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A synoptic review of the ants of California (Hymenoptera: Formicidae)

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ABSTRACT

The taxonomy and composition of the California ant fauna is reviewed, leading to the recognition of 281 species (in 44 genera), of which 255 are considered indigenous and 39 are endemic. Species-level endemism (13.9%) is higher than in adjacent regions, as is the percentage of non-native species (9.3%). About one quarter of the indigenous ant species are endemic to the California floristic province (*sensu* Hickman 1993). Approximately 36 species appear to be undescribed. Most of these undescribed species are assigned code names, which match those used on the "Ants of California" web site (http://www.antweb.org/california.jsp). One new species is described, *Camponotus maritimus* Ward, **sp. nov.**, which corresponds to the taxon previously called *Camponotus maculatus* subsp. *vicinus* var. *maritimus* Wheeler (unavailable quadrinomen). Three species names are revalidated: *Leptothorax calderoni* Creighton **stat. reval.**, **stat. nov.,** *Myrmica glacialis* Emery

stat. reval., stat. **nov.,** and *Temnothorax rudis* (Wheeler) **stat. reval., comb. nov.** The following **new synonymy** is proposed (senior synonym listed first): *Forelius pruinosus* (Roger) = *F. analis* (André); *Monomorium ergatogyna* Wheeler = *M. wheelerorum* DuBois; *Temnothorax andrei* (Emery) = *T. nitens heathii* (Wheeler) = *T. nitens occidentalis* (Wheeler) = *T. ocellatus* (MacKay); *Temnothorax nevadensis* (Wheeler) = *T. lindae* (MacKay) = *T. maryanae* (MacKay); *Temnothorax nitens* (Emery) = *T. mariposa* (Wheeler) = *T. melinus* (MacKay). The genus *Acanthomyops* Mayr is demoted to subgenus (**stat. rev.**) within *Lasius* Fabricius, in accord with recent molecular phylogenetic results. A key to the ant genera of California (based on the worker caste), a synopsis of each genus, a comprehensive bibliography, and a species list are also provided.

Keywords. ant taxonomy, distribution, biogeography, endemism, *Camponotus*, *Lasius*, *Forelius*, *Monomorium*, *Myrmica*, *Leptothorax*, *Temnothorax*

INTRODUCTION

Like other components of the California biota, the ant fauna of this state shows considerable biological diversity and regional endemism. Yet there has been no comprehensive systematic treatment of the ants of California, much less a reliable checklist or a set of identification keys. Part of this stems from the complexity of the fauna and an attendant rash of taxonomic problems whose resolution requires additional study at a larger geographical scale. In light of these constraints, the present paper aims to provide no more than a cursory survey of the ant genera, a provisional list of species, and a guide to the literature. A few necessary taxonomic changes are introduced, mostly involving new synonymy at the species level. A prime motivation for this paper stems from the need to establish a reference checklist for a new web site illustrating the ants of California (http://www.antweb.org/california.jsp). This web site, developed in collaboration with Brian Fisher (California Academy of Sciences), is designed to facilitate identification by providing high-quality digital images of the known California ant species.

The first descriptions of California ants appeared in the nineteenth and early twentieth century, in widely scattered taxonomic papers by Buckley, Emery, Forel, Mayr, W. M. Wheeler and others. Mallis (1941) and Cook (1953) published a species list and a book-length treatment, respectively, of the ants of California but both of these are out-of-date and error-ridden. Revisionary studies on specific groups of ants, carried out within the last 60 years and usually at a continent-wide scale, have had a more salutary effect on our knowledge of the California ant fauna. This includes taxonomic contributions by Bolton (1979), Brown (1950d, 1953g), Buren (1968b), Cole (1968), Creighton (1950a), Francoeur (1973), Gregg (1959, 1969b), Mackay (2000), Snelling (1970, 1973c, 1976, 1982a, 1982b, 1988, 1995a), Trager (1984b, 1991), Ward (1985b, 1999), Watkins (1976, 1985), Wilson (1955a, 2003) and Wing (1968a). Among the more useful publications for those seeking information about the ants of California are the regional treatments of the ants of Deep Canyon, Riverside County (Wheeler & Wheeler 1973e), the California deserts

(Snelling & George 1979), and Nevada (Wheeler & Wheeler 1986g). A popular treatise on the ants of California is in preparation by Roy R. Snelling (pers. comm.).

MATERIALS AND METHODS

There are three principal parts to this paper: (1) a statement and justification of taxonomic changes, (2) a key to the ant genera of California, followed by a brief synopsis of each genus, and (3) a species list (Appendix). Taxa are arranged alphabetically by subfamily, genus and species, following the classification of Bolton (2003). Under the synopsis of California ant genera I have cited literature sources that may be useful for identification of species, as well as papers on general biology. Additional assistance with identification can be obtained by comparing the images of individual species on AntWeb.

The following abbreviations are used for museum collections (following Arnett *et al*. 1993 as far as possible):

CASC California Academy of Sciences, San Francisco, CA, USA
CDAE California Department of Food and Agriculture, Sacramento, CA, USA
LACM Natural History Museum of Los Angeles County, CA, USA
MCSN Museo Civico de Storia Naturale, Genoa, Italy
MCZC Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA
MHNG Muséum d'Histoire Naturelle, Geneva, Switzerland
RAJC Robert A. Johnson Collection, Tempe, AZ, USA
UCDC Bohart Museum of Entomology, University of California, Davis, CA, USA
USNM National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
WPMC William P. Mackay Collection, University of Texas at El Paso, TX, USA

The following worker measurements (in mm) and indices are cited. The first four are taken with the head in full-face (dorsal) view.

HW Head width: maximum measurable head width. This excludes the compound eyes except in two genera of large-eyed ants where, by convention, the eyes are included: *Pseudomyrmex* (after Kempf 1960a) and *Formica* (after Francoeur 1973).
HL Head length: measured along the midline from the anterior clypeal margin to the midpoint of a line drawn across the posterior margin of the head.
EL Eye length: length of the compound eye, measured in the same plane as HL.
FCD Frontal carinal distance: maximum distance between the frontal carinae.
SL Scape length: chord length of the scape, excluding the basal condyle and neck.
PW Pronotum width: maximum width of the pronotum in dorsal view.

FL Profemur length: length of the profemur, measured along its long axis in posterior view.

LHT Length of the hind tibia, measured in dorsolateral view, from the articulation with the femur, excluding the medioproximal condyle, to the distal extremity of the tibia.

DPW Dorsal petiolar width: maximum width of the petiole in dorsal view.

PPW Postpetiolar width: maximum width of the postpetiole (third abdominal segment) in dorsal view.

T4W Maximum width of the fourth abdominal tergite in dorsal view.

CI Cephalic index: HW/HL

REL Relative eye length: EL/HL

SI Scape index: SL/HW

No new taxa are described in this paper, except that a previously unavailable name in *Camponotus* is made available. Instead, most unidentifiable species are assigned code numbers (e.g., *Hypoponera* sp. CA-01), following the example set by the guide to Japanese ants (Morisita *et al*. 1989, 1991, 1992). For forms that are close to a named taxon but whose specific distinctness remains uncertain, I have used the expression "sp. cf.". Thus, "*Paratrechina* sp. cf. *terricola*" refers to a species that is either closely related to, or conspecific with, *Paratrechina terricola* (Buckley). The taxonomic quandaries raised here will hopefully stimulate more detailed systematic investigations. Since most of the ant species listed here are not confined to California, future monographic work will be most useful if it has a broader geographical scope than California alone.

GENERAL FEATURES OF THE CALIFORNIA ANT FAUNA

The ant fauna of California comprises approximately 281 species, representing nine subfamilies, 23 tribes and 44 genera (classification after Bolton 2003). Of this total, 22 species are clearly non-native, and most of these are of Old World origin. The status of four other species (*Dorymyrmex flavus* McCook, *Hypoponera opaciceps* (Mayr), *Lasius neoniger* Emery and *Paratrechina vividula* (Nylander)) is unclear: the distributions of these species within California and their associations with disturbed habitats suggest that they are introduced to the state, while native to other parts of the New World. Among the 255 indisputably indigenous species, 39 (15.3%) are known only from California and a further 28 species extend only slightly beyond the state's borders to southern Oregon and/or northern Baja California. About 63 (24.7%) of the indigenous ant species recorded from the state are endemic to the California floristic province, as defined by Hickman (1993).

This high level of endemism, comparable to that shown by California plants (Hickman 1993), can be contrasted with the situation in neighboring Arizona where ant species richness is greater (~288 native species) but the level of endemism is lower (8.3%) (Table 1).

The harsh Mediterranean climate of California presumably makes it a less favorable environment for ants than regions that experience significant summer rainfall. This factor was cited by Wheeler (1917a: 459) to explain the relative poverty of montane ant communities in California compared to other western states. Geographic barriers also ring much of the state, adding to the insular aspect of the region (Bakker 1984). Climatic and geographic filters have thus produced a California ant fauna with a distinctive composition compared to other southwestern states, not richer in species but having a higher level of endemism.

There is also a greater proportion of exotic species (Table 1), but the introduced taxa are largely confined to disturbed sites at low elevations. As a result, most natural habitats in California are free of non-native ant species. Locations that provide good access to water in the summer (e.g., riparian habitats and artificially irrigated landscapes) are most susceptible to invasion by exotic ants.

TABLE 1. Ant species richness in California and other southwestern states. Endemism estimates for Arizona are approximate. The Texas list (O'Keefe *et al*. 2000) has been corrected for obvious errors.

State	Area (km^2)	# species (# native spp.)	# introduced spp. (%)	# endemic spp. (%)	% endemic (of native spp.)	Data source
California	410,837	281 (255)	26 (9.3)	39 (13.9)	15.3	Present study
Arizona	294,897	300 (288)	11 (3.7)	24 (8.0)	8.3	Cover & Johnson (unpubl.)
New Mexico	314,979	237 (233)	4 (1.7)	7 (3.0)	3.0	Mackay & Mackay (2002)
Texas	692,109	267 (251)	16 (6.0)	10 (3.7)	4.0	O'Keefe *et al*. (2000)

The numbers in Table 1 should be treated as provisional. Further collecting and taxonomic study of ants from California and adjacent regions will undoubtedly lead to the discovery of additional species. In particular, the species totals for New Mexico and Texas can be expected to increase substantially and eventually exceed those of California, although the ranking of levels of endemism is less likely to change. Within California the northeast corner of the state (Modoc Plateau) has not been well collected and additional ant species, of Great Basin distribution, will almost certainly be found there.

TAXONOMIC CHANGES

The preparation of a species list of California ants highlights the necessity of certain taxonomic changes, primarily involving new synonymy. These changes are formally documented and justified below. The expression "stat. nov." signifies a change to a new rank and "stat. rev." indicates a revision in rank to one used previously; "stat. reval." refers to names whose status changes from invalid to valid.

Subfamily Dolichoderinae

Genus *Forelius* Mayr

In a recent taxonomic revision of this genus Cuezzo (2000) recognizes three species from the Nearctic region: *F. mccooki* (McCook 1880), *F. pruinosus* (Roger 1863a) and *F. analis* (André 1893b), with the last-named being removed from synonymy under *F. pruinosus*. All three species are recorded by Cuezzo (2000) from California. *F. mccooki* can be recognized by its abundant standing pilosity, but *F. pruinosus* and *F. analis* cannot be reliably distinguished using the differences cited by Cuezzo (2000). In Cuezzo's worker key *F. analis* is separated from *F. pruinosus* based on the shape of the posterior margin of the head: concave ("sometimes…weak") in *F. analis*, and straight in *F. pruinosus*. Yet, this putative difference is contradicted by Cuezzo's description of the *F. analis* worker—where the posterior margin is said to vary from convex to weakly concave—and by the illustration of a *F. analis* worker (Cuezzo 2000, figure 10) which shows a posterior margin that is convex. (*F. pruinosus* is described, and illustrated, as having the posterior margin of the head straight.) After examining a large series of *Forelius* from the United States and northern Mexico I can find no consistent difference in worker head shape: the posterior margin of the head varies continuously from weakly convex through straight to weakly concave. Color is also variable, ranging from dark brown to yellowish-orange. Some nest series contain both light and dark-colored workers. It is possible that the California populations are not conspecific with *F. pruinosus* (described from Cuba), but these and other western samples seem to grade insensibly into material from farther east and south, including populations in Florida and the West Indies with consistently dark and densely pubescent workers, which correspond to *F. pruinosus* (s.s.). The complex needs further study but because reliable diagnostic differences have not yet been uncovered I treat *F. analis* (type locality Chihuahua, Mexico) as a junior synonym of *F. pruinosus* (**syn. nov.**), thus returning to the conventional treatment of these two names.

It should be noted that even the distinction between *F. mccooki* (standing hairs present on scapes, posterior margin of head, and external face of tibiae) and *F. pruinosus* (standing hairs absent or very sparse on the afore-mentioned structures) occasionally breaks down in western North America, with workers from some localities showing intermediate amounts of pilosity. There is, however, a third distinct (and apparently undescribed) species of *Forelius* in the United States. It is small and dark with a conspicuously shiny mesepisternum, short scapes (SL 0.40-0.48), and sparse standing pilosity. This species ranges from southern Texas to Colombia, and has been found sympatrically with a larger *Forelius* species—apparently *F. pruinosus*—in Mexico, Guatemala and Costa Rica, without showing any sign of intergradation.

