# Collection History and Comparison of the Interactions of the Goldspotted Oak Borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), with Host Oaks in Southern California and Southeastern Arizona, U.S.A.

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# Collection History and Comparison of the Interactions of the Goldspotted Oak Borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), with Host Oaks in Southern California and Southeastern Arizona, U.S.A.

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## Abstract

An invasive population of the goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), is colonizing and killing three species of oaks in San Diego Co., California. However, the interactions of *A. auroguttatus* with oaks in its native range in southeastern Arizona have not been recorded. We present a complete inventory of the North and Central American collection records of *A. auroguttatus* and *Agrilus coxalis* Waterhouse from the literature and from a survey of the holdings of 27 museum and personal collections. We also discuss the relationship between this collection history and the behavior of *A. auroguttatus* as an intracontinental invasive species. Surveys of native populations of *A. auroguttatus* in oak forest stands from four mountain ranges in southeastern Arizona revealed injury patterns on Emory oak, *Quercus emoryi* Torrey, and silverleaf oak, *Quercus hypoleucoides* A. Camus, similar to those observed on other "red" oaks in California. No damage was observed on "white" oaks in Arizona, and observed only rarely on a white oak, *Quercus engelmannii* Greene, in California. In Arizona, adult emergence was confirmed from bark removed from *Q. emoryi*, representing the first developmental record of *A. auroguttatus* from a native host. Late instars of *Agrilus* sp. were also recovered from *Q. hypoleucoides*, but they were not reared to the adult stage for species identification. Nonetheless, our observations of damage and the presence of larvae in the same configuration and location in the outer bark as we would expect for *A. auroguttatus* suggest that *Q. hypoleucoides* is also likely a host. Two hymenopteran parasitoids, *Calosota elongata* Gibson (Eupelmidae) and *Atanycolus simplex* Cresson (Braconidae), and two likely coleopteran predators (Trogossitidae and Elateridae) emerged from, or were collected in southeastern Arizona from, *Q. emoryi* bark infested with *A. auroguttatus*. Based on the museum survey results, the morphological similarity of individuals from the California and Arizona populations, the spatial dynamics of the pattern of infestation in California, the geographic isolation of hosts in California from native populations of the beetle, and the proximity of San Diego Co. to southeastern Arizona, we hypothesize that *A. auroguttatus* was introduced to California from Arizona or less likely from the Mexican states of Baja California, Chihuahua, or Sonora, and that the introduction most likely occurred on oak firewood. Further, we hypothesize that the oak mortality in southern California is occurring from this intracontinental invasive species because the beetle is filling a vacant niche by colonizing and developing in non-coevolved trees with low host resistance in the absence of a diverse and coevolved insect natural enemy complex.

Key Words: *Agrilus coxalis*, *Atanycolus simplex*, *Calosota elongata*, firewood, intracontinental invasive species, oak mortality

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Between 2002 and 2010, aerial survey data revealed an expanding pattern of extensive oak mortality on federal, state, tribal, and private lands in San Diego Co., California (CA). Approximately 21,535 coast live oaks, *Quercus agrifolia* Née (Fagaceae), California black oaks, *Quercus kelloggii* Newberry, and canyon live oaks, *Quercus chrysolepis* Liebm., have died in a 4,903 km$^2$ area centered on the Descanso Ranger District, Cleveland National Forest and Cuyamaca Rancho State Park (Fig. 1A–C). Until recently, this zone of oak mortality was not contiguous with the U.S.-Mexican border on its southern flank, but it now extends from the community of Campo in the southeast to Ramona in the northwest. In 2009, an additional isolated pocket of dying oaks was found at Marion Bear Memorial

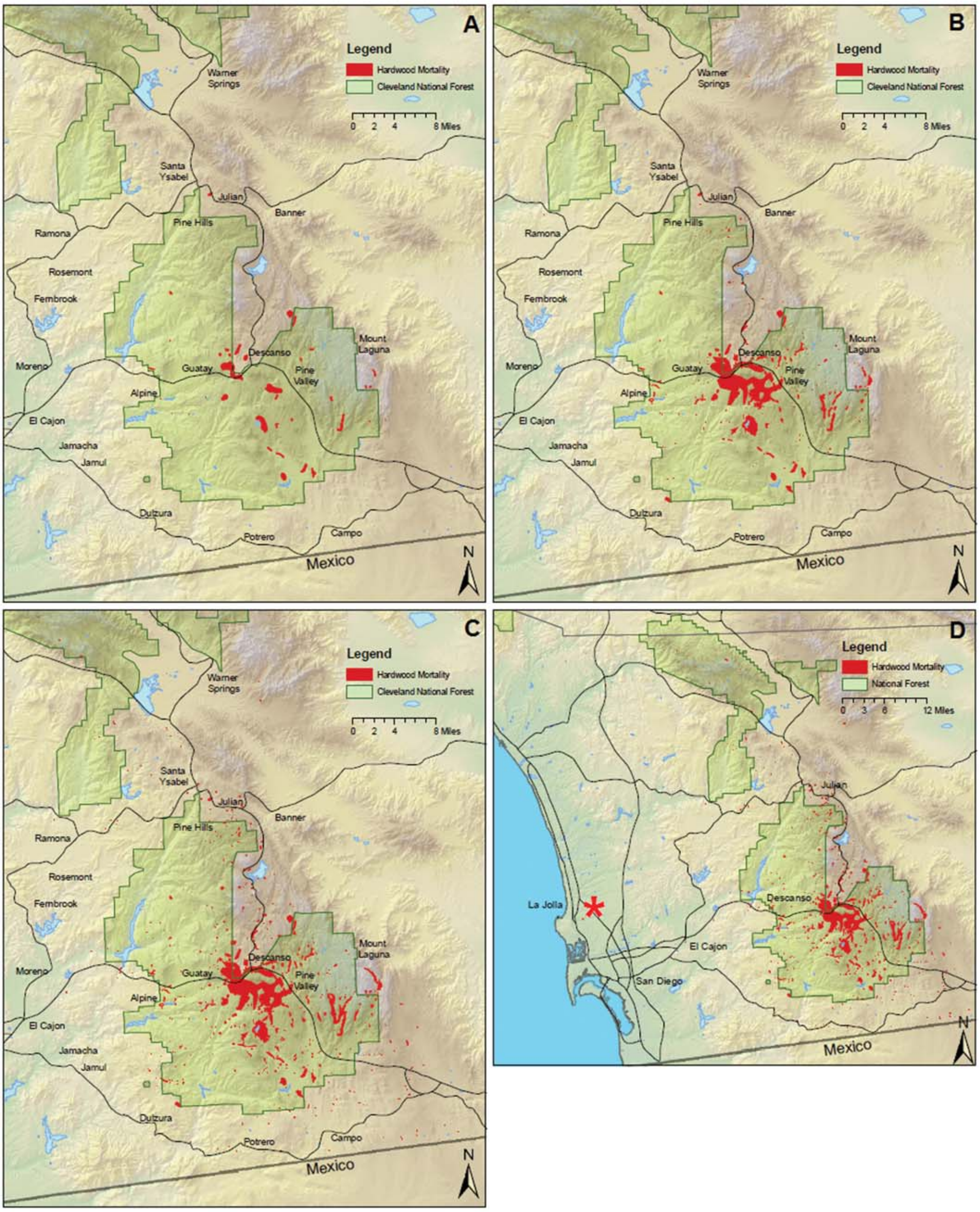


**Fig. 1.** Distibution of oak mortality (red areas) caused by the goldspotted oak borer, *Agrilus auroguttatus*, in San Diego Co., California. A) 2002 to 2004, B) 2002 to 2007, C) 2002 to 2010. This area ranges from 32°42′09.90″N, 116°20′34.67″W to 32°49′41.60″N, 116°51′30.33″W to 32°36′31.45″N, 116°28′06.77″W to 33°11′58.64″N, 116°42′37.96″W. Location of satellite infestation (southwest of red * in map D) found in 2009 is Marion Bear Memorial Park near La Jolla.

