Timothy D. Paine · François Lieutier
Editors

Insects and Diseases of Mediterranean Forest Systems

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Contents

Chapter 21
Invasive Bark and Ambrosia Beetles in California Mediterranean Forest Ecosystems

Steven J. Seybold, Richard L. Penrose*, and Andrew D. Graves

Abstract This chapter discusses the native ranges, histories of introduction, recent research efforts, and the potential impacts of some of 22 species of invasive scolytids in California's Mediterranean forest ecosystems. The diversity of native and ornamental tree species, the varied climatic zones, and the widespread importation of nursery stock and packaged cargo have made California a fertile location for the introduction and establishment of bark and ambrosia beetles. Eight of the twenty two taxa are ambrosia beetles; four are spermophagous (e.g., *Coccotrypes* and *Dactylotrypes* sp.); six are hardwood bark beetles (*Hypothenemus eruditus*, *Scolytus* sp., *Phloeotribus liminaris*, and *Pityophthorus juglandis*); and four are coniferophagous bark beetles (*Hylurgus ligniperda*, *Ips calligraphus*, *Orthotomicus erosus*, and *Phloeosinus armatus*). Five of the species have probable native ranges elsewhere in North America (indigenous exotic species), whereas nearly all of the remaining species have likely origins in Eurasia with at least four of those with clear roots in true Mediterranean ecosystems. Several appear to be from Africa. Many of the species were first detected in heavily urbanized southern California. Detailed overviews are provided for an ensemble of species that have had or could potentially have the most impact on California forest or orchard resources (*H. ligniperda*, *O. erosus*, *P. juglandis*, *Scolytus multistriatus, S. rugulosus*, *S. schevyrewi*, and *Xyleborinus saxeseni*). Another potentially damaging species, the polyphagous shot hole borer, *Euwallacea* nr. *fornicatus*, is treated elsewhere (Chap. 26). The introductions of these taxa range from species that may have invaded over 100–150 years ago (e.g., *Hypothenemus eruditus*, *S. rugulosus*, or *X. saxeseni*) to 10–15 years ago (10 of the 22 species have been detected since 2000). *Dactylotrypes longicollis* (a spermophage); *Euwallacea*

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nr. *fornicatus*; and *Hylurgus ligniperda* represent new generic records for California. Trends and conditions that favor future invasions by other members of this group of insects and a California watch list are presented.

21.1 Introduction

Since the earliest entomological surveys of forests in California (Hopkins 1899) until the latter stages of the twentieth century, the occurrence and impact of invasive species of bark and ambrosia beetles (Coleoptera: Scolytidae, *sensu* Wood 2007; Bright 2014) on trees and shrubs have been almost negligible. The rich endemic fauna in the State (Bright and Stark 1973; Seybold et al. 2008b) seemed to occupy nearly every available *niche* associated with the diverse collection of trees and shrubs in California's many native forest, savanna, and rangeland ecosystems (Bakker 1984). This diversity of native scolytids is no doubt linked to the size of California, its wide climatic and topographic variation, and the attendant diversity of woody plants available as hosts (Hickman 1996). Approximately one-third of California is forested (33,238,000 acres) (USDA Forest Service 2015), and its large metropolitan areas are adorned with major urban forests and parks (e.g., Balboa, Golden Gate, and Griffith Parks) (Anonymous 2015a). Lanner (1999) lists 59 species of native conifers in California, more than any other U.S. state. Griffin and Critchfield (1972) mapped distributions of 86 native forest and woodland tree species and noted that 21 species of trees grow only in the State. In addition, California's urban forests are wildly diverse and replete with a multitude of non-native tree species. Muller et al. (1974) recorded 600 species of indigenous and introduced trees in 86 families in the city of Santa Barbara alone. Thus, the scolytid biodiversity in California is predicated on both diverse native woody plants and an enormous number of exotic woody plants that occur as ornamental plantings or escapees throughout the vast state.

Throughout much of the development of forest entomological investigation in California, the coniferous forests of the Sierra Nevada, Southern Cascade, Transverse, and Coastal Mountain Ranges; the riparian and rangeland hardwood forests; and the urban and periurban collections of adventive trees have been largely unchallenged by invasive insect species in the phloem- and wood-boring guilds (Mattson et al. 1988). In their comprehensive forest entomological monograph, Furniss and Carolin (1977) listed only two bark beetles, the European elm bark beetle, *Scolytus multistriatus* (Marsham), and the shothole borer, *S. rugulosus* (Müller), and one ambrosia beetle, the European shothole borer, *Xyleborus dispar* (F.), as introductions from other continents to the western USA. They treated another ambrosia beetle, the fruit-tree pinhole borer or lesser shot hole borer, *Xyleborinus saxeseni* (Ratzeburg), as a "transcontinental" species, though it is now more widely considered to be a long-naturalized invasive species (Bright and Stark 1973; Rabaglia et al. 2006). All four of these taxa occur in California. In retrospect, an ensemble of other invasive bark beetles, the walnut twig beetle, *Pityophthorus* *juglandis* Blackman (an indigenous exotic, Dodds et al. 2010), the extremely minute bark beetle, *Hypothenemus eruditus* Westwood, the spermophage, *Coccotrypes dactyliperda* (F.), and another invasive ambrosia beetle, *Xyleborus californicus* Wood [now *Cyclorhipidion bodoanum* (Reitter)] (Hobson and Bright 1994) had all been long present in California at the time that this publication was released, but were overlooked by the authors as invasive species. None of these latter species was considered economically significant, so as a group they did not draw the attention of these forest entomologists or their colleagues. Taxonomists, however, were aware that other invasive bark and ambrosia beetles had become established in the western USA prior to the end of the twentieth century (Chamberlin 1939; Wood 1977). For example, Chamberlin (1939) listed six species as introduced Scolytidae in North America [*C. dactyliperda*, *Coccotrypes pygmaeus* (Eichhoff) [= *carpophagus* (Hornung), *Hylastinus obscurus* (Marsham) (on clover, not trees or shrubs), *S. multistriatus*, *S. rugulosus*, and *Xyleborus germanus* Blandford]. Wood (1977) listed 39 introduced species in the USA, but many of these were interception records and not established populations. He noted that many of these invasive species reproduced by means of "facultative arrhenotokic parthenogenesis" whereby one female establishes an entire breeding population. This strategy presumably facilitates their capacity to quickly colonize and invade new habitats.

Since the publication of the monograph by Furniss and Carolin, increasing numbers of invasive bark beetles and woodborers (ambrosia beetles, roundheaded borers, flatheaded borers, and false powderpost beetles) have been detected and have established populations in urban and wildland forests of the West, including California (Lee et al. 2007; Seybold and Downing 2009) (Table 21.1). New invasive bark and ambrosia beetles that have established populations or increased their distributions in California with the potential to significantly impact forest and landscape trees include the redhaired pine bark beetle, *Hylurgus ligniperda* (F.), the Mediterranean pine engraver, *Orthotomicus* (*Ips*) *erosus* (Wollaston), the banded elm bark beetle, *Scolytus schevyrewi* Semenov, the polyphagous shot hole borer, *Euwallacea* nr. *fornicatus* (Eichhoff), and *P. juglandis*. The latter was established in (if not native to) California prior to this recent period, with collection records as early as 1959 from Los Angeles County (Bright 1981; Seybold et al. 2013b; Rugman-Jones et al. 2015). However, surveys over the past 7 years have revealed that this pest of walnut, if not associated indigenously with the native California riparian walnut trees, *Juglans californica* S. Wats. and *J. hindsii* (Jeps.) Rehder, has spread to remote regions of the state and invaded the orchard agroecosystems of English (= Persian) walnut, *J. regia* L., in the Central Valley (Beede and Hasey 1997; Flint et al. 2010; Rugman-Jones et al. 2015). The system of production orchards, which are essentially adventive forests of *J. regia* often surrounded by windbreaks of *J. hindsii*, have been moved with changing land use practices from the greater Los Angeles Basin to the Central Valley in the same time frame that the awareness of the extent of the distribution of *P. juglandis* has changed.

Urban landscapes facilitate the introduction and establishment of invasive species of subcortical insects. They serve as portals where the species can consolidate and build their populations prior to dispersal into wildland forests. Southern California, which is

Table 21.1 Selected major species of invasive bark and woodboring beetles established in the western USA as of 2015[a]

Species	Family	State where initially detected
Heterobostrychus brunneus (Murray)	Bostrichidae	California
Sinoxylon ceratoniae (L.)	Bostrichidae	California
Agrilus anxius Gory	Buprestidae	California/Nevada
Agrilus auroguttatus Schaeffer	Buprestidae	California
Agrilus prionurus Chevrolat	Buprestidae	Texas
Arhopalus syriacus (Reitter)	Cerambycidae	California
Nathrius brevipennis (Mulsant)	Cerambycidae	California
Phoracantha recurva Newman	Cerambycidae	California
Phoracantha semipunctata (F.)	Cerambycidae	California
Dendroctonus mexicanus Hopkins	Scolytidae	Arizona
Euwallacea nr. *fornicatus* (Eichhoff)	Scolytidae	California
Hylurgus ligniperda (F.)	Scolytidae	California
Orthotomicus erosus (Wollaston)	Scolytidae	California
Phloeosinus armatus Reitter	Scolytidae	California
Pityophthorus juglandis Blackman	Scolytidae	Colorado/Utah
Scolytus schevyrewi Semenov	Scolytidae	Colorado/Utah
Trypodendron domesticum (L.)	Scolytidae	Washington
Xyleborinus alni (Niisima)	Scolytidae	Washington
Xyleborus similis Ferrari	Scolytidae	Texas
Xylosandrus crassiusculus (Motschulsky)	Scolytidae	Oregon

[a]Updated from Seybold and Downing (2009). We consider Texas to be part of the continental western USA; these introductions were documented in Haack (2006), except for *P. semipunctata*, which was reported in Scriven et al. (1986); *N. brevipennis* (Linsley 1963; Linsley and Chemsak 1997); *D. mexicanus* (Moser et al. 2005); *H. ligniperda* (Liu et al. 2007); *A. anxius* (Duckles and Švihra 1995; Carlos et al. 2002); *A. auroguttatus* (Coleman and Seybold 2008, Chap. 22); *T. domesticum* (R. Rabaglia, USDA Forest Service, Washington, DC, personal correspondence); and *X. crassiusculus* (LaBonte et al. 2005)

particularly replete with nonindigenous trees and high volumes of imported cargo, appears to have served as an entry point for many of the state's invasive species in this feeding guild. Among the non-native trees are an ensemble of species of Mediterranean pines, such as Aleppo pine, *Pinus halepensis* Mill., Canary Island pine, *Pinus canariensis* Smith, Italian stone pine, *Pinus pinea* L., and Turkish red pine, *Pinus brutia* Tenore, whose attendant subcortical insect fauna in California has not been characterized previously. These trees have been planted widely along city streets, in parks and golf courses, as landscaping in industrial parks, and along highways (particularly at highway on ramps and off ramps) (Fig. 21.1). Both *H. ligniperda* and *O. erosus,* and the roundheaded borer, *Arhopalus syriacus* (Reitter) (Cerambycidae) (Table 21.1), are examples of invasive forest pests that have achieved a toehold in urban or peri-urban environments of California by colonizing these adventive Mediterranean hosts. From there the beetles appeared to have shifted onto native pines as they have moved into California's wildland forests in the U.S. National Forest system.

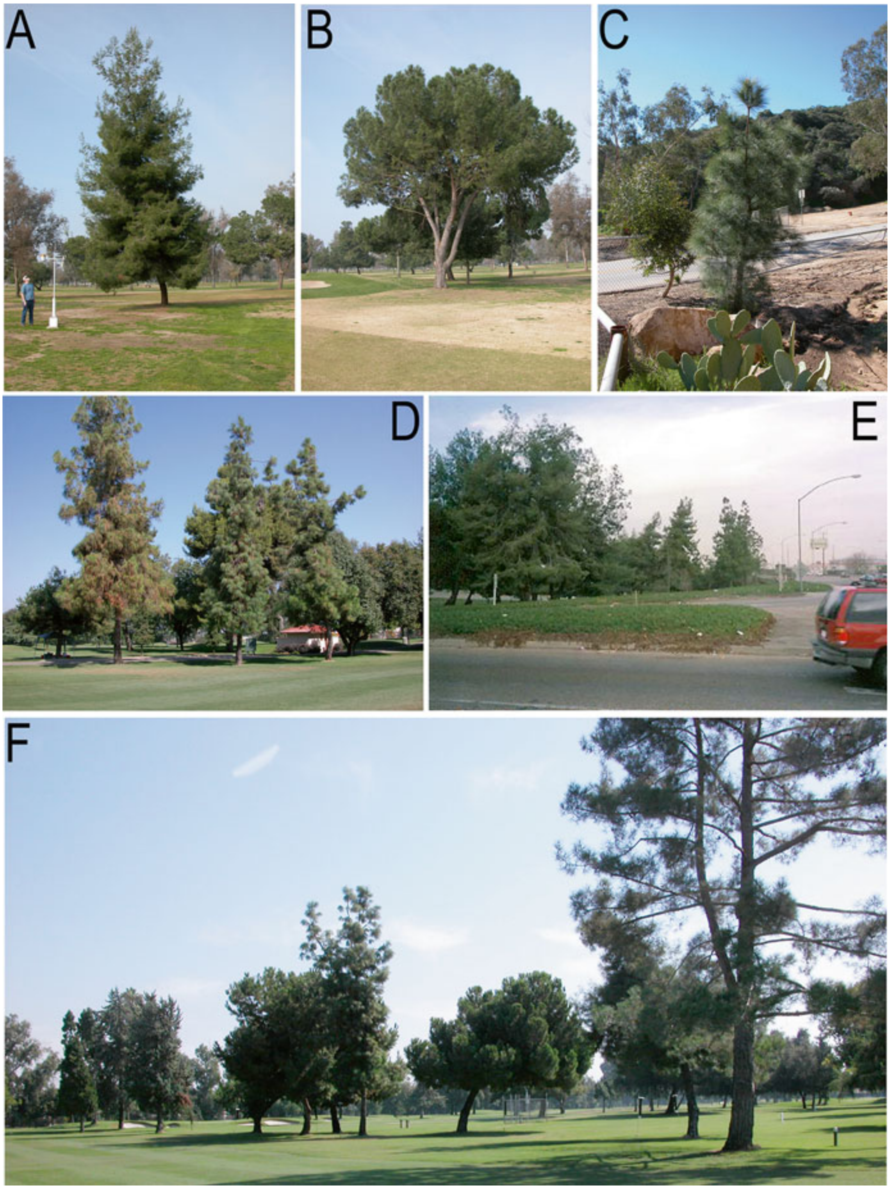


Fig. 21.1 Frequently planted Mediterranean pines in the California urban forest are hosts of invasive species of bark beetles. These hosts include: (**a**) Aleppo pine, *Pinus halepensis* Mill. and (**b**) Italian stone pine, *Pinus pinea* L., both on Valley Oaks Golf Course, Visalia, Tulare Co.; (**c**) Canary Island pine, *Pinus canariensis* Smith at Burbank green waste processing facility, Los Angeles Co.; (**d**) same on grounds of Visalia Country Club, Visalia, Tulare Co.; (**e**) a "stand" of *P. canariensis* and *P. halepensis* on the Highway 58 offramp at Union Avenue, Bakersfield, Kern Co.; and (**f**) a "stand" of *P. halepensis*, *P. canariensis*, and Turkish red pine, *Pinus brutia* Tenore (foreground), on grounds of Visalia Country Club, Visalia, Tulare Co. (SJS, photos)

From 2002 to 2009, one of us (RLP) led an annual detection survey for bark beetles and woodborers in California implemented by personnel from the California Department of Food and Agriculture (CDFA), Pest Detection and Emergency Projects Branch. The primary objective of the survey was to detect exotic species in seven families of xylophagous or phloeophagous Coleoptera and Hymenoptera with an emphasis on the bark and ambrosia beetles. A benefit of the survey is that it also provided baseline data on California's native bark beetle and woodborer fauna, particularly in urban forests. Depending on year, the survey covered 53 (2002) to 101 (2005) locations across 14 (2002) to 40 (2004) counties. Within the state (2002–2005), 35 % of the sites were located in southern California (south of the Tehachapi Mountain range), 28 % of the sites were in the Central Valley, and 37 % of the sites were in northern California (north of the Tehachapi range) outside of the Central Valley. Each year the statewide general survey involved placement of 127 (2002) to 302 (2005) 12-unit Lindgren funnel traps (Lindgren 1983) baited with (1) ethanol, (2) ethanol and α-pinene, or (3) a formulation of the aggregation pheromone of the Eurasian spruce engraver, *Ips typographus* L. The release devices were ethanol [plastic pouch, 275 mg/day (at 20 °C) = ultra high release (UHR)], (−)-α-pinene [plastic pouch, 2 g/day (at 20 °C), UHR], and the *I. typographus* lure (= "exotic *Ips* lure") comprised of racemic ipsdienol (PVC bubble cap, 110 μg/day), 83 %-(−)-*cis*-verbenol (PVC bubble cap, 300–600 μg/day), and 2-methyl-3-buten-2-ol (plastic pouch, 17–19 mg/day) (all at 20 °C). Between 2002 and 2006, the semiochemicals were products of Pherotech Inc., Delta, British Columbia, Canada (now The Scotts MiracleGro Company); in 2007 and thereafter, the products were purchased from Synergy Semiochemical, Burnaby, British Columbia, Canada. The trap cups contained about 100–150 ml of a mixture of water and propylene glycol (50:50 by volume, Sierra Antifreeze, Old World Enterprises, Northbrook, Illinois) to immobilize the insects. Surveys after 2009 (see below) utilized a more diluted form of propylene glycol, with an emphasis on non-ethanol bearing products (Seybold et al. 2013a).