As a nomenclatural side note, the author of *Forelius mccooki* is McCook not Forel, since McCook's 1880 paper provides in his own words a sufficient "description or definition" (ICZN, Article 12) of the ants to make the name available, prior to Forel's (1886b)

more detailed description of the same material. In addition, the date of publication of McCook's paper is 1880 (Ward *et al*. 1996: 275), not 1879 as cited by Bolton (1995b) and others. Cuezzo's (2000) attribution of authorship of *F. mccooki* to Forel is incorrect, but her designation of a lectotype from among material in the Forel collection in MHNG may be considered justifiable, to the extent that Forel's specimens came from McCook and were part of the material to which McCook referred in his 1880 paper.

Subfamily Formicinae

Genus *Camponotus* Mayr

Camponotus maritimus Ward, sp. nov.

(Figures 1-4)

Camponotus maculatus subsp. *vicinus* var. *maritimus* Wheeler 1910g: 305. Unavailable name.
Camponotus vicinus; Creighton 1950a, nec Mayr [in part].
Camponotus vicinus; Snelling 1970, nec Mayr [in part].
Camponotus sp. near *vicinus*; Wetterer *et al*. 2000.
Camponotus cf. *vicinus*; Sanders *et al*. 2001.
Camponotus sp. near *vicinus*; Ward 2005.

Holotype worker, Jasper Ridge, San Mateo Co., California, U.S.A., 150m, 37º24'N 122º14'W, 3.iv.2004, under stone, oak woodland, P.S.Ward#15202 [MCZC]. Paratypes: series of workers, queens and males, same data and nest series as holotype [BMNH, CASC, CDAE, LACM, MCZC, UCDC, USNM, WPMC].

Description, major worker. Medium-sized species, related to *C. vicinus* Mayr, but smaller on average and with a shinier appearance. Masticatory margin of mandibles with five teeth, the first four (counting from apex) acute, the proximal tooth truncate or weakly bifid, and subtended by a small tooth on the outer basal margin of mandible (dentition simpler—five acute teeth only—in smaller workers). Head as long as, or longer than, wide; sides of head weakly convex, diverging posteriorly, and rounding into concave posterior margin (in smaller workers sides of head subparallel and posterior margin convex). Eye about one-quarter of head length and not protruding from side of head in full-face view (breaking outline of head in smallest workers). Anterior clypeal margin crenulate, broadly convex in outline; median clypeal carina prominently developed. Scape relatively short (Figure 3); scape base subcylindrical, not strongly flattened or flared. Frontal carinae separated anteriorly by about one-fifth head width, flaring out posteriorly to about one-third of head width. Mesosoma dorsum convex in profile; dorsal face of propodeum longer than, and rounding into, declivitous face; propodeum markedly compressed from side to side. Petiole simple, scale-like in profile, with blunt summit, and convex in posterior view. Legs relatively short (Figure 4); in largest workers (HW 2.50-3.10 mm), LHT not exceed-

ing 3.00 mm. Body subopaque to sublucid, with a distinctly greater sheen than in workers of *C. vicinus*. Sculpture consisting of fine reticulations, with scattered punctures, coarser on head than on abdominal tergites. Pilosity moderately common on most of body, fine-tipped and golden-yellow; standing pilosity absent from scapes (except apices), external face of tibiae, and sides of head, present on clypeus, midline of head, venter of head, mesosoma, petiole and rest of metasoma. The following numbers of standing setae present on the indicated structures (counts include all sizes of workers): profemur 3-13, pronotum 2-20, mesonotum 2-13, propodeum 3-10, petiole 5-11, abdominal tergite III (exclusive of posterior margin) 4-21, abdominal tergite III posterior margin 5-15, abdominal tergite IV (exclusive of posterior margin) 5-24, abdominal tergite III posterior margin 8-28. Fine, appressed pubescence present on most of body but not forming a dense mat; appressed hairs on abdominal tergites 3 and 4 (gastric tergites 1 and 2) relatively short and sparse and separated by about their lengths. Medium to dark brown, head and metasoma darker, legs, antennal segments 2-12, and scape base usually lighter.

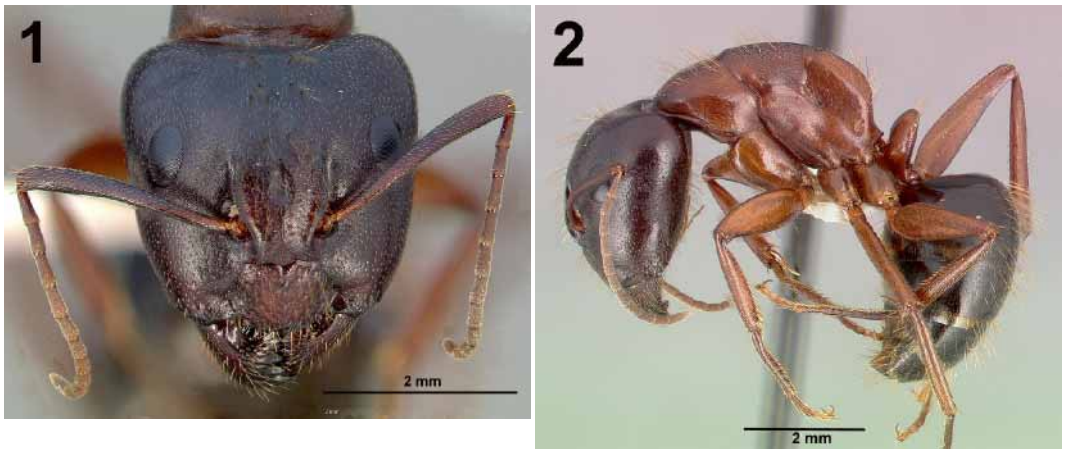
Worker measurements (n = 30). HW 1.08–3.11, HL 1.44–3.17, SL 1.59–2.68, PW 0.93–1.97, LHT 1.78–3.01, CI 0.73–1.00, SI 0.79–1.54, REL 0.21–0.31, LHT/HW 0.94–1.71.

DNA sequence data. The following GenBank sequences are available for *Camponotus maritimus*: 18S ribosomal RNA gene (AY867448), 28S ribosomal RNA gene (AY867464), wingless (AY867433), long wavelength rhodopsin (AY867495) and abdominal-A (AY867480). All sequences derive from a single worker taken from the same nest series as the holotype.

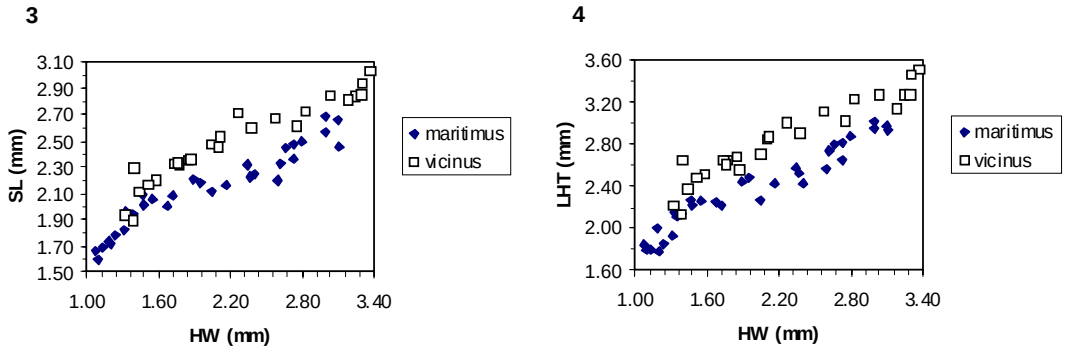
Comments. Wheeler's *maritimus* has remained a quadrinomen, and hence unavailable, since the original description. Creighton (1950a) considered it to represent a synonym of the more widespread species *Camponotus vicinus*, but there are in fact two distinct sympatric species in California. Workers of what is here called *C. maritimus* can be distinguished from those of *C. vicinus* by the narrower scape base, shorter scape, shorter legs, more closely adjacent frontal carinae, shinier integument, and sparser pubescence on abdominal tergites 3 and 4 (appressed hairs separated by about their lengths in *C. maritimus*, by less than their lengths in *C. vicinus*). Plots of SL by HW and LHT by HW separate all but the smallest workers of *C. maritimus* and *C. vicinus* (Figures 3–4), except in southern coastal California. In this latter region there are *vicinus*-like populations in chaparral and coastal sage scrub with atypically short scapes and legs. The workers of these populations can be separated from those of *C. maritimus* by the other characters, especially the duller integument of the head and abdominal tergites 3 and 4, and the denser pubescence on the latter. In addition workers of the southern coastal populations of *vicinus* are exceptionally hairy, with standing pilosity commonly present on the sides of the head, as seen in full-face view, and on the venter of the metafemur (standing pilosity generally absent on these structures in *C. maritimus*).

C. maritimus occurs in coastal regions of California from Mendocino and Lake Coun-

ties to San Diego County (including the Channel Islands), and in the western foothills of the Sierra Nevada. Habitats from which it has been collected include chaparral, serpentine chaparral, serpentine grassland, oak woodland, mixed redwood forest, coniferous forest on serpentine, and coastal scrub. Colonies are most frequently found under stones, less commonly in or under rotten wood.



FIGURES 1-2. *Camponotus maritimus* holotype worker. 1, full-face view of head; 2, lateral view of body.



FIGURES 3-4. Bivariate plots of SL and LHT by HW, for workers of *Camponotus maritimus* and *C. vicinus*.

Localities cited by Wheeler (1910g: 305) in his description of *Camponotus maculatus* subsp. *vicinus* var. *maritimus* are Pacific Grove and San José (H. Heath) and Catalina Island (C. F. Baker). Old specimens collected by Baker, Heath and Wheeler, and placed by Wheeler under "*maritimus*" in the MCZ collection, belong to three species: *C. maritimus* (from Catalina Island and Palo Alto), *C. semitestaceus* Snelling (Palo Alto) and *C. vicinus* Mayr (Pacific Grove). Some of these specimens are labeled as *maritimus* "types" but none of them has true type status because *maritimus* Wheeler is an unavailable name.

For convenience I have chosen the holotype and paratypes of *C. maritimus* Ward from a nest series collected recently at Jasper Ridge near Palo Alto, rather than from the old specimens. Wheeler, it seems, correctly inferred the presence of more than one species but he did not distinguish them with 100% accuracy.

Genus *Lasius* Fabricius

A close relationship between *Acanthomyops* Mayr and *Lasius* has long been recognized (Creighton 1950a, Wilson 1955a, Wing 1968a). Recent molecular studies (Savolainen 2002, Janda *et al.* 2004) demonstrate that *Acanthomyops* is nested phylogenetically within *Lasius*. To maintain monophyly for *Lasius*, *Acanthomyops* cannot be treated as a separate genus. It is here returned to the status of subgenus (**stat. rev.**) in *Lasius*, which generates revised or new combinations in *Lasius* for the following species names: *arizonicus* **comb. rev.**, *bureni* **comb. nov.**, *californicus* **comb. rev.**, *claviger* **comb. rev.**, *clavigeroides* **comb. rev.**, *colei* **comb. nov.**, *coloradensis* **comb. rev.**, *creightoni* **comb. nov**., *interjectus* **comb. rev.**, *latipes* **comb. rev.**, *mexicanus* **comb. rev.**, *murphyi* **comb. rev.**, *occidentalis* **comb. rev.**, *parvula* **comb. rev.**, *plumopilosus* **comb. rev**., *pogonogynus* **comb. rev.**, *pubescens* **comb. rev.**, and *subglaber* **comb. rev.**

Subfamily Myrmicinae

Genus *Leptothorax* Mayr

The ant genus *Leptothorax* formerly comprised a large and heterogeneous assemblage of species but Bolton (2003) redefined it to include only those species closely related to *L. acervorum* Fabricius. Most California species previously placed in *Leptothorax* are now assigned to *Temnothorax* Mayr (see below), with two species remaining in *Leptothorax*.

Leptothorax calderoni Creighton 1950a stat. reval., stat. nov.
(Figure 5)

Leptothorax (*Mychothorax*) *acervorum* race *canadensis* var. *calderoni* Forel 1914c: 617. [Unavailable name.]

Leptothorax (*Mychothorax*) *canadensis calderoni* Creighton 1950a: 276. [First available use of name.] Three syntype workers, one syntype alate queen, Lake Tahoe, California, 6325' (Calderon) [MHNG] [Examined]

Comments. *Leptothorax calderoni* is a large, bicolored species with short standing pilosity and a robust petiole. In California it is sympatric with another species in the *L. mus-*

corum-complex, here called *Leptothorax* sp. CA-01 (this second species might correspond to *L. canadensis* Provancher). In contrast to *Leptothorax* sp. CA-01, the petiole of *L. calderoni* has a less peaked appearance, with the anterior and dorsal faces forming a right angle in lateral view. The two pairs of standing hairs visible in profile on the dorsum of the petiole are separated by notably more than their lengths, whereas in *L.* sp. CA-01 they are separated by about their lengths or less (compare Figures 5 and 6). In addition, *L. calderoni* is larger (worker HW 0.66–0.81; n = 35) with disproportionately longer legs (worker FL 0.56–0.66; n = 35) compared to *L.* sp. CA-01 (worker HW 0.56–0.70, worker FL 0.44–0.56; n = 70). The mesosoma, petiole and postpetiole of *L. calderoni* are orange-brown, the head medium brown and gaster dark brown. Color contrasts tend to be less marked in *L.* sp. CA-01.

