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Taxonomy, Biology, and Distribution of Seed Harvesting Ants in the *Pheidole californica* Complex (Hymenoptera: Formicidae)

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Abstract.—The *Pheidole californica* complex comprises three closely related and partly sympatric species of seed harvesting ants restricted to the western Nearctic region. An analysis of morphological variation in the minor workers and major workers (soldiers) reveals that these species are more variable than previously thought. Nevertheless, morphological characteristics were uncovered that are consistently diagnostic for each species. *Pheidole clementensis* Gregg may be distinguished from both *Pheidole californica* Mayr and *Pheidole creightoni* Gregg by the diagonal rather than longitudinal rugulae between the clypeus and the eye in lateral view. The closely related *P. californica* and *P. creightoni* are most readily distinguished from one another by the angle of their lateral cephalic setae. *Pheidole californica* has decumbent setae forming an angle of forty five degrees or less with the lateral margins of the head in full face view, while the cephalic setae of *P. creightoni* emerge at an angle of approximately ninety degrees. *Pheidole californica* is broadly distributed in the western Nearctic region. *Pheidole creightoni* and *P. clementensis* are more limited in their range, the former being found in foothill or plateau habitats in northern California, Oregon, Washington, and Nevada, while the latter is limited to foothill and coastal habitats of southern California and northern Baja California.

The cosmopolitan genus *Pheidole* is represented in the New World by more than 600 described species, which form a diverse and ecologically important component of many ant communities. Perhaps as a result of their dominance and diversity, the New World *Pheidole* have received considerable taxonomic attention (e.g., Mayr 1870, Emery 1895, Creighton 1950, Gregg 1959), culminating in a recent monograph (Wilson 2003) that more than doubled the number of described species.

Despite this attention the taxonomy of the New World *Pheidole* is not fully resolved. Many taxa are refractory to taxonomic characterization because of similarity between the species, as well as extensive intraspecific variation both within and among populations. *Pheidole californica, P. creightoni,* and *P. clementensis* comprise one such assemblage, here termed the *californica* complex, which is part of the larger "*pilifera* group" of Wilson (2003).

Among the three species included in this study, *P. californica* has both the largest geographic range and highest degree of intraspecific variation. In an attempt to encompass this variation, taxonomists of the late nineteenth and early twentieth century described additional species, and a number of subspecies and varieties (Emery 1895, Wheeler 1915, Cole 1933, 1936), although subsequent taxonomic work acknowledged the synonymy of most of these with *P. californica* (Creighton 1950, Gregg 1959, Wheeler and Wheeler 1986, Wilson 2003).

In spite of all this taxonomic attention *P. californica* remains a difficult ant to characterize, and the precise boundary between it and the other two species included in the study has never been rigorously examined. The purpose of the present contribution is to revise the taxonomy of the *californica* complex and to characterize

each species in a way that takes into account both intra- and interspecific variation.

MATERIALS AND METHODS

At the beginning of this study I traveled to sixteen localities in northern California, Washington, and western Nevada to intensively sample the *californica* complex. Between three and twelve nest series were obtained from each species at a given locality, along a transect that varied in length from one to twelve kilometers. The purpose of this sampling was to obtain baseline data on variation at the level of individual ants, colonies, populations, and species.

In addition to the material obtained specifically for this study, specimens were examined from the collections of Philip S. Ward (PSWC), the Bohart Museum of Entomology, University of California at Davis (UCDC), and the Los Angeles County Museum (LACM).

Measurements of specimens for use in the diagnoses and bivariate plots were taken at 50× using a Wild M5A microscope and a Nikon stage micrometer, and are presented to two decimal places. The following measurements and indices were utilized in this study:

HL Head length: length of the head in full face view, measured from the anterior extremity of the clypeal margin to the midpoint of an imaginary line drawn across the posterior margin of the head (after Ward 2000).

HW Head width: maximum width of head in full face (frontal) view, not including the eyes.

CI Cephalic Index: HW/HL.

EL Eye length: maximum diameter of the eye, measured with the head in lateral view.

REL Relative eye length: EL/HL.

PrW Pronotum width: maximum width of the pronotum, in dorsal view.

DML Dorsal mesosomal length: length of the mesosoma measured in dorsal view, from the anterior extremity of the pronotum near the articulation with the head to the posterior extremity of the propodeum (usually a cuticular flange near the articulation of the petiole). For this measurement, the specimen is adjusted in dorsal view so that the extremities of the pronotum and propodeum are simultaneously in focus.

PPW Postpetiolar width: maximum width of postpetiole in dorsal view.

SPECIES ACCOUNTS

The three species included in this study are members of the "*pilifera* group", a presumably monophyletic set of forty eight species of *Pheidole,* found almost exclusively in the Nearctic region, including Mexico (Wilson 2003). The group is characterized by reduced hypostomal teeth in the major, large eyes in the minor, and by the quadrate shape of the head in both major and minor (Wilson 2003). Within the *pilifera* group Wilson (2003) recognizes a cluster of species that he calls the "*pilifera* complex," which includes the species *P. calens, californica, carrolii, cavigenis, clementensis, creightoni, hoplitica, littoralis, micula, polymorpha, rugulosa, soritis, tepicana,* and *torosa.* Although it is unclear whether these species represent a monophyletic group, they are united by the traits (in the major) of extensive cephalic sculpture and, except in *P. carolli* and *P. littoralis,* transverse rugulae or carinulae on the posterior cephalic vertex ("occipital lobes" in Wilson 2003). Within this cluster of species I recognize a group of three species, here termed the *californica* complex, united by the trait of *highly developed* transverse rugulae (see Wilson 2003: 23) on the cephalic dorsum of the major.

In 1915, W.M. Wheeler described *P. californica* subsp. *micula.* Gregg (1959) later recognized this as a distinct species, *P. micula.* Although I have not examined type

material for this species, I have concluded that *P. micula* is not a member of the *californica* complex, because it lacks highly developed transverse rugulae on the cephalic dorsum of the majors. In his recent monograph, E. O. Wilson (2003) describes the dorsal cephalic sculpture of *P. micula* majors as consisting of transverse *carinulae* that sometimes wrap downward at the sides of the head. Wilson also presents the caveat, in the form of a personal communication from Stefan Cover, that not all specimens of *P. micula* possess such extensive cephalic sculpture. *Pheidole californica*, *P. clementensis*, and *P. creightoni* are unique among the members of the *pilifera*-group in having majors with *highly developed* cephalic sculpture consisting of transverse rugulae, as opposed to carinulae (see Wilson 2003: 23), which cover the posterior cephalic vertex, extend at least one fourth of the way to the clypeus in full face view, and are at least partly visible in lateral view. Thus, I am leaving *P. micula* out of the *californica* complex. Nevertheless, the question of a possible affinity of *P. micula* with members of the *californica* complex warrants further examination.