In some cases, delimitation surveys were carried out to characterize the extent of the distribution of specific taxa by placing one or two additional traps at locations in counties adjacent to previous detection sites. Each year, the traps in the general survey (approx. three per location) were deployed in the field in April or May and insects were collected bi-weekly until October or November in locations selected to maximize detection of immigrant scolytids and other woodborers. These locations included urban and peri-urban parks or industrial landscapes with large densities of introduced woody plants (Fig. 21.2a, b); landfills and green waste facilities (Fig. 21.2c, d); wood recyclers/pallet companies (Fig. 21.2e); mills handling logs/rough-cut lumber from foreign sources; ports; and distribution centers or destinations for foreign commodities such as tools, tiles, and marble, which are often associated with wood packing material (Fig. 21.2f). This material was hypothesized to serve as the "Trojan horse" for many species of invasive subcortical insects (USDA 2000). At some survey sites, ground inspections of moribund, dead, or decadent trees and shrubs or woodpiles were conducted; biological attributes of the invasive species were recorded; and infested materials were returned to the laboratory for further rearing and screening to establish subcortical insect community

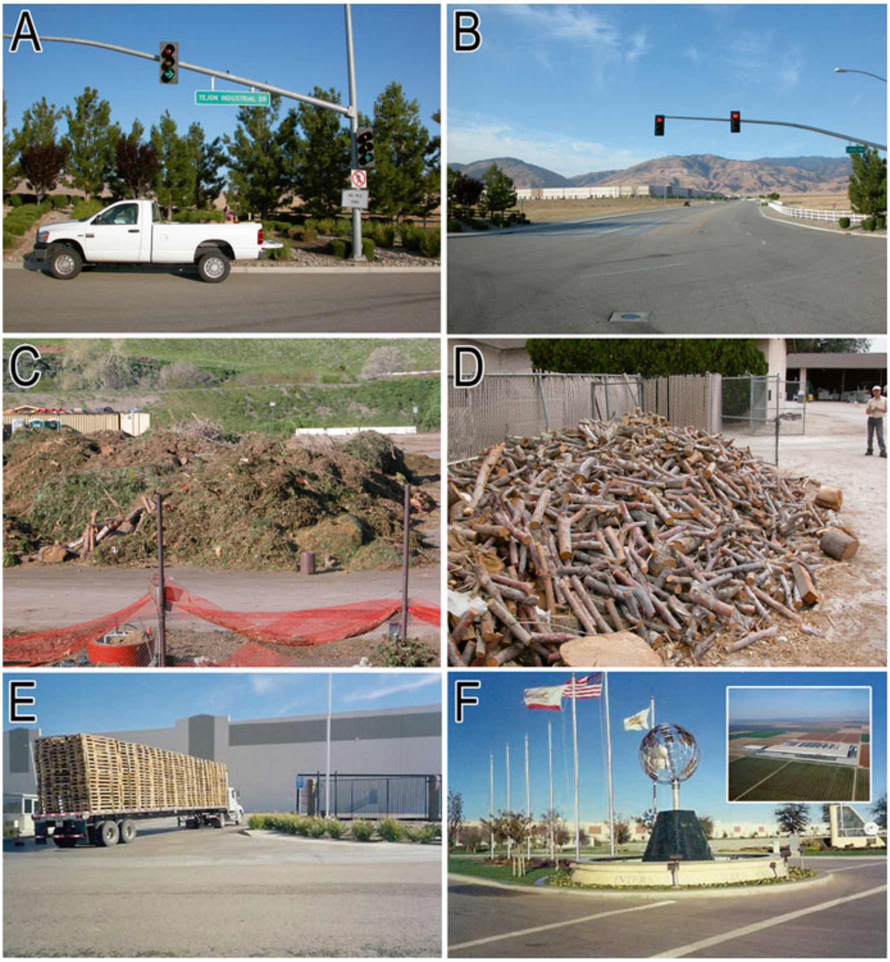


Fig. 21.2 Survey sites for invasive Scolytidae in California included (**a**, **b**) Industrial parks landscaped with adventive tree species (Tejon Industrial Park, Grapevine, California, Kern Co.); (**c**, **d**) Greenwaste processing or storage sites (Burbank and Victorville, California); (**e**) Pallet recycling facilities (Tejon Industrial Park, Grapevine, California); and (**f**) Large scale distribution centers (International Trade and Transportation Center, Seventh Standard Road, Shafter, California, Kern Co., *Inset*, aerial view of the same) (SJS photos)

relationships (Browne 1972). Specimens were curated and pre-identified by the authors; final identifications were confirmed by authorities associated with major North American collections.

Between December 2004 and October 2009, frequent ground surveys of additional sites were conducted by the authors and their colleagues to delimit the distributions and investigate the life histories of several economically important species, and long trapping transects were installed that targeted *O. erosus* (2008–2009) and *H. ligniperda* (2009–2010). These transects led from urban or agricultural areas where these taxa had been detected into U.S. National Forest locations (Seybold 2008; Seybold et al. 2008a). Behavioral studies of the invasive elm bark beetles, *S. multistriatus* and *S. schevyrewi*, were conducted in the greater Sacramento area (northern Central Valley) and in Reno and Carson City, Nevada (western Great Basin) (Lee et al. 2009, 2010, 2011). Surveying continued after 2009 when the principal author began a statewide program of detection and demonstration of the efficacy of the pheromone of *P. juglandis*. This involved monitoring traps in Central Valley orchards and in U.S. National Forest sites (Seybold and Munson 2010; Seybold et al. 2013a, 2015). Some invasive scolytids were also collected or reared as bycatch in various research projects involving the flight behavior and population genetics of *P. juglandis* and other species (Seybold et al. 2012b; Chen and Seybold 2014; Coleman et al. 2014a; Hishinuma et al. 2015; Rugman-Jones et al. 2015). Major California insect collections (Table 21.2, footnotes) were also examined for additional records of interception or establishment prior to 2002. All of these data were integrated into distribution maps for the major invasive species.

Table 21.2 Invasive Scolytidae known to occur in California[a]

Subfamily, tribe, species (common name)	Probable native range[b]	Year first collected in CA	Reference
Hylesininae			
1. Tomicini: *Hylurgus ligniperda* (F.) (Redhaired pine bark beetle)	Europe, Mediterranean	2003	Current study; Liu et al. 2007
2. Phloeotribini: *Phloeotribus liminaris* (Harris) (Peach bark beetle)	Eastern North America	2002	Current study
3. Phloeosini: *Phloeosinus armatus* Reitter (Oriental cypress bark beetle)	Mediterranean, Middle East	1989[c]	Current study; Mendel (1984); Wood (1992); Garrison (1993)
Scolytinae			
4. Dryocoetini: *Coccotrypes advena* Blandford	Asia	2006	Current study
5. Dryocoetini: *Coccotrypes carpophagus* (Hornung)	Africa	2001[d]	Current study; LaBonte and Takahashi (2012)
6. Dryocoetini: *Coccotrypes dactyliperda* (Fabricius)	Africa	1930[e]	Bright and Stark (1973); Wood (1982); Holzman et al. (2009)
7. Dryocoetini: *Dactylotrypes longicollis* (Wollaston)	Canary, Madeira Islands	2009	Current study; Whitehead et al. (2000); Penrose (2010); LaBonte and Takahashi (2012)
8. Scolytini: *Scolytus multistriatus* (Marsham) (European elm bark beetle)	Europe	1951	Armitage (1951); Bright and Stark (1973)
9. Scolytini: *Scolytus rugulosus* (Muller) (Shothole borer)	Europe	1910, 1913[f]	Essig (1915, 1926); Smith (1932, 1945); Bright and Stark (1973); Wood (1982)
10. Scolytini: *Scolytus schevyrewi* Semenov (Banded elm bark beetle)	Asia	2002	Current study; Negrón et al. (2005)

(continued)

Table 21.2 (continued)

Subfamily, tribe, species (common name)	Probable native range[b]	Year first collected in CA	Reference
11. Ipini: *Orthotomicus* (*Ips*) *erosus* (Wollaston) (Mediterranean pine engraver)	Mediterranean, Middle East, Asia	2004	Current study
12. Ipini: *Ips calligraphus* (Germar) (Sixspined ips)	Southeastern USA	1914[g], 1929	Herbert (1916); Wood and Stark (1968); Connor and Wilkinson (1983); Lanier et al. (1991)
13. Xyleborini: *Xylosandrus germanus* (Blandford)	Asia	2003[h]	Current study
14. Xyleborini: *Xyleborus dispar* (Fabricius) (European shothole borer)	Europe	1926	Essig (1926); Bright and Stark (1973); Hobson and Bright (1994)
15. Xyleborini: *Xyleborus californicus* Wood=*Cyclorhipidion bodoanum* (Reitter)	Asia	1944	Wood (1982); Hobson and Bright (1994)
16. Xyleborini: *Xyleborus pfeili* (Ratzeburg)	Eurasia	2003[h]	Current study
17. Xyleborini: *Xyleborus xylographus* (Say)	Eastern North America	1948	Wood (1982); Hobson and Bright (1994)
18. Xyleborini: *Xyleborinus saxeseni* (Ratzeburg) (Fruit-tree pinhole borer/Lesser shothole borer)	Europe	1904[i]	Wood (1982)
19. Xyleborini: *Euwallacea* nr. *fornicatus* (Eichhoff) (Polyphagous shothole borer)	Asia	2003	Current study
20. Cryphalini: *Hypothenemus eruditus* Westwood	Tropical America	1936[j]	Bright and Stark (1973); Wood (1982)
Corthylinae			
21. Pityophthorini: *Pityophthorus juglandis* Blackman (Walnut twig beetle)	SW USA and Mexico	1959	Bright and Stark (1973); Wood (1977); Bright (1981)
22. Corthylini: *Monarthrum mali* (Fitch)	Eastern North America	unknown	Wood (1982)

CSCA California State Collection of Arthropods, Sacramento, CA
EMEC University of California, Essig Museum of Entomology, Berkeley, CA
LACM Los Angeles County Museum of Natural History, Los Angeles, CA
SBNM Santa Barbara Museum of Natural History, Santa Barbara, CA
SDMC San Diego Natural History Museum, San Diego, CA
SJSC San Jose State University, San Jose, CA, J. Gordon Edwards Museum of Entomology
UCDC University of California, The Bohart Museum of Entomology, Davis, CA
UCRC University of California Riverside, Riverside, CA
USNM-US National Museum, Washington, DC
Other collections that we surveyed that do not have codens include California State University Chico, California State University Fresno, California State University Stanislaus, California State

(continued)

Table 21.2 (continued)

University San Francisco, Oakland City Museum, and San Bernardino County Museum. The USDA Forest Service Pacific Southwest Research Station Collection (USDA Forest Service Hopkins U.S. System Index 1929–1955) was also surveyed

[a] Museum survey by the authors included 17 collections. Museum acronyms (Based on Evenhuis, N. L. Abbreviations for Insect and Spider Collections of the World, http://hbs.bishopmuseum.org/codens/codens-inst.html, accessed July 8, 2015

[b] Probable native ranges based on Wood (1977, 1982) and Wood and Bright (1992)

[c] *Phloeosinus armatus* has been known at least since 1989 from southern California (Los Angeles, Los Angeles Co.) where Garrison (1993) reported a specimen collected from firewood. He also noted an additional collection from 1990 in dying branches of Italian cypress, *Cupressus sempervirens* L., in a nursery (Irwindale, Los Angeles Co.). Correspondence among agricultural entomologists from Orange and Los Angeles Cos., CDFA personnel, and SL Wood (Brigham Young University) revealed that this beetle was collected in the early 1990's in Orange Co. and was also found infesting ornamental cypress trees planted in three widely scattered residential areas in southern Los Angeles Co. Wood (1992) briefly reported the establishment in Los Angeles Co. In March 1992, a series of specimens was collected in Redlands (San Bernardino Co.) in a *C. sempervirens* tree. We collected the species in *Cupressus* spp. stem wood from a cut tree in a green waste yard in the Southern Central Valley (S. of Visalia, Tulare Co.), which represents an extension of the state range

[d] As a consequence of this survey, *C. advena* was collected on October 6, 2006 at Whittier Narrows Recreational Area in Los Angeles Co.; C. *carpophagus* was collected in Los Angeles (2004), Orange (2004), Riverside (2006) and San Bernardino (2013) Cos.; and *C. dactyliperda* was collected in Fresno (2004), Riverside (2006), and Tulare (2006) Cos., which represents a range extension in the state for the latter species

[e] San Diego, California, Balboa Park, July 1, 1930, caught at light trap (*CAS*, 1 specimen; *EMEC*, 1 specimen)

[f] Ontario, San Bernardino Co., California, August 1913, breeding in apricot limbs (*CAS*, 2 specimens; *EMEC*, 2 specimens)

[g] F.B. Herbert noted that he observed *I. calligraphus* in 1914–1915 at a site 1.6 km NW of Placerville (El Dorado Co.)

[h] As a consequence of this survey, *X. germanus* was collected on May 30, 2003 at the El Dorado Nature Center in Los Angeles Co., whereas *X. pfeili* was first collected on May 16, 2003 at 3195 Athens Road in Lincoln, Placer Co

[i] Pacific Grove, Monterey Co., November 1904 (*UCRC*), 1 specimen

[j] Los Angeles, March 1936 (*CSCA*), 1 specimen

In this chapter we present an overview of exotic Scolytidae in California with a focus on new species that have been discovered during this survey and subsequent ground reconnaissance. We will explore some of these more significant invasive species from the perspectives of their biology in the new habitat, the case histories of their introductions and establishments, recent research efforts, and potential or realized interactions of the invaders with the native bark and ambrosia beetle fauna in California.

21.2 Invasive Ambrosia Beetles in California

There are records of eight species of ambrosia beetles that have been introduced into California (Table 21.2). Most of these are in the tribe Xyleborini; the exception is *Monarthrum mali* (Fitch), which is in the Corthylini and is an invader from eastern North America (Wood 1982; Wood and Bright 1992). These insects are woodborers that feed as adults and larvae on fungi that grow in their galleries (Solomon

1995; Ranger et al. 2015). They do not construct brood galleries or feed to any great extent in the phloem of trees or shrubs (Solomon 1995). "Host" is a relatively loose term for this group because the trees or shrubs serve primarily as a moistened scaffold or structure in which the fungal food source grows. Thus, any biochemical or physical (e.g., moisture) characteristics of the woody plant are likely to be more indirectly relevant to the feeding and reproductive activity of these species than they are to the phloem feeders (see below).

Of the Xyleborines, fruit-tree pinhole borer or lesser shot hole borer, *Xyleborinus saxeseni* (Ratzeburg), is an interesting case as an invasive species in California (Fig. 21.3, Seybold et al. 2013a). Known as *Xyleborus xylographus* (Say) in the older literature (Essig 1915, 1926; Chamberlin 1939; Bright and Stark 1973), this ambrosia beetle appears to be ubiquitous in North America (Rabaglia et al. 2006) and with a particularly broad distribution in California (Fig. 21.4). It has not only a widespread and transcontinental distribution in North America, but has been collected on five other continents (Wood and Bright 1992). Rabaglia et al. (2006) speculate that it is ultimately a native of Asia, but likely came to North America *via* Europe. It is highly responsive to ethanol used as a semiochemical lure in many generic flight trapping baits across North America and has been a frequently encountered "nuisance" species in many trapping survey programs for bark beetles and woodborers, including ours. It has also been trapped relatively frequently in response to white and black lights (museum survey, *EMEC*). It colonizes both hardwoods and conifers by boring into the xylem and has an enormous host range. Commenting on this host range, Bright and Stark (1973) reported: "possibly no species is exempt from invasion." The breadth of the host range of *X. saxeseni* is illustrated by an April

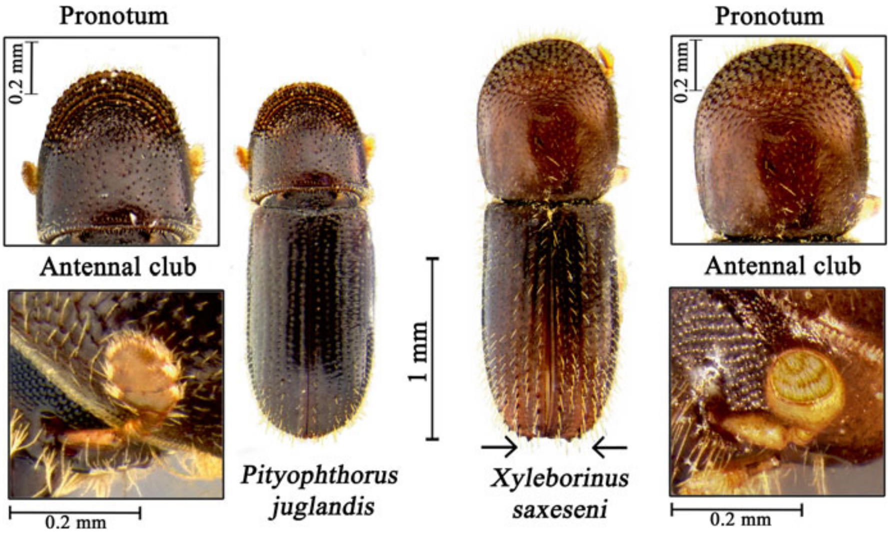


Fig. 21.3 Comparison of dorsal profiles, close up of pronota, and antennal clubs of female walnut twig beetle, *Pityophthorus juglandis* Blackman, and female fruit-tree pinhole borer, *Xyleborinus saxeseni* (Ratzeburg). *Arrows* indicate spines in the elytral declivity and lower right is the truncated antennal club of *X. saxeseni* (Figure by S.M. Hishinuma, UC Davis, from Seybold et al. 2013a)

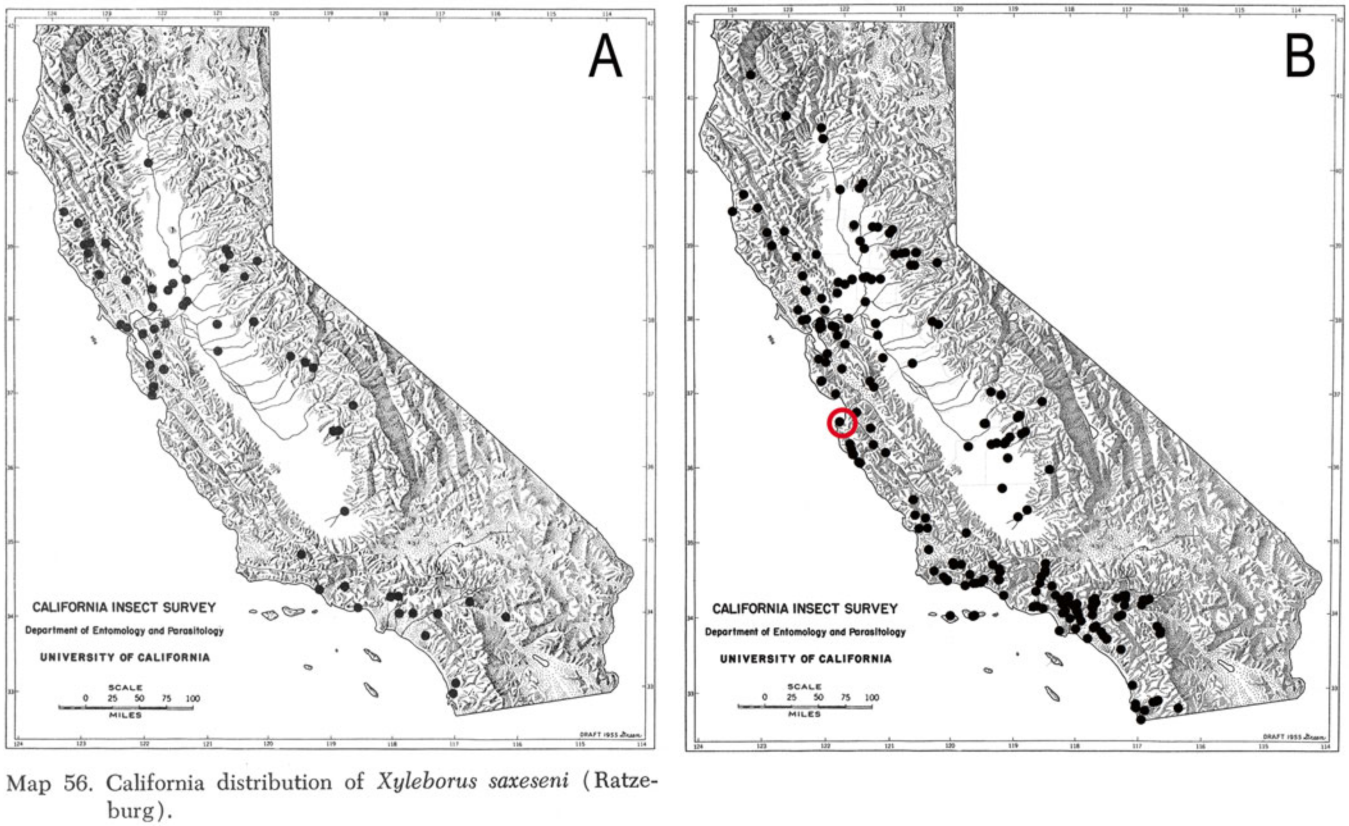


Fig. 21.4 Distribution of the fruit-tree pinhole borer, *Xyleborinus saxeseni* (Ratzeburg), in California. (**a**) California Insect Survey map from Bright and Stark (1973); (**b**) Map from recent literature review, field surveys, and museum survey by the authors (1904-present). *Red circle* indicates the oldest dated collection record in the museum survey (XI-1904, Pacific Grove, Monterey Co., *UCRC*, Table 21.3)

2014 collection on the campus of the University of California Santa Barbara, where it was found boring into the stem of a declining queen or cocos palm, *Syagrus romanzoffiana* (Cham.) Glassman (B. Cabrera, County of Santa Barbara, personal correspondence). Its ubiquity and abundance make it somewhat reminiscent of invasive and now cosmopolitan species of the bird world like house sparrows, *Passer domesticus* L. (Aves: Passeriformes: Passeridae) or common starlings, *Sturnus vulgaris* L. (Aves: Passeriformes: Sturnidae). Male *X. saxeseni* are flightless (apterous) and relatively rare in the population. The males are generally only trapped when the traps are placed on the stem of trees so that they can crawl to the trapping surface.