Most records of *L. calderoni* come from coniferous forest at moderate to high elevations in the Sierra Nevada of California (1470–2680 m), with outlier populations in the northern Coast Ranges and in the San Bernardino Mountains of southern California. Colonies are found in cavities in hard, dead wood. Workers are often conspicuous as foragers on downed logs.

Bolton (1995b) incorrectly listed *L. calderoni* as an unavailable name, overlooking that fact that Creighton's (1950a) treatment of it as a trinomen rendered it available. Creighton considered *L. calderoni* to be a subspecies of *L. canadensis* and a senior synonym of *L. canadensis septentrionalis* Wheeler (1917a). Actually *L. c. septentrionalis* would have seniority if the two were synonyms, but they are not conspecific. They have a similar color pattern but *L. c. septentrionalis* (described from Banff, Alberta and Emerald Lake, British Columbia) has longer setae, a more peaked petiole, and is smaller in size (syntype workers in MCZC examined).

Genus *Monomorium* Mayr

Leaving aside introduced species, the Nearctic *Monomorium* belong to the taxonomically vexing *minimum*-group, revised by DuBois in 1986. Several of the species recognized by DuBois (1986) are problematic, and parts of his keys to workers and queens are unusable. Here I deal only with the two taxa recorded from California: *M. wheelerorum* DuBois is considered to be a junior synomym of *M. ergatogyna* Wheeler (**syn. nov.**) because the putative differences between the two "species" cannot be verified. A key distinguishing feature is said to be the lateral profile of the scutum and scutellum of the queen: flat or slightly depressed in *M. wheelerorum* and convex in *M. ergatogyna*. In populations from northern California, however, this character shows continuous variation between these two conditions, even among queens from the same nest (the species is polygynous). Other supposed queen and worker differences disappear when intra- and interpopulation variation are taken into account. A modern systematic treatment of the *M. minimum*-group is badly needed. Because the queens are apterous in most western populations, interpopula-

tion differentiation is expected to be accentuated, a factor that needs to be considered in any taxonomic study.

Genus *Myrmica* Jurine

The Nearctic species of this genus are currently being revised by André Francoeur (pers. comm.). In accordance with his findings *Myrmica glacialis* Emery is here treated as a valid species (**stat. reval.**, **stat**. **nov**.**).** It was previously considered a synonym of *M. lobifrons* Pergande.

Genus *Temnothorax* Mayr

A recent comprehensive reorganization of the tribe Formicoxenini by Bolton (2003) led to the division of *Leptothorax* (sensu lato) into three genera: *Leptothorax*, *Nesomyrmex* Wheeler and *Temnothorax*, of which the first and last are represented in California. *Temnothorax* includes species previously placed in the subgenus *Myrafant* M. Smith. A revision of the New World *Myrafant* species by Mackay (2000) helped to improve the alpha-taxonomy of the group but various problems remain, particularly among the California species. In preparing a checklist of the ant fauna of this state it became necessary to tackle certain issues left unresolved by Mackay's revision.

There is a rich *Temnothorax* fauna in California, and in the adjacent Baja California peninsula (Johnson & Ward 2002). At least ten undescribed species occur in California, here indicated by code numbers (*Temnothorax* sp. CA-01 to CA-10). These are the subject of ongoing taxonomic study by Roy Snelling (LACM). In this paper I confine myself to clarifying the nomenclature and species limits of some of the described taxa.

Temnothorax andrei (Emery 1895d)

(Figure 7)

Leptothorax andrei Emery 1895d: 322. Holotype worker, Martinez, California (Turner) [MCSN] [Examined]

Leptothorax nitens var. *Heathii* Wheeler 1903d: 245. Twelve syntype workers, Pacific Grove, California [MCZC] [Examined] **Syn. nov.** [Incorrectly synonymized under *nitens* by Creighton 1950a: 265.]

Leptothorax nitens subsp. *occidentalis* Wheeler 1903d: 245. Two syntype workers, Friday Harbor, Washington [MCZC] [Examined] **Syn. nov.** [Incorrectly synonymized under *nitens* by Creighton 1950a: 265.]

Leptothorax ocellatus Mackay 2000: 383. Holotype worker, 5 mi W Mineral, Tehama Co., California, 4250' (D. Chandler) [MCZC] [Examined] **Syn**. **nov**.

Temnothorax andrei (Emery); Bolton 2003: 271. First combination in *Temnothorax*.

Temnothorax ocellatus (Mackay); Bolton 2003: 272. First combination in *Temnothorax*.

Comments. *Temnothorax andrei* is a common species at low and medium elevations (0–1800 m) in California and adjacent western states. The workers are yellow to yellow-brown, lightly sculptured, and with relatively short, blunt-tipped pilosity. The head is predominantly longitudinally reticulate/carinulate with weakly shining interspaces, and with a smooth, shiny median strip of variable extent. A characteristic feature is the presence of a small, isolated shiny patch of cuticle on the head, posteromesad of the compound eye, and surrounded by sculpture. The mesosoma is reticulate-foveolate and subopaque. The propodeal spines are poorly developed and generally reduced to blunt triangular teeth. In profile the petiolar node, while slender, has an abruptly rounded (not cuneate) summit (Fig. 7). During a recent visit to MCSN (Genoa) Alex Wild matched the holotype worker of *T. andrei* to material from California that I had identified as this species. The unique type of *T. ocellatus* falls easily within the range of variation encompassed by *T. andrei*. The original description of *T. ocellatus* misrepresents some features of its morphology. The mesosoma is not as strongly arched as depicted and, although the eyes are small, they are not atypically so for *T. andrei*.

In coastal regions of central and northern California populations of *T. andrei* tend to produce workers that are darker in color, with a shinier head and better developed propodeal spines. While some samples appear strikingly different from the more typical light-colored *T. andrei*, it is difficult to draw a sharp boundary between the coastal and inland populations because of extensive intra- and interpopulation variation. The type series of *T. nitens heathii* (from Pacific Grove) exemplifies this, with some workers having predominantly smooth and shiny heads and others showing varying amounts of fine reticulate/carinulate sculpture. The syntype workers of *T. nitens occidentalis* (from coastal Washington state) also have variably shiny heads. For both *heathii* and *occidentalis*, however, the rounded (non-cuneate) summit of the worker petiole clearly identifies them as being related to *T. andrei* rather than *T. nitens*. A failure by previous investigators to examine critically the types of *heathii* or *occidentalis* led to their being erroneously associated with *T. nitens*.

***Temnothorax nevadensis* (Wheeler 1903d)**

(Figure 9)

Leptothorax nevadensis Wheeler 1903d: 252. Two syntype workers, two syntype males, Kings Cañon, Ormsby Co., Nevada (C. F. Baker) [MCZC] [Examined] Note: original description also includes dealate queen.

Leptothorax melanderi Wheeler 1909e: 81. Holotype worker, Moscow Mountain, Idaho (A. L. Melander) [AMNH] [Not examined]. Synonymy by Mackay 2000: 376.

Leptothorax eldoradensis Wheeler 1915b: 414. Two syntype workers, Mt. Wilson, California (J. C. Bradley) [MCZC] [Examined]. Synonymy by Mackay 2000: 376; here confirmed.

Leptothorax lindae Mackay 2000: 356. Holotype worker, Wolverton Campground, Sequoia Natl. Park, Tulare Co., California (W. & L. Mackay) [MCZC] [Examined]. Paratype workers (same

data) in LACM also examined. **Syn. nov.**

Leptothorax maryanae Mackay 2000: 364. Holotype worker, 4 mi N Fawnskin, San Bernardino Mnts, California (B. & E. Mackay) [MCZC] [Examined] **Syn. nov.**

Temnothorax lindae (Mackay); Bolton 2003: 271. First combination in *Temnothorax*.

Temnothorax maryanae (Mackay); Bolton 2003: 271. First combination in *Temnothorax*.

Temnothorax nevadensis (Wheeler); Bolton 2003: 271. First combination in *Temnothorax*.

Comments. This is another common species of *Temnothorax* in California and other western states, occupying a broad range of habitats, including coastal scrub, chaparral, oak woodland, open coniferous forest, and sagebrush desert. The worker can be recognized by the dark brown to black body color; relatively long and slender pilosity; opaque to sublucid head, with longitudinal rugoreticulate sculpture and scattered foveolae; dense foveolate sculpture on the mesosoma, overlain by weak rugulae; well developed propodeal spines; slender petiole, with anterior face rounding abruptly into posterodorsal face (Fig. 9); and relatively narrow postpetiole (PPW/DPW 1.34–1.51, PPW/T4W 0.33–0.39; n = 6). Size is variable, such that worker HW 0.47–0.70, but usually >0.55. There is considerable variation in the length and slenderness of the propodeal spines but they are always longer than the anteroventral petiolar process. In some *T. nevadensis* workers from eastern California and Nevada the head is rather shiny (sculpture much reduced), but the variation appears to be continuous. Interestingly, a similar trend is seen in the related arboreal species, *T. gallae* (M. R. Smith): near its eastern limit (in Joshua Tree National Park, southeastern California) workers have shinier heads than in populations farther west.

Taking into account the variability inherent in *T. nevadensis*, this species readily encompasses the forms described by Mackay (2000) as *T. lindae* and *T. maryanae* (and placed inexplicably by him in different species complexes, separate from one another and from *T. nevadensis*), plus two of the three taxa previously considered to be subspecies of *T. nevadensis*: *melanderi* and *eldoradensis*. I have not examined the type of *T. melanderi* so some doubt remains here, but the original description and the type locality suggest that the synonymy is justified. On the other hand, *T. rudis*, described as a subspecies of *T. nevadensis*—and synonymized under *T. nevadensis* by Mackay (2000)—is a distinct and easily recognized species, as documented below.

Temnothorax nitens (Emery, 1895d)

(Figure 8)

Leptothorax nitens Emery 1895d: 322. Holotype worker, American Fork Canon, Utah [USNM] [Examined]

Leptothorax nitens var. *mariposa* Wheeler 1917a: 507. Nine syntype workers, Camp Curry, Yosemite, California [LACM, MCZC] [Examined] **Syn. nov.**

Leptothorax mariposa Wheeler; Cole 1958c: 536. Raised to species.

Leptothorax melinus Mackay 2000: 368. Holotype worker, Beartrap Cyn., Socorro Co., New Mexico, 2286 m (W. Mackay #16889) [MCZC] [Examined]. Two paratype workers in LACM

(same data) also examined. **Syn. nov.**
Temnothorax mariposa (Wheeler); Bolton 2003: 271. First combination in *Temnothorax*.
Temnothorax melinus (Mackay); Bolton 2003: 271. First combination in *Temnothorax*.
Temnothorax nitens (Emery); Bolton 2003: 271. First combination in *Temnothorax*.

Comments. *T. nitens* is a common western United States species characterized by a strongly cuneate (wedge-shaped) petiole, as seen in profile (Fig. 8). Body color varies from pale yellow to medium brown. Integument sculpture tends to be light; the head and mesosoma are finely reticulate-foveolate, with extensive shiny areas usually on the front of the head and occasionally on the mesosoma dorsum. The propodeal spines are variable, relatively short but better developed (on average) than in *T. andrei*, and usually as prominent as the anteroventral petiolar process, or more so (Figure 8). In the holotype worker of *T. nitens* the mesosoma dorsum is smooth and shiny centrally, but as noted by others (Wheeler 1903d; Cole 1958c) the head and mesosomal sculpture is highly variable in this species, and both shiny and more heavily sculptured workers can be found in the same nest. I have also observed this in California populations from the Sierra Nevada. The California workers with a shiny promesonotum tend to have weak longitudinal carinulae encroaching anteriorly and laterally, as in the *T. nitens* type.

Mackay's (2000) treatment of *T. nitens* is inconsistent. On the one hand he seems to accept a broad concept of the species, showing it as having a wide distribution in western North America, accepting the previous synonymy of *heathii* and *occidentalis* under *T. nitens* (incorrectly, as it turns out—see under *T. andrei*), and citing biological data from a diverse selection of localities. On the other hand, he describes a colony series from New Mexico as a new species (*melinus*), even though it falls well within the ambit of *T. nitens* (sensu lato). Restricting the use of the name *T. nitens* to workers with an especially shiny mesosoma is difficult to justify, given the patterns of intranidal variation described above. It seems more reasonable to treat it as a polytypic species, with variable effacement of the mesosomal sculpture.

