

# Systematics, Distribution, and Ecology of an Endemic California *Camponotus quercicola* (Hymenoptera: Formicidae)

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**ABSTRACT** The endemic California carpenter ant *Camponotus quercicola* Smith is a little known component of oak woodland habitats containing *Quercus wislizenii* de Candolle and *Q. agrifolia* Née. Close investigation of one site, Stebbins Cold Canyon Reserve, showed that *C. quercicola* was a dominant, arboreal ant species, foraging primarily at night. The 1st description of the sexual castes of *C. quercicola* is provided, together with a guide to distinguish all castes of *C. quercicola* from similar, sympatric *Camponotus* species. We compiled a distribution map based on our own collections and museum specimens. To test the phylogenetic position of *C. quercicola* within the North American *Camponotus* sensu stricto group, we sequenced 385 bp of the mitochondrial gene cytochrome oxidase I from 9 *Camponotus* species. *C. quercicola* did not form a clade with the North American *C. herculeanus* species group to which it was previously assigned. Preliminary results of microsatellite analysis suggested a polygynous colony structure in this species.

**KEY WORDS** *Camponotus quercicola*, life history, polygyny, taxonomy, phylogeny, cytochrome oxidase I

THE ENDEMIC CALIFORNIAN carpenter ant *Camponotus quercicola* Smith was described by Smith (1954), based on a series of workers from Los Angeles County. Smith placed *C. quercicola* within the nominate subgenus *Camponotus*, in or very close to the North American species complex of *C. herculeanus* (L.). *Camponotus quercicola* was reported to be an arboreal and predominantly nocturnal species that did not “appear until very dark” and was “found foraging on and dominating live oaks” at the type locality of Tanbark Flat (Smith 1954). To date, no other publications on the general biology, abundance, and distribution of *C. quercicola* have appeared.

In this article we provide evidence that *C. quercicola* is a dominant nocturnal scavenger or predator on oak trees (*Quercus* spp.) in many parts of California, and suggest that it has been overlooked by other researchers because of its nocturnal and arboreal life style. Colonies of *C. quercicola* live inside live or dead branches of trees, like most other species of the *Camponotus* sensu stricto group (Akre et al. 1994). To the extent that *C. quercicola* is absolutely dependent on oak trees, we would expect a substantial effect on the population structure of *C. quercicola* as a result of destruction and fragmentation of oak woodland in California.

During the course of our field studies we collected males and virgin queens together with workers and brood of *C. quercicola*, enabling the description of these previously unknown castes. This description made it possible to unambiguously identify queens and males of *C. quercicola* in museum material. A distribution map of *C. quercicola* is provided based on

collecting sites of the examined material. Additionally, the phylogenetic position of *C. quercicola* within the subgenus *Camponotus* was evaluated using mitochondrial DNA sequence data. Finally, the abundance and phenology of *C. quercicola* was closely monitored in an oak woodland habitat near Davis, CA (Stebbins Cold Canyon Reserve) and additional data on life history and sociogenetic organization are given.

## Materials and Methods

Museum material was examined from the following collections (codens are those of Arnett et al. 1993): CASC California Academy of Sciences, San Francisco, CA, USA; CDAE California Department of Food & Agriculture, Sacramento, CA, USA; LACM Natural History Museum of Los Angeles County, Los Angeles, CA, USA; UCDC Bohart Museum of Entomology, University of California, Davis, CA, USA; and the USNM National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

All specimen measurements were taken at 25× or 50× under a Wild (Switzerland) microscope with 2 Nikon (Germany) micrometers wired to a digital read-out. All measurements are given in millimeters and the following measurements and indices are cited in the text: HW, maximum head width, measured behind the eyes in workers and queens, but including the eyes in males. HL, length of the head, from the anterior margin of the clypeus to the midpoint of a line drawn across the posterior margin of the head. SL, maximum measurable length of the scape (1st antennal segment), exclude the basal neck. EL, length of the

compound eye, measured with the head in full-face frontal view. PrW, maximum measurable width of the pronotum, as seen in dorsal or (queens, males) anterior view. LHT, length of the metatibia, excluding the median part of the proximal articulation which is received into the femur. See Ward (1989, figure 5). CI, cephalic index: HW/HL; SI, scape index: SL/HL; SI2, scape index, using HW: SL/HW; REL, relative eye length: EL/HL.

**Field Site.** The *C. quercicola* population at Stebbins Cold Canyon Reserve, located  $\approx 18$  km NNW of the town of Vacaville (Solano County), was studied in detail. The reserve is situated within the Inner Coastal Ranges of California and includes 6 distinct habitats based on plant associations. Overall, however, the vegetation of the Cold Canyon basin consists largely of 2 broad plant associations: chaparral and oak woodland (Weathers and Cole 1985). *Quercus wislizenii* is a dominant tree species in the live oak woodland and riparian live oak woodland (Weathers and Cole 1985), and the abundance and phenology studies of *C. quercicola* were conducted in stands of this oak species.

**Molecular Techniques.** DNA was isolated from individual ants using a CTAB-phenol extraction method (Hunt and Page 1994). Specimens were stored in 95% ethanol before DNA isolation.

**Microsatellite Analysis.** Locus ms-C6, developed originally for *C. ligniperdus* (Latreille) (Gertsch et al. 1995), was used for microsatellite analysis of *C. quercicola* colony structure. Polymerase chain reaction (PCR) conditions were the same as described in Gertsch et al. (1995). PCR products were resolved in a 6% denaturing polyacrylamide sequencing gel and bands were developed by a standard silverstaining procedure (courtesy John De Benedictis, UC Davis).