The diagnoses presented in the following species accounts are a summary of morphological features that are usually characteristic of the species and therefore useful in identification. The features that are most consistently diagnostic of species are presented in **bold face.** Intraspecific variation in the remaining traits makes them less useful for identification. In addition, the illustrations (Figs. 5–21) should not be interpreted as comprehensive representations of the respective species. Cephalic sculpture and setae vary dramatically within these species, and most of the differences shown in these figures are not diagnostic for the species. Reliably diagnostic features are indicated in the figures with arrows.

Pheidole californica Mayr 1870
(Figs. 5–8, 21)

Pheidole californica Mayr 1870:987. Description of worker.

Pheidole oregonica Emery 1895:291. Synonymy by Wilson (2003:564).

Pheidole californica var. *incenata* Wheeler 1915: 407. Synonymy by Creighton (1950:173).

Pheidole californica var. *satura* Wheeler 1915:407. Synonymy by Creighton (1950:173).

Pheidole californica subsp. *nevadensis* Wheeler 1915:408. Synonymy by Wheeler and Wheeler (1986:13).

Pheidole californica subsp. *pyramidensis* Emery 1922:105. Replacement name for subsp. *nevadensis* (junior primary homonym of *P. pubiventris* var. *nevadensis* Forel 1901:353). Synonymy by Wheeler and Wheeler (1986:13).

Pheidole californica var. *shoshoni* Cole 1933: 618. Synonymy by Gregg (1959:19).

Pheidole californica var. *hagermani* Cole 1936: 35. Synonymy by Creighton (1950:173).

Pheidole californica Mayr; Wheeler and Wheeler 1972:243 (description of larva).

Major worker measurements (n = 65): HL 0.98–1.28, HW 0.86–1.21, CI 0.87–0.97, EL 0.14–0.22, REL 0.12–0.19, PrW 0.40–0.56, DML 0.83–1.07, PPW 0.17–0.31.

Diagnosis of major worker.—Head in full face view subquadrate. Lateral margins of head weakly to strongly convex. Lobes of posterior cephalic vertex weakly developed, and the notch of the vertex therefore shallow (Fig. 6); rugulae originating on the lateral clypeal margin straight and longitudinal; those rugulae originating on the part of the clypeus directly in front of the eye terminating abruptly at the eye (Fig. 5); eyes usually large in relation to the length of the head (Fig. 5); in full face view, setae emerging laterally from the head **decumbent,** forming an angle of forty five degrees or less with the integument (Fig. 6); propodeal spines in side view typically in the form of equilateral triangles produced from the lateral margination of the propodeum (Fig. 7).

Minor worker measurements (n = 20): HL 0.53–0.72, HW 0.47–0.66, CI 0.86–0.94, EL 0.12–0.16, REL 0.21–0.26, PrW 0.30–0.39, DML 0.67–0.79, PPW 0.12–0.18.

Diagnosis of minor worker.—Mesosoma elongate (DML 0.67–0.79); foveolate (see Wilson 2003: 22) sculpturing dense and

continuous on the mesosoma in side view, covering the mesopleuron, metapleuron, propodeum, and lower parts of the mesonotum; foveolation often continuous onto the sides of the propodeal spines; propodeal spines usually equilaterally triangular in shape and produced from the lateral margination of the propodeum (Fig. 8).

Comments.—Beginning with the work of W.M. Wheeler (1915) and Cole (1933, 1936), the taxonomy of *P. californica* became complicated by the description of several subspecies and varieties, most of which did not differ strongly from *P. californica* sensu stricto. Subsequent work by Creighton (1950), Gregg (1959), Wheeler and Wheeler (1986), and Wilson (2003) consigned most of these names to synonymy with *P. californica.*

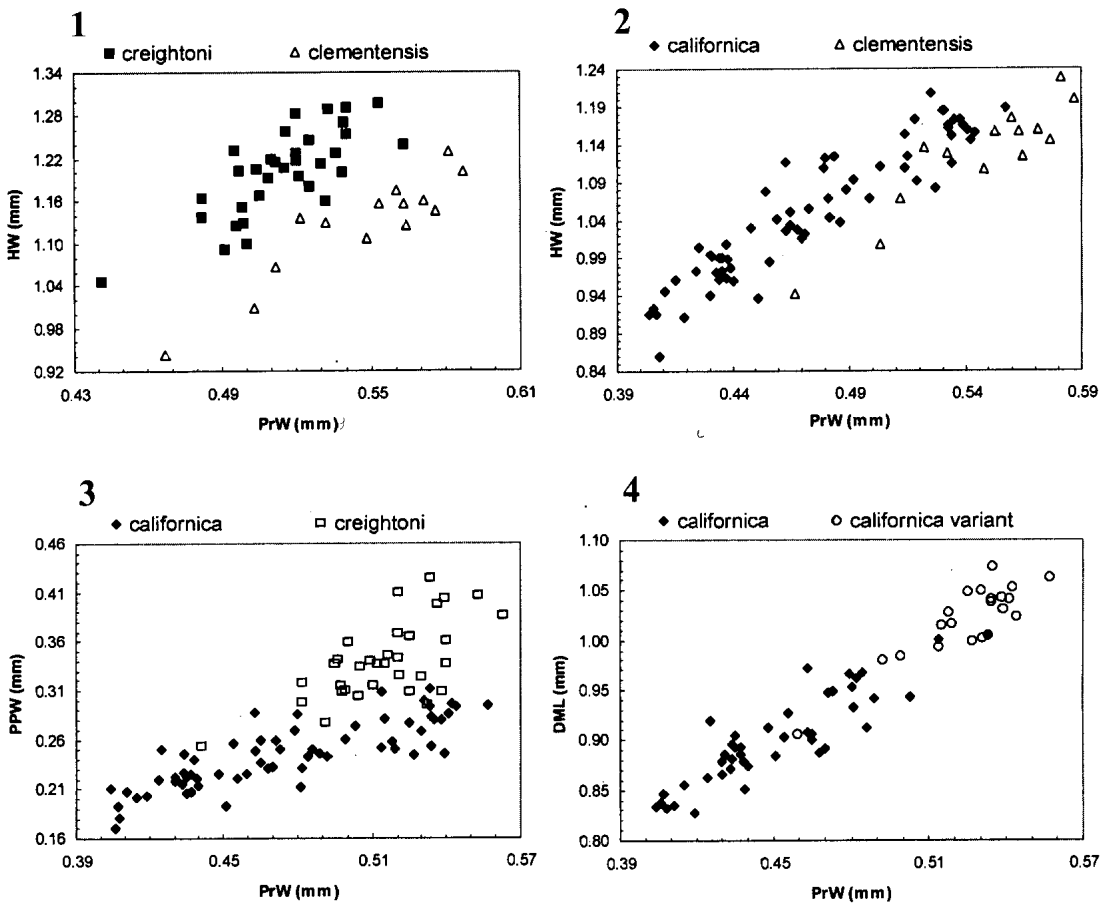
The large geographical range of *P. californica* is correlated with a greater amount of intraspecific variation. Although some local populations of *P. californica* appear to represent distinctive morphological forms, variation is continuous between populations, making it impossible to diagnose the unusual morphs in a useful way. Nevertheless, one morphological variant discovered during the course of the project bears mentioning because of its superficial resemblance to *P. creightoni* (compare Figs. 9–10 with 13–14). The eyes of this *P. creightoni*-like variant of *P. californica* tend to be small in relation to the length of the head (REL 0.12–0.16, n = 21), approaching the condition of *P. creightoni* and *P. clementensis* (compare Fig. 9 with Figs. 13 and 17). In addition, the setae of these ants are shorter and more erect than the setae of most *P. californica,* again approaching the condition of *P. creightoni.* However, these traits vary continuously between the *creightoni*-like variants of *P. californica* and *P. californica* sensu stricto. Additionally, it is important to note that morphology varies continuously within each colony of ants, and between colonies comprising a population, which adds to the difficulty of diagnosing unusual forms of a given species. Figure 21 compares majors of *P. californica* sensu stricto (d-f) with majors of *P. creightoni*-like variants of *P. californica* (a-c) from the same locality, illustrating both variation and continuity in head shape. Bivariate plots also fail to separate these variants from *P. californica* sensu stricto (Fig. 4). At the moment, *creightoni*-like variants of *P. californica,* as described above, are known only from northern California in the vicinity of the Sacramento River delta (see Fig. 25). Although more work will be necessary to determine the origin of these variants, it seems likely, in light of their resemblance to *P. creightoni,* that they are the product of gene flow between this species and *P. californica.*