T. mariposa was originally described as a variety of *T. nitens*. It was synonymized under that species by Creighton (1950a), and later resurrected by Cole (1958c) and raised to species. Cole's argument was that both forms co-occurred in the Yosemite region without intergrading. But examination of a large series of *nitens*-like specimens from throughout the California Sierra Nevada challenges this thesis. It leads me to the conclusion that *T. mariposa* simply connotes larger individuals of *T. nitens* which have correspondingly broader heads and a tendency towards darker body color and coarser sculpture on the side of the mesosoma. There is no evidence of a gap in this size variation (nor in the correlated variation in shape, color and sculpture). The LACM collection has *nitens*-like nest series collected by Cole at Yosemite. His accessions 136, 184, 198, 201, 230, 231 and 233 are identified as "*nitens*" and 239 as "*mariposa*". The "*nitens*" series are collectively smaller and more lightly sculptured than accession 239, but accessions 230, 231 and 233 have workers approaching those of 239 in size and sculpture. Moreover, the syntypes of *T.*

mariposa (LACM, MCZC) agree more closely with the majority series (136 to 233) than with 239, so Cole's attributions and conclusions are difficult to justify.

Temnothorax chandleri (Mackay) is evidently closely related to *L. nitens* and might prove to be conspecific with it. The main diagnostic feature of *T. chandleri* is the heavily sculptured head, which lacks a shiny surface except for a median strip. The type series consisted of three workers, of which the holotype was destroyed while in transit to MCZC (Stefan Cover, pers. comm.). A paratype worker was said to be deposited at the University of New Hampshire (Mackay 2000: 331) but no specimen is present there (Don Chandler, pers. comm.). Thus, the only known type specimen is the paratype worker in WPMC. Here is a description of that specimen which I examined briefly in August 2003:

Petiole cuneate in profile; HW ~0.57 mm; head densely reticulate-foveolate (with weak longitudinal orientation), except for a small shiny central strip which does not extend to the posterior margin; mesosoma densely reticulate-foveolate; propodeal spines short, blunt; dorsum of mesosoma with about 24 short, erect hairs in profile; abdominal tergite IV smooth and shiny except for weak basal striolae; postpetiole moderately broad, length ~0.7× width; pale yellow brown.

This paratype agrees with five workers collected recently at Black Butte Lake, Glenn Co., California (P. S. Ward#14606), in a fallen log of cottonwood (*Populus fremontii*) in riparian woodland. The types of *T. chandleri* were collected from leaf litter at the edge of a slough (Mackay 2000). These limited biological data suggest that *T. chandleri* may be a riparian habitat specialist, whereas *T. nitens* is found in a diverse array of habitats from sea level to ~2600m.

***Temnothorax rudis* (Wheeler 1917a) stat. reval., comb. nov.**
(Figure 10)

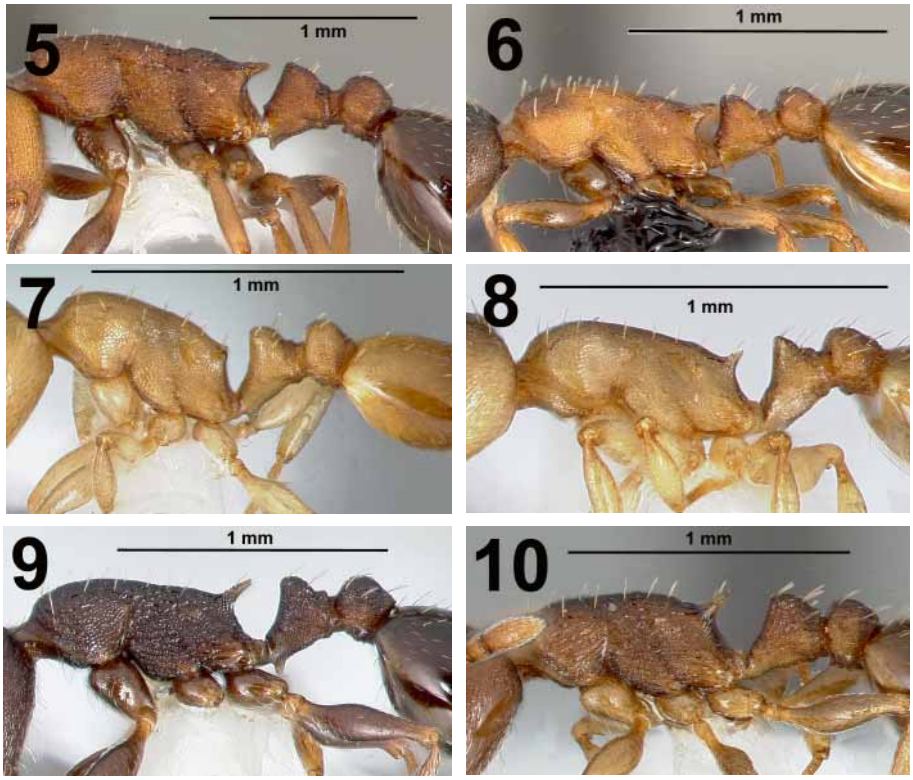
Leptothorax nevadensis subsp. *rudis* Wheeler 1917a: 508. Six syntype workers, Camp Curry, Yosemite, California [MCZC] [Examined]. Note: original description also includes dealate queen, and cites the type locality as Tenaya Canyon, Yosemite Valley. Incorrectly synonymized under *T. nevadensis* by Mackay 2000: 376.

Leptothorax rudis Wheeler; Stuart and Page 1991: 375. Genetic study (*rudis* implicitly raised to species).

Comments. This is a distinct species that occurs sympatrically with *T. nevadensis* in many parts of northern and central California, without showing any sign of intergradation. *T. rudis* is readily distinguished from *T. nevadensis* by petiole shape. In *T. rudis* the petiole is broader in profile, with the anterior and posterodorsal faces meeting at approximately 90º, and the posterodorsal face declining gently (Fig. 10). In *T. nevadensis* the petiole is more slender in profile, with the anterior and posterodorsal faces forming an acute angle (Fig. 9). In addition *T. rudis* has coarser body sculpture and is lighter in color than *T. nevadensis*. *T. rudis* is common in mixed coniferous forests of California, up to about 1750m ele-

vation. Colonies can be found in rotten wood, under stones, in fallen acorns, and in the leaf litter.

Bolton (1995) stated that *rudis* Wheeler 1917a, then combined with *Leptothorax*, was a primary junior homonym of *rudis* Mayr 1868c. Mayr's species, a fossil taxon, was originally combined with *Macromischa*, however, and then later with *Nothomyrmica* (Wheeler 1915i), prior to *Macromischa* being subsumed under *Leptothorax*. Mayr's *rudis* was never treated as a species of *Leptothorax*, so no homonymy arises.



FIGURES 5-10. *Leptothorax* and *Temnothorax* workers, lateral views showing mesosoma, petiole and postpetiole. 5, *Leptothorax calderoni*; 6, *Leptothorax* sp. CA-01; 7, *Temnothorax andrei*; 8, *T. nitens*; 9, *T. nevadensis*; 10, *T. rudis.*

KEY TO CALIFORNIA ANT GENERA BASED ON THE WORKER CASTE

Morphological terminology follows Bolton (1994), on which much of this key is based. The term *mesosoma* is used in preference to alitrunk, to refer to the body part formed from fusion of the thorax and the first abdominal segment (i.e., thorax + propodeum). The *promesonotum* is that part of the mesosoma composed of the pronotum and the mesonotum. *Metasoma* refers to the apparent abdomen, comprising the segments posterior to the

propodeum, i.e., abdominal segment 2 and succeeding segments. In ants abdominal segment 2 forms a node- or scale-like petiole, which is separated by a constriction from the rest of the metasoma. In some species abdominal segment 3 is also node-like and in this case it is said to form a *postpetiole*.

The key has been designed to apply only to those ant species occurring in California but it should also work for most of western North America, excluding Arizona and New Mexico where additional genera occur.

1 Postpetiole present: abdominal segment 3 separated from segment 4 by a strong constriction and distinctly smaller in size, so that anteriorly the metasoma has two node-like segments, the petiole and postpetiole 2
- Postpetiole absent: abdominal segment 3 separated from segment 4 by a weak to moderate constriction or by none at all, and when viewed in profile not distinctly smaller in size (height) than segment 4; metasoma anteriorly with a single, isolated node-like or scale-like segment 26
2 Eye reduced to a single ommatidium or absent; antennal insertions fully exposed in a full-face view of head (Ecitoninae) ..... *Neivamyrmex* Borgmeier
- Eye very rarely reduced, usually consisting of multiple ommatidia; antennal insertions not fully exposed, covered partially by frontal lobes or medial extensions of the antennal sclerites, when the head is observed in full-face view 3
3 Eye very large, eye length about one-half of head length (excluding mandibles); pronotum freely articulating with mesonotum (Pseudomyrmecinae)..... ..... *Pseudomyrmex* Lund
- Eye less than one-half head length; pronotum fused with mesonotum (Myrmicinae) 4
4 Antenna with 6 segments, including a 2-segmented club 5
- Antenna with 10 segments, including a 2-segmented club ..... *Solenopsis* Westwood
- Antenna with 11 segments; club variable 6
- Antenna with 12 segments; club variable 14
5 Mandible elongate and linear, with an apical fork of two spiniform teeth..... ..... *Strumigenys* F. Smith
- Mandible short and subtriangular, with a multi-denticulate masticatory margin ....*Pyramica* Roger
6 Postpetiole attached to the dorsal surface of the following abdominal segment; petiole dorsoventrally flattened, not node-like in profile.....*Crematogaster* Mayr
- Postpetiole attached to the anterior face of the following segment; petiole node-like in profile, not dorsoventrally flattened 7
7 Head in lateral view with a diagonal carina running from above the eye down toward the mandibular insertion; promesonotum with conspicuous tubercles or spines 8
- Head in lateral view lacking such a diagonal carina; promesonotum without conspicu-

ous tubercles or spines 9

8 Frontal lobes expanded laterally and covering the sides of the head below the eyes, in full-face view; body lacking erect pilosity ..... *Cyphomyrmex* Mayr

- Frontal lobes not expanded laterally to cover the sides of the head; body with erect pilosity ..... *Acromyrmex* Mayr

9 Antenna with a distinct 2-segmented apical club..... *Wasmannia* Forel

- Antenna lacking a distinct 2-segmented apical club, either 3-segmented or indistinct 10

10 Eye absent or rudimentary; propodeum unarmed, basal face rounding into declivitous face ..... Solenopsidini new genus

- Eye well developed, with multiple ommatidia; propodeum angulate or spinose 11

11 Lateral portions of clypeus, in front of the antennal insertions, developed in the form of a raised ridge or shield-wall; frontal carinae extending almost to the posterior margin of the head..... *Tetramorium* Mayr (part)

- Lateral portions of clypeus not developed as a raised ridge or shield-wall; frontal carinae very short or absent..... 12

12 Eye with short erect setae projecting between the ommatidia .....*Formicoxenus* Mayr

- Eye lacking erect setae 13

13 Median portion of clypeus with a smooth, longitudinally excavate surface, and lacking carinae ..... *Leptothorax* Mayr

- Median portion of clypeus with several longitudinal carinae .... *Temnothorax* Mayr (part)

14 Hind tibial spur finely pectinate (as seen at 50–100× magnification)..... 15

- Hind tibial spur simple or absent..... 17

15 Metanotal groove absent or very weakly impressed, not breaking the dorsal profile of the mesosoma; psammophore usually present ..... *Pogonomyrmex* Mayr

- Metanotal groove present and interrupting the dorsal profile of the mesosoma; psammophore absent 16

16 Propodeum unarmed; mandible with more than 12 teeth ..... *Manica* Jurine

- Propodeum armed with a pair of spines; mandible with 6–10 teeth .. *Myrmica* Latreille

17 Lateral portions of clypeus, in front of the antennal insertions, developed in the form of a raised ridge or shield-wall; apex of sting with triangular lamellate appendage .... *Tetramorium* Mayr (part)

- Lateral portions of clypeus not developed as a raised ridge or shield-wall; apex of sting without triangular lamellate appendage 18

18 Petiole short and sessile, lacking well differentiated anterior peduncle and dorsal node; ventrolateral margin of head with sharp, longitudinal carina extending from mandibular base to posterolateral corner of head ..... *Myrmecina* Curtis

- Petiole with anterior peduncle and dorsal node; ventrolateral margin of head without sharp, longitudinal carina 19