Although *X. saxeseni* is generally accepted to have invaded North America, it was unusually widespread at a relatively early point in the history of insect collections in western North America (Table 21.3). This suggests that either it was native or it was introduced early during European colonization and then spread rapidly and completely to many forest ecosystems. There are specimens in several California insect collections dating to the period of 1904–1918, which was an era when even the native bark and ambrosia beetle fauna were collected and recorded for the first time in the State (Hopkins 1899). Also, Essig (1915) noted that it was already "widely distributed throughout this State and the Pacific slope" in the early part of the twentieth century (San Diego Co. to Monterey Co. in our museum survey, Table 21.3). It was also collected from the 1920s to the 1950s from relatively remote locations and in native tree species such as the Six Rivers National Forest near Weitchpec (misspelled in the record as Weitchipac)/ Orrick in Humboldt County in tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Rehd.; in the south central Sierra Nevada in Merced County in white fir, *Abies concolor* (Gordon) Lindley ex Hildebrand; and from several out-of-the-way locations in British Columbia (Agassiz, Mission, and Steelhead) in Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco (then known as *Ps. taxifolia*), and hemlock [likely *Tsuga heterophylla* (Raf.) Sarg] (Table 21.3). The breadth of the distribution of *X. saxeseni* in the early 1900s and the degree to which it occurred in remote wildland forests of California and British Columbia raises some doubt about its status as an invader of western North America. Like the striped ambrosia beetle, *Trypodendron lineatum* (Olivier) (Scolytidae) and the ribbed pine borer, *Rhagium inquisitor* (L.) (Cerambycidae), it is possible that *X. saxeseni* was a Holarctic native forest insect to North America. Chamberlin (1939) noted that its distribution included both the eastern and western USA, and that "it may be an introduced species or it may be that our species is native yet identical with the European species of the same name."

Xyleborinus saxeseni and another invasive ambrosia beetle, *C. bodoanum* (Wood 1982; Hobson and Bright 1994; Wood and Bright 1992; Bright 2014) were recently trapped landing on *N. densiflorus* in an ecological study in redwood-tanoak and mixed evergreen forests in the remote Big Sur region of the Santa Lucia Mountains in the California Coastal Range (Beh et al. 2014). Both *X. saxeseni* and *C. bodoanum* were also detected landing on coast live oak, *Quercus agrifolia* Née, in another research study of sudden oak death conducted north of the San Francisco Bay area (McPherson et al. 2008), and females of both also land on and bore into declining walnut trees in the Central Valley (SJS pers. observation). In most instances where they have been encountered together, *X. saxeseni* is

Table 21.3 Historic collection records of fruit-tree pinhole borer, *Xyleborinus saxeseni* (Ratzeburg) in California and other western North American localities[a]

Date	County	Location	Collection method	Specimens
XI-1904	Monterey	Pacific Grove	*ex: Pinus radiata*	1, *UCRC*[b,c]
II-1910/V-1912	Fresno	Camp Greeley	No data	2, *CAS*[d]
IV-29-1915	Ventura	Ventura	*ex:* apricot	1, *EMEC* 1, *CAS*
V-1915	Los Angeles	Whittier	No data	1, *UCRC*[e]
V-14-1915	San Diego	San Diego	No data	1, *EMEC* 1, *CAS*[f]
IX-25-1918	Santa Clara	Mayfield	*ex:* Monterey cypress	1, *USDA-PSW*[g]
VIII-21-1929	Merced	Yosemite, Happy Oaks (= Happy Isles)	*ex*: white fir, *Abies concolor*[h]	2, *CAS*
VI-29-1930	Yuba	Unknown	*ex:* pear stump	1, *LACM*[i]
VI-14-1939	Mendocino	Ryan Creek	No data	1, *CAS*
VIII-24-1953	Humboldt	Weitchipac/Orrick	*ex:* tanoak	6, *USDA-PSW*[j] 15, *CAS*[j]
No date; Accessioned *LACM* 1964	Santa Clara	Harkins Collection, Stanford University Collection	No data	2, *LACM*
No date; Accessioned *LACM* 1964	San Diego	Harkins Collection, Stanford University Collection	No data	1, *LACM*
V-1928	B.C. (Canada)	Agassiz	No data	*CAS*
I-28-1931	B.C.	UBC	*ex:* green Hemlock	*CAS*
VI-1932	B.C.	Mission	*ex: Tsuga heterophylla*	*CAS*
VII-2-1933	B.C.	Steelhead	*ex: Pseudotsuga taxifolia*	*CAS*

[a] From a museum survey by the authors

[b] Museum acronyms as in Table 21.2

[c] *UCRC* ENT 158376

[d] R. Hopping, coll

[e] *UCRC* ENT 157508

[f] H.A. Weinland, coll

[g] Mayfield (=South Palo Alto) in Santa Clara Co. (*ex*: stem and large limbs of recently burned 8″ Monterey cypress, Hopkins No. 15802, *USDA FS PSW* Collection, HUSSI (1929–1955)

[h] H.E. Burke, coll

[i] Yuba Co. (*ex*: reared from pear stump, CA Dept Ag No. 30222, *LACM* Collection)

[j] Six Rivers National Forest near Weitchipac/Orrick in Humboldt Co. in the main stem of a 26 in. diameter tan oak, *Notholithocarpus densiflorus*, Hopkins No. 33920, *USDA FS PSW* Collection, HUSSI (1929–1955). Note that Weitchpec was misspelled as Weitchipac on the label (*CAS* Collection, Hopkins No. 33920A)

abundant and *C. bodoanum* is relatively rare. *Cyclorhipidion bodoanum* (as *Xyleborus californicus*) had been known previous to our survey work from specimens collected in El Dorado (1986), Santa Clara (1944), and Yolo (1949) Cos. (Wood 1982; Hobson and Bright 1994); in this survey we collected it from Butte, Merced, Monterey, Napa, Placer, Sacramento, Shasta, Solano, and Stanislaus Cos., which extends the distribution to the northern limits of the Central Valley of California. We also found a series of specimens in the museum survey (*EMEC*) collected in 1975 from the central Sierra Nevada community of Arnold (Calaveras Co.). In 2012, it was collected for the first time in southern California (Cleveland National Forest, Riverside County) and then in 2014 in San Diego County (Fig. 21.5). The capacity of species such as these to reach remote corners of the state is a testament to their dispersal capacity and their extreme flexibility to find and utilize reproductive sites in host trees.

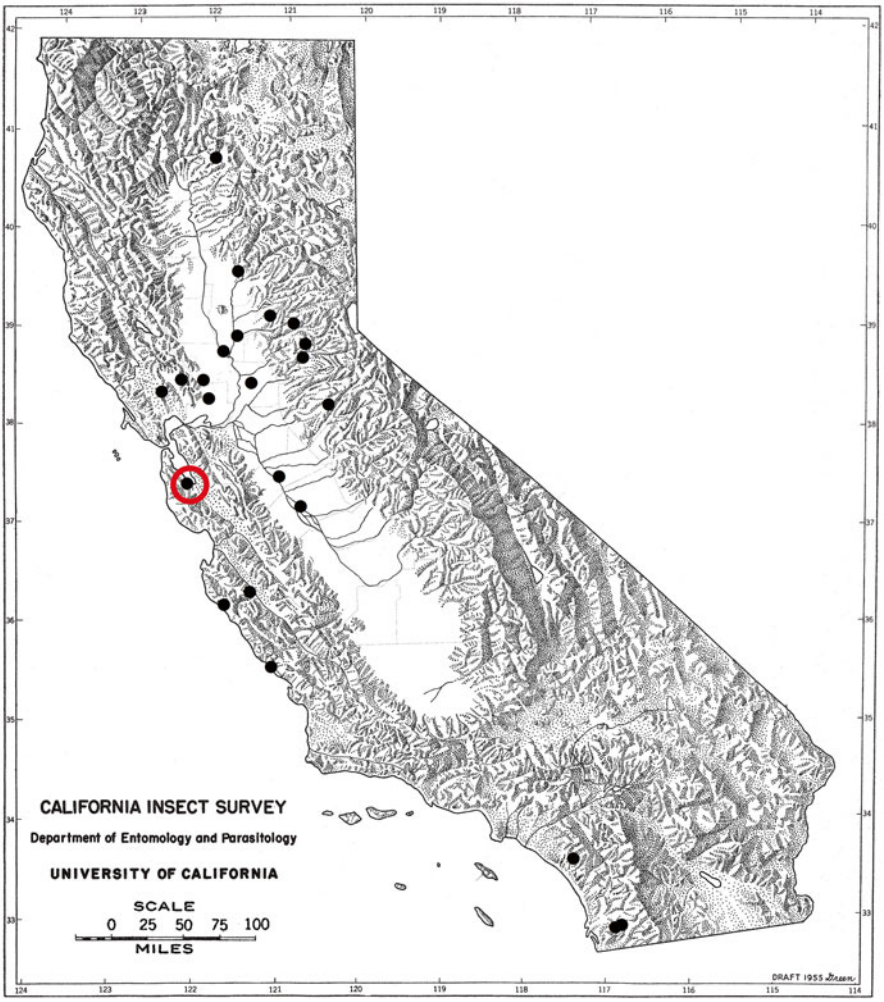


Fig. 21.5 Distribution of the ambrosia beetle, *Cyclorhipidion bodoanum* (Reitter) (formerly *Xyleborus californicus* Wood), in California from recent literature review, field surveys, and museum survey by the authors (1944-present). *Red circle* indicates the oldest dated collection record (III-15-25-1944, Santa Clara Co., *SBMNH*, Wood 1982)

The European shothole borer, *Xyleborus dispar* (Fabricius) was noted by Essig (1926) as an ambrosia beetle pest of a wide variety of trees in Western North America. Its damage to smaller branches and the branch tips bore a resemblance to pear blight, hence it had the common name "pear blight beetle." Essig (1926) noted that it was known from California, Oregon, Washington, and British Columbia, and Linsley and MacLeod (1942) recorded an instance of attacks by *X. dispar* on branches of nectarine trees in Siskiyou County (Northern California), which was the only record listed in Bright and Stark (1973). We have reared it from dying black walnut, *J. nigra* or *J. hindsii x nigra* branches that were removed and brought to the laboratory from Humboldt County (2013), and from frost-damaged small diameter *J. regia* trees from Lake County (2012). In the museum survey (*EMEC*), a male specimen of *X. dispar* was recorded as "taken from walnut" in Corvallis, Oregon (Benton Co.). Despite extensive trapping near walnut trees or rearing from walnut branches and stems, we have not made any additional collections of *X. dispar* related to this host elsewhere in California. Thus, it appears that *X. dispar* is relatively rare with a generally northern distribution in California. Essig (1926) listed a wide range of hosts that included alder, ash, beech, birch, cedar, chestnut, elm, hemlock, maple, oak, pine, poplar, sycamore, tulip tree, and willow as forest trees among many other species normally found in orchards. Presumably, many of these were eastern U.S. records. Jurc et al. (2009) consider *X. dispar* to be polyphagous and reported it colonizing branches from several species of native oaks in Slovenia. Dreistadt et al. (2004) noted that *Xyleborus crassiasculus* (Motschulsky) may be a threat to invade California from neighboring Oregon. The historically northern distribution of *X. dispar* in California suggests that it may have invaded from Oregon as well.

The most dramatic recent addition to the collection of invasive ambrosia beetles in California is the polyphagous shot hole borer (Coleman et al. 2013; Eskalen et al. 2013; Chen et al. 2016, see Chap. 26). This insect is considered to be close phylogenetically to the tea shot hole borer, *Euwallacea fornicatus* (Eichhoff), which has been established for some time in North and Central America and the Pacific Islands with introduced populations in Florida, Hawaii, and Panama (Rabaglia et al. 2006). The tea shot hole borer appears to be native to Asia, but also occurs in Australia and Africa (the Reunion Islands). The polyphagous shot hole borer, which has not yet been assigned a scientific name, was first collected in California on 30 May 2003 near the Port of Long Beach in Whittier Narrows Recreational Area (Los Angeles County) by RLP. It has since expanded its distribution in southern California to include Orange, Riverside, San Bernardino, and San Diego Counties where it mass attacks box elder, sycamore, avocado, and a plethora of other hardwood trees, primarily in riparian areas. It has been a pest of the urban forest and various botanical collections, but is expanding its range into riparian forests in the U.S. National Forest system of southern California and into avocado orchards in San Diego County. The San Diego County population, first detected in 2013, may represent a closely related species or sub-species, which has been referred to provisionally as the Kuroshio shot hole borer. Like *X. saxeseni*, the males of the polyphagous shot hole borer are wingless, relatively sessile, and present at a low proportion relative to the females in the population. Thus, the females are driving the natural dispersal of the introduced population, though like most bark beetles and wood borers, expansion of the invasive population is expected to be highly accelerated by the movement of barked and potentially (in this case) unbarked raw wood products (Haack et al. 2010; Borchert et al. 2011; Jacobi et al. 2012; Jones et al. 2013).

Other new invasive ambrosia beetles in California (Table 21.2) include *Xyleborus pfeili* (Ratzeburg), which was known previously as an invader in Maryland (Vandenberg et al. 2000) and *Xylosandrus germanu*s (Blandford), which is a palaearctic species known from many eastern U.S. states as far west as Michigan and Illinois, and from Ontario and Quebec in Canada (Bright 1968, 2014; Wood 1982; Weber and McPherson 1983; Wood and Bright 1992; Bright and Skidmore 1997, 2002; Douglas et al. 2013). These two species were also recently collected in Oregon (Mudge et al. 2001; LaBonte et al. 2005), and *X. germanus* has been collected in British Columbia in Canada (Bright and Skidmore 2002). *Xyleborus pfeili* was first collected in 2003 near a wood recycling center near Lincoln (Placer Co.) (Table 21.2) and additional collections were made in Placer and eastern Sacramento Cos. *Xylosandrus germanu*s was only collected at El Dorado Regional Park (Los Angeles Co.), but is considered to be established there because it was collected both in 2003 and 2007 (Table 21.2). One other species of immigrant *Xyleborus* that has been previously recorded in California is *X. xylographus* Say (not to be confused with the old references to *X. saxeseni*). *Xyleborus xylographus* was known previously in California only from specimens collected (1948) in the Sierra Nevada in El Dorado Co. (Wood 1982; Hobson and Bright 1994), but in this survey we collected it from Marin, Orange, Shasta, Solano, Sonoma, Sutter, and Trinity Cos., which extends the distribution to the northern Central Valley, to coastal California, and to southern California.