Pheidole californica is probably most closely related to *P. creightoni,* from which it may be distinguished by the angle of its lateral cephalic setae (see diagnoses and key). The two species overlap broadly for all of the metric measurements that were taken (see *measurements* in the diagnoses), and bivariate plots do not separate the two species to a significant degree (Fig. 3). The affinity of the two species is also born out in the qualitative characteristics of coloration, body sculpture, and nest structure, all of which vary continuously between the species. Refer to the diagnoses of *P. clementensis* and *P. creightoni* for information on sympatry with *P. californica.*

Material examined (PSWC, UCDC, LACM).

MEXICO **Baja California:** 10.8mi E Meling Ranch, 4750′ (R. A. Johnson); 28km E Ensenada, 750m (P. S. Ward); Sierra Juarez, 12.3mi N Laguna Hanson, 5260′ (R. A. Johnson).

UNITED STATES **California:** *Alameda Co.:* Murietta Caves (R. M. & G. E. Bohart); Tesla Road, A.E.C. [Atomic Energy Commission site] (D. C. Rentz); *Alpine Co.:* Markleeville (R. R. Snelling) ; *Amador Co.:* 9km WNW Plymouth, 200m (P. S. Ward); *Butte Co.:* 13.3km N Paradise, 840m (D. O. Burge); 16.3km ENE Chico, 260m (D. O. Burge); 6.1mi. NE jct. hwy. 99 & Neal road (R. R. Snelling and P. Mehlhop); 9km N Oroville, 360m (P. S. Ward); Chico, Bidwell Park (T. Byler); Chico, Upper Bidwell Creek (L. Gheiza); Oroville (T. R. Haig); *Contra Costa Co.:* Black Diamond



Figs. 1–4. Bivariate plots of metric measurements in major workers of *Pheidole californica, P. creightoni,* and *P. clementensis.* HW = head width, PrW = pronotum width, PPW = postpetiolar width, DML = dorsal metasomal length.

Mines Regional Preserve, 360m (P. S. Ward); Mt. Diablo State Park, 670m (P. S. Ward); *El Dorado Co.:* 9km SW Pilot Hill, 340m (P. S. Ward); 14km NW Shingle Springs, 340m (P. S. Ward); *Fresno Co.:* Black Mountain, 7km ESE Prather, 1050m (P. S. Ward); Table Mountain Reserve, 300m (A. L. Wild); *Glenn Co.:* 8km ESE St. John Mtn., 750m (A. L. Wild); *Kern Co.:* Paine Wildflower Preserve, 70m (A. L. Wild); *Lake Co.:* McLaughlin Reserve, 19km ESE Lower Lake, 640m (P. S. Ward); McLaughlin Reserve, 19km ESE Lower Lake, 650m (A. L. Wild); *Lassen Co.:* 4km ENE Wendel, 1370m (P. S. Ward); 6km SE Wendel, 1230m (P. S. Ward); Eagle Lake, 1600m (P. S. Ward); Hallelujah Jct., 1440m (A. L. Wild); Hallelujah Junction, 1440m (D. O. Burge); Hallelujah Junction, 1440m (P. S. Ward); *Los Angeles Co.:* 2mi S Pearblossom, 3200′ (C. D. George); *Mendocino Co.:* 4.7km NNE Hopland, 292m (D. O. Burge); 4.7km NNE Hopland, 304m (D. O. Burge); *Modoc Co.:* Eagleville (R. R. Snelling) ; Stronghold, 4000′ (W. S. Creighton); *Monterey Co.:* 14km S Jolon, Fort Hunter Liggett MR, 360m (P. S. Ward); 14km SW Jolon, Fort Hunter Liggett MR, 640m (P. S. Ward); *Napa Co.:* 3km ESE Napa Junction, 150m (P. S. Ward); Mt George, 8km NE Napa, 320m (P. S. Ward); *Orange Co.:* 1mi NW El Toro, 450′ (R. J. Hamton); Pleasants Peak, Santa Ana Mtns., 1140m (P. S. Ward); *Placer Co.:* 2.54km SSW Dutch Flat, 940m (D. O. Burge); *Sacramento Co.:* 7.8km W Galt, 5m (D. O. Burge); Rancho Cordova, 25m (P. S. Ward); *San Diego Co.:* 18km E Mt. Laguna, 300m (P. S. Ward); 5mi N Descanso, 3000′ (J. H. Hunt); Chula Vista (CV2 edge), 160m (A. V. Suarez); Chula Vista (E end), 160m (P. S. Ward); Chula Vista (Paseo del Rey), 78m (A. V. Suarez); UC Elliott Reserve, 150m (A. V. Suarez); *San Mateo Co.:* Jasper Ridge, 150m (P. S. Ward); North Peak, Montara Mtn., 550m (P. S. Ward); San Bruno Mtn., 330m (P. S. Ward); *Santa Barbara Co.:* Santa Cruz Island (J. Longino); Santa Cruz Island Field Station, 70m (P. S. Ward); *Santa Clara Co.:* 10km SE San Jose, 240m (P. S. Ward); Palo Alto (Cala Heath); Stanford University (collector unidentified) ; *Santa Cruz Co.:* Boulder Creek, 800–900′ (J. Keesaw); Santa Cruz (R.