**Phylogenetic Analysis.** Six *Camponotus sensu stricto* species were used for the molecular systematic analysis. Three species belonged to the North American *C. herculeanus* species group [*C. herculeanus*, *C. modoc* Wheeler, and *C. pennsylvanicus* (DeGeer)] to which Smith (1954) assigned *C. quercicola*. Additionally, 1 *C. herculeanus* and 2 *C. ligniperdus* specimens from Germany were included, as well as *C. laevigatus* (F. Smith), which is another western species in the subgenus *Camponotus* with no special affinity toward the *C. herculeanus* species group. Also included in this analysis were species from other *Camponotus* subgenera—*C. (Myrmothrix) floridanus* (Buckley), *C. (Myrmothrix) atriceps* (F. Smith), *C. (Myrmentoma) essigi* M. Smith—and 2 representatives of other Formicidae genera: *Formica moki* Wheeler and *Lasius pallitarsis* (Provancher). The latter species was used as the outgroup. Voucher specimens of all species have been deposited in the Bohart Museum of Entomology (UCDC), with duplicates in the Museum of Comparative Zoology, Harvard University (MCZC).

We amplified 385 bp of the mitochondrial cytochrome oxidase I (COI) gene using primers provided by Ted Schultz, Smithsonian Institution (unpublished data). PCR conditions were as follows: 0.5 U *Taq* DNA polymerase (GIBCO/BRL, Gaithersburg, MD); standard 10 $\times$  buffer (GIBCO/BRL); final concentration

of  $MgCl_2$  2 mM. We ran 35 PCR cycles of 1 min at 95°C (denaturing), 1 min 47°C (annealing), and 1 min 30 s at 72°C (elongation). PCR products were purified using the microcon 100 microconcentrators (Amicon, Bedford, MA), followed by automated sequencing of double-stranded products. All sequences were unambiguously aligned by eye. The program PAUP (Swofford 1998) was used for maximum parsimony analysis.

## Results

### Taxonomic Treatment.

*Camponotus quercicola* M. R. Smith, 1954: 211. HOLOTYPE, worker, Tanbark Flat, Los Angeles County, California (T. C. Lawrence) (USNM) [examined].

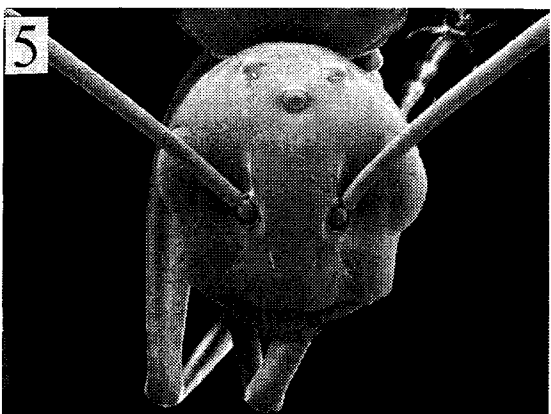
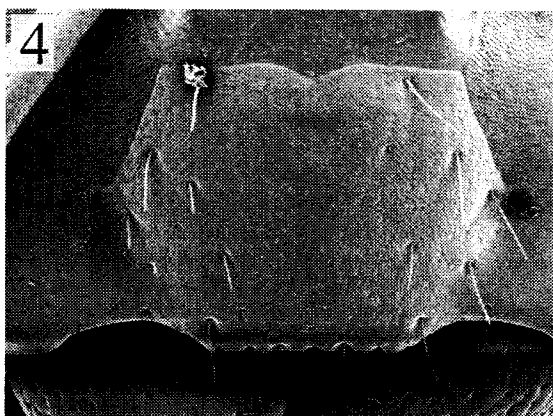
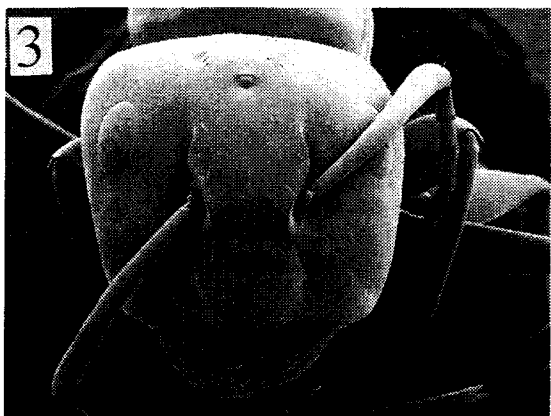
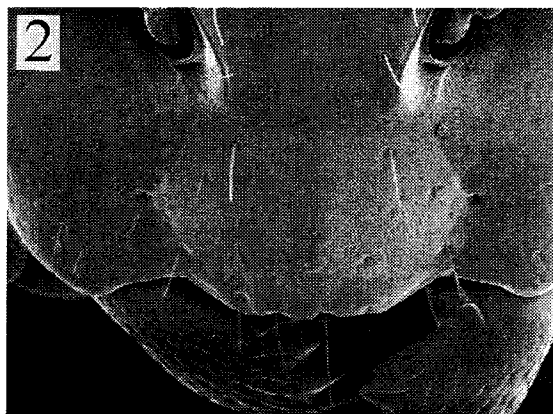
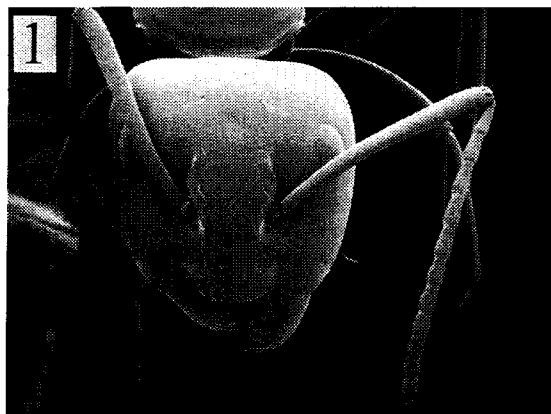
*Camponotus quercicola*; Wheeler & Wheeler, 1986: 60. Worker in key.