19 Dorsum of head and mesosoma without standing pilosity..... *Cardiocondyla* Emery
- Dorsum of head and mesosoma with standing pilosity..... 20
20 Anteromedian portion of clypeus notably elevated and bounded by a pair of carinae that diverge anteriorly 21
- Anteromedian portion of clypeus not abruptly elevated and lacking a pair of anteriorly diverging carinae 23
21 Propodeum unarmed ..... *Monomorium* Mayr
- Propodeum armed with a pair of teeth or spines 22
22 Antennal club 3-segmented; propodeal spiracle large and located close to the declivitous face of the propodeum, separated from latter by no more than the diameter of the spiracle .....*Rogeria* Emery
- Antennal club 4-segmented; propodeal spiracle relatively small and separated from the declivitous face of the propodeum by more than the spiracle diameter..... .....*Stenamma* Westwood
23 Antennal club 3- (rarely 4-) segmented..... 24
- Antenna lacking a distinct club 25
24 In profile promesonotum domed and distinctly elevated above the propodeal dorsum; workers dimorphic ..... *Pheidole* Westwood
- In profile entire mesosoma dorsum flat to weakly convex, promesonotum not domed or markedly elevated above the level of the propodeum; workers monomorphic..... .....*Temnothorax* Mayr (part)
25 Head narrow, longer than broad; mandible slender and triangular, outer margin not strongly curving towards the midline; psammophore absent ..... *Aphaenogaster* Mayr
- Head broad, subquadrate; mandible short and thick, outer margin strongly curving towards the midline; psammophore usually present ..... *Messor* Forel
26 Pygidium (last visible abdominal tergite) flattened and bordered laterally with a row of peg-like teeth or spines that converge distally (Cerapachyinae)....*Cerapachys* F. Smith
- Pygidium (last visible abdominal tergite) convex and rounded, lacking a row of teeth or spines 27
27 Distinct constriction between abdominal segments 3 and 4; terga and sterna of abdominal segments 3 and 4 laterally fused 28
- No constriction between abdominal segments 3 and 4; terga of abdominal segments 3 and 4 overlapping the corresponding sterna, not laterally fused with them 30
28 Articulation of petiole (second abdominal segment) to third abdominal segment very broad; petiole without a distinct posterior face (Amblyoponinae)..... ..... *Amblyopone* Erichson
- Articulation of petiole (second abdominal segment) to third abdominal segment narrow; petiole with a distinct posterior face 29
29 Pronotum freely articulating with the mesonotum; abdominal tergite 4 not strongly enlarged and not curved ventrally; apex of metasoma directed posteriorly (Ponerinae)

.....*Hypoponera* Santschi

- Pronotum fused immovably to the mesonotum; abdominal tergite 4 strongly enlarged and curved ventrally; apex of metasoma directed anteriorly (Proceratiinae)..... ..... *Proceratium* Roger

30 Apex of metasoma with a circular orifice, often fringed with short setae (the acidopore) (Formicinae)..... 31

- Apex of metasoma with a slit-shaped orifice (Dolichoderinae)..... 38

31 Antenna with 9 segments ..... *Brachymyrmex* Mayr

- Antenna with 11 segments ..... *Plagiolepis* Mayr
- Antenna with 12 segments 32

32 Metapleural gland absent; antennal insertions well separated from the posterior clypeal margin; in profile mesosoma dorsum usually evenly convex ... *Camponotus* Mayr

- Metapleural gland present; antennal insertions adjacent to the posterior clypeal margin; in profile promesonotum separated from the dorsal face of the propodeum by a distinct impression 33

33 Maxillary palp segments 3 and 4 greatly elongated, segment 3 (counting from base) half the head length or more; psammophore present .....*Myrmecocystus* Wesmael

- Maxillary palp segments 3 and 4 not greatly elongated, segment 3 much less than half the head length; psammophore absent 34

34 Ocelli present; propodeal spiracle elliptical to oval..... 35

- Ocelli absent or indistinct; propodeal spiracle circular to subcircular 36

35 Mandible triangular, with seven or more distinct teeth on the masticatory margin ....*Formica* Linnaeus

- Mandible falcate (sickle-shaped) and lacking distinct teeth ..... *Polyergus* Latreille

36 Dorsum of head and mesosoma with coarse setae, arranged in distinct pairs; eye situated in relatively anterior position, at or in front of midlength of side of head .... *Paratrechina* Motschoulsky

- Pilosity on dorsum of head and mesosoma variable, but not arranged as coarse setae in pairs; eye situated in relatively posterior position, behind midlength of side of head 37

37 Mandible with six teeth; antennal scape long, surpassing posterior margin of head by more than half its length; mesonotum in dorsal view strongly constricted behind pronotum ..... *Prenolepis* Mayr

- Mandible with seven or more teeth; antennal scape shorter, surpassing posterior margin of head by less than a third its length; mesonotum in dorsal view not strongly constricted behind pronotum .....*Lasius* Fabricius

38 Propodeum with a prominent conical tooth at the junction of the dorsal and declivitous faces; maxillary palp segment 3 elongate, subequal in length to segments 4–6; apical mandibular tooth much enlarged..... *Dorymyrmex* Mayr

- Propodeum rounded or subangulate at the junction of the dorsal and declivitous faces,

but without a conical tooth; maxillary palp segment 3 short, subequal in length to segments 4; apical mandibular tooth not notably enlarged 39

39 Mesosoma dorsum lacking standing pilosity 40

- Mesosoma dorsum with standing pilosity 41

40 Petiole flattened, plate-like, and without a conspicuous, dorsally protruding scale (petiole often overhung by the succeeding abdominal segment); dorsal face of propodeum much shorter than the declivitous (posterior) face ..... *Tapinoma* Foerster

- Petiole with a well developed, dorsally protruding scale; dorsal face of propodeum subequal in length to declivitous face ..... *Linepithema* Mayr

41 In profile mesosoma dorsum without an impressed metanotal groove, the promesonotum and propodeum forming a continuous surface; workers variable in size within a colony ..... *Liometopum* Mayr

- In profile mesosoma dorsum interrupted by a well marked metanotal groove; workers showing little intra-colony size variation 42

42 Petiole lacking an erect scale; side of mesosoma with conspicuous microreticulate sculpture; dark brown-black, with contrastingly paler tarsi ..... *Technomyrmex* Mayr

- Petiole with well developed erect scale; side of mesosoma without conspicuous microreticulate sculpture; varying in color from yellowish-orange to dark brown, but without contrastingly paler tarsi ..... *Forelius* Emery

SYNOPSIS OF CALIFORNIA ANT GENERA

Subfamily Amblyoponinae

Genus *Amblyopone* Erichson

Ants in the genus *Amblyopone* have cryptic foraging habits and are specialist predators on geophilomorph centipedes and other arthropods living in soil or rotten wood. Two species are known from California: *A. oregonensis* (Wheeler) is found in shaded, medium-elevation coniferous forests in northern California, while *A. pallipes* (Haldeman) is widespread in chaparral and low elevation woodland.

Species identification: Ward (1988). Additional references: Brown (1960a), Creighton (1940b), Haskins (1928), Lattke (1991d), Lacau and Delabie (2002), Traniello (1978, 1982).

Subfamily Cerapachyinae

Genus *Cerapachys* F. Smith

Ants in this genus are subterranean predators on other ants and they are not commonly

encountered in California. Workers of *C. augustae* Wheeler have been recorded from three localities in southern coastal California (specimens in LACM and UCDC), while males of *C. davisi* M. R. Smith have been collected at light in desert locations in Imperial and San Bernardino Counties (Snelling & George 1979).

Species identification: male key in Mackay and Mackay (2002). Additional references: Brown (1975), Smith (1942b), Snelling and George (1979), Wheeler (1902e, 1903j).

Subfamily Dolichoderinae

Genus *Dorymyrmex* Mayr

These generalist, ground-nesting ants are frequent in open habitats at medium to low elevations. The two commonest species, *D. bicolor* Wheeler and *D. insanus* (Buckley), are usually distinguishable on the basis of color, with the former being bicolored (head and mesosoma orange- or reddish-brown, metasoma brownish-black) and the latter unicolorous dark brown, but some samples are intermediate in color. Snelling (1995a) describes additional worker differences in head shape and eye size, but these characters are quite variable and are not always reliable. This group of ants continues to be burdened with taxonomic uncertainties, possibly as a result of occasional interspecific hybridization.

Species identification: key in Snelling (1995a). Additional references. Berkelhamer (1984), Johnson (1989b), Martinez (1995), Snelling and George (1979), Trager (1988a), Wheeler and Wheeler (1986g).

Genus *Forelius* Emery

These are hyperactive, thermophilic, ground-nesting ants, with two species (*F. mccooki* and *F. pruinosus*) in California. Colonies are polygynous, and the workers have conspicuous foraging trails. Some nest series consist of individuals phenotypically intermediate between *F. mccooki* and *F. pruinosus*, indicating the possibility of introgression between the two forms. Taxonomic difficulties with the group have been discussed previously (under “Taxonomic Changes”).

Species identification: key in Wheeler and Wheeler (1986g). Additional references: Cuezzo (2000), Holway *et al.* (2002), Scheffrahn *et al.* (1984), Shattuck (1992c), Snelling and George (1979), Yensen *et al.* (1980).

Genus *Linepithema* Mayr

The introduced Argentine ant, *L. humile* (Mayr), is abundant in many urban and agricul-

tural locations in lowland California, and it has invaded natural habitats along rivers and in some coastal regions. Workers avidly tend plant nectaries and honeydew-producing hemipterans. *L. humile* aggressively eliminates epigeic (above-ground foraging) native ant species (Ward 1987; Human & Gordon 1996; Holway 1998). Most California populations of *L. humile* exhibit a unicolonial population structure, in which there is little or no intraspecific aggression, and they have reduced genetic diversity compared to native populations in Argentina (Tsutsui *et al*. 2000). Additional references (a sampling only): Buczkowski *et al*. (2004), Carney *et al.* (2003), Gordon *et al*. (2001), Heller (2004), Holway (1999), Holway *et al*. (1998, 2002), Holway and Suarez (2004), Human and Gordon (1997), Ingram and Gordon (2003), Knight and Rust (1990), Longcore (2003), Newell and Barber (1913), Sanders *et al*. (2001), Shattuck (1992a, 1992c), Smith (1965), Suarez *et al.* (1998, 1999, 2001), Tsutsui and Case (2001), Tsutsui *et al*. (2003), Vega and Rust (2001).

Genus *Liometopum* Mayr

This genus is represented in California by two species, both widespread. These ants have populous colonies that inhabit the trunks of large living trees, especially those of oak and pine. *L. occidentale* Emery tends to be associated with deciduous trees, while *L. luctuosum* Wheeler is found most frequently in conifers. The workers forage in large files and are generalist scavengers and predators, as well as active tenders of aphids and scale insects.

Species identification: key in Wheeler and Wheeler (1986g). Additional references: Disney (1982), Gulmahamad (1995), Kistner *et al*. (2002), Shapley (1920), Snelling and George (1979), Wheeler (1905h).

Genus *Tapinoma* Foerster

T. melanocephalum (Fabricius) is an introduced species, not definitively established in the state. *T. sessile* (Say) is a very common ant, found in almost all habitats in California except deserts and areas invaded by *Linepithema humile*. *T. sessile* shows substantial variation in size and color. At scattered locations in California a bicolored (orange and black) form of *T. sessile* occurs sympatrically with the typical unicolored dark brown/black morph. Workers of intermediate color have also been observed, suggesting that the two forms are conspecific. An alternative interpretation is that there are two species which occasionally exchange genes, perhaps analogous to the situation between *Forelius mccooki* and *F. pruinosus* and between *Dorymyrmex bicolor* and *D. insanus*.

Species identification: key in Creighton (1950a). Additional references: Meissner and Silverman (2001), Smith (1965), Wang and Brook (1970).

Genus *Technomyrmex* Mayr

This genus is represented by a single introduced species in the *T. albipes* complex, which occasionally establishes residence in hothouses (e.g., in Golden Gate Park, San Francisco). The group is under taxonomic revision by Barry Bolton (pers. comm.). References: Deyrup (1991), Ogata *et al.* (1996), Smith (1965), Tsuji *et al.* (1991), Yamauchi *et al.* (1991).

Subfamily Ecitoninae

Genus *Neivamyrmex* Borgmeier

This is the only genus of army ants found in California. These are nomadic, predacious ants that engage in group foraging. Workers are usually active at night, and often forage below the soil surface. Other ant species (both adults and brood) appear to be the principal prey items of *Neivamyrmex*, although the habits of the smaller, subterranean species are not well known.

Species identification: Snelling and Snelling (2005). Additional references: Borgmeier (1955), Gotwald (1995), Snelling and George (1979), Ward (1999), Watkins (1972, 1976, 1977b, 1985), Wheeler and Wheeler (1984a, 1986g).

Subfamily Formicinae

Genus *Brachymyrmex* Mayr

The name *B. depilis* Emery is provisionally attached to the single species of *Brachymyrmex* that occurs in California. It is widespread but infrequently encountered, in part because of its small size and inconspicuous foraging behavior. This is a ground-nesting species, recorded in California from sea level to ~1900m. References: Creighton (1950a), Page (1982), Smith (1979), Wheeler and Wheeler (1986g), Yensen *et al.* (1980).

Genus *Camponotus* Mayr

Species of *Camponotus* (carpenter ants) are found in almost all terrestrial habitats of California, and include both ground-nesting and arboreal species. The workers are generalist scavengers and predators, and are most active at dusk and at night. Identification of the California species can be difficult. The keys cited below do not cover all of the species in this state, several of which are undescribed. The images on AntWeb provide additional assistance in identification. See also the description of *Camponotus maritimus* above (under "Taxonomic Changes").

Species identification: keys in Wheeler and Wheeler (1986g) and Mackay and Mackay (2002). Additional references: Brady *et al*. (2000), Chen *et al*., (2002), Creighton and Snelling (1967), Degnan *et al*. (2004), Gadau *et al*. (1999), Hansen and Akre (1985), MacArthur (2005), Sameshima *et al*. (1999), Sauer *et al*. (2000), Smith (1979), Snelling (1968b, 1970, 1988).

