía), 200', Feb 29, 1992 (RAJC); 0.5 mi S San Gregorio, Mar 5, 1992 (RAJC); 1.8 mi E Río San Gregorio, Mar 6, 1992 (RAJC); 3.05 mi E San Gregorio, Mar 4, 1992 (RAJC); 1.2 mi E Hwy 1 on road to Sierra San Francisco, 200', Jan 27, 1995 (RAJC); Jct Hwy 1 & Rd to Sierra San Francisco, 180', Mar 13, 2003 (RAJC); 1.8 mi W Hwy 1 on road to San Isidro, Mar 2, 1992 (RAJC); 13.5 mi W Hwy 1 on road to San Isidro, Mar 2, 1992 (RAJC); 5.05 mi NE San Isidro, Mar 2, 1992 (RAJC); 10.9 mi SE Vizcaíno, 120', Jan 26, 1995 (RAJC); 25 km W Vizcaíno, 200', Jan 7, 1991 (LACM; RAJC); 6.9 mi W Vizcaíno, 250', Jan 26, 1995 (RAJC); 12.5 mi E Bahía Tortuga, 220', Mar 8, 1998 (RAJC; UCDC); 1 mi E Rancho San José Magdalena, Feb 15, 1993 (RAJC); 4.9 mi SE San Juanico, Mar 6, 1992 (RAJC); 7.4 mi N San Juanico, Mar 6, 1992 (RAJC); base of Cerro las Mulas, Feb 17, 1993 (RAJC); Cerro las Mulas, May 10, 1992 (RAJC); Cabo San Lucas, 140', Feb 2, 1996 (RAJC); Hwy 1 at 15.1 mi E Guamúchil, Feb 29, 1992 (RAJC); Hwy 1 at 20.6 mi E Guamúchil & 4 mi S Volcán Tres Vírgenes, Feb 29, 1992 (RAJC); Hwy 1 at 8.3 mi E Guamúchil (in Santa María Wash), Mar 2, 1992 (RAJC); Santa María Wash at 0.2 mi S Hwy 1 (6.3 mi E Guamúchil), Mar 28, 1992 (RAJC); Hwy 1 at 19.5 mi S Ciudad Constitución, 120', Jan 31, 1998 (RAJC); Hwy 22 at 6 mi W Ciudad Constitución, 50', Feb 4, 1996 (RAJC); Hwy 1 at 3.5 mi S Mulegé, Feb 29, 1992 (RAJC); Hwy 1 at 20.5 mi S Mulegé, Mar 1, 1992 (RAJC); Hwy 1 at 27.3 mi SE border of Baja California, 100', Feb 28, 1992 (RAJC); Hwy 1 at 37.3 mi SE border of Baja California (10.6 mi NW Gustavo Diaz Ordaz), Mar 28, 1992 (RAJC); Hwy 1 at 3.3 mi E Ejido Alfredo V. Bonfil, Feb 12, 1993 (RAJC); Hwy 1 at 6.05 mi S Gustavo Diaz Ordaz (53.95 mi S border Baja California), Mar 28, 1992 (RAJC); Hwy 53 at 21.7 mi N Villa Insurgentes, Mar 2, 1992 (RAJC); Hwy 1 at 43.6 mi NW Villa Insurgentes, 1430', Mar 14, 2002 (RAJC); Hwy 53 at 22.4 mi N Ejido Francisco Villa (at turnoff to Comondú), Mar 2, 1992 (RAJC); Hwy 53 at 3.8 mi N Ejido Villa Francisco (at turnoff to Comondú), Mar 2, 1992 (RAJC); Hwy 53 at 5.5 mi NE Ejido Francisco Villa (at turnoff to Comondú), Mar 3, 1992 (RAJC); La Purísima, Mar 2–3, 1992 (RAJC); Hwy 1 at 4.0 km S Jct to Santiago, 520', Mar 19, 2014 (RAJC); Hwy 1 at turnoff to Ribera, 240', Mar 21, 2014 (NHMW; RAJC); E of Punta Chele, May 21, 1992 (RAJC); La Paz, Sept 4, 1959 (LACM); Hwy 1 at 11.0 mi S La Paz, 520', Mar 16, 2002 (RAJC); Ramal el Chivato, S of El Cien, Sep 17, 1983 (LACM); Loreto, Feb 1923 (LACM; USNM); 2 km N Loreto, 5 m, Dec 20, 2015 (MMPC); 6 mi N El Triunfo, Jul 15, 1938 (USNM); 4 km ESE Guerrero Negro, 10 m, Jan 2, 1990 (UCDC); 2.2 mi N Rancho Caracol, 500 m, Jul 11–12, 1999 (UCDC); Juncalito, 5 m, Jul 13, 1995 (UCDC). **Locations not found: Baja California Sur:** Virgen María, Jan 25, 1967 (LACM) (Figure 27A).

Etymology. Pergande did not indicate the derivation of the specific epithet, *julianus*, but it seems likely that it referred to the type locality “San Julio”, given that Julian is Julio.

Discussion. *Veromessor pergandei* and *V. stoddardi* are the only congeners that might be sympatric with *V. julianus*. *Veromessor julianus* cannot be confused with either species, and it is diagnosed by: (1) well developed

psammophore, (2) long propodeal spines ($\geq 2\times$ longer than distance between their bases), and (3) metasternal process about twice as long as high, apex more or less flat, translucent in profile. This species is recognized in the field based on their large colonies ($> 40,000$ workers) that forage in long columns from near dusk and into the night (Creighton, 1953; Johnson, 2000a, 2000b). *Veromessor julianus* may be sympatric with *V. andrei* near Bahía San Quintin, but the former species is easily distinguished by its well developed psammophore; the psammophore is poorly developed in *V. andrei*.

Wheeler and Creighton (1934) described *V. julianus* subsp. *clarior* because it differed from the typical *V. julianus* by: (1) having a more quadrate head, (2) shorter antennal scapes that just reach the posterior margin, (3) mesopropodeal suture notably impressed dorsally, (4) propodeal spines longer, thinner, and more elevated meeting the plane of the basal surface of the propodeum at 45° , (5) cephalic striae finer, and (6) granulation on the mesosoma much less pronounced. They also noted that *julianus* subsp. *clarior* was much more hairy than the typical *julianus*, especially in regard to the gular ammochaetae and abdominal hairs, and with a clear, yellowish-red color, the gaster piceous brown, usually with a yellowish spot at the base of the first segment.

In the same paper, Wheeler and Creighton (1934) described the other subspecies, *V. julianus* subsp. *manni*, as having an impressed mesopropodeal suture (as in subsp. *clarior*), but differing from subsp. *clarior* in its smoother cephalic sculpture, with striae scarcely visible in smaller workers, but the propodeal spines were more similar to those in the typical *julianus*. Color less clear than that of *clarior*, with the head tending toward a muddy, brownish-red, and the yellowish spot at the base of the first gastral tergum reduced or absent. *Veromessor julianus* subsp. *manni* was also smaller than the typical *julianus* and *julianus* subsp. *clarior*, but the authors noted that these size differences may not remain after examining additional specimens.

All three subspecies of *V. julianus* were described from few workers such that the authors examined little variation within each subspecies. Numerous series now are available so that subspecies variation can be examined, and these series demonstrate that all of the above characters described to separate these forms vary within a nest series. For example, Wheeler and Creighton (1934) noted that the mesopropodeal suture was impressed on *V. julianus* subsp. *clarior* and *V. julianus* subsp. *manni*, but that the suture was not impressed in *V. julianus*. Examination of long nest series demonstrates that the mesopropodeal suture is impressed below the level of the propodeum in some workers, but not impressed in others, such that there is no consistent variation across subspecies.

As noted in the above discussion regarding the subspecies, workers of *V. julianus* have two color forms: (1) bicolored, with an orangish head and mesosoma and a darker gaster, and (2) dark brown with the head often slightly darker than the mesosoma. Workers within a colony generally consist of one color form, but workers with the alternate color are present occasionally. In combination with lack of morphological differences between the two subspecies, bivariate plots for several morphological characters display similar allometries for both color forms (Figure 26). Both color forms also occur in proximate locales on the peninsula.

Queen color correlates with worker color in the dark brown form as colonies with dark brown workers contain concolorous dark brownish queens. Alternatively, colonies with bicolored workers (orangish head and mesosoma, brownish gaster) contain orangish queens and sometimes concolorous brownish queens indicating that these two color forms are not consistent for alate queens.

Our molecular phylogeny indicates that the color forms belong to two clades. We then conducted preliminary molecular species delimitation analyses using STACEY (Jones, 2017) and DELINEATE (Sukumaran, Holder, & Knowles, 2021), which consistently show *V. julianus* lineages to be a single species (M.L. Borowiec, unpub. data). We leave a more comprehensive exploration of possible divergence among these lineages to our phylogenetic study (M.L. Borowiec, unpub. data) but note here that more definitive conclusions will require additional sampling, including more samples of intermediate phenotypes. Here, we consider *V. julianus* subsp. *clarior* and *V. julianus* subsp. *manni* to be junior synonyms of *V. julianus*, and we synonymize both subspecies under *V. julianus*.

Wheeler and Creighton (1934) misspelled the type locality for *V. julianus* subsp. *clarior* as Commondu, Lower California; the correct spelling is Comondú (= San José de Comondú), which is in Baja California Sur, Mexico. For *V. julianus* subsp. *manni*, Wheeler and Creighton (1934) gave type locality as “Purissima, Lower California”, collected by W.M. Mann. However, no type material was located from “Purissima” and we believe their original citation to be spurious. We did locate two workers collected at Las Parras, Baja California, by W.M. Mann [USNM] with the additional label “not a syntype?, M. R. Smith”. We believe that Las Parras is the correct type locality, such that both of these workers are syntypes of *V. julianus* subsp. *manni*. We designated the bottom worker as a lectotype and placed such a label on the pin. Las Parras is a few miles west of Loreto.

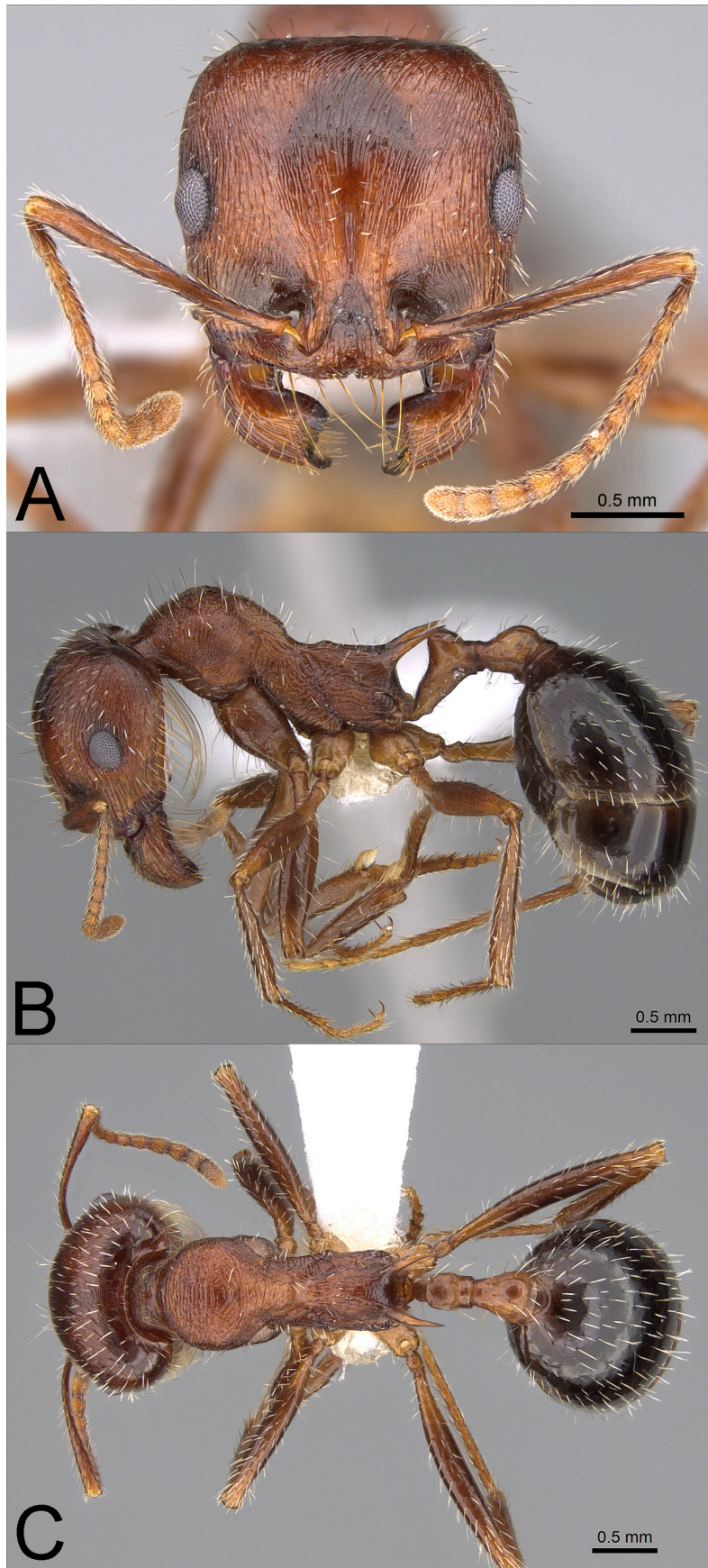


FIGURE 20. Photograph of *Veromessor julianus* worker (bicolored form): (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0922837). Photographs by Michele Esposito from www.AntWeb.org.

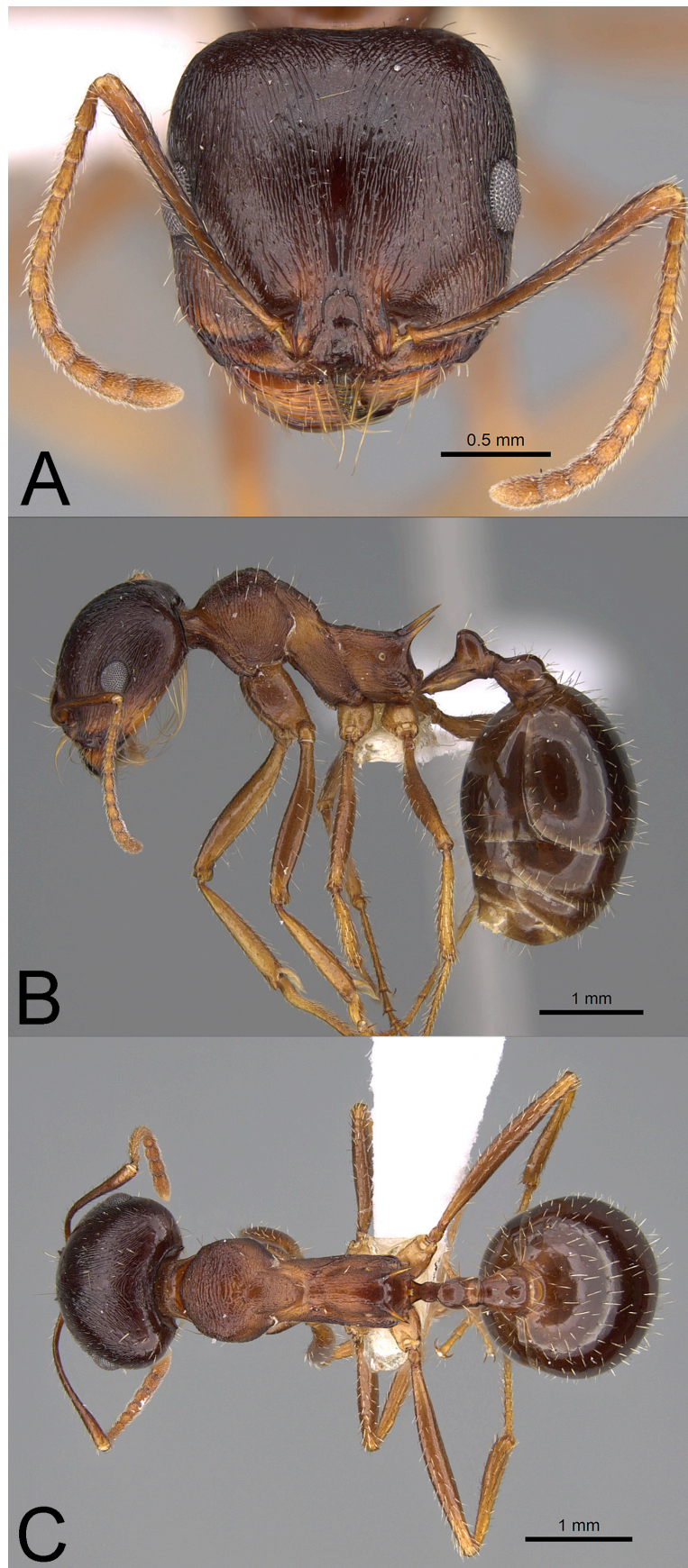


FIGURE 21. Photograph of *Veromessor julianus* minor worker (dark form): (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0922836). Photographs by Michele Esposito from www.AntWeb.org.

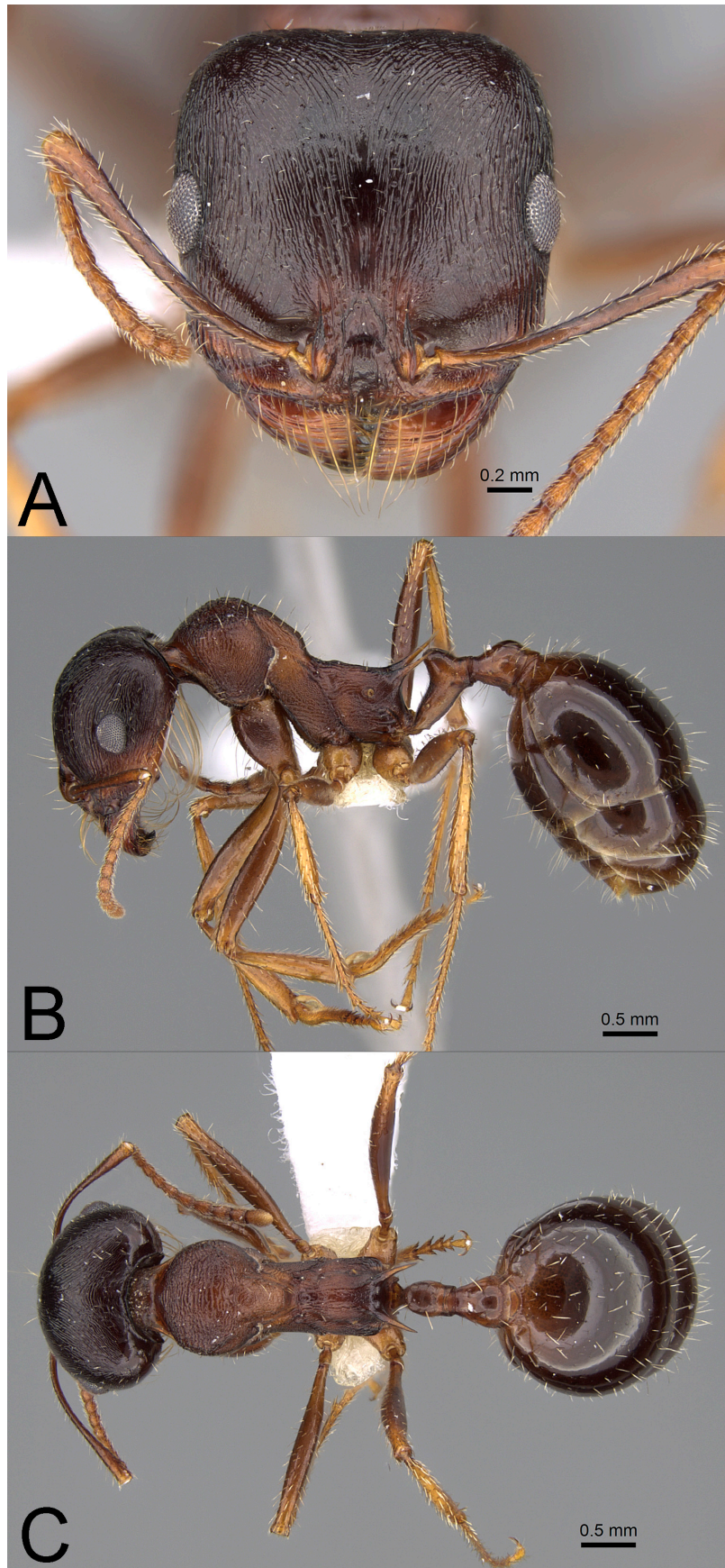


FIGURE 22. Photograph of *Veromessor julianus* major worker (dark form): (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0922835). Photographs by Michele Esposito from www.AntWeb.org.

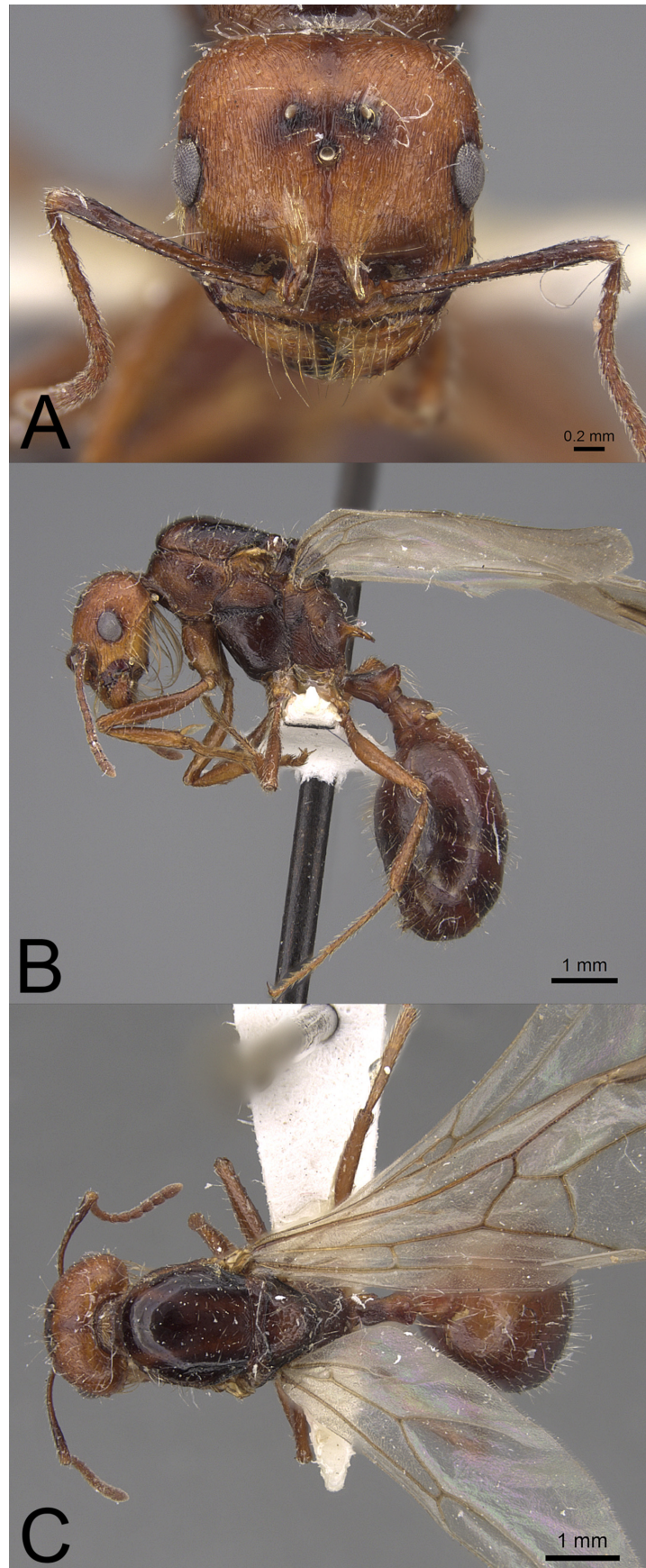


FIGURE 23. Photograph of *Veromessor julianus* alate queen (light form): (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0923146). Photographs by Wade Lee from www.AntWeb.org.

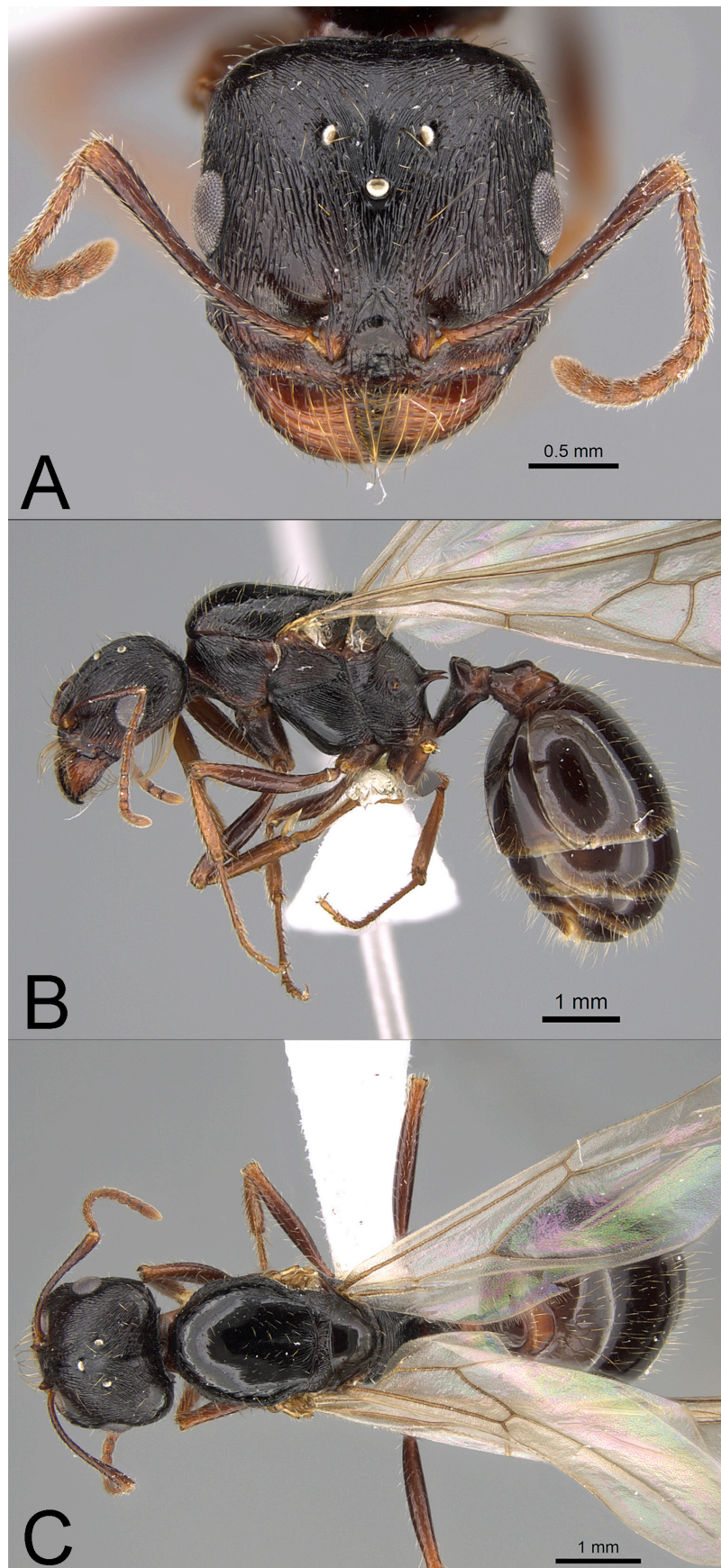


FIGURE 24. Photograph of *Veromessor julianus* alate queen (dark form): (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0922838). Photographs by Michele Esposito from www.AntWeb.org.

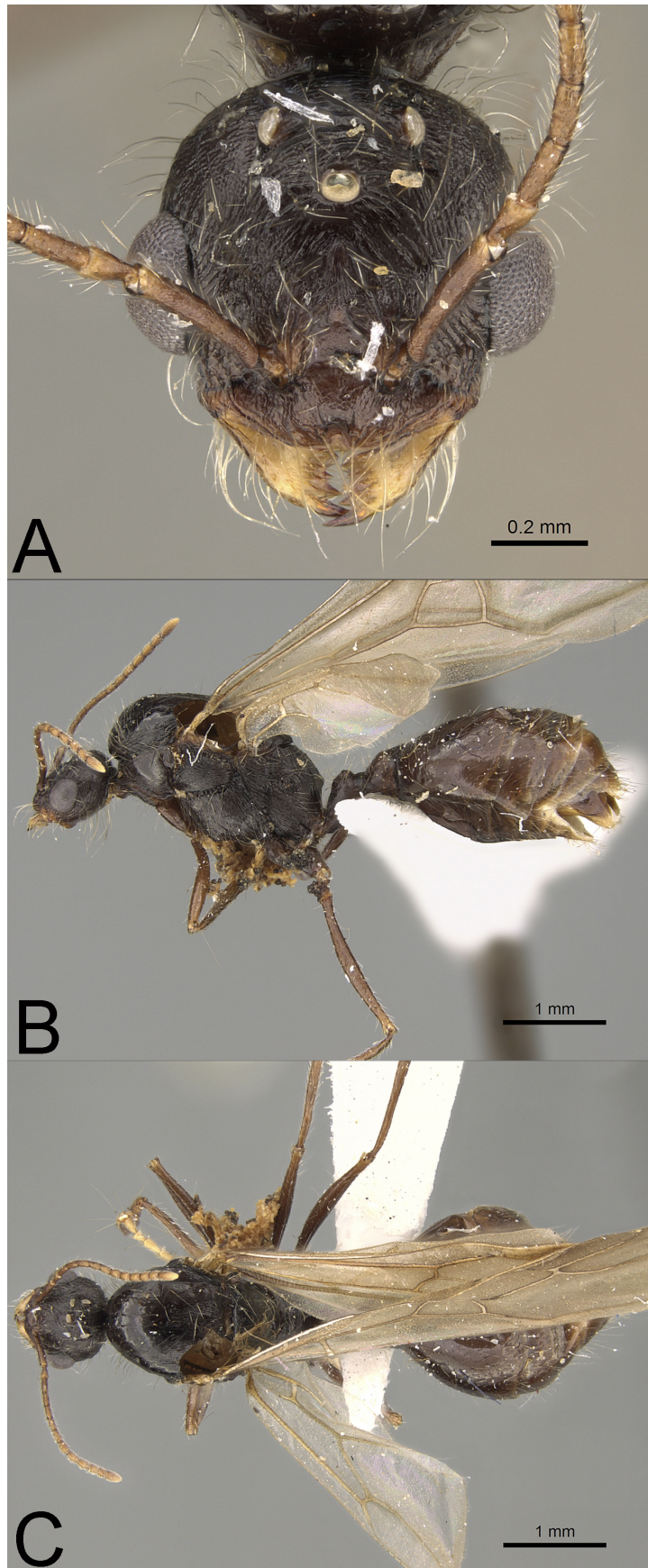


FIGURE 25. Photograph of *Veromessor julianus* male: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0923344). Photographs by Michele Esposito from www.AntWeb.org.

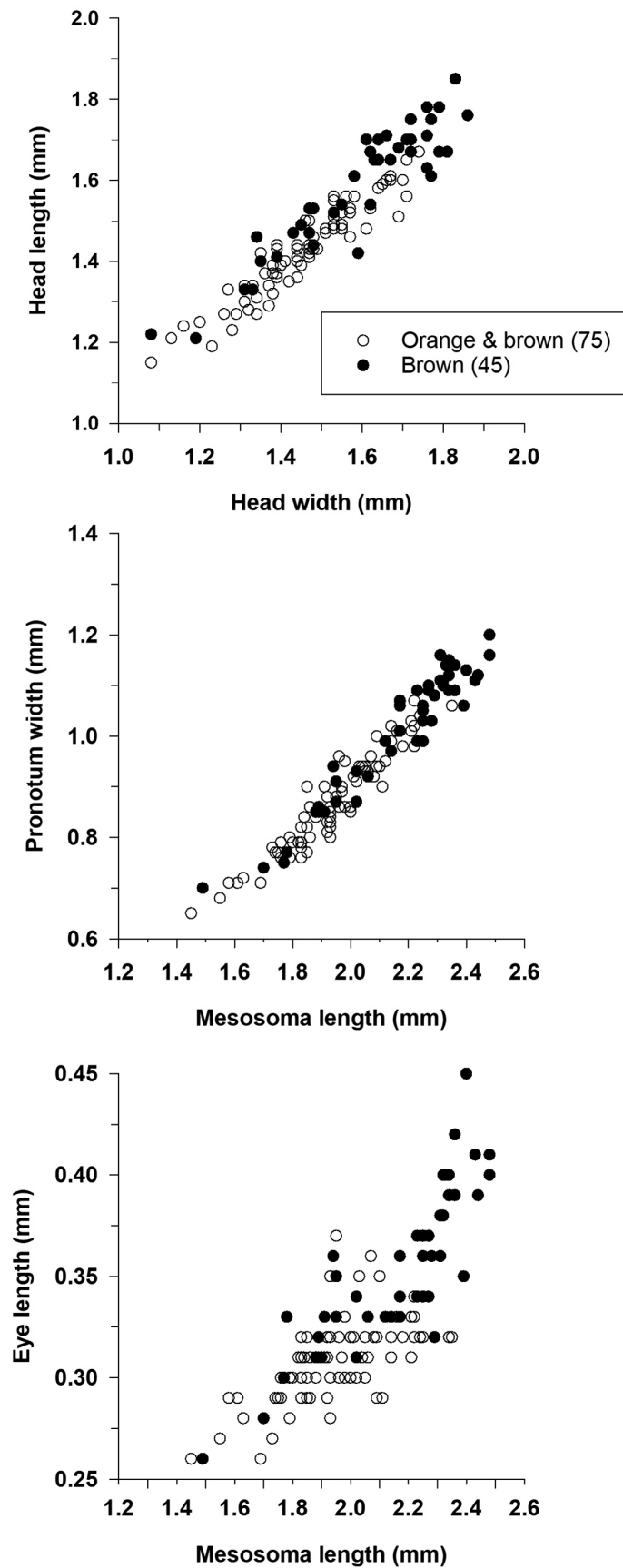


FIGURE 26. Bivariate plots for workers of the two color forms (bicolored and dark) of *Veromessor julianus*: (A) head width versus head length, (B) mesosoma length versus pronotum width, and (C) mesosoma length versus eye length. Sample size for each color form is in parentheses.

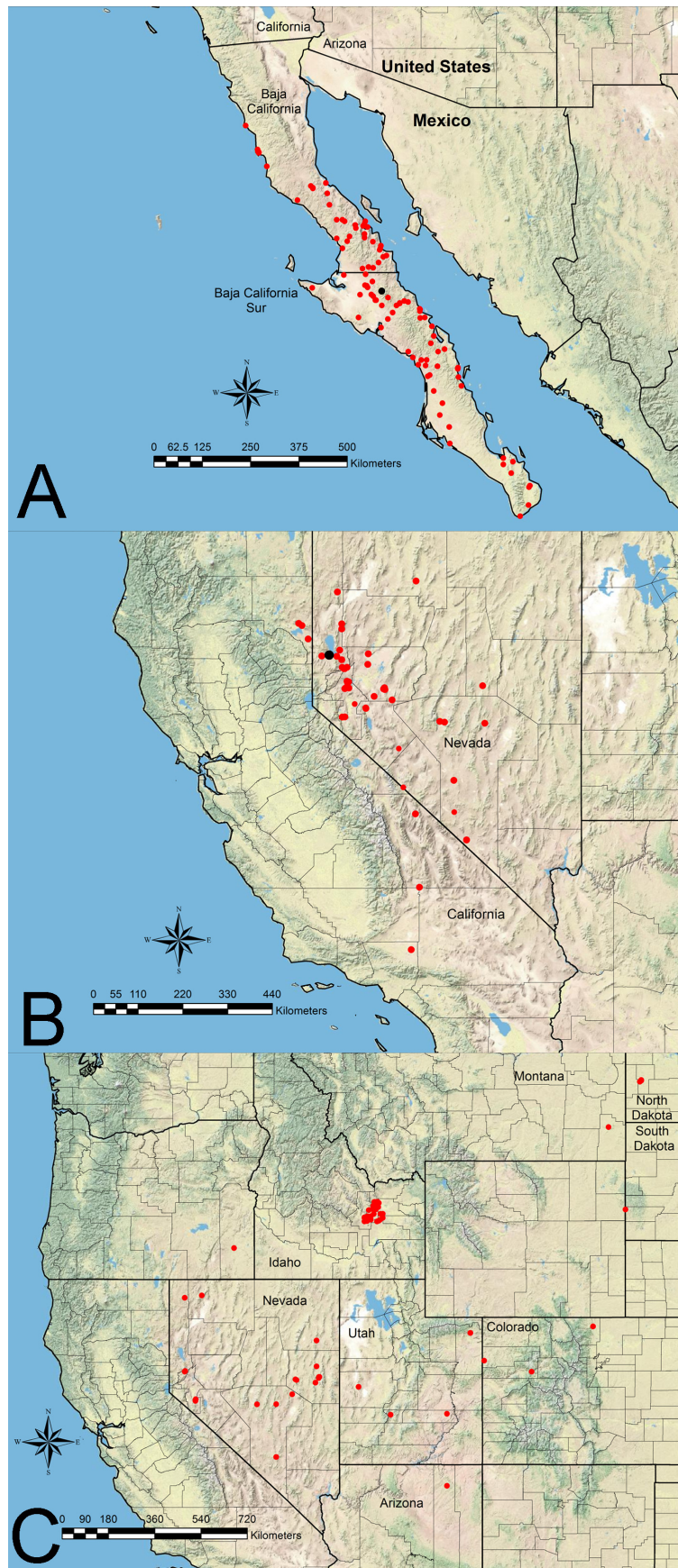


FIGURE 27. Geographic distribution of: (A) *Veromessor julianus*, (B) *V. lariversi*, and (C) *V. lobognathus*. The larger black circle in each panel denotes the type locality.