Measurements [in millimeters], workers ( $n = 30$ ). HW 1.45–3.46, HL 1.78–3.39, PrW 1.23–2.31, LHT 2.36–3.56, CI 0.81–1.02, SI 0.88–1.17, SI2 0.86–1.44, REL 0.22–0.29, LHT/HW 1.03–1.63.

Measurements [in millimeters], queens ( $n = 10$ ). HW 3.20–3.74, HL 3.28–3.62, PrW 2.70–2.94, LHT 3.42–3.58, CI 0.97–1.06, SI 0.76–0.86, SI2 0.72–0.88, REL 0.24–0.26, LHT/HW 0.92–1.09.

Measurements [in millimeters], males ( $n = 7$ ). HW 1.64–1.86, HL 1.69–1.94, PrW 1.93–2.21, LHT 2.78–3.16, CI 0.92–1.00, SI 1.13–1.23, SI2 1.16–1.32, REL 0.34–0.37, LHT/HW 1.65–1.77.

**Worker Diagnosis.** Polymorphic but showing only moderate variation in size and allometry (see range of values for HW, PrW, LHT, CI, and SI); clypeus ecarinate or with, at most, a weak, bluntly rounded longitudinal ridge along the midline; anteromedial margin of clypeus more or less straight, slightly crenulate, and not set off sharply from lateral portions (Figs. 1 and 2); scape base subcylindrical; mesosoma convex in profile, the dorsal face of the propodeum rounding into the declivitous face without a distinct angular juncture between the 2; posterior margin of mesonotum with well-marked suture and, in all but smallest workers, separated from the propodeum by a short, transverse sclerite (mesoscutellum or metanotum); mesosoma strongly compressed posteriorly, the dorsal face of the propodeum longer than wide (dorsal view) but generally subequal to, or shorter than, the declivitous face (lateral view); petiole scale-like; body sublucid, covered with weak reticulate sculpture and scattered fine punctures, the latter becoming coarser around the genae; standing pilosity scarce, lacking on the scapes and tibiae (excluding their apices) and usually absent from the pronotum; 0–10 standing hairs visible in outline in the malar region, with the head in full-face view; standing pilosity also present on the frons and vertex, gula (except the smallest workers), mesonotum (0–4 erect setae), propodeum (2–10 erect setae), and petiole; abdominal tergites III and IV with 1–5 and 2–6 erect hairs, respectively, excluding the posterior rows (5–13 and 7–17, including the posterior rows); pubescence short and inconspicuous, appressed hairs separated by more than their lengths on the gastric



Figs. 1-6. SEM micrographs of *C. quercicola* worker, queen, and male. (1) Frontal view of worker head, HW = 2.866 mm. (2) Close-up of clypeus, same specimen. (3) Frontal view of queen head, HW = 3.722 mm. (4) Close-up of clypeus, same specimen. (5) Frontal view of male head, HW = 1.814 mm. (6) Close-up of clypeus, same specimen.

tergites. Body black, legs dark reddish-brown to black. For additional details see Smith (1954).

**Queen Description.** Masticatory margin of mandibles with 5 teeth. Head about as broad as, or somewhat broader than, long (CI 0.97-1.06). Sides of head only slightly convex (almost straight) and converging to-

ward the mandibular insertions (Fig. 3). Posterior margin of head varying from more or less straight to slightly concave, when the head is seen in full-face, frontal view. Clypeus evenly convex from side to side and front to back, lacking median carina; anteromedial margin of clypeus flat to slightly emarginate, weakly

crenulate, and only slightly exceeding, in anterior reach, the anterolateral margins of the head (Fig. 4). Scape relatively short, scape index 0.76–0.86; scape base subcylindrical. First funicular segment 1.41–1.55 times length of 2nd funicular segment, which is, in turn, slightly shorter than (0.9 times) the length of the 3rd funicular segment. Frontal carinae diverging moderately, reaching a maximum distance of 0.37–0.40 times head width, then curving slightly toward midline, disappearing before the level of the upper margin of the compound eye; frontal groove present along midline of head between the frontal carinae. Eye length  $\approx 1.3$  times eye width, as seen in an oblique lateral view of head; eye length, as seen in full-face frontal view, 0.24–0.26 times head length. Convexity of eye only slightly greater than that of the surrounding head surface, and eye not protruding from lateral margin of head in full-face view. Ocelli distinct, median ocellus located slightly posterior to the upper margin of compound eye, in full-face view. Mesosoma with full complement of thoracic sclerites; mesoscutum with a faint anteromedial line, and with parapsidal lines, notauli absent; legs relatively short, LHT/HW 0.92–1.09. Petiolar scale thin, dorsal margin sharp-edged in lateral view and, in anterior view, slightly to strongly notched. Most of body sublucid, covered in fine reticulate sculpture and scattered small punctures. Punctures most conspicuous on head, especially between compound eye and mandibles, where they achieve largest size ( $\approx 0.015$  mm in diameter), and are separated from one another by  $\approx 3$ –4 diameters. Standing pilosity mostly straight, fine-tipped, golden, and relatively sparse. Standing pilosity lacking on scapes, mesofemur, metafemur, and external faces of tibiae. Clypeus with  $\approx 12$ –20 erect hairs, excluding those on the anterior margin; a few short erect setae usually present on the gena. With the head in full-face view, malar region with 0–8 hairs visible in profile. For other particular parts of the body the number of standing hairs as follows: frons and vertex 10–22 (these arranged in 2 parallel rows, 1 on each side of the midline), gula 6–22, posterior face of profemur 0–2, pronotum 0–3, mesonotum 4–10, mesoscutellum 7–14, metanotum 0–2, propodeum above propodeal spiracle 4–9, dorsum of petiole 7–13, abdominal tergite III, exclusive of posterior row, 0–6, abdominal tergite III, posterior row, 6–10, abdominal tergite IV, exclusive of posterior row, 0–5, and abdominal tergite IV, posterior row 9–14 (totals of 7–15 and 10–18 standing hairs, on abdominal tergites III and IV, respectively). Standing setae forming the posterior rows on abdominal tergites III and IV separated by  $\approx 0.7$  times their lengths or more. Appressed pubescence present on much of body but inconspicuous; appressed hairs on abdominal tergites III–VI very short ( $\approx 0.05$  mm long) and relatively sparse, separated by more than their lengths. Body, including mandibles, black, the legs dark brown. Antenna black, becoming slightly lighter at the apex.