Park near La Jolla, CA, on the edge of metropolitan San Diego to the west of the core area (Fig. 1D). Throughout San Diego Co., drought was considered the principal cause of this tree mortality for many years, and various pathogens have been suspected, but never confirmed, as mortality agents. Tree mortality has been consistent over the past eight years and continues to spread from the area centered on the communities of Descanso, Guatay, and Pine Valley (Fig. 1A–C).

In June 2008, the goldspotted oak borer, *Agrilus coxalis* Waterhouse (Coleoptera: Buprestidae), was identified as the primary cause of this oak mortality (Coleman and Seybold 2008a, b). Hespenheide (1979) synonymized *Agrilus auroguttatus* Schaeffer (collected only in southeastern Arizona [AZ] at that time) with *Agrilus coxalis* (collected only in southern Mexico [Veracruz, Chiapas] and Guatemala at that time). However, given several morphological differences, the apparent disjunct nature of the distribution of the populations, and the morphological similarity of the specimens from the Arizona (AZ) (native) and CA (introduced) populations, Hespenheide and Bellamy (2009) assigned subspecific status to the AZ/CA (*Agrilus coxalis auroguttatus* Schaeffer) and Mexican/Guatemalan (*Agrilus coxalis coxalis* Waterhouse) populations. Most recently, Hespenheide *et al.* (2011) re-examined the species complex, and based on the male genitalia, they concluded that the AZ/CA and Mexican/Guatemalan forms do indeed comprise separate species with the original nomenclature (*A. auroguttatus* and *A. coxalis*, respectively). Westcott (2005) reported a specimen collected in southern Baja California, Mexico that is *A. auroguttatus* (Hespenheide *et al.* 2011). Life history data on any member of the species complex was absent prior to 2008 (Coleman and Seybold 2008b, 2010).

Ground surveys in 2008 established that the distribution of *A. auroguttatus* in southern CA is contiguous with the zone of tree mortality. Observations documented through these surveys provided the first records of larval habits, host association, damage, and tree mortality associated with *A. auroguttatus* (Coleman and Seybold 2008b). Symptoms of infestation are wet, dark-colored stains on the bark surface, D-shaped adult exit holes through the bark, and reduction of foliage in the tree crown (Coleman and Seybold 2008a; Coleman *et al.* 2011; Hishinuma *et al.* 2011). Bark removed by foraging acorn, *Melanerpes formicivorus* (Swainson), and Nuttall's, *Picoides nuttallii* (Gambel), woodpeckers (both Piciformes: Picidae) is also a common sign of infestation on *Q. agrifolia*.

*Agrilus auroguttatus* attacks susceptible oaks aggressively along the main stem and largest branches, favors the lower bole, and rarely injures the upper branches. No additional insect species are associated with early *A. auroguttatus* injury in CA. The abundant *A. auroguttatus* larval galleries are dark-colored and form a meandering pattern on the wood surface. The larvae feed in the phloem and primarily on the xylem surface, and as a consequence, patches of cambium are killed, branches die back, and eventually trees die after several years of continuous infestation.

*Agrilus auroguttatus* was first detected in southern CA in 2004 during an exotic wood borer survey by the California Department of Food and Agriculture (Westcott 2005). A preliminary survey of the collection history of *A. auroguttatus* and *A. coxalis* (Coleman and Seybold 2008b, 2009) revealed that *A. coxalis* was first recorded in the 1880s in Guatemala and southern Mexico, whereas *A. auroguttatus* was first recorded in the early 1900s in southeastern AZ. The species status of specimens collected in Costa Rica and Honduras remains unresolved (H.A. Hespenheide, personal communication). Thus, the species complex is native to North and Central America. Coleman and Seybold (2008b) presented two hypotheses for the newly recognized occurrence of *A. auroguttatus* in CA: 1) *A. auroguttatus* was introduced by human activity as a discrete population into southern California from its native range; or 2) *A. auroguttatus* expanded its range by natural dispersal from either AZ or Mexico (Westcott 2005).

Herein we report the results of a more intensive survey of museum collections to document the complete historical distributions of *A. auroguttatus* and *A. coxalis*. We also report on the interactions of *A. auroguttatus* with oaks in southeastern AZ to document its behavior in its native range and provide more insight into its biology and population dynamics in CA. We discuss the most probable hypothesis for its introduction into CA and emphasize the potential impact of movement of oak firewood from within the current zone of infestation as a pathway for the accelerated expansion of the population of *A. auroguttatus* in CA.

## Material and Methods

**Museum Survey.** We surveyed nine museum collections in CA and AZ and contacted three coleopterists in CA and Oregon with expertise in the Buprestidae (C.L. Bellamy, H.A. Hespenheide, and R.L. Westcott) for the holdings of *A. auroguttatus* and *A. coxalis* in their personal collections or their knowledge of holdings in other collections that we could not visit in person. Furthermore, we contacted 12 other major collections in the U.S. and Canada by e-mail for holdings of these species and reviewed the literature for other evidence of collection records. Determined and undetermined specimens of Buprestidae were surveyed in all collections that we visited in person. Label information was recorded for positively verified specimens. Data from museum collections were compiled with previously published information to determine the historical record of the *A. coxalis* complex in North and Central America.

The following museum and personal collections were included in the survey. Acronyms (all USA unless otherwise indicated) are based on Evenhuis (2010). AMNH-American Museum of Natural History, New York, NY; BMNH-The Natural History Museum, London, UK; BPBM-Bernice P. Bishop

Museum, Honolulu, HI; BYU-Provo, Brigham Young University, Monte L. Bean Life Science Museum, Provo, UT; CAS-California Academy of Sciences, San Francisco, CA; CHAH-Henry A. Hespenheide, personal collection, Los Angeles, CA; CIDA-College of Idaho, Orma J. Smith Museum of Natural History, Caldwell, ID; CLBC-Charles L. Bellamy–affiliated with CSCA; CMNC-Canadian Museum of Nature, Ottawa, Ontario, Canada; CNCI=CNC-Canadian National Collection of Insects, Ottawa, Ontario, Canada; CSCA-California State Collection of Arthropods, Sacramento, CA; EBCC-Universidad Nacional Autónoma de México, Estación Biológica Chamela, San Patricio, Jalisco, Mexico; EMEC-University of California, Essig Museum of Entomology, Berkeley, CA; FMNH-Field Museum of Natural History, Chicago, IL; FSCA- Florida State Collection of Arthropods, Gainesville, FL; GHNC- Gayle H. Nelson, personal collection, now in FSCA; LACM-Los Angeles County Museum of Natural History, Los Angeles, CA; MCZ-Museum of Comparative Zoology, Harvard University, Cambridge, MA; RHTC-Robert H. Turnbow, personal collection, Ft. Rucker, AL; RLWE-Richard L. Westcott, personal collection, Salem, OR; SBNM-Santa Barbara Museum of Natural History, Santa Barbara, CA; SDMC-San Diego Natural History Museum, San Diego, CA; TAMU-Texas A&M University, College Station, TX; UAIC- University of Arizona Insect Collection, Tucson, AZ; UCDC-University of California, The Bohart Museum of Entomology, Davis, CA; UCR-University of California-Riverside, Riverside, CA; and USNM-National Museum of Natural History, Washington, DC.