Biology. Nests of *V. julianus* occur in open sites. Colonies of *V. julianus* have not been censused, but observations indicate that they contain tens of thousands of workers. Nests consist of a small tumulus lacking chaff to a large disc surrounded by chaff; nests sometimes have multiple entrances (Creighton, 1953; R.A. Johnson, pers. obs.). Workers of *V. julianus* forage in columns with workers fanning out to forage at the distal end of the column; workers clear a narrow trail through vegetation when necessary (Creighton, 1953; Johnson, 2000b). During winter and spring, foraging columns of *V. julianus* form prior to dusk, and foraging continues into the night with workers returning early the next morning (Johnson, 2000a), and it appears to forage during the day in at least some parts of its range (Creighton, 1953). Workers are weakly polymorphic.

Gland chemistry has not been examined in *V. julianus*. Like other large-colony congeners, workers of *V. julianus* have a large pygidial gland reservoir with a textured tergal cuticle (Hölldobler *et al.*, 2013).

Mating flights of *V. julianus* occur in February–March with few sexuals being released over 1–2 or more weeks. Flights occur during early morning (8:30–10:00 MST) at temperatures from 16–23° C, and occur during mild breezes or overcast skies, but they were precluded by light rain or moderate breezes (Johnson, 2000a). Mating appears to occur in the air.

Queens are haplometrotic (Johnson, 2000a). Dry mass of alate queens averages 11.1 ± 0.4 mg. Alate queens contain an average of 47.4 ± 1.9 ($n = 5$) ovarioles, and mated queens contain an average of 1.225 ± 0.02 ($n = 2$) million sperm. Dry mass for virgin males averages 1.9 ± 0.2 mg, and they contain an average of 4.4 ± 0.17 ($n = 3$) million sperm (R.A. Johnson, unpub. data). Queens have a relatively low heat tolerance compared to other desert ants with most queens dying in hydrated conditions at 42° C and all at 43° C over a 2 h period (Johnson, 2000a). Ventilation patterns and metabolic rate of workers and alate queens are discussed in Lighton and Berrigan (1995).

Veromessor julianus is a hot desert species that is endemic to the Baja California peninsula of Mexico at elevations from 0–625 m (see Johnson, 2000a; Johnson & Ward, 2002). It is most common in sandy soils but it also occurs on rocky hillsides and bajadas. *Veromessor julianus* has a parapatric distribution with *V. pergandei*, with the former species occurring in slightly more mesic microhabitats, i.e., in wetter soils and/or at higher elevations (Johnson, 2000a; R.A. Johnson, pers. obs.). This species occurs in the Baja California desert, Gulf of California xeric scrub, San Lucan xeric scrub, and Sierra de la Laguna dry forests ecoregions, as defined by Olson *et al.* (2001) (Figure 27A).

Veromessor lariversi

(Figures 1E, 28, 29A–C, 31–32)

Distribution—Figure 27B

Veromessor lariversi Smith, 1951: 94 (worker). Types examined: holotype worker [USNM: USNMMENT00529582], #61266, 6 paratype workers [LACM], 5 paratype workers [MCZC], 13 paratype workers [USNM], UNITED STATES, Nevada: Washoe County, Nevada Dominion Mine, Pyramid Mining District, Mullen Gap at 5 miles west of Pyramid Lake (Ira La Rivers, 8 May 1951); Cole, 1955: 52 (queen).

Messor lariversi (Smith); Bolton 1982: 341 (first combination in *Messor*).

Veromessor lariversi Smith; Ward, Brady, Fisher, and Schultz, 2015: 13 (revived combination in *Veromessor*).

Worker diagnosis. This species is uniquely characterized by the following combination of features: (1) light yellowish to yellowish-orange or yellowish-red, gaster sometimes slightly darker, (2) medial lobe of clypeus arugose, smooth and shining, not thick and protuberant in profile, not elevated above lateral lobes in frontal view, (3) mandibles with 7, or rarely 8 teeth, (4) dorsal base of scape not flattened, slightly widened; maximum basal width of scape less than maximum preapical width, (5) MOD distinctly greater than OMD, $OI > 28.0$, (6) cephalic dorsum with few discontinuous, medial, longitudinal rugae that weaken laterally and disappear posterior to eyes, posterior margin smooth and shining, rugae more coarse and well-defined in front of and below eyes, dorsum mostly smooth and shining with scattered piligerous punctures, (7) psammophore well developed; ventral surface of head capsule with many long J-shaped hairs arranged in a distinct row around the outer margin of the ventral region of the head capsule, (8) dorsum and sides of pronotum weakly roughened and shining *or* weakly to strongly coriarius to lineogranulate, weakly shining; mesonotum with piligerous punctures to moderately punctulate-granulate, weakly shining to shining; mesopleura variable: faintly to strongly lineogranulate *or* strongly granulate between few, irregular longitudinal rugae *or* faintly granulate between longitudinal rugae dorsally and moderately to strongly granulate and arugose ventrally, (9) sides of propodeum weakly punctate-granulate between longitudinal or

oblique rugae **or** lineogranulate; propodeal spines divergent, triangular, acuminate, length similar to width at base; length less than distance between their bases and length $< 0.5 \times \text{MOD}$; infraspinal facet and propodeal declivity micropunctate, shining, and (10) metasternal process higher than long, apex subangulate. Additional diagnostic characters that separate *V. lariversi* from *V. pseudolariversi* are: (1) in profile, the anteroventral margin of the postpetiole is continuous, lacking a minute process, and (2) relatively smaller eye with fewer ommatidia (Figures 28, 29A–C, 30).

Measurements. holotype ($n = 25 + 10$ paratypes). HL 1.31 (1.06–1.42); HW 1.23 (0.93–1.37); MOD 0.39 (0.33–0.43); OMD 0.32 (0.26–0.38); SL 1.17 (0.87–1.27); PNW 0.81 (0.59–0.98); HFL 1.48 (0.95–1.62); ML 1.75 (1.29–1.93); PW 0.23 (0.16–0.26); PPW 0.40 (0.29–0.45). Indices: SI 95.12 (80.56–107.53); CI 93.89 (83.041–104.00); OI 31.71 (28.57–38.38); HFI 120.33 (87.96–129.90).

Queen diagnosis. This caste is diagnosed by the following combination of features: (1) head and mesosoma dark orangish-brown to dark brownish-orange; gaster slightly lighter orangish-brown, (2) medial lobe of clypeus not thick and protuberant in profile, not elevated above lateral lobes in frontal view, medial lobe mostly smooth and arugose with numerous micropunctures, (3) mandibles with 7 teeth, (4) dorsal base of scape slightly flattened, but not widened; maximum basal width of scape less than maximum preapical width, (5) MOD distinctly greater than OMD, (6) cephalic dorsum with prominent longitudinal rugae medially, around eyes, and on malar area; rugae faint to lacking between medial rugae and eyes; rugae lacking posterior to ocelli, posterior margin smooth and shining, (7) psammophore well developed, (8) sides of pronotum moderately granulate between fine longitudinal rugae; mesoscutum and mesoscutellum smooth and weakly shining with scattered piligerous punctures; anepisternum moderately shining between fine, longitudinal rugae; katapisternum largely smooth and shining with longitudinal rugae near anterior and posterior margins, (9) propodeum moderately coriarius between longitudinal and oblique rugae; propodeal spines triangular, about as long as width as base, apex bluntly rounded, length less than the distance between their bases; infraspinal facet and propodeal declivity smooth and weakly shining, and (10) metasternal process higher than long, apex rounded. An additional diagnostic character is that in profile, the anteroventral margin of the postpetiole is continuous, lacking a minute process (Figure 31).

Measurements. ($n = 4$). HL 1.55–1.61; HW 1.53–1.62; MOD 0.43–0.54; OMD 0.36–0.43; SL 1.29–1.39; HFL 1.78–1.84; ML 2.78–2.98; PW 0.40–0.44; PPW 0.63–0.74. Indices: SI 79.63–88.54; CI 95.03–101.94; OI 27.22–34.39; HFI 109.88–119.61.

Male diagnosis. This caste is diagnosed by the following combination of features: (11) head dark brownish, rest of body light orangish-brown, (12) clypeus weakly convex, anterior margin nearly straight across middle, (13) mandibles with 3 or 4 small teeth or denticles basad of apical tooth, (14) anterior ocellus well above level of tops of eyes, (15) anepisternum mostly smooth and shining with numerous weak punctures; katapisternum mostly smooth and shining, (16) propodeum lacking denticles, with few widely spaced longitudinal rugae, especially laterad, (17) metasternal process prominent, triangular, acuminate, and (18) subpetiolar process digitiform with lamella tapering posterad (Figures 1E, 32).

Measurements. ($n = 1$). HL 0.81; HW 0.72; MOD 0.40; SL 0.35; HFL 1.66; ML 1.99; PW 0.30; PPW 0.43; AOD 0.12; IOD 0.25; OOD 0.23. Indices: SI 48.61; CI 88.89; OI 55.56; HFI 230.56.

Additional material examined. **UNITED STATES: California:** *Inyo Co.*: Eureka Valley, Mar 1978 (LACM); Deep Springs, Sep 28, 1978 (LACM). *Lassen Co.*: 1.5 km NE Wendel, 1250 m, Jul 6, 2008 (UCDC); 13 km at 9.5° N Doyle, 1240 m, Jun 27, 2004 (UCDC); 5.3 mi NE Litchfield, 4200', Jul 24, 1969 (LACM). *Los Angeles Co.*: Saddle Back Butte, 3020', Apr 28, 1998 (LACM). *San Bernardino Co.*: China Lake at Paxton Dunes at 13 mi NNE Ridgecrest, 2200', Apr 13–29, 1982 (UCDC). **Nevada:** *Churchill Co.*: Sand Mountain, T17N, R32E, 4200', Apr 22, 1979 (LACM); Sand Mountain at 25 mi SE Fallon, Mar 18–Aug 1, 1980 (UCDC); Blow Sand Mtns (T15N, R30E), 4500', Jun 29, 1979 (LACM); 16 mi N Fallon, 3500', Jun 8, 1971 (LACM); 28 mi N Fallon, 4000', Jun 8, 1971 (LACM); Sand Spring Dune, 1200 m, Jun 30–Jul 2, 1996 & Aug 2, 1996 & Jun 5, 2000 & Jul 3, 2008 & Jul 3, 2012 (CASC; MCZC; MLBC; UCDC). *Esmeralda Co.*: Hwy 266 at 0.1 mi N California state line, 4980', Jul 22, 1992 (RAJC). *Humboldt Co.*: 10 mi NNE Winnemucca (T37N, R38E, Sect 9), 4400', Jun 24, 1971 (LACM). *Lander Co.*: Big Smoky Valley, T10N, R43E, Sect 17, 5900', May 3, 1971 (LACM). *Lyon Co.*: Silver Springs Junction, Jun 28–29, 1954 (LACM; MCZC); 2 mi ESE Silver Springs, 4000', Jul 18–20, 1973 (LACM; MCZC; RAJC); Smith, Sep 13, 1953 (LACM); 3 mi E Smith, May 23, 1971 (LACM; RAJC); 6 km E Weeks, 1280 m, Jun 28, 1998 (UCDC); 0.2 mi NW Jct Hwy 477 & I-80, 4120', Jul 24, 2018 (RAJC); Fort Churchill State Historic Park, 1285 m, Jul 1, 2010 & Jul 2, 2012 & Jul 1, 2014 & Jun 29, 2016 & Jul 27, 2018 (MLBC; MMPC; RAJC; UCDC); Hwy 95 at 6.9 mi E Jct Hwy 208, 4400', Jul 28, 2018 (NHMW; RAJC). *Mineral Co.*: Schurz, 4250' May 3, 1965

(LACM; MCZC); T14N, R33E, Sect 11, 5800', May 17, 1971 (LACM); 1.4 mi SE Jct Hwys 95 & 360, 4350', Jul 10, 2019 (RAJC). *Nye Co.*: Round Mountain, 5900', Jul 15, 1954 (LACM); Cactus Range, May 12, 1953 (LACM); Big Dunes at 10 mi W Lathrop Wells, 2600', May 1, 1970 (LACM; RAJC); Nevada Test Site, near Mercury, Jun 1962 (USNM); Hot Creek Valley at Moore's Station (T7N, R51E), 7000', Aug 21, 1969 (LACM); Hwy 95 at 16.3 mi SE Scotty's Junction, 3980', Jul 10, 2019 (RAJC). *Washoe Co.*: Wadsworth, Jun 30, 1971 (LACM); 1.7 mi NW Wadsworth, 4000', Sep 10–11, 1975 (LACM); 2.8 mi W Wadsworth, May 30, 1963 & May 26, 1965 & Jun 21, 1968 (LACM); 3 mi W Wadsworth, Nov 21, 1968 (LACM); 4 km WSW Wadsworth, 1270 m, Jun 30, 2002 (UCDC); 24 mi S Gerlach, 3900', Jun 11, 1971 (MCZC); 21 mi N Gerlach, 4100', Jun 15, 1971 (LACM; RAJC); 18 mi S Gerlach, 4500', Jun 11, 1971 (LACM); 5 km S Nixon, 1185 m, Jul 8, 1982 (UCDC); 10 mi N Nixon, 4000', Jun 11, 1971 (LACM); S end Pyramid Lake, 1140 m, Jul 6, 1990 (MCZC; UCDC); T23N, R20E, Sect 19, 5000', May 12, 1974 (LACM) (Figure 27B).

Etymology. This species was named after Ira La Rivers, biologist at University of Nevada, Reno, who collected the type series.

Discussion. Smith (1951) described *V. lariversi* from a holotype and 37 paratype workers; the holotype and 25 paratypes were deposited at USNM. All USNM specimens have the type labels USNM 61266 [listed as 61265 in Smith (1951)], but none of these specimens had a holotype label. All but one pin had a USNM 61266 PARATYPE label; the one exception was a pin with PARA crossed out. This pin also had a black dot on the triangle, and this specimen was presumed to be the holotype. Consequently, we placed a holotype label on this specimen.

Numerous series were subsequently collected by M. R. Smith, A. C. Cole, and R. R. Snelling that were all identified as *V. lariversi* until morphological variation in these series was conveyed to us by Phil Ward. Subsequent examination revealed that many of these series consisted of a species morphologically distinct from, but closely related to *V. lariversi*. Morphological differences that separate the two species include that workers of *V. lariversi*: (1) in profile, ventral margin of postpetiole continuous, lacking a minute process (Figure 29A), (2) in dorsal view and in profile, the pronotum and mesonotum arugose, weakly to strongly coriarius to punctulate-granulate (Figure 29B–C), and (3) a relatively smaller eye with fewer facets (Figure 30). For workers of *V. pseudolariversi*: (1) in profile, anteroventral margin of postpetiole discontinuous with margin interrupted by a minute process, margin concave anterior to process (Figure 29D), (2) in dorsal view and in profile, the pronotum with discontinuous to continuous, irregular to irregular, transverse rugae; dorsum of mesonotum with one to few weak, irregular, usually discontinuous, longitudinal rugae (Figure 29E–F), and (3) a relatively larger eye with more facets (Figure 30). Queens of the two species also differ in size. Worker allometry is similar for both species, but queens of *V. pseudolariversi* are distinctly smaller than those of *V. lariversi* and their males are larger (Figure 33), in addition to other morphological traits given in the key to queens. A molecular phylogeny based on UCEs shows that these two lineages are sister, reciprocally monophyletic, and quite divergent. This phylogeny included specimens from Fort Churchill State Historic Park in Lyon County, Nevada, where both lineages occur sympatrically (M.L. Borowiec, unpub. data).

Cole (1955) described the queen of *V. lariversi* (Cole Coll. No. NEV-352), but no queens from this series were present in loans that we examined. However, eight workers from the NEV-352 series were examined and identified as *V. lariversi*, verifying that this description was of *V. lariversi*. Cole (1963) later redescribed the queen and described the male from Cole Coll. No. NEV-784. Unfortunately, no individuals from the NEV-784 series were available in our loans to verify this identification. It seems probable that this series was actually *V. pseudolariversi* given the much smaller size of the queen (6.59–6.72 mm in length) compared to the 9.4 mm length indicated in his earlier description of the *V. lariversi* queen (Cole, 1955). That this description is that of *V. pseudolariversi* is also supported in that Figure 3B of Cole (1963) shows a small process on the anteroventral margin of the postpetiole of the male. Cole also described the male as rather uniformly black, which better fits the description for the male of *V. pseudolariversi* (see Figure 44) compared to the light brownish male of *V. lariversi* (Figure 32). Other morphological characters were described too briefly to further verify this presumption.

Veromessor lariversi is broadly sympatric with several congeners including *V. smithi*, *V. lobognathus*, and *V. pseudolariversi*. This species is easily separated from all congeners except for the very similar *V. pseudolariversi* (see above). Workers of *Veromessor lariversi* are separated from *V. smithi* by: (1) smaller size (HW = 0.93–1.37 mm), (2) body concolorous light yellowish to yellowish-orange or yellowish-red, gaster often slightly darker, (3) maximum basal width of scape less than maximum preapical width, and (4) mandibles with 7 teeth. For *V. smithi*: (1) larger size (HW = 1.33–1.61 mm), (2) concolorous orangish-brown to rust colored, (3) maximum basal width of scape greater than maximum preapical width, and (4) mandibles with 8 teeth.

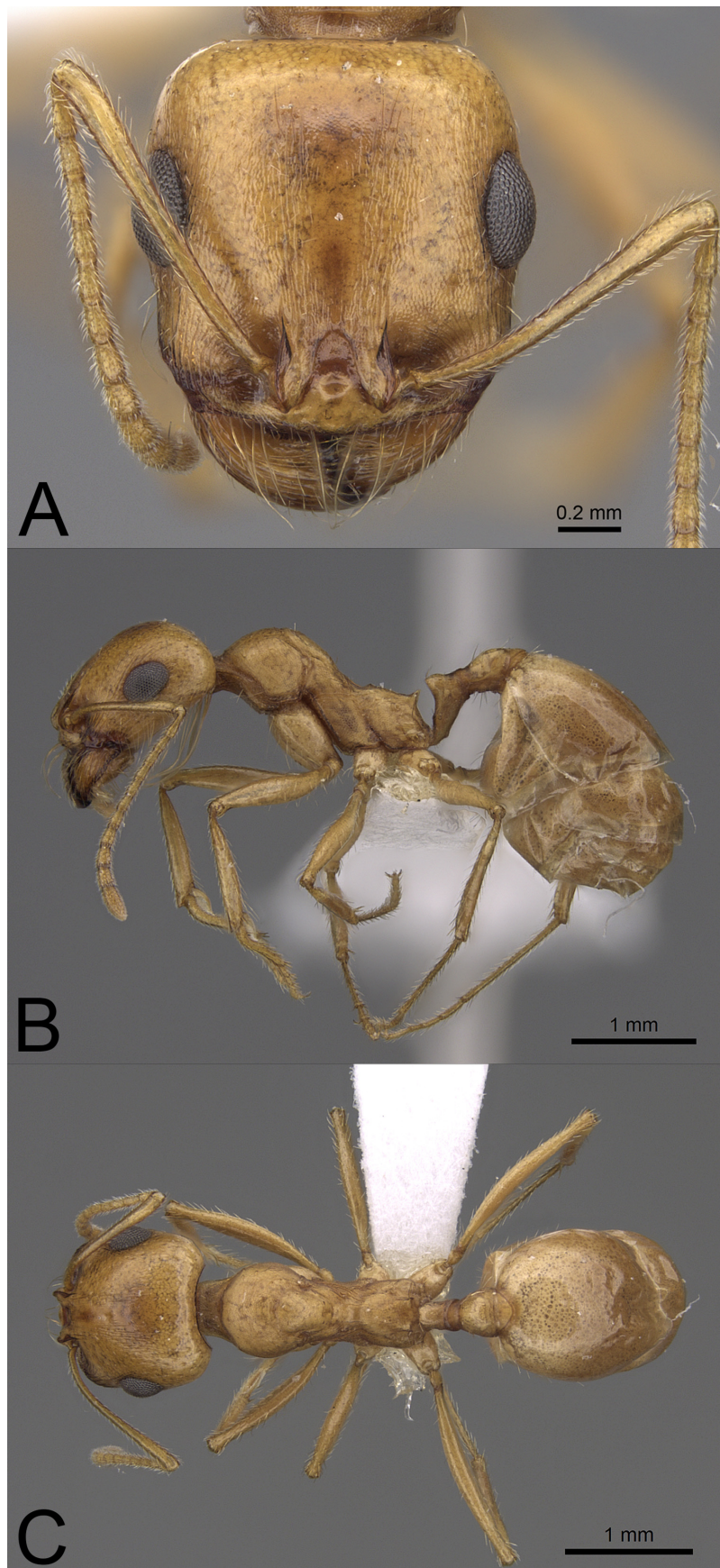


FIGURE 28. Photograph of *Veromessor lariversi* worker: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0923148). Photographs by Wade Lee from www.AntWeb.org.

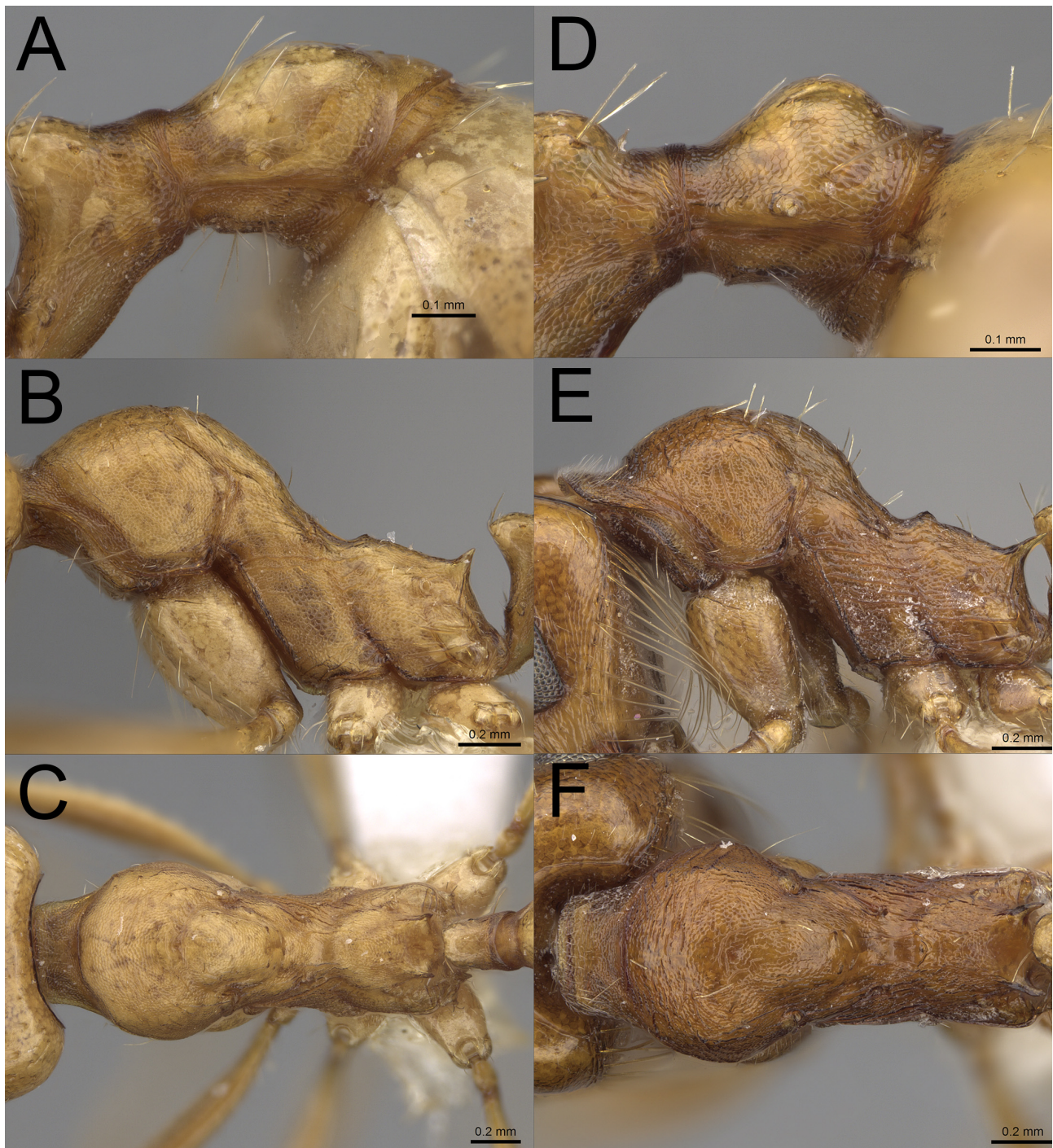


FIGURE 29. Photographs of diagnostic characters to distinguish between workers of *Veromessor lariversi* Smith and (A–C) *V. pseudolariversi* (D–F). Photographs of *V. lariversi* worker (CASENT0923148): (A) anteroventral margin of postpetiole lacking a minute process, margin with a continuous profile, and (B) in profile and (C) in dorsal view, pronotum and mesonotum arugose and weakly to strongly coriaceous to punctulate-granulate. Photographs of *V. pseudolariversi* paratype worker (CASENT0923121): (D) anteroventral margin of postpetiole with a minute process that interrupts the continuous profile, margin weakly concave anterior to process, and (E) in profile and (F) in dorsal view, pronotum with discontinuous to continuous, wavy to irregular transverse rugae; dorsum of mesonotum with one to few weak, wavy to irregular, usually discontinuous longitudinal rugae. Photographs by Michele Esposito and Wade Lee from www.AntWeb.org.

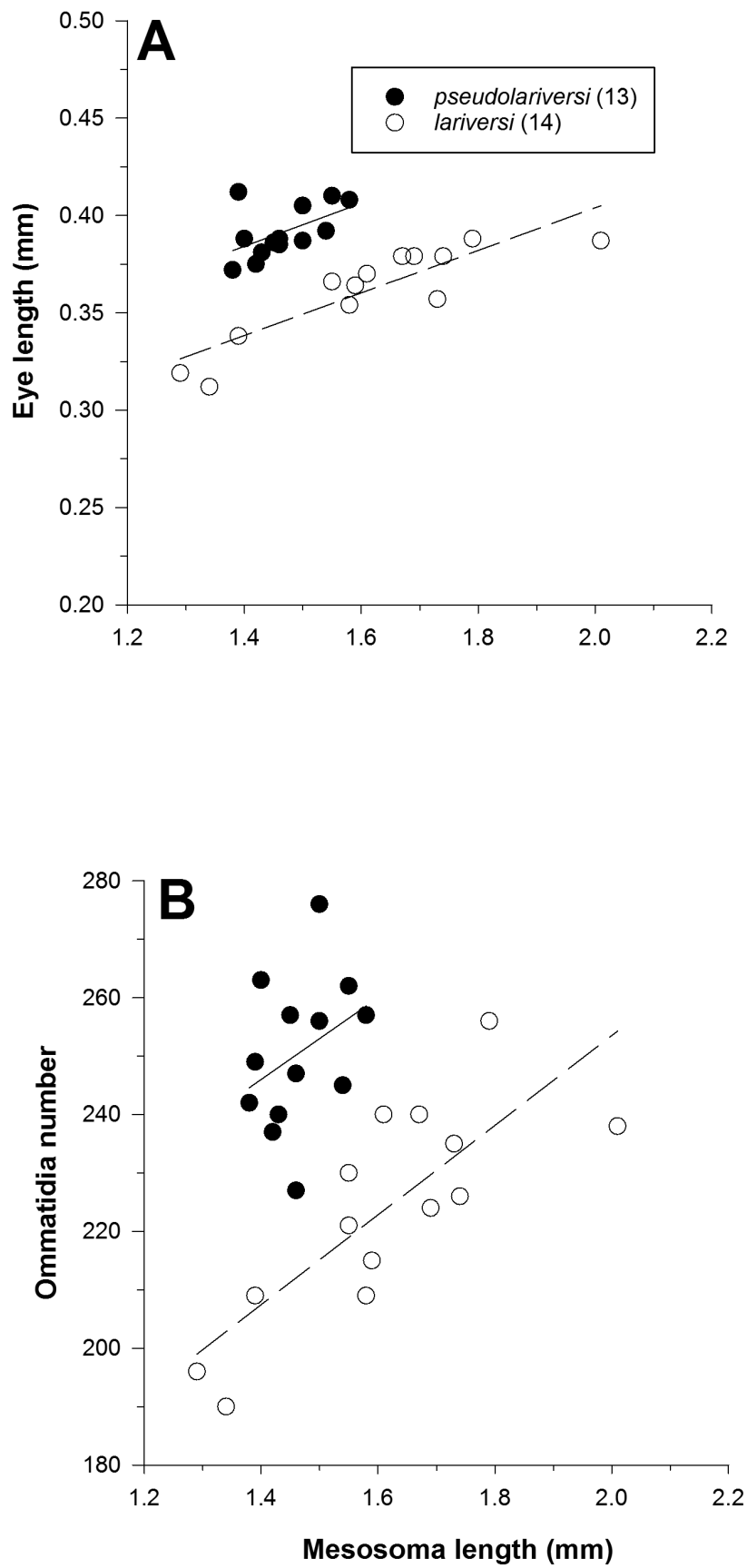


FIGURE 30. Bivariate plots for workers of *V. lariversi* and *V. pseudolariversi*: (A) mesosoma length versus number of eye facets, and (B) mesosoma length versus eye length. Sample size for each species is in parentheses.

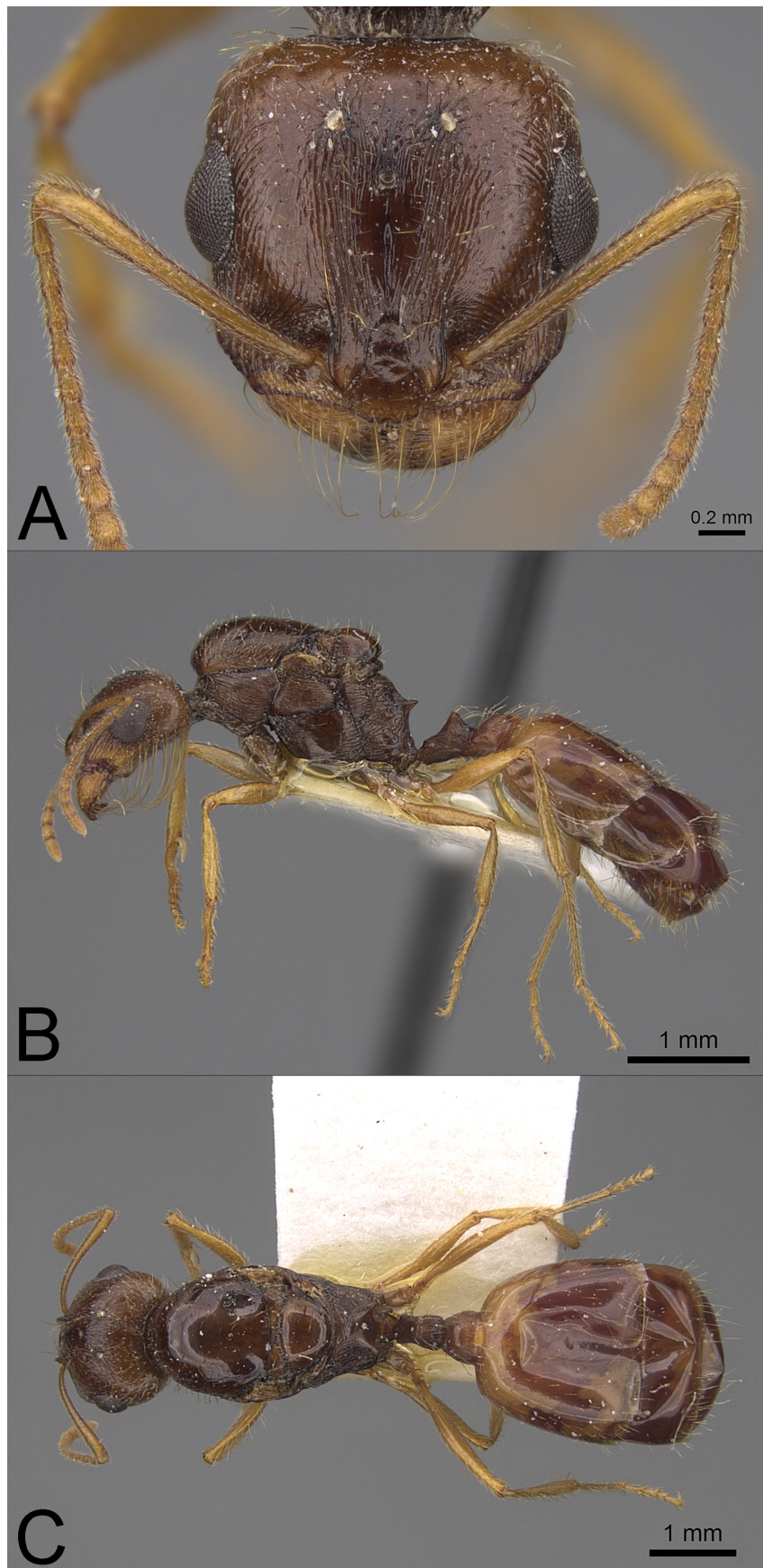


FIGURE 31. Photograph of *Veromessor lariversi* dealate queen: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (LACMENT363890). Photographs by Wade Lee from www.AntWeb.org.

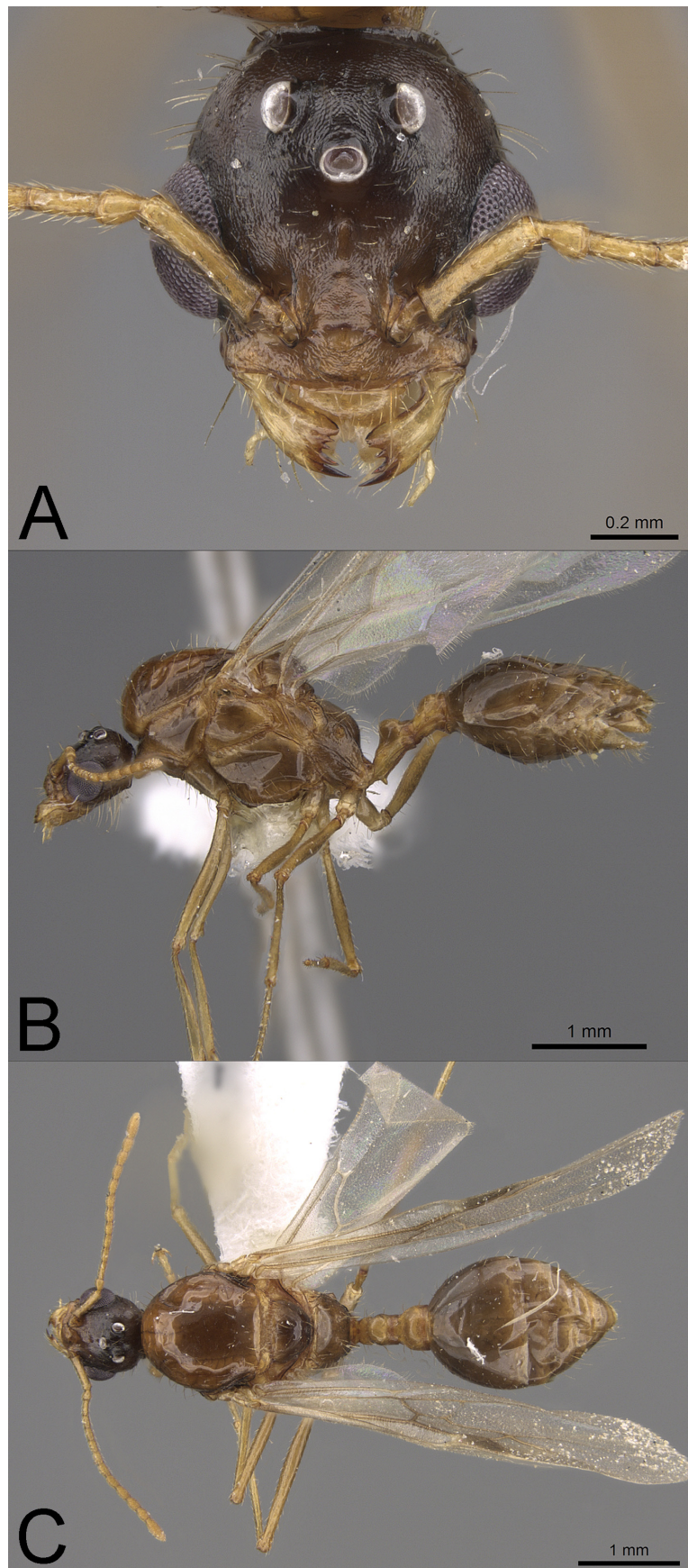


FIGURE 32. Photograph of *Veromessor lariversi* male: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0761204). Photographs by Michele Esposito from www.AntWeb.org.