**Male Description.** Mandible slender, masticatory margin with a single prominent apical tooth, then rounding into the basal margin. Head generally longer than wide (see CI values). In full-face view, the pos-

terior margin of head forming a semicircular arch above the upper margin of the compound eyes (Fig. 5). Clypeus broader than long, anteromedial margin straight (and weakly crenulate), and rounding gradually into the less protruding lateral portions (Fig. 6); clypeus essentially lacking a median longitudinal carina, but with a weak posteromedial protrusion or ridge; above this ridge in some males there is a broad, arched-transverse suture which separates the posterior 5th of the clypeus from the remainder. Scape straight, slender, longer than head length. Frontal carinae similar to those of queen, but continuing to diverge posteriorly. Eyes protruding only moderately from the sides of the head, eye length approximately one-third of head length; ocelli small, 0.12–0.16 mm in diameter and separated from one another by several diameters. Mesosoma structure like that of queen. Legs rather long, LHT/HW  $> 1.60$ . In lateral view petiolar scale appearing low, thick, with a vertical anterior face, and posteriorly rounded summit; in anterior view dorsal margin slightly emarginate. Head and mesosoma subopaque to sublucid, gaster shinier, but all of body less shiny than that of queen. Body with fine reticulate sculpture and scattered inconspicuous punctures. Standing pilosity scarce, fine-tipped, silvery-golden, lacking on scapes and extensor surfaces of tibiae; a few hairs on the clypeus and malar area, none on the frons, 3–6 on the vertex, and 4–7 on the gula; mesosomal and petiolar pilosity similar to that of queen, except that propodeum above propodeal spiracle with only 2–4 standing hairs (but additional setae present lower down on the propodeum, below the spiracle, that are absent in queens and workers); standing pilosity on abdominal tergites III and IV distributed as follows: abdominal tergite III, exclusive of posterior row, 4–7, abdominal tergite III, posterior row, 2–5, abdominal tergite IV, exclusive of posterior row, 5–9, and abdominal tergite IV, posterior row 4–9 (totals of 8–12 and 9–18 standing hairs, on abdominal tergites III and IV, respectively). Appressed pubescence scattered and generally very inconspicuous; appressed hairs on abdominal tergites III–VI short, separated by more than their lengths, except for denser medial patches. Body black, the distal ends of appendages lighter brown.

**Variation.** In populations of *C. quercicola* from northern California the queens and workers tend to have broader heads, shorter scapes and legs, and reduced malar pilosity, compared with those from the type locality (Tanbark Flat) and other localities in southern California (unpublished data). A scarcity of records from intermediate localities—probably because of a lack of collecting—precludes a detailed evaluation of this variation, but it appears to be clinal in nature.

**Comments.** Within the subgenus *Camponotus* (*Camponotus*), the workers and queens of *C. quercicola* can be recognized by the combination of sparse pilosity, inconspicuous pubescence, shiny integument, uniformly dark black body, and by the relative length of the appendages (see scape indices and LHT/HW). Among the 9 other described species of this

subgenus in North America, *C. laevigatus* is easily distinguished from *C. quercicola* by the abundant erect pilosity on all parts of its body including the scapes and tibiae; *C. modoc*, *C. pennsylvanicus*, and *C. chromaiodes* Bolton by their duller integument and denser covering of appressed pubescence and standing pilosity on the gastric tergites; *C. novaeboracensis* (Fitch) by its less shiny head and more abundant pilosity, especially on the gaster (abdominal tergite IV usually with >16 standing hairs, inclusive of the posterior row); *C. herculeanus* by the same features and additionally by its shorter scape and legs (queen LHT/HW <0.90); and *C. americanus* Mayr, *C. schaefferi* Wheeler, and *C. texanus* Wheeler by their lighter orange-brown coloration and more abundant standing pilosity (posterior face of profemur with >2 hairs; abdominal tergite IV usually with >16 standing hairs, including the posterior row). Of the above species, only *C. laevigatus* and *C. modoc* are known to occur sympatrically with, or in close proximity to, populations of *C. quercicola*.

Among California species of *Camponotus* (*Tanaemyrmex*), some uniformly dark workers and queens of *C. vicinus* Mayr resemble superficially those of *C. quercicola*, but they can be distinguished by the much denser pilosity on abdominal tergites III and IV in addition to the flattened scape base and the carinate clypeus characteristic of the subgenus *Tanaemyrmex*.