**Field Survey in Arizona.** Between December 2008 and October 2009, we conducted a ground survey of oak stands in four mountain ranges in the Coronado National Forest in southeastern AZ for recent oak mortality, in anticipation of linking mortality to the activity of *A. auroguttatus* (Fig. 2). Aerially detected hardwood mortality is not available for this region (USDA Forest Service 2010a), so comparison of long-term oak mortality between AZ and CA (*e.g.*, Fig. 1) is not possible, but oak mortality can be described as occurring at latent levels in AZ. The native oak component in these four ranges is comprised primarily of Arizona white oak, *Quercus arizonica* Sarg., Emory oak, *Quercus emoryi* Torrey, Gambel oak, *Quercus gambelii* Nutt., gray oak, *Quercus grisea* Liebm., and silverleaf oak, *Quercus hypoleucoides* A. Camus.

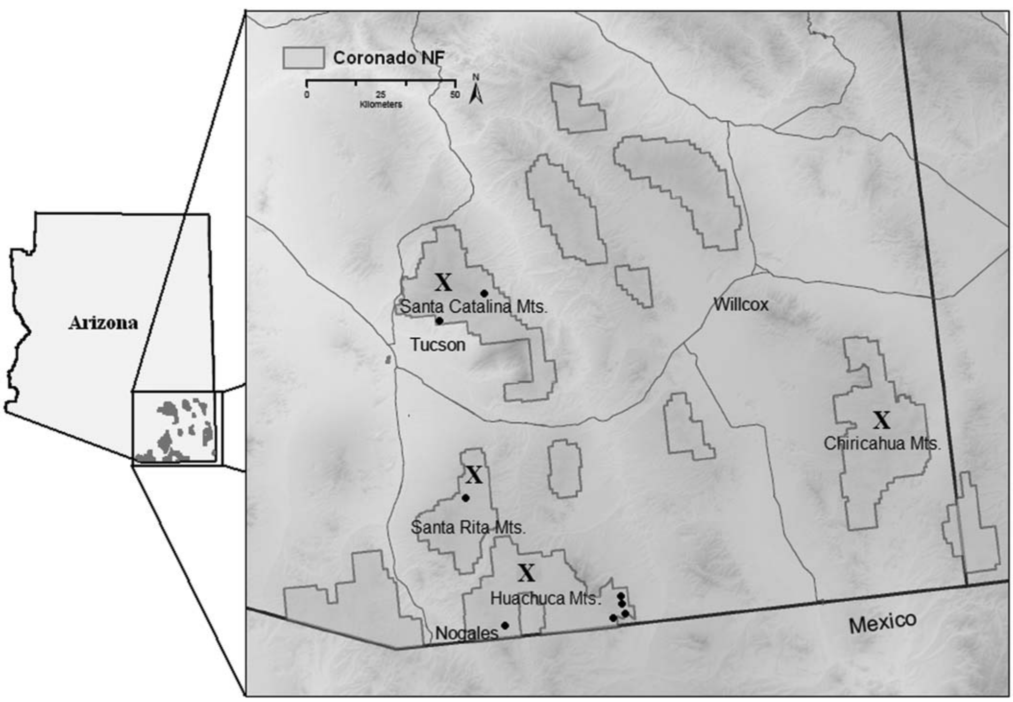


**Fig. 2.** The four mountain ranges (Santa Catalina, Santa Rita, Huachuca, and Chiricahua) in the Coronado National Forest in southeastern Arizona where historical collections of *Agrilus auroguttatus* were made. General localities (**X**) are noted on the four mountain ranges, but a few exact localities (●) were available from collection labels.

Arizona white oak, Emory oak, gray oak, and silverleaf oak are commonly found interspersed in the same forest stands at lower elevations (1,372–1,981 m), whereas Gambel oak is restricted primarily to higher elevations (1,981–2,438 m).

**Field Survey in California.** Between 2008 and 2010, we reared or hand-sampled *A. auroguttatus* and associated insects from logs of *Q. agrifolia* or *Q. kelloggii*, from standing trees in the Descanso Ranger District of the Cleveland National Forest or in William Heise County Park, Julian, CA. Between January and April 2010, recently killed *Q. agrifolia* were felled and logs were collected at Heise Park. Logs from the lower portion of the main stems from infested trees were quartered and placed into 1.8 × 1.8 m laboratory rearing cages (BioQuip, Gardena, CA). Cages were monitored for insect emergence from April to September 2010. The main stems of heavily infested and recently killed *Q. agrifolia* and *Q. kelloggii* were sampled by removing the outer bark and exposing the phloem at multiple locations in the Descanso Ranger District (Pine Creek Trailhead, Noble Canyon Trailhead, Glencliff Fire Station, Wooded Hills Campground, Pine Valley community, Descanso Ranger Station, and Laguna Mountain Recreation Area) and Heise Park. *Agrilus auroguttatus* and other insects were sampled from the standing trees from larval galleries and pupal cells of *A. auroguttatus*.

## Results

**Museum Survey.** A total of 78 specimens (37 *A. coxalis* and 41 *A. auroguttatus*) collected prior to 2008 were recorded from museum collections and the literature (Table 1). The first collection of *A. auroguttatus* in CA is still represented by three adults collected in 2004 from San Diego Co. The museum survey revealed several new collections from Mexican states and U.S. mountain ranges, but no new records from Guatemalan departments when compared to previously reported localities (Waterhouse 1889; Schaeffer 1905; Fisher 1928; Hespenheide 1979; Westcott 2005; Coleman and Seybold 2008b; Hespenheide and Bellamy 2009). The new Mexican state records include one record of *A. coxalis* from Jalisco (Tuito, FSCA) and two records of *A. coxalis* from Tamaulipas (Santa Engracia, FMNH and Tula, USNM). The new U.S. records include four records of *A. auroguttatus* from the Chiricahua Mountains of AZ (CAS, FMNH-3) and two records of *A. auroguttatus* from the Santa Catalina Mountains of AZ (FSCA, UAIC). The two new Mexican state records represent a significant northward extension of the range of what we assume is *A. coxalis* on the Mexican mainland. There were no records of *A. auroguttatus* from Sonora or Chihuahua, immediately south of southeastern AZ.

The survey confirmed that *A. auroguttatus* occurs in the Chiricahua Mountains of AZ (Cochise Co.) with one specimen collected in 1908 (CAS, Van Dyke personal collection) and several series of specimens collected between the early 1900s and 1957 (FMNH, J.N. Knull, personal collection). The collections from the Santa Catalina Mountains from Upper Bear Canyon (1965 and 1968) represent a new record for this mountain range, and the most northern collection in southeastern AZ (Pima Co.). Besides the Chiricahua and Santa Catalina Mountains, *A. auroguttatus* has been frequently collected from various canyons in two other mountain ranges of southeastern AZ (Huachuca and Santa Rita, Fig. 2). Thus, it is known from three counties in AZ (Cochise, Pima, and Santa Cruz Cos., primarily localities in the Coronado National Forest) and one county in CA (San Diego Co.); *A. coxalis* has been collected from nine states in Mexico and at least four departments in Guatemala. No specimens of *A. auroguttatus* or *A. coxalis* were found in any of the undetermined holdings from the collections in the survey. Two female specimens from the Honduran department of Olancho (FSCA) were also noted in the survey. They are likely *A. coxalis*, but future collection of males from this locality will be necessary to determine their relationship with Costa Rican specimens, which may represent a separate undescribed species (H. A. Hespenheide, personal communication).