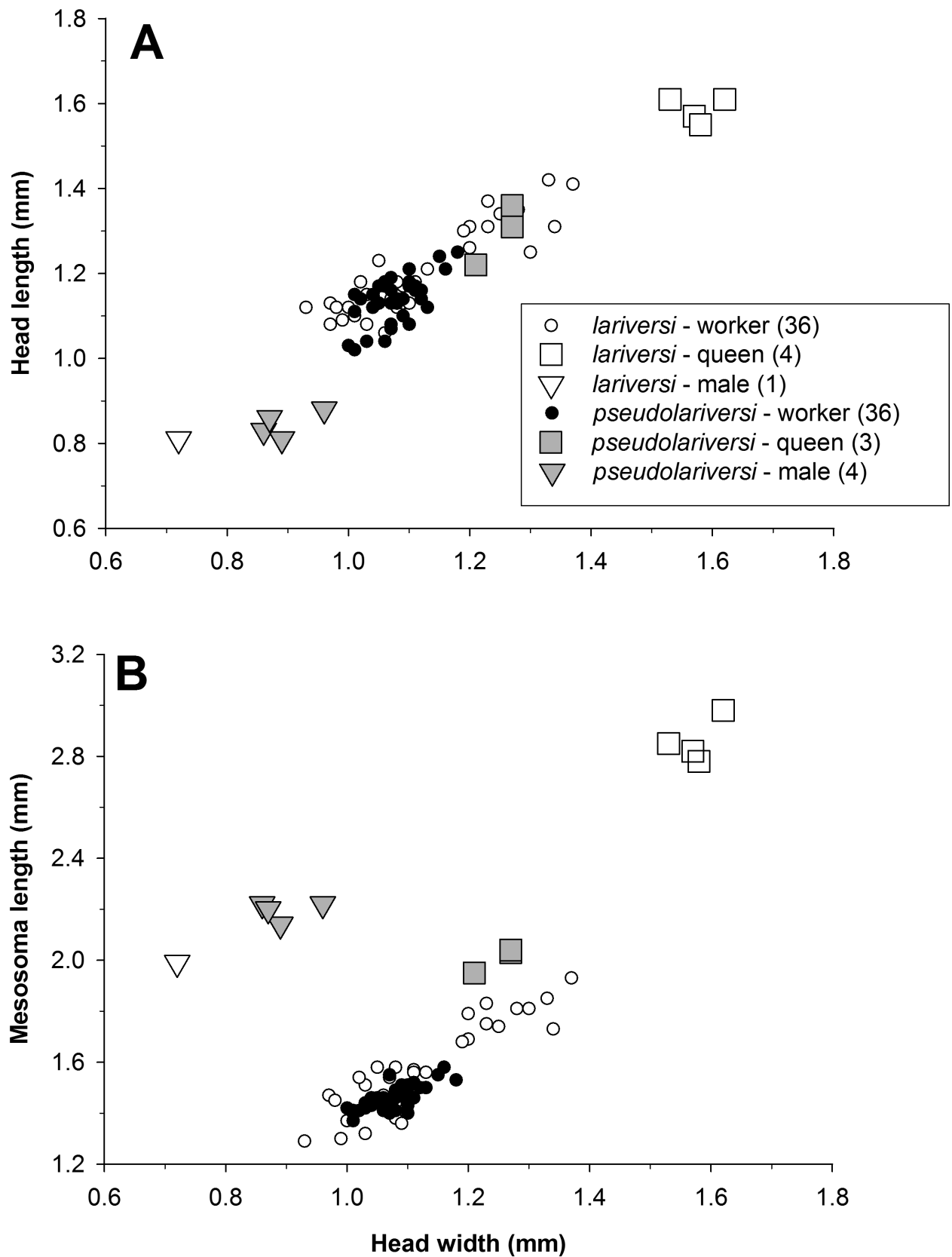


FIGURE 33. Bivariate plots for workers, queens, and males of *Veromessor lariversi* and *V. pseudolariversi*: (A) head width versus head length and (B) head width versus mesosoma length. Sample size for each caste is in parentheses.

Veromessor lariversi workers are separated from *V. lobognathus* based on: (1) smaller size (HW = 0.93–1.37 mm), (2) body concolorous light yellowish to yellowish-orange or yellowish-red, gaster often slightly darker, (3) dorsum of pronotum weakly to strongly punctulate-granulate to lineogranulate, usually arugose, (4) maximum basal width of scape less than maximum preapical width, and (5) mandibles with 7 teeth. In *V. lobognathus*: (1) larger in size (HW = 1.28–1.82 mm), (2) light to dark orangish-brown to reddish-brown head and mesosoma, (3) dorsum of pronotum with weakly to strongly irregular rugae and numerous secondary rugae to rugoreticulate, (4) maximum basal width of scape greater than maximum preapical width, and (5) mandibles with 8 teeth.

Biology. The biologies are probably similar for *V. lariversi* and *V. pseudolariversi*, but it is difficult to ascribe published information to one species or the other because series numbers were not referenced in papers, voucher series were not collected, or series were absent from loans that we examined. Papers that discuss biology of “*V. lariversi*” include Bennett (2000), Cole (1955; 1966), Creighton (1953), Smith (1951), Snelling and George (1979), and Wheeler and Wheeler (1986). The following information on biology includes only that which could be verified from examined series or field observations of *V. lariversi*.

Veromessor lariversi workers are solitary, nocturnal foragers (R.A. Johnson, pers. obs.). Nests are usually polydomous with craters up to 10–15 cm in diameter, but sometimes consist only of an entrance lacking a crater. Colonies reach up to about 1,000 workers (Cole, 1955) and are presumably monogynous. Workers are mostly monomorphic. Snelling and George (1979) collected both *V. lariversi* and *V. pseudolariversi* in California, and they indicated that colonies appear to aestivate in summer months. It seems more likely that these authors observed inactive colonies given that both RAJ and MLB have observed *V. lariversi* foraging in June.

Gland chemistry has not been examined in *V. lariversi*. Neither has the pygidial gland been examined, but we expect that this species has a small pygidial gland reservoir and lacks a textured tergal cuticle, as does its sister species, *V. pseudolariversi*, and all other small-colony congeners (see Hölldobler *et al.*, 2013).

Mating flights have not been observed, but dealate queens have been collected from May 26–Jun 29, indicating that mating flights occur during summer. Cole (1963) found two dealate queens in one excavated nest, but it is unclear if this record was for *V. lariversi* or *V. pseudolariversi*.

Veromessor lariversi is a mostly Great Basin Desert species with a few records from the Mohave Desert. This species appears to be most common in sandy soils at elevations from 785–2,120 m. There is also one record from Los Angeles County, California, which suggests that *V. lariversi* is more widespread than indicated by current collection records. This species occurs in the Great Basin shrub steppe, Mohave Desert, and Snake-Columbia shrub steppe ecoregions, as defined by Olson *et al.* (2001) (Figure 27B).

Veromessor lobognathus

(Figures 1F, 12B, 34–36)

Distribution—Figure 27C

Messor lobognathus Andrews, 1916: 82, fig. 1 (worker). Syntypes examined: 1 worker [MCZC], 1 worker [USNM], UNITED STATES, Colorado: Glenwood Springs, 5,750', no date (T.D.A. Cockerell); Cole, 1963: 680 (queen, male); Wheeler and Wheeler, 1957: 143, figs. 1b, 2 (larvae). See also Wheeler and Creighton, 1934: 371, plate II, fig. 6. USNM worker here designated **LECTOTYPE** [CASENT0105632].

Veromessor lobognathus (Andrews); Wheeler and Creighton, 1934: 362 (first combination in *Veromessor*).

Messor lobognathus Andrews; Bolton, 1982: 341 (revived combination in *Messor*).

Veromessor lobognathus (Andrews); Ward, Brady, Fisher, and Schultz: 2015: 13 (revived combination in *Veromessor*).

Lobognathus Enzmann, 1947: 152 [as subgenus of *Veromessor*]. [Erroneous entry for *Veromessor lobognathus* (Andrews); see Brown, 1949: 49].

Worker diagnosis. This species is uniquely characterized by the following combination of features: (1) light to dark orangish-brown to reddish-brown, gaster usually slightly lighter, (2) medial lobe of clypeus with weakly to strongly irregular longitudinal or oblique rugae, medial lobe not thick and protuberant in profile, not elevated above lateral lobes in frontal view, (3) mandibles with 8 teeth, (4) dorsal base of scape flattened and widened; maximum basal width of scape greater than maximum preapical width, (5) MOD distinctly less than OMD, $OI < 25.0$, (6) cephalic dorsum with prominent irregular, longitudinal rugae, usually with numerous short lateral branches, rugae often becoming rugoreticulate posterior to eyes; interrugae on cephalic dorsum moderately punctate to strongly granulate, weakly dull to dull, (7) psammophore moderately well developed; ventral surface of head capsule with

both J-shaped hairs and straight or evenly curved hairs, J-shaped hairs arranged in a V-shaped row which does not reach the posterior part of the lateroventral margin of head capsule, (8) in dorsal view, pronotum rugoreticulate, sometimes with one to few irregular transverse rugae along anteromedial margin; sides of pronotum with irregular longitudinal rugae with numerous short, lateral branches; mesonotum with strongly irregular longitudinal trending rugae to rugoreticulate; mesopleura with strongly irregular longitudinal rugae, usually with numerous short lateral branches, dorsal one-third often rugoreticulate or nearly so, (9) propodeal spines elongate, slender, straight in profile and weakly curving inward in dorsal view, length $1.0\text{--}1.5\times$ the distance between their bases and length $> 1.0\times$ MOD; infraspinal facet rugose, weakly shining to smooth and strongly shining; propodeal declivity weakly coriarius, strongly shining, and (10) metasternal process small, triangular, longer than high, apex bluntly rounded (Figures 12B, 34).

Measurements. lectotype ($n = 38$). HL 1.77 (1.30–1.69); HW 1.85 (1.28–1.82); MOD 0.35 (0.31–0.41); OMD 0.53 (0.34–0.49); SL 1.54 (1.20–1.54); PNW 1.10 (0.79–1.10); HFL 2.22 (1.41–1.98); ML 2.28 (1.61–2.29); PW 0.36 (0.26–0.36); PPW 0.53 (0.44–0.60). Indices: SI 83.24 (78.95–97.66); CI 104.52 (98.46–118.12); OI 21.08 (20.47–25.00); HFI 120.00 (105.00–120.00).

Queen diagnosis. This caste is diagnosed by the following combination of features: (1) light to dark orangish-brown to reddish-brown, gaster usually slightly darker, (2) medial lobe of clypeus with coarse, irregular rugae that traverse in all directions, anteromedial margin sometimes sharply depressed, (3) mandibles with 8 teeth, (4) dorsal base of scape flattened and widened; maximum basal width of scape greater than maximum preapical width, (5) MOD slightly less than to slightly greater than OMD, (6) cephalic dorsum with wavy to irregular longitudinal rugae, medial rugae not diverging to diverging toward posterior corners, rugae often becoming more irregular to weakly rugoreticulate along posterior margin; interrugae strongly punctulate and roughened, dull to weakly shining, (7) psammophore moderately well developed, (8) sides of pronotum weakly coriarius, weakly shining between longitudinal rugae; mesoscutum with longitudinal rugae; mesoscutellum finely striatopunctate with scattered fine, irregular rugae; anepisternum moderately shining between fine longitudinal rugae; katepisternum weakly coriarius, weakly shining with few short rugae near margins, (9) propodeum with regular to irregular longitudinal and oblique rugae, propodeal spines elongate-triangular, acuminate, length slightly less than distance between their bases; infraspinal facet weakly coriarius, weakly shining; propodeal declivity smooth and shining, and (10) metasternal process longer than high, apex broadly rounded (Figure 35).

Measurements. ($n = 12$). HL 1.48–1.86; HW 1.65–1.99; MOD 0.39–0.52; OMD 0.35–0.47; SL 1.30–1.62; HFL 1.78–2.10; ML 2.49–2.91; PW 0.37–0.42; PPW 0.69–0.74. Indices: SI 76.57–84.57; CI 102.98–114.86; OI 22.61–26.67; HFI 99.48–112.64.

Male diagnosis. This caste is diagnosed by the following combination of features: (11) light brown to brownish-black, (12) medial lobe of clypeus thick and abruptly descendant at anteromedial margin; anterior margin nearly straight across middle, (13) mandibles usually with 1 (rarely 2) denticles basad of preapical tooth, (14) ocelli well above level of top of eyes, (15) anepisternum moderately shining, weakly punctulate between fine, longitudinal striae that are often lacking on lower one-fourth or more or entire anepisternum mostly smooth and shining; katepisternum with short rugae near margins, rest of katepisternum weakly to moderately coriarius or entire katepisternum mostly smooth and shining, (16) propodeum weakly to moderately coriarius between moderately coarse longitudinal rugae to mostly smooth and shining with weaker longitudinal rugae; spines or denticles absent; in profile, juncture of dorsal surface and propodeal declivity weakly angulate to rounded, (17) metasternal process low and obtuse to acute, and (18) subpetiolar process prominent and acute (Figures 1F, 36).

Measurements. ($n = 12$). HL 0.82–0.96; HW 0.77–0.86; MOD 0.33–0.38; OMD 0.09–0.12; SL 0.34–0.46; HFL 1.73–1.99; ML 2.13–2.58; PW 0.28–0.34; PPW 0.54–0.61; AOD 0.09–0.11; IOD 0.24–0.31; OOD 0.27–0.30. Indices: SI 43.59–59.74; CI 84.78–100.00; OI 39.76–46.15; HFI 205.95–246.15.

Additional material examined. UNITED STATES: *Arizona:* Navajo Co.: Black Mesa, 1991 m, Jul 21, 2008 (MCZC). *Colorado:* Larimer Co.: Owl Canyon near Hwy 287, 5700' & 6100', Jul 22, 1952 (LACM; USNM). *Rio Blanco Co.:* 20 mi SW Rangely, 6500', Aug 26, 1952 (not examined, see Gregg, 1955). *Idaho:* Bingham Co.: INEL (= Idaho National Laboratory) at East Butte (T2N, R32E, Sect 14), 1957 m, May 30, 1987 (CIDA; RAJC); INEL at Middle Butte (T2N, R32E, Sect 20), 5550' & 6100', Jun 24, 1989 (CIDA; RAJC); T3N, R33E, Sect 24, 1528 m, Jun 1, 1993 (CIDA); INE at 2.2 mi NE Jct. Hwy 20/Rd T-21, 1528 m, Jun 1, 1993 (RAJC). *Butte Co.:* AEC-NRTS (=Idaho National Laboratory), Jun 29, 1967 (CIDA); AEC-NRTS at 30 mi W Idaho Falls, 4947', Jun 14, 1967 (LACM); T2N, R28E, Sect 23NE, at 44 km ESE Arco, 1518 m, May 28, 1987 (CIDA); INEL (T2N, R29E, Sect 1),

1503 m, May 22, 1987 & Jul 1, 1989 & Aug 13, 1989 & Jul 6, 1990 (CIDA; RAJC); Road T-11 (T3N, R28E, Sect 1), 1561 m, May 29, 1993 (CIDA); INEL at W border on Road T-2 (T3N, R28E, Sect 18), 1615 m, Jun 22, 1988 (CIDA); INEL at dead end of Road T-2 (T3N, R28E, Sect 19), 5275', Jun 22, 1988 (CIDA); 1 mi S Teakettle Butte (T2N, R28E, Sect 19), 1584 m, May 31, 1993 (CIDA; RAJC); Rd T-10 (T3N, R28E, Sect 32), 1567 m, Jun 22, 1988 (CIDA); T3N, R29E, Sect 7, 1567 m, May 29, 1993 (CIDA); INEL on Road T-12 (T3N, R29E, Sect 33), 1588 m, Jun 2, 1993 (CIDA); INEL at Powerline Rd (T4N, R30E, Sect 14), 1417 m, Jul 6, 1990 (CIDA); INEL at hilltop above Hwy 33 (T5N, R30E, Sect 3), 4987', Jun 23, 1988 (CIDA); INEL at 1 km W Jct Franklin & Lincoln Blvds (T5N, R31E, Sect 4), 1462 m, Jun 9, 1991 (CIDA); INEL at site boundary on Kyle Road Canyon (T6N, R30E, Sect 3), 5440', May 27, 1988 (CIDA; RAJC); 15.7 km ENE Howe (T6N, R30E, Sect 24), 1481 m, Jul 3, 1987 (CIDA); 2 km SSW Howe, 1510 m, Aug 24, 2017 (JTLC); INEL at N Big Lost Sinks (T6N, R30E, Sect 27), 1554 m, Jul 8, 1990 (CIDA); INEL at Richard Butte (T7N, R31E, Sect 4), 1554 m, Jul 7, 1990 (CIDA; RAJC). *Clark Co.*: INEL at W border (T8N, R30E, Sect 36), 1615 m, Jun 9, 1991 (CIDA; RAJC); INEL at Hwy 28 at 1 mi SE Jct Hwy 22 (T8N, R31E, Sect 36), 1536 m, Jun 9, 1991 (CIDA); 1 mi E Jct Hwys 28 & 22 (T8N, R31E, Sect 35), 5040', Sep 1, 1991 (CIDA); INEL at Hwy 22 (T8N, R31E, Sect 34), 1554 m, Jun 29, 1988 (CIDA); INEL at Hwy 28 (T8N, R31E, Sect 36), Sep 1, 1991 (CIDA). *Jefferson Co.*: INEL at Rd T-4 (T4N, R33E, Sect 13), 1533 m, Jul 3, 1989 (CIDA; RAJC); INEL Rd T-2 (T4N, R33E, Sect 17), 5010', Jun 14, 1994 (CIDA); T6N, R32E, Sect 15, 1460 m, Jun 1, 1993 (CIDA); INEL along Hwy 28 (T7N, R32E, Sect 11), 1253 m, Jun 9, 1991 (CIDA); INEL at 0.9 mi N Hwy 33 (T6N, R32E, Sect 15), 4820', Jun 1, 1993 (RAJC). *Montana*: *Carter Co.*: 10 mi SW Ekalaka (T1N, R57E), 3500', Jun 13, 1966 (UAIC). *Nevada*: *Elko Co.*: Palomino Ridge, 6300', Jul 15, 1970 (LACM; RAJC). *Humboldt Co.*: 91 mi SSW Denio (T42N, R27E, Sect 11), 5200', May 24, 1971 (LACM). *Lyon Co.*: 14 mi SSE Yerington, 5100', May 20, 1971 (LACM; RAJC); 16 rd mi SSE Yerington, 5200', Jun 16, 1979 (LACM); Pine Grove Rd at 0.9 mi S Jct Hwy 208, 4610', Jul 22, 2018 (NHMW; RAJC). *Nye Co.*: Currant Pass Summit (18 mi NE Currant), 6500', May 5, 1974 (LACM); AEC-NTS near Mercury (= Ranier Mesa), 7000', Jun 21–Jul 26, 1962 (LACM; UAIC; USNM); Morey Mine in Hot Creek Valley, 7100', Jun 18, 1970 (LACM); Nye, 9 km NNW Belmont, 2505 m, Jul 12, 2019 (UCDC). *Storey Co.*: 2 mi E Clark, 4700', Jul 20, 1971 (LACM); Clark Mine at 27 km E Sparks, 1420 m, Jul 3, 1994 (RAJC); 20 km WSW Fernley, 1430 m, Jul 3, 1994 (UCDC). *Washoe Co.*: Hanging Rock Canyon, 1750 m, Jun 5–6, 1999 (UCDC). *White Pine Co.*: Ely, Jun 25, 1954 (LACM; USNM); T18N, R64E, 7000' & 7500', Jul 15, 1970 (LACM); White Pine Mtns (T17N, R57E, Sect 17), 6700', Apr 29, 1971 (LACM); White Pine Mtns, T17N, R57E, Sect 22, 6700', Apr 29, 1971 (RAJC); 2 mi E McGill, 7500', Jul 15, 1970 (RAJC); 49 km N Ely, 2005 m, Jul 14, 2019 (UCDC). *North Dakota*: *Billings Co.*: Roosevelt National Park near Medora, May 12, 1954 & Jun 28, 1957 & Jul 5, 1957 & Jun 1–13, 1958 & Aug 2, 1958 & Jun 10, 1960 (LACM; USNM); Roosevelt National Park, T140N, R102W, Sect 1, May 28, 1957 (LACM; USNM); Roosevelt National Park, T140N, R102W, Sect 12, May 9–10, 1960 (LACM). *Oregon*: *Malheur Co.*: 7.0 mi ENE Jct Hwys 78 & 95, 1095 m, Jun 21, 2020 (MLBC). *South Dakota*: *Custer Co.*: T3S, R1E, Sect 18, 4750', Jun 10–15, 1963 (UAIC). *Utah*: *Duchesne Co.*: 11 mi W Duchesne (T3S, R6W), 6200', no date (not examined, see Wheeler & Wheeler, 1967). *Millard Co.*: Valley in House Range, 2235 m, Apr 7, 2013 (JTLC); House Range at Notch Peak, 2230 m, Apr 7, 2013 (JTLC). *Piute Co.*: Tushar Mtns, 1.8 mi S Jct Rt 89 & FSR 125, Jul 21, 2009 (MCZC). *Uinta Co.*: 15 km NNE Vernal, 1720 m, Jul 15, 2013 (JTLC) (Figure 27C).

Etymology. The specific epithet, *lobognathus*, (Gr. *lobos* = lobed, and *gnathos* = jaw) presumably refers to the mandibles, which Andrews described as “large and stout, peculiarly lobed apically.”

Discussion. *Veromessor lobognathus* is broadly sympatric with several congeners including *V. smithi*, *V. lariversi*, and *V. pseudolariversi*. Workers of *Veromessor lobognathus* are separated from *V. smithi* based on: (1) propodeal spines longer, length greater than distance between their bases and length $\geq 1.0 \times \text{MOD}$, and (2) eyes smaller ($\text{MOD} = 0.31\text{--}0.41$, $\text{OI} = 20.5\text{--}25.0$). In *V. smithi*: (1) propodeal spines short, length less than distance between their bases and length $< 0.5 \times \text{MOD}$, and (2) eyes larger ($\text{MOD} = 0.38\text{--}0.49$, $\text{OI} = 24.8\text{--}33.5$).

Veromessor lobognathus is separated from workers of *V. lariversi* and *V. pseudolariversi* based on: (1) light to dark orangish-brown to reddish-brown head and mesosoma, (2) maximum basal width of scape greater than maximum preapical width, and (3) mandibles with 8 teeth. For both *V. lariversi* and *V. pseudolariversi*: (1) body concolorous light yellowish to yellowish-orange or yellowish-red, (2) maximum basal width of scape less than maximum preapical width, and (3) mandibles with 7 teeth.

A molecular phylogeny that used UCEs shows *V. lobognathus* and *V. smithi* are sister lineages (M.L. Borowiec, unpub. data).

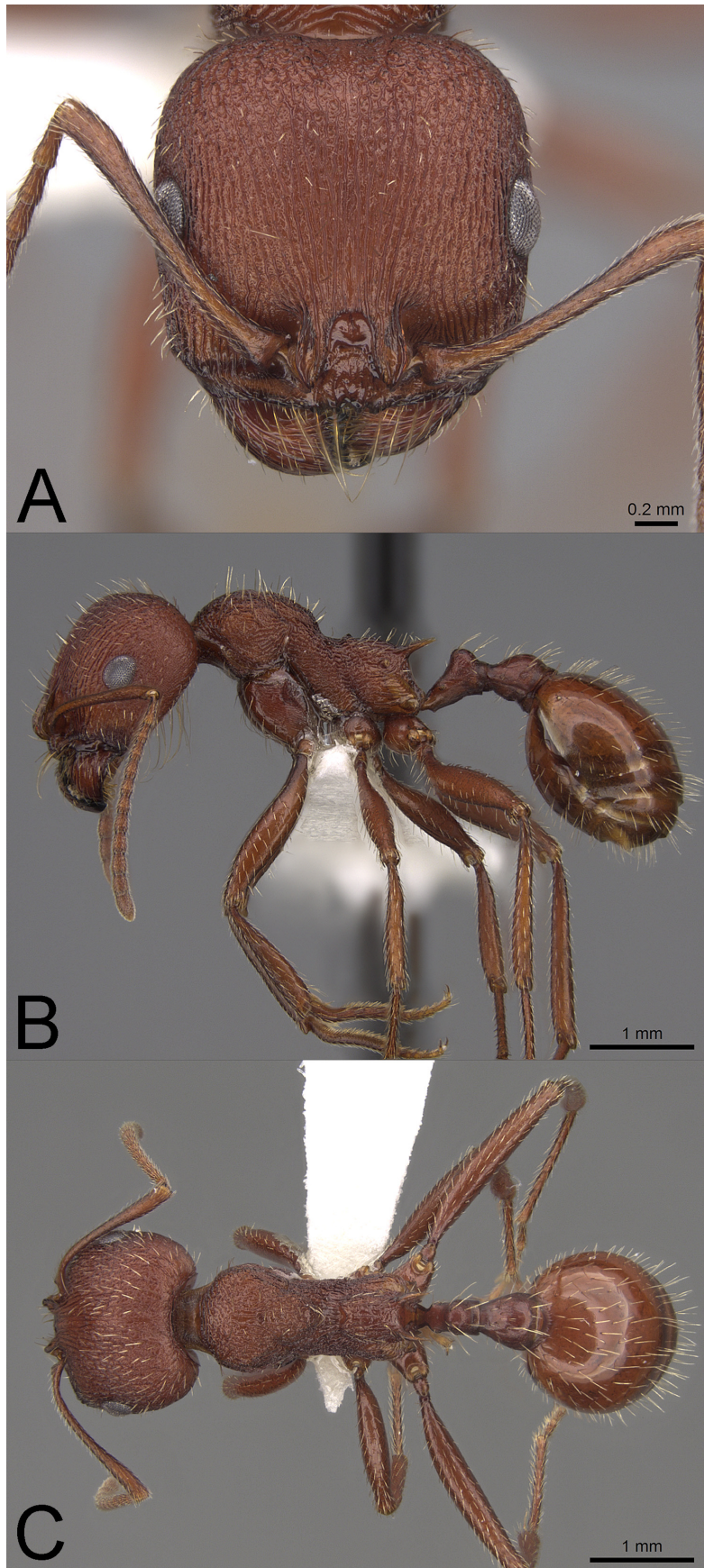


FIGURE 34. Photograph of *Veromessor lobognathus* worker: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (MCZ-ENT00736317). Photographs by Wade Lee from www.AntWeb.org.

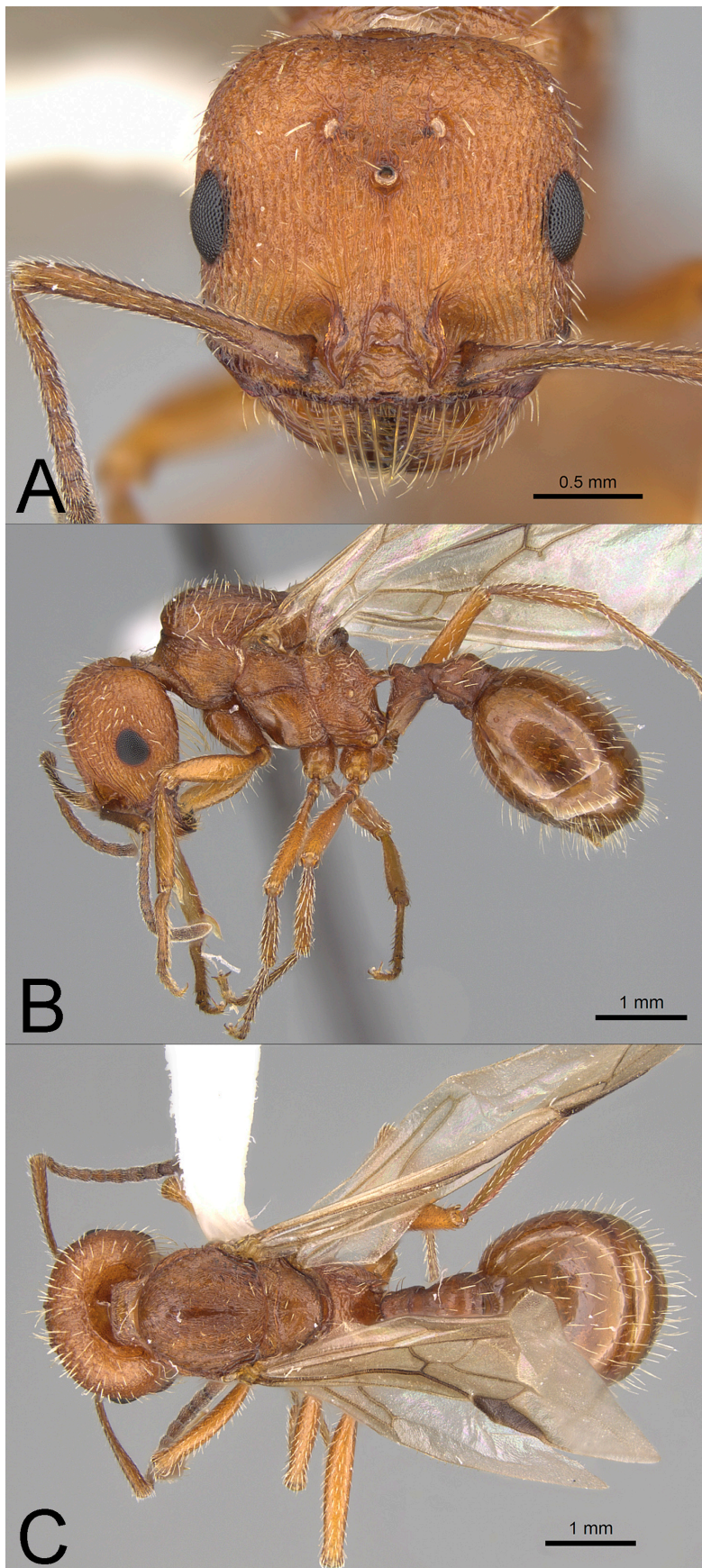


FIGURE 35. Photograph of *Veromessor lobognathus* alate queen: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0922832). Photographs by Michele Esposito from www.AntWeb.org.

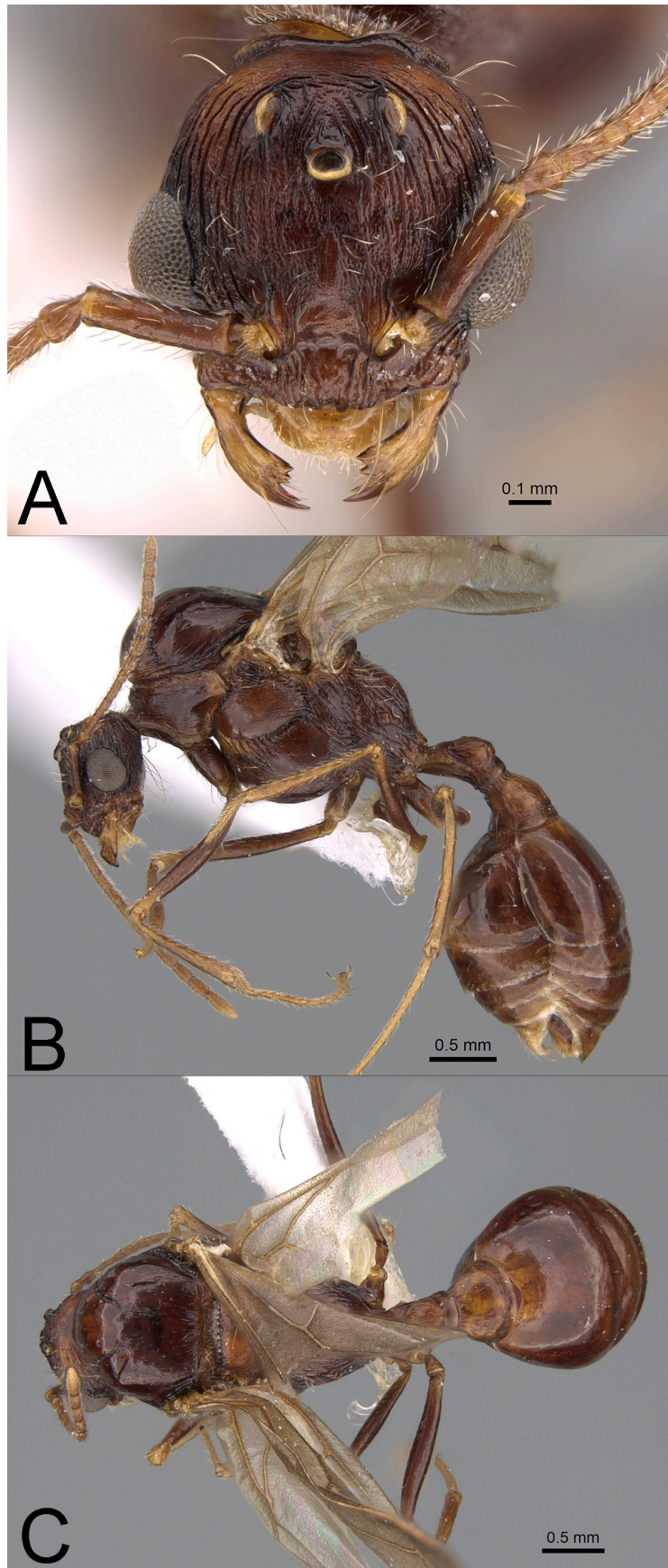


FIGURE 36. Photograph of *Veromessor lobognathus* male: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0922830). Photographs by Michele Esposito from www.AntWeb.org.

Biology. *Veromessor lobognathus* workers are solitary, diurnal foragers that suspend activity when soil temperatures become high (Cole, 1963; Wheeler & Wheeler, 1959). Workers also forage nocturnally (M. Bennett, pers. comm.), presumably when daytime temperatures are consistently high. Nests are usually placed under rocks or workers construct a small tumulus mound in areas where the soil contains numerous small stones (Clark & Blom, 2007; Cole, 1966; Wheeler & Wheeler, 1965). The largest of several excavated colonies contained 627 workers, numerous larvae, and numerous sexuals (55 alate queens, 149 males) (Cole, 1963; Wheeler & Wheeler, 1959), suggesting that colonies contain up to about 1000 workers. Number of reproductive queens in colonies of *V. lobognathus* is unknown, but two museum series contained two dealate queens (R.A. Johnson, pers. obs.), and Wheeler and Wheeler (1959) found 10 dealate queens in a nest. Additional nests should be excavated to determine if colonies contain multiple reproductive queens.

The chemistry of several glands has been examined in workers of *V. lobognathus*. The mandibular and venom glands lack volatile compounds, while the postpharyngeal gland contained linear and methyl-branched higher hydrocarbons, and the Dufour gland contained a mixture of hydrocarbons (do Nascimento, Jackson, Morgan, Clark, & Blom, 1993). Like other small-colony congeners, workers of *V. lobognathus* have a small pygidial gland reservoir and lack a textured tergal cuticle (Hölldobler *et al.*, 2013).

Mating flights have not been observed, but sexuals have been collected in nests from 24 June–2 August, suggesting that flights occur during summer (probably late June through July).

Veromessor lobognathus is a mostly mid-elevation species that occurs at 1,060–2,275 m, and it is generally found at higher elevations in western portions of its range (Wheeler & Wheeler, 1965). It appears to be most common in pinyon pine-juniper habitats similar to those occupied by *V. smithi*, but it also occurs in rockier foothill habitats, especially in eastern portions of its range. This species occurs in the Great Basin shrub steppe, Snake-Columbia shrub steppe, Colorado Plateau shrublands, Western short grasslands, and Northern short grasslands ecoregions, as defined by Olson *et al.* (2001). Incursions into the Mohave Desert are restricted to higher elevations, such as Rainier Mesa on the Nevada Test Site (Figure 27C).