In the Sierra Nevada of California, there is an aberrant queen form of *C. modoc* (or possibly an undescribed species) that is very shiny and whose gastric tergites are short-pubescent and almost devoid of standing pilosity. Known only from 4 alate queens (UCD collection), and without any associated workers, this odd form can be distinguished from queens of *C. quercicola* by its smaller size (HW 2.88–3.16, compared with 3.20–3.74 in *C. quercicola*); pointed or convex dorsal margin of petiole (emarginate in *C. quercicola*); coarser punctation on the head; lighter orange-red legs that contrast with the dark body; more abundant pilosity on the mesosoma and petiole (latter with 12–20 erect setae); and virtual lack of standing pilosity on the posterior margins of abdominal tergites III and IV. With respect to all these characters except size and gastric pilosity the 4 queens are more similar to *C. modoc* than to *C. quercicola*.

In California, males of *C. quercicola* can be separated from all other similar-sized *Camponotus* males (i.e., those in the subgenera *Camponotus* and *Tanaemyrmex*) by the patterns of pilosity and by the relative length of the legs. California *Camponotus* (*Tanaemyrmex*) males have more abundant pilosity on the head, mesosoma and gaster. In males of *C. (Camponotus) laevigatus* the standing pilosity extends also to the scapes and legs. Males of *C. (Camponotus) modoc* can be distinguished from those of *C. quercicola* by their duller integument, longer and denser pubescence on the gaster, and shorter legs (LHT/HW  $\approx$  1.45–1.64). *Camponotus modoc* males also tend to have more standing pilosity on the gaster but less on the gula and malar area, than those of *C. quercicola*.

**Material Examined.** California Calaveras County: Mokelumme Hill [as "Mokel Hill"] (T. E. Blaisdell)

(CASC); Colusa County: 8 km W Fouts Springs, 1,600 m (P. S. Ward) (UCDC); Contra Costa County: Alamo (D. G. Welch) (CDAE); Lafayette (R. R. Finger, Jr.) (CDAE); Mt. Diablo State Pk., 670 m (P. S. Ward) (UCDC); El Dorado County: Pine Hill, W of Rescue (R. Harris) (UCDC); Snowline Camp (C. D. MacNeill) (CASC); Glenn County: 17 km W Elk Crk., 1,060 m (P. S. Ward) (UCDC); Lake County: Anderson Spr. (W. B. Bauer & J. S. Buckett) (UCDC); Los Angeles County: Big Rock Creek, 4,500 feet (R. R. Snelling) (LACM); Bouquet Canyon (N. Westerland) (LACM); Crystal Lake Recreation Area (L. Stange) (LACM); S. fork, Big Rock Crk., 4,500 feet (R. R. Snelling) (LACM); Tanbark Flat (R. W. Bushing) (UCDC); Tanbark Flat (T. C. Lawrence) (LACM, USNM); Tanbark Flat (A. Menke) (LACM); Tanbark Flat (R. R. Snelling) (CDAE); Tanbark Flat (L. Stange) (LACM); Tanbark Flat, San Gabriel Mts, 2,700 feet (R. R. Snelling) (LACM); Mariposa County: Yosemite, 3880–4000 feet (collector unstated) (CDAE); Mendocino County: Hopland Field Stn., 240 m (P. S. Ward) (UCDC); Monterey County: N Fork, San Antonio R., Los Padres Nat'l For., 460 m (P. S. Ward) (UCDC); Tassajara Hot Spgs, 1,500 feet (O. Bryant) (CASC); Napa County: Monticello Dam (R. R. Finger, Jr.) (CDAE); Placer County: 25 km E Foresthill, 1,370 m (P. S. Ward) (UCDC); 8 miles E Auburn (E. E. Grissell) (UCDC); Foresthill (E. Klee) (CASC); Foresthill [as "Forest Hill"] (collector unstated) (CASC); Granite Bay (J. Shipley) (UCDC); Riverside County: Banning, Mill Canyon (Chenault) (CASC); Joshua Tree N.M., L. Covington Flat (M. Knox & E. Sleeper) (CASC); Joshua Tree N.M., U. Covington Flat (E. L. Sleeper) (CASC); Pinyon Tree (Joshua Tree) (E. L. Sleeper) (CASC); San Bernardino County: "Mountains, San Bdn Co." (C. Pierce) (LACM); 0.5 miles N Crestline (G. R. Noonan) (CASC); Mountain Home Village [as "Mtn. Home"] (M. Narog) (USNM); Pine Mtn. (D. Dahlsten) (UCDC); San Diego County: 13 km ESE Mt. Laguna, 1280 m (P. S. Ward) (UCDC); 5 miles N Descanso, 3,000 feet (J. H. Hunt) (LACM); San Joaquin County: Stockton (R. Castro) (CDAE); Santa Barbara County: Santa Barbara (G. E. Woodhams) (CDAE); Solano County: Cold Canyon, 19 km NNW Vacaville, 120 m (S. G. Brady) (UCDC); Cold Canyon, 19 km NNW Vacaville, 120 m (D. M. Olson) (UCDC); Cold Canyon, 19 km NNW Vacaville, 120 m (P. S. Ward) (UCDC); Cold Canyon, 19 km NNW Vacaville, 300 m (P. S. Ward) (UCDC); Sonoma County: 3 km N Sonoma, 290 m (P. S. Ward) (UCDC); Tuolumne County: 1 km S Mather, 1,390 m (P. S. Ward) (UCDC); Ventura County: Ozena Campground [as "Camp Ozena"] Upper Cuyama [River] (C. W. Kirkwood) (LACM); Reyes Creek [as "Reyer Cr."] (C. W. Kirkwood) (LACM); Yolo County: 6 km SW Winters, 45 m (D. A. Holway) (UCDC); 6 km WNW Rumsey, 190 m (P. S. Ward) (UCDC); Yuba County: Bullard's Bar (R. E. Rice) (UCDC); Sierra Foothill Rge F S, 18 miles NE Marysville (M. B. Hertlein) (UCDC); UC Sierra Foothill Research & Extension Center, 200 m (P. S. Ward) (UCDC).