21.3 Invasive Spermophagous and Miscellaneous Bark Beetles in California

To date, four scolytid species that feed on seeds of palms and other plants have been introduced into California (Table 21.2). The host range of this guild is rather unusual as it includes fresh and dry seeds of many plants (Wood and Bright 1992), as well as petioles of leaves (Bright and Skidmore 2002); logs of conifers (Bright 2014); and buttons made of "vegetable ivory" (Wood 1977) (Appendix 21.I). The earliest introduction of a member of this feeding group to California appears to have been with *Coccotrypes dactyliperda* (F.), for which the oldest record in our survey was 1930 in San Diego Co. (Fig. 21.6a). Chamberlin (1939) considered this species to have been established in Hawaii, but only introduced, not established, in the continental USA. He noted that Van Dyke had collected it from the Canary Island date palm, *Phoenix canariensis* Chabaud, in Los Angeles. Holzman et al. (2009) confirmed the general timing of the introduction by stating that it first occurred in

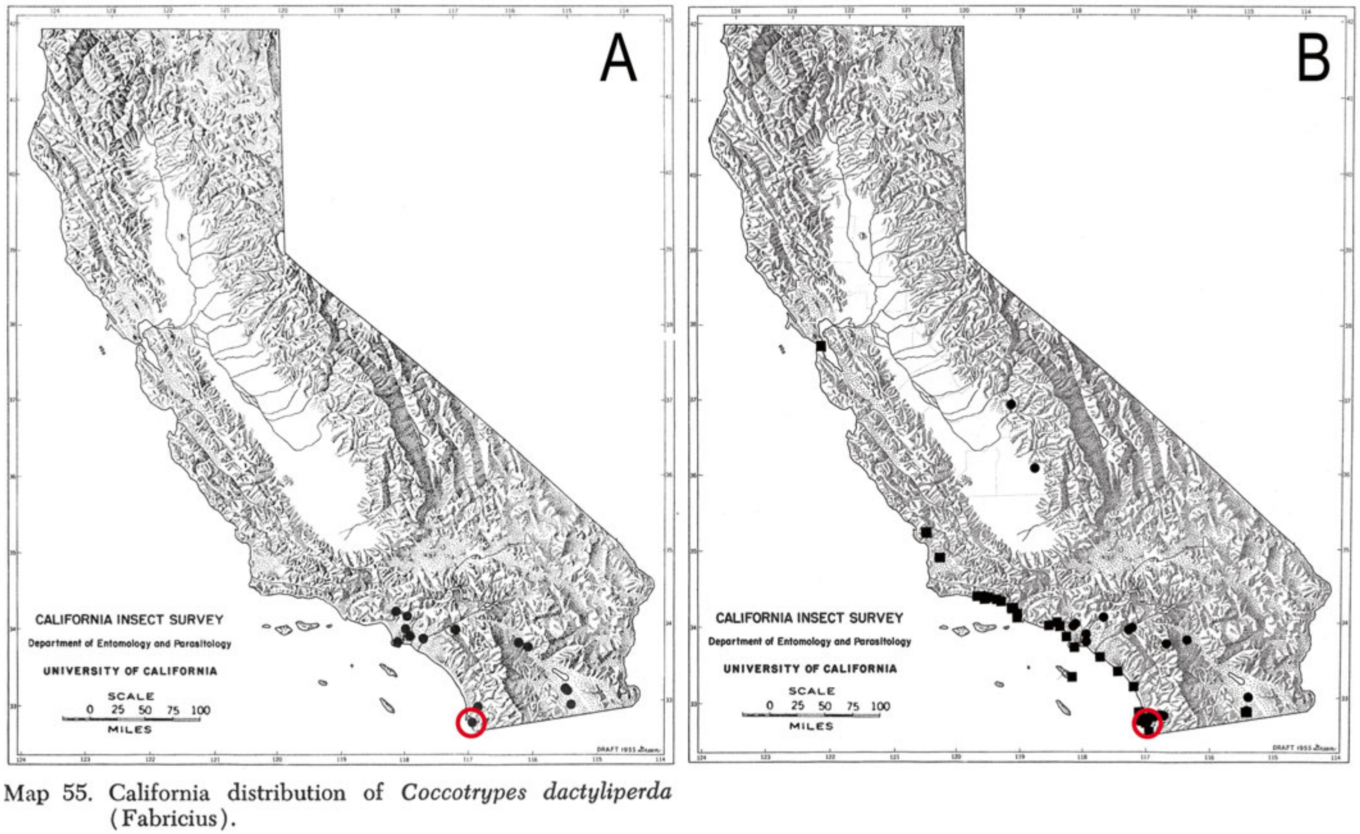


Fig. 21.6 Distribution of the spermophage, *Coccotrypes dactyliperda* (F.), in California from field survey data and museum records. (**a**) California Insect Survey map from Bright and Stark (1973); (**b**) Map from field and museum survey by the authors (1930-present) with squared entries from Holzman et al. (2009). *Red circles* indicate the oldest dated collection record (VII-1-1930, Balboa Park, San Diego, San Diego Co., *CAS* and *EMEC*)

California about 80 years ago. Our survey yielded records of *C. dactyliperda* from Fresno (2004), Riverside (2006), and Tulare (2006) Cos., which represent a range extension in the state (Fig. 21.6b). Holzman et al. (2009) also report a northern extension of the range along the Central Coast. Its distribution in the USA also includes Arizona, Florida, and Texas (Wood and Bright 1992). Two other more recently introduced species in this genus are *C. advena* Blandford and *C. carpophagus* (Hornung), both of which were first detected in the trapping survey or a related Early Detection Rapid Response survey executed by CDFA (Table 21.2). *Coccotrypes advena* was first collected in a survey trap on 6 October 2006 in Whittier Narrows Recreational Area near South El Monte in Los Angeles County (identified by D.E. Bright) and known only from this site based on collections in 2006 and 2007. It is likely from Southeast Asia (Indonesia) (Wood 1977), but also occurs in Australia, the Pacific Islands (including Hawaii, Bright and Skidmore 1997), the Caribbean (including Puerto Rico, Bright 2014), and South and Central America. It was first reported from North America (Florida) by Wood (1982) and again by Atkinson and Peck (1994), though the latter authors implied that it might not actually be established in south Florida. This species has a rather large host range (Wood and Bright 1992), and presumably colonizes the seeds of most of these hosts (Appendix 21.I). Another spermophage, *Dactylotrypes longicollis* (Wollaston), feeds on seeds of the date palm, *Phoenix dactylifera* L., and of *P. canariensis* (Whitehead et al. 2000; LaBonte and Takahashi 2012). So far it is only known in North America by several collection records in southern California (Orange and Los Angeles Cos.) (Penrose 2010; LaBonte and Takahashi 2012). These types of beetles constitute a threat to the California date industry, which has its origins in the Mediterranean.

Another unusual invasive species of scolytid in California is *Hypothenemus eruditus*. The collection history of this species is typical of a California invasive in that the earliest records (1936) were in urban southern California, and subsequent collections have been from urban, or disturbed habitats and agroecosystems. Bright and Stark (1973) suggest that the California distribution of *H. eruditus* is along the southern Pacific Coast, but we have found it to be widespread in the Central Valley as well (Fig. 21.7). Wood (1982) notes that it has bred in everything from the cover of a book (hence the name "*eruditus*"), to fungal fruiting bodies, and fruiting stalks of grass. The galleries may also be in the central axis (pith) of twigs and leaf stalks, or they may engrave the xylem surface in the more typical phloeophagous habit. The host range is enormous (Wood and Bright 1992; Bright and Skidmore 1997, 2002; Wood 2007; Bright 2014), and the intraspecific genetic diversity may also be quite high as Wood (2007) noted 72 synonyms. Wood (2007) also reported that *H. eruditus* may be the most widely distributed and abundant species of scolytid in the world. The structure of the female-constructed galleries and the larval mines has been described as "irregular" (Wood 2007). Although *H. eruditus* is not thought to be an ambrosia beetle, like many of the ambrosia beetles mentioned above, the males are flightless and they mate with their female siblings (Wood 2007). We reared this species from 5 to 7.5 cm and larger diameter branches of *J. regia*, *J. californica*, and *Pterocarya* spp. collected from Los Angeles and Solano Counties

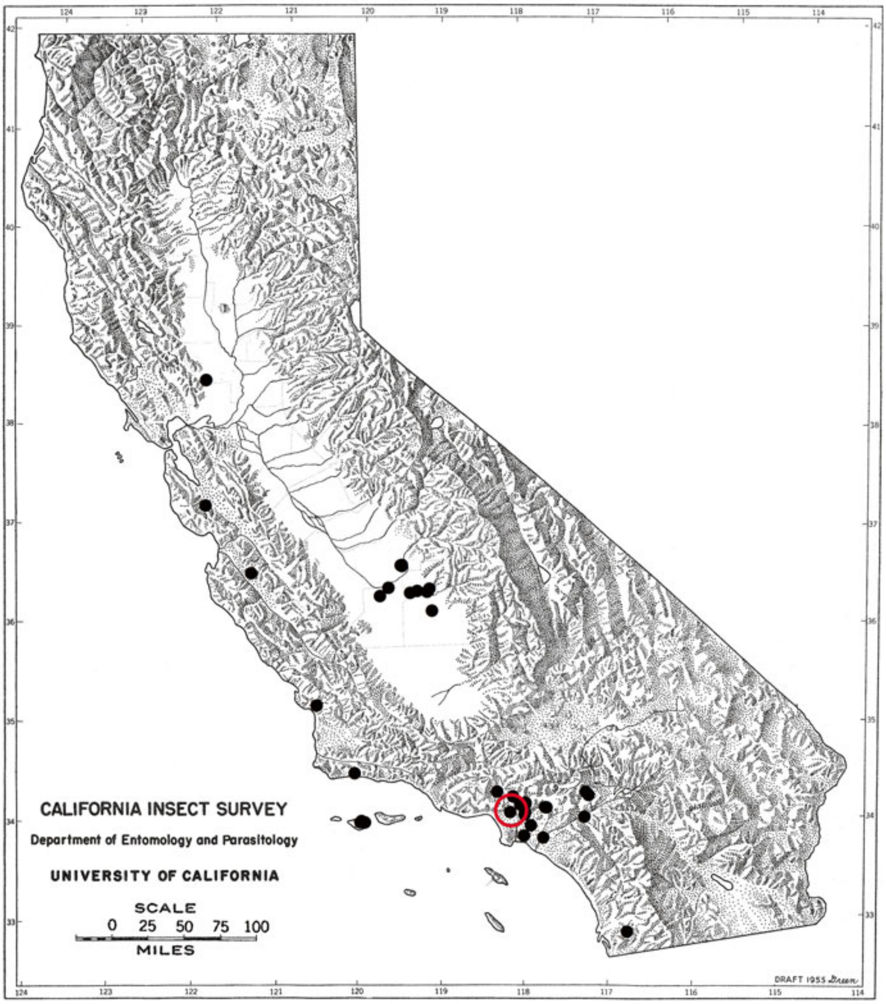


Fig. 21.7 Distribution of the minute bark beetle, *Hypothenemus eruditus* Westwood, in California from field and museum survey by the authors (1936-present). *Red circle* indicates the oldest dated collection record (III-1936, Los Angeles, Los Angeles Co., *CSCA*)

(Hishinuma et al. 2015). We have also reared it on several occasions from crown gall (*Agrobacterium tumefaciens*)-infected paradox walnut rootstocks (burls) collected in Kings County. It (and *X. saxeseni*) was also captured in funnel traps placed in three *J. regia* orchards as part of a *P. juglandis* seasonality study in Fresno and Tulare Counties when antifreeze laden with ethanol was inadvertently used in the trap cups instead of the recommended propylene glycol-based product (Seybold et al. 2013a). Because of its extremely small size (females, 1.0–1.3 mm; males, 0.7–0.8 mm in length, Mifsud and Knížek 2009), this species and its congeners are typically ignored in various research and survey efforts involving forest insects. Wood (2007) also attributed (in part) the large number of synonyms to the small size of *H. eruditus* and the inability of taxonomists to see the characters necessary to make an accurate species determination.

21.4 Invasive Phloem–Feeding Bark Beetles of Economic Importance in California

21.4.1 Scolytus

There are three species of introduced *Scolytus* in California. One is a pest of rosaceous fruit and nut trees [*Scolytus rugulosus* (Müller)], and two are pests of elms [*Scolytus multistriatus* (Marsham) and *Scolytus schevyrewi* Semenov]. As a threesome, they represent interesting comparative histories of establishment. Furthermore, the more recent invasion of North America by *S. schevyrewi* has created a case of competitive displacement whereby population densities of *S. multistriatus* appear to be on the decline as *S. schevyrewi* usurps the habitat (Lee et al. 2009).

21.4.1.1 Shothole Borer, *Scolytus rugulosus* (Müller)

North American populations of the shothole borer, *Scolytus rugulosus*, are thought to have been derived from Europe (Furniss and Carolin 1977), though Wood (1982) notes the strong potential for distinct geographic races from Europe and Asia, and it appears that no one has tried to evaluate the populations in North America for this diversity with modern molecular methods. Michalski (1973) also remarks on the morphological diversity of the specimens that he examined, with special emphasis on Central Asian populations. Wood and Bright (1992) list 13 subspecies or synonyms for *S. rugulosus*, also a reflection of this diversity of the species. In addition to southern Canada and every state of the USA, *S. rugulosus* has been collected in Chihuahua and Durango, Mexico, as well as in Argentina, Brazil, Chile, Peru, and Uruguay in South America (introduced) (Wood 1982, 2007; Wood and Bright 1992; Bright and Skidmore 1997). No major changes in status of the distribution or host range were reported in Bright and Skidmore (2002) or Bright (2014).

Scolytus rugulosus is a Palaearctic species that colonizes fruit trees and appears to have arrived in California long before the development of industrial-style agriculture; its origins in North America are unclear (Essig 1915, 1926; Bright and Stark 1973). Bright and Stark (1973) suggest that it was first collected or introduced into the USA in 1878, whereas Smith (1932) states that “It is believed to have been accidently introduced into the United States some time prior to 1877.” From specimens in the Canadian National Collection, the first record in Canada is from 1917 in Prince Edward County, Ontario (Douglas et al. 2013). Wood (1977) suggests an even earlier introduction for *S. rugulosus* into the USA (colonial period). However, although five native bark and ambrosia beetles were present, *S. rugulosus* was not among the 42 species of Coleoptera recovered in the archaeoentomological study of refuse pits from seventeenth century colonial Boston (1635–1662) (Bain 1998).

Its entry into California most certainly came much later than colonial times. Smith (1932) noted that "The first authentic record of the occurrence of this pest in California is found in the files of E.O. Essig, who discovered it in Ventura County in 1910." However, Essig (1915) wrote that, "So far this species is recorded as limited in California to the deciduous fruit section adjacent to Ontario, San Bernardino County." Specimens in the *CAS* and *EMEC* from this era (1913) support this assertion (Table 21.2). It was also collected in 1915 in Chino (San Bernardino Co.) and El Modena (Orange Co.), and in 1916 in Pasadena (Los Angeles Co.) (museum survey, *EMEC*). Thus, if *S. rugulosus* were introduced into Ventura County it appears to have quickly established populations further south in the state, and particularly, in San Bernardino County (see red circles in Fig. 21.8). Smith (1932) also reported that it moved rapidly through the state such that by 1932 it was known to occur in the majority of counties in California (Fig. 21.8) and was responsible for injury to fruit trees in the Santa Clara, San Joaquin, and Sacramento Valleys, as well as in parts of southern California. It is somewhat amazing that during a period of rather limited transportation, *S. rugulosus* had the capacity to disperse and hitchhike its way throughout nearly the entire state of California in less than 20 years (1915–1932). It is also possible that Essig's discovery in Ventura Co. in 1910 raised awareness about *S. rugulosus* amongst growers and the limited pest detection community at the time such that already resident populations of the pest in other regions of the state were more quickly identified and documented. Nonetheless, this appears to be another case of an invader whose founder populations colonized southern California.

The ubiquity and abundance of *S. rugulosus* in California is underscored by its long and consistent collection record throughout the state (Fig. 21.8b, c); it is particularly abundant in the Central Valley for obvious reasons and with the major growth of the almond industry in recent years. For example, in 2011–2012, the senior author collected extremely large numbers of specimens on purple and green sticky panel traps targeting detection of the goldspotted oak borer, *Agrilus auroguttatus* Schaeffer, at an almond and oak firewood processing site in Bakersfield (Kern County). From time-to-time *S. rugulosus* has been trapped dispersing through walnut orchards, likely when moving from one almond or fruit orchard to another. In cherry orchards in the state of Washington, Doerr et al. (2008) describe the dispersal of *S. rugulosus* from debris piles of fruit tree cuttings some 50 m distant to the edges of the orchard where they attacked healthy trees.

The beetle utilizes the phloem of branches or small diameter stems as host material. Feeding by adults and larvae at the phloem/xylem interface can lead to girdling, which can cause branch or tree death. When forming brood galleries, females colonize first and construct a short (1–4 cm) uniramous and generally longitudinal egg gallery without a nuptial chamber (Michalski 1973; Wood 1982). The females generally initiate the entrance hole on a lenticel where the soft spongy tissue may allow for easier access and leverage for tunneling through the outer bark (Smith 1932, 1945). Colonization attempts on healthy host trees may lead to a resin exudate (gumming) from entrance holes, which can kill the adults (Smith 1945; UC-IPM 2015). In stressed hosts, gumming may not occur in response to colonization attempts. One male joins the female, and the male removes the frass from the gallery. This gallery is etched relatively deeply onto the surface of the xylem and pupal

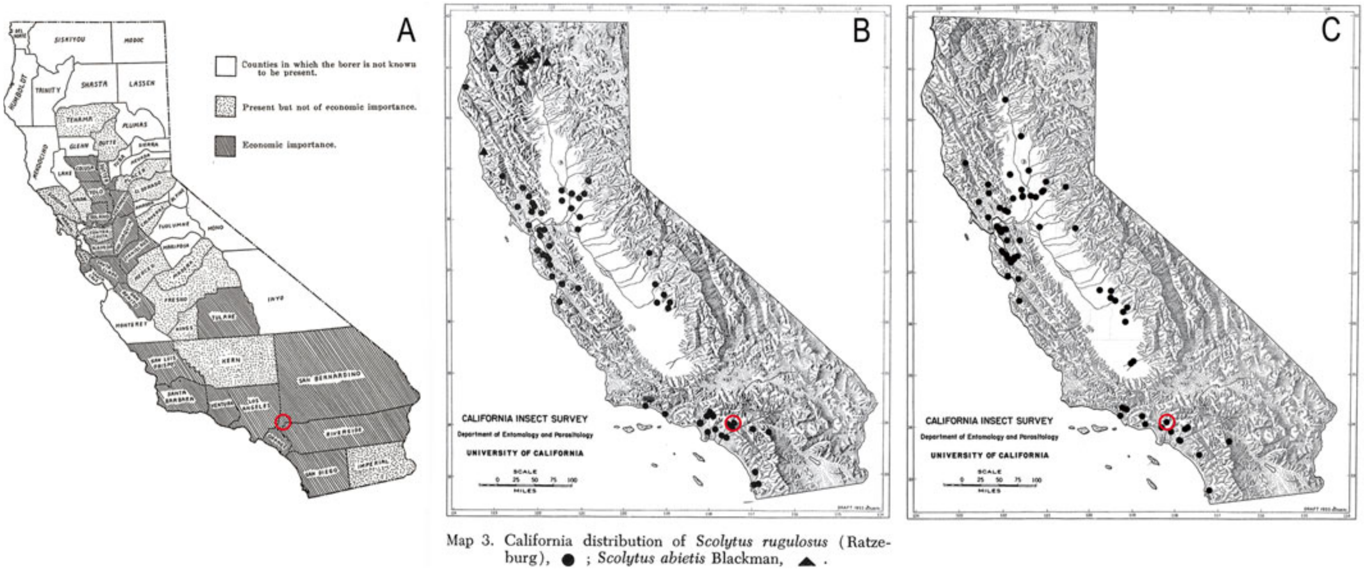


Fig. 21.8 Distribution of the shothole borer, *Scolytus rugulosus* (Müller), in California from the literature and from field survey data and museum records. (**a**) Distribution map from Smith (1932); (**b**) California Insect Survey map from Bright and Stark (1973); (**c**) Map from field and museum survey by the authors (1913-present). *Red circles* indicate the oldest dated collection record (VIII-1913, Ontario, San Bernardino Co., *CAS* and *EMEC*, Essig 1915, 1926; Smith 1932, 1945). The discovery of *S. rugulosus* in Ventura Co. by E.O. Essig in 1910 (Smith 1932) was not substantiated by any corresponding specimens in any of the collections in our museum survey

cells are frequently created deep in the wood (1–2 cm below the surface) (Michalski 1973; Furniss and Carolin 1977; Wood 1982). The gallery system has been described as "centipede-like" (UC-IPM 2015), but the galleries often overlap as a consequence of the aggregating adults, so they lose their distinction. Adults may also kill small twigs by feeding at the base of the bud; these wounds also exude considerable resin or gum (Smith 1945; Furniss and Carolin 1977). In California, Smith (1945) suggested that there are 3–4 generations in the warmest parts of the range, whereas Dreistadt et al. (2004) report 2+ generations per year with adults active primarily from April to June and the larvae as the primary overwintering stage.