Genus *Formica* Linnaeus

In California the members of this genus are most prevalent in montane habitats, although a few species occur in drier, low elevation sites. *Formica* species are ground-nesting ants with generalist foraging habits. Francoeur's (1973) authoritative revision of the *Formica fusca*-group allows the species in that group to be relatively easily identified. Taxonomic difficulties still plague the *Formica rufa*-group, which contains most of the remaining species in California.

Species identification: keys in Francoeur (1973), Wheeler and Wheeler (1986g), Snelling and Buren (1985) and Mackay and Mackay (2002). Additional references: Agosti (1994b), Agosti and Bolton (1990b), Buren (1968a), Cole (1956d, 1956f, 1956g), Creighton (1940a, 1950a), Dlussky (1967), Francoeur and Snelling (1979), Gösswald (1989, 1990), Savolainen (1998), Smith (1979), Trager *et al*. (2005), Wilson and Brown (1955).

Genus *Lasius* Fabricius

These ground-nesting ants also tend to prefer cooler habitats at middle to high elevations. Workers are generalized scavengers and often tend hemipterans. Species in the subgenera *Acanthomyops* and *Chthonolasius* are temporary social parasites on other *Lasius* species. Species of *Acanthomyops* were previously considered to represent a different genus, but are now known to be phylogenetically nested within *Lasius* (see above under "Taxonomic Changes").

Species identification: keys in Wilson (1955a), Wing (1968) (*Acanthomyops*), and Mackay and Mackay (2002). Additional references: Agosti and Bolton (1990b), Cole (1956a, 1958a), Hasegawa (1998), Janda *et al*. (2004), MacKay (1998), Savolainen (2002), Seifert (1988a, 1992b), Umphrey and Danzmann (1998), Wheeler and Wheeler (1986g).

Genus *Myrmecocystus* Wesmael

These are the well-known "honeypot ants", whose colonies include a subgroup of specialized workers (repletes) devoted to storage of liquid food in their swollen abdomens. Spe-

cies of *Myrmecocytus* are restricted to the western United States and northern Mexico and are found primarily in desert habitats. Snelling's (1976) landmark revision of the genus also contains much useful biological information.

Species identification: keys in Snelling (1976, 1982b). Additional references: Diniz-Filho and Fowler (1998), Duncan and Lighton (1994a, 1994b), Hölldobler (1976b, 1986), Kay and Whitford (1978), Kronauer *et al*. (2003, 2004), Lloyd *et al*. (1989), Rissing (1984), Snelling (1969b, 1971a), Snelling and George (1979), Smith (1979), Wheeler and Wheeler (1986g).

Genus *Paratrechina* Motschoulsky

These ground-dwelling ants are infrequently encountered in natural habitats of California, except *P. hystrix* Trager, a desert species. *P. vividula* (Nylander) is common in many urban locations, and behaves like an introduced species, although it is assumed to be native to Mexico (Trager 1984b). A second tramp species, *P. longicornis* (Latreille), of Old World origin, is established at some locations in southern California.

Species identification: keys in Trager (1984). Additional references: Creighton (1950a), MacKay (1998), Smith (1965), Saporito *et al.* (2004), Wetterer *et al*. (1999).

Genus *Plagiolepis* Mayr

A single introduced species, *P. alluaudi* Emery, has been recorded from the state (Catalina Island). The genus is of Old World origin. References: Smith (1958b), Smith (1979), Wilson and Taylor (1967).

Genus *Polyergus* Latreille

The members of this genus are obligate slave-raiders of other ants, mostly species in the *Formica fusca*-group. The California populations of *Polyergus* are here treated as a single variable species, *P. breviceps* Emery. This implies synonymy of *P. laeviceps* Wheeler (type locality: Mt. Tamalpais, California) under *P. breviceps* but no formal change is proposed here because the entire complex needs comprehensive taxonomic evaluation. Within California there is considerable interregional variation in worker morphology and biology (including the host species attacked), but I have seen no evidence of more than one species occurring in any given locality. One might expect there to be pronounced interpopulation variation in *P. breviceps* because of the limited dispersal of the queens (Topoff 1999). References (partial list): Agosti (1994b), Creighton (1950a), Greenberg *et al*. (2004), Hasegawa *et al.* (2002), Hölldobler (1985), Topoff (1990, 1999), Wheeler (1968).

Genus *Prenolepis* Mayr

P. imparis Say is very common in mesic habitats at low and medium elevations throughout most of the state. Nests are located deep in the ground, and workers do not forage during the hottest periods of summer. A collection of unusually small alate queens from one locality in the foothills of the Sierra Nevada appears to represent a second, undescribed species, which might be a social parasite of *P. imparis* (Wild 2002). References: Creighton (1950a), Fontenla (2000), Lynch *et al.* (1980), Smith (1965), Tschinkel (1987), Wheeler (1930c).

Subfamily Myrmicinae

Genus *Acromyrmex* Mayr

These leaf-cutting ants are represented in California by a single species, *Acromyrmex versicolor* (Pergande), confined to the southern deserts. The harvested leaves are used to culture a basidiomycete fungus, which is the principal food of the ants. References: Gamboa (1975, 1976), Johnson and Rissing (1993), Julian and Fewell (2004), Mueller *et al*. (2001), Reichardt and Wheeler (1996), Rissing *et al.* (1986, 1989), Snelling and George (1979), Weber (1972).

Genus *Aphaenogaster* Mayr

Of the six species of this genus occurring in California, one (*A. occidentalis* (Emery)) is widespread in mesic habitats, four are confined to deserts, and one species (*A. patruelis* Forel) is endemic to the Channel Islands and Isla Guadalupe. All are ground-nesting ants, with somewhat generalized scavenging habits.

Species identification: keys in Creighton (1950a), Wheeler and Wheeler (1986g) and Mackay and Mackay (2002). Additional references: Creighton (1955), De Andrade (1995), Hölldobler and Carlin (1990), Hölldobler *et al*. (1995), Johnson (2000a, 2001), Jones and Phillips (1989), Sanders and Gordon (2002), Schulz (1994), Smith (1963c), Umphrey (1996), Wheeler and Creighton (1934).

Genus *Cardiocondyla* Emery

These minute ants are of Old World origin but several species have become widespread vagrants. Two of these occur in disturbed (mostly urban) habitats in California, where they nest in sidewalks and along roadways. Both are able to survive in sites invaded by

the Argentine ant (*Linepithema humile*). The males of *Cardiocondyla* occur in two forms: dispersing winged males and wingless, worker-like (ergatoid) males that mate in the nest.

Species identification: keys in Seifert (2003). Additional references: Anderson *et al*. (2003), Creighton and Snelling (1974), Cremer and Heinze (2003), Gulmahamad (1997), Heinze (1999), Heinze and Hölldobler (1993B), Heinze *et al.* (2004), Kugler (1984), MacKay (1995), Snelling (1974).

Genus *Crematogaster* Lund

This large cosmopolitan genus is represented in California by both arboreal and ground-nesting species. Nine species have been recorded from the state but taxonomic uncertainties undermine this statistic. *C. opuntiae* Buren is quite similar to, and possibly conspecific with, *C. californica* Wheeler; the differences between *C. coarctata* Mayr and *C. mormonum* Wheeler are slight and unreliable; and the record of *C. larreae* Buren from California may be a misidentification. The North American species of this genus are much in need of a taxonomic update.

Species identification: keys in Buren (1968b). Additional references: Buren (1959), Longino (2003), Mackay and Mackay (2002), Scheffrahn and Rust (1989), Snelling and George (1979), Wheeler and Krutzsch (1994).

Genus *Cyphomyrmex* Mayr

There are two species of *Cyphomyrmex* recorded from California, both ground-nesting and infrequently encountered. These fungus-growing ants collect caterpillar frass and other organic matter, on which they cultivate fungal mycelia or (in some species) yeasts.

Species identification: keys in Snelling and Longino (1992). Additional references: De Andrade (2003), Kempf (1964d, 1966), Schultz *et al*. (2002), Weber (1972).

Genus *Formicoxenus* Mayr

A single species, *F. diversipilosus* (M. Smith) occurs in northern California, where it lives as a "guest-ant" in the mound nests of species in the *Formica rufa*-group, such as *F. integroides* Wheeler and *F. obscuripes* Forel. Colonies of *Formicoxenus* occupy dead twigs within the larger mound nests, and apparently scavenge organic material gathered by the host ant. References: Alpert and Akre (1973), Bolton (2003), Buschinger (1979a), Francoeur *et al*. (1985), Lenoir *et al.* (1997), Smith (1939c), Snelling (1965a).

Genus *Leptothorax* Mayr

Most species formerly placed in this genus have been reassigned to *Nesomyrmex* and *Temnothorax*, leaving *Leptothorax* much more narrowly and precisely circumscribed (Bolton 2003). Nevertheless, the species-level taxonomy of the North American *Leptothorax* remains in a state of chaos. There are at least two species in California: one can be easily identified as *L. calderoni* (see "Taxonomic Changes" above), while the remaining collections—here assigned the code name *Leptothorax* sp. CA-01—cannot be identified with certainty. They belong to the *muscorum*-complex, which is widespread in temperate North America and Eurasia, and within which species limits are ill-defined. References: Bolton (2003), Brown (1955a), Buschinger and Heinze (1993), Cole (1954d), Creighton (1950a), Douwes and Stille (1987), Francoeur (1986b), Francoeur *et al.* (1985), Heinze (1989b, 1991, 1998), Heinze *et al.* (1996), Loiselle et al. (1990), Möglich (1979).

Genus *Manica* Jurine

All four North American species of this Holarctic genus occur in California, where they are confined to montane and high desert locations. Detailed notes on the distribution and nesting habits of the species are given by Wheeler and Wheeler (1970a). One species, *M. parasitica* Creighton, is known only from peculiar shiny workers collected in the nests of *M. bradleyi* (Wheeler), of which it is presumed to be a parasite, but its taxonomic status remains unclear.

Species identification: keys in Wheeler and Wheeler (1986g). Additional references: Creighton (1934), Fales *et al.* (1972), Went *et al.* (1972), Wheeler and Wheeler (1968b, 1970a), Wheeler (1914e).

Genus *Messor* Forel

These are granivorous ants whose nest entrances are usually surrounded by conspicuous piles of seed chaff. The seven California species are found mostly in open, dry habitats. There is some evidence that the Nearctic species of *Messor* are more closely related to a group of New World *Aphaenogaster* (those belonging to the erstwhile genus *Novomessor*) than to the Old World species of *Messor* (Bennett 2000). If confirmed this would warrant redefinition of *Messor* and resurrection of *Veromessor*, the genus name previously applied to the Nearctic species. Unfortunately *Aphaenogaster* itself is likely to be paraphyletic and a comprehensive overhaul of the entire tribe Pheidolini, in which these ants have been placed, is needed.

Species identification: keys in Smith (1956a) and Wheeler and Wheeler (1986g). Additional references: Bennett (2000), Boulton *et al.* (2003), Brown (1999a, 1999b),

Brown and Human (1997), Cahan *et al.* (1998), Cole (1963a), Creighton (1953a), Davidson (1977a, 1978), Helms Cahan (2001), Hobbs (1985), Johnson (2000a, 2001), O'Dowd and Hay (1980), Rissing and Wheeler (1976), Ryti and Case (1988), Waser (1998), Went *et al*. (1972), Wheeler and Rissing (1975a, 1975b), Wheeler and Creighton (1934).

Genus *Monomorium* Mayr

California appears to have a single indigenous species of this genus, *M. ergatogyna*, a ground-nesting species which is widely but patchily distributed throughout the state except at high elevations. The reasons for treating *M. wheelerorum* as a junior synonym have been discussed above (under "Taxonomic Changes"). The introduced Pharaoh's ant, *M. pharaonis* (Linnaeus), is a frequent pest in buildings in urban California. A second introduced species, similar to *M. pharaonis* but with a more elongate head and more shagreened sculpture, has been collected once in the state (images and locality information on AntWeb).

Species identification: keys in Wheeler and Wheeler (1986g). Additional references: Adams and Traniello (1981), Andersen *et al.* (1991), Berndt and Eichler (1987), Bolton (1987), DuBois (1986, 2000), Fernández (2005), Heterick (2001), Jones *et al*. (1982a, 1982b), Knight and Rust (1990).

Genus *Myrmecina* Curtis

The members of this genus are small, cryptobiotic ants that live in soil, leaf litter and rotten logs. Studies of two Asian species suggest that these ants are specialized as mite predators (Masuko 1995). California has a single species, *M. americana* Emery, that is known from scattered low-elevation sites throughout the state. It was previously considered to represent a distinct, endemic taxon (*M. californica* M. R. Smith). The California populations exhibit considerable variation in color and sculpture, however, making it difficult to establish a clear distinction between them and other western populations of *M. americana*. References: Brown (1967c), Buschinger (2003), Buschinger and Schreiber (2002), Masuko (1995), Murakami *et al.* (2002), Smith (1948), Snelling (1965b), Ward (1988).

Genus Myrmica Latreille

This is a Holarctic genus of ground-nesting ants, with generalized foraging habits. Like most members of the genus, the California species are found predominantly in temperate habitats such as coniferous forests and montane meadows, but one rare species (*M. rugiventris* (M. R. Smith)) occurs in chaparral, oak woodland and coastal scrub. A revision of the Nearctic species is in preparation by André Francoeur.