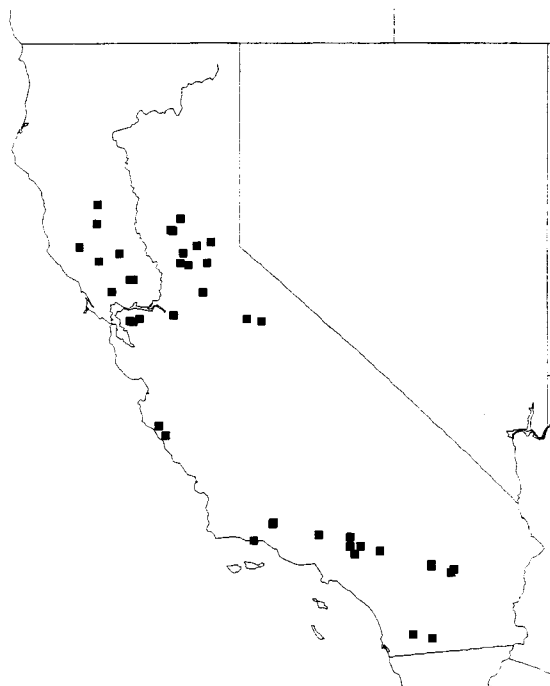


Fig. 7. Distribution of *C. quercicola*.

**Distribution.** To date, *C. quercicola* has been collected only in California, from Glenn and Yuba Counties south to San Diego County and east to Joshua Tree National Park (Fig. 7). It is likely to also occur in adjacent parts of northern Baja California where *Quercus agrifolia* Née is found. Most collections come from oak woodland habitats, most frequently sites with *Q. agrifolia* or *Q. wislizenii*. The range of elevations, for collections for which this information was given, is 45–1,600 m.

**Life History.** In our observations in northern and central California, foraging workers of *C. quercicola* were seen and collected on *Q. wislizenii*, *Q. agrifolia*, *Q. lobata* Née, and *Q. kelloggii* Newb. Nesting was confirmed for *Q. wislizenii* (Stebbins Cold Canyon Reserve and Sierra Foothill Research and Extension Center) by the simultaneous collection of workers and brood in dead branches of this oak species. In other instances we observed workers and males retreating into cavities within the trunks of trees, indicating that the nests were located in rotten wood within the bole of living trees. In the Stebbins Cold Canyon Reserve every investigated mature *Q. wislizenii* tree ( $n = 25$ ) in an area of  $\approx 500 \text{ m}^2$  of live oak woodland and riparian oak woodland habitat was occupied by *C. quercicola* foragers. During nocturnal surveys in this area (on 6 different nights, from May to September 1997 and April to August 1998), *C. quercicola* was the only ant observed to forage on oak trees, and we never observed other ants at honey baits placed on these trees. These observations indicate that *C. quercicola* is indeed the dominant ant species for-

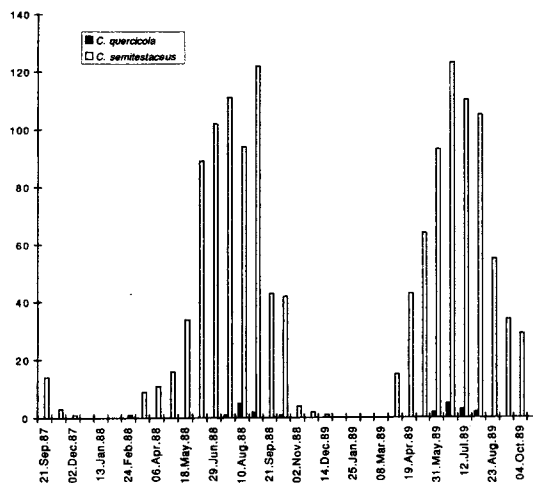


Fig. 8. Comparison of ground-foraging worker activity in *C. quercicola* and *C. semitestaceus* at Stebbins Cold Canyon Reserve, based on pitfall trap data from a 2-yr period. The abscissa is divided into 3-wk sampling intervals and the 1st d of every other sampling period is given. Ordinate is total number of workers trapped during each sampling period.

aging on *Q. wislizenii* during the night in the summer months.

*Camponotus quercicola* is primarily a nocturnal species. It was rarely observed in daylight, which might explain why it has been seldom encountered and reported, despite its fairly wide distribution and abundance. In the Stebbins Cold Canyon Reserve, workers of *C. quercicola* seem to spend most of their time in or on trees. Nevertheless, workers of *C. quercicola* were regularly found in low numbers in pitfall traps on the ground (Fig. 8) during a 2-yr observation period in the Reserve, which indicates that they do occasionally forage on the ground. Workers appear to forage individually, but they occurred at honey baits (placed as drops on the surface of tree bark) in increasing numbers over time, suggesting some form of recruitment. However, we never observed active recruiting (e.g., tandem running or group recruitment).

Individual foragers were observed to carry small live caterpillars ( $n = 2$ ), an unidentified adult dipteran ( $n = 1$ ) and bird droppings ( $n = 1$ ); but most foragers were seen to go up into the tree canopy and return with an expanded gaster, indicating that they had collected liquids. Lawrence (in Smith 1954) mentioned that the ants were feeding on "exudates" on the trees but never specified the nature of these "exudates." For other *Camponotus* species it is known that a significant portion of their diet is from aphids, scale insects, or membracids (Pricer 1908, Sanders 1964, Pfeiffer 1996). Therefore, it may be that the liquid collected by the *C. quercicola* workers was homopteran honeydew.

