# Distribution and Biogeography of the North American Termite Genus *Zootermopsis* (Isoptera: Termopsidae)

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**ABSTRACT** The modern distribution of species of the North American termite genus *Zootermopsis* Emerson is described based on reexamination of museum specimens and extensive new field collections. A recently discovered diagnostic morphological character (shape and position of the right mandibular subsidiary tooth in nonsoldier castes) and the enhanced resolution facilitated by hydrocarbon analysis were used to revise distribution maps for each species. The historical biogeography of species of *Zootermopsis* and their host trees is discussed, with emphasis on the state of California where paleoclimatic and paleobotanic patterns are best known. Evidence demonstrating two substantially allopatric distributions of hydrocarbon phenotypes within the *Z. nevadensis* complex, in combination with studies of interphenotype agonistic behavior and genetic variation, suggests reproductive isolation between the two *Z. nevadensis* hydrocarbon variants.

**KEY WORDS** *Zootermopsis*, biogeography, insect hydrocarbons

DAMPWOOD TERMITES, *Zootermopsis* Emerson, occur only in western North America. *Z. laticeps* (Banks) is a large, easily identified species with a highly restricted range that is disjunct from others in the genus. It colonizes dead wood within live branches and trunks of trees growing in riparian habitats in central and southeastern Arizona, southwestern New Mexico, and northern Mexico (Banks & Snyder 1920, Castle 1934, Nutting 1965, Weesner 1970). The distributions of *Z. angusticollis* (Hagen) and *Z. nevadensis* (Hagen) have been reported to range within the Pacific coastal United States north to British Columbia and into parts of Idaho, Montana, and western Nevada (Banks & Snyder 1920; Castle 1934, 1944; Light 1935; Spencer 1945; Snyder 1954; Weesner 1965, 1970; Vickery & Kevan 1983). The two species were considered sympatric along much of the coast, even occurring in the same host logs (Castle 1934, Weesner 1970).

The distributions of *Zootermopsis* species have not been more clearly defined because of the absence of reliable techniques for species diagnosis. However, as a result of studies to characterize cuticular hydrocarbon patterns among specimens of *Zootermopsis*, Haverty et al. (1988) correlated unique hydrocarbon phenotypes with the relatively reliable morphological characters of alate color and size and shape of the wings. Haverty and his collaborators concluded that *Z. angusticollis* and *Z. laticeps* each have distinct hydrocarbon phenotypes (called phenotypes II and IV, respectively), and that two additional hydrocarbon patterns (phenotypes I and III) correspond to specimens fitting the morphological description of *Z. nevadensis*. Haverty et al. (1988) noted that inland and southern California *Z. nevadensis* colonies had hydrocarbon phenotype I; colonies with the *Z. nevadensis* phenotype III pattern occurred along the coast of northern California and the Pacific Northwest.

Using the hydrocarbon phenotypes as a sorting character, Thorne found an exact correspondence between shape and position of the subsidiary tooth of the right mandible of nonsoldier castes and the *Zootermopsis* hydrocarbon groupings of II, IV, and [I + III] (Thorne & Haverty 1989). This morphological character enables accurate separation of *Z. laticeps*, *Z. angusticollis*, and *Z. nevadensis* without relying on seasonal collection of alates or on often ambiguous morphological characters on soldiers. The mandibular tooth does not, however, enable morphological discrimination of specimens of the two *Z. nevadensis* hydrocarbon phenotypes (I and III).

Haverty & Thorne (1989) examined patterns of agonistic behavior among *Zootermopsis* individuals from colonies of known hydrocarbon phenotypes. This study demonstrated that intrapheno-

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[3] Deceased. Department of Entomology, University of Arizona, Tucson, AZ 85721. After his retirement and until his death in March 1992, W.L. Nutting worked on this project with the first and second authors by collecting live material in Arizona and by gathering data from his personal termite collections from Arizona, New Mexico, and Mexico. We dedicate this paper to our friend and colleague, Professor William L. Nutting.

type agonism among nonreproductive castes is consistently low no matter what the geographic origin of the termites. Interphenotype agonism is typically high among Z. *laticeps* and all others. Agonism is also high between Z. *nevadensis* phenotypes I and III. Thus, these two chemically diagnosed Z. *nevadensis* groups clearly recognize one another, although they remain morphologically indistinguishable. A further pertinent result of the agonistic bioassays was that although agonism is consistently high between Z. *angusticollis* and Z. *nevadensis* phenotype III individuals, agonism between Z. *angusticollis* and Z. *nevadensis* phenotype I individuals is frequently low.

Based on the unique hydrocarbon phenotypes, agonistic behavior, and apparent allopatric distributions, Haverty & Thorne (1989) named the two hydrocarbon variants of Z. *nevadensis* as subspecies: phenotype I called Z. *nevadensis* subsp. *nevadensis* (because its range includes the type locality) and Z. *nevadensis* subsp. *nuttingi*. Subsequent work on allozyme variation (Korman et al. 1991) and DNA hybridization (Broughton & Kistner 1991) suggests genetic differences between the Z. *nevadensis* subspecies. However, because of a high level of ambiguity, the genetic data alone do not support elevating the variants to species status. Alate flight phenologies (based on museum specimen labels and limited published data) are also being examined as an indication of possible temporal reproductive isolation between the two subspecies, but records reviewed to date are insubstantial and equivocal.

In the present article we synthesize what has been learned using the three recently developed diagnostic techniques (hydrocarbon analysis, subsidiary mandibular tooth, and agonistic behavior) to revise distribution maps of the genus *Zootermopsis*. The range of each cuticular hydrocarbon phenotype is reported based upon extensive new field collections. A large number of specimens from museum collections was reexamined and determined with respect to the nonsoldier mandibular character. Discussion focuses on the historical biogeography of the species of *Zootermopsis* and their link with host trees, especially within the state of California where paleoclimatic and paleobotanic patterns are best known.

## Materials and Methods

**Sampling and Identification of Cuticular Hydrocarbon Phenotypes.** Collections for hydrocarbon analyses were made in Oregon, California, and Arizona from September 1986 through August 1987. The purpose of these collections was to sample areas that have been reported in the literature to support populations of *Zootermopsis*. Xeric and mesic areas, higher and lower elevations of the Sierra Nevada, the Cascade Range, the Coast Range and the San Gabriel, San Bernardino, and San Jacinto Mountains in California were sampled. Two east–west transects were made across the Coast Range and the Cascade Range in Oregon. Riparian areas of southeastern Arizona and the mountainous region in central Arizona were also visited. In addition, occasional samples were provided by associates and included in our hydrocarbon analyses.