**Field Survey in Arizona.** During the detection survey, we observed D-shaped exit holes, meandering dark-colored larval galleries on the xylem surface, and pupal cells in the outer bark of several individuals of *Q. emoryi* and *Q. hypoleucoides* in canyons where historic collections of *A. auroguttatus* were made (*e.g.*, Madera Canyon, Santa Rita Mountains, Pima and Santa Cruz Cos.; Miller and Carr Canyons, Huachuca Mountains, Cochise Co.; Pinery and Rucker Canyons, Chiricahua Mountains, Cochise Co.; and Willow Canyon, Santa Catalina Mountains, Pima Co., Fig. 2, Table 2). Injury symptoms were similar to those discussed by Coleman and Seybold (2008b). Callus tissue was also observed around and over the galleries. For example, in February 2009, late instar *Agrilus* were collected from the outer bark of one specimen of *Q. emoryi* (61 cm diameter at breast height, DBH, and approximately 30 m tall) that had died recently at Box Canyon in the Santa Rita Mountains (Pima Co.). The tree showed no signs of visible external injury or pathogen infection, and had likely died as a consequence of infestation by *A. auroguttatus* (*i.e.*, there was no evidence of any predisposing factors). The larvae from this original collection did not complete development, so we could not verify the species at that time, but we suspected that it was *A. auroguttatus*. We visited the

**Table 1.** Chronological presentation of records for *Agrilus coxalis* and *Agrilus auroguttatus* from a survey of museum collections and the literature.

| Date | Locality | Collection | Site Description | Notes/Comments/Collector |
|---|---|---|---|---|
| ***Agrilus coxalis*** | | | | |
| undated | Juquila, Mexico | BMNH | | From Waterhouse (1889); Hespenheide (1979), lectotype |
| undated | Córdova, Mexico | BMNH | | From Waterhouse (1889); Hespenheide (1979), paratype |
| undated | Capetillo (Sacatepéquez), Guatemala | BMNH | | From Waterhouse (1889); Hespenheide (1979), paratype |
| undated | S. Geronimo (San Jerónimo, Baja Verapaz), Guatemala | BMNH | | From Waterhouse (1889); Hespenheide (1979), paratype |
| III-21-1939 | Tamaulipas, Mexico | FMNH | Santa Engracia | From J.N. Knull personal collection† |
| VII-5-1956 | Chiapas, Mexico | EMEC | 8.1 km SE San Cristobal de las Casas | G.H. Nelson |
| VII-5-1956 | Chiapas, Mexico | FSCA | 5 km SE San Cristobal de las Casas | D.D. Linsdale |
| VII-13-1965 | Chiapas, Mexico | GHNC | 3.2 km NW Pueblo Nuevo, LLU Bio. Station | |
| VII-13-1965 | Chiapas, Mexico | FSCA | 21 km NW of Pueblo Nuevo, LLU Bio. Station | G.H. Nelson |
| V-11-12-1969 | Chiapas, Mexico | CMNC | 16.1 km E Teopisca | H.F. Howden (Hespenheide and Bellamy 2009) |
| V-14-1969 | Chiapas, Mexico | CMNC | 25.8 km E Teopisca | H.F. Howden |
| V-17-1969 | Chiapas, Mexico | CMNC | 12.9 km NE San Cristobal de las Casas | H.F. Howden |
| V-26-1969 | Chiapas, Mexico | CNCI | 6.4 km SE San Cristobal | J.M. Campbell |
| V-30-1969 | Chiapas, Mexico | CNCI | Laguna Montebello Parq. Nat., 1524 m elev. | In Malaise trap |
| VI-8-1969 | Chiapas, Mexico | CNCI | 4.8 km NE San Cristobal | B.V. Peterson |
| VI-5-1974 | Chiapas, Mexico | CLBC | 11.3 km SE Teopisca | C.W. and L.B. O'Brien and G.B. Marshall |
| VII-19-1981 | Veracruz, Mexico | EMEC | Jalapa, Veracruz | C. Gold |
| VII-3-5-1986 | Chiapas, Mexico | CHAH | San Cristobal de las Casas, vic. El Chivero, 2438 m elev. | E. Giesbert (Hespenheide and Bellamy 2009) |
| V-25-1987 | Chiapas, Mexico | CLBC | 11 km NE San Cristobal de las Casas | E.G. and T.J. Riley and D.A. Rider |
| VI-3-6-1989 | Zacapa, Guatemala | CHAH | 12–14 km S San Lorenzo, 305–610 m | E. Giesbert (Hespenheide and Bellamy 2009) |
| IX-28-1989 | Chiapas, Mexico | CSCA | 10 km E San Cristobal de las Casas | R.L. Penrose |
| VI-20-1990 | Chiapas, Mexico | RHTC | 30 km W Comitán | R.L. Turnbow |
| VI-21-1990 | Chiapas, Mexico | FSCA | Laguna Montebello Parq. Nat., 1524 m elev. | M. C. Thomas |
| VII-15-1990 | Jalisco, Mexico | FSCA | 12 km NW Tuito | J. E. Wappes |
| VII-25-30-1990 | Chiapas, Mexico | TAMU | Municipio San Cristobal San Felipe, 2194 m elev. | R.W. Jones from Malaise trap |
| IX-1-1990 | Chiapas, Mexico | EBCC | 16 km SO Ocosingo | F.A. Noguera |
| V-24-1991 | Chilasco, Baja Verapaz, Guatemala | CMNC | 7.8 km W Chilasco, 1700 m elev. | H. and A. Howden |
| VI-10-1991 | Zacapa, Guatemala | FSCA | San Lorenzo Rd, 1524–1818 m elev. | J. E. Wappes, 5 specimens |
| VI-10-15-1991 | San Lorenzo, San Marcos, Guatemala | CHAH | vic. San Lorenzo, 1768 m | E. Giesbert (Hespenheide and Bellamy 2009) |
| V-10-1994 | Tamaulipas, Mexico | USNM | 16.1 km E Tula, 1189 m elev. | Oak forest; J.E. Wappes |
| VII-5-2001 | Oaxaca, Mexico | RLWE | 10 km E Mitla, 1890 m elev. | Beating oak |

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**Table 1.** Continued.

| Date | Locality | Collection | Site Description | Notes/Comments/Collector |
|---|---|---|---|---|
| ***Agrilus coxalis*** | | | | |
| V-23-2002 | Olancho, Honduras | FSCA | Montaña del Malacate | R. Turnbow, 2 female specimens |
| ***Agrilus auroguttatus*** | | | | |
| undated | Cochise Co., AZ | MCZ | Palmerlee | |
| undated | AZ | FMNH | Huachuca Mts. | From J.N. Knull personal collection†, 2 specimens, Chas. Schaeffer co-types |
| VI-16 | Cochise Co., AZ | FMNH | Palmerlee, Huachuca Mts. | From J.N. Knull personal collection†, determined by C. Schaeffer |
| VII-26 | AZ | CAS | Santa Rita Mts. | From Chamberlain personal collection†; Also in Fisher (1928) |
| VII-26 | Cochise Co., AZ | CAS | Palmerly | From Chamberlain personal collection†; catalog #231, paratype |
| VIII-4 | Cochise Co., AZ | | Rams (Ramsey) Cn., Huachuca Mts. | From Fisher (1928); C. Schaeffer personal collection |
| VIII-15 | Cochise Co., AZ | | Palmerlee, Miller Cn., Huachuca Mts. | From Fisher (1928); C. Schaeffer personal collection |
| IX-14 | AZ | FMNH | Chiricahua Mts. | From J.N. Knull personal collection† |
| VIII-2-1905 | AZ | AMNH | Huachuca Mts. | "R.C." [Ramsey Canyon] |
| VIII-4-1905 | Cochise Co., AZ | USNM | Palmerlee, Miller Cn., Huachuca Mts. | From C. Schaeffer personal collection, 3 specimens, including 1 cotype†, Also noted in Schaeffer (1905), beating black oak branches§ |
| VII-22-1907 | AZ | OSU | Miller Canyon, Huachuca Mts. | H.A. Kaeber |
| VIII-10-1908 | AZ | CAS | Chiricahua Mts. | From Van Dyke personal collection† |
| VIII-15-1940 | Pima Co., AZ | CAS | Madera Cn. Foothills, Santa Rita Mts. | Donated 1962† |
| VII-12-1950 | AZ | FMNH | Huachuca Mts. | From J.N. Knull personal collection†, 3 specimens, including 1 collected on VII-19-1950 |
| VII-15-1953 | AZ | FMNH | Chiricahua Mts. | From J.N. Knull personal collection†, 2 specimens |
| VII-17-1957 | AZ | FMNH | Chiricahua Mts. | From J.N. Knull personal collection†, 4 specimens |
| VI-17-1963 | Santa Cruz Co., AZ | CIDA | Santa Rita Mountains, Madera Canyon, 1706 m | |
| VII-24-1965 | Pima Co., AZ | UAIC | Upper Bear Canyon, Santa Catalina Mts. | † |
| VII-6-1968 | Pima Co., AZ | FSCA | Bear Canyon, Santa Catalina Mts. | K. Stephan, det. J.N. Knull |
| VII-20-1969 | Cochise Co., AZ | FSCA | Carr Canyon, Huachuca Mts. | G.H. & D.E. Nelson |
| VI-12-1975 | Santa Cruz Co., AZ | FSCA | Washington Camp, T23S, R16E, S35, Canelo Hills/Patagonia Mts. (W of Huachuca Mts.) | K. Stephan, 2 specimens, det. G.H. Nelson |
| VIII-30-31-1977 | Baja California Sur, Mexico | RLWE | Sa. Victoria, Sierra de La Laguna, trail W of La Laguna, 1830 m elev. | 1 male specimen, beating *Quercus* sp.; Also in Westcott (2005) |