V. Chamberton); UC Santa Cruz campus, 230m (P. S. Ward); *Shasta Co.*: 1km WNW Lamoine, 630m (P. S. Ward); Enterprise, 175m (P. S. Ward); *Siskiyou Co.*: 17km SW Scott Bar, 640m (P. S. Ward); 26.8km S Tule Lake, 1420m (D. O. Burge); Weed (A. C. Cole); *Solano Co.*: 10km NE Dixon, 15m (P. S. Ward); 13km NW Dixon, 35m (P. S. Ward); 13km NW Rockville, 85m (P. S. Ward); Allendale (R. Waegell); Cold Canyon, 19km NNW Vacaville, 107m (D. O. Burge); Cold Canyon, 19km NNW Vacaville, 120m (P. S. Ward); Cold Canyon, 19km NNW Vacaville, 120m (D. M. Olson); Cold Canyon, 19km NNW Vacaville, 600m (P. S. Ward); Jepson Prairie, 18km S Dixon, 10m (P. S. Ward); South end of Lake Solano, 40m (R. Waegell); *Sonoma Co.*: 1km NNE Sonoma, 170m (P. S. Ward); 2km ENE Glen Ellen, 150m (P. S. Ward); 6km N Sonoma, 300m (P. S. Ward); Pepperwood Ranch, 15km N Santa Rosa, 360m (P. S. Ward); Sonoma, 25m (P. S. Ward); *Stanislaus Co.*: 22km WSW Patterson, 350m (D. O. Burge); Del Puerto Canyon, 22km WSW Patterson, 350m (P. S. Ward); Del Puerto Canyon, Frank Raines Regional Park, 340m (A. L. Wild); *Sutter Co.*: 7km NNW Sutter, 210m (P. S. Ward); *Tehama Co.*: 6km E Payne's Creek, 720m (P. S. Ward); 8.02km SSE Paynes Creek, 308m (D. O. Burge); 17.3km ESE Redbluff, 352m (D. O. Burge); hwy. 36, 5.8mi NE jct. w/hwy 99 (R. R. Snelling and P. Mehlhop); Redding (A. C. Cole); *Tuolumne Co.*: 3km SW Cold Springs, 1700m (P. S. Ward); 2mi W Chinese Camp (J. I. Stage); Sweetwater Campground, Stanislaus N.F. (S. Bloem); *Ventura Co.*: 29km WNW Stauffer, 1460m (P. S. Ward); *Yolo Co.*: 2.2km WSW Davis, 18m (D. O. Burge); 2km SSE Dobbins, 560m (P. S. Ward); 10 km N Davis, 10m (P. S. Ward); 10km W Winters, 60m (P. S. Ward); 13km W Rumsey, 710m (P. S. Ward); Berryessa Peak, 930m (P. S. Ward); Davis (P. S. Ward); Grasslands Regional Park, 8km SE Davis, 10m (P. S. Ward); *Yuba Co.*: Sierra Foothill Range, 18mi NE Marysville (F. A. Ludtke). **Idaho:** *Elmore Co.*: 5.5mi E Hammett (R. R. Snelling); *Gooding Co.*: Hagerman (A. C. Cole); *Owyhee Co.*: 3.3mi S Given's Hot Springs (R. R. Snelling); *Twin Falls Co.*: Twin Falls (A. C. Cole). **Nevada:** *Humboldt Co.*: Calico Mtns., 35mi N Gerlach (W. S. Creighton); *Washoe Co.*: 5km S Nixon, 1185m (P. S. Ward); 8.67km W Nixon, 1140m (D. O. Burge); Hanging Rock Canyon, 1750m (P. S. Ward); S end Pyramid Lake, 1140m (P. S. Ward). **Oregon:** *Deschutes Co.*: Smith Rock State Park, 880m (P. S. Ward); *Josephine Co.*: 8km SSW Cave Junction, 430m (P. S. Ward); *Lake Co.*: 5mi S Plush (R. R. Snelling); *Wasco Co.*: Maupin (W. S. Creighton). **Utah:** *Salt Lake Co.*: Salt Lake City (Grundmann). **Washington:** *Adams Co.*: McMannaman Lake, 260m (P. S. Ward); *Grant Co.*: Frenchman Coulee, 260m (P. S. Ward); *King Co.*: Seattle (T. Kincaid); *Okanogan Co.*: Riverside, 290m (D. O. Burge); *Whitman Co.*: Wawawai (W. M. Mann).

Pheidole creightoni Gregg 1955
(Figs. 13–16)

Pheidole creightoni Gregg 1955: 19 (w, q, m).

Major worker measurements (n = 34): HL 1.15–1.37, HW 1.05–1.30, CI 0.88–0.96, EL 0.17–0.21, REL 0.13–0.17, PrW 0.44–0.56, DML 0.94–1.10, PPW 0.25–0.42.

Diagnosis of major worker.—Head subquadrate in full face view (Fig. 14); lobes of the anterior cephalic vertex developed, so that in full face view the medial notch is pronounced (Fig. 14); rugulae that originate on the lateral clypeal margin straight and longitudinal; those rugulae originating on the part of the clypeus directly in front of the eye terminate abruptly at the eye (Fig. 13); eyes small in relation to the length of the head (REL 0.13–0.17; Fig. 13); due to the development of the lobes of the posterior cephalic vertex, eyes appear to be placed near the posterior clypeal margin, often within the first third or fourth of the length of the head in lateral view (Fig. 13); pilosity short and erect; in full face view, setae emerging laterally from the head **erect,** forming an angle of approximately ninety degrees with the integument (Fig. 14); propodeal spines in side view generally in the form of long blunt pegs (Fig. 15); lateral margination of the propodeum not usually well developed.

Minor worker measurements (n = 8): HL 0.53–0.62, HW 0.48–0.57, CI 0.89–0.93, EL 0.13–0.15, REL 0.22–0.26, PrW 0.31–0.35, DML 0.67–0.75, PPW 0.14–0.17.

Diagnosis of the minor worker.—Mesosoma elongate (DML 0.67–0.75); foveolate sculpturing patchy on the mesosoma in side view, interspersed on the metapleuron, mesopleuron, and propodeum with patches of smooth, shining integument; propodeal spines normally sharp and elongate (Fig. 16); lateral margination of the propodeum usually weakly developed.

Comments.—At five localities *P. creightoni* and *P. californica* are known to co-occur (Fig. 24). At four of these sites the species appear to be distinct, but at Dye

Creek, California, a fraction of the colonies (2 out of 9) sampled along a three kilometer transect yielded workers that were difficult to assign to either species. The morphology of these ants is curiously intermediate between *P. californica* and *P. creightoni*, "bridging the gap" between the two species. In general, the unusual colonies yielded workers with the size and coloration of *P. creightoni*, but with the decumbent lateral cephalic setae that are diagnostic of *P. californica*. In general, ants from the two unusual colonies resemble collections of *P. californica* (three out of nine colonies along the transect) much more than *P. creightoni* (four out of nine colonies along the transect), and they were treated as *P. californica* for the analysis of morphometric data.