Veromessor pergandei

(Figures 1G, 6E, 37–40)

Distribution—Figure 41A

Aphaenogaster pergandei Mayr, 1886: 448 (worker). Syntypes examined: 9 workers [USNM] #55467, UNITED STATES, California: no location, May 1884; Wheeler and Creighton, 1934: 376 (minor worker, queen, male); Wheeler & Wheeler, 1972: 240 (larvae); Wheeler & Wheeler, 1987: 303, figs. 1–6 (larvae). See also Wheeler and Creighton, 1934: 374, plate II, fig. 3. USNM worker here designated **LECTOTYPE** [USNMMENT00531691].

Stenamma (*Veromessor*) *pergandei* (Mayr); Emery, 1895: 307 (first combination in *Stenamma* [*Veromessor*]).

Novomessor pergandei (Mayr); Emery, 1915: 73 (first combination in *Novomessor*).

Messor (*Veromessor*) *pergandei* (Mayr); Forel, 1917: 235 (first combination in *Messor* [*Veromessor*]).

Veromessor pergandei (Mayr); Wheeler and Creighton, 1934: 374 (first combination in *Veromessor*).

Novomessor (*Veromessor*) *pergandei* (Mayr); Enzmann, 1947: 152 (first combination in *Novomessor* [*Veromessor*]).

Veromessor pergandei (Mayr); Creighton, 1950: 157 (revived combination in *Veromessor*).

Messor pergandei (Mayr); Bolton, 1982: 341 (revived combination in *Messor*).

Veromessor pergandei (Mayr); Ward, Brady, Fisher, and Schultz, 2015: 13 (revived combination in *Veromessor*).

Worker diagnosis. This species is uniquely characterized by the following combination of features: (1) concolorous dark brownish-black to black, (2) medial lobe of clypeus thick and protuberant in profile, elevated above lateral lobes in frontal view with a blunt medial tooth or projection along with several coarse, lateral, longitudinal rugae, (3) mandibles with 8 teeth, (4) dorsal base of scape weakly flattened, weakly widened; maximum basal width of scape much less than maximum preapical width, (5) MOD less than to greater than OMD; in profile, lower margin of eye narrowed and abruptly rounded to bluntly subangulate, $OI < 29.0$, (6) cephalic dorsum with fine, closely spaced, longitudinal rugae on medial area from clypeus to near posterior margin of eyes and below eyes, rest of head weakly to strongly coriarius, moderately shining; rugae on smaller workers usually more restricted to lacking, (7) psammophore well developed; ventral surface of head capsule with many long J-shaped hairs arranged in a distinct row around the outer margin of the ventral surface of head capsule, (8) mesosoma lacking rugae, moderately to strongly coriarius, weakly to moderately shining, (9) propodeal spines acuminate, not curved in profile, not curved

in dorsal view to weakly curved inward for workers with longer spines; length less than the distance between their bases; infraspinal facet and propodeal declivity moderately to strongly coriaceous, weakly to moderately shining, and (10) metasternal process small, more or less coniform, about as long as high, apex bluntly rounded (Figures 6E, 37–38).

Measurements. lectotype ($n = 62$). HL 1.77 (1.09–1.89); HW 1.72 (1.10–2.03); MOD 0.43 (0.27–0.49); OMD 0.42 (0.22–0.50); SL 1.38 (0.96–1.57); PNW 1.04 (0.61–1.22); HFL 1.59 (1.32–2.23); ML 2.07 (1.21–2.41); PW 0.31 (0.20–0.42); PPW 0.47 (0.28–0.67). Indices: SI 80.23 (72.45–94.59); CI 97.18 (83.62–111.69); OI 25.00 (20.00–28.46); HFI 92.44 (87.42–130.00).

Queen diagnosis. This caste is diagnosed by the following combination of features: (1) head and mesosoma blackish to black; gaster dark brown, (2) medial lobe of clypeus thick and protuberant in profile, elevated above lateral lobes in frontal view with a blunt medial tooth or projection along with several coarse, lateral, longitudinal rugae, (3) mandibles with 8 teeth, (4) dorsal base of scape weakly flattened and weakly widened; maximum basal width of scape much less than maximum preapical width, (5) MOD distinctly less than OMD, (6) cephalic dorsum with fine, closely spaced, longitudinal rugae that often fade or disappear near posterior margin; interrugae weakly to moderately coriaceous, weakly shining, (7) psammophore well developed, (8) sides of pronotum smooth and shining, often with fine, closely spaced longitudinal rugae along posterior margin; mesoscutum and mesoscutellum smooth and shining with scattered piligerous punctures, rarely with lateral longitudinal striae on mesoscutum; mesopleura moderately coriaceous, but often with fine rugae anterad on anepisternum and posterad on katapisternum, (9) propodeum with fine, longitudinal and oblique rugae, interrugae moderately punctulate, weakly shining; propodeal spines short, triangular, bluntly tipped; length much less than the distance between their bases; infraspinal facet and propodeal declivity smooth and shining to moderately to strongly coriaceous, weakly shining, and (10) metasternal process small, elongate-triangular, slightly higher than long, apex bluntly subangulate (Figure 39).

Measurements. ($n = 12$). HL 1.78–2.04; HW 1.86–2.30; MOD 0.48–0.60; OMD 0.34–0.48; SL 1.48–1.74; HFL 1.79–2.39; ML 3.32–4.01; PW 0.42–0.64; PPW 0.71–0.90. Indices: SI 66.37–83.33; CI 100.00–117.42; OI 23.77–30.73; HFI 87.44–117.19.

Male diagnosis. This caste is diagnosed by the following combination of features: (11) color blackish, (12) medial lobe of clypeus thickened and abruptly descendant along anterior margin; anterior margin evenly to abruptly concave medially, (13) preapical tooth small, mandibles with 1–3 small triangular denticles or teeth basad of preapical tooth, (14) anterior ocellus level with top of eyes, (15) mesopleura weakly shining, strongly coriaceous to strongly punctate, anepisternum with some very fine, longitudinal rugae or distinctly lineopunctate, (16) sides of propodeum strongly punctate-granulate between rugae; propodeal teeth absent or very short and obtuse; in profile, juncture of dorsum of propodeum and propodeal declivity rounded, (17) metasternal process longer than high, rounded in profile, and (18) subpetiolar process small and obtuse to large and triangular with apex rounded (Figures 1G, 40).

Measurements. ($n = 12$). HL 1.14–1.48; HW 1.23–1.46; MOD 0.50–0.59; OMD 0.19–0.24; SL 0.52–0.69; HFL 1.94–2.58; ML 2.84–3.90; PW 0.57–0.73; PPW 0.98–1.29; AOD 0.11–0.16; IOD 0.38–0.44; OOD 0.42–0.51. Indices: SI 39.69–51.15; CI 95.52–109.52; OI 36.99–44.35; HFI 135.66–193.13.

Additional material examined. MEXICO: Baja California: 2 mi W Laguna Salada, 200', Jan 9, 1993 (RAJC); 5.0 mi S Hwy 3 to Mike's Sky Ranch, 3600', Mar 17, 2003 (RAJC); San Fernando, Jul 31, 1938 (USNM); Calamajué (as Calamujuet), no date (USNM); San Julio, no date (USNM); Hwy 3 at 12.8 mi E [Colonia] Lazaro Cardenas, Feb 28, 1992 (RAJC); 18.55 mi SE [Colonia] Lazaro Cardenas, Feb 26, 1992 (RAJC); Hwy 3 at 1 mi SE [Colonia] Lazaro Cardenas, Feb 26, 1992 (RAJC); Hwy 3 at 2.7 mi NW [Colonia] Lazaro Cardenas, Feb 26, 1992 (RAJC); San Felipe, Aug 23, 1959 (UAIC); Valle San Felipe, 1360', Mar 4, 1998 (RAJC); 5.9 mi SE San Felipe at 1 mi W Punta Estrella, 100', Feb 26, 1992 (RAJC); 6 mi W Jct Hwys 3 & 5, Feb 26, 1992 (RAJC); 0.3 mi S La Puerta, Feb 23, 1993 (RAJC); 0.5 mi W Huerfanito, 50', Mar 9, 1992 (RAJC); Bahía de los Ángeles, 10', Jan 9, 1991 (LACM; RAJC); 11.5 mi S Bahía de los Ángeles, Mar 9, 1992 (RAJC); 24.4 mi SE Bahía de los Ángeles, 300', Mar 9, 1992 (RAJC); Hwy 1 at 11.65 mi W Bahía de los Ángeles, Mar 9, 1992 (RAJC); Hwy 1 at 18.15 mi W Bahía de los Ángeles, Mar 9, 1992 (RAJC); 19 km NW Bahía de los Ángeles, Jun 1, 1997 (UCDC); Hwy 1 at 7 km S Jct to Bahía de los Ángeles, Jan 6, 1991 (RAJC); Hwy 1 at 7 mi S Bahía de los Ángeles turnoff, Jan 6, 1991 (LACM; RAJC); 14 km ENE Jct Hwy 1 & rd to Bahía de los Ángeles, 480 m, Apr 6, 1998 (UCDC); 14.7 mi NW El Progreso, 960', Mar 10, 1992 (RAJC); 2.5 mi NE El Progreso, 960', Jan 29, 1995 (RAJC); 38.5 mi NW Catavina at 1 mi N El Progreso, Feb 10, 1993 (RAJC); 5.2 mi W Catavina, 1250', Feb 14, 1997 (RAJC); 30.9 mi S Puertocitos, 50', Feb 27, 1992

(RAJC); 41.7 mi S Puertocitos, 50', Feb 27, 1992 (RAJC); 5 mi W Playa San Rafael, Mar 9, 1992 (RAJC); 2.3 mi NW Las Arrastras, 1150', Feb 27, 1992 (RAJC); 6.5 mi N Las Arrastras de Arriola, 1000', Feb 19, 1994 (RAJC); 7.7 mi SE Las Arrastras, 1450', Feb 27, 1992 (RAJC); 8.5 mi N Rancho Arrastras, 820', Jan 25, 1995 (RAJC); 7 mi N Las Arrastras de Arriola, Jun 8, 1967 (LACM); E base Sierra San Pedro Martir at Trailhead to Canyon Diablo, 1260', Mar 4, 1998 (RAJC); Hwy 1 at 3.3 mi E Ejido Alfredo V. Bonfil, Feb 12, 1993 (RAJC); 6 mi NW Rancho Santa Ynez, 1800', Jan 10, 1976 (CIDA); 9 km NW Rancho Santa Ines, 550 m, Apr 12, 1997 (CIDA); Valle Montevideo at 18 km W Bahía de los Ángeles, 380 m, no date (CIDA); SW end of Isla de la Guarda, 60 m, Jul 30, 1996 (UCDC); Cañon de Guadalupe, 550 m, Mar 30, 2001 (UCDC); 27 km W Punta Arena at 19 km N San Borja, Apr 9–10, 1976 (UCDC). **Baja California Sur:** 1 mi W El Mesquital, Feb 16, 1993 (RAJC); 16 km E San Ignacio in Santa María Wash, Jan 9, 1991 (RAJC); 16 km SE San Ignacio, Jan 9, 1991 (LACM; RAJC); Hwy 1 at 15.1 mi E Guamúchil, Feb 29, 1992 (RAJC); Hwy 1 at 24.2 mi NW Santa Rosalía, 1450', Mar 13, 2002 (RAJC). **Sonora:** *Mpio. Caborca:* Río Asunción & Cerro Cañedo, 2.8 km (by air) ESE of Caborca, 305 m, Jan 17, 2016 (RAJC). *Mpio. Cucurpe:* Rancho Puerto Blanco at Cerro Proveedora, 8.2 km (by air) WSW Caborca, 260 m, Feb 14, 2010 (RAJC). *Mpio. General Plutarco Elías Calles:* 6.4 km (by air) SW Jct Hwys 2 & 8, 445 m, Mar 1, 2012 (RAJC); Sierra los Tanques at 5.3 km (by air) WSW Jct Hwys 2 & 8, 410 m, Feb 26, 2013 (RAJC); Sierra los Tanques at 6.8 km (by air) SW Jct Hwys 2 & 8, 415 m, Feb 27, 2013 (RAJC); 2.8 mi W Los Vidrios, 960', Mar 11, 1992 (RAJC). *Mpio. Hermosillo:* 6.5 km (by air) NNE center Hermosillo, 380 m, Dec 26, 2011 (RAJC); Hermosillo, Aug 12, 1959 (UAIC); SW Hermosillo nr Estadio de Sonora, 185 m, Feb 11, 2014 (RAJC); Arroyo el Chiltepín at 17 km NNE Hermosillo, 270 m, Mar 3, 2012 (RAJC); Siete Cerros at 8.6 km (by air) ENE Miguel Alemán, 90 m, Jan 19, 2016 (RAJC); Hwy 15 at 14 km N Hermosillo, 320 m, Oct 3, 2010 (RAJC); Cerrito de la Virgen at 5 km SSW Hermosillo, 285 m, Nov 10, 2010 (RAJC); Isla Tiburón at Bahía Sausal, 5 m, Dec 18, 1997 (UCDC). *Mpio. La Colorada:* 18.9 km (by air) S Cobachi, 425 m, Oct 18, 2011 (RAJC). *Mpio. Mazatán:* 2.3 km (by air) ESE Mazatán, 560 m, Jun 18, 2012 (RAJC). *Mpio. Puerto Peñasco:* Pinacate Reserve at Tecolote Campground, 215 m, Mar 4, 2012 (RAJC); Pinacate Reserve on Rd to Tecolote Campground at 49.5 km (by air) W Sonoyta, 210 m, Mar 4, 2012 (RAJC); Pinacate Reserve at Crater Elegante, 295 m, Mar 5, 2012 (RAJC); Pinacate Biosphere Reserve at Pápago Tanks, 210 m, Feb 24, 2013 (RAJC); Pinacate Biosphere Reserve at Cerro Lava, 235 m, Feb 25, 2013 (RAJC); Pinacate Reserve on rd to Visitor Center, S Sierra Blanca, 70 m, Mar 5, 2012 (RAJC); Pinacate Desert, no date, 1982 (LACM). *Mpio. Pitiquito:* Puerto Libertad, Jul 26, 1945 (USNM); 28.6 mi NE Puerto Libertad, 1570', May 29, 1994 (RAJC). *Mpio. Rayón:* 8.0 km (by air) SSE Rayón, 535 m, Feb 4, 2011 (RAJC); 11.5 mi S Seri Desemboque, 30', Nov 29, 1996 (RAJC). *Mpio. San Luis Río Colorado:* 36.6 km (by air) SE El Golfo de Santa Clara, 15 m, Feb 27, 2017 (RAJC). *Mpio. Trincheras:* El Boludo, no date (USNM). **UNITED STATES: Arizona:** *La Paz Co.:* 6 mi W Bouse, Mar 20, 1980 (UAIC); Vicksburg at 0.1 mi N Jct I-10, 1170', Apr 24, 2018 (RAJC); Ehrenberg, 260', Apr 24, 2018 (RAJC). *Maricopa Co.:* Arlington, Jun 16, 1919 (USNM); Tempe in Kyrene area, Mar 6, 1928 (UAIC; USNM); Tempe, May 1905 (UAIC); 4 mi SE Vulture Mine, 1960', Nov 8, 1993 (RAJC); I-10 at Salome Rd exit, 1230', May 18, 1993 & Sep 28, 2018 (RAJC); Salt River Recreation Area at Phon D Sutton, 1350', Jan 16, 1993 (RAJC); Chandler, Dec 25, 1936 (LACM); Phoenix, Mar 24, 1933 (USNM); North Scottsdale, Feb 27, 1986 (UCDC); Gila Bend, Nov 22, 1932 (UAIC); Gila Bend Mtns, Aug 8, 1917 (UAIC); Hwy 85 at 10.9 mi S Jct I-10, 920', May 3, 2018 (RAJC). *Mohave Co.:* Detrital Valley, 2040', Apr 28, 1993 (RAJC); 4 mi E Littlefield, 2000', Oct 9, 1976 (UAIC). *Pima Co.:* College Park, Tucson, Feb 13–Mar 23, 1933 (UAIC); Tucson, May 1905 & May 22, 1909 & Nov 22, 1910 & Dec 26, 1934 & Sep 19, 1935 & Mar 20, 1938 & no date (UAIC; USNM); 12 mi N Tucson, Mar 20, 1973 (LACM); Tucson Mtns (T13S, R11E, Sect 9), Aug 2, 1972 (CIDA). *Pinal Co.:* 25 mi S Phoenix, May 17, 1932 (USNM); McCartney Rd at 0.7 mi E I-10, 1430', Feb 21, 2001 (RAJC); 2.0 mi E Jct I-10 & McCartney Rd, 1430', Apr 29, 2005 (RAJC); 1.0 mi E Jct McCartney Rd & I-10, 1450', Feb 11, 1991 (RAJC); 1.0 km N Jct I-10 & McCartney Rd, 1470', Aug 26, 2014 (RAJC); 7 km E Casa Grande, Feb 11, 1991 (LACM; RAJC); 1.2 km NE Jct I-10 & McCartney Rd, 1440', Feb 15, 2018 (RAJC); Hwy 79 at 0.1 mi S Tom Mix Monument, 2360', Dec 4, 2005 (RAJC); 8.4 mi SW Picacho, 1550', Jul 6, 2012 (RAJC). *Yuma Co.:* Yuma (as Youma), no date (USNM); Yuma, May–Jun, 1958 (UAIC); 4 mi SE Yuma, Feb 28, 1960 (UCDC); Mohawk Dunes, May 11–16, 1996 & Jun 10–24, 1996 (UAIC); Mohawk Dunes at 9.7 mi E Tacna, 460', Mar 21, 2001 (RAJC); Topock, Apr 14, 1926 (UCDC); nr railroad at Dateland, 460', Dec 16–21, 2010 & Oct 3, 2018 (RAJC; UCDC); 1 mi NE Dateland, 460', Dec 18, 1992 (RAJC); 9 mi E San Luis, Feb 18, 1980 (UAIC); Yuma at Araby Rd at 0.2 mi N I-8, 190', Oct 3, 2018 (RAJC). *No county:* no loc, no date (USNM); Gila Desert, Apr 6, 1935 (LACM). **California:** *Fresno Co.:* 27 km SSE (202°) Mendota, 200 m, Mar 28, 2005 (UCDC); Jacalitos Canyon, Mar 25, 1967 (UCDC); Monvero Dunes

Research Nature Area, 300 m & 585 m, Mar 23, 2015 (MLBC; MMPC). *Imperial Co.*: 9.3 mi S Walter's Camp, Apr 10–11, 1998 (UCDC); Glamis Dunes, Dec 16, 1982 (UCDC); Glamis Dunes at 6 mi N Ogilby, Mar 19, 1980 (UAIC); Glamis, 300', Oct 3, 2018 (RAJC); Fort Yuma, Apr 29, 1909 (USNM); 8 mi E Calipatria, Nov 12, 1921 (USNM); Government Wells near Coyote Wells, 0', Jul 29, 1917 (USNM); Salton Sea, no date (USNM); Salton Sea, Mecca Beach Campground, -60 m, Apr 18, 2014 (MLBC); Coyote Wash, Mar 28, 1919 (USNM); Dixieland, Jul 24, 1917 (USNM); Coyote Mtns, Painted Gorge, Mar 12–13, 1994 (LACM); Ocotillo, 370', Apr 25, 2018 (NHMW; RAJC); 2.8 mi NNW Ocotillo, 300', Feb 28, 1999 (LACM); 6.9 mi SSE Ocotillo, 320', Feb 28, 1999 (LACM); Algodones Dunes, Ogilby Rd at 0.6 km S I-8, 62 m, Mar 11, 2009 (UCDC); Algodones Dunes, 90 m, Sept 11–15, 2007 & Apr 28–May 2, 2008 (UCDC); no loc, no date, 1911 (USNM). *Inyo Co.*: Ballarat, Mar 27, 1961 (UCDC); 6 mi W Ballarat, Apr 5, 1931 (USNM); Racetrack, Death Valley National Monument, 3700', Mar 26, 1969 & Mar 1, 1970 (UAIC); Ubehebe Crater, Death Valley National Monument, Mar 19, 1931 (USNM); Death Valley National Monument, Jul 2, 1944 (USNM); Grapevine Ranger Station, Death Valley National Monument, 2300', Oct 30–Nov 27, 1968 & Mar 12, 1969 & Jun 7–21, 1973 (RAJC; UAIC); 6 km N Badwater, Death Valley National Park, 200 m, Mar 26, 1998 (UCDC); 5 km N Ashford Mill, Death Valley National Park, 60 m, Mar 26, 1998 (UCDC); Cottonwood Canyon, Death Valley National Park, 250 m, Mar 27, 1998 (UCDC); 12.5 km SE Stovepipe Wells, -15 m, Dec 27, 2012 (MMPC); Death Valley (no loc), Oct 20, 1938 & Apr 16, 1976 (LACM; UCDC); Hanaupah Canyon Rd, 330 m, Mar 26, 1998 (UCDC); Hwy 168 at 1 mi E Big Pine, 1200', Jul 22, 1992 (RAJC); 2.2 mi SW Independence, 4620', May 24, 2008 (RAJC); Saline Valley Dunes at 30 km E Independence, May 26, 1993 (UCDC); Furnace Creek, Jan 11, 1981 (UCDC); 5.5 km WNW Furnace Creek, -80 m, Dec 24, 2012 (MMPC); Grapevine Mtns, Titus Canyon, Feb 12, 1967 (LACM); 1 mi W Jct Hwy 395 & Road J41, 3000', Feb 16, 1985 (UCDC). *Kern Co.*: Boron, Jul 19, 1988 (UCDC); Edwards, Jul 20, 1988, UCDC; Mohave, Nov 11, 1914 & May 1, 1952 & no date, 1976 (UCDC; USNM); Bakersfield, Apr 3–6, 1938 (LACM; USNM); Ricardo, Nov 8, 1929 (USNM); Inyokern, Mar 21, 1931 (USNM); 2 km ESE Ricardo, Red Rock Canyon State Park, 740 m, 16 Mar 2003 (UCDC); Hwy 223 at 4 mi E Arvin, Jun 12, 1971 (LACM); Tehachapi, Jul 18, 1931 (LACM); Sand Canyon at 3 mi W Brown, Mar 30, 1963, (UCDC); Red Rock Canyon State Park, 800 m, Mar 18, 2003 (UCDC); China Lake, Jul 21, 1988 (UCDC). *Kings Co.*: Kettleman, Jun 30, 1988 (UCDC); 4 mi S Kettleman Canyon, Nov 17, 1959 (LACM). *Los Angeles Co.*: Claremont, no date & Dec 8, 1910 & Apr 1921 (UAIC; UCDC; USNM); Acton at 12 mi S Palmdale, 2720', May 3, 2001 (UCDC); Los Angeles, no date (USNM); Glendale, May 16, 1941 (UCDC); no loc, no date (USNM). *Orange Co.*: Corona del Mar, Apr 1, 1932 (USNM). *Riverside Co.*: Palm Canyon, Jun 22, 1931 & no date, 1956 (USNM); 1000 Palms Canyon, Mar 4, 1940 (LACM); Elsinore, Jan 4, 1919 (USNM); San Jacinto, no date (USNM); Palm Springs, Mar 23–25, 1918 & Apr 15, 1930 & Aug 24, 1944 (UAIC; USNM); SE of Palm Springs, Dec 1, 1930 (USNM); Coachella Valley at Garnet, no date (USNM); Painted Canyon, Mar 8, 1930 (USNM); Whitewater, Apr 13, 1963 (LACM); Whitewater Canyon at 0.6 mi N I-10, 1470', Apr 25, 2018 (RAJC); Banning, Apr 19, 1924 (LACM); 3 mi NW Desert Hot Springs, Apr 11, 1952 (LACM); Mule Mtns at Coon Hollow, 525', Feb 1, 1967 (LACM); San Jacinto Creek, Apr 7, 1939 (LACM); Magnesia Canyon, Jul 20, 1952 (UCDC); Perris, no date & Jul 11, 1988 (UAIC; UCDC; USNM); Temecula (MWD land), 379 m, Jul 11, 1997 (UCDC); 12 mi S Thermal, Jul 21, 1967 (UCDC); Deep Canyon, Dec 4, 1967 & Apr 18–Jul 24, 1969 & Dec 7, 1970 & no date (UAIC); W rim Deep Canyon, 2000' & 2500', May 8, 1969 & May 7, 1979 (UAIC); Black Hill (T6S, R6E, Sect 19), 3000', Mar 9, 1970 (UAIC); Chiriaco Summit, Apr 25, 1986 (UAIC); Dos Palmas Spring (T6S, R5E, Sect 26), Apr 29, 1969 (UAIC); 15.5 km NE Temecula, 470 m, May 3, 2016 (MMPC); 9 km S Desert Center, 690 m, Apr 17, 2014 (MLBC; MMPC); Salton Sea at Mecca Beach Campground, -60 m, Apr 18, 2014 (MLBC); no loc, May 3, 1951 & no date (UAIC); no loc, Apr 4, 1942 (LACM). *San Bernardino Co.*: 50 km NNW Baker, Jan 12, 1981 (UCDC); Fenner, Mar 9, 1919 & Jun 18, 1931 (LACM; USNM); Hesperia, Nov 18, 1928 (USNM); Barstow, Apr 6, 1930 (USNM); Morongo Valley, Mar 29, 1952 (UCDC; USNM); Morongo Valley, Dry Morongo Canyon, Apr 7, 1963 & Jul 10, 1963 (LACM; UAIC); Soda Spring, May 8, 1991 & Feb 1992 (CIDA; LACM); Yermo, Apr 24, 1952 (LACM); Joshua Tree National Monument, 3000', Apr 26, 1952 (LACM); Joshua Tree, 3000', Apr 26, 1952 (LACM); Yucca Valley, Jun 29, 1934 (LACM); Hwy 372 at 4.5 mi NNE Landers turnoff, 3390', Sep 30, 2018 (RAJC); Needles, May 1905 & Jul 8, 1931 (LACM; UAIC); 2 mi N Iron Mtn, Feb 6, 1984 (LACM); Kelso Sand Dunes, Mar 27, 1973 (LACM); Kelbacker Rd at 2 mi S Kelso, 2158', Apr 18, 2000 (UCDC); Loma Linda, no date (UAIC); Hwy 247 at Barstow (near Mohave National Reserve Hdqtrs), 2470' Apr 25, 2018 (RAJC); Hwy 95 at 6.6 mi S Needles, 900', May 3, 2018 (RAJC); no loc, no date (LACM; USNM). *San Diego Co.*: Pinyon Ridge, no date, 1931 (USNM); Culp Valley Rd at 0.5 mi W Hwy 22, 3080', Apr 1, 1997 (RAJC); Culp Valley campground, 1015 m, Jan 1, 2014 (MLBC);

Sentenac Canyon, 2400', Apr 23, 1952 (LACM); Jacumba, May 30, 1940 (LACM); Moosa Canyon, Apr 20, 1892 (USNM); 16 km S Ocotillo Wells, 180 m, Feb 28, 1988 (UCDC); 14 km SSW Borrego Springs, 620 m, Feb 26, 1988 (UCDC); Anza Borrego State Park at Yaqui Well, Mar 22, 1978 (UAIC); Borrego Springs, 620' & 195 m, Jul 31, 2003 & Dec 31, 2013 & Apr 25, 2018 (MLBC; RAJC); Lakeside, Dec 22, 1910 (UAIC). *San Luis Obispo Co.*: Carrizo, Mar 1939 (LACM). *No county*: Mohave Desert, Jul 1931 & no loc, no date (LACM; UAIC; USNM); Death Valley, Mar 4, 1941 (UCDC); Cala (=California), no date (LACM; USNM); Colorado Desert, Aug 11, 1917 (UAIC); Mohave Desert, Bar S Ranch, Nov 18, 1928 (USNM); Panamint Valley, Mar 24, 1930 (USNM). *Nevada*: *Clark Co.*: Mesquite, 1600', Apr 2, 1970 (RAJC); Boulder City, 2500', May 24, 1975 & Jun 27, 1977 & no date (LACM; UAIC); 4 mi SE Henderson, 2200', Apr 20, 1971 (LACM); 2 mi SSE Riverside, 2200', Apr 4, 1971 (LACM); 17 mi E Searchlight, Nov 24, 1969 (LACM); T26S, R65E, Nov 24, 1969 (LACM); Newberry Mtns, no date, 1954 (LACM). *Esmeralda Co.*: Hwy 72 (= Hwy 267?) at State Line, 4000', Oct 31, 1967 (LACM). *Nye Co.*: Amargosa Desert near Beatty, Mar 8, 1931 (USNM); Amargosa River at 14 mi SSE Beatty, 2700', Mar 26, 1972 (RAJC); 9 mi SSW Beatty, 3000', Apr 15, 1970 (LACM); Devil's Hole, 2600', May 5, 1968 (LACM); Rock Valley near Mercury, Apr 21, 1971 (LACM); Lathrop Wells, 2300', Apr 14, 1964 (LACM); Mercury, May 26, 1960 & Jul 1, 1961 (LACM; USNM); Ash Meadows, Mar 24, 1996 (UCDC). **Locations that could not be geolocated. UNITED STATES: Arizona: Pima Co.**: Catalina Mtns at South Fenner Canyon, 3000', Mar 9, 1919 (UAIC). **Questionable locales (outside of geographic range): UNITED STATES: Arizona: Santa Cruz Co.**: Mt. Wrightson, 7000–8000' Oct 22, 1960 (UAIC). **California: Mariposa Co.**: Big Tree, Jan 1940 (UCDC). **Santa Clara Co.**: Palo Alto, no date (USNM). **Florida: Charlotte Co.**: Punta Gordo, Feb 2, 1919 (USNM) (Figure 41A).

Etymology. The specific epithet, *pergandei*, was derived from the type series being obtained from Theodore Pergande, an early American entomologist of German descent.

Discussion. *Veromessor pergandei* is sympatric with the congeners *V. andrei*, *V. julianus*, and *V. stoddardi*. However, workers of *V. pergandei* are easily separated from these species based on: (1) well developed psammophore, (2) blunt toothlike projection on medial lobe of clypeus, (3) mostly concolorous dark brownish-black to black, and (4) lack of rugae on mesosoma and the cephalic dorsum posterior to eyes. In *V. andrei* and *V. stoddardi*: (1) psammophore poorly developed, (2) blunt toothlike projection lacking on medial lobe of clypeus, (3) coloration mostly orangish to reddish or reddish-brown (though *V. andrei* sometimes can be dark brownish-black to black), and (4) weak to coarse rugae on mesosoma and cephalic dorsum posterior to eyes. *Veromessor pergandei* is distinguished from *V. julianus* by: (1) propodeal spines short, length less than the distance between their bases, (2) dorsum of pronotum coriarius, lacking rugae, (3) mesopleura mostly coriarius, lacking rugae, (4) blunt toothlike projection on medial lobe of clypeus, and (5) in profile, eye narrowed below with a distinct ventral angle. In *V. julianus*: (1) propodeal spines long, length > 2.0× the distance between their bases, (2) dorsum of pronotum with irregular transverse rugae, (3) mesopleura with longitudinal rugae or lineogranulate, (4) blunt toothlike projection lacking on medial lobe of clypeus, and (5) in profile, eye rounded below. *Veromessor pergandei* is recognized in the field based on their large colonies (> 35,000 workers) of blackish to black workers that forage in long columns (Rissing, 1988; Tevis, 1958; Went, Wheeler, & Wheeler, 1972).

A molecular phylogeny that used UCEs shows *V. pergandei* is sister to the clade containing *V. lariversi* and *V. pseudolariversi* (M.L. Borowiec, unpub. data).

Biology. *Veromessor pergandei* is the best studied species in the genus. Nests are usually in sandy soils and consist of one entrance (occasionally more than one, especially during mating flights) with a circular gravel mound up to 50 cm in diameter; nests extend to a depth of 3–4 m or more with a distinctly angled shaft (Johnson, 1992; Tevis, 1958; Tschinkel, 2015; Wheeler & Creighton, 1934). Workers are weakly polymorphic (Gordon, 1978; Rissing, 1987).

Colonies contain tens of thousands of workers; Went *et al.* (1972) estimated > 35,000 workers in one foraging column, suggesting colonies contain several times that number of workers. Colonies forage most days of the year, but forager number decreases drastically during winter months. Foraging time varies seasonally according to temperature: colonies forage diurnally when days are cool, and they become crepuscular-matinal as temperatures increase. Colonies sometimes forage nocturnally when nights are warm (Snelling & George, 1979; Tevis, 1958; Went *et al.*, 1972; Wheeler & Rissing, 1975b), but colonies appear to be strictly diurnal in eastern portions of their range (R.A. Johnson, pers. obs.).

Workers forage in a well-defined, pheromone-based column that is up to 40 m long, with workers fanning out to forage individually at the distal end of the column; colonies sometimes have two or three foraging columns (Plowes,

Colella, *et al.*, 2014; Ryti & Case, 1986; Went *et al.*, 1972; Wheeler & Rissing, 1975b; Wheeler & Creighton, 1934). Pheromones are the primary mechanism for workers orienting in foraging columns, but workers also respond to sun position and experimental shifts in polarized light, and they display backtracking when displaced from foraging columns. Workers also use path integration in both the foraging column and in the fan (Freas, Congdon, Plowes, & Spetch, 2019, 2020; Freas, Plowes, & Spetch, 2019; Plowes *et al.*, 2019; Plowes, Ramsch, Middendorf, & Hölldobler, 2014).

Foraging columns rotate around the nest such that colonies visit the entire area surrounding their nests, suggesting that columns function for both food acquisition and territorial interactions (Rissing, 1988). Scouts are not used to assess foraging column direction (Went *et al.*, 1972; Wheeler & Rissing, 1975b), but rather direction of the daily foraging column is determined by chemicals secreted from the pygidial gland (see below and Hölldobler *et al.*, 2013). In the laboratory, workers can detect recruitment pheromones of previous foraging columns for 7–10 days (B. Hölldobler, pers. comm.), suggesting a mechanism for colonies to adjust day to day direction of the foraging column. Secretions from the pygidial gland (primarily n-tridecane) appear to initiate the foraging column (Hölldobler *et al.*, 2013), while a trail pheromone (primarily 1-phenylethanol) released from the poison gland maintains recruitment to the foraging fan (Plowes, Colella, *et al.*, 2014). The recruitment effect from the poison gland is enhanced when adding pygidial gland secretions (Plowes, Colella, *et al.*, 2014). Benzaldehyde was also a major compound in their pygidial gland secretions, but this chemical was not detected in mandibular gland secretions, as suggested by Blum, Padovani, Curley, and Hawk (1969). Like other large-colony congeners, workers of *V. pergandei* have a large pygidial gland reservoir with a textured tergal cuticle (Hölldobler *et al.*, 2013).

Colonies of *V. pergandei* also assess and respond to natural seed density because day to day change in foraging column direction is higher in years with low compared to high seed density (Johnson, 1989). Similarly, when novel seeds are presented in an experimental patch, foragers sample fewer seeds before harvesting one in years with low seed density compared to years with high seed density (Johnson, 1991). However, foraging column length does not change with seed density (Rissing, 1988; Rissing & Wheeler, 1976). Fighting occurs between foraging columns that encounter one another, resulting in “black piles of dead ants” (Wheeler & Rissing, 1975b), but more often columns avoid foraging toward nearest neighbors (Ryti & Case, 1986, 1988a).

That workers of *V. pergandei* are weakly polymorphic has been used to test foraging efficiency based on the idea of “size matching” between worker body size and food item size. These studies show that the correlation of body size and seed size varies among colonies, and even when size correlations are significant, they often account for < 5% of the variance (Davidson, 1978; Gordon, 1978; Rissing, 1981; Rissing & Pollock, 1984; Waser, 1998).

Worker size variation was also found to be inversely correlated with number of potentially competing seed-harvester ant species over an approximately 650 km longitudinal cline (Davidson, 1978). This geographic pattern of size variation was suggested to be an adaptive response to the local competitive environment because colonies could exploit a broader range of seed resources (sizes) in locales with fewer competitors, while diets narrowed in areas with more competitors. Two lines of evidence lend doubt to this interpretation. First, the correlation between worker body size and food item size (i.e., size matching) varies among colonies, and even when correlations are significant, they often account for < 5% of the variance (Davidson, 1978; Gordon, 1978; Rissing, 1981; Rissing & Pollock, 1984; Waser, 1998). Second, worker size and amount of worker size variation changed seasonally at two widespread locales (Gordon, 1978; Rissing & Pollock, 1984), and at both sites, amount of intracolony variation within a year was similar to the total amount of geographic variation found by Davidson (1978). This suggests that site differences noted by Davidson were related to variations in timing of the cycle rather than to the local competitive environment. Additionally, variation in timing of the body size cycle appeared to occur across sites in southern California, as observed during informal surveys during April–May 2018. These surveys indicated that colonies in low desert habitats contained small workers, while those in high desert habitats contained larger workers (R.A. Johnson, pers. obs.). In combination, these data indicate that seasonal variation in worker size is a species-specific trait in *V. pergandei*, but the underlying mechanism causing this variation is unknown.