The host range is rather broad, and the beetle seems quite capable of exploiting declining branches or stems of many fruit trees (*Malus, Prunus, Pyrus*, etc., and allied species (Appendix 21.I). Dreistadt et al. (2004) list the following pre-disposing factors: root diseases, insufficient irrigation, infestations of other insect pests, whereas Doerr et al. (2008) emphasize that a lack of orchard sanitation may be the key factor leading to colonization of residual healthy trees (in this case, cherry trees). Another stress factor related to the success of *S. rugulosus* is sun scald on newly planted trees or on pruning wounds created in the summer (UC IPM 2015).

It appears that *S. rugulosus* colonizes and kills healthy limbs and trunks when population densities are high, so management steps to reduce density are critical (Dreistadt et al. 2004). These steps include: (1) pruning off heavily infested limbs; (2) removing heavily infested trees from orchards; (3) practicing good orchard sanitation, which involves burning or removing infested or unifested prunings before the growing season starts (UC-IPM 2015). It is important not to leave branches, stems or stumps anywhere near where healthy trees are growing. There are no chemical ecological tools for managing *S. rugulosus*, but a female-produced aggregation pheromone component (4-methyl-3-hexanol) has been isolated from the closely related *S. amygdali* Guerin-Meneville (Ben-Yehuda et al. 2002). This semiochemical may have utility in detecting both *S. rugulosus* and *S. amygdali*. Both of these species were evaluated for their damage to fruit trees in the Mediterranean region (Israel) and the levels of damage to stone (64 % of sampled areas) and pome (18 % of sampled areas) were influenced by "grove" management, resistance to infestation by a local buprestid species; climatic conditions; and the conditions (health) of trees neighboring the orchard under survey (Mendel et al. 1997). Thus, the behavior and management of this pest in the Mediterranean *sensu stricto* appears to be similar to the situation in California.

21.4.1.2 European Elm Bark Beetle, *Scolytus multistriatus* (Marsham)

The European elm bark beetle, *Scolytus multistriatus*, was first detected in North America in 1909 in Massachusetts (Chapman 1910). In contrast to the uncertainty surrounding the introduction of *S. rugulosus*, the entrance of *S. multistriatus* into California was documented by Armitage (1951) when it was collected on the campus of San Jose State University (Santa Clara County) from an ornamental slippery elm, *Ulmus fulvus* (= *U. rubra* Muhl.), tree in what appeared to be a well-established population (Fig. 21.9a, red circle). It was soon thereafter (1955) collected in southern California (Glendale, Los Angeles Co., museum survey, *EMEC*) from Siberian elm,

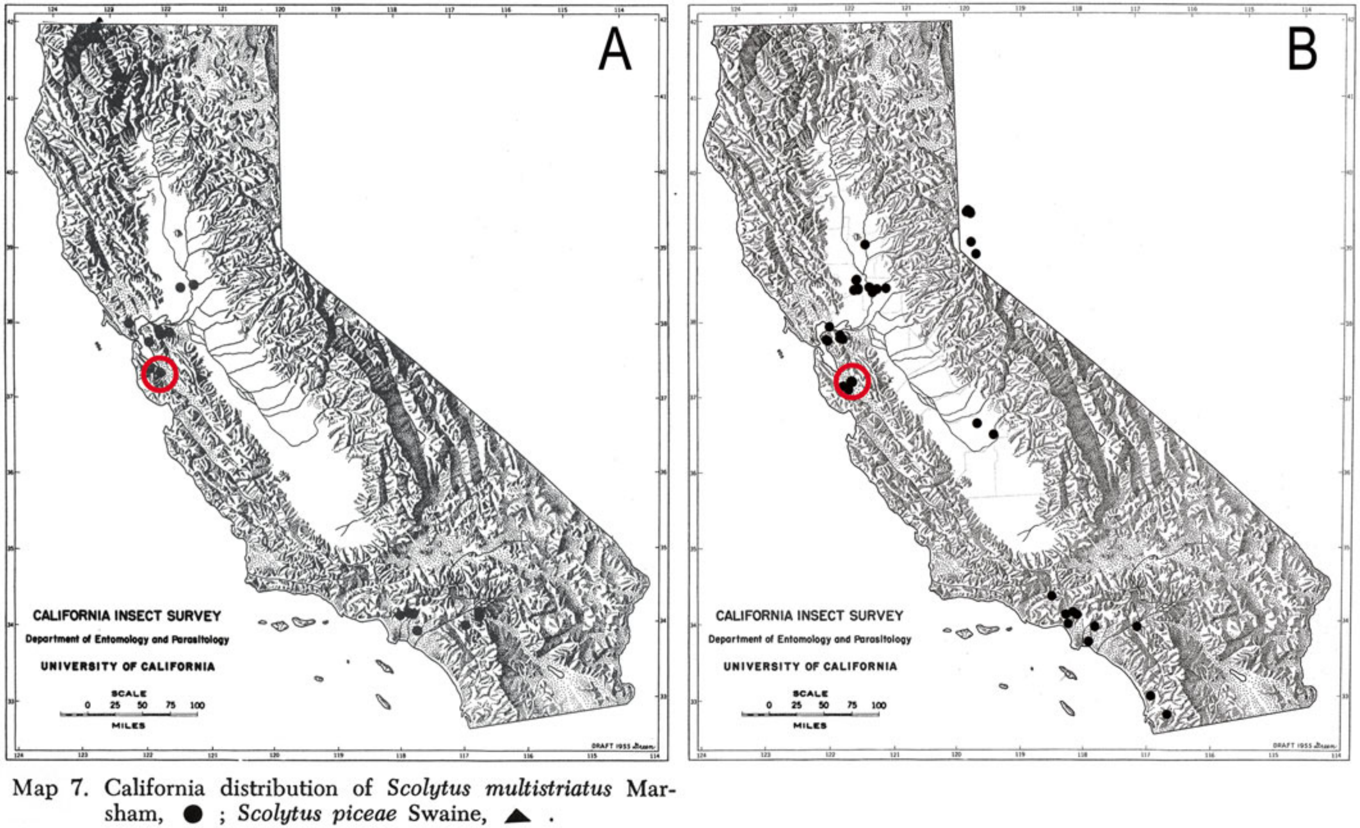


Fig. 21.9 Distribution of the European elm bark beetle, *Scolytus multistriatus* (Marsham), in California from the literature and from field survey data and museum records. (**a**) California Insect Survey map from Bright and Stark (1973); (**b**) Map from field and museum survey by the authors (1951-present). Note Nevada collection records from Carson City, Gardnerville, and Reno. *Red circles* indicate the oldest dated collection record (III-1-1951, San Jose, Santa Clara Co., *CSCA* and *EMEC*, Armitage 1951)

U. pumila L. Although *S. multistriatus* could have made a "long march" across the continent from its original introduction point in the East (Chapman 1910), it appears to have arrived in California as its first destination west of the Mississippi River (Armitage 1951). The remaining portions of the continent were invaded later punctuated by announcements of its "progress" from regulatory and detection entomologists and plant pathologists (Parker et al. 1947; Davidson and Newell 1957; Davidson et al. 1964; Barger and Hock 1971; Claflin and Dooling 1973; Ives and Petty 1976; Buth and Ellis 1981). This likely was a consequence of flight dispersal and elm firewood transport. By 1970, *S. multistriatus* was found in most of the contiguous United States except for Montana, Arizona, and Florida (Barger and Hock 1971), but it has since been collected in Montana in 1973 (Claflin and Dooling 1973), in Arizona in 1976 (B. Celaya, personal communication in Lee et al. 2009), and in Florida in 1997 (T. H. Atkinson, personal communication in Lee et al. 2009).

Since the 1930s, *S. multistriatus* has been known to be a principal vector of the pathogen that causes Dutch elm disease (DED) (Readio 1935), a disease that resulted in 50–75 % mortality of pre-1930s American elm, *Ulmus americana* L., populations in the northern and eastern USA (Bloomfield 1979). The causative agents of DED are the fungi *Ophiostoma himal-ulmi* Brasier & M.D. Mehrota, *Ophiostoma novo-ulmi* Brasier, and *Ophiostoma ulmi* (Buisman) Nannf. (Harrington et al. 2001), and the vector-pathogen interactions have been well studied in Europe (Webber 1990, 2000, 2004; Webber and Brasier 1984). In California, *S. multistriatus* is considered to be widely distributed, but the fungal pathogen is only thought to occur in the San Francisco Bay Area and the greater Sacramento area (Dreistadt et al. 2004). Our survey did not target *S. multistriatus* by using its aggregation pheromone, so the distribution reported here should be considered an underestimate of the true range of the species in California (Fig. 21.9b). This species was largely detected in the survey in urban areas where *U. americana*, and English elm, *U. minor* Mill., are grown as street trees. Surprisingly, it was also trapped in some of the agricultural sites in the Central Valley, perhaps dispersing through orchards between rural residences with planted elm trees.

The chemical ecology of *S. multistriatus* was reviewed in Negrón et al. (2005) (see next section), but there is one unusual host interaction of *S. multistriatus* in California that bears emphasis. A widely planted elm in the Central Valley and in southern California is Chinese elm, *U. parvifolia* Jacq. In flight assays in the Sacramento area, Lee et al. (2010) reported that the response of *S. multistriatus* toward uninfested *U. parvifolia* was low and not different from unbaited traps. This low preference for *U. parvifolia* was consistent with work reported by Švihra and Koehler (1981) where *S. multistriatus* showed a greater flight response to bolts of *U. pumila*, than to *U. parvifolia*. Although *S. multistriatus* has been reported to infest *U. parvifolia* (Brown 1965), many females provided with this host in the laboratory died before ovipositing and survival of progeny was low (Švihra and Volney 1983; Švihra 1998). Dreistadt et al. (2004) also note that the galleries of *S. multistriatus* are "more meandering" on *U. parvifolia* as well, thus this host may tolerate invasion by this beetle. Sanitation of cut elm wood is considered a sound management practice for *S. multistriatus* as long as the wood can be tarped for at least 7 months (Švihra 1987).

21.4.1.3 Banded Elm Bark Beetle, *Scolytus schevyrewi* Semenov

The banded elm bark beetle, *Scolytus schevyrewi*, native to Asia, was detected in the USA in 2003 (Negrón et al. 2005; Lee et al. 2006). In Asia, *S. schevyrewi* occurs in the northern Chinese provinces of Beijing, Hebei, Heilongjiang, Henan, Ningxia, Shaanxi, and Xinjiang, as well as in Korea, Mongolia, Russia, Kazakhstan, Uzbekistan, Kyrgyzstan, Turkmenistan, and Tajikistan (Michalski 1973; Krivolutskaya 1983; Wang 1992; Wood and Bright 1992; Bright and Skidmore 1997, 2002; Liu and Haack 2003). A seven-state survey revealed that *S. schevyrewi* was much more abundant than *S. multistriatus*, in areas of Colorado and Wyoming (Lee et al. 2009). This pattern of competitive displacement is likely to unfold both to the west and east of these Rocky Mountain states, and based on bycatches in various methylbutenol-baited survey traps for the walnut twig beetle, this displacement appears to be underway in California and Minnesota (SJS, personal observation). The key mechanistic components that facilitate the displacement appear to be the competitive advantage of *S. schevyrewi* larvae under the bark, and the more rapid response of *S. schevyrewi* to uninfested elm hosts established through flight studies (Lee and Seybold 2010; Lee et al. 2010, 2011).

Corresponding with the advent of the Age of the Internet, the entomological community became rapidly aware of *S. schevyrewi* as a North American invader in April 2003 when it was detected in a USDA Forest Service-USDA APHIS Plant Protection and Quarantine survey trapping program (Early Detection Rapid Response Pilot Project-EDRR) around pallet recycling sites near Aurora, Colorado and Ogden, Utah (Negrón et al. 2005; Lee et al. 2006, 2007, 2009; LaBonte 2010). However, the nearly simultaneous discovery of *S. schevyrewi* across the western USA in 2003–2004 indicated that the insect was not a recent introduction, but had been present in North America for many years. Indeed, a survey of museum collections and detection records revealed that *S. schevyrewi* had been collected in 1994, 1998, and 2000 in Colorado, New Mexico, and Oklahoma, respectively (Negrón et al. 2005). The specimens had likely been either amongst the unidentified material or misidentified and co-mingled with *S. multistriatus* in these collections. Of relevance to California, were specimens of *S. schevyrewi* collected in 2002 from southern California (Los Angeles Co., City of Industry, 1 July 2002, T. Galindo, collector; Table 21.2, Fig. 21.10) from funnel traps baited with ethanol and α-pinene. This species is now known from 28 U.S. states, as well as five Canadian Provinces (Alberta, British Columbia, Manitoba, Ontario, and Saskatchewan) (CFIA 2007; Lee et al. 2009; Humble et al. 2010; Bousquet et al. 2013; Douglas et al. 2013). It is present in at least 13 California counties ranging from San Diego in the south to Lassen in the north (Fig. 21.10). Surprisingly, it had not yet appeared to have invaded the northern Central Valley during the period of our survey.

The nearly decade long period from when specimens were accessioned into museum collections and the discovery of *S. schevyrewi* in North America was due in part to the morphological similarity of the species with *S. multistriatus* (Negrón et al. 2005). Although *S. schevyrewi* generally resembles *S. multistriatus*, the

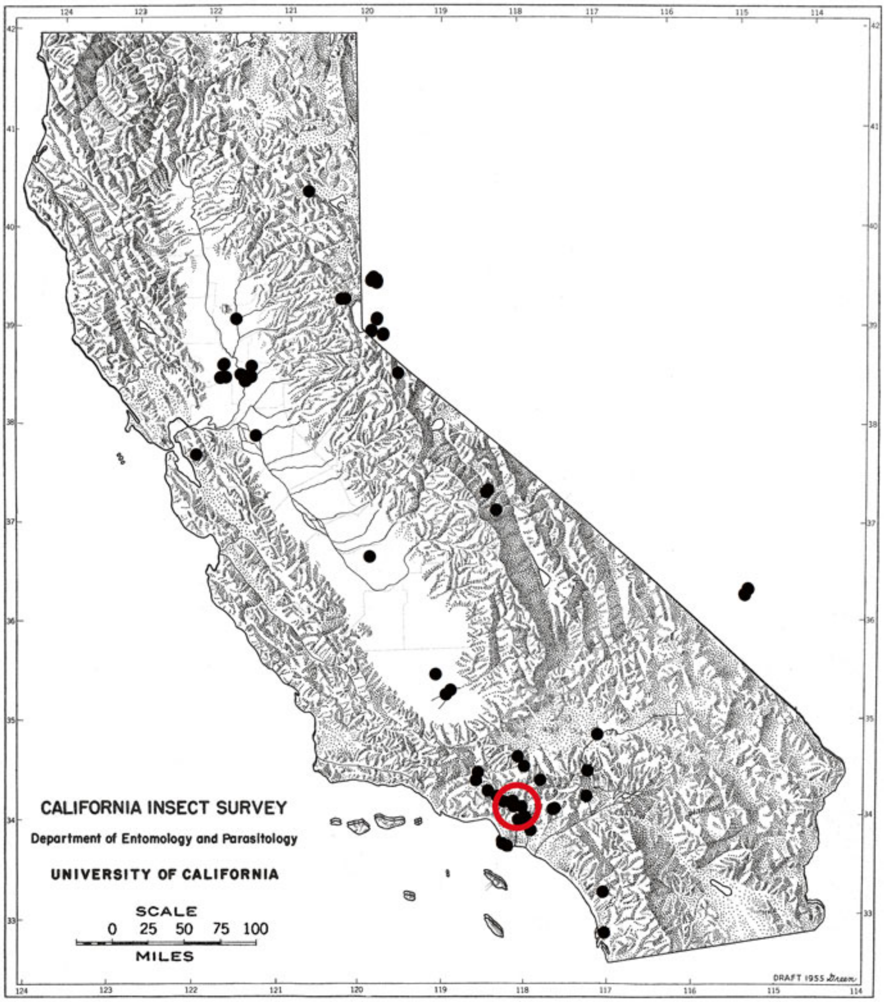


Fig. 21.10 Distribution of the banded elm bark beetle, *Scolytus schevyrewi* Semenov, in California from field and museum survey by the authors (2002-present). Note Nevada collection records from Carson City, Genoa, Las Vegas, and Reno. *Red circle* indicates the oldest dated collection record (VII-1-2002, City of Industry, Los Angeles Co., *CSCA*)

former often has a light-to-dark band across its wing covers (elytra), whereas the latter has tooth-like structures along the margin of some of the ventrites. The two species can be distinguished by size, ventral spine placement, presence/absence of elytral band, and the posteriolateral "teeth" (Lee et al. 2006, 2007; LaBonte 2010). There are also differences in the morphology of the single spine on the second ventrite and its alignment with the anterior margin of the ventrite (Lee et al. 2006). Johnson et al. (2008) provided a molecular technique for separating *S. schevyrewi* and *S. multistriatus* adults and larvae. Information on the basic biology of *S. schevyrewi* in its native range is sparse. The native host range was reviewed by Negrón et al. (2005); additional details of aspects of its host associations in North America are presented in Appendix 21.I). It appears to have a strong preference for *Ulmus pumila* in the western USA, and when cut logs (bolts) of this host were allowed to be colonized by wild populations in the field, *S. schevyrewi* did not differ in emergence density from 10- versus 24-cm-diameter bolts (Lee et al. 2011). In contrast, in research with *S. multistriatus* in northern California, Hajek and Dahlsten (1985a) reported that *Ulmus procera* Salisb. branch diameter demonstrated a strong positive relationship with the density of *S. multistriatus* eggs, attacks, gallery lengths, and emerged adults. In Colorado, *S. schevyrewi* often landed on elm bolts between 12:00 p.m. and 4 p.m.; and near large elm trees, they were captured more frequently on sticky traps at 1.8 and 3.7 m aboveground than higher along the main stem (Lee et al. 2011).

Banded elm bark beetle females construct single vertical egg galleries in the phloem that are about 4–6 cm long and lack a nuptial chamber. Males move about the bark surface searching for entrance holes and mate with multiple females at these entrances. Between 20 and 120 eggs are laid and females guard the egg gallery until death. Larvae develop through four or five instars and migrate to the outer bark to pupate. There are two to three generations in the USA. Larvae, pupae, and adults overwinter, and the adults start emerging in early spring. In Colorado/Nevada, *S. schevyrewi* initiated flight in April/March and ceased in October/September, whereas *S. multistriatus* initiated flight in April/May and ceased in October/September (Lee et al. 2011).