During our collection trips, we separated each sample point by at least 8 km. Most of our collections were made along main roads, and, infrequently, along logging roads. At a given site, we searched for colonies of *Zootermopsis* in logs, stumps, standing dead trees, and dead wood in live trees. When termites were found, we usually did not collect the entire colony. Typically, we gathered just enough material for hydrocarbon analysis and voucher specimens (usually 10–15 individuals including, if possible, at least one soldier). Whenever possible, we identified the host wood to species.

Termites were separated from debris in the field, in the laboratory, or in temporary travel quarters. Specimens to be extracted were frozen in the laboratory, removed from the freezer, and allowed to reach ambient temperature before extraction. Cuticular lipids were extracted, and hydrocarbons were separated and characterized as described by Haverty et al. (1988). Samples or colonies were identified to hydrocarbon phenotype on the basis of diagnostic hydrocarbon patterns (Haverty et al. 1988).

**Determination of Preserved Material from Museum Collections.** A large portion of the Z. *laticeps* locality information is based upon the personal collection and observations of W. L. Nutting. In addition, collections of fresh material for hydrocarbon analysis were made by M. I. Haverty and W. L. Nutting.

Preserved *Zootermopsis* specimens were requested from national and regional collections (see *Acknowledgments* for specific museums) for morphological analysis based on the subsidiary tooth of the right mandible of nonsoldier castes (Thorne & Haverty 1989). For sample vials containing three or more termites, the right mandible of one individual (preferably a late instar or a nymph, pseudergate, or alate) was probed into a visible position or removed for examination under a dissecting microscope. In the occasional circumstance that diagnosis was ambiguous (normally because of a recent molt or a broken mandible), a second individual was examined. Previous determinations were confirmed or revised in accordance with the mandible character. Locality information of all specimens was noted and later compiled with longitude and latitude coordinates. Additional label information, such as elevation of collection site, host species, and presence of mature alates in the sample, was also recorded if available.

**Table 1. Collection localities for *Z. nevadensis* subsp. *nevadensis* determined by characterization of cuticular hydrocarbons**

| State | County | Locality |
|---|---|---|
| California | Butte | 25 mi S Elam Creek Info Ctr, Hwy 32 |
| | | Forbestown |
| | Eldorado | Grizzly Flat |
| | | Omo Ranch |
| | Glenn | Mendocino Nat'l Forest Black Butte Rd |
| | Los Angeles | near Wrightwood |
| | | 1 mi from Vincent Gap |
| | | Dawson Pass |
| | | Eagles Roost Picnic Area |
| | | Mt. Waterman Ski Area |
| | | Chilao Flat |
| | Madera | Bass Lake Ranger Station |
| | | Westfall Ranger Station |
| | Mono | Mammoth |
| | Napa | 6 mi N Napa, Silverado Trail |
| | Nevada | Near Hobart Mills |
| | Plumas | 3 mi S Clio |
| | | Crescent Mills |
| | | 4 mi N Chester |
| | | 2 mi W Chester |
| | Riverside | Idyllwild (Saunders Meadow) |
| | | Alvin Meadow W of Idyllwild |
| | | Pine Cone W of Idyllwild |
| | | Black Mtn Rd N of Idyllwild |
| | San Bernardino | Baylis Park Picnic Area |
| | | Deer Lick Ranger Stn |
| | | Butler Peak Lookout |
| | | Onyx Point |
| | | near Heart Bar Camp |
| | | Jenks Lake |
| | Shasta | 0.6 mi E Burney |
| | | 5.6 mi E Burney |
| | | 6 mi N Burney |
| | | Hat Creek |
| | Sierra | Near Calpine |
| | Tehama | Payne's Creek |
| | | Hwy 36, 20 mi W Red Bluff |
| | Tuolumne | Yosemite Nat'l Park (North Gate, Hwy 120) |

**Table 2. Collection localities for *Z. angusticollis* determined by characterization of cuticular hydrocarbons**

| State or Province | County | Locality |
|---|---|---|
| British Columbia | | University of Victoria campus |
| California | Alameda | Dublin |
| | | Oakland |
| | Del Norte | Oregon Mountain |
| | Humboldt | near Willow Creek, Hwy 299 |
| | | 35 mi E Arcata |
| | | 8 mi N Hoopa, Hwy 962 |
| | | Orleans |
| | | Van Dusen Park, Hwy 36 |
| | | Bridgeville |
| | Mendocino | 6 mi NNW Cloverdale, Hwy 128 |
| | | Fish Rock Rd at Hwy 128 |
| | | Navarro |
| | | Hwy 20 W Willits |
| | Monterey | Pacific Grove–Cypress Point |
| | San Bernardino | Forest Falls in Mill Creek Canyon |
| | | Waterman Canyon |
| | Siskiyou | Happy Camp |
| | | 20 mi W Happy Camp, Hwy 96 |
| | Trinity | 7 mi W Big Bar, Hwy 299 |
| | | 6 mi E Dinsmore |
| Oregon | Benton | Mary's Peak |
| | | nr Alsea |
| | | McDonald Forest |
| | Coos | Myrtle Point |
| | | Remote |
| | Douglas | Camas Valley |
| | | 25 mi E Roseburg |
| | | 50 mi E Roseburg, Hwy 138 |
| | Lincoln | nr Cold Springs |
| | Linn | 42 mi W Sisters, Hwy 20 |
| | | Cascadia |
| | | Foster Lane nr Sweethome |
| Washington | Clallam | Tatoosh Island |

## Results

Collection records of *Zootermopsis* specimens used in the hydrocarbon analyses are tabulated in Tables 1–4; hydrocarbon phenotypes are mapped separately in Figs. 1–4. The museum collection data are presented in Tables 5–7, with summary maps indicating sites for the *Z. nevadensis* complex (Fig. 5), *A. angusticollis* (Fig. 6), and *Z. laticeps* (Fig. 7). Host records (combined from the hydrocarbon collection expeditions, museum labels, and literature accounts) are listed in Table 8.

*Zootermopsis nevadensis* subsp. *nevadensis* (hydrocarbon phenotype I) occurs in low to upper-mid elevations ($\leq$2,600 m) on the east and west slopes of the Sierra Nevada, the east side of the crest of the Coast Range adjacent to the Sacramento Valley, and in the higher elevations ($\geq$1,500 m) above the chaparral of the San Gabriel, San Bernardino, and San Jacinto Mountains of southern California (Tables 1 and 5; Figs. 1 and 5). Thus far, *Z. nevadensis* subsp. *nevadensis* has not been collected north of McCloud, CA.