Two additional studies have examined worker polymorphism in *V. pergandei*. One study examined nest architecture, finding that groups of polymorphic workers constructed nests that were longer with a more complex architecture than groups of single-sized workers (Kwapich, Valentini, & Hölldobler, 2018). The other study examined the interaction between predatory spiders (*Steatoda* spp. and *Asagena* spp.) and *V. pergandei* workers. Workers of *V. pergandei* become ensnared in the spider webs, and presence of an ensnared nestmate increased the probability of web removal and nestmate retrieval. Web removal was accomplished by larger-bodied workers (Kwapich & Hölldobler, 2019).

Foragers of *V. pergandei* learn several components related to handling and search efficiency of seeds (Johnson, 1991). In an experimental patch of novel seeds, workers initially handled then dropped multiple novel seeds before harvesting one, apparently to learn seed characters such as mass and shape. Number of seeds handled before one was harvested decreased over time, but workers still harvested heavier than average seeds because they handled but rejected lightweight seeds. Handling time per seed and trip time (travel time to and from the nest and time inside the nest) decreased for individuals within one foraging period. In terms of memory, tactile-associated behaviors, such as handling time per seed and number of seeds handled, were lost quickly compared to olfactory-associated behaviors such as seed recognition and acceptance (Johnson, 1991). Rate of learning to recognize a novel seed species was negatively associated with measures of seed species diversity (Johnson, Rissing, & Killeen, 1994). Workers also assess distance from the nest given that more seeds are handled before one is harvested when the experimental seed patch is farther from the nest while still harvesting seeds that are heavier than the average of those offered in the patch (Rissing & Pollock, 1984). That workers specialize on harvesting particular seed species may result from learning to identify and handle acceptable seeds (Rissing, 1981).

Alate production is influenced by intraspecific competition and precipitation. Food-supplemented and neighbor-removed colonies produced more sexuals than control colonies (Ryti & Case, 1988a). Affect of food supplementation on production of sexuals was further examined in another field experiment in which food was supplemented early (when queens were laying reproductive eggs) or late (after queens presumably stopped laying reproductive destined eggs), along with a worker removal treatment and a control treatment. Early fed colonies produced more alates and a more strongly female-biased sex ratio than other treatments, while worker removal treatments produced the fewest alates and least female-biased sex ratios. Late fed colonies produced sexuals with the heaviest wet masses (males and females) and dry masses (only males) (Ode & Rissing, 2002). Number of sexuals produced and flight activity also decreased in very dry years (Cahan, 2001b).

Mating flights occur from mid-February through early April and usually occur over up to several weeks, with few sexuals released on a given day. Mating flights occur during mid-morning on sunny days with little wind (Creighton, 1953; Johnson, 2000a; Pollock & Rissing, 1985). Mating occurs in the air (S.W. Rissing, pers. comm; R.A. Johnson, pers. obs.).

Queens of *V. pergandei* mate with multiple males (Kwapich, Gadau, & Hölldobler, 2017; Ode & Rissing, 2002). Patriline number ranged from one to seven (mean = 3.80, $n = 9$ colonies) with an effective mating frequency (M_e) of 2.56 (Kwapich *et al.*, 2017). The most productive colonies had significantly fewer patrilines, a larger peak forager population, and a larger annual foraging range (Kwapich *et al.*, 2017). Dry mass of alate queens averages 20.5 ± 0.3 mg. Alate queens contain an average of 71.6 ± 3.6 ($n = 5$) ovarioles, and mated queens contain an average of 2.90 ± 0.17 ($n = 4$) million sperm. Dry mass for virgin males averages 5.7 ± 0.2 mg, and they contain an average of 26.9 ± 1.39 ($n = 5$) million sperm (R.A. Johnson, unpublished data). Queens of *V. pergandei* have a lower tolerance to high temperatures than do most other desert ants with most queens dying at 42°C and all dying at 43°C over 2 h (Johnson, 2000a).

Queen founding behavior varies across the geographic range: single queens (haplometrosis) initiate nests in western portions of the range, that is, southwestern Arizona and southern California, whereas multiple, unrelated queens (pleometrosis) initiate nests in eastern and northwestern portions of the range, that is central and western Arizona, southeastern California, and southern Nevada (Hagen, Smith, & Rissing, 1988; Helms Cahan & Helms, 2012; Johnson, 2000a; Pollock & Rissing, 1985; Rissing, Johnson, & Martin, 2000; Ryti, 1988). Pleometrotic queens cooperate to produce the first brood of workers, with worker production being a linear function of queen number (Rissing & Pollock, 1986, 1991). Additional variation occurs in pleometrotic parts of the range because colonies reduce to one queen in eastern areas, whereas multiple queens persist in mature colonies (primary polygyny) in northwestern portions of the range (Helms & Helms Cahan, 2012; Rissing & Pollock, 1986; 1987). Worker aggression and elimination of queens were correlated with region of origin. In areas of queen reduction, queens were as likely to be killed by workers as by other queens (Helms, Newman, & Helms Cahan, 2013). In southeastern California, the shift from haplometrosis to pleometrosis occurs across a narrow transition zone with the shift to pleometrosis correlating with reduced precipitation, decreased vegetative biomass, and lower colony density (Cahan, 2001a, 2001b; Cahan, Helms, & Rissing, 1998). Queen mass varies across the three reproductive strategies: queens in haplometrotic areas are heaviest, those in areas of pleometrosis with queen reduction (secondary monogyny) are intermediate in mass, and those in areas of primary polygyny are lightest (Helms Cahan & Helms, 2014). Variation in these queen founding strategies correlated with brain monoamine content. Serotonin levels were significantly

higher in life stages where queens displayed aggression, suggesting the serotonin modulates aggression in queens of *V. pergandei* (Muscedere *et al.*, 2016). Regions with alternate queen social forms currently meet in contact zones where gene flow and selection on alternate social forms should occur. Two types of genetic data infer that these three reproductive strategies/zones represent intraspecific behavioral variation rather than the existence of cryptic species. Microsatellite data indicated significant genetic differentiation across the sites, but differentiation across the three reproductive zones did not correspond to the spatial pattern of genetic structure among sites (Helms & Helms Cahan, 2012). A molecular phylogeny based on UCEs gave similar results, showing that colonies in the three reproductive zones did not segregate into separate clades (M.L. Borowiec, unpub. data).

Pleometrotic colony founding has been studied in eastern portions of their geographic range (southcentral Arizona). These pleometrotic queens are unrelated, they coexist without dominance, and they appear to actively prefer associations because single queens more readily abandon nests to join associations than do queens already in groups (Hagen *et al.*, 1988; Helms Cahan & Helms, 2012; Krebs & Rissing, 1991; Rissing & Pollock, 1986). All queens lay a similar number of eggs, and the first workers emerge earlier and more workers are produced (number is a linear function of queen number) by pleometrotic compared to haplometrotic queens (Rissing & Pollock, 1991). After the first workers emerge, queens become aggressive, and colonies reduce to one queen. Laboratory colonies brood raid adjacent colonies and those with pleometrotic queens are more successful than haplometrotic colonies (Rissing & Pollock, 1987). This advantage resulted from the additional workers produced by pleometrotic queens because brood raiding success increased for haplometrotic colonies that were worker-supplemented (Rissing & Pollock, 1991). Brood raiding between incipient colonies and mature colonies killing incipient colonies also occurs in the field (Pfennig, 1995; Raczkowski, 2003; R.A. Johnson, pers. obs.). Field experiments to test the benefits of pleometrosis have had variable results. In one study, experimental haplometrotic and pleometrotic colonies survived to the first worker stage at a similar rate and had a similar longevity (Pfennig, 1995), while pleometrotic colonies emerged at a higher rate and outlived haplometrotic colonies in another study at the same site (Raczkowski, 2003). Surviving colonies then enter their growth phase and probably start producing reproductive sexuals after 3–4 years; colonies likely live 10–20+ years (Tevis, 1958; Wheeler & Rissing, 1975a).

Rainfall is critical for recruitment of *V. pergandei* colonies in central Arizona where queens found nests cooperatively. In a laboratory experiment, survival, condition, and brood condition increased with water level for single queens. In a two-way experiment with queen number and water level as main effects, queen survival was positively influenced by both water level and queen number. Water level also was a significant effect for three measures of queen condition in the latter experiment, but queen number was not significant for any of these measures, suggesting that enhanced worker production is the primary advantage of pleometrosis. A discriminant analysis using recruitment and rainfall data over 20 years for a site in central Arizona, USA, documented that recruitment occurred only in years in which rainfall for both January–March and April–June (the critical period for nest founding and survival of incipient nests) exceeded the long-term mean amount of rainfall. This discriminant analysis also predicted that no recruitment occurred when long-term mean rainfall for January–March and April–June at the site were included as ungrouped periods. This suggests that pleometrosis in *V. pergandei* evolved to enhance colony survival in areas with harsh abiotic (desiccating) conditions, facilitating colonization of habitats in which solitary queens could not establish even in wet years (Johnson, 2021).

Mature colonies of *V. pergandei* are overdispersed (Ryti & Case, 1984, 1986), but foundress queens have a clumped dispersion (Pfennig, 1995; Ryti & Case, 1988b). In one study, new foundress nests were usually associated with mature colonies (Pfennig, 1995), while new foundress nests were farther than expected from mature conspecific nests in another study (Ryti & Case, 1988b). Moreover, foundress queens prefer to initiate nests in open, exposed sites (Rissing & Pollock, 1989; R.A. Johnson, pers. obs.), such that these queens more likely choose microsites *per se* rather than locations based on presence or absence of mature colonies. Ryti and Case (1988b) continued monitoring these foundress nests finding that they were randomly dispersed after three months (when the first minors emerged) due to mortality caused by such as raids by adjacent foundress nests and mature colonies (see above).

Colonies of *V. pergandei* relocate their nest up to 10 times per year, with the surface extent of active and abandoned nests extending 10–15 m in diameter (Tevis, 1958). Nothing is known about causes of nest relocation in *V. pergandei*.

Veromessor pergandei also affect the distribution and abundance of plants. Nest mounds/refuse piles of *V. pergandei* colonies contained more plant species than adjacent control plots, and plants on mounds/refuse piles produced more, and sometimes heavier, seeds than plants in adjacent control plots (Rissing, 1986).

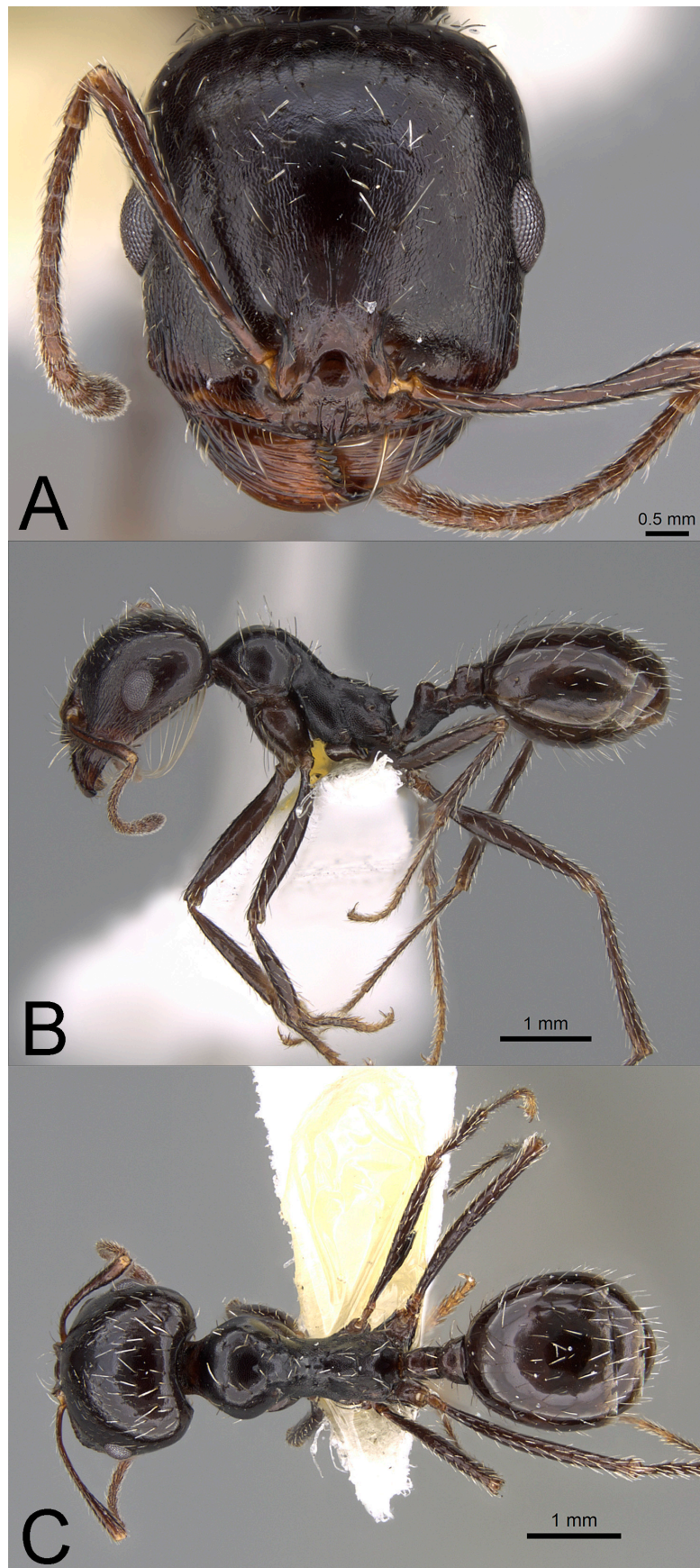


FIGURE 37. Photograph of *Veromessor pergandei* minor worker: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0922827). Photographs by Michele Esposito from www.AntWeb.org.

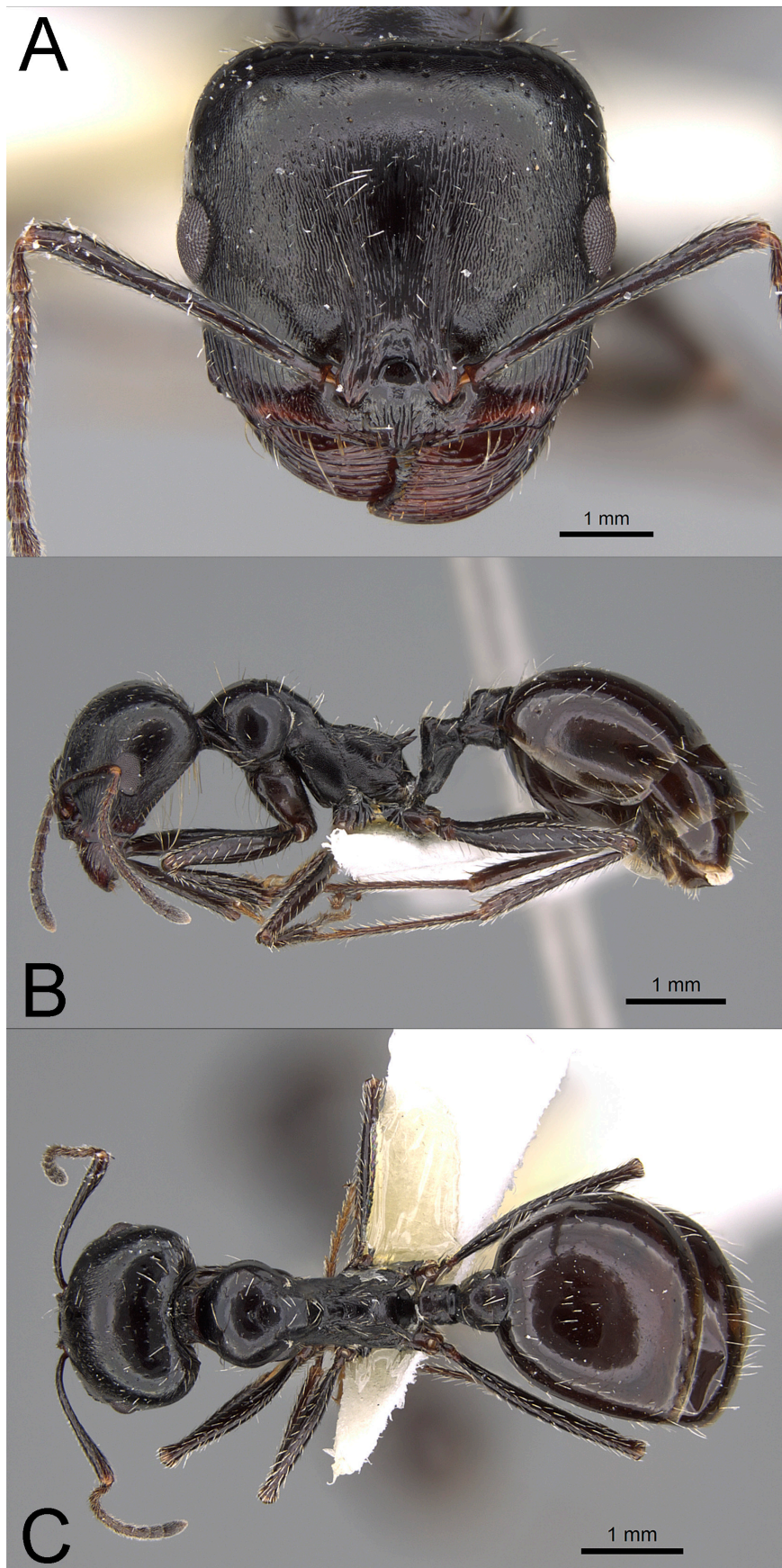


FIGURE 38. Photograph of *Veromessor pergandei* major worker: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0922826). Photographs by Michele Esposito from www.AntWeb.org.

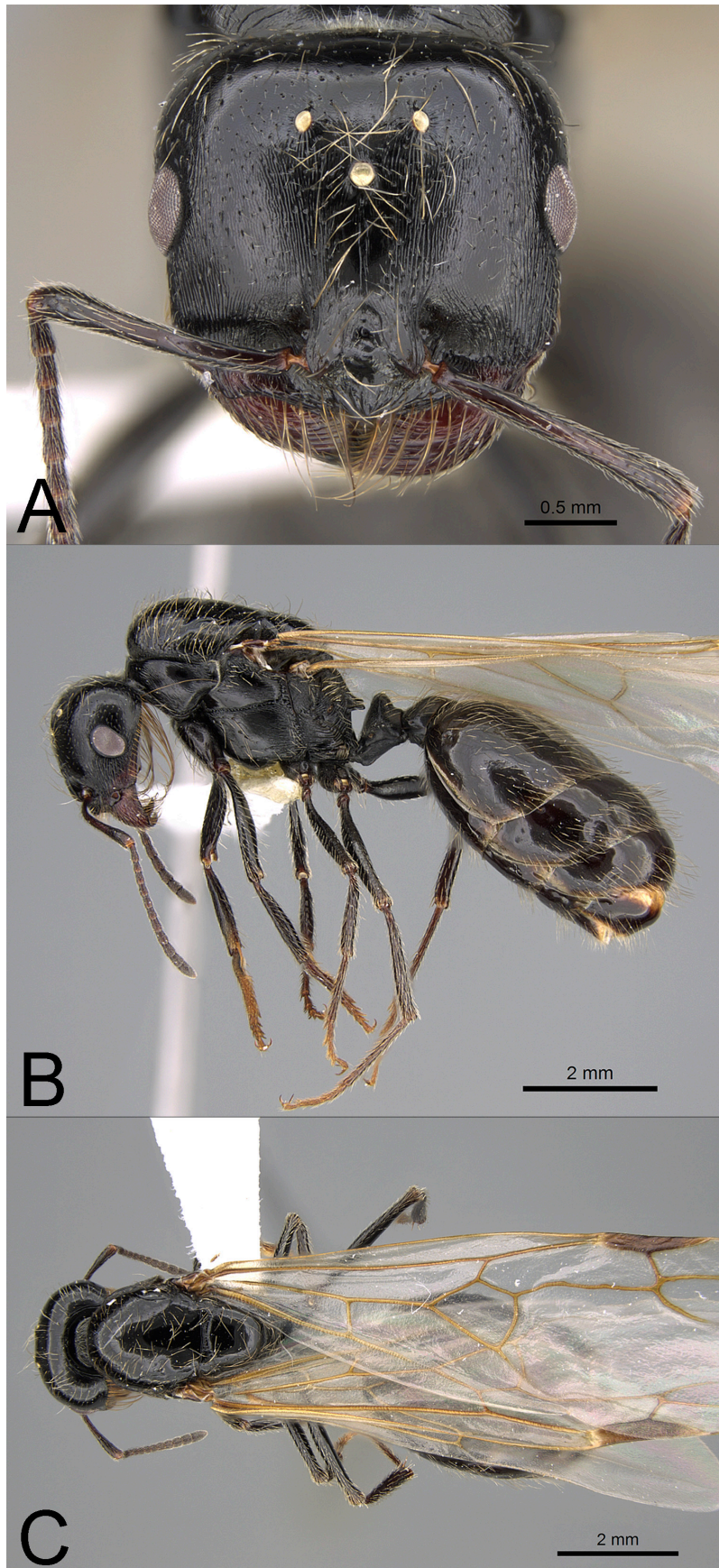


FIGURE 39. Photograph of *Veromessor pergandei* alate queen: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0922829). Photographs by Michele Esposito from www.AntWeb.org.

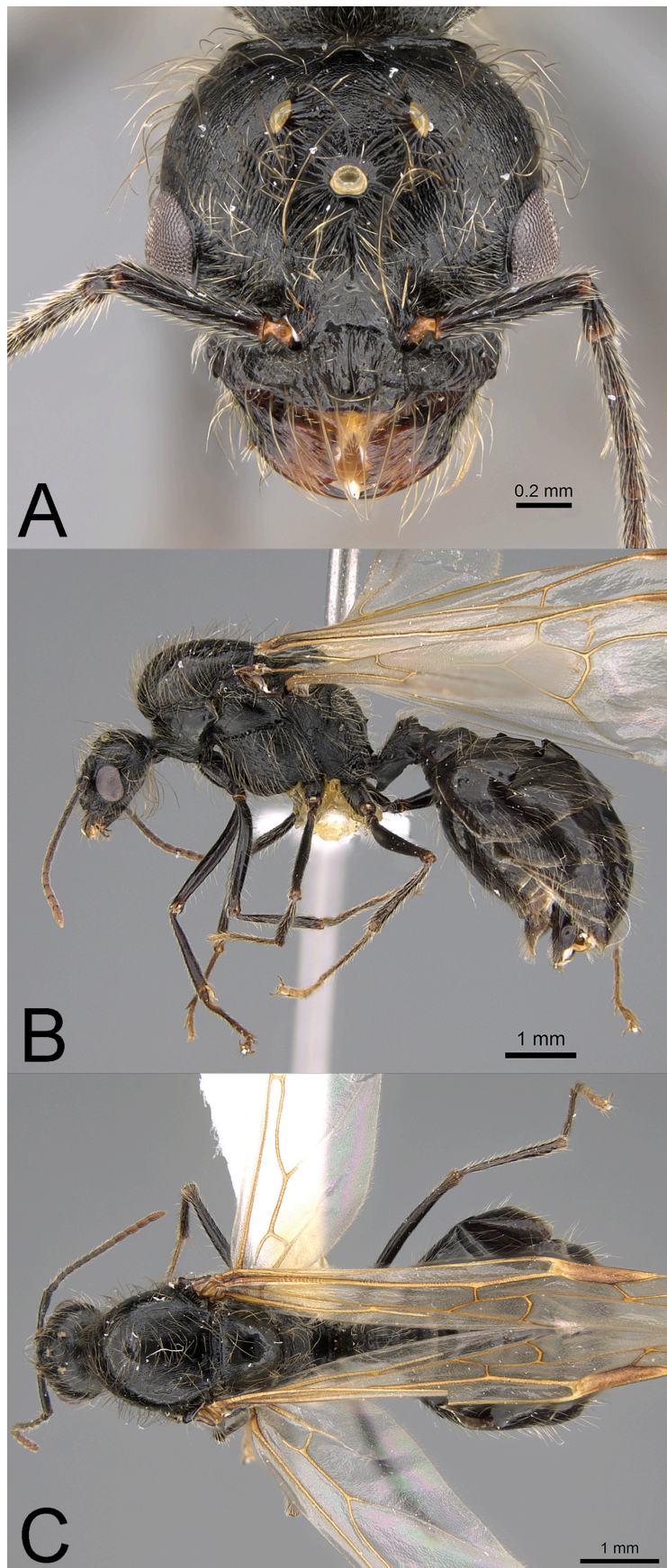


FIGURE 40. Photograph of *Veromessor pergandei* male: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0922828). Photographs by Michele Esposito from www.AntWeb.org.

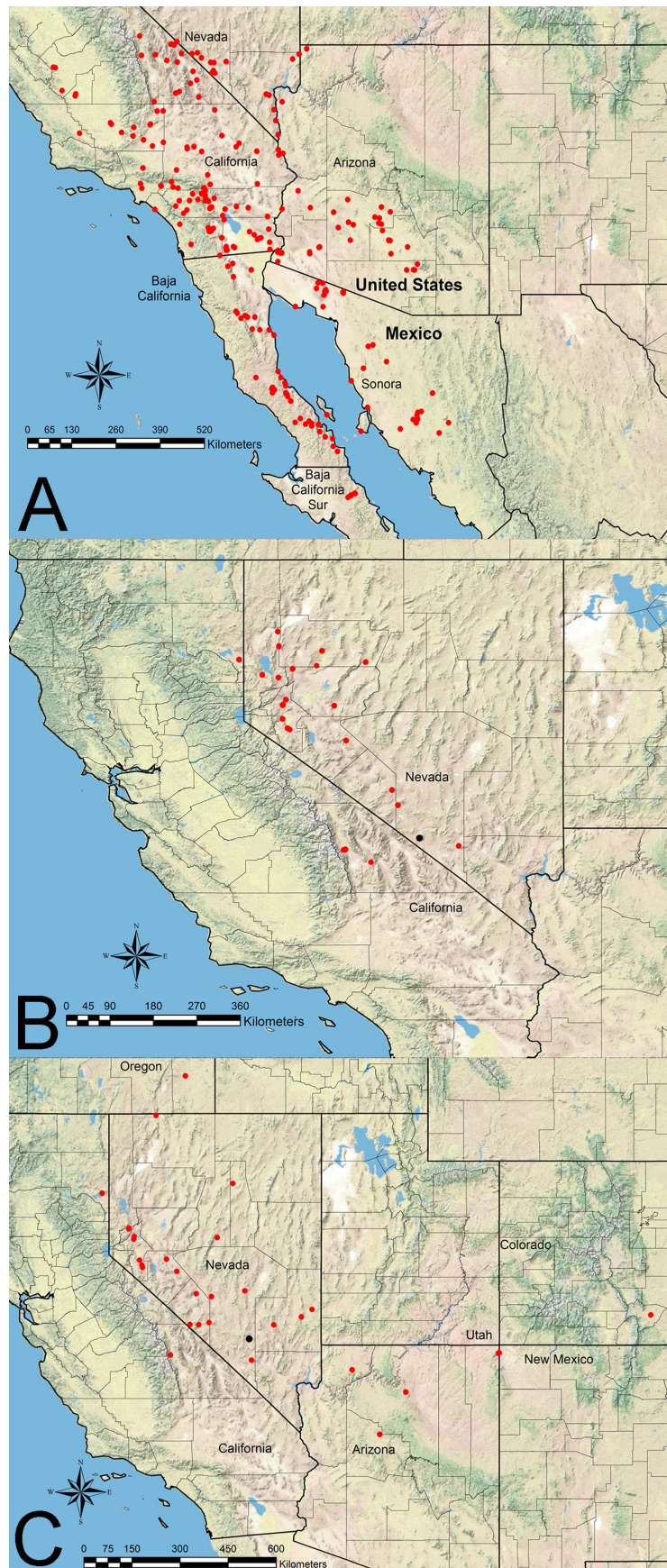


FIGURE 41. Geographic distribution of: (A) *Veromessor pergandei*, (B) *V. pseudolariversi*, and (C) *V. smithi*. The larger black circle in panels B & C denotes the type locality.

Desert ants such as *V. pergandei* experience major physiological challenges because their small size and high surface to volume ratio make them prone to desiccation. One adaptation to minimize water loss is that workers have low water loss rates that are comparable to those of other desert arthropods (Johnson, 2000c; Lighton, Quinlan, & Feener, 1994). Nevertheless, workers lose a significant amount of water during a foraging period (Feener & Lighton, 1991; Lighton *et al.*, 1994). This water is presumably regained before the next foraging period, but the source of this water is unknown (Feener & Lighton, 1991; Johnson, 2000c; Johnson, Kaiser, Quinlan, & Sharp, 2011). Cuticular abrasion caused by digging increases water loss rate in both workers and queens, and this damage is partially repaired over time in queens (Johnson, 2000c; Johnson *et al.*, 2011). Moreover, *V. pergandei* appears to survive in hot, xeric environs because of avoidance rather than tolerance to heat and desiccation. Ventilation patterns and metabolic rate of workers and alate queens are discussed in Lighton and Berrigan (1995).

Several genera of spiders (*Asagena*, *Euryopsis*, *Steatoda*) (Hale *et al.*, 2018; Kwapich & Hölldobler, 2019) and horned lizards (*Phrynosoma* spp.) prey on workers of *V. pergandei* (R.A. Johnson, pers. obs.).

Veromessor pergandei inhabits the Sonoran, Colorado, and Mohave Deserts, in areas that collectively encompass the hottest, most arid portions of North America; colonies occur in sandy soil at elevations from -80–1,400 m (Creighton, 1950, 1953; Johnson, 1992, 2000b; Tevis, 1958; Wheeler & Wheeler, 1973). This species occurs in the Mohave desert, Sonoran desert, Baja California desert, Gulf of California xeric scrub, and California coastal sage and chaparral ecoregions, as defined by Olson *et al.* (2001) (Figure 41A).

***Veromessor pseudolariversi* Johnson, Borowiec, Snelling & Cole NEW SPECIES**

(Figures 1H, 29D–F, 42–44)

Distribution—Figure 41B

Holotype worker [USNM: CASENT0923119]: UNITED STATES, Nevada: Nye County, 7 mi SSE Beatty, 36°49'N 116°44'W, 3000' (909 m), 5 April 1970 (G.C. & J. Wheeler NEV#782A). Paratypes, same data as holotype: CASC (10 workers), LACM (19 worker), MCZC (12 workers), MLBC (6 workers), NHMW (2 workers), RAJC (40 workers), UAIC (6 workers), UCDC (6 workers), USNM (16 workers).

Veromessor lariversi: Cole, 1963: 680, figs. 1b, 2b, 3b (queen, male), description apparently used *V. pseudolariversi* that was misidentified as *V. lariversi* (see discussion under *V. lariversi*).

Veromessor lariversi: Holldobler *et al.*, 2013: 866, misidentified as *V. lariversi*.

Worker diagnosis. This species is uniquely characterized by the following combination of features: (1) light yellowish to yellowish-orange or yellowish-red, gaster sometimes slightly darker, (2) medial lobe of clypeus arugose, smooth and shining, not thick and protuberant in profile, not elevated above lateral lobes in frontal view, (3) mandibles with 7 teeth, (4) dorsal base of scape not flattened, slightly widened; maximum basal width of scape less than maximum preapical width, (5) MOD distinctly greater than OMD, $OI > 32.0$, (6) cephalic dorsum mostly smooth and shining with scattered piligerous punctures between few discontinuous, medial longitudinal rugae that weaken laterally and disappear posterior to eyes, posterior margin smooth and shining, rugae more coarse and well-defined in front of eyes, (7) psammophore well developed; consisting of J-shaped hairs arranged in a distinct row around the outer margin of ventral surface of the head capsule, (8) dorsum of pronotum weakly roughened and shining to lineogranulate or with few weak discontinuous irregular transverse rugae; sides of pronotum weakly to moderately punctulate-granulate, weakly shining, between few coarse longitudinal rugae; mesonotum with piligerous punctures to moderately punctulate-granulate, weakly shining to shining; mesopleura with moderately coarse, wavy to irregular, longitudinal rugae, (9) sides of propodeum weakly to moderately punctulate-granulate between few longitudinal or oblique rugae; propodeal spines divergent, elongate-triangular, acuminate, length similar to width at base, less than the distance between their bases, and length $< 0.5 \times MOD$; infraspinal facet weakly coriarius, weakly shining; propodeal declivity smooth and shining, and (10) metasternal process higher than long, apex subangulate. Additionally, in profile, the anteroventral margin of postpetiole interrupted by a transverse ridge, appearing as a minute process, margin weakly concave anterior to process (Figures 29D–F, 42).

Measurements. holotype ($n = 26 + 9$ paratypes). HL 1.16 (1.02–1.25); HW 1.11 (1.00–1.18); MOD 0.41 (0.35–0.41); OMD 0.28 (0.24–0.32); SL 1.04 (0.86–1.10); PNW 0.74 (0.65–0.78); HFL 1.25 (0.98–1.28); ML 1.46 (1.37–1.58); PW 0.22 (0.18–0.24); PPW 0.35 (0.29–0.37). Indices: SI 93.69 (74.78–99.00); CI 95.69 (87.83–101.92); OI 36.94 (32.14–37.61); HFI 112.61 (94.94–118.10).

Description. Head quadrate to longer than wide (CI = 87.83–101.92); posterior margin flat to weakly convex in full-face view. Medial area of cephalic dorsum mostly smooth and shining with faint to weakly prominent, wavy to weakly irregular rugae laterad to near posterior margin of eyes; cephalic rugae most prominent between frontal lobes and eyes and on malar area, usually with one to two rugae continuing posterad along dorsal and ventral margins of eyes. Scattered piligerous punctures on posterior one-half of cephalic dorsum. Interrugae on cephalic dorsum weakly shining to shining; posterior corners weakly roughened to weakly coriarius, weakly shining to smooth and shining. Medial lobe of clypeus weakly convex, arugose, weakly coriarius, weakly shining to smooth and shining with numerous long, curved, bristle-like, yellowish macrochaetae projecting from anterior margin and lateroventral margin of mandibles. Mandibles with seven teeth. Eyes large (MOD = 0.35–0.41 mm; $0.30\text{--}0.36\times\text{HL}$; $\text{OI} > 32.0$). In profile, eyes situated near middle of head; eyes distinctly larger than OMD (OMD = $0.63\text{--}0.89\times\text{MOD}$). In full-face view, eyes protruding beyond lateral margins of head. Antennal scapes (SI = 74.78–99.00) surpassing posterior corners of head by slightly less than length of first funicular segment. Dorsal base of scape not flattened to weakly flattened, weakly widened; maximum basal width of scape less than maximum preapical width. Psammophore well developed; consisting of J-shaped hairs arranged in a distinct row around the outer margin of the ventral region of head capsule.

Promesonotal profile strongly convex with promesonotal suture weakly to moderately impressed. Dorsum of pronotum weakly roughened and shining to lineogranulate or with several weak irregular, discontinuous, transverse rugae anterad; sides of pronotum moderately to strongly granulate-punctulate, weakly shining, between several irregular, discontinuous, mostly vertical rugae that are usually restricted to anterior one-half. Mesonotum moderately to strongly punctulate-granulate or coriarius, weakly shining; mesopleura with moderately coarse, wavy to irregular rugae that traverse longitudinally to posterodorsally. Sides of propodeum weakly to moderately punctulate-granulate between few longitudinal or oblique rugae that continue from mesopleura but weaken or disappear on sides of propodeum; propodeal spines divergent, elongate-triangular, acuminate, length similar to width at base, less than distance between their bases, and $< 0.5\times\text{MOD}$; infraspinal facet lacking a well-defined keel, weakly coriarius, weakly shining; propodeal declivity smooth and shining. Propodeal spiracles circular facing posterad. Legs weakly to moderately coriarius, weakly shining to smooth and shining.

In profile, peduncle of petiole long, thickening posterad, meeting anterior surface of petiolar node in a broadly continuous curve. In profile, posterior surface of petiolar node strongly convex; petiolar node asymmetrical with anterior surface longer than posterior surface, apex weakly rounded to weakly subangulate. In dorsal view, petiolar node about as long as wide, narrowing to a broadly rounded anterior margin. Sides and posterior surface of petiolar node weakly sculptured to coriarius, weakly shining. Dorsum of postpetiole convex in profile; in dorsal view, sides subparallel posterad, narrowing anterad; length and width similar; dorsum weakly sculptured to weakly punctulate-granulate, weakly shining to smooth and shining; in profile, ventral margin of postpetiole discontinuous with margin interrupted by a minute process anterad, margin weakly concave anterior to process. First gastral tergum weakly to moderately coriarius, weakly shining to shining.