Species identification: keys in Creighton (1950a), Wheeler and Wheeler (1986g) and Mackay and Mackay (2002). Additional references: Bolton (1988a), Evans (1995, 1996a, 1996b), Francoeur (2005), Radchenko (1994a, 1994d), Seifert (1988b), Weber (1939b, 1947b, 1948a, 1950c).

Genus *Pheidole* Westwood

This is one of the world's largest ant genera, with more than 600 species recognized in the New World alone (Wilson 2003). The native California *Pheidole* are all ground-dwelling species, found in open, dry habitats. A few of the species are generalized scavengers, but most belong to a group of seed-harvesting specialists, the *P. pilifera*-group, with fifteen species in the state. There are also three introduced species, currently of limited distribution and confined to urban areas.

Species identification: keys in Gregg (1959), Wheeler and Wheeler (1986g) and Wilson (2003). Additional references: Clark *et al.* (1986), Cole (1956c), Creighton and Gregg (1955), Davidson (1977a), Johnson (2000a, 2000b, 2001), Langen *et al*. (2000), Martinez (1992, 1996, 1997), Snelling (1992b), Snelling and George (1979), Ward (2000), Wheeler and Wheeler (1973e).

Genus *Pogonomyrmex* Mayr

The species in this genus are seed-harvesting ants, whose nest mounds are often conspicuously decorated with pebbles. The workers are diurnal and have a potent sting. Several of the taxa belong to difficult complexes, and species boundaries remain unclear. In neighboring Arizona a series of stabilized hybrid lineages has been documented in the *P. barbatus*-complex (Helms Cahan *et al.* 2002).

Species identification: keys in Cole (1966), Wheeler and Wheeler (1986g) and Mackay and Mackay (2002). Additional references: Davidson (1977a), De Vita (1979), Gordon (1999), Groark (2001), Helms Cahan *et al*. (2002), Hölldobler (1976a, 1976c), Johnson (2000a, 2001), Knudtson (1978), Kusnezov (1951e), Lei (2000), MacKay (1980, 1981, 1982), MacKay and MacKay (1989), O'Dowd and Hay (1980), Olsen (1934), Parker and Rissing (2002), Ryti and Case (1988), Schmidt (1998), Shattuck (1987), Snelling (1982a), Taber (1990, 1998), Taber *et al.* (1987, 1988), Wheeler (1902a, 1914e).

Genus *Pyramica* Roger

Three species of *Pyramica* have been recorded from California, of which two are endemic and one is introduced from the Old World. These are rare, cryptobiotic ants, thought to be specialist predators on springtails and other small arthropods.

Species identification: keys in Ward (1988) and Bolton (2000). Additional references: Bolton (1999), Brown (1953g), Brown and Wilson (1959b), Dejean (1985b), Wilson (1954a).

Genus *Rogeria* Emery

A single, apparently undescribed species of this predominantly Neotropical genus has been collected once in Orange County (images and locality data on AntWeb). References: Kugler (1994).

Solenopsidini new genus

The sole species in this undescribed genus has blind, subterranean workers and is known only from desert regions of southwestern United States. A description is in preparation, based on collections of workers, queens and males from southeastern Arizona (Cover & Deyrup 2005). Alates of apparently the same species have been collected in southern California. Mackay and Mackay (2003) recorded the same species from New Mexico and tentatively assigned it to the genus *Tranopelta* Mayr.

Genus *Solenopsis* Westwood

Two groups of *Solenopsis* occur in California. "Fire ants" are relatively large, ground-dwelling species, with generalized foraging habits, aggressive workers and a painful sting. They include the widespread native species, *S. xyloni* McCook, and the recently introduced *S. invicta* Buren (red imported fire ant). "Thief ants" are small to minute species, previously placed in the subgenus *Diplorhoptrum*. These ants are predominantly subterranean, and difficult to identify.

Species identification: keys in Trager (1991) (fire ants), Wheeler and Wheeler (1986g) and Mackay and Mackay (2002). Additional references: Buren (1972), Creighton (1930b), Gorman *et al*. (1998), Jones *et al*. (1982a), Knight and Rust (1990), Korzukhin *et al*. (2001), Morrison (2002), Porter and Savignano (1990), Ross and Trager (1991), Taber (2000), Thompson (1989).

Genus *Stenamma* Westwood

The species in this genus nest in soil and rotting wood, usually in mesic habitats. *Stenamma* workers have rather cryptic foraging habits, and are often encountered in litter

samples. California appears to a center of ongoing diversification for the group, resulting in a number of taxonomic difficulties. For identification purposes the images on AntWeb should be examined in consultation with the keys in Snelling (1973c).

Species identification: keys in Snelling (1973c). Additional references: Cole (1966b), DuBois (1998), Smith (1957b), Wheeler and Wheeler (1986g).

Genus *Strumigenys* F. Smith

Strumigenys is a predominantly tropical genus, represented in California by a single, non-native species, *S. silvestrii* Emery. Species in this genus whose biology has been studied are specialist predators of springtails and other small arthropods. References: Bolton (1999, 2000), Brown (1959f), Brown and Wilson (1959b), Dejean (1987), Wilson (1954a).

Genus *Temnothorax* Mayr

Most of the California species formerly placed in *Leptothorax* have now been assigned to *Temnothorax* (Bolton 2003). With at least twenty species in California, this is a diverse group showing wide variation in habitat and nest-site preferences. About a third of the species are arboreal. Most species appear to be generalist scavengers.

Species identification: keys in Wheeler and Wheeler (1986g) and Mackay (2000), in conjunction with the new synonymy introduced here (see above under "Taxonomic Changes") and images on AntWeb. Additional references: Bolton (2003), Cole (1958c), Creighton (1950a), Deyrup and Cover (2004), Douwes and Stille (1987), Möglich (1979), Smith (1949e), Wheeler (1903d).

Genus *Tetramorium* Mayr

There is one native species of *Tetramorium* in California, *T. spinosum* (Pergande), which occurs in open dry habitats of southern California, and one introduced European species, *T. caespitum* (Linnaeus) (the pavement ant), which is found in urban and agricultural areas of central and northern California. Both are ground-nesting, with generalist foraging habits. Four other non-native species, of tropical origin, have been recorded occasionally from the state.

Species identification: keys in Bolton (1979). Additional references: Astruc *et al.* (2001), Brown (1957d), Bruder and Gupta (1972), Knight and Rust (1990), Longhurst *et al.* (1980), Martinez (1993), Merickel and Clark (1994), Sanetra and Buschinger (2000), Steiner *et al.* (2005).

Genus *Wasmannia* Forel

Wasmannia auropunctata (Roger) has been recorded occasionally from southern California. Native to the Neotropics, this aggressive species has not become established in California, probably because of climatic unsuitability. It is considered ecologically destructive in other areas where it has successfully invaded. References: Jourdan (1997), Le Breton *et al*. (2004), Longino and Fernández (2005), Lubin (1984), Ulloa-Chacón and Cherix (1990), Wetterer and Porter (2003).

Subfamily Ponerinae

Genus *Hypoponera* Santschi

This is a cosmopolitan genus of small predacious ants, nesting in soil and rotten wood. Four species are known from California, of which one (*Hypoponera* sp. CA-01) is apparently undescribed and not included in the keys cited below. It is similar to *Hypoponera opacior* (Forel) from which it can be distinguished by the orange-brown body color (usually dark brown in California *H. opacior*), narrower head (CI 0.77-0.83, as opposed to 0.83-0.87 in *H. opacior*), and conspicuous standing pilosity on the venter of the head (such pilosity sparse in California populations of *H. opacior*).

Species identification: keys in Creighton (1950a), Wheeler and Wheeler (1986g) and Mackay and Mackay (2002). Additional references: Delabie and Blard (2002), Duffield *et al.* (1976), Foitzik *et al.* (2002), Taylor (1967a).

Subfamily Proceratiinae

Genus *Proceratium* Roger

A single, rare species of *Proceratium* has been recorded from California. Endemic to the state, *P. californicum* Cook is known from valley oak woodland in the Central Valley and from woodland, chaparral and grassland sites in adjacent foothill localities. It is presumed to be a specialist, subterranean predator; some other members of the genus have been shown to prey on spider eggs. References: Baroni Urbani and de Andrade (2003), Brown (1958g, 1958j, 1980c), de Andrade and Baroni Urbani (2003), Onoyama and Yoshimura (2002), Snelling (1967), Ward (1988).

Subfamily Pseudomyrmecinae

Genus *Pseudomyrmex* Lund

Ants in this predominantly Neotropical genus nest in hollow dead twigs and other preformed plant cavities. Two species occur in California: *P. apache* Creighton is widespread at middle and low elevations within the California floristic province, often nesting in branches of manzanita (*Arctostaphylos*), while *P. pallidus* (F. Smith) is confined to southern California.

Species identification: Ward (1985b). Additional references: Creighton (1953b, 1954), Peters (1997), Starks *et al*. (1998), Ward (1989a, 1990, 1993).

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APPENDIX. List of ant species known to occur in California, arranged alphabetically by subfamily and genus.

Species	Status	Notes
Amblyoponinae		
Amblyopone oregonensis (Wheeler 1915b)		
Amblyopone pallipes (Haldeman 1844)		
Cerapachyinae		
Cerapachys augustae Wheeler 1902e		
Cerapachys davisi M. R. Smith 1942b		Species is known from males only.
Dolichoderinae		
Dorymyrmex bicolor Wheeler 1906i		Evidence of occasional introgression with *D. insanus*.
Dorymyrmex flavus McCook 1880	I?	Probably introduced into California (Snelling 1995a).
Dorymyrmex insanus (Buckley 1866)		
Dorymyrmex sp. CA-01		
Forelius mccooki (McCook 1880)		Evidence of occasional introgression with *F. pruinosus.*
Forelius pruinosus (Roger 1863a)		
Linepithema humile (Mayr 1868b)	I	
Liometopum luctuosum Wheeler 1905h		
Liometopum occidentale Emery 1895d		
Tapinoma melanocephalum (Fabricius 1793)	I	
Tapinoma sessile (Say 1836)		
Technomyrmex sp. cf. *albipes* (F. Smith 1861b)	I	
Ecitoninae		
Neivamyrmex californicus (Mayr 1870b)	E2	
Neivamyrmex leonardi (Wheeler 1915b)		Probably conspecific with *N. minor.*
Neivamyrmex minor (Cresson 1872)		Species is known from males only.
Neivamyrmex mojave (M. R. Smith 1943f)		Species is known from males only.
Neivamyrmex nigrescens (Cresson 1872)		
Neivamyrmex nyensis Watkins 1977b		
Neivamyrmex opacithorax (Emery 1894d)		
Neivamyrmex pilosus mexicanus (F. Smith 1859c)		
Neivamyrmex swainsonii (Shuckard 1840a)		
Neivamyrmex sp. CA-01	E1	Description in preparation (Snelling & Snelling 2005).
Formicinae		
Brachymyrmex depilis Emery 1893k		
Camponotus anthrax Wheeler 1911d	E2	
Camponotus bakeri Wheeler 1904e	E1, E2	
Camponotus clarithorax Creighton 1950a	E2	Based on unavailable name *clarithorax* Emery 1893k.
Camponotus dumetorum Wheeler 1910g	E2	

Camponotus essigi M. R. Smith 1923b		
Camponotus festinatus (Buckley 1866)		
Camponotus hyatti Emery 1893k		
Camponotus laevigatus (F. Smith 1858a)		
Camponotus maritimus Ward, sp. nov.	E1, E2	Based on unavailable name *maritimus* Wheeler 1910g.
Camponotus modoc Wheeler 1910g		
Camponotus ocreatus Emery 1893k		
Camponotus quercicola M. R. Smith 1954b	E2	
Camponotus sansabeanus (Buckley 1866)		
Camponotus sayi Emery 1893k		
Camponotus semitestaceus Snelling 1970		Based on unavailable name *semitestaceus* Emery 1893k.
Camponotus vicinus Mayr 1870b		
Camponotus yogi Wheeler 1915b	E2	
Camponotus sp. CA-01	E2	
Camponotus sp. CA-02	E2	
Formica accreta Francoeur 1973		
Formica adamsi whymperi Wheeler 1917a		Based on unavailable name *whymperi* Forel 1904b.
Formica aerata Francoeur 1973		
Formica altipetens Wheeler 1913i		
Formica argentea Wheeler 1912c		Replacement name for *argentata* Wheeler 1902e.
Formica aserva Forel 1901l		
Formica canadensis Santschi 1914a		
Formica dakotensis Emery 1893k		
Formica densiventris Viereck 1903		
Formica francoeuri Bolton 1995	E2	Replacement name for *pilicornis* Emery 1893k.
Formica fusca Linnaeus 1758		
Formica gnava Buckley 1866		
Formica hewitti Wheeler 1917a		
Formica integroides Wheeler 1913i		Based on unavailable name *integroides* Emery 1893k.
Formica lasioides Emery 1893k		
Formica lepida Wheeler 1913i	E1, E2	
Formica longipilosa Francoeur 1973	E1, E2	
Formica manni Wheeler 1913i		
Formica microphthalma Francoeur 1973		
Formica moki Wheeler 1906i		
Formica neoclara Emery 1893k		
Formica neogagates Viereck 1903		Based on unavailable name *neogagates* Emery 1893k.
Formica neorufibarbis Emery 1893k		
Formica nevadensis Wheeler 1904i		
Formica obscuripes Forel 1886b		
Formica oreas Wheeler 1903g		
Formica pacifica Francoeur 1973		
Formica perpilosa Wheeler 1913i		Based on unavailable name *perpi-*