The presence of typical *P. californica* and *P. creightoni* at Dye Creek points to hybridization as a possible explanation for the existence of morphologically intermediate colonies of *Pheidole* at that site. Within northern California, the range of *P. californica* appears to extend from the northern Sacramento Valley into the surrounding foothills and plateau areas, while the range of *P. creightoni* appears to extend from the foothill and plateau regions to the edge of the Sacramento Valley (see Fig. 24). It may be that that the Dye Creek region forms part of a hybrid zone between the two species. Resolution of this problem will probably require both genetic analysis and more intensive sampling in the foothills area of northern California.

Material examined (PSWC, UCDC, LACM).

UNITED STATES **California:** *Mendocino Co.:* 4.59km NNE Hopland, 292m (D. O. Burge); 7.7km NNE Hopland, 825m (D. O. Burge); Hopland Field Station, 240m (P. S. Ward); *Siskiyou Co.:* 1.5mi NE Gazelle, 2600' (R. R. Snelling); Weed (A. C. Cole); *Tehama Co.:* 17.3km ESE Redbluff, 352m (D. O. Burge); 34.4km N Forest Ranch, 756m (D. O. Burge); *Trinity Co.:* Weaverville, Democrat Gulch (D. M. Gordon). **Nevada:** *Lander Co.:* Battle Mtn. (A. C. Cole); *Humboldt Co.:* Winemucca (A. C. Cole); *Lyon Co.:* Fort Churchill State Historic Park, 1280m (P. S. Ward); *Washoe Co.:* 8.67km W Nixon, 1140m (D. O. Burge); S end Pyramid Lake, 1140m (P. S. Ward). **Oregon:** *Jackson Co.:* 3mi E Applegate (W. S. Creighton); *Josephine Co.:* 8km SSW Cave Junction, 430m (P. S. Ward). **Washington:** *Grant Co.:* Corfu (C. H. Lavers).

Pheidole clementensis Gregg 1969
(Figs. 17–20)

Pheidole clementensis Gregg 1969: 93 (w).

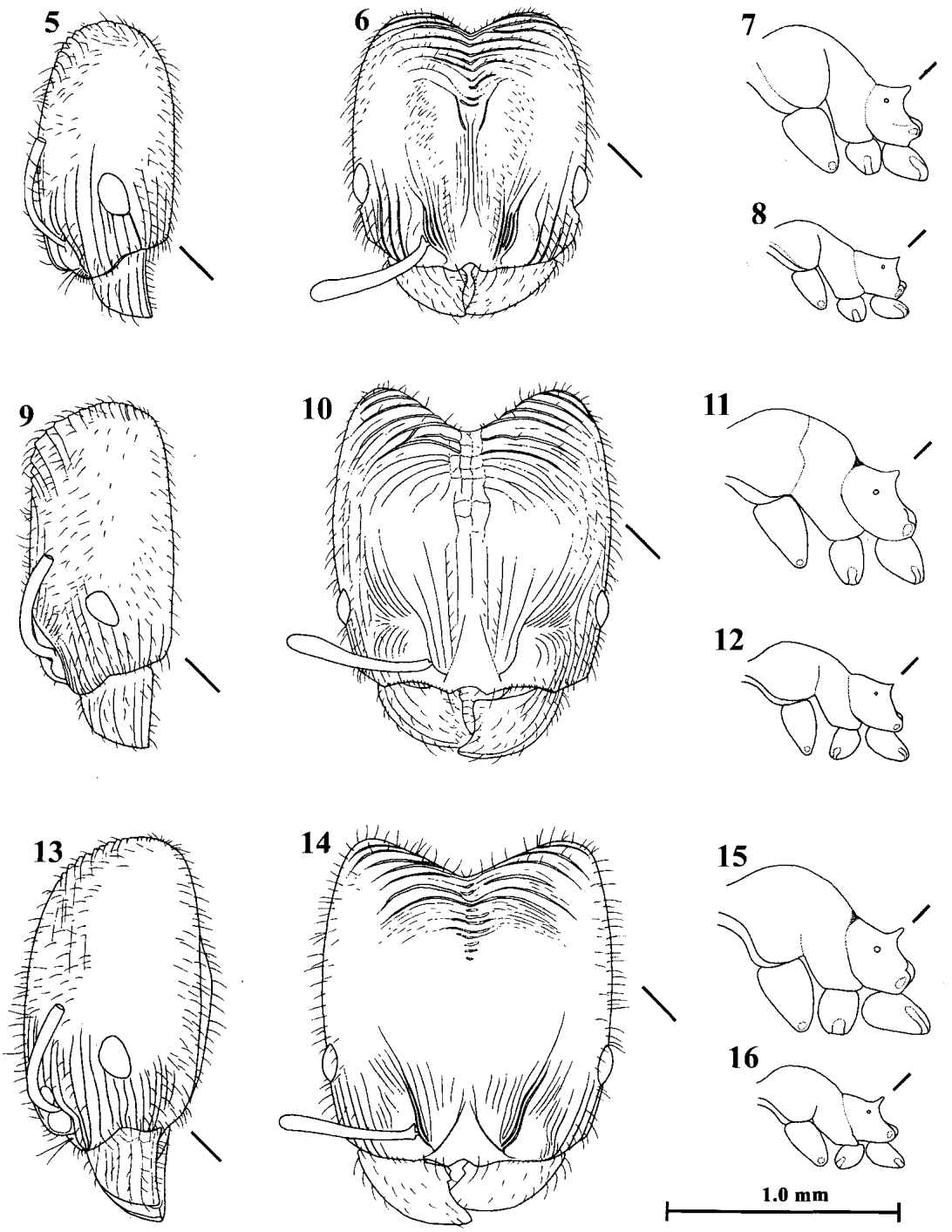
Major worker measurements (n = 14): HL 1.09–1.37, HW 0.94–1.23, CI 0.85–0.90, EL 0.14–0.18, REL 0.11–0.14, PrW 0.47–0.59, DML 0.92–1.11, PPW 0.23–0.34.

Diagnosis of major worker.—Head usually rectangular (subquadrate and elongate) in full face view, lateral margins parallel and only mildly convex (Fig. 18); transverse rugulae near the vertex of the head extremely coarse, such that in side view the head usually appears to have "brow ridges" (Fig. 17); in lateral view, rugulae originating on the part of the clypeus directly anterior to the eye arranged **diagonally** (rather than longitudinally), running towards the ventral surface of the head, below the eye (Fig. 17); eyes small relative to the length of the head (REL 0.11–0.14; Fig. 17); eyes located near the posterior clypeal margin, often within the first third or fourth of the length of the head in side view (Fig. 17); propodeal spines in side view generally in the form of long blunt pegs (Fig. 19); lateral margination of the propodeum usually weakly developed.