Populations of *S. schevyrewi* have damaged drought-stressed elms in the arid Rocky Mountain and Intermountain regions where *U. pumila* is a primary shade tree. For example, in 2004, 333 infested *U. pumila* trees were removed from Newcastle, Wyoming (Lee et al. 2007). As it displaces *S. multistriatus*, *S. schevyrewi* could threaten American elm populations across the USA. Beetles emerging from diseased American elm logs carried spores of *Ophiostoma novo-ulmi*, the causative agent of Dutch elm disease (Jacobi et al. 2007). Later studies showed that the pathogen could also be transmitted to healthy elms (Jacobi et al. 2013). Before mating, *S. schevyrewi* feeds in twig crotches; this behavior may facilitate transmission of the pathogen by the beetles to living trees.

In the 1970s, studies of the chemical ecology of *S. multistriatus* revealed aggregation behavior based on both female-produced pheromone components and host co-attractants (summarized in Negrón et al. 2005). The role of behavioral chemicals in the aggregation behavior of *S. schevyrewi* is poorly understood. In funnel trap flight assays of semiochemicals in Colorado or Nevada, Lee et al. (2011) demonstrated that *S. schevyrewi* had moderate responses, 3 to 10-fold greater than unbaited control traps, to Multilure (a commercial lure for *S. multistriatus*), 2-methyl-3-buten-2-ol (MB) combined with multistriatin, and MB combined with a plant extract that is included in a commercial formulation of Multilure. In contrast, *S. multistriatus* had a 226 to 259-fold greater response to Multilure than to the control. Both *Scolytus* species showed electroantennographic (EAG) responses to MB, racemic multistriatin, and (+)- and (−)-α-pinene (a host *Ulmus* monoterpene), with the greatest sensitivity to multistriatin. *Scolytus schevyrewi* was more responsive to (−)-α-pinene than was *S. multistriatus* (Lee et al. 2011).

The co-colonization of *Ulmus* by the two *Scolytus* spp. was characterized through tests of long-range flight responses to infested or uninfested small cut logs of *Ulmus americana, U. parvifolia,* and *U. pumila* (Lee et al. 2010). Trials were conducted in Colorado and Wyoming to test the flight response of *S. schevyrewi*; in California to test the response of *S. multistriatus*; and in Nevada to test the responses of both species simultaneously. Studies with *S. schevyrewi* showed that males and females aggregated toward *Ulmus* spp. host volatiles but provided no evidence of a putative aggregation pheromone during the 0–48 or 48–96-h period of infestation. In contrast, *S. multistriatus* was attracted to *U. pumila* over unbaited controls, more to *U. pumila* infested with conspecific females than without, and more during the 48–96- versus 0–48-h period of infestation. This confirmed that male and female *S. multistriatus* aggregated toward host volatiles and that females produced an aggregation pheromone. In a cross-attraction study, *S. schevyrewi* displayed neither flight preference nor interruption to *U. pumila* infested with conspecifcs, heterospecifics, or a mix of both species. Response of *S. multistriatus* was too low to draw conclusions. Although *S. multistriatus* aggregates moderately to host volatiles and strongly to female-derived pheromones emitted after a few days, *S. multistriatus* may have a relative disadvantage by selecting elm hosts more slowly than *S. schevyrewi*, which aggregates very strongly to host volatiles and does not appear to be deterred by the presence of its heterospecific. As noted above, the differential long-range host location strategy may be one factor in a chain of behavioral events that leads to advantageous host colonization and development by *S. schevyrewi*.

Lee and Seybold (2010) examined the sequence of behavioral interactions between the species on and below the bark surface. At the first step in the sequence, host acceptance behavior (i.e., time to tunnel into the host) was monitored among female *S. schevyrewi* and *S. multistriatus*. There was no substantial difference in host acceptance behavior when females were offered small cut logs (bolts) of *U. pumila* infested with con- or heterospecific females. At the second step, mating and oviposition usually follow after a female has excavated a gallery. Mean oviposition per parental female in 1 week was not significantly different among treatments: *S. schevyrewi* at medium density of 2.86 parental females per dm^2, at high density of 5.71 per dm^2; *S. multistriatus* at medium density, at high density; and mixed species (i.e., *S. schevyrewi* and *S. multistriatus* combined, with each at medium density). At the third step, progeny production and progeny size were monitored among the same density treatments, but the number of parental beetles and size of bolts were doubled. Differences in progeny production would reflect larval competition, since the number of eggs initially laid was not different. Both *S. schevyrewi* and *S. multistriatus* were sensitive to intraspecific competition because size of progeny was smaller in high than medium density treatments, but total progeny production was similar at both densities. *Scolytus schevyrewi* was a stronger interspecific competitor than *S. multistriatus*. Smaller *S. multistriatus* progeny, and fourfold more *S. schevyrewi* progeny were produced when both species developed on the same host. Thus, these proximal behavioral events contribute toward the mechanism for competitive displacement in the context of the host colonization behavior of these two elm *Scolytus*.

21.4.2 *Walnut Twig Beetle,* **Pityophthorus juglandis** *Blackman*

The walnut twig beetle is a very small (1.5–2.0 mm or about 1/16 in long), reddish brown bark beetle that bores through the outer bark and into the phloem of the branches and main stem of walnut, butternut, or wingnut trees (Seybold et al. 2013a, b; Hishinuma et al. 2015). This species is characterized by its relatively small size and four to six concentric ridges (asperities) on the upper surface of the pronotum (the shield-like cover behind and over the head) (Fig. 21.11). Like most bark beetles, the larvae are white, C-shaped, and found in the phloem. For this species, the egg galleries created by the adults are generally horizontal (across the grain) and the larval galleries tend to be vertical (along the grain). The male beetle bores into the bark first, creating a push-pin-sized hole in the cracks and furrows or lenticels and leaf scars on the bark surface. Several females then join the male and create the gallery system. The males produce an aggregation pheromone (Seybold et al. 2015), which attracts more males and females to the colonization site and results in a mass attack. The insect appears to be ubiquitous in California, occurring in both walnut orchards and in native black walnut trees growing in windbreaks and surrounding riparian areas. Its distribution reaches from San Diego County in the south to Humboldt and Siskiyou Counties in the north (Fig. 21.12b). It will colonize not only standing live trees, but also recently fallen dead tree stems or branches with fresh phloem.

The discovery of the devastating thousand cankers disease of walnut trees in the western USA (Tisserat et al. 2009, 2011; Utley et al. 2009, 2013; Seybold et al. 2013b) focused attention on the biology and distribution of *P. juglandis* as the disease pathogen's vector. The pathogen, *Geosmithia morbida* Kolařík. Freeland, Utley, & Tisserat, is a mitosporic filamentous fungus that causes restricted necrotic lesions in the phloem of most species of walnut, *Juglans* spp. L. (Tisserat et al. 2009; Utley et al. 2009; Kolařík et al. 2011); butternut, *Juglans cinerea* L. (Serdani et al. 2013); and wingnut, *Pterocarya* spp. Kunth (Hishinuma et al. 2015). Numerous spores (conidia) have been observed on the surface of the wing covers of *P. juglandis* (Fig. 21.13). A group of phoretic mite species (Fig. 21.14) may also be involved in the transfer of the pathogen beneath the bark, as they are with *S. multistriatus* and the Dutch elm disease pathogen, *Ophiostoma novo-ulmi* (Moser et al. 2010). Thus, a plethora of entrance holes created through the outer bark by *P. juglandis* for feeding and/or reproduction result in the transfer of *G. morbida* conidia or yeast propagules to the phloem. The myriad small necrotic areas in the phloem coalesce on the branches and main stem of *Juglans* or *Pterocarya*, likely restricting the flux of carbohydrate within the tree and causing branch dieback and, depending on species, even tree mortality. The time from initial colonization of *Juglans* or *Pterocarya* spp. by *P. juglandis* or initial observations of leaf discoloration in the crown until eventual death of the diseased tree varies with host species, size of the tree, locality, and population density of the vector and pathogen, but crown dieback and sometimes even mortality may occur in a matter of several years (Anonymous 2015b). When the disease has run its course in trees, the xylem surfaces of the branches and even

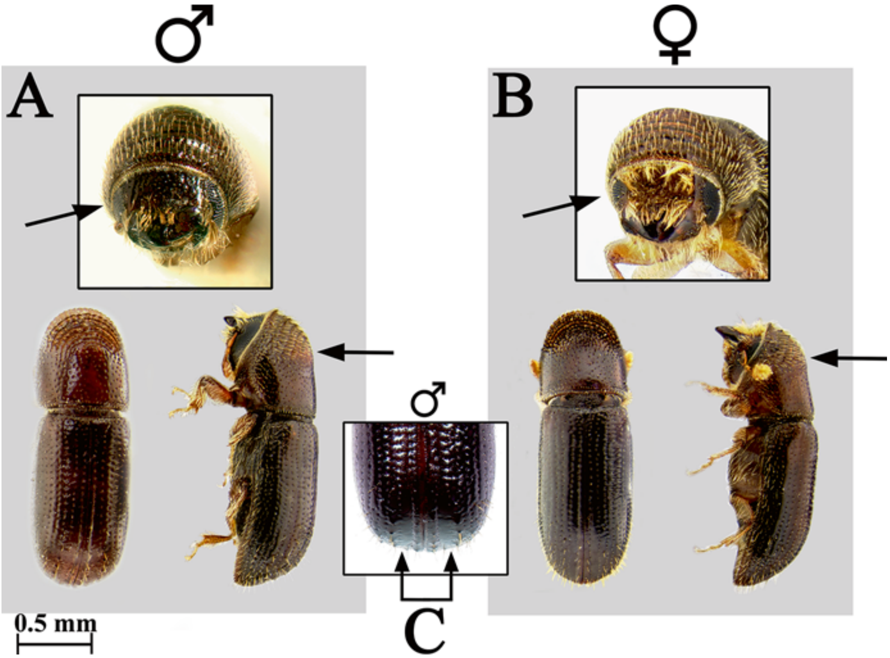


Fig. 21.11 Comparison of morphological characters of male (**a**) and female (**b**) walnut twig beetle, *Pityophthorus juglandis* Blackman. *Arrows* indicate the degree of pubescence on the male and female frons; the apex, which occurs before the midpoint on the anterior half of the pronotum of males and females; and granules on the male elytral declivity (**c**) (Figure by S.M. Hishinuma, UC Davis and ADG, from Seybold et al. 2013a)

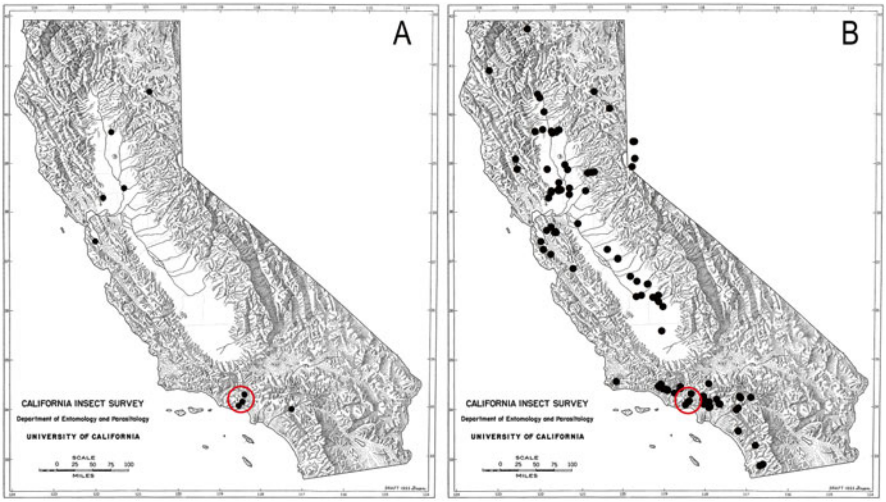


Fig. 21.12 Distribution of the walnut twig beetle, *Pityophthorus juglandis* Blackman in California from the literature and from field survey data and museum records. (**a**) Map from collection records from 1959–1990, with initial collection locations in San Fernando and Tarzana, Los Angeles County (1959 and 1960) *circled* in *red* and (**b**) cumulative collection records from 1959–2015 from field and museum survey by the authors (Note Nevada collection records from Carson City, Genoa, and Reno)

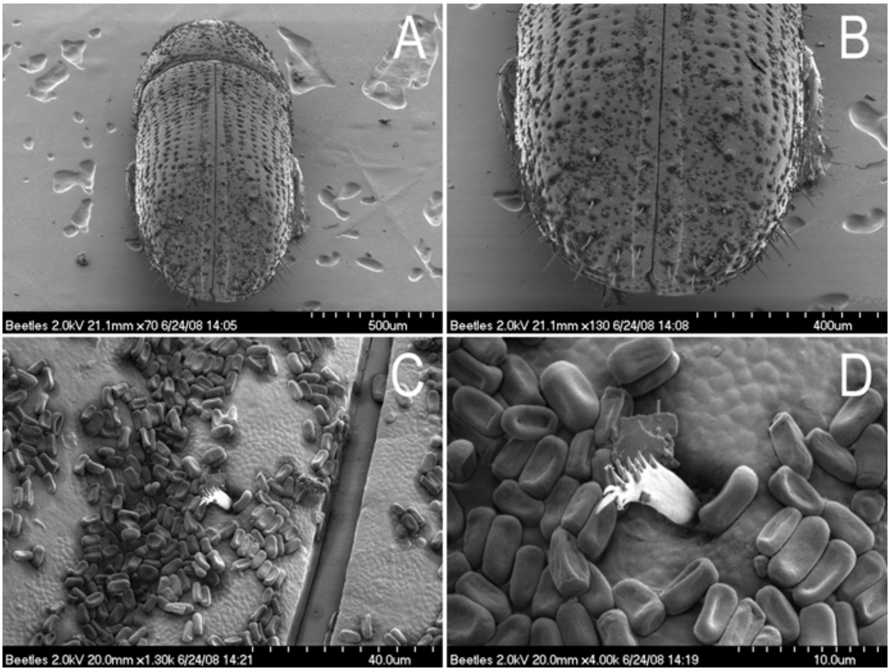
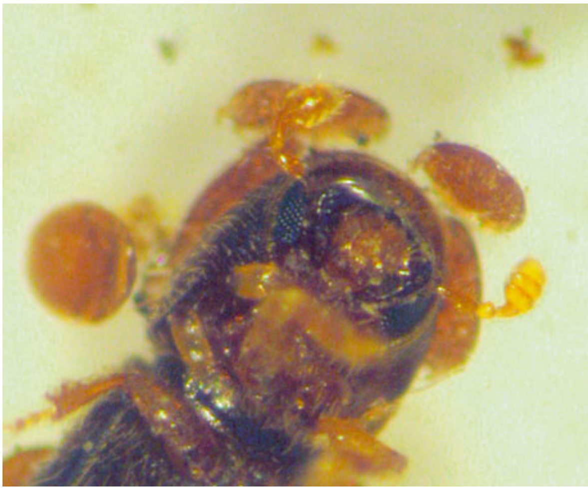


Fig. 21.13 Scanning electron micrographs of the cuticular surface of male walnut twig beetle, *Pityophthorus juglanidis* Blackman, illustrating the presence of conidia likely from *Geosmithia morbida*: (**a**) Posterior perspective of male showing coating of dry spores on surface (scale bar at lower right = 500 µm); (**b**) Posterior perspective of male with the focus on the elytral declivity (scale bar at lower right = 400 µm); (**c**) Enlargement of area around a seta on the elytral suture showing large number of conidia (scale bar at lower right = 40 µm); and (**d**) Enlargement of area around the same seta showing morphology of conidia in and around the setal pit (scale bar at lower right = 10 µm) (Beetles collected in Davis, Yolo County, California, June 13, 2008; photographed June 24, 2008, by ADG and by Delilah F. Wood, USDA Agricultural Research Service Western Regional Research Center, Albany, California)

Fig. 21.14 Male walnut twig beetle, *Pityophthorus juglandis* Blackman, with phoretic mites *Saproglyphus* 51939 n. sp. dn, *Tarsonemus minimax* F., and *Trichouropoda* 51943 n. sp. dn that might be involved in the transfer of *Geosmithia morbida* beneath the bark of *Juglans* spp. (Mite identification, John C. Moser, USDA Forest Service, Southern Research Station, Pineville, Louisiana and ADG photo)



the main stem are often marked by the numerous transverse egg galleries created by female *P. juglandis*.

In California, the insect-fungal complex is widespread in endemic native riparian stands of *Juglans hindsii* (in northern California) and *J. californica* (in southern California) (Griffin and Critchfield 1972; Flint et al. 2010), and cases of the disease on various horticultural varieties of *J. regia* in commercial orchards have been numerous (Geiger and Wood s2009; Graves et al. 2009, 2010; Flint et al. 2010; Yaghmour et al. 2014). Urban plantings, trees along rural highways and agricultural lands, and collections of trees in parks and germplasm reserves have all shown disease symptoms. The insect-fungal complex has also been recorded in California from "Royal" hybrid trees, *J. hindsii x nigra*, and from "Paradox," the horticulturally important *J. hindsii x regia* hybrid used widely in the nut industry as a commercial rootstock for *J. regia*.