Since 1985, we have collected >50 separate colonies of *Z. nevadensis* subsp. *nevadensis* and have collected it almost exclusively from *Pinus* species (Table 8). In a few instances we found colonies in white fir, *Abies concolor* and Douglas-fir, *Pseudotsuga menziesii*, but never in incense-cedar, *Libocedrus decurrens*. These species, in addition to ponderosa pine, *Pinus ponderosa*, and sugar pine, *P. lambertiana*, constitute the predominant components of the Sierra Nevada mixed-conifer forest type. Thus far, the only hardwood in which we have encountered *Z. nevadensis* subsp. *nevadensis* is oak, *Quercus* spp. (two occasions).

*Zootermopsis angusticollis* and *Z. nevadensis* subsp. *nuttingi* are sympatric throughout most of their range (Tables 2, 3, 5, and 6; Figs. 2, 3, 5 and 6). They generally occur in mesic and hydric habitats of the Coast Range and Cascade Mountains of California and Oregon. On a western

**Table 3. Collection localities for *Z. nevadensis* subsp. *nuttingi* determined by characterization of cuticular hydrocarbons**

| State or Province | County | Locality |
|---|---|---|
| British Columbia | | Greater Victoria Water District |
| California | Humboldt | near Willow Creek, Hwy 299 |
| | | 25 mi E Arcata, Hwy 299 |
| | | 35 mi E Arcata |
| | | 9 mi N Willow Creek |
| | | Van Dusen Park, Hwy 36 |
| | | Bridgeville |
| | Lake | Lake Pillsbury |
| | Mendocino | 6 mi NNW Cloverdale, Hwy 128 |
| | | Fish Rock Rd at Hwy 128 |
| | | Navarro |
| | | Potter Valley |
| | | nr Covelo |
| | | Hwy 20 W Willits |
| | Monterey | Pacific Grove–Cypress Point |
| | Napa | N of Calistoga, Hwy 28, at county line |
| | Shasta | Harrison Gulch Rng Stn 48 mi W Red Bluff |
| | | Harrison Gulch Hwy 36 |
| | | 2.5 mi N Whiskeytown, Hwy 299 |
| | | nr French Gulch |
| | | Trinity Mtn Station |
| | Siskiyou | hwy 89 near Bartle Gap |
| | | 2 mi E McCloud |
| | | 23 mi NE Weed, Hwy 97 |
| | | 6 mi S Butte Valley, Hwy 97 |
| | | 15 mi N Orleans, Hwy 96 |
| | | Oak Knoll Ranger Stn 20 mi W I-5, Hwy 96 |
| | | near Horse Creek Post Office |
| | | Happy Camp |
| | | 20 mi W Happy Camp, Hwy 96 |
| | Trinity | Buckhorn Summit, W of Redding, Hwy 299 |
| | | Douglas City, Hwy 299 |
| | | 2 mi W Weaverville, Hwy 299 |
| | | Cedar Flat, Hwy 299 |
| | | Gray Falls Campgrnd, Hwy 299 |
| | | Jackass Springs, 32 mi N of Hwy 299 |
| | | 40 mi N Hwy 299 near Clair Engle Lake |
| | | 6 mi E Dinsmore |
| | | Forest Glen |
| Oregon | Coos | Myrtle Point |
| | Douglas | 25 mi E Roseburg |
| | | Steamboat Inn, Hwy 138 |
| | | 50 mi E Roseburg, Hwy 138 |
| | Lincoln | near Cold Springs |
| | Linn | Cascadia |

transect from the Harny Basin across the Cascade Mountain Range, neither *Z. angusticollis* nor *Z. nevadensis* subsp. *nuttingi* are likely to be encountered in logs or tree stumps until "indicator species" (such as Oregon grape, rhododendron, bracken fern, sword fern, dogwood, and alder) are present. Typically, in areas east of (or lacking) this shrub composition, the logs and stumps of ponderosa pine (and less often lodgepole pine) appear too dry to support *Zootermopsis* populations; the dampwood termites are replaced by carpenter ants.

**Table 4. Collection localities for *Z. laticeps* determined by characterization of cuticular hydrocarbons**

| State | County | Locality |
|---|---|---|
| Arizona | Cochise | Benson |
| | | Charleston Crossing |
| | | Fairbank |
| | | Hereford |
| | | Lewis Crossing, Rio San Pedro @ Hwy 90 |
| | | St. David |
| | Graham | Pima |
| | Santa Cruz | Nogales |
| | | Patagonia |
| | | Rio Rico |
| | | Ruby Road, nr Santa Cruz River |

*Zootermopsis angusticollis* and *Z. nevadensis* subsp. *nuttingi* are found north into Washington and British Columbia (Tables 2, 3, 5 and 6), with occasional records of *Z. nevadensis* (subspecies uncertain) in Idaho and Montana (Table 5). *Z. angusticollis* and *Z. nevadensis* (subspecies uncertain, likely *nevadensis*) have both been collected in Baja California.

In California north of the San Francisco Bay area up into northwestern Oregon, *Z. angusticol-*

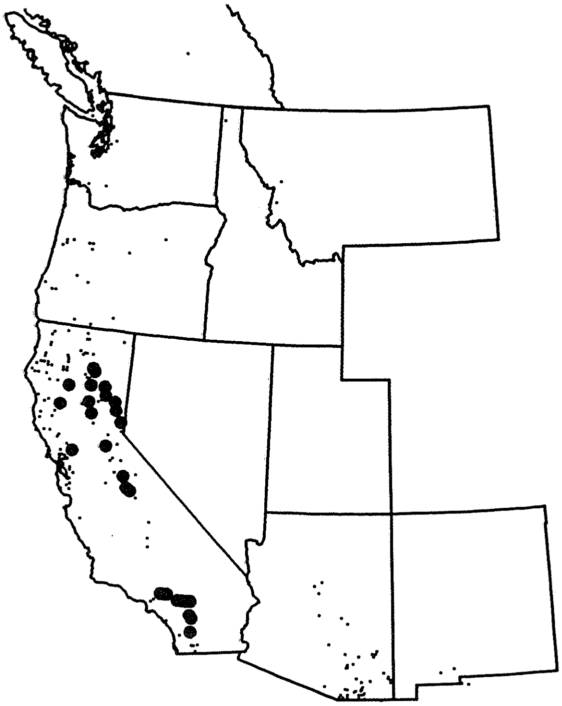

**Fig. 1.** Collection locations of *Zootermopsis nevadensis* subsp. *nevadensis* (Hydrocarbon phenotype I) for hydrocarbon analysis (large dots). Small dots represent collection localities for hydrocarbon samples and museum specimens for all *Zootermopsis* taxa.