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**Table 1.** Continued.

| Date | Locality | Collection | Site Description | Notes/Comments/Collector |
|---|---|---|---|---|
| ***Agrilus auroguttatus*** | | | | |
| VII-21-2000 | Cochise Co., AZ | FSCA | Copper Canyon, 1850 m elev., Montezuma Canyon Rd, 31°21′45″N 110°18′01″W, Huachuca Mts. | D. Yanega, det. G.H. Nelson, UCRC ENT 40897 |
| VI-18 to VII-18, VII-19 to VIII-19-2003 | Santa Cruz Co., AZ | CHAH | Upper Madera Canyon | F.T. Hovore, I.P. Swift (Hespenheide and Bellamy, 2009) |
| VII-16-30-2004 | San Diego Co., CA | CSCA | Paco Picacho Campground, Cuyamaca State Park | Also in Westcott (2005), 2 specimens |
| VI-18-2004 | San Diego Co., CA | CSCA | Chamber Park, Cuyamaca State Park | Also in Westcott (2005) |
| VI-20 to VII-21-2005 | Cochise Co, AZ | CHAH | Carr Canyon, 1981 m | F.T. Hovore, at bait (Hespenheide and Bellamy 2009) |
| VII-24-2006 | San Diego Co., CA | CSCA | Julian, 4945 Heise Park Road | Funnel trap catch with exotic *Ips* lure |
| VI-27-2008 | San Diego Co., CA | CAS | Noble Canyon Trailhead, Cleveland NF | T.W. Coleman, purple flight intercept traps near *Quercus agrifolia* |
| | No holdings | BPBM | | Surveyed March 2009 |
| | No holdings | BYU | | Surveyed March 2009 and April 2010 |
| | No holdings | LACM | | Surveyed Dec. 2008 |
| | No holdings | SBNM | | Surveyed Jan. 2009 |
| | No holdings | SDMC | | Surveyed Dec. 2008 |
| | No holdings | UCDC | | Surveyed Nov. 2008 |
| | No holdings | UCR | | Surveyed Dec. 2008 |

† These specimens were accessioned under *A. auroguttatus*.
§ Another specimen from this series is accessioned in the MCZ. This single undated specimen (collected by C. Schaeffer) was from the H.C. Fall collection.

same tree on 1–2 May 2009, when additional *Agrilus* larvae and pupae were collected (Table 2). The outer bark of the tree from the root collar to ~1.5 m above the forest floor was removed, collected, and returned to the laboratory. These bark samples were placed in emergence cages and monitored daily.

As a second example, in October 2009, we collected late instar *Agrilus* in pre-pupal behavior in the outer bark of a recently dead specimen of *Q. hypoleucoides* in Miller Canyon, Huachuca Mountains (Cochise Co.). This tree also had similar injury symptoms and larval gallery patterns to those created by *A. auroguttatus* in CA. No evidence of occurrence of *A. auroguttatus* was noted on any of the "white" oak species observed in southeastern AZ (*i.e.*, *Q. arizonica* or *Q. grisea*).

*Agrilus auroguttatus* was the only phloem/wood borer that emerged from bark samples collected in AZ. A total of 104 adult *A. auroguttatus* were reared from *Q. emoryi* bark samples collected in May 2009 from Box Canyon. No adults were reared from *Q. hypoleucoides* bark samples. In the laboratory, emergence began 13 May and continued until 2 June. Peak emergence for *A. auroguttatus* in the laboratory occurred on 16 May with 16 adults.

Of the 27 *A. auroguttatus* larvae and pupae that we observed in the bark exterior when we took the samples, four were parasitized (15% parasitism rate). A total of 18 parasitoid larvae were found feeding externally in aggregation on the four *A. auroguttatus* larvae (Table 3). One of these parasitoids completed development on 3 June 2009, and was described by G. A. P. Gibson (Canadian National Collection of Insects, Agriculture and Agri-Food Canada) as *Calosota elongata* Gibson (Hymenoptera: Eupelmidae) (Gibson 2010). Additional adult specimens of *C. elongata* were collected on 6 July (4 specimens), 7 July (3 specimens), 12 July (2 specimens), 13 July (2 specimens), and 14 July, 2009 (1 specimen). These specimens of *C. elongata* were all female except for one. Seven (six females, one male) additional specimens were collected from the rearing cages when they were dismantled in October 2009. A larger parasitoid (6 adults) also emerged from the bark samples. Its emergence preceded that of *A. auroguttatus* and began on 6 May 2009; the last adult wasp of

**Table 2.** Survey locations in southeastern Arizona for oak mortality and activity of *Agrilus auroguttatus*.

| Date | Locality | County | GPS Coordinates | Notes/Comments |
|---|---|---|---|---|
| XII-2008 | Madera Canyon, Santa Rita Mountains | Santa Cruz | N 31.71475° W 110.87559° | *A. auroguttatus* injury signs and pupal cells in outer bark on *Q. hypoleucoides* (61.9 cm DBH†) |
| II-2009 | Box Canyon, Santa Rita Mountains | Pima | N 31.79961° W 110.75921° | *A. auroguttatus* injury signs and *Agrilus* sp. larvae in outer bark on *Q. emoryi*, (61.2 cm DBH) |
| II-2009 | Carr Canyon, Huachuca Mountains | Cochise | N 31.44535° W 110.28618° | D-shaped exit holes and bark staining on *Q. hypoleucoides* |
| V-2009 | Box Canyon, Santa Rita Mountains | Pima | N 31.79961° W 110.75921° | Injury signs, *Agrilus* sp. larvae, and parasitoids observed in outer bark on *Q. emoryi* (61.2 cm DBH) |
| IX-2009 | Miller Canyon, Huachuca Mountains | Cochise | N 31.742687° W 110.25411° | Larval galleries and *Agrilus* sp. larvae in outer bark of *Q. emoryi* (73.2 cm DBH) |
| IX-2009 | Rucker Canyon, Chiricahua Mountains | Cochise | N 31.74999° W 109.39748° | Two recently killed *Q. emoryi* with D-shaped exit holes (54.4 and 38.9 cm DBH) |
| IX-2009 | Chiricahua National Monument, Chiricahua Mountains | Cochise | N 31.00854° W 109.38030° | Three recently killed *Q. emoryi* with D-shaped exit holes and *Agrilus* sp. larvae (73.4, 52.1, and 73.0 cm DBH) |
| IX-2009 | Pinery Canyon, Chiricahua Mountains | Cochise | N 31.97136° W 109.34537° | Recently killed *Q. emoryi* with D-shaped exit holes (60.2 cm DBH) |
| X-2009 | Miller Canyon, Huachuca Mountains | Cochise | N 31.41660° W 110.27461° | D-shaped exit holes, bark staining, and *Agrilus* sp. larva in outer bark on *Q. hypoleucoides* (61.2 cm DBH) |
| X-2009 | Willow Canyon, Santa Catalina Mountains | Pima | N 32.43441° W 110.75285° | Injury signs and *Agrilus* sp. larvae in outer bark on *Q. emoryi* (37.6 cm DBH) |