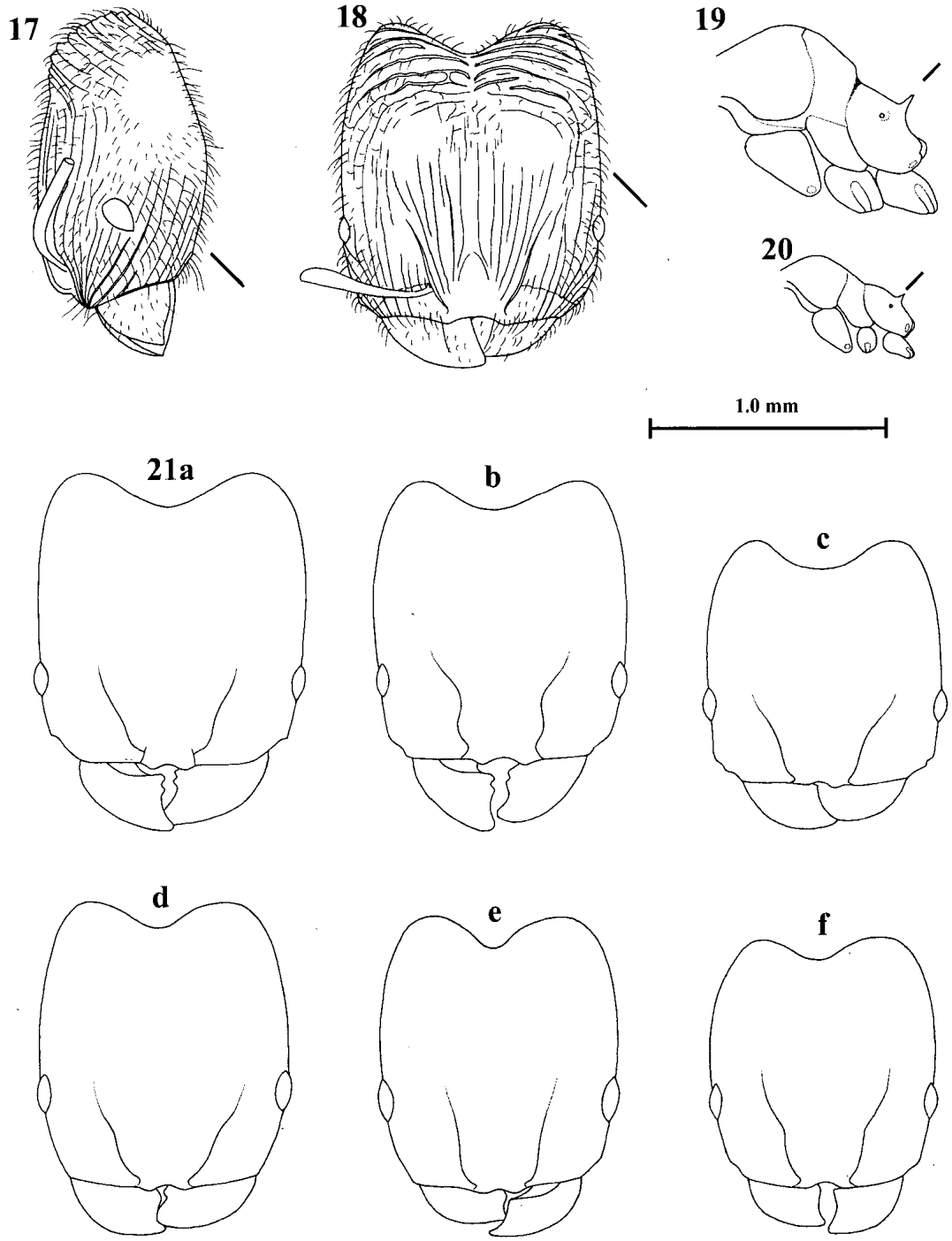
Minor worker measurements (n = 6): HL 0.52–0.61, HW 0.47–0.55, CI 0.89–0.92, EL 0.11–0.14, REL 0.19–0.22, PrW 0.30–0.35, DML 0.62–0.73, PPW 0.11–0.14.

Diagnosis of minor worker.—Mesosoma short (DML 0.62–0.73); foveolate sculpturing on the lateral mesosoma nearly non-existent, replaced by small, indistinct patches of sculpture mixed with more extensive areas of smooth and shining integument; propodeal spines short, thin, and sharp-tipped (Fig. 20); lateral margination of the propodeum usually weakly developed.

Comments.—Majors of *P. clementensis* may be distinguished from majors of *P.*



Figs. 5–16. *Pheidole* major workers, full face view of head (6, 10, 14), lateral view of head (5, 9, 13), and lateral view of mesosoma (7, 11, 15). *Pheidole* minor workers, lateral view of mesosoma (8, 12, 16). Note that sculpturing and setae of the antennal scapes and mesosoma have been omitted for clarity. 5–8: *P. californica*, 16.4 km ENE Chico, California; 9–12: *P. creightoni*-like variant of *P. californica*, 4.59 km NNE Hopland, California; 13–16: *P. creightoni*, 34.4 km N Forest Ranch, California.



Figs. 17–21. *Pheidole clementensis* major worker, full face view of head (18), lateral view of head (17), and lateral view of mesosoma (19). Minor worker, lateral view of mesosoma (20). *Pheidole californica* major workers, full face view of head with sculpture, pilosity, and antennae omitted (21a–f). 17–20: *P. clementensis*, Meling Ranch, Baja California, Mexico. 21a–c, three specimens of the *P. creightoni*-like variant of *P. californica*, from a single colony; 21d–f, three specimens of *P. californica* sensu stricto from a single colony. 21 a–f: 19km NNW Vacaville, California.

californica and *P. creightoni* by the angle of the rugulae between the eye and the clypeus in side view (see diagnoses). *Pheidole clementensis* overlaps more broadly with *P. californica* than *P. creightoni* for the metric measurements that were taken (see measurements in diagnoses), and bivariate plots tend to separate *P. creightoni* from *P. clementensis* more readily than they separate *P. californica* from *P. clementensis* (compare Figs. 1 and 2).

The range of *P. clementensis* overlaps broadly with the range of *P. californica* (Figs. 22–23), and the two species are sympatric at several sites. Although collections of the species from these sympatric zones are few, no intermediate forms are known, and hybridization does not appear to occur. The known range of *P. clementensis* is far removed from that of *P. creightoni* (Fig. 23).

Material examined (PSWC, UCDC, LACM).

MEXICO: **Baja California:** 8mi E El Rosario bridge (R. A. Johnson); Meling Ranch, 2450′ (R. A. Johnson); Sierra San Borja 9.9mi N San Borja, 1970′ (R. A. Johnson).

UNITED STATES: **California:** *Los Angeles Co.:* San Clemente Is., Pyramid Head (R. R. Snelling); *Orange Co.:* 1mi NW El Toro, 450′ (R. J. Hamton); *Riverside Co.:* Lake Skinner, 462m (A. V. Suarez); Skinner Reservoir, 4470′ (T. Prentice); *San Diego Co.:* Camp Pendleton (J. H. Hunt); Chula Vista (E end), 160m (P. S. Ward); Miramar Naval Air Station (T. Prentice).