Erect, mostly short to medium-length, yellowish pilosity sparse on head. Moderately abundant semidecumbent to decumbent pilosity on scape, becoming slightly denser distally; abundant decumbent hairs on funicular segments. In profile, dorsum of mesosoma with up to 10–12 erect, yellowish hairs, longest hairs about $0.3\times\text{MOD}$. Hairs on gastral terga short, sparse, arising from piligerous punctures. Legs with moderately abundant suberect to decumbent, yellowish setae. Body mostly concolorous yellowish-orange to orangish-yellow, gaster often slightly more yellowish to yellowish-brown (Figures 29D–F, 42).

Queen diagnosis. This caste is diagnosed by the following combination of features: (1) mostly concolorous yellowish-brown to medium orangish-brown, (2) medial lobe of clypeus not thick and protuberant in profile, not elevated above lateral lobes in frontal view, medial lobe mostly smooth and arugose with numerous micropunctures to coriarius, (3) mandibles with 7 teeth, (4) dorsal base of scape weakly flattened, weakly widened; maximum basal width of scape less than maximum preapical width, (5) MOD distinctly greater than OMD, (6) cephalic dorsum with prominent longitudinal rugae adjacent to midline, above and below eyes, and on malar area; rugae lacking posterior to ocelli, posterior margin mostly smooth and shining, (7) psammophore well developed, (8) sides of pronotum moderately granulate between fine longitudinal rugae; mesoscutum smooth and shining, sometimes with faint rugae and scattered piligerous punctures; mesoscutellum smooth and strongly shining; mesospleura roughened and dull between wavy mostly longitudinal rugae, rugae faint to disappearing along posterodorsal margin of katapisternum, (9) propodeum moderately coriarius between longitudinal and oblique rugae; propodeal spines triangular, about

as long as width at base, length shorter than the distance between their bases; infraspinal facet and propodeal declivity weakly coriarius, weakly shining to shining, and (10) metasternal process higher than long, apex rounded. Additionally, in profile, the anteroventral margin of postpetiole interrupted by a transverse ridge, appearing as a minute process, margin weakly concave anterior to process (Figure 43).

Measurements. ($n = 3$). HL 1.22–1.31; HW 1.21–1.36; MOD 0.43–0.48; OMD 0.25–0.27; SL 1.0–1.11; HFL 1.30–1.32; ML 1.95–2.04; PW 0.29–0.31; PPW 0.45–0.48. Indices: SI 81.62–85.95; CI 96.95–107.09; OI 33.86–39.67; HFI 96.32–109.09.

Male diagnosis. This caste is diagnosed by the following combination of features: (11) dark brownish-black, (12) medial lobe of clypeus with several irregular longitudinal rugae with prominent medial carina that bifurcates near anterior margin, (13) preapical tooth small; mandibles with 1–2 minute teeth basad of preapical tooth, (14) in frontal view, anterior ocellus slightly above level of top of eyes, (15) mesopleura dull to weakly shining; anepisternum with fine longitudinal rugae, katepisternum with fine rugae that traverse ventrally from anterodorsal margin then curve posterad to posterior margin, (16) propodeum with moderately strong rugae, interrugae moderately coriarius; propodeal spines consist of denticles, (17) metasternal process elongate, digitiform, and (18) subpetiolar process triangular, slightly longer than high. Additionally, in profile, ventral margin of postpetiole discontinuous with margin interrupted by a minute process anterad, margin weakly concave anterior to process (Figures 1H, 44).

Measurements. ($n = 4$). HL 0.81–0.88; HW 0.86–0.96; MOD 0.44–0.48; OMD 0.080–0.12; SL 0.32–0.41; HFL 1.50–1.59; ML 2.14–2.22; PW 0.33–0.37; PPW 0.51–0.52; AOD 0.07–1.08; IOD 0.22–0.27; OOD 0.27–0.28. Indices: SI 36.78–46.51; CI 101.16–109.88; OI 49.44–51.16; HFI 164.58–178.65.

Additional material examined. **UNITED STATES: California:** Inyo Co.: 2 mi W Lone Pine, 4300', Jul 17, 1952 (CASC); 3 mi W Lone Pine, 4300', May 2–3, 1952 & Jul 17, 1952 & Apr 7, 1959 (LACM; MCZC; UAIC; USNM); Alabama Hills at 4.7 mi W Lone Pine, 5080', May 23, 2008 (RAJC); Jct Hwy 190 & Saline Valley Rd, 4860', May 24, 2008 (RAJC). **Lassen Co.:** 13 km at 9.5°N Doyle, 1240 m, Jun 27, 2004 (UCDC). **Nevada:** Churchill Co.: T24N, R26E, Sect 8, 4500', Jun 10, 1975 (LACM); Fairview Valley at Jct Hwys 31 & 50, 4100', May 17, 1971 (LACM). **Esmeralda Co.:** Goldfield, 5800', Oct 19, 1952 (LACM). **Lyon Co.:** 0.2 mi NW Jct Hwy 477 & I-80, 4120', Jul 24–25, 2018 (RAJC); 2 mi ESE Silver Springs, 4000', Jul 18, 1973 (LACM); Mason Valley at 0.6 mi S Jct Hwy 208 & Pine Grove Rd, 4490', Sep 8, 2014 (RAJC); 6 mi S Mason, 4400', May 20, 1971 (LACM); 2 km SW Weeks, 1280 m, Jul 2, 2006 (UCDC); Fort Churchill State Historic Park, 1285 m, Jul 2, 1996 & Jul 1–2, 2010 & Jul 3, 2008 & Jul 2, 2012 & Jul 29, 2016 (MLBC; MMPC; UCDC). **Mineral Co.:** Petrified Summit, 6200', Jun 26, 1970 (LACM). **Nye Co.:** Wagner, 4000', Oct 17, 1952 (LACM); near Mercury, Jul 4–11, 1962 (LACM); Big Dune at 10 mi W Lathrop Wells, May 31, 1970 (LACM). **Pershing Co.:** 7 Devils Spring, 3780', May 18, 1965 (LACM); 11 mi NW Lovelock, T25N, R30E, Sect 20, 5000', Apr 23, 1971 & Jun 23, 1971 (LACM; RAJC). **Washoe Co.:** Gerlach, 4100', Jun 11, 1971 (LACM); 18 mi S Gerlach, 4500', Jun 11, 1971 (RAJC); 19 mi S Gerlach, 4500', Jun 11, 1971 (RAJC); 5 km S Nixon, 1185 m, Jul 7, 2004 (UCDC); T23N, R21E, Sect 20, 1320 m, Aug 10, 1972 (LACM) (Figure 41B).

Etymology. The specific epithet, *pseudolariversi*, refers to its close similarity to *V. lariversi*, as exemplified by numerous series having been misidentified as *V. lariversi* until differences were conveyed to us by Phil Ward.

Discussion. *Veromessor pseudolariversi* is broadly sympatric with several congeners including *V. smithi*, *V. lariversi*, and *V. lobognathus*. *Veromessor pseudolariversi* workers are separated from *V. lobognathus* and *V. smithi* by: (1) smaller size (HW = 0.93–1.37 mm), (2) body concolorous light yellowish to yellowish-orange or yellowish-red, gaster often slightly darker, (3) maximum basal width of scape less than maximum preapical width, and (4) mandibles with 7 teeth. For *V. lobognathus* and *V. smithi*: (1) larger in size (HW = 1.28–1.82 mm), (2) concolorous orangish-brown to rust colored, (3) maximum basal width of scape greater than maximum preapical width, and (4) mandibles with 8 teeth.

Veromessor pseudolariversi is most similar to the closely related *V. lariversi*, as reflected by the fact that numerous series of *V. pseudolariversi* were misidentified as *V. lariversi*. However, these two species display consistent differences in morphology. Morphological differences that separate the two species include that workers of *V. pseudolariversi*: (1) in profile, anteroventral margin of postpetiole discontinuous with margin interrupted by a minute process, margin concave anterior to process (Figure 29D), (2) in dorsal view and in profile, the pronotum with discontinuous to continuous, irregular, transverse rugae; dorsum of mesonotum with one to few weak, irregular, usually discontinuous, longitudinal rugae (Figure 29E–F), and (3) a relatively larger eye with more facets (Figure 30). For workers of *V. lariversi*: (1) in profile, ventral margin of postpetiole continuous, lacking a minute process

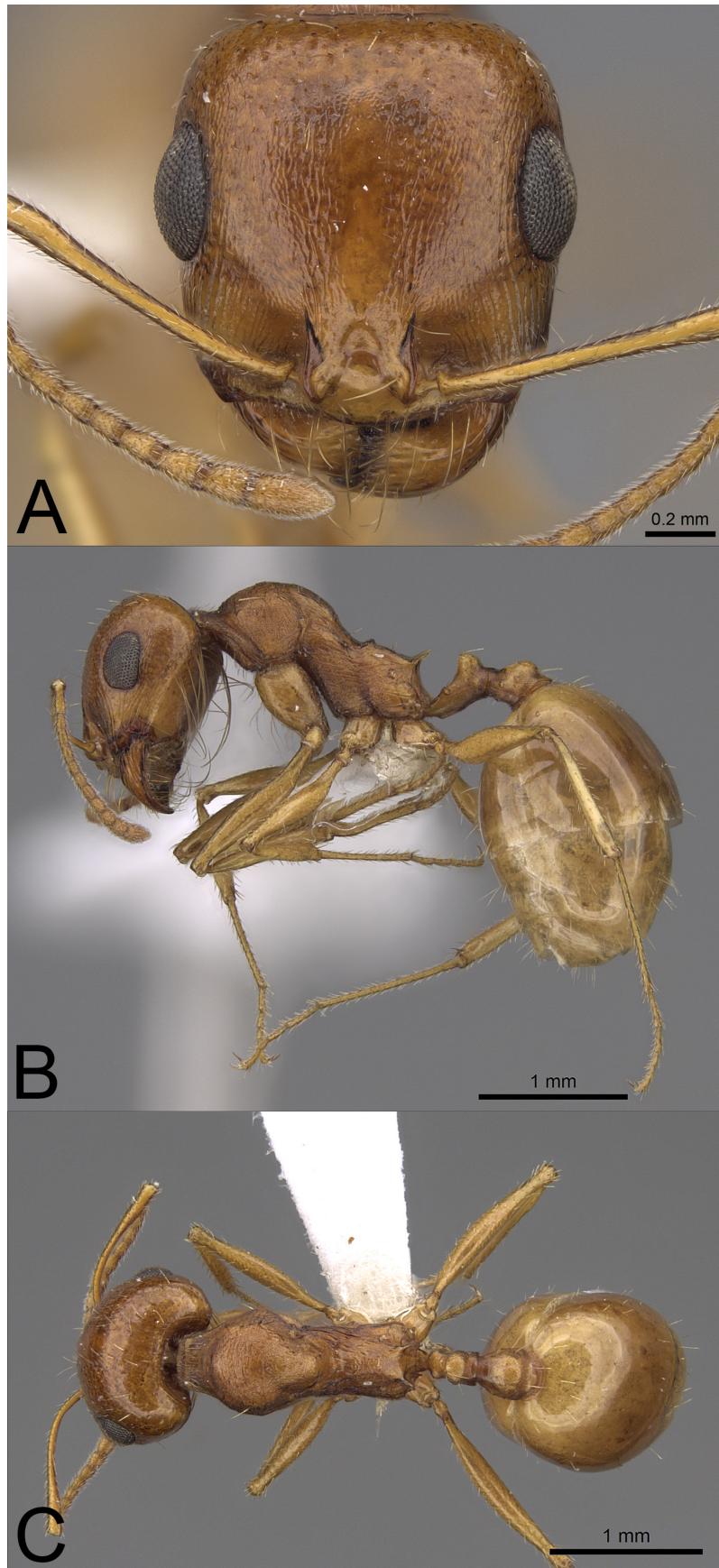


FIGURE 42. Photograph of *Veromessor pseudolariversi* holotype worker: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CAsENT0923119). Photographs by Wade Lee from www.AntWeb.org.

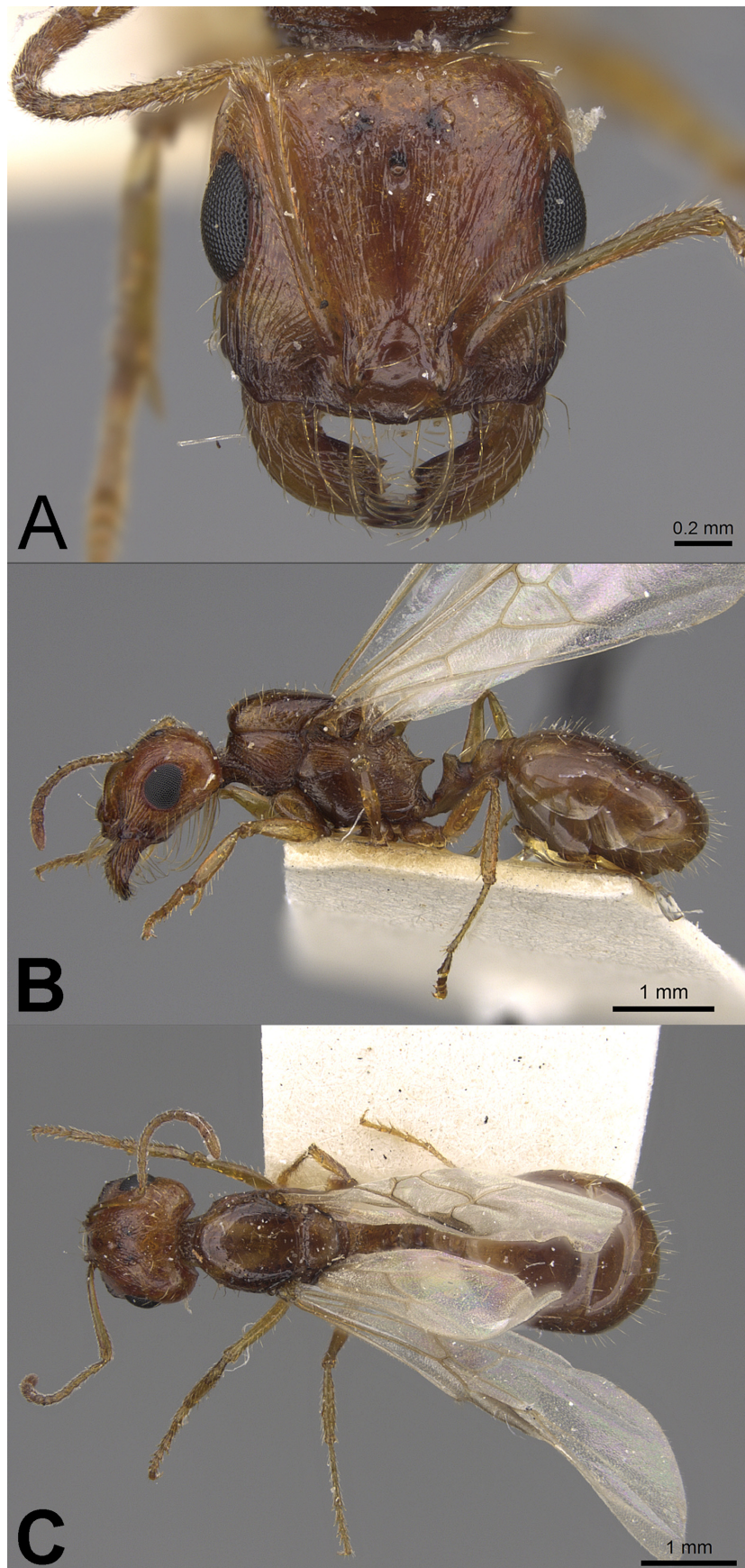


FIGURE 43. Photograph of *Veromessor pseudolariversi* alate queen: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (LACMENT370281). Photographs by Wade Lee from www.AntWeb.org.



FIGURE 44. Photograph of *Veromessor pseudolariversi* male: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0869851). Photographs by Robert Johnson from www.AntWeb.org.

(Figure 29A), (2) in dorsal view and in profile, the pronotum and mesonotum arugose, weakly to strongly coriarius to punctulate-granulate (Figure 29B–C), and (3) a relatively smaller eye with fewer facets (Figure 30). Queens and males of the two species also differ in size. Worker allometry is similar for both species, but queens of *V. lariversi* are distinctly larger than those of *V. pseudolariversi*, but their males are smaller (Figure 33). A molecular phylogeny that used UCEs shows that specimens that can be identified as *V. lariversi* and *V. pseudolariversi* using the above characters form sister but divergent, reciprocally monophyletic lineages, including specimens occurring in sympatry at Fort Churchill State Historic Park in Lyon County, Nevada (M.L. Borowiec, unpub. data).

Biology. As noted in the species account for *V. lariversi*, the biology of *V. lariversi* and *V. pseudolariversi* are probably similar, but it is difficult to ascribe published information to one species or the other because series were not referenced in papers, voucher series were not collected, or series were absent from loans that were examined. The following information on biology includes only that which could be verified from examined series of *V. pseudolariversi* or field observations.

Veromessor pseudolariversi workers are solitary, nocturnal foragers. Nests are usually polydomous and range from an entrance lacking a tumulus up to tumuli 10–15 cm in diameter (R.A. Johnson, pers. obs.). Colonies reach up to about 1,000 workers, and they are presumably monogynous. Workers are mostly monomorphic. Snelling and George (1979) collected both *V. lariversi* and *V. pseudolariversi* in California, and they indicated that colonies appear to aestivate during summer months. It seems more likely that these authors observed inactive colonies given that both RAJ and MLB have observed *V. pseudolariversi* foraging in June.

Gland chemistry has not been examined in *V. pseudolariversi*. Like other small-colony congeners, workers of *V. pseudolariversi* have a small pygidial gland reservoir and lack a textured tergal cuticle (Hölldobler *et al.*, 2013).

Mating flights have not been observed, but males were collected on June 11 and dealate queens were found on the ground at night and early morning on 29 June–3 July, indicating that mating flights occur during summer, probably during pre-dawn hours. Cole (1963) found two dealate queens in one excavated nest, but it is unclear if this record was for *V. lariversi* or *V. pseudolariversi*.

Veromessor pseudolariversi is a mid-elevation species of the Great Basin Desert that occurs at elevations from 1,145–1,305 m. This species occurs in the Great Basin shrub steppe, Mohave desert, and Western short grasslands ecoregions, as defined by by Olson *et al.* (2001) (Figure 41B).

Veromessor smithi

(Figures 1I, 6D, 45–47)

Distribution—Figure 40C

Veromessor smithi Cole, 1963: 678, figs. 1a, 2a, 3a (worker, queen, male). Holotype worker [LACM: LACMENT164497]: UNITED STATES, Nevada: Nye County, Nevada Test Site, Area 12 desert near Mercury, 3300', 15 July 1962 (A.C. Cole NEV-721). Additional paratype series from same locality, 15 July 1962—A.C. Cole NEV-722: LACM (3 workers, 3 alate queens, 6 males); 17 July 1962—A.C. Cole NEV-739: USNM (101 workers, 7 alate queens, 1 dealate queen, 4 males); 4 July 1962—A.C. Cole NEV-741: LACM (4 workers, 3 alate queens, 1 male), UAIC (4 workers); 20 June 1962—A.C. Cole NEV-744: LACM (6 workers); 20 Jun 1962—A.C. Cole NEV-745: LACM (6 workers); 20 June 1962—A.C. Cole NEV-757: LACM (1 worker, 1 alate queen, 1 male); 20 June 1962—A.C. Cole NEV-758: LACM (3 workers, 3 alate queens, 3 males); 23 Jun 1962—A.C. Cole NEV-759: LACM (4 workers, 1 alate queen, 1 male). See also Wheeler and Wheeler, 1972: 240 (larvae).

Messor smithi (Cole); Bolton, 1982: 341 (first combination in *Messor*).

Veromessor smithi Cole; Ward, Brady, Fisher, and Schultz 2015: 13 (revived combination in *Veromessor*).

Worker diagnosis. This species is uniquely characterized by the following combination of features: (1) yellowish-red or dull reddish to reddish-brown, (2) medial lobe of clypeus smooth and shining, sometimes with rugae anterad, medial lobe not thick and protuberant in profile, not elevated above lateral lobes in frontal view, anteromedial margin often sharply depressed, (3) mandibles with 8, or rarely 9 teeth, (4) dorsal base of scape flattened and notably widened; maximum basal width of scape greater than maximum preapical width, (5) MOD less than to greater than OMD, $OI > 24.5$, (6) cephalic dorsum with prominent, wavy, longitudinal rugae that diverge toward posterior corners, rugae posterior to eyes usually becoming more irregular, often with short lateral branches, rugae sometimes fading or disappearing along posterior margin, becoming punctulate-granulate; interrugae on cephalic dorsum weakly coriarius or weakly granulate, weakly shining, (7) psammophore moderately well developed;

ventral surface of head capsule with both J-shaped hairs and straight or evenly curved hairs, J-shaped hairs arranged in a V-shaped row which does not reach the posterior part of the lateroventral margin of the head capsule, (8) dorsum of pronotum with strongly irregular rugae to rugoreticulate, interrugae weakly to strongly coriaceous or weakly granulate; sides of pronotum with strongly irregular rugae to weakly rugoreticulate, interrugae strongly granulate; mesonotum with strongly irregular longitudinal trending rugae to rugoreticulate; mesopleura with strongly irregular rugae to rugoreticulate dorsad, rugae mostly longitudinal ventrad, interrugae granulate, (9) propodeal spines triangular, acuminate; length less than to sometimes approaching the distance between their bases; infraspinal facet and propodeal declivity weakly sculptured, strongly shining, and (10) metasternal process small, more or less coniform, about as long as high, apex acuminate to bluntly subangulate (Figures 6D, 45).

Measurements. holotype ($n = 8 + 24$ paratypes). HL 1.50 (1.33–1.58); HW 1.50 (1.33–1.61); MOD 0.47 (0.38–0.49); OMD 0.44 (0.32–0.48); SL 1.40 (1.23–1.44); PNW 0.92 (0.81–1.01); HFL 1.59 (1.38–1.77); ML 2.11 (1.76–2.07); PW 0.29 (0.25–0.31); PPW 0.47 (0.37–0.46). Indices: SI 93.33 (84.83–98.50); CI 100.00 (97.79–108.27); OI 31.33 (24.84–33.57); HFI 106.00 (95.83–116.43).

Queen diagnosis. This caste is diagnosed by the following combination of features: (1) light ferruginous orange to orangish-red, gaster sometimes light orangish-brown, (2) medial lobe of clypeus mostly smooth and shining or rarely with irregular rugae, medial lobe not thick and protuberant in profile, not elevated above lateral lobes in frontal view, (3) mandibles with 8 teeth, (4) dorsal base of scape flattened and widened; maximum basal width of scape greater than maximum preapical width, (5) MOD slightly greater than OMD, (6) cephalic dorsum with longitudinal rugae that diverge toward posterior corners with rugae usually weakening to disappearing posterior to ocelli, weakly punctate-granulate, weakly shining; interrugae on cephalic dorsum weakly punctulate, weakly shining, (7) psammophore moderately well developed, (8) mesocutum and mesoscutellum smooth and shining with scattered piligerous punctures; anepisternum weakly shining and densely punctate between longitudinal rugae; katepisternum shinier, with weaker rugae or mostly granulate, but usually smooth and arugose anteroventrally, (9) propodeum with weak irregular longitudinal and oblique rugae; propodeal spines triangular, acuminate, length about the same as width at base; length much less than distance between their bases; interspinal surface and propodeal declivity weakly coriaceous, shining, and (10) metasternal process small, more or less coniform, about as long as high, apex acuminate to bluntly subangulate (Figure 46).

Measurements. ($n = 8 + 4$ paratypes). HL 1.40–1.63; HW 1.43–1.69; MOD 0.41–0.48; OMD 0.30–0.45; SL 1.20–1.42; HFL 1.55–1.82; ML 2.06–2.38; PW 0.28–0.36; PPW 0.57–0.57. Indices: SI 82.99–93.75; CI 97.30–106.25; OI 26.04–33.33; HFI 103.33–119.44.

Male diagnosis. This caste is diagnosed by the following combination of features: (11) yellowish-brown to light medium brown, (12) medial lobe of clypeus abruptly depressed across anterior margin, anterior margin straight across middle, (13) preapical tooth small; mandibles with one or two minute denticles or teeth basad of preapical tooth, (14) anterior ocellus above level of top of eyes, (15) mesopleura very weakly sculptured, but anepisternum usually punctulate and with some widely spaced, very fine rugae; katepisternum mostly smooth and shining to weakly roughened, (16) propodeum weakly sculptured with some widely spaced, longitudinal rugae; spines or denticles absent; in profile, juncture of dorsal surface and propodeal declivity rounded to subangulate, (17) metasternal process elongate, slender, often with a withered look, and (18) subpetiolar process short, triangular to spine-like (Figures 1I, 47).

Measurements. ($n = 5 + 7$ paratypes). HL 0.77–0.91; HW 0.68–0.75; MOD 0.34–0.41; OMD 0.08–0.11; SL 0.23–0.36; HFL 1.42–1.75; ML 1.91–2.29; PW 0.26–0.31; PPW 0.39–0.51; AOD 0.09–0.12; IOD 0.23–0.30; OOD 0.19–0.27. Indices: SI 31.04–50.00; CI 80.23–90.91; OI 49.28–60.29; HFI 201.33–247.14.

Additional material examined. UNITED STATES: *Arizona*: Apache Co.: Carrizo Mtns at Black Rock Dike, 2033 m, Jun 12, 2009 (MCZC); Carrizo Mts at Red Goat Wash, 1724 m, Jun 5, 2009 (MCZC). *Coconino Co.*: 32 km W Cameron on old Rt 64, 1746 m, Jul 28, 2011 (MCZC). *Mohave Co.*: 4 mi NW Nixon Springs, Aug 5, 1969 (LACM). *Yavapai Co.*: Prescott National Forest, USFS Rd 680 at 0.4 mi E Hwy 89 & 7.1 mi N Paulden, 4850', Mar 10, 1993 & Apr 20, 1999 & Jul 25, 1999 (RAJC; UCDC). *California*: Inyo Co.: 4.8 mi SW Independence, 5580', May 24, 2008 (RAJC). *Lassen Co.*: 6 km SE Wendel, 1230 m, Jul 7, 2002 (UCDC). *Colorado*: Huerfano Co.: 3 mi N Walsenburg, Aug 26, 1951 (LACM). *Nevada*: Esmeralda Co.: 20 mi WNW Tonapah, 4800', Jun 19, 1970 (LACM); 4 mi NW Pigeon Spring, 6100', May 28, 1970 (RAJC); Lida Junction, 4800', no date (not examined; see Wheeler & Wheeler, 1986); 1.4 mi E Lida, 5910', Jun 16, 2020 (RAJC). *Eureka Co.*: 5 mi SSW Beowawe, 4500', Jul 2, 1971 (RAJC). *Humboldt Co.*: 3 mi SSW Denio, 5200', Apr 2, 1970 (RAJC). *Lander Co.*: Big Smoky Valley

(T17N, R45E, Sect 6), 6100', May 3, 1971 (RAJC). *Lincoln Co.*: 6 mi E Panaca, 5800', no date (not examined; see Wheeler & Wheeler, 1986); 4 mi W Caliente, 5600', no date (not examined; see Wheeler & Wheeler, 1986); 10 mi SW Crystal Springs, 5500', no date (not examined; see Wheeler & Wheeler, 1986). *Lyon Co.*: 8 mi SSE Yerington, 4600', May 20, 1971 (RAJC); 16 rd mi SSE Yerington, 5200', Jun 16, 1979 (LACM); Pine Grove Rd at 10.6 mi S Jct Hwy 208, 5200', Jul 23, 2018 (NHMW; RAJC); 7 km SW Silver Springs, 1380 m, Sep 29, 1993 (RAJC); Churchill Butte, 6000' & 1830 m, Jun 11, 1975 & Jul 3, 1994 (RAJC; UCDC). *Mineral Co.*: Dead Horse Wells, 4100', no date (not examined; see Wheeler & Wheeler, 1986); Petrified Summit, 6200', no date (not examined; see Wheeler & Wheeler, 1986). *Nye Co.*: Hot Creek Valley at 10 mi NE Warm Springs, 5200', no date (not examined; see Wheeler & Wheeler, 1986); 6 mi E Tonopah, 5600', no date (not examined; see Wheeler & Wheeler, 1986). *Storey Co.*: Clark Mine at 27 km E Sparks, 1420 m, May 24, 1994 (not examined; M. Bennett, pers. comm.); 20 km WSW Fernley, 1430 m, Jul 3, 1994 (UCDC). *New Mexico*: *San Juan Co.*: Carrizo Mtns at Arnold Cliff Ranch, 1824 m, Aug 20, 2010 (MCZC). *Oregon*: *Malheur Co.*: Jct Hwys 95 & 78, no date (LACM) (Figure 41C).

Etymology. This species was named after Dr. M.R. Smith, who spent numerous years dedicated to the meticulous study of ants.

Discussion. *Veromessor smithi* is broadly sympatric with several congeners including *V. lobognathus*, *V. lariversi*, and *V. pseudolariversi*. Workers of *Veromessor smithi* are separated from *V. lobognathus* based on: (1) propodeal spines short, length less than distance between their bases and length $< 0.5 \times \text{MOD}$, (2) eyes larger ($\text{MOD} = 0.38\text{--}0.49$, $\text{OI} = 24.8\text{--}33.5$), and (3) area between eyes and frontal lobes weakly coriarius and weakly shining to shining between faint to prominent weakly irregular to regular rugae. In *V. lobognathus*: (1) propodeal spines longer, length greater than distance between their bases and length $\geq 1.0 \times \text{MOD}$, (2) eyes smaller ($\text{MOD} = 0.31\text{--}0.41$, $\text{OI} = 20.5\text{--}25.0$), and (3) area between eyes and frontal lobes strongly granulate and dull between prominent strongly irregular rugae to weakly rugoreticulate.

Workers of *Veromessor smithi* are separated from *V. lariversi* and *V. pseudolariversi* by: (1) larger in size ($\text{HW} = 1.33\text{--}1.61$ mm), (2) concolorous orangish-brown to rust colored, (3) maximum basal width of scape greater than maximum preapical width, and (4) mandibles with 8, or rarely 9 teeth. For *V. lariversi* and *V. pseudolariversi*: (1) smaller in size ($\text{HW} = 0.93\text{--}1.37$ mm), (2) body concolorous light yellowish to yellowish-orange or yellowish-red, gaster often slightly darker, (3) maximum basal width of scape less than maximum preapical width, and (4) mandibles with 7 teeth.

The type locality for *V. smithi* is the Nevada Test Site in Area 12 (= Rainier Mesa), which is along the northern edge of the Nevada Test Site.

A molecular phylogeny that used UCEs shows *V. smithi* and *V. lobognathus* are sister lineages (M.L. Borowiec, unpub. data).

Biology. Little is known about the biology of *V. smithi*. Workers are solitary, crepuscular and nocturnal foragers (Cole, 1963; 1966; M. Bennett, pers. comm.). Nests are placed in open, exposed areas and typically consist of one to two small circular craters about 10–15 cm in diameter (Cole, 1966). Colonies are small, with one excavated colony containing 275 workers, 1 dealate queen, 27 alate queens, and 97 males (Cole, 1963).

Gland chemistry has not been examined in *V. smithi*. Like other small-colony congeners, workers of *V. smithi* have a small pygidial gland reservoir and lack a textured tergal cuticle (Hölldobler *et al.*, 2013).

Mating flights have not been observed, but sexuals have been collected in nests from 12 Jun–27 July (Cole, 1966), suggesting that mating flights occur during late June–July. One dealate brachypterous queen was also examined by RAJ (RAJC; Wheeler and Wheeler NEV#1709).

Veromessor smithi occurs at elevations from 760–2,275 m. It appears to be most common in pinyon pine-juniper habitats similar to those inhabited by *V. lobognathus*. Collections from southwestern Oregon, northwestern New Mexico, and southcentral Colorado indicate that *V. smithi* is much more widely distributed than indicated by current records, and it also likely occurs in Utah and western Colorado. This species occurs in the Great Basin shrub steppe, Snake–Columbia shrub steppe, Colorado Plateau shrublands, Arizona Mountains forests, Western short grasslands, and Mohave desert ecoregions, as defined by Olson *et al.* (2001); the two Mohave desert records are from mid-elevations (Figure 41C).



FIGURE 45. Photograph of *Veromessor smithi* worker: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (MCZ-ENT00671466). Photographs by Wade Lee from www.AntWeb.org.

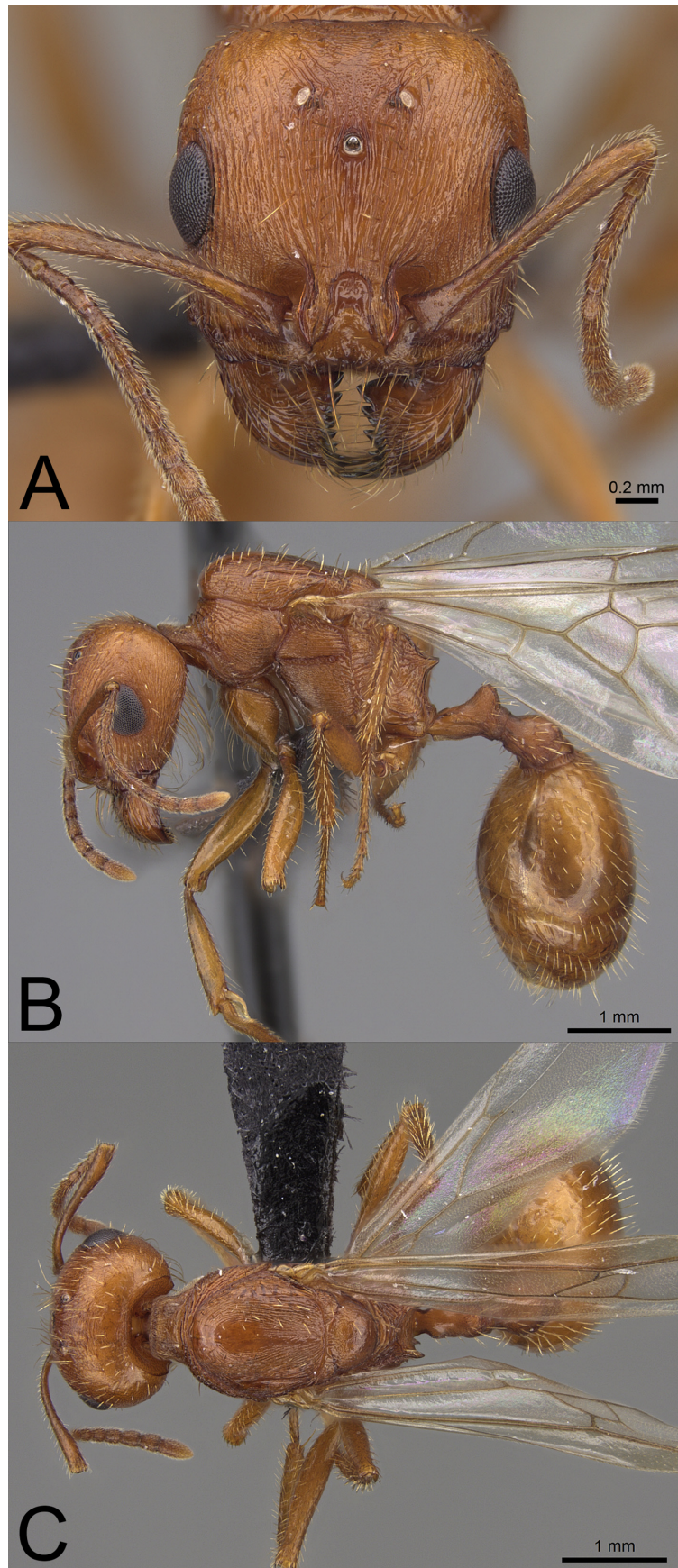


FIGURE 46. Photograph of *Veromessor smithi* alate queen: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (MCZ-ENT00671476). Photographs by Wade Lee from www.AntWeb.org.