† DBH, tree diameter at breast height, measured at 1.47 m.

this taxon emerged 18 May 2009. This species was identified as *Atanycolus simplex* Cresson (Hymenoptera: Braconidae) by Michael J. Sharkey (Department of Entomology, University of Kentucky). Four adult specimens of *Temnochila* Erichson sp. (Trogossitidae), potential predators, were also collected when the emergence cages were dismantled. During surveys in October 2009, larvae of Trogossitidae and Elateridae were also recovered from beneath the bark of *A. auroguttatus*-infested *Q. emoryi* that had died recently in the Huachuca and Chiricahua Mountain Ranges. Each larva was recovered from *A. auroguttatus* larval galleries or pupal cells in the outer bark.

**Field Observations in California.** Since the original biological observations of *A. auroguttatus* in CA were reported (Coleman and Seybold 2008b), we report here only additional information on the host range and community of insects associated with this buprestid. In March 2010, we noted adult exit holes and meandering larval galleries on several specimens of Engelmann oak, *Quercus engelmannii* Greene, on the Descanso Ranger District of the Cleveland National Forest. However, we did not recover larvae or adults of *A. auroguttatus* from this species of white oak. We also reared several specimens of *A. simplex* from *A. auroguttatus*-infested logs from *Q. agrifolia* in CA (Table 3), but observed no larval or adult specimens of *C. elongata* in association with *A. auroguttatus* in CA. However, a snakefly larva (*Agulla* Navis, Raphidioptera: Raphidiidae) and a trogossitid larva were each encountered on one occasion while sampling for *A. auroguttatus* larvae during the dormant season on the Cleveland National Forest at the Pine Creek Trailhead (November 2009; Pine Valley, CA) and William Heise County Park (March 2010; Julian, CA), respectively. Both larvae were found in pupal cells of *A. auroguttatus* in *Q. agrifolia* (Table 3).

## Discussion

*Agrilus auroguttatus* and *A. coxalis* are native to North and Central America, and because of the absence of data on these taxa in the economic entomology literature, they appear historically to have presented no significant threat to the health of oak stands in southeastern AZ, Mexico, and Guatemala. These species have been rarely collected in their native regions over the past century. However, *A. auroguttatus* is currently ubiquitous and abundant within the zone of oak mortality in San Diego Co., CA. Oak mortality was initially

**Table 3.** Subcortical insect associates of *Agrilus auroguttatus* reared or collected from infested *Quercus emoryi* and *Quercus agrifolia* bark from survey locations in southeastern Arizona and San Diego Co., California.

| Taxon | Likely relationship to *A. auroguttatus* | Host species | Collection date, locality, and observations |
|---|---|---|---|
| *Calosota elongata* (Hymenoptera: Eupelmidae) | Parasitoid | *Q. emoryi* | V-1-2-2009; Box Canyon, AZ; found as ectoparasitoid on mature *Agrilus* sp. larvae; adult wasps reared later from bark infested with *A. auroguttatus* |
| *Atanycolus simplex* Cresson (Hymenoptera: Braconidae) | Parasitoid | *Q. emoryi* | V-1-2-2009; Box Canyon, AZ; adult wasps reared from bark infested with *A. auroguttatus* |
| | | *Q. agrifolia* | III-3-2010; W. Heise Co. Park; CA; adult wasps reared from logs infested with *A. auroguttatus* |
| (Coleoptera: Trogossitidae) | Predator | *Q. emoryi* | V-1-2-2009; Box Canyon, AZ; adult *Temnochila* sp. beetles reared from bark infested with *A. auroguttatus* |
| | | *Q. emoryi* | X-30-2009; Miller Canyon, AZ; Larval beetles collected from *A. auroguttatus* larval galleries in outer bark |
| | | *Q. agrifolia* | III-3-2010; W. Heise Co. Park, Julian, CA; Larval beetles collected from *A. auroguttatus* pupal cell in outer bark |
| (Coleoptera: Elateridae) | Predator | *Q. emoryi* | X-31-2009; Chiricahua National Monument, AZ; Larval beetles collected from *A. auroguttatus* pupal cell in outer bark |
| *Agulla* sp. (Raphidioptera) | Predator | *Q. agrifolia* | XII-30-2009; Pine Valley, CA; Larva collected from pupal cell in outer bark |

detected on the Descanso Ranger District, Cleveland National Forest and at Cuyamaca Rancho State Park, so the *A. auroguttatus* infestation is believed to have originated in the vicinity of these two areas. In 2003, the majority of oak mortality was primarily surrounding the communities of Descanso, Guatay, and Pine Valley (Fig. 1). In the following years (2004 to 2008), the zone of oak mortality expanded outward from these communities (Fig. 1). As of fall 2008, neither mortality nor infested trees were present at the U.S.-Mexican border. However, *A. auroguttatus*-infested trees along the border were detected for the first time in 2009 and infestation rates there are currently very low, suggesting a nascent infestation in this area that is spreading from the north.

Increased levels of oak mortality have not been aerially mapped further south of the U.S. and Mexican border, but the spatial pattern of infestation on the U.S. side does not support a range expansion from Mexico. We predict that oak mortality will be evident in northern Baja California, Mexico in the next few years as the infestation spreads south from San Diego Co. Confirmed oak hosts for *A. auroguttatus* in California have limited distributions in northern Baja California, and do not extend much farther east in San Diego Co. The Mojave and Sonoran Deserts extend from southern Nevada to Sinaloa, Mexico and are dominated primarily by annual species and low shrubs, such as creosote bush, *Larrea tridentata* (Sessé and Moc. ex DC.) Coville (Zygophyllaceae), and white bursage, *Ambrosia dumosa* (A. Gray) Payne (Asteraceae) (Shreve and Wiggins 1964). Thus, these deserts geographically isolate the oak hosts, and isolate the population of *A. auroguttatus* in CA from the native *A. auroguttatus* populations in southeastern AZ. Because the zone of tree mortality is isolated by the Mohave and Sonoran Deserts to the east and by a band of healthy host type to the south and southeast, and because initial tree mortality was mapped away from the border, we conclude that the hypothesis of continuous range expansion by natural dispersal into CA from AZ and/or Mexico is extremely unlikely. The recent recognition (Hespenheide and Bellamy 2009, Hespenheide *et al.* 2011) that the CA population is similar morphologically to the AZ population suggests that the tree-killing population of *A. auroguttatus* in CA originated from AZ. Molecular genetic analyses of these populations are underway to test this hypothesis. The lone collection record of *A. auroguttatus* in 1977 from southern Baja California (Westcott 2005, Table 1) suggests that either a second introduction has occurred there or that the native range of *A. auroguttatus* may extend southward in a dispersed fashion into central Mexico on both the Baja Peninsula and the mainland.