Initial results using the microsatellite marker ms-C6 demonstrated that 1 of 8 investigated colonies of *C. quercicola* was polygynous (i.e., the colony had multiple reproductive queens). Analyzing 11 workers collected from the same tree, we found 6 alleles and 6

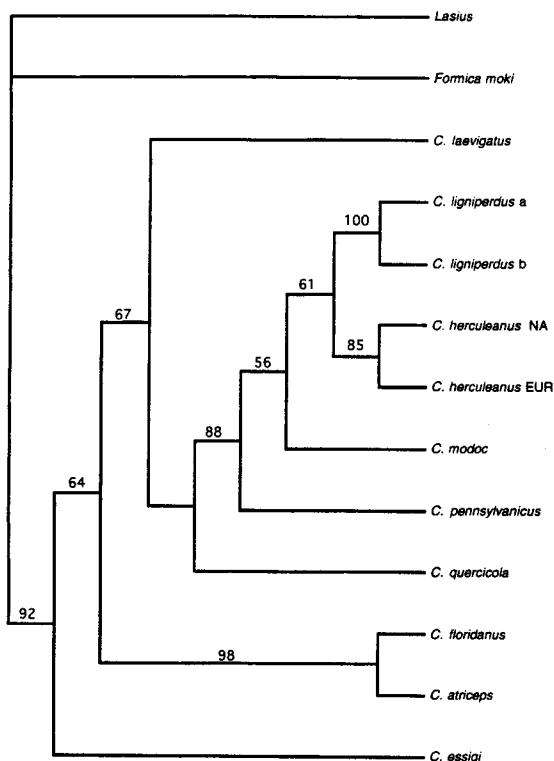


Fig. 9. Phylogeny of selected *Camponotus* species. Shown is the single most parsimonious tree derived from branch-and-bound analysis (unweighted) of 385 bp of COI sequence data. Numbers above branches are bootstrap percentage values (1,000 pseudoreplicates) for clades found in both the most parsimonious and bootstrap majority rule trees.

different genotypes. Alleles were given letters from A to F. Observed genotypes and number of workers with this genotype are as follows: A/F (1), B/F (1), C/C (1), C/D (3), and C/E (5). The genotypes found were not compatible with 1 reproductive queen; the minimum number of queens necessary to explain these genotypes is 2, with 1 queen single-mated and 1 queen double-mated.

**Systematic Relationships.** We obtained molecular data in the form of 385 bp of COI from 13 specimens. These data were analyzed using the branch-and-bound method implemented by PAUP (Swofford 1998), resulting in a single most parsimonious tree (tree length = 266; consistency index = 0.62; retention index = 0.60). This phylogeny (Fig. 9) shows a clade consisting of the European *C. ligniperdus* together with all members of the North American *C. herculeanus* species group excluding *C. quercicola*. This result is supported by an 88% bootstrap percentage (Fig. 9). Furthermore, the 6 species of the subgenus *Camponotus* (*Camponotus*) included in our analysis (*C. herculeanus*, *C. laevigatus*, *C. ligniperdus*, *C. modoc*, *C. pennsylvanicus*, and *C. quercicola*) form a clade with 67% bootstrap support.

## Discussion

We describe the worker, male, and queen castes of *C. quercicola*, and provide a guide to distinguish all castes of this species from similar, sympatric *Camponotus* ants. *C. quercicola* shows a fairly wide distribution in California (Fig. 7) and according to our results must be considered an important ant species of some oak woodland habitats in the state, especially those containing *Q. agrifolia* and *Q. wislizenii*. At Stebbins Cold Canyon Reserve we found that *C. quercicola* is the dominant ant on live oak trees at night (*Q. wislizenii*). The low number of *C. quercicola* workers found in pitfall traps, when compared with that of other species such as *C. semitestaceus* Snelling (Fig. 8), indicates that they only occasionally forage on the ground. *Camponotus quercicola* may also play an important role in the interaction of oak trees with other herbivorous insect species, given the possibility that they tend homopteran honeydew producers. Additionally, foragers of *C. quercicola* were seen to prey on other herbivorous insect species.

The finding of polygyny in 1 *C. quercicola* colony was surprising because polygyny is rare in *Camponotus* species (Akre et al. 1994). We collected these workers from the same area of 1 tree and they did not show any aggression toward each other. Therefore, it seems likely that all workers belonged to the same colony, but we cannot exclude the possibility that these workers represent multiple colonies. It may be part of the oligogyny syndrome found in *C. herculeanus* and *C. ligniperdus* (Hölldobler 1962, Gadau et al. 1998) but this needs more detailed investigation to verify.

Affinities of *C. quercicola* within the subgenus *Camponotus* remain somewhat unclear. Results of the molecular systematic study of *Camponotus* (*Camponotus*) species placed *C. quercicola* outside a well-supported clade containing *C. herculeanus*, *C. ligniperdus*, *C. pennsylvanicus*, and *C. modoc* (Fig. 9). Morphologically, *C. quercicola* bears some resemblance to *C. schaefferi* and *C. texanus*, all 3 species having—in contrast to most other North American *Camponotus* (*Camponotus*)—extremely short, inconspicuous pubescence; a shiny and finely punctulate integument; and scattered, fine, golden pilosity on the gaster. In addition, *C. quercicola* and *C. schaefferi* show some biological similarities, both nesting in dead wood within living oak trees. If it is true that *C. schaefferi* and *C. texanus* are closely related to *C. quercicola*, then we might recognize 2 species groups within the subgenus *Camponotus*, a Holarctic species group centered around *C. herculeanus* (including *C. modoc* as a western Nearctic species confined to higher elevations) and a southwestern Nearctic species group including *C. quercicola*. We are currently developing a data set that will address the issue of relationships among these and other species in *Camponotus* (*Camponotus*).