21.4.2.1 Distribution and Taxonomy

Walnut twig beetle is thought to be native to Arizona, southern California, and New Mexico, USA and Chihuahua, Mexico (Bright 1981; Wood and Bright 1992; Seybold et al. 2013b), however, its status as an invasive or native species in California is confusing. From the first collection in California (Fig. 21.12a), it has expanded its range to cover much of the state (Fig. 21.12b) and to include nine western (Arizona, California, Colorado, Idaho, New Mexico, Nevada, Oregon, Utah, and Washington) and seven eastern (Indiana, Maryland, North Carolina, Ohio, Pennsylvania, Tennessee, and Virginia) U.S. states (Cranshaw 2011; Seybold et al. 2012a, 2013b; University of Maryland Extension 2014; Wiggins et al. 2014; Indiana Department of Natural Resources 2015). This range has expanded nationally from four U.S. counties in 1960 (Fig. 21.15a) to 127 counties in September 2015 (Fig. 21.15b), with the majority of the *P. juglandis* genetic diversity present among purportedly ancestral populations in Arizona and New Mexico (Rugman-Jones et al. 2015). The current U.S. distribution ranges south to north from Cochise and Hildago Counties (southern Arizona and New Mexico, respectively, 31°24′N) to Spokane and Kootenai Counties (northeastern Washington and northern Idaho, respectively, 47°43′N), and west to east from Humboldt and Benton Counties (California, 123°38′W and Oregon, 123°13′W, respectively) to Bucks County (Pennsylvania, 75°89′W) (Seybold et al. 2012a) (Fig. 21.15b). There is only one collection record from northern Mexico in U.S. collections (*CAS*, *USNM*), and neither *P. juglandis* nor *G. morbida* have been detected in Canada as of December 2015 (Troy Kimoto, Canadian Food Inspection Agency, personal communication). The distribution of *P. juglandis* in North America is not continuous within the geographic limits described here. It has likely been governed by the presence of *Juglans* or *Pterocarya* spp. trees in the landscape and by the degree of human-mediated movement of *Juglans* spp. raw logs or barked wood products (Seybold et al. 2012a). Offsite plantings of

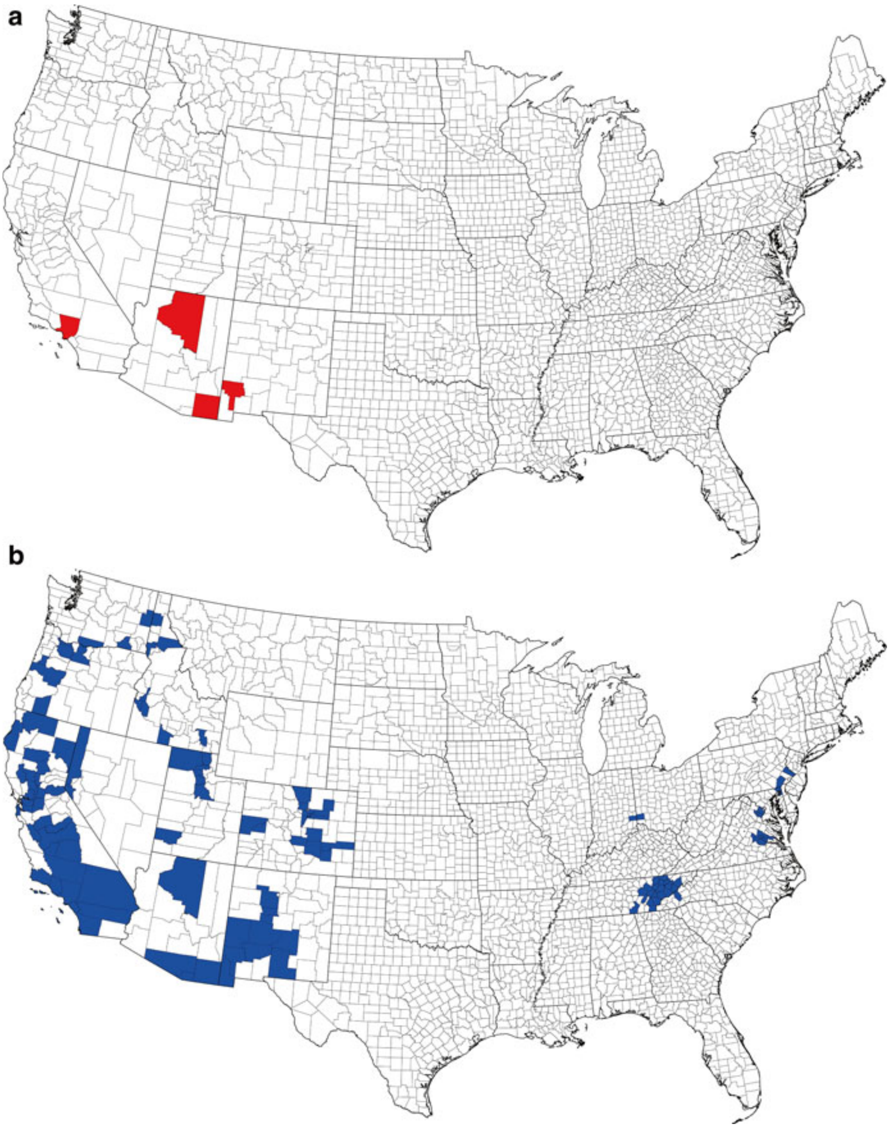


Fig. 21.15 United States of America county distribution records of the walnut twig beetle, *Pityophthorus juglandis* Blackman: (**a**) historic distribution as of 1960 (Bright 1981; Wood and Bright 1992); and (**b**) current distribution (September 2015) based primarily on recent collections by the authors and various cooperators (Figure modified from Rugman-Jones et al. 2015)

eastern black walnut, *J. nigra* L., in the western USA likely facilitated the expansion of the distribution of *P. juglandis* and thousand cankers disease (Tisserat et al. 2011).

Prior to the discovery of thousand cankers disease in the western USA, the North American collection record of *P. juglandis* was sparse. *Pityophthorus juglandis* was initially collected on 15 July 1896 from "black" walnut in Lone Mountain, New Mexico (near Silver City in Grant Co.); this female holotype (*USNM* type No. 41271) was the basis of the species description by Blackman (1928). Blackman (1928) listed little walnut, *Juglans rupestris* Englm. ex Torr., as the host; *J. rupestris* has been synonymized with *Juglans microcarpa* Berland. However, given the locality and our current understanding of native walnut distributions, Arizona walnut, *Juglans major* (Torr. ex Sitsgr.) Heller, was the likely original host for this collection (USGS 2014). Subsequent collections by J.L. Webb (1907), D.J. and J.N. Knull (1947), S.L. Wood (1958–1960) and W.F. Barr (1958) widened the distribution to include Arizona (Cochise and Coconino Cos.) and Chihuahua in Mexico (summarized in Bright 1981). Bright and Stark (1973) reported two records in California: (1) San Fernando, Los Angeles Co. by an unnamed collector on *J. nigra* (specimen reported by Bright and Stark (1973) to be in the California State Collection of Arthropods, Sacramento, CA, *CSCA*) and (2) Tarzana, Los Angeles Co. by an unnamed collector on *J. californica* (specimen reported by Bright and Stark (1973) to be in the *USNM*) (Fig. 21.12a, circled in red). No specific collection dates were reported for these California specimens, but later in their text Bright and Stark (1973) wrote that "It is a recent introduction to the state; the first record is 1959." Bright and Stark (1973) also wrote, "*Geographic distribution and host range*. – *P. juglandis* is distributed in the southwestern states, Arizona, California, and New Mexico where its hosts, walnut trees, are grown," which might suggest that *P. juglandis* was originally native to California. Wood (1977) underscored this uncertainty when he wrote, "Since native potential hosts occur in the area (California), there is a question as to whether an oversight in collecting prior to 1959 occurred or an introduction actually did occur." Indeed, in the Pacific Coast states, the native distributions of *J. californica* and *J. hindsii* extend from southern California (*californica*, Griffin and Critchfield 1972) to southern Oregon (*hindsii*, Griffin and Critchfield 1972; Callahan 2008), and perhaps even into southern Washington for the latter (SJS, pers. observation), suggesting that the ancestoral distribution of *P. juglandis* could have included these states. Nonetheless, population genetics analyses from many collection sites in California, Oregon, and Washington hint at a relatively recent invasion of the Pacific Coast states by *P. juglandis* (Rugman-Jones et al. 2015). Bright (1981) did not report any additions to the California distribution, but listed the specimen documenting the Tarzana locality to be in the *CSCA*, rather than the *USNM*. Wood and Bright (1992) and Bright and Skidmore (1997, 2002) did not report any additions to the western North American distribution of *P. juglandis*; Wood and Bright (1992) listed the host range as *J. californica*, *J. major*, and *J. nigra*. Furniss and Carolin (1977) noted that *P. juglandis* in California and Arizona was one of the few western species in the genus that colonized a hardwood. Cranshaw (2011) and Seybold et al. (2012a) provided updates to the national distribution (Fig. 21.15b).

Pityophthorus juglandis is one of two U.S. representatives of a 19 species subgeneric group of *Pityophthorus* (*Juglandis* group) that is characterized by adults with concentric rows of pronotal asperities; by a generally convex and slightly impressed elytral declivity; by declivital interstriae 1 and 3 that are nearly equal in height; and by glabrous discal elytral interstriae (Bright 1981, 1985; Atkinson 1993). Only *P. juglandis* and *P. pecki* Atkinson (southern Florida, Atkinson and Peck 1994) amongst *Juglandis* group species are known from the USA and only *P. juglandis* is known to colonize walnut. The remaining species in the group have only been collected in Central America or Mexico. Eleven of the nineteen species were described by Wood (1964, 1971, 1976); five by Bright (1985); two by Blackman (1928, 1942); and one by Atkinson (1993). In addition to *P. juglandis*, Blackman (1942) described *P. pudicus* from a specimen collected in the Port of New York from *Sambucus* sp. wood associated with a packing crate originating from Guadalajara, Jalisco, Mexico (Blackman 1942; Bright 1981). Bright (1985) broadened his concept of the *Juglandis* group when he included *P. cracentis*, which has a "distinctly, but slightly impressed" elytral declivity.

Adult *P. juglandis* can be distinguished from most of the other members in the group by the "evenly convex elytral declivity on which interstriae 1 and 3 of the male bear distinct granules, by the broadly flattened, densely pubescent female frons, by the irregular rows of asperities on the anterior surface of the pronotum, by the close, deep punctures on the posterior portion of the pronotum, by the generally distinct rows of punctures in declivital striae 1 and 2, and by the host" (Bright 1981). Bright (1985) modified his key such that *P. juglandis* is now considered to have "punctures in striae 1 and 2 that are indistinct to obsolete," and "declivital interstriae 1 and 3 each with a row of small granules in the male." Bright (1981) considered *P. detentus* Wood to have the most morphological similarity to *P. juglandis*, but the former has a generally shorter body length, declivital interstriae 1 and 3 devoid of granules in both sexes, and pronotal asperities arranged in fairly regular concentric rows. This congener has only been collected in Central America from various shrubs and vines. A Mexican species, *P. insuetus* Bright, collected on the Compositae, also keys out near *P. detentus* (and *P. juglandis*) (Bright 1985), but is smaller with a "more deeply impressed elytral declivity and more distinct strial punctures in striae 1 and 2 on the declivity" (Bright 1985). In the national detection survey, *P. juglandis* has been most frequently confused with *P. crinalis* Blackman and *P. lautus* Eichhoff, two species that can colonize eastern North American hardwoods and *Rhus* spp. (Bright 1981; Atkinson and Peck 1994; Seybold et al. 2013a). These two species are in the *Lautus* subgeneric group; *P. lautus* has been collected on rare occasions from *Juglans*, but *P. crinalis* has not (Bright 1981; Katovich and Ostry 1998).

21.4.2.2 Biology and Community Ecology

Walnut twig beetles overwinter primarily in the larval and adult stages beneath the bark. The beetle is completely dependent on walnut, butternut, or wingnut trees as hosts, and the emerging adult males (and soon thereafter the females) colonize branches of all sizes, but generally not those smaller than 1.5–2 cm (0.5–0.75 in.) in diameter. Unlike many other species of twig beetles (*Pityophthorus*), *P. juglandis* will even attempt to colonize the main stem of trees. These attempts are often successful when the trees are in advanced stages of decline. Entrance holes are not initiated below the soil line. It is never solely a twig-infesting beetle, even in its putative native host (*J. major*) and range (Arizona and New Mexico), where it also colonizes the larger branches and main stem of trees. Dead *J. major* trees with *P. juglandis* galleries on the main stem were observed in this region (Graves et al. 2011, ADG, unpublished data).

In California, adult *P. juglandis* is active in flight nearly year round (Chen and Seybold 2014). It has been caught in pheromone-baited flight traps during every month, although at extremely low levels in December and January. Flight appears to be triggered when ambient air temperatures exceed 65 °F (18–19 °C). Other physical factors such as wind speed, light intensity, and relative humidity also appear to play a role in mediating flight. The beetle prefers to fly when temperature is moderate and wind speed, light intensity, and relative humidity are low; it can be particularly active at dusk (Seybold et al. 2012b; Chen and Seybold 2014). Maximum flight occurs in May and June and then again in September and October. Adult flight activity declines drastically in November (Chen and Seybold 2014). There are three larval instars and likely 2–3 generations per year in California (Dallara et al. 2012, P.L. Dallara, personal correspondence).

In California walnut trees, the only other related insect that might be confused with *P. juglandis* is *X. saxeseni*. Although *X. saxeseni* resembles *P. juglandis* in size and shape, there are clear morphological differences visible under a dissecting microscope or hand lens (Fig. 21.3). Also, as an ambrosia beetle *X. saxeseni* bores into the xylem of walnut trees and feeds on fungi that grow in its galleries. Thus, it colonizes trees that are typically in a later stage of decline than those favored by *P. juglandis*.

Colonization of walnut in California by *P. juglandis* is accompanied by the entry of a series of other subcortical insects that exploit the “carcass” of the declining tree or its insect denizens. The herbivores include the aforementioned *X. saxeseni*, *Cyclorhipidion bodoanum*, and *Hypothenemus eruditus* (Scolytidae); *Rhyncolus cercocarpus* (Thatcher) and *Stenomimus* nr. *pallidus* (Boheman) (both Curculionidae); *Xylotrechus nauticus* (Mannerheim), *Nathrius brevipennis* (Mulsant), and *Phymatodes juglandis* Leng (all Cerambycidae); *Dicerca hornii* Crotch, *Chrysobothris analis* LeConte, *Chrysobothris wintu* Wellso & Manley, and *Anthaxia* sp. (all Buprestidae); *Amphicerus cornutus* (Pallas) and *Scobicia declivis* LeConte (both Bostrichidae); and *Petalium californicum* Fall and *Priobium punctatum* (LeConte) (both Anobiidae). Predaceous insects include *Narthecius simulator* Casey and *Parandrita cephalotes* (LeConte) (both Laemophloeidae), *Temnochila chlorodia* (Mannerheim) (Trogositidae) (rare), and *Agulla* (=*Raphidia*) sp. (Raphidioptera: Raphidiidae), whereas probable parasitoids include *Neocalosoter pityophthori* (Ashmead) (Hymenoptera: Pteromalidae) and *Plastonoxus westwoodi* Kieffer (Hymenoptera: Bethylidae). The pteromalid can be quite abundant when *P. juglandis* are reared from infested branches. Also, the cerambycid *N. brevipennis* has been trapped landing in large numbers (>150) over a 1-week period on live branches or cut branches of *Juglans* in various behavioral assays. *Temnochila chlorodia* has been reared from *Juglans* cut logs under circumstances when both *P. juglandis* and *X. nauticus* have been present. It is likely that *T. chlorodia* had fed on

X. nauticus larvae beneath the bark (Linsley and MacLeod 1942), but in one collection jar in our emergence study, over 20 *P. juglandis* adults were consumed by adult *T. chlorodia*, indicating that this predatory interaction may also occur. It would not be unusual for *T. chlorodia* to be associated with a hardwood bark beetle as Hajek and Dahlsten (1985b) reported that this predator was relatively common in collections of English elm, *Ulmus procera* Salisb. (=*U. minor* cultivar Atinia), that harbored *S. multistriatus* at two sites in northern California. In that survey, however, larval *T. chlorodia* consumed larval *S. multistriatus*.

21.4.2.3 Damage

In addition to the physical damage created by the feeding of the adults and larvae in the phloem, penetration of the bark and transfer of *G. morbida* spores to the phloem by the adults result in an infection of the phloem and necrotic lesions (cankers) that encircle the gallery system. The numerous regions of necrotic tissue from gallery construction and fungal infection may coalesce over time and girdle individual branches and main scaffolds, leading to branch flagging and crown decline (Graves et al. 2009). Presumably the flow of carbohydrates is disrupted as a consequence of the phloem necrosis. In both orchard-grown English walnut trees and landscape black walnut trees, the pattern of decline generally begins in the crown and moves downward as beetles colonize larger and larger diameter portions of the trees. However, in some instances (e.g., in trees previously impacted by crown gall, *Agrobacterium tumefaciens*, shallow bark canker, *Brennaria (=Erwinia) nigrifluens*, or other diseases), *P. juglandis* first colonizes the Paradox or black walnut rootstock or the lower portion of the main trunk of the scion. Although *P. juglandis* appears to have preferences in host selection behavior among species of *Juglans* (S.M. Hishinuma, personal correspondence), all cultivars of English walnut seem to be susceptible to colonization by the beetle. Exhaustive and specific host suitability tests of these cultivars have not been carried out. As the crown is gradually killed in black walnut trees, epicormic branches may sprout from the trunk. This has rarely been observed with *J. regia* trees.

Colonization of walnut trees by *P. juglandis* appears to be a progressive process that can take many years. Trees that are over- or under-watered or that have various root diseases or mistletoe infections may be more susceptible to colonization and may experience an accelerated decline. Ultimately, it appears that colonization by *P. juglandis* and infection by *G. morbida* initiates a decline that is fatal for the tree. The mortality caused by the disease has been largely unquantified in California *J. regia* orchards because in most instances, growers remove the infested walnut trees from orchards before the trees succumb. The decline and mortality have been more obvious in landscape black walnut trees, which are often ignored for many years as their health has waned along California's rural roads and highways. Very little is known of the distribution and impact of *P. juglandis* in wildland forests of the eastern or western USA (Graves et al. 2011; Wiggins et al. 2014). A funnel trapping survey of four national forests of southern California (Angeles, Cleveland, Los Padres, and San Bernardino) revealed limited encroachment of *P. juglandis* on three of the forests (Seybold and Munson 2010), but an extensive distribution and high flight activity in the Los Padres National Forest (Ventura County), which contains the bulk of the native distribution of *J. californica* (Griffin and Critchfield 1972). In an impact survey on national forest lands in Arizona, southern California, and New Mexico, Graves et al. (2011) found cases of dead walnut trees with evidence of *P. juglandis* galleries on six national forests. Of 139 *J. californica* in the southern California survey plots, approximately 5 % were dead and showed evidence of *P. juglandis*; of 194 *J. major* in Arizona and New Mexico, 6.7 % were dead and showed evidence of *P. juglandis*. Crown condition in both regions was worse when *P. juglandis* had been present feeding and reproducing on the trees, which could be interpreted as symptoms of die back occurring in association with the beetle. In the California survey plots, approximately 30 % of the trees had evidence of *P. juglandis*, whereas in the Arizona/New Mexico plots, approximately 50 % of the trees had this evidence (Graves et al. 2011, ADG, unpublished data).

21.4.2.4 Management

Monitoring and Detection

Capturing and identifying the tiny beetle is the key to early detection of the disease in new areas. Detailed guidelines are available for using pheromone-baited traps to detect and monitor *P. juglandis* (Seybold et al. 2013a). A two-page guide for field use and instructional videos are also available at http://www.ipm.ucdavis.edu/thousandcankers. The purpose of this trapping is to detect an incipient population of *P. juglandis* or delimit a known population of *P. juglandis* where it has been recently discovered. The trap and guidelines were developed in northern California native black walnut and English walnut orchard ecosystems with relatively high population densities of *P. juglandis*. The system uses a small multiple-funnel trap baited with the male-produced aggregation pheromone. The trap captures both sexes of the *P. juglandis* while attracting few other insect species, including only low numbers of most other bark or ambrosia beetles (Coleoptera: Scolytidae), making detection of *P. juglandis* easier. The baited traps have been used primarily to detect *P. juglandis* populations. Little information is available on how the traps could be used to assess population levels. If *P. juglandis* is detected in traps, a survey of nearby walnut trees is warranted to assess the extent of beetle infestation and other TCD symptoms. The outer bark can be peeled away to reveal *P. juglandis* galleries in the phloem, a key diagnostic feature for diagnosing the thousand cankers disease complex.