**Fig. 2.** Collection locations of *Zootermopsis angusticollis* (Hydrocarbon phenotype II) for hydrocarbon analysis (large dots). Small dots represent collection localities for hydrocarbon samples and museum specimens for all *Zootermopsis* taxa.

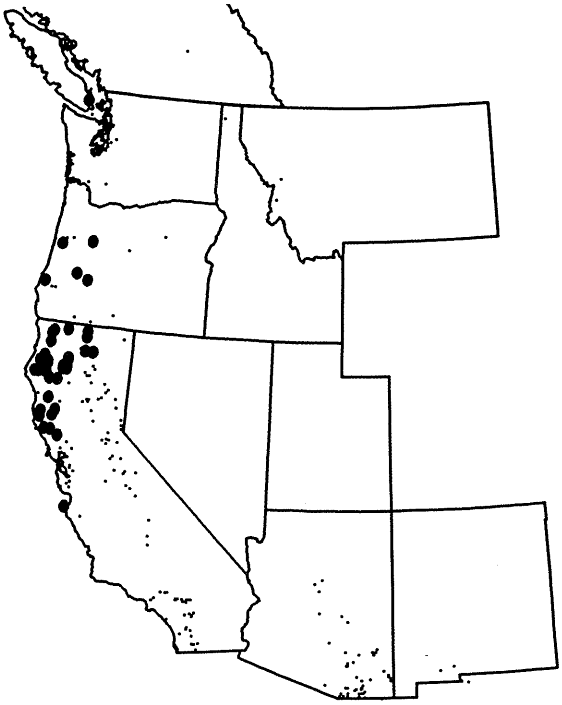

**Fig. 3.** Collection locations of *Zootermopsis nevadensis* subsp. *nuttingi* (Hydrocarbon phenotype III) for hydrocarbon analysis (large dots). Small dots represent collection localities for hydrocarbon samples and museum specimens for all *Zootermopsis* taxa.

*lis* and *Z. nevadensis* subsp. *nuttingi* are most frequently found in Douglas-fir, the dominant conifer of this area. Both can occasionally be found in ponderosa pine (in the more xeric sites), western red cedar, *Thuja plicata*, redwood, and occasional hardwood species (Table 8). From the San Francisco Bay area south to the Monterey Bay area, both termite species are found predominantly in Monterey pine, *P. radiata*, and Douglas-fir, again the prevailing conifer species. In southern California, *Z. angusticollis* occurs only in lower elevations (<1,500 m) and is found in hardwoods and typically low-elevation conifers such as Jeffrey pine, *P. jeffreyi*. Based on hydrocarbon phenotype, we have not collected *Z. nevadensis* subsp. *nuttingi* south of Monterey County. Most museum specimens of *Z. nevadensis* (Table 5) from southern California are from higher elevations and are likely *Z. nevadensis* subsp. *nevadensis*. However, possible localities for *Z. nevadensis* subsp. *nuttingi*, based on museum specimens, might be those in San Diego, Santa Barbara, and Ventura counties (Table 5).

Thus, in regions surveyed to date, the distribution of the two subspecies of *Z. nevadensis* appears to be largely allopatric (Figs. 1 and 3). The single exception to this pattern is that one sample of *Z. nevadensis* subsp. *nevadensis* was collected in the Napa Valley of California (Table 1), a region typically inhabited by *Z. nevadensis* subsp. *nuttingi*. It is possible that those *Z. nevadensis* subsp. *nevadensis* were imported into the Napa Valley in the oak firewood in which they were collected. Equally plausible is that the Napa Valley represents the southwestern margin of the distribution of *Z. nevadensis* subsp. *nevadensis* in the Coast Range. Further sampling is warranted in the Napa Valley, and also along transects across the northern Coast Range of California. Current results suggest that the two *Z. nevadensis* variants meet or perhaps overlap in this region; further resolution would be of interest.

All of the numerous collections of *Z. nevadensis* we have made thus far fall into either hydrocarbon phenotype I or III (Haverty et al. 1988). We have found no hydrocarbon hybrids as have been found in the two species of *Solenopsis* introduced into the southeastern United States (Vander Meer et al. 1985, Ross et al. 1987). The two subspecies of *Z. nevadensis* will infli-breed under laboratory conditions and produce offspring with intermediate hydrocarbon profiles (M.I.H., unpublished data).

The distribution and habits of *Z. laticeps* are clearly different from the other species of *Zoo-*

**Fig. 4.** Collection locations of *Zootermopsis laticeps* (Hydrocarbon phenotype IV) for hydrocarbon analysis (large dots). Small dots represent collection localities for hydrocarbon samples and museum specimens for all *Zootermopsis* taxa.

*termopsis*. The collections made to document the hydrocarbon pattern of Z. *laticeps* (Table 4; Fig. 4) expand the locality data from museum specimens (Table 7, Fig. 3). For this study, our collecting was restricted to southeastern Arizona (Table 4). However, Z. *laticeps* has been collected by Nutting (1965) and others as far north in Arizona as Sedona and as far south as Cerocahui, Chihuahua, Mexico. The extent of the southern distribution of this species has not been determined. Collections have been made from very low elevations in Arizona such as Florence (≈500 m) and Pima (≈1,000 m) and from very high elevations such as Rose Canyon Lake, AZ (≈2,600 m). The apparent limiting factor is the presence of a suitable hardwood host.

*Zootermopsis laticeps* is strictly riparian. In the collections made by Nutting (1965) and more recently by us (W.L.N. and M.I.H.), Z. *laticeps* has been found only in dead wood within or attached to live wood of trees; this species is never found in logs or stumps of dead trees. The moisture provided by the live tissue may be critical to the termites.

Although suitable hosts occur west of the Colorado River (*Populus, Salix,* and *Plantanus*), Z. *laticeps* has not been found in riparian localities west of the Sonoran Desert. Likewise, with an abundance of *Pinus* and *Pseudotsuga* in central, eastern, and southeastern Arizona, neither Z. *angusticollis* nor Z. *nevadensis* has been collected there. The Sonoran, Colorado, and Great Basin deserts appear to be effective geographic isolating barriers.

## Discussion

**Historical Perspective.** An historical biogeographical analysis attempts to understand biotic distribution patterns in relation to pertinent physical events and biological interactions. The premise, as stated by Mayr (1970), is that the history of a taxon is reflected in its distribution pattern.

Physical events over geologic time have profoundly affected the survival, evolution, and present distribution of flora and fauna. These planetary events include lithosphere plate tectonics (causing continental drift); climatic changes including regional temperature oscillations, glaciers, and associated variations in sea level; and the barrier-forming development of mountain ranges, great rivers, and inland seas.