		losa Wheeler 1902b.
Formica podzolica Francoeur 1973		California records from Francoeur (1973:168).
Formica propinqua Creighton 1940a		Based on unavailable name *propinqua* Wheeler 1917a.
Formica puberula Emery 1893k		
Formica ravida Creighton 1940a		Based on unavailable name *ravida* Wheeler 1913i.
Formica sibylla Wheeler 1913i		
Formica sp. cf. *sibylla*	E1, E2	
Formica subelongata Francoeur 1973	E2	
Formica subnitens Creighton 1940a		
Formica subpolita Mayr 1886d		
Formica transmontanis Francoeur 1973		
Formica xerophila M. R. Smith 1939f		
Formica sp. CA-01		In the *F. microgyna* subgroup, within the *F. rufa*-group.
Lasius alienus (Foerster 1850a)		
Lasius atopus Cole 1958a	E1, E2	
Lasius sp. cf. *atopus*	E1, E2	
Lasius californicus Wheeler 1917a	E2	
Lasius crypticus Wilson 1955a		
Lasius flavus (Fabricius 1782)		
Lasius humilis Wheeler 1917a		
Lasius latipes (Walsh 1863)		
Lasius murphyi Forel 1901j		
Lasius neoniger Emery 1893k	I?	Possibly introduced into California (Wilson 1955a).
Lasius niger (Linnaeus 1758)		
Lasius pallitarsis (Provancher 1881b)		
Lasius subumbratus Viereck 1903		
Lasius umbratus (Nylander 1846b)		
Lasius vestitus Wheeler 1910h		
Lasius sp. CA-01	E2	Near *L. umbratus*; known only from queens and males.
Myrmecocystus christineae Snelling 1982b	E1	
Myrmecocystus colei Snelling 1976	E1, E2	
Myrmecocystus creightoni Snelling 1971a	E2	
Myrmecocystus ewarti Snelling 1971a		
Myrmecocystus flaviceps Wheeler 1912e		
Myrmecocystus hammettensis Cole 1938b		
Myrmecocystus kathjuli Snelling 1976	E1	
Myrmecocystus kennedyi Snelling 1969b		Based on unavailable name *kennedyi* Cole 1936b.
Myrmecocystus koso Snelling 1976		
Myrmecocystus lugubris Wheeler 1909f		
Myrmecocystus mendax Wheeler 1908g		
Myrmecocystus mexicanus Wesmael 1838		
Myrmecocystus mimicus Wheeler 1908g		
Myrmecocystus navajo Wheeler 1908g		

Myrmecocystus placodops Forel 1908c		
Myrmecocystus romainei Hunt & Snelling 1975		Based on unavailable name *romainei* Cole 1936b.
Myrmecocystus semirufus Emery 1893k	E2	
Myrmecocystus tenuinodis Snelling 1976		
Myrmecocystus testaceus Emery 1893k		
Myrmecocystus wheeleri Snelling 1971a	E2	
Myrmecocystus yuma Wheeler 1912e		
Paratrechina hystrix Trager 1984b		
Paratrechina longicornis (Latreille 1802a)	I	
Paratrechina sp. cf. *terricola*		
Paratrechina vividula (Nylander 1846a)	I?	Considered native to Texas and Mexico (Trager 1984b).
Paratrechina sp. CA-01	E1, E2	
Plagiolepis alluaudi Emery 1894b	I	
Polyergus breviceps Emery 1893k		
Prenolepis imparis (Say 1836)		
Prenolepis sp. CA-01	E1, E2	
Myrmicinae		
Acromyrmex versicolor (Pergande 1893)		
Aphaenogaster boulderensis M. R. Smith 1941		
Aphaenogaster cockerelli André 1893b		
Aphaenogaster megommata M. R. Smith 1963c		
Aphaenogaster occidentalis (Emery 1895d)		
Aphaenogaster patruelis Forel 1886b	E2	
Aphaenogaster uinta Wheeler 1917a		
Cardiocondyla mauritanica Forel 1890b	I	
Cardiocondyla minutior Forel 1899a	I	
Crematogaster californica Wheeler 1919h		Based on unavailable name *californica* Emery 1895d.
Crematogaster coarctata Mayr 1870b		
Crematogaster depilis Wheeler 1919h		Based on unavailable name *depilis* Wheeler 1908h.
Crematogaster hespera Buren 1968b		
Crematogaster larreae Buren 1968b		California records need confirmation.
Crematogaster marioni Buren 1968b	E2	
Crematogaster mormonum Wheeler 1919h		Based on unavailable name *mormonum* Emery 1895d.
Crematogaster mutans Buren 1968b		
Crematogaster opuntiae Buren 1968b		May be conspecific with *C. californica*.
Cyphomyrmex flavidus Pergande 1896		
Cyphomyrmex wheeleri Forel 1900h		
Formicoxenus diversipilosus (M. R. Smith 1939c)		
Leptothorax calderoni Creighton 1950a		Based on unavailable name *calderoni* Forel 1914c.
Leptothorax sp. CA-01		Represents one or more species in the *muscorum* complex.

Manica bradleyi (Wheeler 1909e)		
Manica hunteri (Wheeler 1914e)		
Manica invidia Bolton 1995		Replacement name for *mutica* Emery 1895d.
Manica parasitica (Creighton 1934)	E1, E2	
Messor andrei (Mayr 1886d)	E2	
Messor chamberlini Wheeler 1915b	E1, E2	
Messor chicoensis (M. R. Smith 1956a)	E1, E2	
Messor lariversi (M. R. Smith 1951d)		
Messor pergandei (Mayr 1886d)		
Messor smithi (Cole 1963a)		
Messor stoddardi (Emery 1895d)	E2	
Monomorium ergatogyna Wheeler 1904e		
Monomorium pharaonis (Linnaeus 1758)	I	
Monomorium sp. nr. *pharaonis*	I	
Myrmecina americana Emery 1895d		
Myrmica americana Weber 1939b		
Myrmica discontinua Weber 1939b		
Myrmica glacialis Emery 1921c		Based on unavailable name *glacialis* Forel 1904b.
Myrmica incompleta Provancher 1881b		
Myrmica rugiventris (M. R. Smith 1943b)		
Myrmica tahoensis Weber 1948a		Based on unavailable name *tahoensis* Wheeler 1917a.
Myrmica sp. CA-01	E1, E2	
Pheidole barbata Wheeler 1908h		
Pheidole bicarinata Mayr 1870b		
Pheidole californica Mayr 1870b		
Pheidole cerebrosior Wheeler 1915b		
Pheidole clementensis Gregg 1969b	E2	
Pheidole clydei Gregg 1950		
Pheidole creightoni Gregg 1955a		
Pheidole desertorum Wheeler 1906i		
Pheidole fervens F. Smith 1858a	I	
Pheidole gilvescens Creighton & Gregg 1955		Based on unavailable name *gilvescens* Wheeler 1908h
Pheidole hyatti Emery 1895d		
Pheidole micula Wheeler 1915b	I	
Pheidole moerens Wheeler 1908a	I	
Pheidole paiute Gregg 1959		
Pheidole pilifera (Roger 1863a)		May be a distinct species, *pacifica* Wheeler 1915b, in CA.
Pheidole psammophila Creighton & Gregg 1955		
Pheidole rugulosa Gregg 1959		
Pheidole sciophila Wheeler 1908h		
Pheidole teneriffana Forel 1893f	I	
Pheidole vistana Forel 1914d		
Pheidole xerophila Wheeler 1908h		
Pheidole yaqui Creighton & Gregg 1955		
Pogonomyrmex anzensis Cole 1968	E1	

Pogonomyrmex brevispinosus Cole 1968	E1, E2	
Pogonomyrmex californicus (Buckley 1867)		
Pogonomyrmex colei Snelling 1982a		
Pogonomyrmex desertorum Wheeler 1902d		Occurrence in California needs confirmation.
Pogonomyrmex imberbiculus Wheeler 1902a		
Pogonomyrmex magnacanthus Cole 1968		
Pogonomyrmex maricopa Wheeler 1914f		
Pogonomyrmex montanus MacKay 1980	E2	
Pogonomyrmex occidentalis (Cresson 1865b)		
Pogonomyrmex rugosus Emery 1895d		
Pogonomyrmex salinus Olsen 1934		
Pogonomyrmex subdentatus Mayr 1870b		
Pogonomyrmex subnitidus Emery 1895d		
Pogonomyrmex tenuispinus Forel 1914d		
Pyramica californica (Brown 1950d)	E1, E2	
Pyramica membranifera (Emery 1869b)	I	
Pyramica reliquia (Ward 1988)	E1, E2	
Rogeria sp. CA-01	E1, E2	
Solenopsidini, gen. nov., sp. nov.		Description in preparation (Cover & Deyrup 2005).
Solenopsis amblychila Wheeler 1915b		
Solenopsis aurea Wheeler 1906i		California "*aurea*" may be light-colored *S. xyloni*.
Solenopsis invicta Buren 1972	I	
Solenopsis molesta (Say 1836)		Identification of species as *molesta* needs confirmation.
Solenopsis salina Wheeler 1908h		
Solenopsis tennesseensis M. R. Smith 1951c		Replacement name for *longiceps* M. R. Smith 1943a.
Solenopsis texana catalinae Wheeler 1904e		Taxonomic status of *catalinae* is unclear.
Solenopsis truncorum Forel 1901j		
Solenopsis xyloni McCook 1880		
Solenopsis sp. CA-01	E1, E2	
Stenamma californicum Snelling 1973c		
Stenamma diecki Emery 1895d		
Stenamma sp. cf. *diecki*	E1, E2	
Stenamma dyscheres Snelling 1973c	E1, E2	
Stenamma exasperatum Snelling 1973c	E1, E2	
Stenamma heathi Wheeler 1915b	E2	
Stenamma sp. cf. *heathi*	E1, E2	
Stenamma punctatoventre Snelling 1973c		
Stenamma sp. 1 cf. *punctatoventre*	E1, E2	
Stenamma sp. 2 cf. *punctatoventre*	E1, E2	
Stenamma sp. 3 cf. *punctatoventre*	E1, E2	
Stenamma sequoiarum Wheeler 1917a	E1, E2	
Stenamma sp. cf. *sequoiarum*	E1, E2	
Stenamma smithi Cole 1966b		
Stenamma snellingi Bolton 1995		Replacement name for *occidentale*

		M. R. Smith 1957b.
Stenamma sp. cf. *snellingi*		
Stenamma sp. CA-01	E1, E2	
Strumigenys silvestrii Emery 1906c	I	
Temnothorax andrei (Emery 1895d)		
Temnothorax chandleri (Mackay 2000)	E1, E2	May be conspecific with *T. nitens*.
Temnothorax gallae (M. R. Smith 1949e)	E2	
Temnothorax neomexicanus (Wheeler 1903d)		
Temnothorax nevadensis (Wheeler 1903d)		
Temnothorax nitens (Emery 1895d)		
Temnothorax oxynodis (Mackay 2000)	E1, E2	
Temnothorax rudis (Wheeler 1917a)		
Temnothorax rugatulus (Emery 1895d)		
Temnothorax whitfordi (Mackay 2000)		
Temnothorax sp. CA-01	E2	*Leptothorax* sp. nr. *silvestrii* of Johnson & Ward (2002).
Temnothorax sp. CA-02	E2	*Leptothorax* sp. BCA-2 of Johnson & Ward (2002).
Temnothorax sp. CA-03	E2	*Leptothorax* sp. BCA-3 of Johnson & Ward (2002).
Temnothorax sp. CA-04		
Temnothorax sp. CA-05	E1, E2	
Temnothorax sp. CA-06	E1, E2	
Temnothorax sp. CA-07	E2	*Leptothorax* sp. BCA-9 of Johnson & Ward (2002).
Temnothorax sp. CA-08		
Temnothorax sp. CA-09	E1, E2	
Temnothorax sp. CA-10		
Tetramorium bicarinatum (Nylander 1846b)	I	
Tetramorium caespitum (Linnaeus 1758)	I	
Tetramorium insolens (F. Smith 1861b)	I	
Tetramorium pacificum Mayr 1870b	I	
Tetramorium simillimum (F. Smith 1851)	I	
Tetramorium spinosum (Pergande 1896)		
Wasmannia auropunctata (Roger 1863a)	I	
Ponerinae		
Hypoponera opaciceps (Mayr 1887)	I?	
Hypoponera opacior (Forel 1893j)		
Hypoponera punctatissima (Roger 1859)	I	
Hypoponera sp. CA-01		
Proceratiinae		
Proceratium californicum Cook 1953	E1, E2	
Pseudomyrmecinae		
Pseudomyrmex apache Creighton 1953b		
Pseudomyrmex pallidus (F. Smith 1855c)		

* E1 = endemic to California; E2 = endemic to California floristic province (Hickman, 1993); I = introduced species.