IDENTIFICATION

The following short key may be used to differentiate major workers of the three species of the *californica* complex. All species have highly developed cephalic sculpture consisting of transverse rugulae that cover the posterior cephalic vertex, extend at least one fourth of the way to the clypeus in full face view, and are at least partly visible in lateral view.

1. Rugulae originating on lateral clypeal margin (directly anterior to eye) straight and longitudinal, terminating abruptly at the eye (Figs. 5, 9, 13) 2
– Rugulae originating on lateral clypeal margin (directly anterior to eye) arranged diagonally rather than longitudinally, running *beneath* the eye (Fig. 17) ..... ***P. clementensis* Gregg**

2. In full face view, setae emerging laterally from the head *decumbent,* forming an angle of forty five degrees or less with the integument (Fig. 6) ..... ***P. californica* Mayr**
– In full face view, setae emerging laterally from the head *erect,* forming an angle of approximately ninety degrees with the integument (Fig. 14) ..... ***P. creightoni* Gregg**

Gregg's (1959) key to the *Pheidole* of North America is also useful for identifying members of the *californica* complex. In light of newly discovered variation in critical traits, however, some couplets of the key must be modified. Couplets 23 and 27 refer to the development of the post petiolar connules, a trait that varies considerably within *P. californica* and *P. creightoni.* In general, *P. creightoni* has more highly developed postpetiolar connules than *P. californica,* but the difference is not diagnostic. Couplet 27 of Gregg's key should be simplified to the following in order to prevent misidentification of *P. creightoni* that do not have well-developed postpetiolar connules.

27. Rugae on cephalic vertices of the major straight or wavy, but not reticulate; lateral postpetiolar connules *usually* very prominent 28
– Rugae on cephalic vertices of the major notably reticulate and often coarse, but not reticulate; lateral postpetiolar connules *usually* blunt 29

Couplet 24, which is based on the head length (HL) of the major, must be modified in order to encompass newly discovered variation in this trait.

24. Head of major 0.85mm in length, or less 25
Head of major 0.98mm in length, or more 26

In their original form, couplets 33 and 34 of Gregg's key differentiate four subspecies of *P. californica*. As these subspecies are in synonymy with *P. californica*, I have provided a replacement for couplets 33 and 34 that now includes *P. clementensis*, which was described subsequent to the publication of Gregg's (1959) key. Although Gregg's (1969) description of *P. clementensis* includes a modification of the 1959 key that is intended to separate the new species from *P. californica*, the "brow ridges" to which Gregg's couplet refers are not a consistent characteristic of the species. Some specimens of *P. californica* have similar sculpture, and specimens of *P. clementensis* without "brow ridges" are known from southern California. The following couplet (adapted from the short key above) should replace Gregg's couplets 33 and 34.

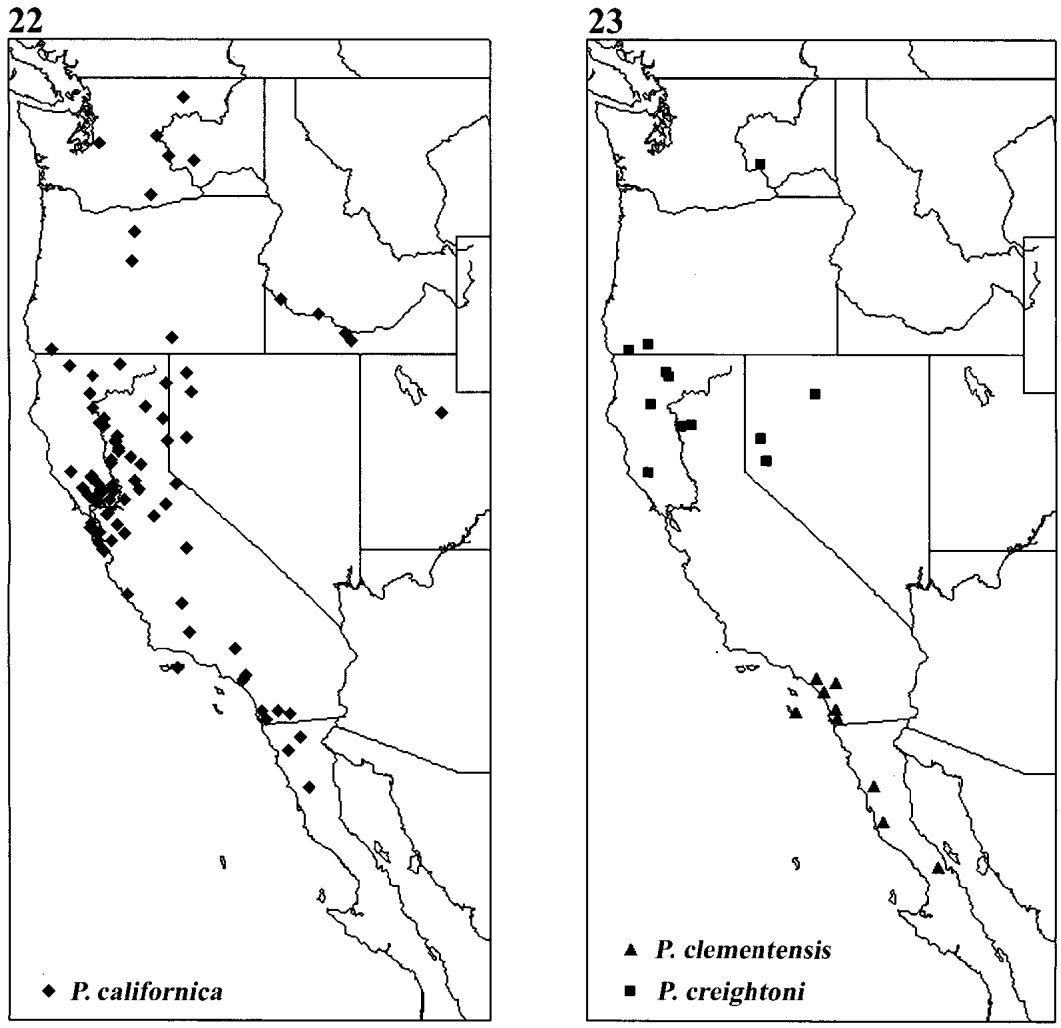
33. Rugulae originating on lateral clypeal margin (directly anterior to eye) arranged diagonally rather than longitudinally, running *beneath* the eye (Fig. 17) ..... ***P. clementensis*** **Gregg**
– Rugulae originating on lateral clypeal margin (directly anterior to eye) straight and longitudinal, terminating abruptly at the eye (Fig. 5) ..... ***P. californica*** **Mayr**

BIOLOGY AND DISTRIBUTION

The biological observations included in the following synopses are those that appear to be characteristic of the species. Nevertheless, these traits vary considerably within each species. Distribution data are based on my own collections and information associated with specimens that I examined in existing collections, which means that they are biased towards accessible areas. Thus, gaps on each map may indicate a lack of field work within a particular region rather than a true gap in the distribution of the species.