Intercalated with the distribution, radiation, and evolution of any single taxon will be the complex historical biogeography of interacting organisms, particularly those closely associated with the ecology of the focal taxon. In the case of dampwood termites and trees, the latter provide both food and lifetime harborage for the insects. Most individuals in these termite colonies live their entire life cycle without ever leaving their host logs. Winged fertile termite offspring (alates or swarmers) fly from their natal nest log only once to find a mate quickly and retreat back into suitable wood to initiate additional sequestered colonies. Therefore, in an attempt to understand the current distribution of *Zootermopsis* (and of the subgeneric taxa), we examined what is known of the paleobotany and biogeography of key host trees, particularly the coniferous genera *Pinus* (pines) and *Pseudotsuga* (Douglas-fir).

Before discussing the floristic biogeography, it is important to point out that significantly less is known about the history of the termites. The worldwide distribution of the Isoptera suggests that the order originated in the Paleozoic or early Mesozoic (Fig. 8) before the breakup of Pangea (Emerson 1952, 1955; see also Thorne & Carpenter 1992). All six major families of living termites were probably in existence and dispersed over the great land masses by the late Mesozoic (Snyder 1950, Emerson 1952). The earliest known fossil termites are of the subfamily Hodotermitinae (the Hodotermitidae are closely related to the Termopsidae), found in the early Cretaceous (Spain 130 million years ago (mya) [Lacasa-Ruiz & Martinez-Delclos 1986] and in Brazil 110 mya [Krishna 1990]). There is no fossil evidence yielding clues as to the origin of *Zootermopsis*,

**Table 5. Collection localities of *Z. nevadensis* specimens from museums**

| State or Province | County | Locality |
|---|---|---|
| British Columbia | | Camas Hill, Metchosin 10 mi W Victoria |
| | | Cloverdale (near Vancouver?) |
| | | Colista |
| | | Royal Oak |
| | | Thetis Lake Park, Langford 30 mi N Victoria |
| | | Vancouver Island |
| | | Vernon |
| California | Butte | Forest Ranch |
| | | Jarboe Pass |
| | | Paradise |
| | Calaveras | Calaveras Big Trees Park, near Arnold Murphy's |
| | Contra Costa | Richmond |
| | Eldorado | Blodgett Forest |
| | | Camino |
| | | China Flat |
| | | Placerville |
| | | Sly Park |
| | | Snowline Camp |
| | | Wright's Lake |
| | Fresno | Shaver Lake |
| | Humbolt | Eel River |
| | | Kneeland |
| | | Rohnerville |
| | Kern | Alden Creek Public Campground |
| | | Alta Sierra |
| | Lake | Middleton |
| | Lassen | Bridge Creek Campground |
| | Los Angeles | Cloudburst Camp |
| | | Crystal Lake |
| | Madera | Yosemite |
| | Mariposa | near Fish Camp |
| | Mendocino | Eagle's Nest |
| | | Eel River |
| | | Howard Creek |
| | | Leggett State Park |
| | Modoc | Cedar Pass Campground |
| | | Davis Creek |
| | Monterey | Chew's Ridge |
| | | Pacific Grove |
| | Napa | 20 mi N Napa, Copell Creek |
| | Placer | Tahoe City |
| | | Lake Tahoe |
| | Plumas | Bucks Lake |
| | | Meadow Valley |
| | | Seneca, near Lake Almanor |
| | Riverside | Idyllwild |
| | | Hemet Valley |
| | | Herkey Creek, near Lake Hemet |
| | | San Jacinto Mountains |
| | San Diego | Kitchen Creek, Laguna Mountains |
| | | Mt. Laguna |
| | | Mt. Palomar |
| | | Pine Valley |
| | | Julian |
| | Santa Barbara | Santa Cruz Island |
| | Santa Clara | San Jose |
| | Santa Cruz | Big Basin Redwood State Park |
| | Siskiyou | Ash Creek Ranger Station, near McCloud |
| | | Dunsmuir |
| California | Siskiyou | Mt. Shasta City |
| | | Bray |
| | Shasta | Redwoods |
| | | Mt. Lassen National Park (Manzanita Lake?) |
| | Sonoma | Plantation |
| | Trinity | Bell Creek |
| | | Carrville |
| | | Coffee Creek Ranch, near Carrville |
| | Tulare | Johnsondale |
| | Tuolumne | Groveland |
| | | Strawberry |
| | | Yosemite Valley |
| | | Tuolumne River |
| | Ventura | Grade Valley |
| | Yuba | Dry Creek near Smartville |
| Idaho | Bonner | Preist Lake |
| Montana | Ravalli | Hamilton |
| | Missoula | Missoula |
| Oregon | Curry | Rouge River |
| | Columbia | Goble |
| | Grant | Ritter |
| | Jackson | Ashland |
| | Klamath | Keno |
| | Lake | Bly |
| | Lincoln | Waldport |
| | Tillamook | Tillamook Burn |
| Washington | Cowlitz | Castle Rock |
| | Skamania | Butte Camp |
| | | Muddy River |
| | | Spirit Lake |
| | Whatcom | Point Roberts |
| | ??? | Fox Island |

although a fossil species tentatively placed in *Zootermopsis* (*Z. coloradensis* (Scudder)) was found in the Oligocene Florissant deposits of Colorado (Emerson 1933). The DNA hybridization study of Broughton & Kistner (1991) implies an origin of the genus ≈50 mya.

In contrast to the fossil record of termites, the floristic biogeography does provide insights into patterns compatible with the modern distribution of *Zootermopsis*. Focusing on California, the following general synopsis emerges: California's current plant diversity, numerically and geographically, is a result of recurrent climatic fluctuations over geologic time in a region in which diverse topographic and edaphic conditions were emerging concurrently. The repeated warming and cooling trends, varying in duration and intensity, cyclically allowed plants to radiate and expand distributions, then forced contractions and strandings which resulted either in local extinctions or in isolated (relict) populations. A more detailed chronology of these events follows (for reference, geologic time periods are summarized in Table 9).