Native hosts of *A. auroguttatus* have limited distributions in southeastern AZ and in New Mexico. The native U.S. ranges of *Q. emoryi* and *Q. hypoleucoides* are restricted to the southern edge of the Mogollon Rim that bisects AZ and southwestern New Mexico (USDA Forest Service 2009). The isolated distributions of these oak species may limit the northern edge of the range of *A. auroguttatus* in AZ. *Quercus emoryi* and *Q. hypoleucoides* are also found on several additional mountain ranges in the Coronado National Forest (Dragoon, Galiuro, and Pinaleno) and in southwestern New Mexico, and the distributions of these two oaks also extend south into the northern states of Mexico (Sonora and Chihuahua). Although no collections of *A. auroguttatus* have been reported from Mexico immediately south of southeastern AZ or from New Mexico immediately east, we suspect that populations may be present in these similar oak savanna habitats. Thus, we speculate that *A. auroguttatus* is also native to northern Mexico and New Mexico, and further surveys and collecting will be necessary to confirm this hypothesis.

The origin and population dynamics of the CA population of *A. auroguttatus* are topics of intense interest. We hypothesize that *A. auroguttatus* was introduced into southern CA during the last 10–15 years as a consequence of importation on oak firewood. Firewood movement into southern San Diego Co. from unknown regions within Mexico was reported to have occurred for the last 20 years, and the southern CA zone of tree mortality is a relatively short automobile trip via U.S. Interstate 8 from the oak forests of southeastern AZ (Coleman and Seybold 2008b). Infested firewood could have been imported from southern Baja California, Sonora, or Chihuahua, Mexico, or through vacation traffic from AZ. Firewood movement has been implicated in the transportation of other woodboring tree pests including the emerald ash borer, *Agrilus planipennis* Fairmaire (Petrice and Haack 2006; Haack *et al.* 2010), and continues to be a potential threat for moving *A. auroguttatus* within CA.

Because the long-term drought regime and other climatic factors appear to have been similar in both San Diego Co. and southeastern AZ (NOAA 2009), it appears that biotic factors (natural enemies, interspecific competitors, host resistance) may play a greater role in explaining the outbreak in CA and the relatively quiescent level of tree mortality that we noted in southeastern AZ. Both the enemy release and biotic resistance hypotheses have been widely debated as explanations for the successful establishment of invasive species, particularly for invasive plants (Maron and Vilà 2001; Keane and Crawley 2002; Colautti *et al.* 2004).

The near absence of a diverse and coevolved natural enemy complex for *A. auroguttatus* in CA and the initial discovery and prevalence of *C. elongata* in AZ (Gibson 2010) support the hypothesis that the invasive population was introduced and may explain, in part, the eruptive behavior of the population in CA. Other eupelmids are known to be parasitoids of wood borers, bark beetles, and gall wasps, and similar parasitism levels (18%) were found for larvae of the native bronze birch borer, *Agrilus anxius* Gory, in areas of the U.S. and Canada (Katovich *et al.* 2000). Thus, *C. elongata* may contribute significantly to *A. auroguttatus* mortality and provide some natural regulation of its host's population in southeastern AZ. It may also show promise as a biological control agent in CA. *Calosota elongata* populations were discovered in December 2010 with *A. auroguttatus* in the Cleveland National Forest, Descanso Ranger District (L. J. Haavik, unpublished data). However, the distribution of this parasitoid appears limited when compared to the expansion of *A. auroguttatus* in CA and the infestation rate is much lower than what was determined in AZ. Molecular genetic analyses of the populations of *C. elongata* are also underway in hopes of associating the population sources of the herbivore and parasitoid. Additional research is needed to assess the host specificity and prevalence of *C. elongata* in AZ.

*Atanycolus simplex* has a broad distribution in the U.S. and has been associated with *A. planipennis*, the twolined chestnut borer, *Agrilus bilineatus* (Weber), the elm borer, *Saperda tridentata* Olivier (Cerambycidae), and various other buprestid and cerambycid species (Quicke and Sharkey 1989; Krischik and Davidson 2007; USDA Forest Service 2010b). *Atanycolus simplex* has also been associated with the oak cordwood borer, *Xylotrechus nauticus* (Mannerheim) (Cerambycidae) (Linsley 1964), which emerges frequently from hardwoods throughout CA. Although the single record of *A. simplex* from *A. auroguttatus*-infested *Q. agrifolia* collected in CA (Table 3) could have been associated with *X. nauticus*, which often also develops in logs such as these, our experience with rearing *A. simplex* from outer bark of *Q. emoryi* infested with *A. auroguttatus* from Pima Co. AZ suggests that *A. simplex* probably parasitizes *A. auroguttatus* in CA as well. This braconid appears to have a wider host range and, because of this lack of host specificity, may not be as suitable as *C. elongata* for augmentative release as a potential biological control agent for *A. auroguttatus* in CA.

Our survey did not reveal any evidence for egg parasitism, so we are not aware if there are any potential differences between AZ and CA. Egg parasitoids are important regulators of populations of other subcortical forest insects. For example, egg parasitism levels of 50% have been reported for *A. anxius* (Carlson and Knight 1969), and the egg parasitoid *Avetianella longoi* Siscaro (Hymenoptera: Encyrtidae) has been reported to have a profound impact on the population density of the eucalyptus longhorned beetle, *Phoracantha semipunctata* (F.)

(Cerambycidae) (Luhring *et al.* 2004). Therefore, more intensive surveys for egg parasitoids of *A. auroguttatus* are needed in both CA and southeastern AZ.

Predators such as bark gnawing beetles (Trogossitidae) and click beetles (Elateridae) may also contribute to the natural regulation of *A. auroguttatus* populations in AZ. A trogossitid and a snakefly larva were both also observed in association with *A. auroguttatus* in CA. Snakeflies and bark gnawing beetles are generalist predators and commonly prey on bark and wood-boring beetles of pines and hardwoods in the western U.S. (Furniss and Carolin 1977).

Differences in interspecific competition may also play a role in the comparative population dynamics of *A. auroguttatus* in CA and AZ. Evans and Hogue (2004) characterize the patterns of distribution of Coleoptera in CA as influenced by three basic regional faunas: Vancouveran, Southern Sonoran, and Californian. Probably the most relevant regional faunal influence for the biogeography of *Agrilus* in CA is the Southern Sonoran fauna, which connects the fauna of CA with AZ and northwestern Mexico. Certainly, this is the most relevant when we consider the status of *A. auroguttatus* in CA. Although the Sonoran faunal elements expanded their ranges northward into CA during the past 10,000 years (Evans and Hogue 2004), apparently CA's *Agrilus* fauna did not partake in this range expansion. The *Agrilus* fauna of CA is relatively depauperate (H. Hespenheide, personal communication), whereas AZ's fauna is relatively rich. Although we did not encounter them in our survey, in the Chiricahua Mountains, eight species of *Agrilus* (*Agrilus abditus* Horn, *Agrilus asperulus* Waterhouse, *Agrilus chiricahuae* Fisher, *Agrilus geronimoi* Knull, *Agrilus palmerleei* Knull, *Agrilus quercicola* Fisher, *Agrilus quercus* Schaeffer, and *Agrilus waltersi* Nelson) have been collected as adults in association with *Quercus* L., and *Agrilus parkeri* Knull has been reared from *Q. hypoleucoides* (H. Hespenheide, personal communication). There are also species of *Chrysobothris* (Solier) (Buprestidae) in AZ on oaks that are not present in CA (H. Hespenheide, personal communication). Presumably, some of these would be competitors with *A. auroguttatus* in AZ if they colonized the same portion of the tree. In CA, the subcortical community of herbivores associated with *A. auroguttatus* includes oak bark beetles, *Pseudopityophthorus* Swaine spp., oak ambrosia beetles, *Monarthrum* Kirsch spp., (both Curculionidae: Scolytinae), the lead cable borer, *Scobicia declivis* LeConte (Bostrichidae), *X. nauticus*, and *Phymatodes* Mulsant spp. (Cerambycidae) (Coleman and Seybold 2008b), as well as *Chrysobothris femorata* (Olivier) and *Chrysobothris wintu* Wellso and Manley (Swiecki and Bernhardt 2006; Wellso and Manley 2007). These species generally colonize oaks after larvae of *A. auroguttatus* have been well established in the phloem. Thus, in CA there appears to be limited interspecific competition for this niche, whereas in southeastern AZ there is the potential for a wider range of subcortical competitors.