Pheidole californica.—This species is found in the greatest diversity of habitats, from valley grasslands to higher elevation mountainous or plateau areas (5 to 1750m, mean = 600m) in Arizona, California, Idaho, Nevada, Oregon, Utah, Washington, and Baja California (Fig. 22). *Pheidole californica* readily colonizes disturbed habitats such as road verges, fallow fields, and vacant lots. Nest entrances are usually small and inconspicuous, making them difficult to find except when they are located in patches of bare soil. Midden piles are accumulated, but this species does not usually collect chaff around the nest in the manner of *P. creightoni*. Foraging usually takes place in the evening and during the night. Foraging is conducted primarily by minor workers. Nuptial flights tend to occur in the evening and early night at most localities. In Davis, California, nuptial flights at a specific group of colonies were observed to begin in early May, and continue sporadically until late June.

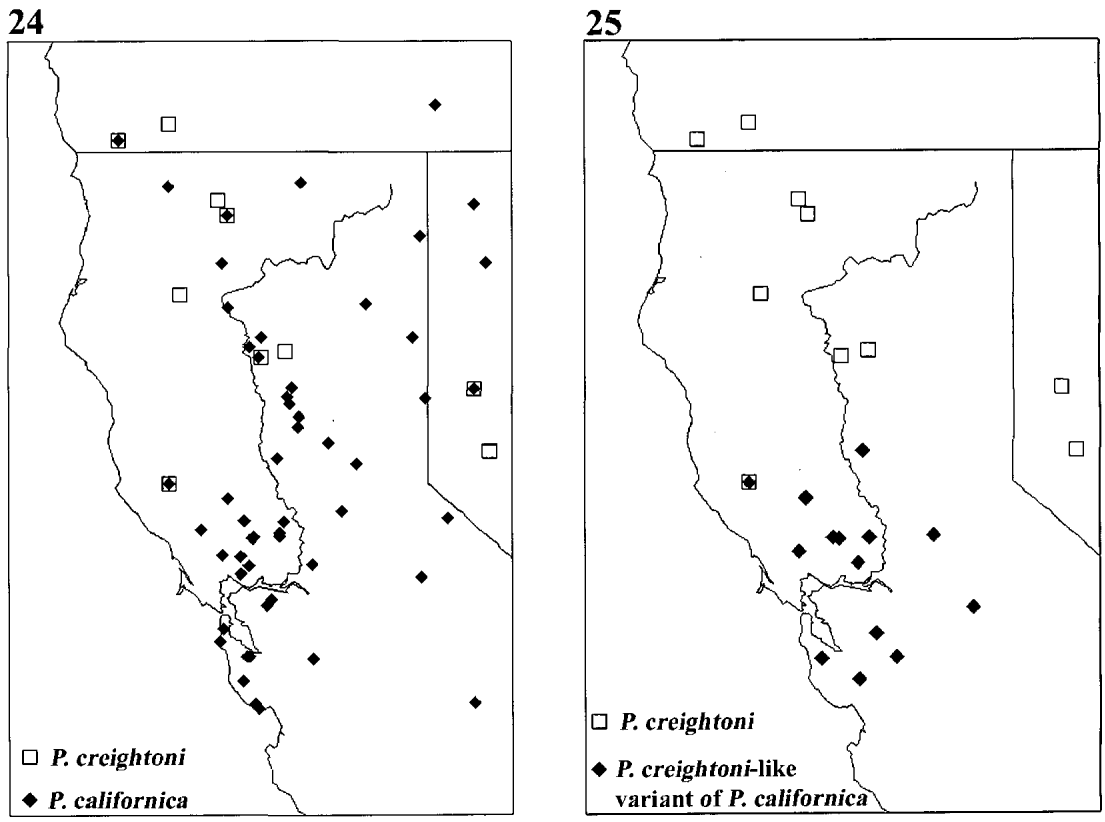
Pheidole creightoni.—This species is found in foothill, mountain, and plateau



Figs. 22–23. Known distributions in the western United States and northern Mexico of *Pheidole californica* (22), and *P. creightoni* and *P. clementensis* (23).

areas of California, Oregon, Washington, and Nevada (Fig. 23) at a higher average elevation than *P. californica* (300 to 1300m, mean = 725m). *Pheidole creightoni* is often found in less disturbed habitats than *P. californica*. Nest entrances are conspicuous, and usually located within tufts of grass or at the edge of partially buried stones. Significant amounts of discarded seed chaff are usually associated with nests, forming a soft "crater" around the entrance, or a mound adjacent to the nest. The foraging habits of *P. creightoni* are similar to those of *P. californica*, although foraging columns of the former tend to contain a higher proportion of major workers.

At several study sites where *P. creightoni* co-occurs with the seed harvesting ant *Messor andrei* (Mayr) these species tend to nest in close proximity. This phenomenon was first noted by W. S. Creighton, who originally collected *P. creightoni* in southern Oregon (Gregg 1955). At both Dye Creek and Hopland Research and Extension Center, California, *P. creightoni* colonies were discovered in close proximity to *M. andrei* nests. In one instance at Hopland Research and Extension Center, a mature colony of *P. creightoni* was located



Figs 24–25. Known distributions in northern California, western Nevada, and southern Oregon of *P. californica* and *P. creightoni* (24), and *P. creightoni* and the *P. creightoni*-like variant of *P. californica* (25).

only 20cm from the entrance of a large and active colony of *M. andrei*, the *Pheidole* nest being surrounded by the chaff piles and foraging trails of *M. andrei*. Colonies of *P. californica* were never observed in close proximity to nests of *M. andrei*. Given that *P. creightoni* and *M. andrei* are both seed harvesting species, and thus potential competitors, it seems paradoxical that they would preferentially nest in close proximity to one another.

Pheidole clementensis.—This species is found in arid and semi-arid habitats of southern California and northern Baja California (Fig. 23) at moderate elevations (160 to 800m, mean = 530m). Based on collection data from specimens examined, nesting is most often beneath stones, but the author has not made any personal observations.

DISCUSSION AND CONCLUSIONS

Pheidole californica is the most variable member of the *californica* complex at both the local and geographic scale, with marked differences in morphology among populations, among nests within a population, and among the members of a single colony. In spite of this variability, which has led to poor characterization of the species and confusion with other members of the complex, I have identified some traits that consistently separate *P. californica* from its closest relatives.

High levels of morphological variation in *P. californica* may be correlated with the large range of the species. It is possible that barriers to dispersal within the wide geographical range of *P. californica* have led to divergence in this species, while the comparatively small range of *P. creightoni*

and *P. clementensis* has led to a correspondingly lower amount of variation.

Another possible source of variation in the *californica* complex is hybridization between species. At several localities *P. californica* and *P. creightoni* are sympatric, and at one of these sites there is some evidence of hybridization. Thus, it may be that the confusing variation among and within some populations of *P. californica* is partly due to the influence of introgression with *P. creightoni*. Genetic work may be required for the resolution of this and other questions related to variation in members of the *californica* complex.

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