The genus *Pinus* attained a high diversity in eastern Asia, the eastern United States, and western Europe by the end of the Cretaceous (Axelrod 1986, Millar 1993). At this time, Laurasia had begun to split into North America and Europe,

**Table 6. Collection localities of *Z. angusticollis* specimens from museums**

| State or Province | County | Locality |
|---|---|---|
| British Columbia | | Chatham Island |
| | | Galiano Island |
| | | Huxley Island |
| | | Langford |
| | | Mitlenatch Island |
| | | Royal Oak |
| | | Thetis Lake Park, Langford |
| | | Vancouver |
| | | Victoria |
| | | White Rock |
| California | Alameda | Berkeley |
| | | Berkeley Hills |
| | Butte | Chico |
| | Contra Costa | Crockett |
| | | Danville |
| | Kern | Alta Sierra |
| | Lake | Middleton |
| | Los Angeles | Los Angeles |
| | | Pasadena |
| | | South Pasadena |
| | Marin | Inverness |
| | | Inverness Ridge |
| | | Ross |
| | Mendocino | 5 mi E Anchor Bay |
| | Monterey | Pacific Grove |
| | | Carmel |
| | Orange | San Juan Creek |
| | San Bernardino | Mill Creek |
| | | San Bernardino |
| | San Diego | Escondido |
| | | Mt. Laguna |
| | | Palomar |
| | San Francisco | Golden Gate Park |
| | Santa Barbara | Santa Barbara |
| | Santa Clara | Los Gatos Canyon |
| | | Stevens Creek Canyon |
| | | San Jose |
| | Shasta | 2 mi W Viola |
| Oregon | ??? | Boyer |
| | Benton | Corvallis |
| | Crook | Ochoco Mtns. |
| | Klamath | Keno |
| Washington | Grays Harbor | Hoquiam |
| | King | Carnation |
| | | Renton |
| | | Seattle |
| | Pierce | Ft. Lewis |

**Table 7. Collection localities of *Z. laticeps* specimens from museums**

| State | County | Locality |
|---|---|---|
| Arizona | Cochise | Douglas |
| | | Hereford |
| | | Paradise |
| | | Lewis Crossing (in live cottonwood stump) |
| | | Ida Canyon, Huachuca Mtns. |
| | | SW Research Stn, Portal |
| | | Turkey Cr., Chiricahua Mtns. |
| | | Pinery Canyon, Chiracahua Mtns. |
| | | Cochise Stronghold, Dragoon Mtns. |
| | | Ramsey Canyon, Huachuca Mtns. |
| | | Garcia |
| | | Palmerlee |
| | | Miller Canyon, Huachuca Mtns. |
| | | Cave Canyon, Huachuca Mtns. |
| | | Lindsey Ranch, 2 mi SE Charleston |
| | | Dos Cabezas |
| | Coconino | Sedona |
| | Gila | Globe |
| | | Six Shooter Canyon, Pinal Mtns. |
| | | Workman Creek, Sierra Ancha |
| | Graham | Safford |
| | | Galiuro Mtns. |
| | | Noon Creek, Pinaleno Mtns. |
| | | Solomon |
| | Maricopa | Camp Creek |
| | Pima | Brown Canyon, Baboquivari Mtns. |
| | | Sabino Canyon, Santa Catalina Mtns. |
| | | Edgar Canyon, Santa Catalina Mtns. |
| | | Upper Bear Canyon, Santa Catalina Mtns. |
| | | Rose Canyon, Santa Catalina Mtns. |
| | Pinal | Florence |
| | | Peppersauce Canyon, Santa Catalina Mtns. |
| | Santa Cruz | Madera Canyon |
| | | Patagonia |
| | | Canelo (Flying B Ranch) |
| | | W Slope Patagonia Mtns. |
| | | Peña Blanca Spring |
| | | O'Donnell Canyon, 1/2 mi N Ewing Ranch |
| | Yavapai | Clemenceau |
| | | Beaver Cr. Campground, 2 mi E jct. 17 & 179 |
| Chihuahua (Mexico) | | Cerocahui (frass with mandible) |
| | | Rio Tomachic, W of Madera |
| New Mexico | Doña Ana | Las Cruces |
| | Ana | Strahman's Farm, 5 mi S Mesilla (in pecan) |
| Texas | El Paso | El Paso |

and an expansive north–south midcontinental seaway extended through the entire North American continent, impeding east–west migration of species (Noonan 1986). By the early Tertiary (Paleocene), a low mountain axis of the Rocky Mountains had formed, but the remaining topography of the western United States differed greatly from today. None of the Californian mountain ranges had formed, a tropical sea covered much of the Pacific states, and a shore existed along the region of the present Sierra Nevada and Klamath mountains (Axelrod 1977, Raven & Axelrod 1978). The warm and humid conditions of the Paleocene caused pines to disappear from middle latitudes (to 70°), and the lack of topographic relief meant that there were no cooler refugia at higher elevations. As a result, many pine species became extinct or retreated to high latitude refugia during this period (Millar 1993).

The Eocene continued warm and wet. The Eocene climate oscillated with substantial tem-

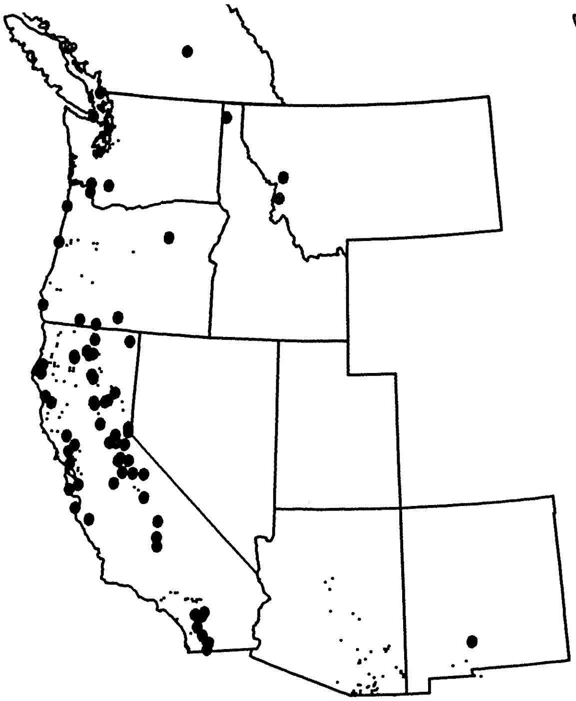

**Fig. 5.** Museum record localities for *Zootermopsis nevadensis* morphotype (large dots). Small dots represent collection localities for hydrocarbon samples and museum specimens for all *Zootermopsis* taxa.