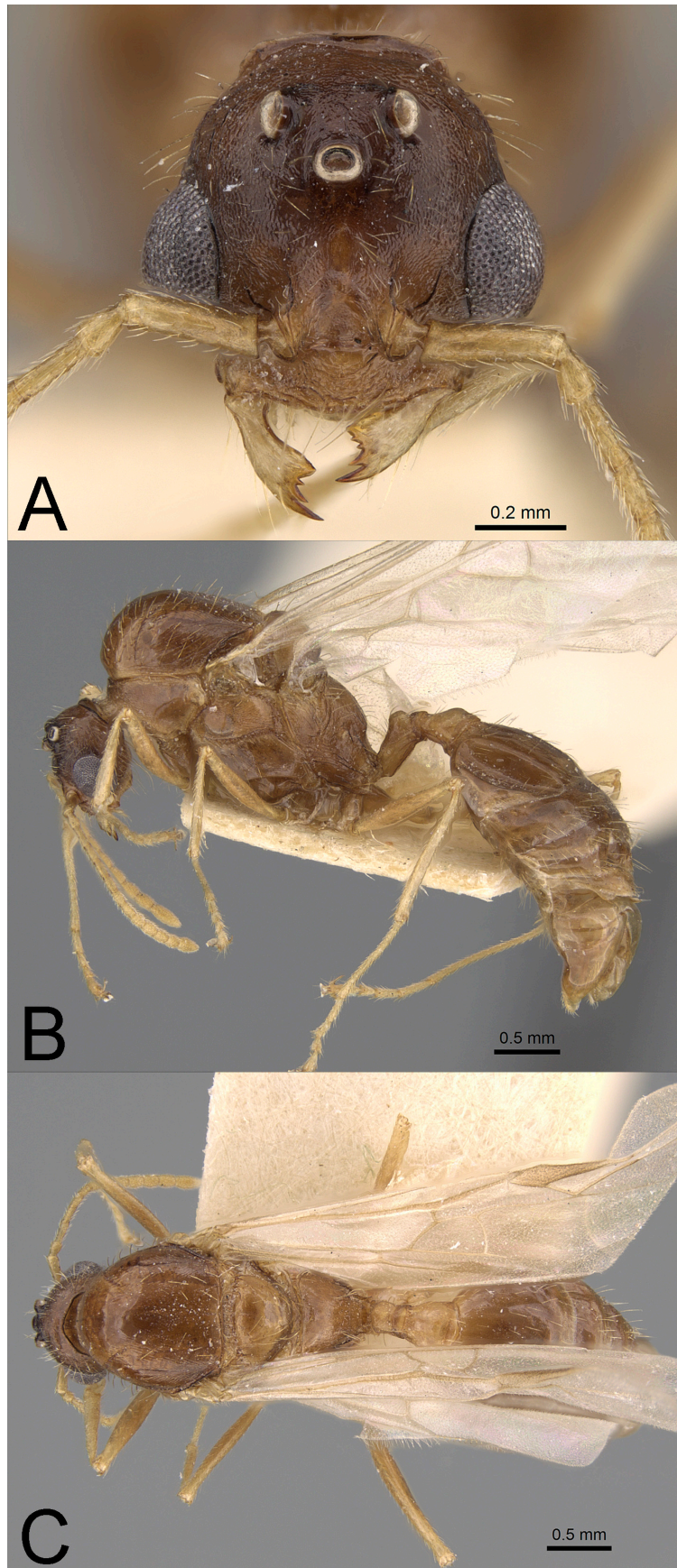


FIGURE 47. Photograph of *Veromessor smithi* paratype male: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (LACMENT364058). Photographs by Michele Esposito from www.AntWeb.org.

Veromessor stoddardi

(Figures 1J, 48–51)

Distribution—Figure 52

Stenamma (Messor) stoddardi Emery, 1895: 307 (worker). Syntypes examined: 2 workers [LACM], 7 workers [USNM], #55466, UNITED STATES, California: Riverside County, San Jacinto (Hyatt?). See also Wheeler and Creighton 1934: 385, plate II, fig. 1. USNM worker here designated **LECTOTYPE** [USNMMENT00922798].

Novomessor stoddardi (Emery); Emery, 1915: 73 (first combination in *Novomessor*).

Novomessor (Veromessor) stoddardi (Emery); Forel, 1917: 235 (first combination in *Novomessor* [*Veromessor*]).

Veromessor stoddardi (Emery); Wheeler and Creighton, 1934: 385 (first combination in *Veromessor*).

Novomessor (Veromessor) stoddardi (Emery); Enzmann, 1947: 152 (revived combination in *Novomessor* [*Veromessor*], in key).

Veromessor stoddardi (Mayr); Creighton, 1950: 157 (revived combination in *Veromessor*).

Messor stoddardi (Emery); Bolton, 1982: 341 (first combination in *Messor*).

Veromessor stoddardi Ward, Brady, Fisher, and Schultz, 2015: 13 (revived combination in *Veromessor*).

Worker diagnosis. This species is uniquely characterized by the following combination of features: (1) head and mesosoma orangish-red to orangish-brown, gaster blackish-orange to blackish, (2) medial lobe of clypeus lacking medial groove but with several lateral longitudinal rugae, medial lobe not thick and protuberant in profile, not elevated above lateral lobes in frontal view, (3) mandibles with 8 teeth, (4) antennal scape narrowest immediately distad of basal bend, (5) MOD distinctly less than OMD, $OI < 25.0$, (6) cephalic dorsum moderately shining between fine, widely spaced, longitudinal rugae; antennal fossa lacking concentric rugae, (7) psammophore poorly developed; ventral surface of head capsule with scattered straight or evenly curved hairs, but J-shaped hairs mostly absent, (8) dorsum of pronotum with fine, wavy to weakly irregular, longitudinal rugae; sides of pronotum with longitudinal rugae that fade to disappear posterad, posterior one-third often granulate; mesonotum mostly smooth and shining, lacking rugae or with longitudinal rugae that are distinctly weaker than those on dorsum of pronotum; mesopleura with rugae that traverse longitudinally to posterodorsally, interrugae weakly coriarius to moderately granulate, (9) propodeal spines short, acuminate, length less than distance between their bases; infraspinal facet and propodeal declivity rugose or weakly to strongly coriarius, weakly to moderately shining, and (10) metasternal process large, narrowed laterally, slightly higher than long with angulate apex; anterior and posterior surfaces decline steeply; partly translucent (Figures 48–49).

Measurements. lectotype ($n = 66$). HL 1.72 (1.03–1.80); HW 1.80 (0.93–1.83); MOD 0.33 (0.21–0.33); OMD 0.44 (0.23–0.44); SL 1.22 (0.83–1.45); PNW 1.02 (0.62–1.11); HFL 1.63 (0.92–1.71); ML 2.20 (1.27–2.20); PW 0.34 (0.19–0.38); PPW 0.50 (0.26–0.52). Indices: SI 67.68 (66.85–100.69); CI 104.65 (87.07–109.20); OI 18.33 (16.09–24.75); HFI 90.56 (68.03–114.85).

Queen diagnosis. This caste is diagnosed by the following combination of features: (1) head dark orangish-brown to reddish-brown, gaster slightly lighter; pronotum, dorsal portion of anepisternum, mesoscutellum, propodeum dark orangish-brown; rest of mesosoma dark blackish-orange to blackish, (2) medial lobe of clypeus lacking medial groove but with several lateral longitudinal rugae, (3) mandibles with 8 teeth, (4) dorsal surface of base of scape slightly flattened; maximum basal width of scape similar to maximum preapical width, (5) MOD slightly greater than OMD, (6) cephalic dorsum with fine, wavy to irregular longitudinal rugae that fade to disappear near posterior margin; interrugae moderately shining, (7) psammophore poorly developed, (8) sides of pronotum weakly to moderately punctate between fine longitudinal rugae; mesoscutum and mesoscutellum smooth and shining with scattered piligerous punctures; anepisternum shining, weakly punctate between fine longitudinal rugae, both rugae and punctuation weak to absent ventrad; katepisternum mostly shining and superficially roughened with short, longitudinal striae anterad and posterad, (9) sides of propodeum weakly shining and densely punctate between longitudinal and oblique rugae; propodeal spines triangular, acuminate, distinctly shorter than distance between their bases; infraspinal facet shining, superficially punctate above, propodeal declivity smooth and shining, and (10) metasternal process large, narrowed laterally, slightly higher than long with angulate apex; anterior and posterior surfaces decline steeply; partly translucent (Figure 50).

Measurements. ($n = 6$). HL 1.56–1.72; HW 1.61–1.75; MOD 0.40–0.44; OMD 0.34–0.41; SL 1.20–1.32; HFL 1.61–1.69; ML 2.77–2.97; PW 0.39–0.45; PPW 0.61–0.67. Indices: SI 74.07–76.97; CI 96.99–110.76; OI 24.12–26.71; HFI 93.71–101.24.

Male diagnosis. This caste is diagnosed by the following combination of features: (11) blackish brown,

appendages light brown, (12) medial lobe of clypeus abruptly descendant distad, disc weakly shining with coarse oblique to longitudinal rugae, (13) mandibles with 3–4 teeth basad of preapical tooth, (14) anterior ocellus above level of top of eyes, (15) anepisternum weakly shining, finely punctate between closely spaced, moderately coarse, longitudinal rugae; katapisternum shinier, disc weakly roughened, posterad with moderately coarse oblique to longitudinal rugae, (16) propodeum densely punctate between coarse, mostly longitudinal rugae, interrugae weakly shining; propodeal spines triangular, acuminate, length less than distance between their bases, (17) metasternal process distinctly higher than long, apex narrowly rounded, and (18) subpetiolar process short, elongate-triangular to spiniform or digitiform, apex acuminate to rounded (Figures 1J, 51).

Measurements. ($n = 2$). HL 1.15–1.19; HW 1.12–1.15; MOD 0.45–0.46; OMD 0.11–0.14; SL 0.46–0.52; HFL 1.96–2.07; ML 3.07–3.12; PW 0.46–0.49; PPW 0.83–0.90; AOD 0.12–0.13; IOD 0.32–0.32; OOD 0.40–0.42. Indices: SI 41.07–45.22; CI 94.12–100.00; OI 40.00–40.18; HFI 175.00–180.00.

Additional material examined. **MEXICO: Baja California:** 38.5 mi NW Catavina at 1 mi N El Progreso, Feb 10, 1993 (RAJC; UCDC); Sierra San Borja at 9.9 mi N San Borja, 1970', Mar 11, 1998 (RAJC); 4.4 mi W Meling Ranch, 2450', Mar 25, 2001 (CIDA; NHMW; RAJC; UCDC); Meling Ranch, 2200', no date (not examined; R. Snelling, pers. obs.); 4 mi S Misión Descanso, 700', May 14, 1952 (LACM; UAIC); Rosarito Beach, Jun 14, 1938 (CASC; LACM; USNM); 19 mi N Ensenada, 1100', May 15, 1952 (LACM; USNM); 4 mi S La Misión, 700', May 14, 1952 (USNM); Rancho Cañadas at 13 km NE Camalú, 260 m, Aug 26, 1994 (not examined; M. Bennett, pers. comm.); 2.8 mi E San Telmo, Jul 14, 1979 (UCDC); 14 km ENE Jct Hwy 1 at Road to Bahía de los Ángeles, 480 m, Apr 7, 1998 (UCDC); "The Oaks" at 5 mi N Santo Thomas, May 9, 1999 (UCDC); 10 mi E San Quintin, no date (not examined; R. Snelling, pers. obs.). **UNITED STATES: California: Monterey Co.:** FS Hastings Natural History Reserve, Apr 25, 1941 (LACM); Paraiso Springs, no date (not examined; R. Snelling, pers. obs.); no loc, Jun 1963 (USNM). **Riverside Co.:** Cleveland National Forest, Forest Service Rd 8S01 at 3 mi E Jct 8S01 & 8S04 (W of Lake Elsinore), May 7, 1984 (LACM); Lake Skinner, 462 m, Jul 29, 1996 (UCDC). **San Bernardino Co.:** Chino Hills State Park at 6 km S Los Serranos, 250 m, Jun 13, 1994 (not examined; M. Bennett, pers. comm.). **San Diego Co.:** San Isidro, 200', May 13–15, 1952 & Jul 9, 1952 (LACM; USNM); Descanso, Feb 1898 (USNM); 5 mi E Descanso, 3000' (not examined; R. Snelling, pers. obs.); Santa Ysabel Ecological Reserve, 957 m, Jun 2003 (UCDC); Sweetwater River, 100 m, May 29–Jun 3, 2003 (UCDC); Sycamore Crossing, Peñasquitos Canyon, 25 m, May 1, 2004 (UCDC). **Santa Barbara Co.:** 4 km E San Marcos Pass, 980 m, May 5, 1986 (JTLC); 21 km ESE Santa Ynez, 980 m, May 5, 1986 (not examined; M. Bennett, pers. comm.) (Figure 52).

Etymology. The specific epithet, *stoddardi*, was presumably derived from someone named Stoddard, but no reference to this person has been located.

Discussion. The poorly developed psammophore distinguishes *V. stoddardi* from all congeners except *V. andrei* and *V. chicoensis*. *Veromessor andrei* is the only congener with a poorly developed psammophore that is likely to co-occur with *V. stoddardi*. The two species can be distinguished based on: (1) *V. stoddardi* has short propodeal spines (length less than the distance between their bases), (2) strongly polymorphic workers, and (3) weak, regular rugae on cephalic dorsum posterior to eyes and dorsum of pronotum. In *V. andrei*: (1) propodeal spines long (length $\geq 3\times$ the distance between their bases), (2) workers mostly monomorphic, and (3) notably coarse rugae on cephalic dorsum posterior to eyes and dorsum of pronotum. *Veromessor stoddardi* is most similar to the closely related species *V. chicoensis*, from which it can be distinguished by: (1) antennal scape narrowest immediately distad of basal bend; maximum basal width of scape about equal to maximum preapical width, and (2) in dorsal view, the mesonotum usually smooth and shining, rugae distinctly weaker than those on pronotum. In *V. chicoensis*: (1) antennal scape narrowest near midlength; maximum basal width of scape greater than maximum preapical width, and (2) in dorsal view, rugae on mesonotum similar to those on pronotum, interrugae weakly dull (also see discussion under *P. chicoensis*).

Workers of these two species display few consistent morphological differences, but queens and males differ in both morphology and size. Worker allometry is similar for both species (see above), but queens and males of *V. stoddardi* are distinctly larger than those of *V. chicoensis* (Figure 19). A molecular phylogeny based on UCEs shows that both species form divergent, reciprocally monophyletic lineages (M.L. Borowiec, unpub. data).

Wheeler and Creighton (1934) wrongly restricted the type locality of *V. stoddardi* to San Diego County, indicating, "the type series comes from several localities all in San Diego County, California. It seems preferable, for this reason to regard San Diego County as the type locality." This is a remarkable statement given that none of the type material came from San Diego County. The locality cited in the description by Emery (1895) is San Jacinto, Riverside County, California, and this is the correct type locality, as noted by Creighton (1950).

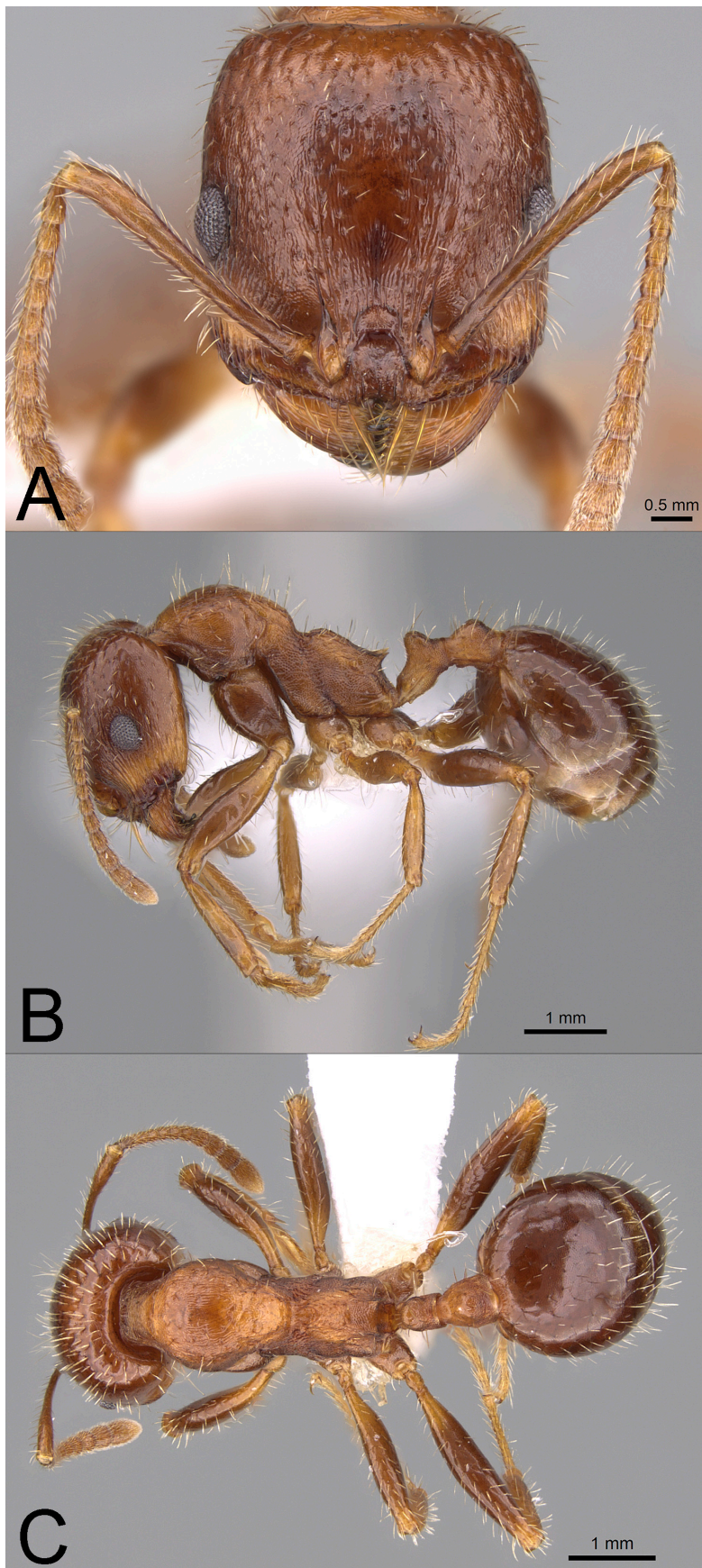


FIGURE 48. Photograph of *Veromessor stoddardi* minor worker: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0922825). Photographs by Michele Esposito from www.AntWeb.org.

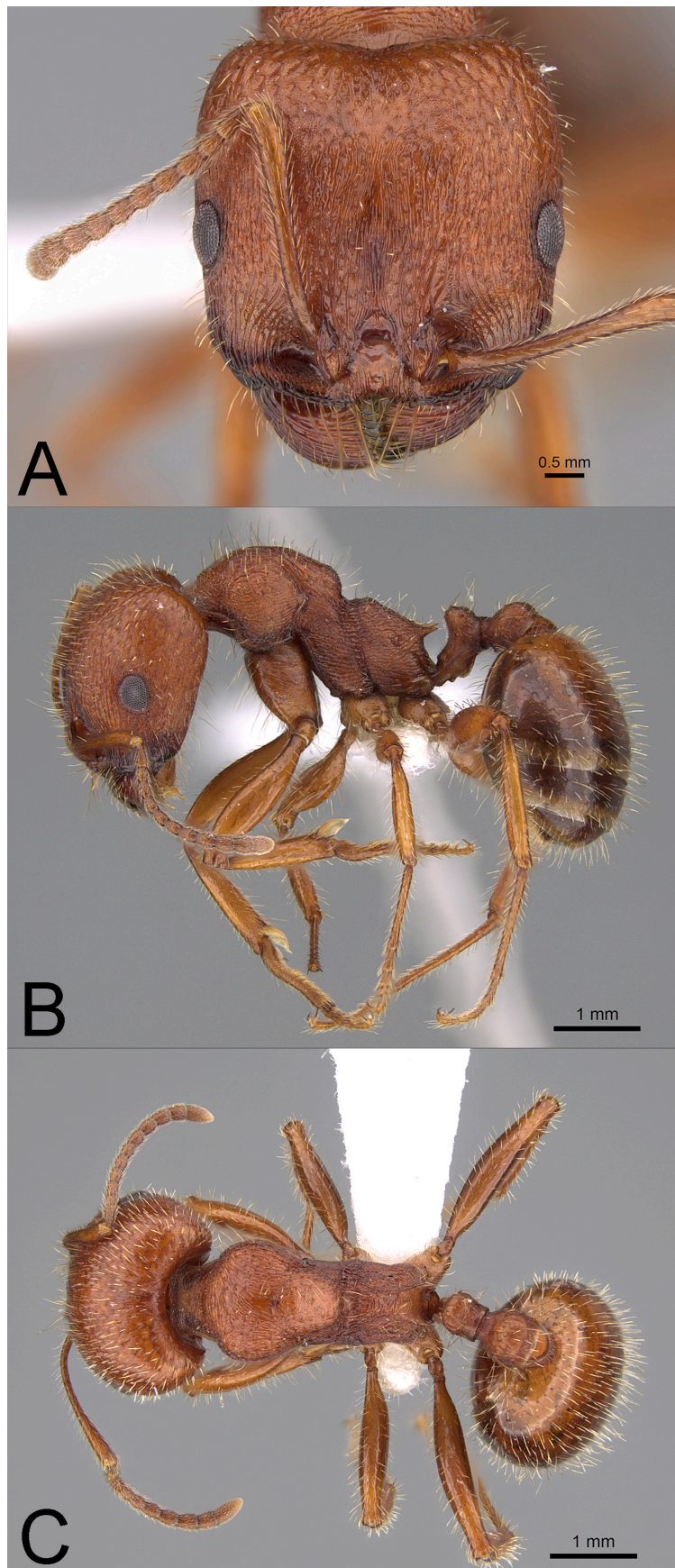


FIGURE 49. Photograph of *Veromessor stoddardi* major worker: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (CASENT0922824). Photographs by Michele Esposito from www.AntWeb.org.

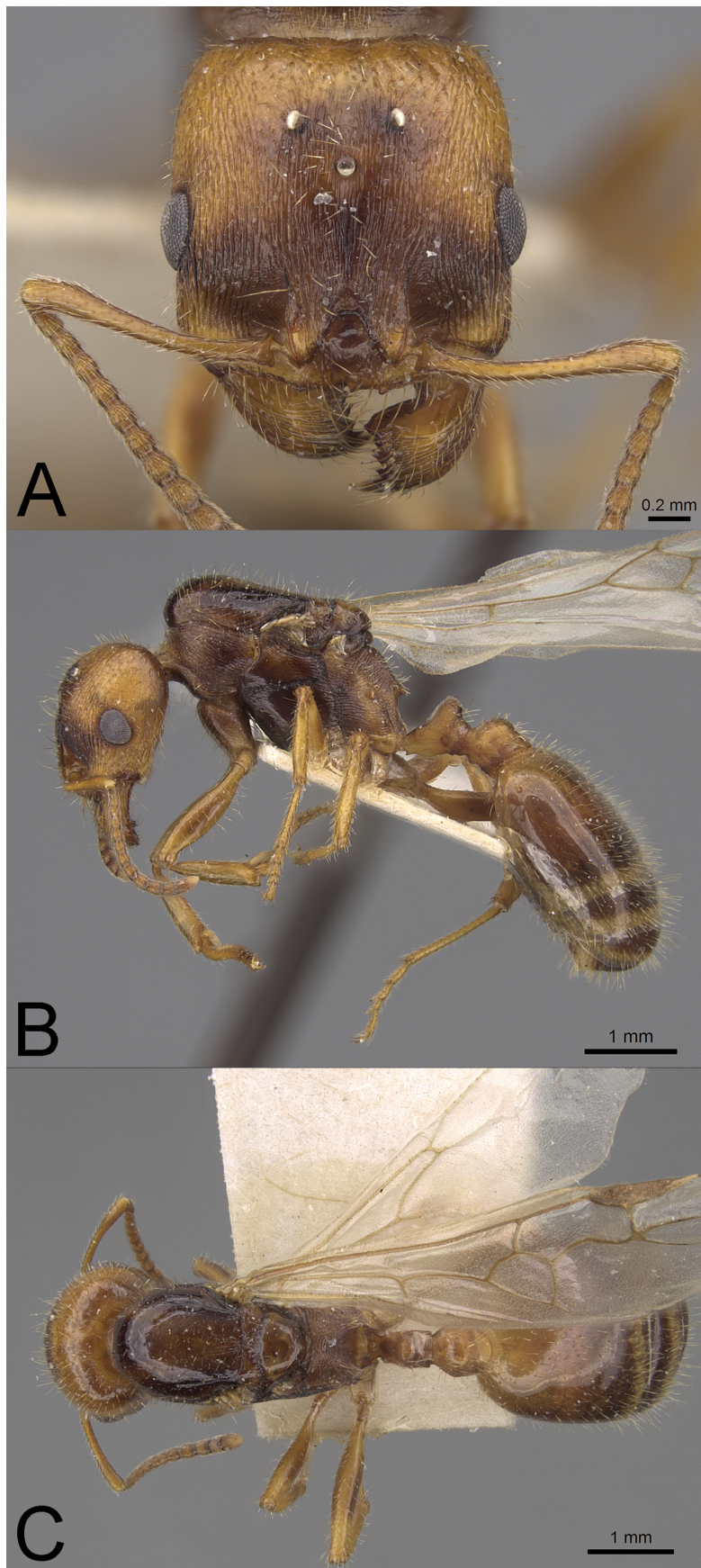


FIGURE 50. Photograph of *Veromessor stoddardi* alate queen: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (LACMENT370303). Photographs by Wade Lee from www.AntWeb.org.

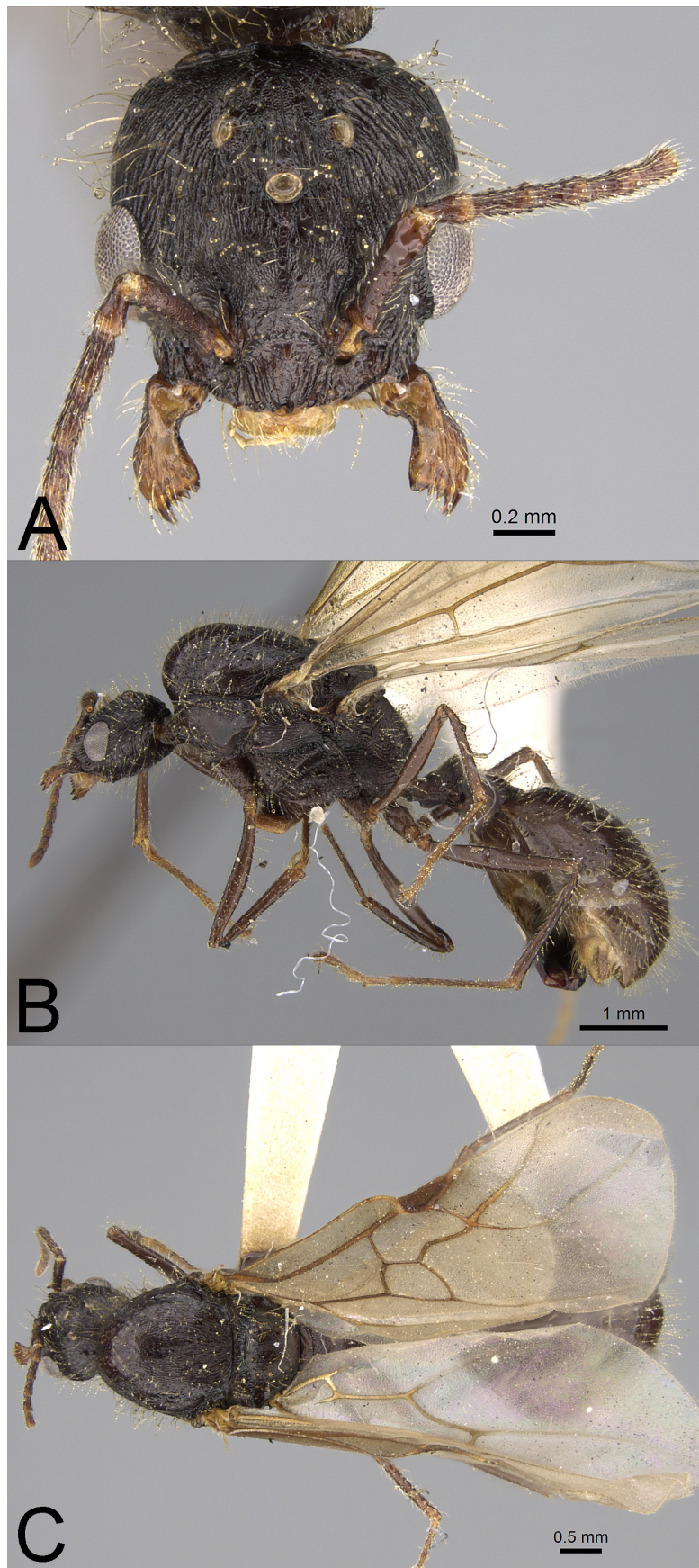


FIGURE 51. Photograph of *Veromessor stoddardi* male: (A) frontal view of head, (B) lateral view of body, and (C) dorsal view of body (LACMENT364104). Photographs by Michele Esposito from www.AntWeb.org.

Biology. Workers of *V. stoddardi* are solitary foragers that commence activities near dusk and forage through the night (M. Bennett, pers. comm.). Another observer indicated that colonies have long foraging columns (K.L. Jorda, pers. comm.), such that more information is needed to understand foraging biology of this species. Colonies probably contain 1,000–2,000 workers (Creighton, 1953; R.A. Johnson, pers. obs.). Workers are strongly polymorphic. Nests are often placed in hard clay soil and often have two to three entrances (Creighton, 1953).

Gland chemistry has not been examined in *V. stoddardi*. Like other small-colony congeners, workers of *V. stoddardi* have a small pygidial gland reservoir and lack a textured tergal cuticle (Hölldobler *et al.*, 2013).

Mating flights occur near dusk and post-dawn hours in June and July (Creighton, 1953; M. Bennett, pers. comm.). Nothing is known about mating frequency or colony founding.

Veromessor stoddardi occurs at elevations from 60–980 m, and it appears to be mostly restricted to soils with higher clay content (M. Bennett, pers. comm.). This species occurs in the Baja California desert, California coastal sage and chaparral, and California montane chaparral and woodlands ecoregions, as defined by Olson *et al.* (2001) (Figure 52).

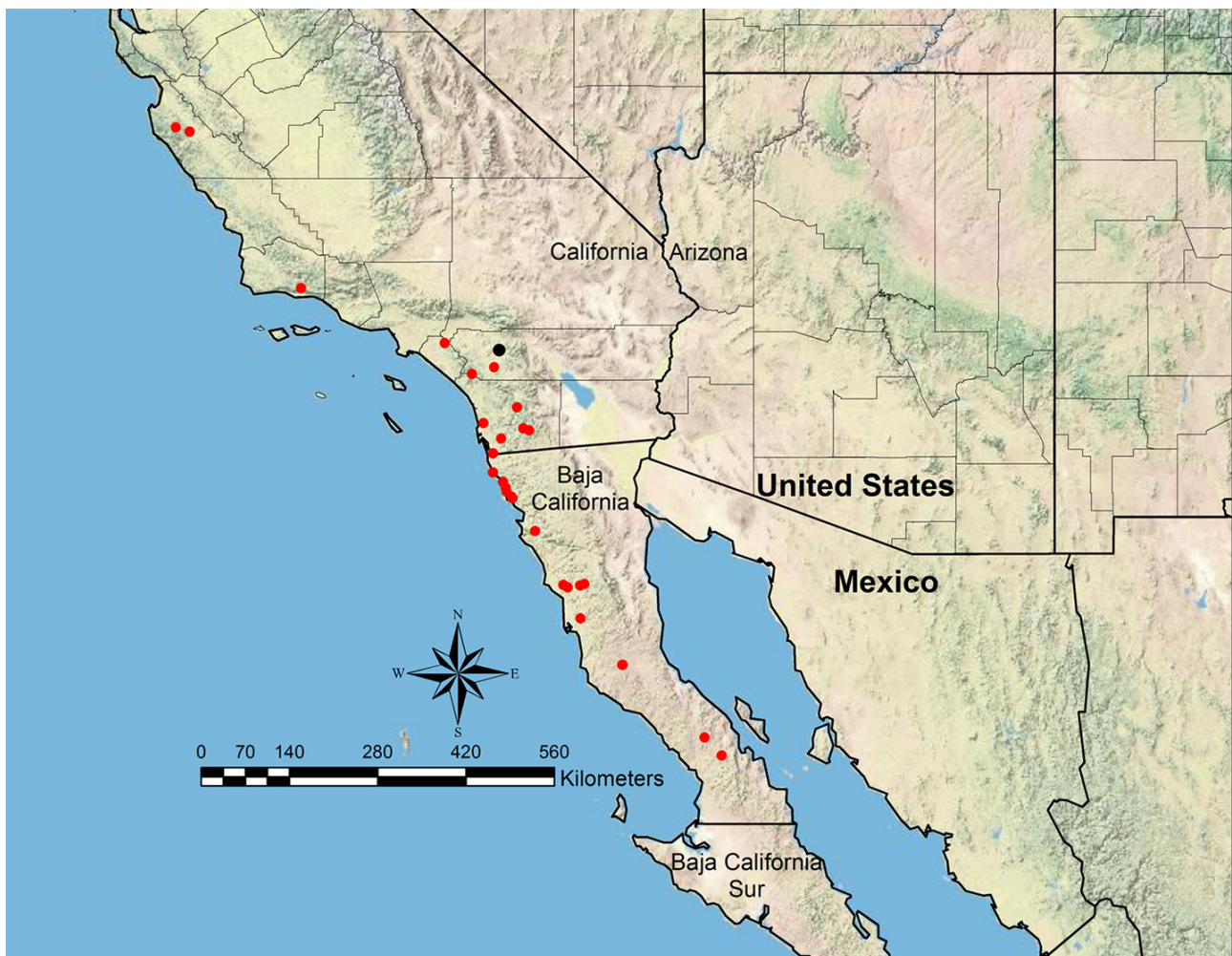


FIGURE 52. Geographic distribution of *Veromessor stoddardi*. The larger black circle denotes the type locality.

Additional notes

We also note a putative new species of *Veromessor* that is unavailable to describe until additional material is collected. Two workers of this species were collected from the northern end of the Mohawk Dunes, Yuma County, Arizona, during summer (year unknown). These specimens were examined by Roy Snelling, who stated that they were a new species closely related to *V. pergandei*. These two specimens were undoubtedly deposited at LACM, but the senior author could not find these workers during a visit to LACM in 2018, and they are presumed lost. The senior author and others (including RRS) have revisited Mohawk Dunes multiple times through the years without

finding additional specimens, and we write this addendum so that other collectors can be on the lookout for this species. We presume that this is a small-colony, nocturnal species given the difficulty finding additional specimens. As a note on geographic range, there are numerous sand dunes in the area, and we presume this species would also occur south into the sand dunes of the Gran Desierto Altar in northwestern Sonora, Mexico. We predict ecology of this species (Table 1 and below), which we list as *V. sp. cf. pergandei*.

Biology of *Veromessor*

Veromessor is an interesting genus because it contains relatively few species, yet notable interspecific variation occurs in several morphological and ecological traits. Morphological variation occurs in degree of psammophore development, degree of worker polymorphism and worker body size, size of the propodeal spines, and eye size and structure; ecological variation occurs in colony size and associated foraging method, seasonality of mating flights, and queen size and colony founding strategy. We also discuss mating frequency given that queens of *V. pergandei* mate with multiple males. Interspecific variation in each character is discussed below, while a companion paper maps these traits onto a molecular phylogeny (M.L. Borowiec, unpub. data). Moreover, species of *Veromessor* are used in ecological, sociobiological, and behavioral studies such that it is important to understand if trait evolution results from convergent evolution or common ancestry. Distribution patterns also are discussed because some species display parapatric distributions, while other species are broadly sympatric but may or may not occur at the same locales or in the same habitats (see also Bennett, 2000; Johnson, 2000b).

Psammophore development

The psammophore consists of numerous long hairs that extend from the lateroventral margin of the head. The function of these hairs is unknown, but it has been suggested that they are used to carry sand or soil (Porter & Jorgensen, 1990; Spangler & Rettenmeyer, 1966; Wheeler, 1907). Psammophores can also be used to carry seeds. Johnson (1991) observed *Pogonomyrmex rugosus* workers carry multiple seeds in their psammophore when presented with a patch of novel seeds, whereas *V. pergandei* did not use their psammophore to carry multiple seeds. Psammophores are rare in ants, but they are common in species that inhabit arid areas, with up to one-third of the species in some desert areas possessing psammophores (Bernard, 1948).

The psammophore ranges from poorly to well developed across species of *Veromessor*, with development diagnosed by number and distribution of J-shaped hairs on the ventral surface of the head capsule (=hypostomal region). As discussed by Bennett (2000), the psammophore in species of *Veromessor* can be placed into four categories of increasing development: (1) J-shaped hairs mostly absent, with scattered straight or evenly curved hairs, (2) J-shaped hairs present but not arranged in a distinct row, usually mixed with straight or evenly curved hairs, (3) J-shaped hairs arranged in a V-shaped row which does not reach the posterior part of the lateroventral margin of the head capsule, usually mixed with straight or evenly curved hairs, and (4) J-shaped hairs arranged in a distinct row around the lateroventral margin of the the head capsule (Table 1, Figure 6).