Our preliminary observations in CA suggest that *A. auroguttatus* tends to prefer coast live oak and California black oak (both "red" oaks, subgenus *Quercus*, section *Lobatae* [Nixon 1993; Manos *et al.* 1999]) more than canyon live oak (an intermediate oak species, *i.e.*, neither a red nor a white oak, subgenus *Quercus*, section *Protobalanus*) (Coleman and Seybold 2009). Until recently, we had not recorded any observations of injury by *A. auroguttatus* to Engelmann oak, which is a white oak species (subgenus *Quercus*, section *Quercus*) with a limited distribution in southern CA. We attribute the rarity and opportunistic colonization of the non-preferred host *Q. engelmannii* by *A. auroguttatus* to the extremely high population density of the beetle in San Diego Co. Two other red oaks in AZ, *Q. emoryi* and *Q. hypoleucoides*, are likely native hosts for *A. auroguttatus*, but we found no evidence that the AZ white oaks, *Q. arizonica* and *Q. grisea*, are colonized by *A. auroguttatus* or any phloem- or wood-boring buprestids.

We hypothesize that phloem thickness, bark structure, and/or host chemistry may influence susceptibility to *A. auroguttatus*. Red oaks in CA or their progenitors may have had a limited coevolutionary relationship with *A. auroguttatus* and related species, thus rendering them more susceptible to the buprestid than the red oaks in southeastern AZ, whose longer association with *A. auroguttatus*, and specific bark characteristics and chemistry, may provide some measure of host resistance. White oaks in both CA and AZ appear to have higher levels of host resistance, perhaps associated with their fibrous, furrowed bark and thin phloem (vs. thick, spongy phloem in red oaks). In CA, two additional native red oak species, Shreve oak, *Quercus parvula* Greene var. *shrevei* (C.H. Mull.) Nixon, and interior live oak, *Quercus wislizenii* A. DC, which grow farther north in the state, may also be susceptible to colonization and injury by *A. auroguttatus*. Two other oaks in CA that are likely to have a more distant coevolutionary relationship with *A. auroguttatus* are the adventive white oak species, Holm (= Holly) oak, *Quercus ilex* L., and cork oak, *Quercus suber* L. These are European species that are widely planted as ornamentals in urban areas of southern CA and the Central Valley. Additional observations and experiments on the physiological host range of *A. auroguttatus* are needed to test these hypotheses.

*Agrilus auroguttatus* is an intracontinental invasive species that has come to CA. Although it originates from the same continent as the area of introduction, it is native to a different, but parallel, ecosystem in a different geographic region (concept summarized in Dodds *et al.* [2010]). We hypothesize that this non-native species is feeding on new hosts in CA with limited host resistance, filling a vacant niche, and perhaps has a limited ensemble of coevolved insect natural enemies, which would ordinarily regulate the herbivore population. Similarly, in 2003, the soapberry borer, *Agrilus prionurus* Chevrolat, was first associated with mortality of high-value western soapberry, *Sapindus saponaria* var. *drummondii* (Hook. and Arn.) L. D. Benson (Sapindaceae), in Bastrop Co., Texas, and it has since spread to additional counties within the state (Billings and Pase 2008). *Agrilus prionurus* has also been rarely collected in its native region of Mexico and very little is known about its biology. Other examples of subcortical intracontinental invasive species in the U.S. are the bronze birch borer (Carlos *et al.* 2002), the locust borer, *Megacyllene robiniae* (Forster) (Cerambycidae) (Galford 1984), the longhorned beetle *Neospondylis upiformis* (Mannerheim) (Cerambycidae) (Smith and Hurley 2005), the sixspined ips, *Ips calligraphus* (Germar) (Wood and Stark 1968) and the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (both Scolytinae) (Dodds *et al.* 2010), and the Nantucket pine tip moth, *Rhyacionia frustrana* (Scudder) (Tortricidae) (Yates *et al.* 1981). As international examples, the fir bark beetle, *Polygraphus proximus* Blandford (Scolytinae), has been reported as newly invasive in western Eurasia from its native distribution in the eastern region of the continent (Baranchikov *et al.* 2010) and the oak splendor beetle, *Agrilus biguttatus* (F.), has been found recently in Denmark, which is a northward shift in its historic range in central Europe (Pederson and Jørum 2009). The introduction of *A. auroguttatus* into CA is somewhat unique relative to these other instances of intracontinental invasive species because 1) there is a relatively short distance between the locations of the source and introduction point (approximately 560 km) and 2) there is an apparent relatively extreme susceptibility of the hosts at the introduction point. Most cases of intracontinental invasive species introductions of subcortical forest insects have not led to extensive tree mortality. Human-defined political borders are insignificant when dealing with regions of distinct flora and fauna. Increased trade, nursery stock movement, a changing climate, and firewood movement may lead to additional forest health problems from intracontinental invasive species, and the recent decline of walnut in the U.S. due to thousand cankers disease and the walnut twig beetle, *Pityophthorus juglandis* Blackman (Scolytinae), may be another manifestation of this problem (Graves *et al.* 2009, 2010; Seybold *et al.* 2010).

The native distributions of the three primary CA hosts of *A. auroguttatus* extend north through most of the state along the coastal foothills and along the Sierra Nevada (Coleman and Seybold 2009), and oak stands throughout CA are primarily even-aged and dominated by an older size class, which appears to be more susceptible to *A. auroguttatus*. Firewood movement represents a significant pathway for introducing this species into these regions. The buprestid is currently injuring and killing *Quercus* spp. between 30 and 1,830 m elevation in southern CA. Previous collection records in its native region extend to 1,981 m elevation (Table 1). Average minimum temperature in the current zone of infestation in San Diego Co. ranges from –12 to –9°C; this range of low temperatures also extends to northern CA along the coast and the lower elevations of the Sierra Nevada mountain ranges (Jordan 2001). These similar mean annual minimum temperatures are also found in southeastern AZ. Thus, this new pest to CA oaks has the potential to impact more northern regions in CA, and the prospect of *A. auroguttatus* and sudden oak death (caused by the pathogen *Phytophthora ramorum* Werres, de Cock, and Man [Rizzo and Garbelotto 2003]) acting simultaneously on *Q. agrifolia* in CA presents a severe threat to this key oak species. As a foundation species of the CA coastal oak savanna, loss of *Q. agrifolia* may result in "dramatic changes in assemblages of associated species with cascading impacts on food webs and fluxes of energy and nutrients" (Ellison *et al.* 2010). Thus, *A. auroguttatus* represents the most significant and aggressive phloem/wood-boring pest of several CA oak species (Swiecki and Bernhardt 2006; Geiger and Woods 2009), and it has the potential to significantly alter California's landscape by killing many mature trees and impacting the distribution and structure of the fuel load in areas frequently impacted by wildfire. Evans and Hogue (2004) outlined the future of beetle biogeography in CA as a consequence of 1) new discoveries of extant species, 2) natural range extensions of populations currently residing in adjoining states or Mexico, or 3) deliberate or inadvertent introductions of exotic species. Ironically, it appears that *A. auroguttatus* has enriched the coleopteran fauna of CA as an inadvertent introduction from an adjoining state. This enhancement of biodiversity, however, appears to be accompanied by a rather severe economic consequence for the forests of the state.

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