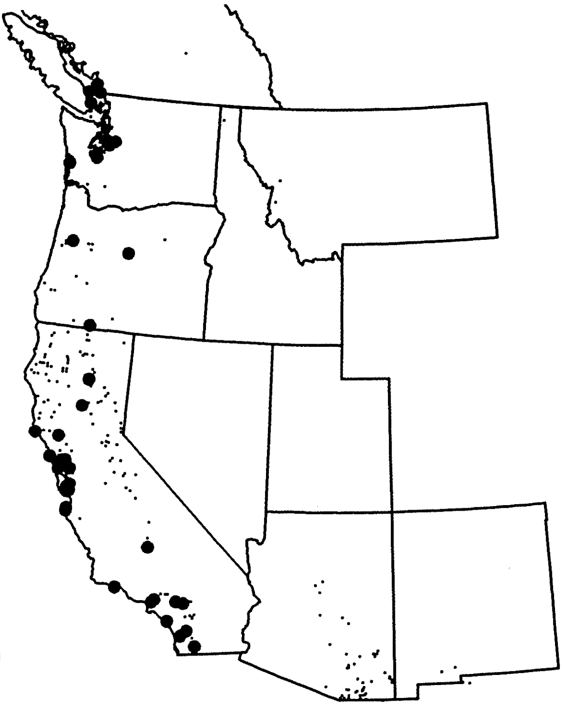

**Fig. 6.** Museum record localities for *Zootermopsis angusticollis* (large dots). Small dots represent collection localities for hydrocarbon samples and museum specimens for all *Zootermopsis* taxa.

perature fluctuations, causing pines to shift into three refugia: high and low latitudes and into the few upland regions of middle latitudes in western North America (Millar 1993). Evolution and radiation of pine species occurred within Eocene refugia (ponderosa pine, for example, was divided into disjunct populations, some of which met much later in the Cenozoic) (Millar 1993).

The end of the Eocene brought a dramatic climatic event: an average temperature drop of 10–13°C in just 1 million yr, paralleled by a broad decrease in rainfall and increased seasonality. The cooler temperatures allowed pines to begin migrating out of their refugia and to become more widespread in middle latitudes during the Oligocene and Miocene (Millar 1993).

During the Oligocene, two major types of conifer forest emerged: montane conifers mixed with deciduous hardwoods typified midaltitudes (750–1,350 m); specialized subalpine conifers occurred at higher elevations (Axelrod 1977). The mid-Continental Seaway retreated from North America, and the continental ice sheets of the Oligocene melted in a relatively mild Miocene climate.

Following the mid-Miocene, a cooling and drying trend continued, and the mixed conifer and subalpine forests shifted coastward (Axelrod 1976, 1977; Raven & Axelrod 1978), with species diversity falling as summer rainfall declined. A rich forest (ancestral to the present Sierra Nevada mixed conifer forest), however, covered the Great Basin and Columbia Plateau. Southern California was covered with tropical seas and was situated in the present area of Baja California until plate movement occurred in the late Miocene.

The Sierra Nevada, peninsular ranges, coast ranges, and Siskiyou–Klamath regions uplifted in the Pliocene, geological processes which continued into the Quaternary (Raven & Axelrod 1978). The uplift of the Sierras provided California protection from the more extreme interior continental climates, resulting in a Mediterranean climate with reduced summer rainfall and greater temperature ranges (Raven 1977, Raven & Axelrod 1978). Vegetation drought stress occurred as a result of elevated summer temperatures. The summer drought became more severe (into the Pleistocene), restricting numerous mixed conifer forest species to northwestern California and cooler portions of Oregon, Washington, and Idaho. These species also became confined to mesic mountainous areas over the interior and toward the coast. During this time, the deciduous hardwood component was largely lost from these forests (Wolfe 1969). The lack of floral zonation in the Klamath region is thought

**Fig. 7.** Museum record localities for *Zootermopsis laticeps* (large dots). Small dots represent collection localities for hydrocarbon samples and museum specimens for all *Zootermopsis* taxa. Collections from Chihuahua, Mexico, are not shown on the map (see Table 7).

**Table 8. Host species associated with collections of *Zootermopsis*. Hosts are listed in order of most frequent to least frequent occurrence.**

| *Zootermopsis* spp. | Host (common and scientific names) |
|---|---|
| *Z. nevadensis* subsp. *nevadensis* | Ponderosa pine (*Pinus ponderosa* Laws.) |
| | Jeffrey pine (*Pinus Jeffreyi* Grev. & Balf.) |
| | Digger pine (*Pinus sabiniana* Dougl.) |
| | Coulter pine (*Pinus Coulteri* D. Don) |
| | Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) |
| | White fir (*Abies concolor* (Gord. & Glend.) Lindl.) |
| | Sugar pine (*Pinus lambertiana* Dougl.) |
| | Oak (*Quercus* sp.) |
| *Z. angusticollis* | Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) |
| | Monterey pine (*Pinus radiata* D. Don) |
| | Ponderosa pine (*Pinus ponderosa* Laws.) |
| | Monterey cypress (*Cupressus macrocarpa* Hartw.) |
| | Redwood (*Sequoia sempervirens* (D. Don) Endl.) |
| | Western red cedar (*Thuja plicata* Donn) |
| | Madrone (*Arbutus menziesii* Pursh) |
| | Bay (*Umbellularia californica* (Hook. & Arn.) Nutt.) |
| | Red alder (*Alnus rubra* Bong.) |
| | Oak (*Quercus* sp.) |
| | Birch (*Betula occidentalis* Hook.)[a] |
| | Eucalyptus (*Eucalyptus* sp.)[a] |
| | Jeffrey pine (*Pinus Jeffreyi* Grev. & Balf.)[a] |
| *Z. nevadensis* subsp. *nuttingi* | Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) |
| | Monterey pine (*Pinus radiata* D. Don) |
| | Ponderosa pine (*Pinus ponderosa* Laws.) |
| | Monterey cypress (*Cupressus macrocarpa* Hartw.) |
| | Digger pine (*Pinus sabiniana* Dougl.) |
| | Redwood (*Sequoia sempervirens* (D. Don) Endl.) |
| | Western red cedar (*Thuja plicata* Donn) |
| | Oak (*Quercus* sp.) |
| *Z. laticeps* | Cottonwood (*Populus Fremontii* S. Wats.) |
| | Willow (*Salix Gooddingii* Ball) |
| | Live oak (*Quercus* sp.)[a] |
| | Sycamore (*Plantanus Wrightii* Wats.)[b] |
| | Alder (*Alnus oblongifolia* Torr.)[b] |
| | Pecan (*Carya illinoensis* (Wangenh.) K. Koch)[c] |

[a] Incidental host records from museum collection labels.
[b] Host record from Nutting (1966).
[c] Host record from Weesner (1970).

to be relictual and facilitated by less topographic relief in the local area.

The recent Pleistocene Epoch was characterized by a series of 16–18 glacier cycles of varying lengths (Bowen 1979). The effect of the climatic periods associated with glaciation is reflected not in floristic species composition but rather in a North–South gradient pattern. Species extinctions were uncommon, but distributions shifted south then north (or up then down in elevation) following the glacier cycle (Millar 1993). *Pseudotsuga* took over as the dominant in the conifer forests of the Northwest (Columbia Plateau–Cascade region) (Wolfe 1969).