Across species of *Veromessor*, psammophore development loosely corresponds with habitat. The three species with the most poorly developed psammophores (*V. andrei*, *V. chicoensis*, *V. stoddardi*) are restricted to the more mesic California coastal ranges, the California Central Valley, and Sierra Nevada foothills. *Veromessor chamberlini* has a moderately well developed psammophore, and it is also restricted to more mesic southern California coastal habitats. The two other species with a moderately well developed psammophore (*V. lobognathus*, *V. smithi*) are widespread and inhabit cooler, higher elevation areas such as pinyon pine-juniper habitats. Two species with well developed psammophores (*V. julianus*, *V. pergandei*) inhabit low elevation, hot desert environs, while the other two species (*V. lariversi*, *V. pseudolariversi*) inhabit both low elevation, hot desert and mid-elevation, cool desert environs; all four species often occur in sandy habitats (see also Wheeler, 1907). This interspecific variation suggests that degree of psammophore development is subject to environmental pressures.

TABLE 1. Summary of morphological and ecological traits for species of *Veromessor*.

Species ^{&}	Psammophore development [*]	Propodeal spine length ⁺	Degree of worker polymorphism	Colony size; foraging strategy	Timing of mating flights	Colony founding strategy
<i>andrei</i>	2	≥ 3.0	monomorphic	large; column	summer	semi-claustral; obligate forager
<i>chamberlini</i>	3	≥ 3.0	monomorphic	small; solitary	summer	?
<i>chicoensis</i>	1	< 1	polymorphic	small; solitary or with short column	summer	semi-claustral; obligate forager?
<i>julianus</i>	4	≥ 2	weakly polymorphic	large; column	late winter/spring	?
<i>lariversi</i>	4	< 1	monomorphic	small; solitary	summer	?
<i>lobognathus</i>	3	1-1.5	monomorphic	small; solitary	summer	?
<i>pergandei</i>	4	< 1	weakly polymorphic	large; column	late winter/spring	fully claustral
<i>sp. cf. pergandei</i>	?	?	?	small; solitary?	late winter/spring?	?
<i>pseudolariversi</i>	4	< 1	monomorphic	small; solitary	summer	?
<i>smithi</i>	3	< 1	monomorphic	small; solitary	summer	?
<i>stoddardi</i>	1	< 1	polymorphic	small; solitary or with short column	summer	?

[&]species are listed in alphabetical order, except for *sp. cf. pergandei*, which is an undescribed species in which known specimens are presumed lost. See text under Additional notes.

^{*}variation in psammophore development with regard to number and distribution of long J-shaped hairs on the ventral surface of the head capsule (=hypostomal regions) (see text): (1) J-shaped hairs mostly absent with scattered straight or evenly curved hairs, (2) J-shaped hairs present but not arranged in a distinct row, usually mixed with straight of evenly curved hairs, (3) J-shaped hairs present arranged in a V-shaped row which does not reach the posterior part of the lateroventral margin of head capsule, usually mixed with straight or evenly curved hairs, (4) J-shaped hairs present, many long J-shaped hairs arranged in a distinct row around the outer margin of the ventral region of the head capsule.

⁺approximate length of propodeal spines relative to distance between their bases.

Propodeal spines

The function of propodeal spines is unclear, but the two primary hypotheses are that these spines function for defense or structural support (Blanchard & Moreau, 2017; Sarnat, Friedman, Fischer, Lecroq-Bennet, & Economo, 2017; R. Keller, pers. comm.). Interestingly, size of the propodeal spines varies greatly across the few species of *Veromessor*. The spines are short (length less than to similar to distance between their bases) in *V. chicoensis*, *V. lariversi*, *V. pergandei*, *V. pseudolariversi*, *V. smithi*, and *V. stoddardi*, medium length (length about 1.0–1.5× as long as the distance between their bases) in *V. lobognathus*, long (length $\geq 2\times$ as long as the distance between their bases) in *V. julianus*, and very long (length $\geq 3\times$ as long as the distance between their bases) in *V. andrei* and *V. chamberlini* (Table 1).

Eye size and structure

The eyes of insects possess an incredible array of adaptations to enhance vision across the gamut of light levels that they experience. One commonly studied contrast relates to differences in eye structure between nocturnal and diurnal species, with nocturnal species typically having larger eyes and larger eye facets. Cuticular pigment level also often is correlated with level of ambient light, with species having little or no cuticular pigment typically living in dim light to lightless environments.

Eye structure and pigment level varied between nocturnal and diurnal species of *Veromessor*, as well as in three other ant genera (*Myrmecocystus*, *Aphaenogaster*, *Temnothorax*) (Johnson & Rutowski, 2022). *Veromessor* contains two species (*V. lariversi* and *V. pseudolariversi*) that are pale in color, i.e., light yellowish to yellowish-orange, while all other congeners are darker (Johnson & Rutowski, 2022). Differences in pigment level correlated with foraging time—pale species mostly are strict nocturnal foragers whereas dark species usually forage diurnally, or foraging activity is temperature dependent (diurnal during cool seasons, nocturnal during hottest seasons), and several species are largely matinal-crepuscular-nocturnal foragers (*V. julianus*, *V. smithi*, and *V. stoddardi*).

As predicted, both pale species had large eyes, but they displayed a different eye structure. *Veromessor pseudolariversi* had larger eyes and more eye facets than *V. lariversi*, but mean facet diameter was similar for the two species (Figures 30 & 53), despite their being sister species. All three variables (eye size, facet number, facet diameter) were larger for these two species than for all other dark congeners except for *V. smithi*. Compared to *V. pseudolariversi*, the eyes of *V. smithi* were smaller and had fewer facets, but facet diameter was similar. Compared to *V. lariversi*, the eyes of *V. smithi* were larger and facet diameter was larger, but facet number was similar (Figure 53). Moreover, eyes of the two pale species of *Veromessor* evolved to maximize sensitivity over resolution, which is the pattern typical for most nocturnal insects with apposition eyes (Greiner, 2006; Stöckl, Smolka, O’Carroll, & Warrant, 2017).

Worker polymorphism and worker body size

The genus *Veromessor* is interesting because workers range from monomorphic to polymorphic (Table 1). Most species are monomorphic (*V. andrei*, *V. chamberlini*, *V. lariversi*, *V. lobognathus*, *V. pseudolariversi*, *V. smithi*), but two species are weakly polymorphic (*V. julianus*, *V. pergandei*) and two species are polymorphic (*V. chicoensis*, *V. stoddardi*). All species of *Veromessor* that display some degree of polymorphism show monophasic allometry, which is the most primitive form of polymorphism in which growth is nonisometric (Wills, Powell, Rivera, & Suarez, 2018; Wilson, 1953). Worker polymorphism has been examined in detail only in the weakly polymorphic *V. pergandei*, where workers display an annual cycle of mean body size with the largest workers present during winter months (Gordon, 1978; Rissing, 1987). Additionally, some tasks are related to worker size in *V. pergandei*. For example, *Steatoda* and *Asagena* spiders prey on workers of *V. pergandei*, but only the largest 30% of workers remove webs of these species from the foraging column, and only the largest workers retrieve nestmates that are ensnared in webs (Kwapich & Hölldobler, 2019). Groups of polymorphic workers also dig longer nests with more branching than do groups of monomorphic workers, and larger workers build tunnels with a larger diameter (Kwapich *et al.*, 2018). Further studies should examine distribution of body sizes within and across colonies for all species. These studies should include seasonal and geographic variation in worker body size given the annual cycle displayed by colonies

of *V. pergandei* (Rissing, 1987), along with the size-frequency distribution for foragers within colonies, as graphed by Rissing and Pollock (1984).

Species of *Veromessor* also show morphological similarities and differences within groups of ecologically similar species. The three large-colony species (*V. andrei*, *V. julianus*, *V. pergandei*) form one group of ecologically similar species, while small-colony species form three groups of ecologically similar species: (1) *V. lariversi* and *V. pseudolariversi*, (2) *V. lobognathus* and *V. smithi*, and (3) *V. chicoensis* and *V. stoddardi*. Two of the large-colony species, *V. julianus* and *V. pergandei*, have a similar allometry for head width versus head length and mesosoma length versus pronotum width. For *V. andrei*, the allometry for mesosoma length versus pronotum width is similar to that of *V. julianus* and *V. pergandei*, but head length in *V. andrei* is greater than head width for any given worker size in the other two species. Workers of *V. andrei* are also less variable in size than those of *V. julianus* and *V. pergandei* (Figure 54).

The ecologically similar pairs of small-colony species display two patterns. First, body size varies across groups with there being a group of smaller species (*V. lariversi*, *V. pseudolariversi*), a group of larger species (*V. lobognathus*, *V. smithi*), and a group of polymorphic species (*V. chicoensis*, *V. stoddardi*). The former two groups also have one species that has greater variation in body size (Figure 55). *Veromessor chamberlini* does not readily fit into any of these species groups.

Colony size and foraging method

Species of *Veromessor* display a dimorphism in colony size with three species (*V. andrei*, *V. julianus*, *V. pergandei*) having colonies that probably greatly exceed 50,000 workers, while the other seven species have colonies that typically range from several hundred to 1,000–2,000 or more workers. All three large-colony species forage in columns that extend 10–40 m from the nest, with workers dispersing into a fan to forage individually near the end of the column (for a review see Plowes, Johnson, & Hölldobler, 2012). In contrast, all small-colony species use solitary foraging, although *V. chamberlini*, *V. chicoensis*, and *V. stoddardi* sometimes forage in short columns (Table 1; M. Bennett, pers. comm.; R.A. Johnson, pers. obs.).

Colony size and foraging strategy also correlate with development of the pygidial gland. The three large-colony, column foraging species possess a well developed pygidial gland that consists of large paired clusters of glandular cells, large paired reservoir sacks, and a pair of distinct textured cuticle structures associated with the gland. In contrast, the pygidial gland reservoir and textured tergal cuticle structures are lacking or rudimentary in six of the seven small-colony species (not examined in *V. lariversi*) (Hölldobler *et al.*, 2013). These two groups of species should be examined for additional differences in glands and gland chemistry.

Seasonality of mating flights

Most desert ants have summer mating flights that are triggered by rain (Johnson, 2000b, 2001). In contrast, all species of *Veromessor* have mating flights that appear to be triggered by photoperiod, i.e., flights do not occur in response to rains. All species of *Veromessor* appear to release few sexuals per day over a period of up to several weeks. Photoperiod-triggered mating flights appear to be a derived trait given that species of *Novomessor*, the mostly closely related genus (Ward *et al.*, 2015), have mating flights triggered by summer rains (Johnson, 2000b). Most species of *Veromessor* have summer mating flights (June–August), whereas those of *V. julianus* and *V. pergandei* occur during late winter–early spring (Johnson, 2000a). The late winter–spring flights for these two species correlate with their being the only two species of *Veromessor* that are restricted to hot desert habitats (Wheeler & Wheeler, 1973). Queens of both species have poor heat tolerance compared to species of *Novomessor* and *Pogonomyrmex* (see Johnson, 2000a), suggesting that *Veromessor* queens could not survive hot summer soil temperatures (see also Rissing, Johnson, & Pollock, 1986). Moreover, it seems probable that shifting mating flights from summer to late winter–early spring was prerequisite to these two species invading hot desert habitats (Johnson, 2000a, 2001). Based on these patterns, we predict that mating flights of *V. sp. cf. pergandei* (sexuals are unknown) occur during late winter or spring (Table 1).

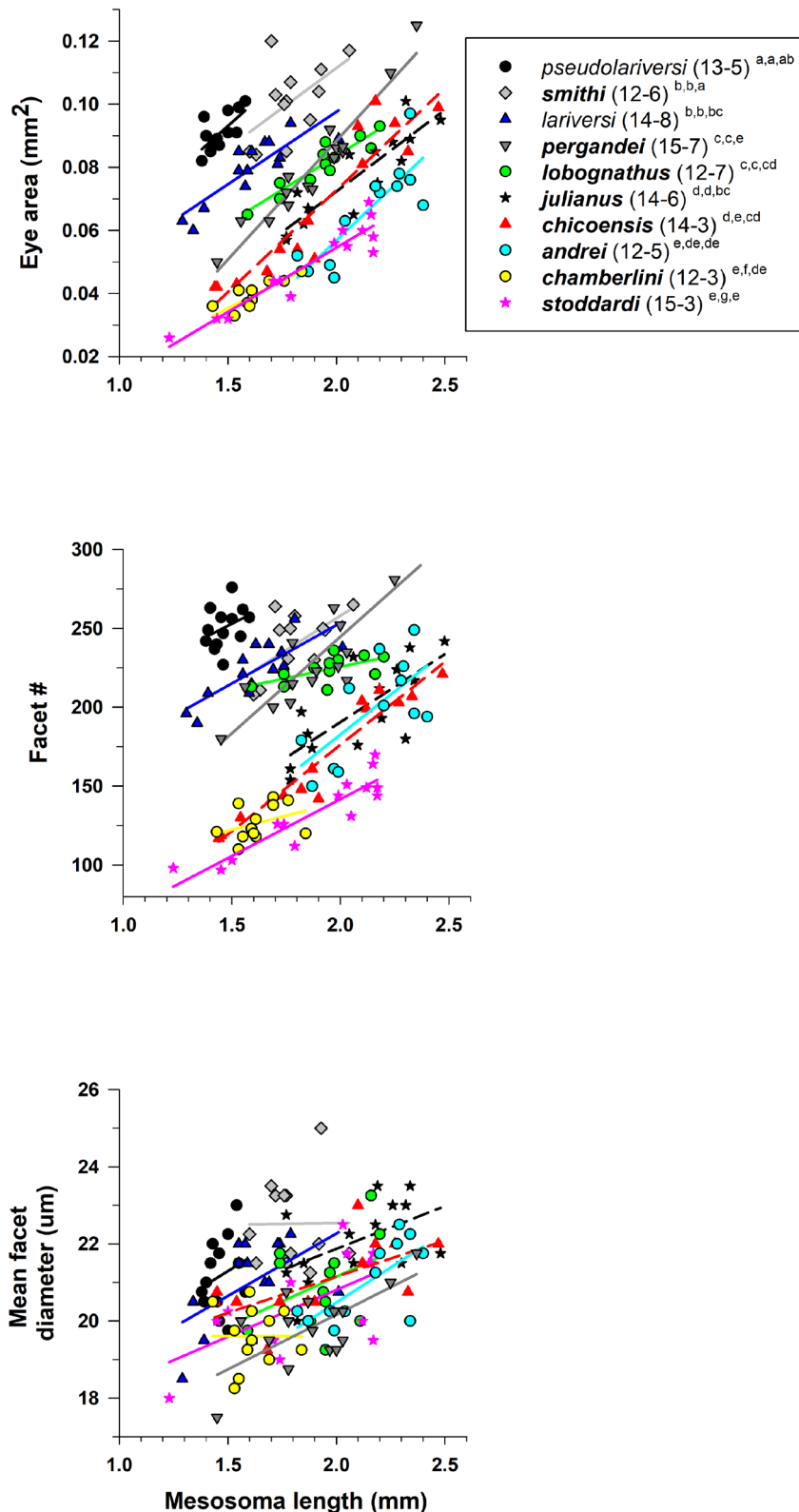


FIGURE 53. Eye area (mm²) (A), facet number (B), and mean facet diameter (µm) (C) for pale and dark colored species of *Veromessor*. Two species are pale (*V. lariversi*, *V. pseudolariversi*—open symbols and regular font), while the other eight species are dark (filled symbols and bold font). For each species, number of workers examined and number of colonies they were derived from is given in parentheses. Significant differences ($P < 0.05$) among species are denoted after each species name by the letters *a–g*: $a > b > c > d > e > f > g$; the three sets of letters for each species correspond to panels A, B, and C, respectively. Groupings are based on univariate F tests within MANCOVA followed by pairwise comparisons using a least significant differences test (see also Johnson & Rutowski, 2022).

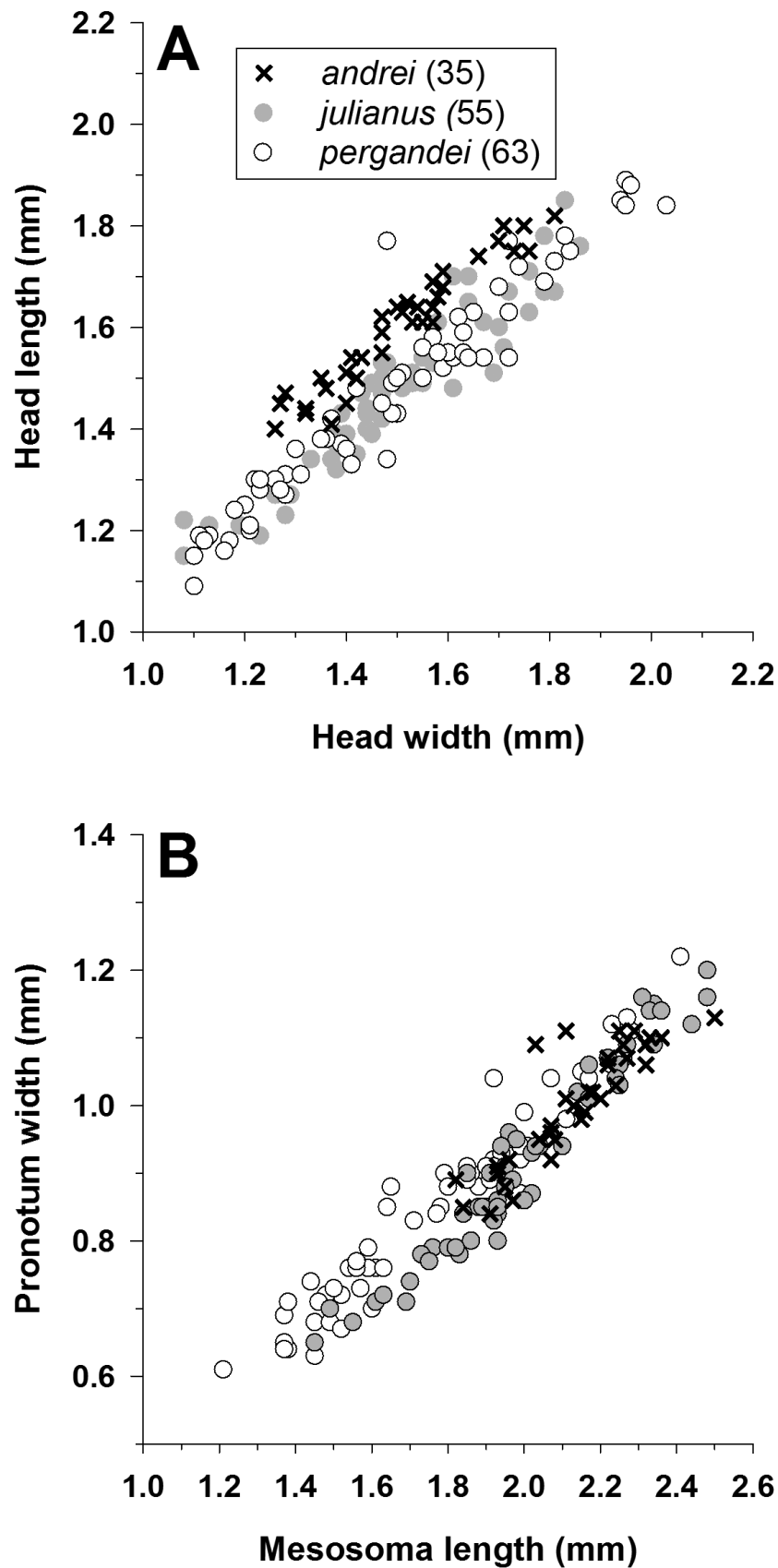


FIGURE 54. Bivariate plots for workers showing head width versus head length (A) and mesosoma length versus pronotum width (B) for the three large colony species of *Veromessor* (*V. andrei*, *V. julianus*, *V. pergandei*). Sample size for each species is given in parentheses.

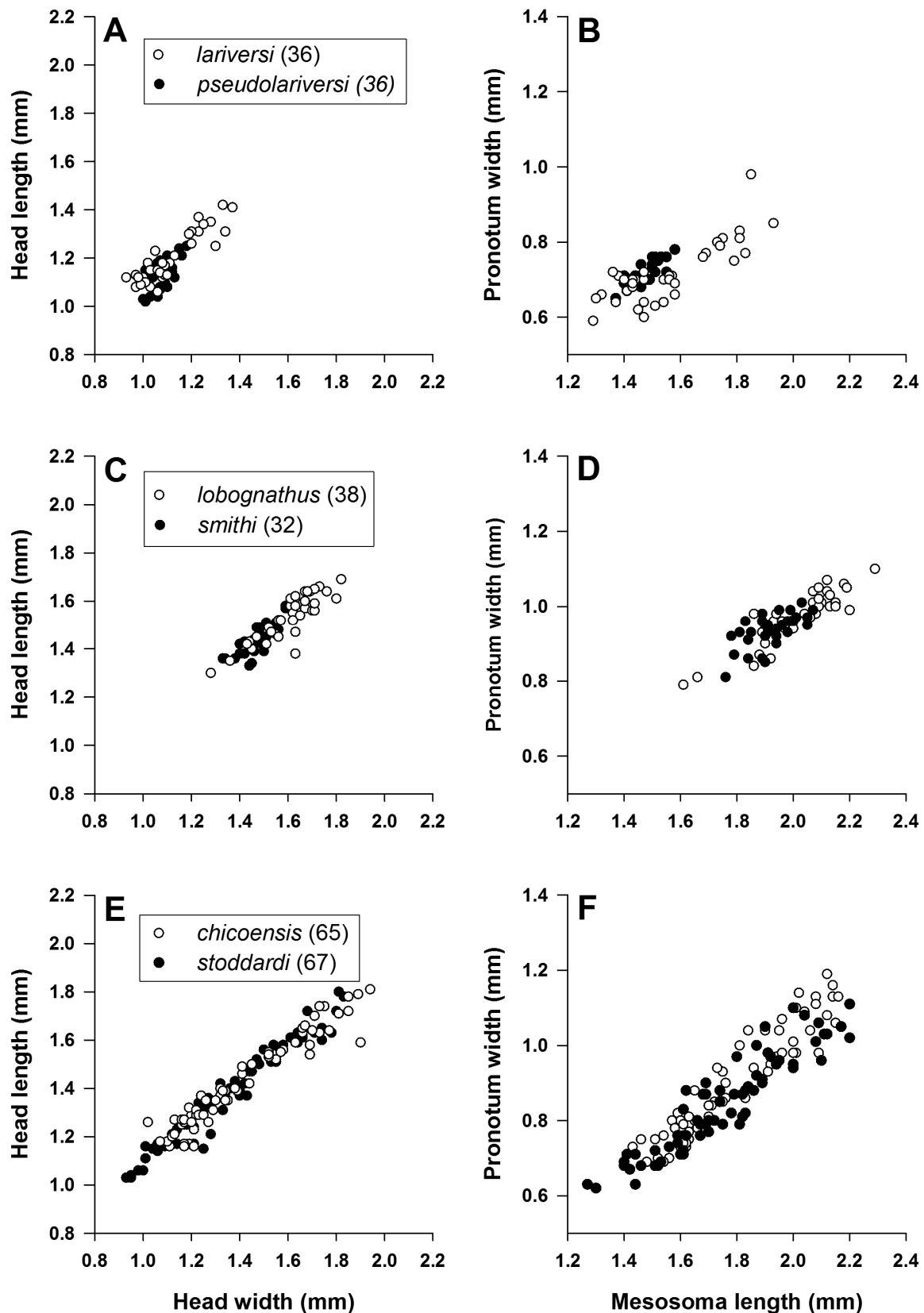


FIGURE 55. Bivariate plots for workers showing head width versus head length (left panels) and mesosoma length versus pronotum width (right panels) for ecologically similar pairs of small colony species of *Veromessor*: *V. lariversi* and *V. pseudolariversi* (A–B), *V. lobognathus* and *V. smithi* (C–D), *V. chicoensis* and *V. stoddardi* (E–F). Note that the x-axis scale is the same for all panels on the left and for all panels on the right so that sizes can be compared directly across species groups. Sample size for each species is given in parentheses.

Mating frequency

Obligate multiple mating (effective queen mating frequency ≥ 2) is rare in ants (but see Denny, Franks, Powell, & Edwards, 2004; Overson, Fewell, & Gadau, 2016; Villesen, Murakami, Schultz, & Boomsma, 2002; Wiernasz, Perroni, & Cole, 2004). Little is known about mating frequency in species of *Veromessor*, but we include this topic to highlight the need for data so as to determine if species variation correlates with life history traits such as colony size. Mating frequency is known only for *V. pergandei*, in which queens mate with multiple males; patriline number ranges from one to seven (mean = 3.80, $n = 9$ colonies) with an effective mating frequency (M_e) of 2.56 (Kwapich *et al.*, 2017; Ode & Rissing, 2002). Additionally, the most productive colonies of *V. pergandei* had significantly fewer patrilines, a larger peak forager population, and a larger annual foraging range (Kwapich *et al.*, 2017).

Queen size and colony founding strategy

The evolution of queen size and method of colony founding is a promising research area given the wide variation in known queen founding strategies combined with the large variation in queen body size across species of *Veromessor* (Figure 56). The three large-colony, column foraging species have the largest queens in the genus, with an average dry mass of 20.5 mg for *V. pergandei* (see also Cahan & Rissing, 2005), 11.1 mg for *V. julianus*, and 7.5 mg for *V. andrei* (see above). The queens of *V. julianus* and *V. pergandei* are the largest queens in the genus, and these also are the only two species that are restricted to hot desert habitats (Wheeler & Wheeler, 1973), where increased body size can increase longevity under desiccating conditions (Johnson, 1998, 2021; Wiernasz & Cole, 2003). At the low end of the scale, size of *V. chicoensis* queens is similar to that of their workers (Figure 19), and undoubtedly this species has the lowest queen to worker dimorphism in the genus. The queens of *V. smithi* are also relatively small, with a size similar to or only slightly larger than that of workers (workers: HW = 1.33–1.61 mm, HL = 1.33–1.58 mm, ML = 1.76–2.07 mm; queens: HL = 1.40–1.63 mm, HW = 1.40–1.63 mm, ML = 2.06–2.38 mm). A similar range of queen body size also occurs in *Pogonomyrmex*, where queens of *P. schmitti* are similar in size to their workers (Johnson, 2015; Johnson & Cover, 2015).

Little is known about colony founding strategies for species of *Veromessor*. All species of *Veromessor* probably have independent colony founding, but this has only been documented in *V. andrei*, *V. julianus*, and *V. pergandei*. *Veromessor julianus* is haplometrotic (Johnson, 2000a), whereas *V. pergandei* displays geographic variation in founding strategy (see above). The larger queens of *V. pergandei* are fully claustral, while the smaller queens of *V. andrei* appear to be semi-claustral with obligate queen foraging based on their absence of storage proteins (Brown, 1999b). Nothing is known about colony founding for queens of small-colony species. However, if body size correlates with colony founding strategy, then queens for most to all small-colony species are predicted to be semi-claustral obligate foragers. For example, the very small size for queens of *V. chicoensis*, especially relative to worker size, suggests that this species is semi-claustral with obligate queen foraging. We also note that queens of *V. pseudolariversi* are very small (Figure 56), but they are much larger than their workers compared to the queens of *V. lobognathus* and *V. smithi*. Interestingly, *V. lariversi* and *V. pseudolariversi* have similar geographic ranges and are sympatric at several sites, but the queens differ in size with those of *V. pseudolariversi* being the smallest in the genus, while those of *V. lariversi* are the largest among small-colony species (Figure 56). Additional studies should examine colony founding strategies and variation in queen body size. For most of these species, it is doubtful that sufficient numbers of founding queens could be located to experimentally test founding strategy (e.g., Johnson, 2002, 2006). However, founding strategy might be inferred by comparing storage protein levels for alate queens across species (see Hahn, Johnson, Buck, & Wheeler, 2004).

Distribution patterns

Veromessor is mostly restricted to western North America with species inhabiting arid and semi-arid habitats, grasslands, sclerophyll woodlands, and desert scrublands. Distribution patterns of *Veromessor* are discussed in two groups that correspond to colony size—species that have large colonies (>50,000 workers) and species that have small colonies (usually < 1,000–2,000 workers) (see also Johnson, 2000b). The three large-colony species (*V.*

andrei, *V. julianus*, *V. pergandei*) have mostly parapatric distribution patterns with their ranges showing little to no overlap across the narrow contact zones that separate the species (herein we define parapatric as species that occupy separate but adjoining areas, such that only a small fraction of individuals in each species encounter the other species) (see Figure 1, pg 83 in Johnson, 2000b). *Veromessor julianus* is restricted to central and southern parts of the Baja California peninsula in Mexico, as well as a narrow band along cool Pacific coastal areas north to Bahía San Quintin (Johnson, 2000a, 2000b) (Figure 27A). Alternatively, *V. pergandei* occurs in the more xeric desert areas along the east coast of the peninsula south to northern Baja California Sur. Where these two species come in contact, *V. pergandei* occurs in more xeric microhabitats, i.e., in drier soils and/or at lower elevations (Johnson, 2000a). The different micro- and macrohabitats occupied by *V. julianus* and *V. pergandei* correlate with queen body size as queens of *V. pergandei* are larger than those of *V. julianus* (see also Wiernasz & Cole, 2003).

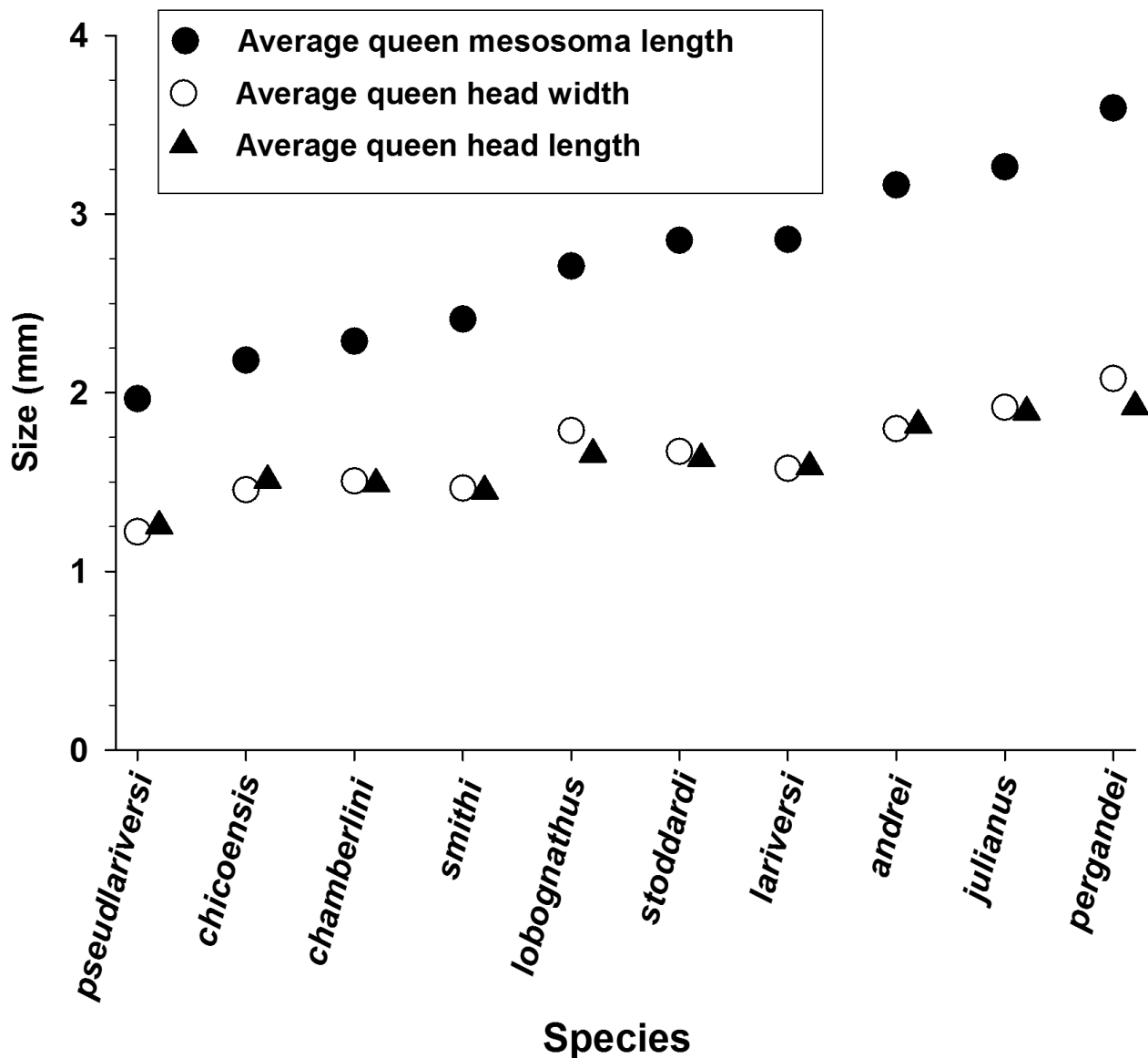


FIGURE 56. Queen body size across species of *Veromessor* based on average head width, average head length, and average mesosoma length. Species are ordered (left to right) from shortest to longest mesosoma length.

Veromessor julianus and *V. andrei* contact each other only near Bahía San Quintin, Baja California, Mexico (Figures 10A, 27A). *Veromessor pergandei* and *V. andrei* rarely coexist as the latter species inhabits the cool foothills of the California coastal range and inland valleys from northwestern Baja California to southern Oregon. In contrast, *V. pergandei* inhabits hot desert areas to the east and only occasionally penetrates to the adjacent coastal valleys, but rarely above elevations of 1,100–1,200 m (see also Johnson, 2000a, 2000b); there are also several records for *V. pergandei* in hot coastal areas of California such as in the Central Valley (Figure 41A).

The other seven species of *Veromessor* have relatively small colonies with number of workers ranging from several hundred to 1,000–2,000 or more. Distribution patterns of these species can be divided into three groups: (1) three California species (*V. chamberlini*, *V. chicoensis*, *V. stoddardi*) that occur in non-desert areas of the California coastal range west of the Sierra Nevada from northern to southern California, with one species extending into central Baja California, (2) four broadly sympatric species (*V. lariversi*, *V. lobognathus*, *V. pseudolariversi*, *V. smithi*) that occur east of the Sierra Nevada in California and are most common in Nevada, with ranges sometimes extending into Arizona and adjacent states, and (3) one species (*V. sp. cf. pergandei*) that appears to be restricted to sand dunes of hot desert habitats in southwestern Arizona and probably northwestern Sonora, Mexico.

The first group consists of three species (*V. chamberlini*, *V. chicoensis*, *V. stoddardi*) that are restricted to California and Baja California. *Veromessor chicoensis* is geographically isolated from the other two species as it is restricted to the Sacramento and San Joaquin Valleys of northern and central California (Hamm & Kamansky, 2009) (Figure 10C). *Veromessor stoddardi* is most closely related to *V. chicoensis* (M.L. Borowiec, unpub. data), and these two species have a mostly contiguous distribution with *V. chicoensis* in northern coastal range areas, while *V. stoddardi* occurs in southern coastal range areas, with the nearest locales being about 170 km apart (Figures 10C, 52). *Veromessor chamberlini* occurs on Santa Cruz and Santa Rosa Islands and across locales along the southern base of the San Gabriel Mountains and in coastal areas north to near the San Francisco Bay area (Figure 10B).

The four species in the second group occur in California east of the Sierra Nevada and have broadly sympatric distributions. These species form two groups based on habitat of occurrence. *Veromessor lobognathus* and *V. smithi* typically inhabit mid-elevation, pinyon pine–juniper habitats, rocky bajadas, and buttes. Both species are sympatric at some locales (Figures 27C, 41C), but it is not known if these two species have different microhabitat preferences. Alternatively, *V. lariversi* and *V. pseudolariversi* typically inhabit high desert habitats, often in sandy soils. Both species have a similar geographic distribution and both species are sympatric at some sites (Figures 27B, 41B). It is not known if these two species have different microhabitat preferences.

The final species, *V. sp. cf. pergandei*, is only known from one hot desert habitat locale in sand dunes of southwestern Arizona.

Conclusions

The ant genus *Veromessor* consists of relatively few species, yet these species display wide variation in numerous traits. A companion paper reconstructs a phylogeny for the genus to better understand their species relationships and evolution of these traits. Most studies have focused on *V. pergandei*, and we encourage researchers to study the biology of this interesting genus with emphasis on species that have small colonies.

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