Based on the distribution map and our field observations, *C. quercicola* can be expected to occur in oak woodland habitats in the Sierra Nevada Foothills and the Coastal Ranges, which contain *Quercus wislizenii*, *Q. agrifolia*, or *Q. kelloggii*. A comparison of the dis-

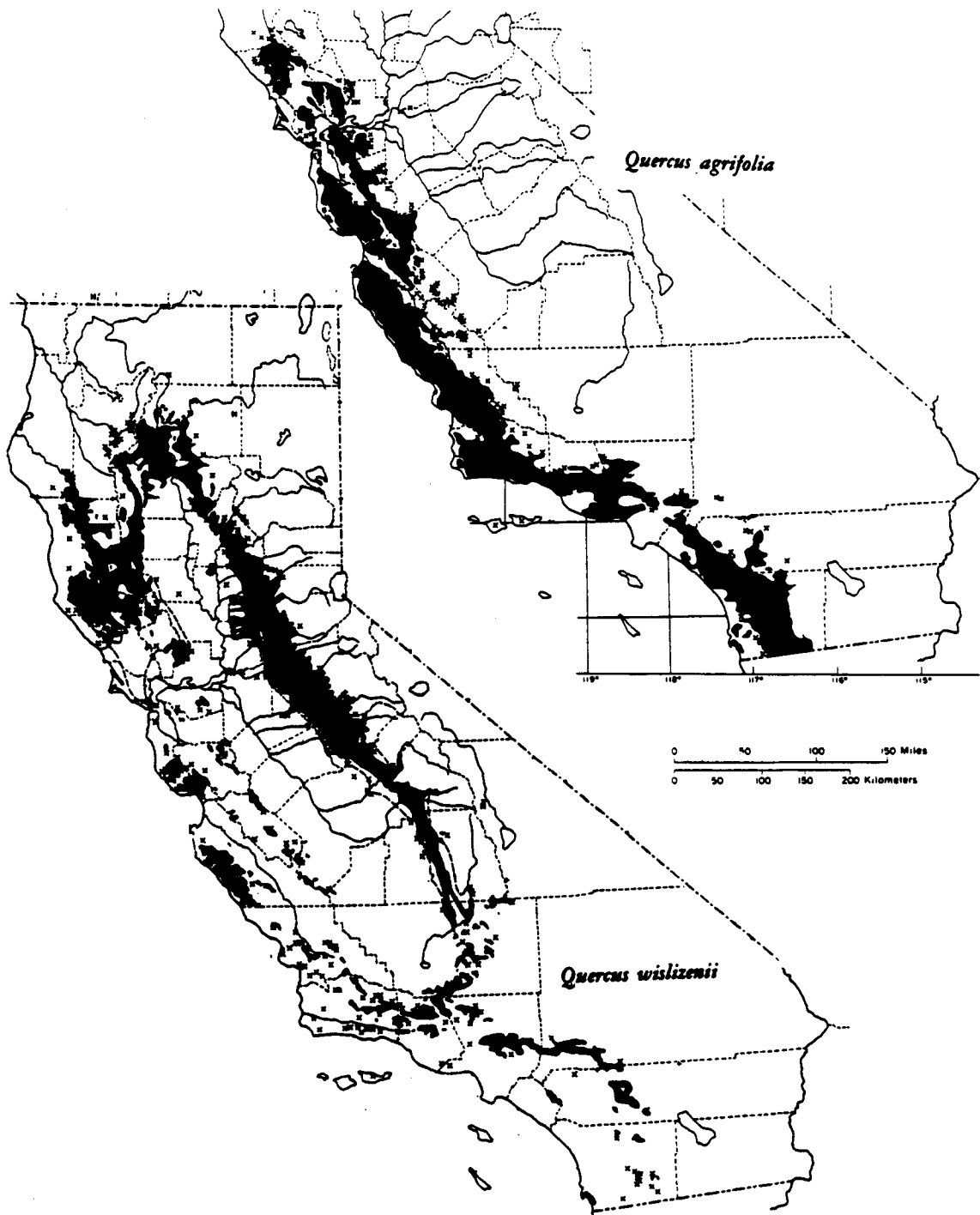


Fig. 10. Distribution of *Q. wislizenii* and *Q. agrifolia* (modified from Griffin and Switchfield 1976). Shaded areas, groups of stands >2 miles across. x, stands <2 miles across or of unknown size.

tribution map of *C. quercicola* (Fig. 7) with the distribution maps of *Q. wislizenii* and *Q. agrifolia* (Fig. 10) shows strong concordance, a pattern consistent with the close association of *C. quercicola* and these 2

species of oak. Note that *C. quercicola* was never found on blue oak (*Q. douglasii*), so that oak woodland dominated by this species may not support populations of *C. quercicola*.



It is unclear which species of oak is inhabited by *C. quercicola* in Joshua Tree National Park (see material examined), because none of the oak tree species commonly used by *C. quercicola* occurs within the boundaries of this park. *Q. chrysolepis* Liebm. is 1 of 4 *Quercus* species growing in the park, and this species also occurs in some Sierra foothill locations where *C. quercicola* was collected (e.g., Colusa County, 8 km W Font's Spring; Placer County, 25 km E Foresthill). Therefore, *Q. chrysolepis* must also be considered a potential nesting and foraging site for *C. quercicola*.

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