The differences in the present forests of California finally emerged in the Holocene, more specifically during the brief and recent Xerothermic episode (8,000–4,000 yr ago). During that interval of warm and dry climate, Douglas-fir became restricted northward of the central part of the Sierra Nevada (Raven & Axelrod 1978). In southern California, some disjunct relict taxa (e.g., ponderosa pine) remain in isolated pockets but they disappeared from most areas (Raven & Axelrod 1978). The narrow, xeric subzones at the boundaries of more diverse mixed conifer forests were colonized by ponderosa pine, Jeffrey pine, and Douglas-fir. Each of these species is able to cope with those relatively poor sites because of their associations with ectotrophic mycorrhizae (Axelrod 1986).

**Biogeography of *Zootermopsis*.** All implications suggest that the dampwood termites were carried along with the pines and other hosts in their episodic retreats and reinvasions during the climatic and topographical shifts of the past 50 million yr. Some of the paleobotanical patterns

| ERA | PERIOD | | EPOCH |
|---|---|---|---|
| CENOZOIC | QUATERNARY | | HOLOCENE<br>LAST 10,000 YEARS |
| | | | PLEISTOCENE<br>2 - 5 MYA |
| | TERTIARY | NEOGENE | PLIOCENE<br>7 MYA |
| | | | MIOCENE<br>26 MYA |
| | | PALEOGENE | OLIGOCENE<br>34 MYA |
| | | | EOCENE<br>54 MYA |
| | | | PALEOCENE<br>60 - 65 MYA |
| MESOZOIC | CRETACEOUS<br>136 MYA | | |
| | JURASSIC<br>180 - 190 MYA | | |
| | TRIASSIC<br>225 MYA | | |

**Fig. 8.** Geologic timetable reference chart.

correlate well with the present distribution of *Zootermopsis* species, and logical deductions can be made regarding historical biogeography.

In the early Tertiary, ancestors of modern *Zootermopsis* must have been living in the region between the western boundary of the midcontinental seaway and the shore of the tropical sea covering much of the Pacific states (shoreline along the axis of the present Sierra Nevada and Klamath mountains). *Zootermopsis* and its close relatives are known only from temperate climates, so it may be that the genus was confined to relatively northern latitudes of the western North American region during the tropical periods of the Paleocene. As temperature oscillations and the complementary shift in pine habitats occurred in the Eocene, *Zootermopsis* probably moved with their hosts, confined to high latitudes and upland refugia during warm and wet intervals. Cooler temperatures enabled a more widespread distribution of pines in middle latitudes during the Oligocene and Miocene; during this time, *Zootermopsis* may have been widespread as well. Dampwood termites likely expanded their range coastward following the mid-Miocene, in conjunction with the forest migration to the coast during this cool and dry period. There may also have been colonization southward as the tropical seas receded from southern California.

From this potentially broad *Zootermopsis* distribution in the late Miocene, the geological uplifts of the Pliocene, combined with the droughts of the late Tertiary and glacial cycles of the Quaternary, served to differentiate microhabitats suitable for *Zootermopsis.* The conifer forests became restricted to northern California and cooler regions of Oregon, Washington, and Idaho. Inland and southern populations were confined to mesic, mountainous areas. At the end of the last glacial episode, isolated, relict forests (and, presumably, *Zootermopsis*) remained disjunct from neighboring populations; a pattern constricted even more during the recent Xerothermic episode of the Holocene.

Considering individual *Zootermopsis* taxa, it seems clear that Z. *laticeps* became separated from the other species, isolated by geographic barriers such as the Rocky Mountains and the deserts of the American Southwest. Modern Z. *laticeps* have not only a distinct range but a distinct habitat as well, living in the dead wood of live riparian, hardwood trees. Morphologically, Z. *laticeps* is the most primitive of living *Zootermopsis* (Emerson 1933), a pattern substantiated by genetic differences (Broughton & Kistner 1991). The timing of the divergence between the Z. *laticeps* lineage and the Pacific Coastal *Zootermopsis* is estimated at ≈13 mya based on DNA hybridization studies (Broughton & Kistner 1991).

The isolated collections of Z. *nevadensis* subsp. *nevadensis* at higher elevations in southern California parallel the distribution of relict pine associations also confined to those mountains. The predominantly coastal distribution of Z. *angusticollis* and Z. *nevadensis* subsp. *nuttingi* may be associated with the Miocene movement of forests toward the coast and subsequent isolation caused by the formation of the San Joaquin Valley.

Central to our study is the apparent recent or incipient speciation of Z. *nevadensis* into the variants Z. *nevadensis* subsp. *nevadensis* and Z. *nevadensis* subsp. *nuttingi.* These two groups are morphologically indistinguishable, but they are largely or totally allopatric with consistent, diagnostic hydrocarbon patterns. The recent paleoclimatic history of the Pacific Coastal states, and associated influences on floristic biogeography, may provide clues regarding the relatively recent geographic division of the ancestral species, leading to allopatric or parapatric differentiation of Z. *nevadensis* subsp. *nevadensis* and Z. *nevadensis* subsp. *nuttingi.*

In light of our evidence demonstrating substantially allopatric distributions of *Zootermopsis* hydrocarbon phenotypes I and III, it is appropriate to reconsider taxonomic status within the *Z. nevadensis* complex. Intraphenotype aggression is rare, but soldiers, pseudergates, and nymphs having hydrocarbon phenotype I frequently behave agonistically toward phenotype III individuals and vice versa, indicating that nonreproductive termites discriminate between the variants (Haverty & Thorne 1989). Laboratory matings between phenotypes produce viable immatures with an intermediate hydrocarbon phenotype, but such hybrids have not been collected in the field. The evidence for reproductive isolation between the two *Z. nevadensis* variants is compelling based upon the largely allopatric distribution demonstrated in this paper, but precise distributions along the zone of potential overlap (Napa Valley and the northern coast range of California) needs to be established. Hydrocarbon differentiation (Haverty et al. 1988) and genetic variation (Broughton & Kistner 1991, Korman et al. 1991) also support the incipient or complete speciation hypothesis. Precise data on alate flight phenologies might provide further evidence, although timing of reproductive flights is influenced by microclimatic factors, and it may therefore be difficult to compare among locations or years.

At this point we refrain from elevating the status of the two *Zootermopsis* variants from subspecies to species. Instead, we choose the conservative tactic of leaving the two groups as subspecies until more data are available. Given the primitive, even "relictual," nature of the genus *Zootermopsis*, recent radiation within the group is a notable evolutionary process.

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