Ideally, pheromone-baited *P. juglandis* traps should be deployed from March through November when ambient air temperatures exceed 65 °F (18–19 °C) (Seybold et al. 2012b; Chen and Seybold 2014). Depending on available resources, more targeted detection protocols may include: (1) Trapping for about 6 weeks from late August through mid-October or late April through mid-June; or (2) Trapping for 3 weeks during May and June and 3 weeks during September and October. A primary consideration when selecting locations for traps and choosing a density of traps in the landscape is whether the objective is to detect an incipient population or delimit a known population. A higher density of traps might be used if the extent of an introduced population is to be assessed. If the goal is to detect a new population of *P. juglandis* over a large land area (e.g., an entire state), only a much lower density of traps would be economically feasible. Whatever the overall goal, traps must be placed near walnut trees.

Control

Currently, sanitation of woody debris is the primary strategy for *P. juglandis* management within orchards. Removal of infested wood piles and prunings should be conducted during the winter months in advance of the primary period of *P. juglandis* emergence and flight activity in the spring (April–June). When possible, infested material should be burned to reduce the build-up of beetle populations. Once a tree becomes infested, no control is available, so it is critically important that growers, practicing arborists, and landscapers be aware of this beetle and the accompanying disease and not move any infested wood. The minute beetles can survive undetected beneath the bark in dry walnut wood; they may emerge later and transmit the disease to other walnut trees. It can take up to 7 months to "clear" infested, firewood-sized pieces of English walnut wood of the *P. juglandis*. It may take longer to disinfest larger pieces of wood with thicker phloem and greater surface area of invaginated bark.

Currently, no insecticides have been shown to reduce mortality rates of trees infested with *P. juglandis*, and chemical control is not recommended at this time. Research is proceeding with systemic insecticides injected into the base of trees, but this will be practical only for valuable shade trees in residential or arboretum settings, but not for forest or orchard applications that involve many trees. Thus, it is important that infested wood is not moved off-site. Infested trees should be taken down, and ground or burned (where allowed) on-site. Because the beetles are very small and difficult to detect, it is important that freshly-cut walnut branches, logs, or burls not be moved or shipped from infested areas, not even for woodworking purposes. Seasoning wood on-site for 2–3 years should allow *P. juglandis* and other woodborers time to emerge at the site of infestation, but it is prudent to have all wood inspected by a knowledgeable entomologist or cooperative extension specialist prior to movement of the material from the site, even when properly seasoned and debarked. The disinfestation of the wood can be accelerated by steam heating the wood to a minimum outer sapwood temperature of 56 °C maintained for 40 min, which is effective for eliminating *P. juglandis* and *G. morbida* from logs of *J. nigra* (Mayfield et al. 2014). However, previously treating barked wood (steam heat or fumigation) does not preclude future attacks by *P. juglandis* if the phloem is still fresh for colonization (Audley 2015; Audley et al. 2016).

21.4.3 *Mediterranean Pine Engraver,* Orthotomicus erosus *(Wollaston)*

The Mediterranean pine engraver, *O. erosus*, is approx. 2.7–3.5 mm long, reddish- to dark brown, and has a moderately concave elytral declivity with four spines on each margin (Fig. 21.16a, b). The second spine is the largest or broadest of the four and is very pronounced in males (Fig. 21.16c, d). Other related species in California that might be confused with *O. erosus* include the pine engraver, *Ips pini* (Say); *Orthotomicus caelatus* (Eichhoff), *Ips latidens* LeConte, and *Ips spinifer* (Eichhoff) (Wood 1982). *Ips pini* also has four declivital spines, but in males the third spine is largest, whereas in females all four spines are similar in size and shape. The other three species only have three declivital spines. Further details on identification of *O. erosus* are available in Cavey et al. (1994) and Lee et al. (2005, 2007).

Aukema et al. (2010) rated *O. erosus* as one of 62 “high impact” nonindigenous, invasive forest insects in the continental USA. These were species of regulatory

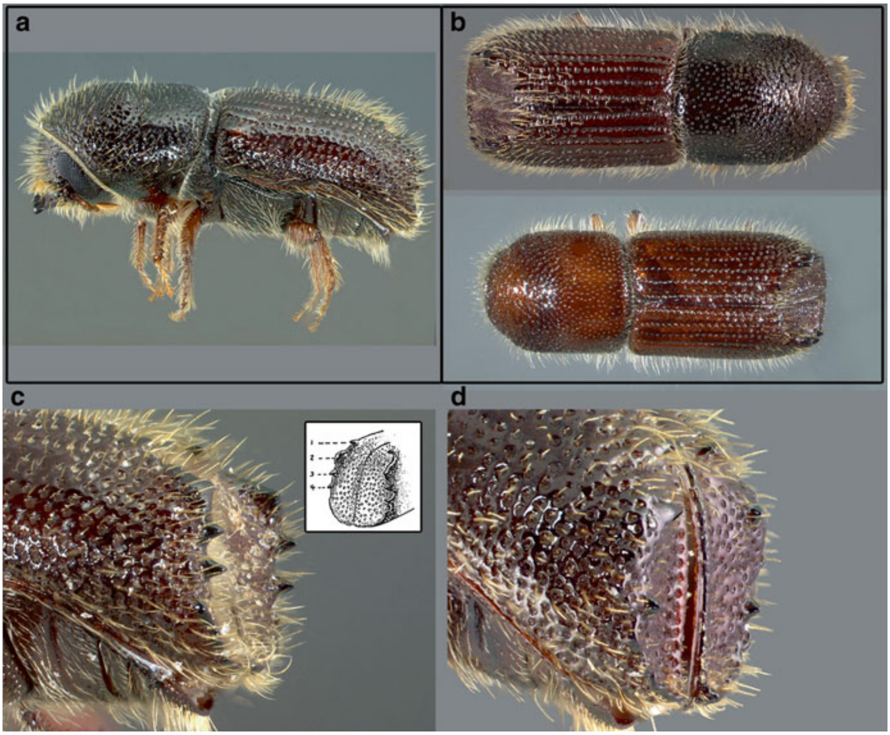


Fig. 21.16 Lateral view of female (**a**) and dorsal views of male (**b**) Mediterranean pine engraver, *Orthotomicus* (*Ips*) *erosus* (Wollaston). The margin of the elytral declivity of males (**c**) is armed with four pronounced spines (inset); the spines are reduced in size on the margin of the elytral declivity of females (**d**) (Photo credits, Dr. Anthony G. Gutierrez (Chief) and Danielle N. Thomas, Molecular Biology Lab, Entomological Sciences Program, U.S. Army CHPPM, Aberdeen Proving Ground, Maryland). Drawing of male elytral declivity (21.16c, *inset*) showing morphology of spines (Cavey et al. 1994)

significance or that had caused notable damage to U.S. forest or urban forest trees. Three hundred and ninety three other invasive forest insects were not considered to be of high impact. *Orthotomicus erosus* was first trapped in California on 25 May 2004 at Chaffee Zoo in the city of Fresno (Fresno Co.) (Fig. 21.17, see red circled collection point), and soon thereafter in five other California counties (Kern, Los Angeles, Madera, Merced, and Tulare), suggesting an established population in the southern Central Valley. At the site of initial detection, 90 % of the 471 specimens were captured in the funnel trap baited with ethanol + α-pinene. In 2005 and 2006, additional survey trapping detected *O. erosus* in Kings, Monterey, San Luis Obispo, and Yolo Cos. Ground checking by the authors and their colleagues at multiple locations in 2004–2007 in Fresno, Tulare, and Kern Cos. revealed large populations of *O. erosus* larvae, pupae, and adults overwintering from December to February. In these areas, *O. erosus* was collected from beneath the bark of several large standing pine stumps (up to approx. 1 m in diameter) and primarily from cut logs (approx. 20 to 50 cm diameter) of widely planted Mediterranean and other non-indigenous pines: *P. halepensis*, *P. pinea*, *P. canariensis*, Scots pine, *P. sylvestris* L., and *P. brutia* (Fig. 21.1). The ground surveys also revealed that *O. erosus* had colonized (and was reared from) cut logs of deodar cedar, *Cedrus deodora* (Roxb.) G. Don, collected in Kingsburg, Tulare Co. The bulk of its current distribution (Fig. 21.17) does not overlap with the distributions of native pines in California, but during the initial surveys vacated galleries were observed on one native species, Monterey pine, *P. radiata* D. Don, in an adventive planting of Christmas trees in Tulare Co., whereas adults were reared from a large cut branch of another native species, gray pine, *P. sabiniana* Douglas ex D. Don, from a green waste pile in Fresno Co. *Orthotomicus erosus* appears to have completely invaded the Central Valley as a specimen was recorded in 2013 from a survey trap in far northern Shasta County (Fig. 21.17).

Several observations in 2004–2007 suggested that *O. erosus* was not an immediately recent introduction, but had been in California for at least 3 years prior to its initial detection. First, the beetle was widely distributed and abundant throughout the eastern half of the southern Central Valley where ornamental pines occur as islands in the landscape. *Orthotomicus erosus* had apparently had sufficient time to locate these trees and debris piles composed of their branches and stems. Second, evidence of *O. erosus* galleries on a weathered and standing, dead tree (*P. halepensis*, approx. 50 cm diameter at breast height) near the community of Arvin in Kern Co. was linked with both a remote location and an older instance of colonization (i.e., at least 3 years prior to the observation in December 2004). Further, in 2004 and 2005, weathered and de-barked, cut pine logs with evidence of *O. erosus* galleries on the wood surface were observed at a golf course in Fresno (Fresno Co.) and at a composting facility south of Visalia (Tulare Co.), both of which indicated older instances of colonization. Thus, the distances between the observation points of some of these remnant galleries, the widespread occurrence of *O. erosus* in the state (Fig. 21.17), and its marked abundance, all suggest that 2000–2001 is a very conservative minimum estimate of the initial introduction of the species to California. The flight trap survey guided by CDFA revealed the presence of these populations; forest entomologists simply would not normally survey the urban forest resources of the southern Central Valley, which is primarily an agroecosystem.

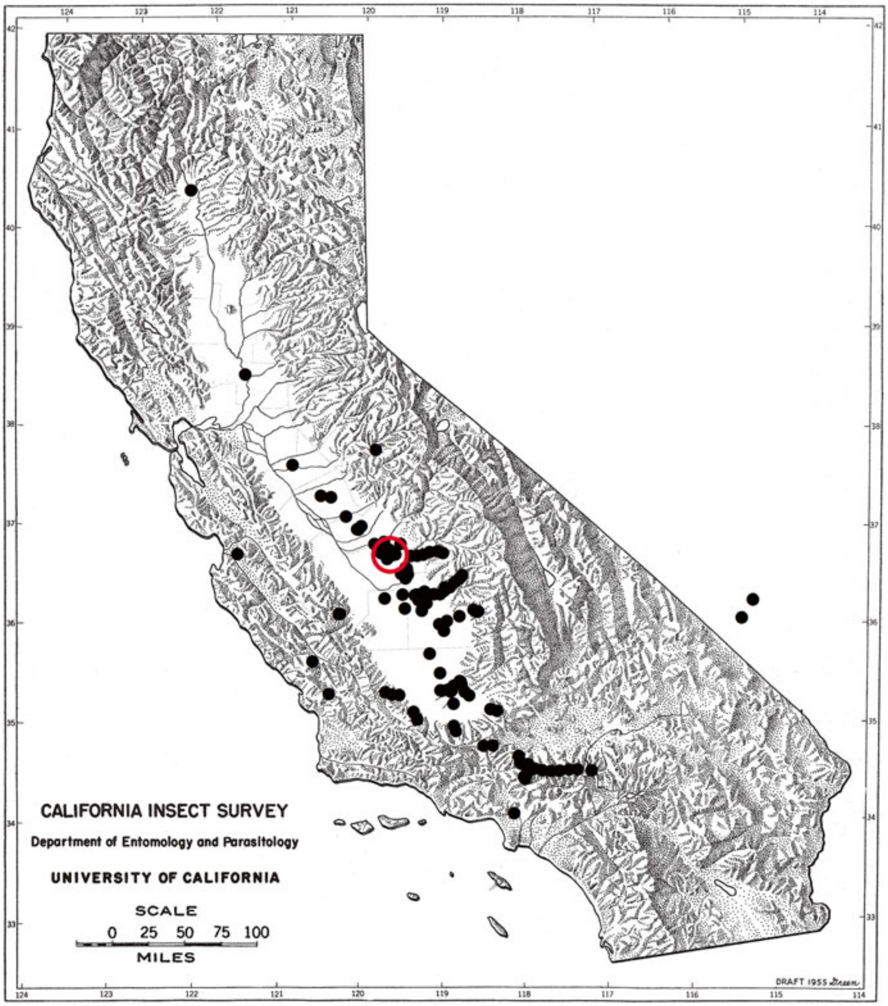


Fig. 21.17 Distribution of the Mediterranean pine engraver, *Orthotomicus* (*Ips*) *erosus* (Wollaston), in California from field survey by the authors (2004-present). Initial collection point *circled* in *red* (V-25-2004, Chaffee Zoo, Fresno, Fresno Co.). Note extreme northern collection point in Shasta Co. (Anderson) and central Sierra Nevada collection point in Tuolumne Co. (Yosemite). The latter is in a region of native coniferous forest. Also note the Clark Co. Nevada collection records from Blue Diamond and Las Vegas (December 2015)

How *O. erosus* entered California is unknown, but it may have arrived with solid wood packing material associated with imported goods. In a survey of 1985–2000 interception records from the USDA APHIS Port Information Network, Haack (2001) concluded that *O. erosus* was the second most frequently intercepted scolytid species at U.S. ports (385 interceptions). The most frequent countries of origin were Spain, Italy, China, Turkey, and Portugal (in descending order). Crating was the most frequently infested type of wooden article, and the associated products were most often tiles, marble, and granite. Ironically, in the analysis, California was not among the top five U.S. states where *O. erosus* had been intercepted. Of the 385 interceptions, only 15 were made at California ports: 14 at Long Beach and one at San Francisco. Of the 15 California interceptions, 12 were made on cargo from China, and one each from France, Korea, and Portugal (RA Haack, pers. comm.). In 2011 it was detected in a survey trap in Cumberland County, North Carolina, but apparently it was not collected again or verified as established by ground survey (NAPIS 2014). In 2015, it was detected with ethanol + α-pinene-baited funnel traps in Blue Diamond and Las Vegas, Nevada (Clark Co.) (Fig. 21.17, JB Knight, Nevada Department of Agriculture, pers. comm.).

Orthotomicus erosus is a well-documented pest of pines and perhaps other conifers throughout its native range in the Mediterranean Basin, the Middle East, Central Asia, and China (Mendel and Halperin 1982; Mendel 1983; Wood and Bright 1992; Yin and Huang 1992; Bright and Skidmore 1997, 2002; Eglitis 2000a; Bright 2014). Very little is known of its occurrence in China, but it has been reported from Anhui, Fujian, Guangdong, Guangxi, Guizhou, Henan, Hunan, Jiangsu, Jiangxi, Liaoning, Qinghai (Hengduan Mountains), Shaanxi, Shandong, Sichuan, Yunnan, and Zhejiang provinces (Yin and Huang 1992; Chen et al. 1998; Bright 2014). In July 2007, this widespread occurrence and host range of the pest in China was confirmed by one of us (SJS), through an examination of the holdings of the Chinese Academy of Sciences insect collection in Beijing. Pfeffer (1994) notes that *O. erosus* is distributed in southern Europe (north to southern Austria), the Crimea, the Caucasus, Asia Minor, the Mediterranean and nearby Atlantic islands (including Madeira Island), Palestine, and North Africa.

Whether its native distribution reaches into central Europe (northern Austria, Germany, Latvia, and Poland) is not clear from the literature (Grüne 1979; Wood and Bright 1992; Yin and Huang 1992; Eglitis 2000a). The species appears to have become otherwise cosmopolitan; it has been reported to have been introduced in Chile (1986), England (1921), Fiji (1985), Finland (1990), South Africa (1976), Swaziland (1983), and Sweden (1988) (Bevan 1984; Browne 1968; Ciesla 1988; Gillerfors 1988; Siitonen 1990; Tribe 1990, 1992; Wood and Bright 1992; Bright and Skidmore 1997, 2002; Eglitis 2000a). Kirkendall (1989) described research on within-family competition between larvae of various bark beetle species in the Ipini, including Norwegian populations of *O. erosus*.

However, the establishment of *O. erosus* in Fiji (1985) (Wood and Bright 1992; Eglitis 2000a) has since been shown to have been incorrect based on a misidentification (Brockerhoff et al. 2006). Furthermore, examination of the records from northern Europe reveals that *O. erosus* is also not likely to be present currently in the British Isles or Scandinavia. Atkinson (1921) reported "large numbers" of all life stages of *O. erosus* in felled *P. sylvestris* in Gloucestershire, England (the "Forest of Dean") and considered the species to be "firmly established." However, Duffy (1953) did not list *O. erosus* among "imported" or "doubtfully indigenous" species of British bark beetles, implying that he considered it indigenous. In contrast, Browne (1968) noted *O. erosus* as established in England, but "too rare to be of any importance," whereas Bevan (1987) ignored *O. erosus* completely in his treatment of forest insects of Britain. Recent collections have only involved interceptions at ports or from cargo without any further evidence of an established population of *O. erosus* in the country (C Tilbury, Forest Research, UK Forestry Commission, Surrey, and MVL Barclay, British Museum of Natural History, London, personal communication, Barclay 2003). In Sweden (Gillerfors 1988; Schroeder 1990) and Finland (Siitonen 1990), reports of *O. erosus* are also from interception records (in this case from imported pulpwood) without any subsequent evaluation of the biology, ecology, impact, or establishment of the species. Siitonen (1990) describes the interception of *O. erosus* in pine pulpwood imported to Finland from Siberia. Since Siberia or any eastern portion of the former Soviet Union has not been documented previously as part of the native range of *O. erosus* (Wood and Bright 1992), there is a strong likelihood that this report of *O. erosus* may also have been a misidentification. Finally, upon further examination, the Norwegian population of *Orthotomicus* used in the competition studies turned out to be *O. proximus* (Eichhoff) rather than *O. erosus* (LR Kirkendall, University of Bergen, pers. comm.), and there are no current records of indigenous or introduced populations in Norway (K Thunes, Norwegian Forest Research Institute, pers. comm.). The cold temperature tolerances of *O. erosus* from California were studied in the laboratory in the Minnesota Department of Agriculture-University of Minnesota BL2 Quarantine Facility in St. Paul, Minnesota, and the mean supercooling point for adult *O. erosus* was approximately −17 °C (1.4 °F) in October, −22 °C (−7.6 °F) in December and January, and −16 °C (3.2 °F) in March (Venette et al. 2009). When adults were cooled to different temperatures and examined for mortality, no significant mortality was observed until temperatures approached the mean supercooling point (Venette et al. 2009). These authors stated that, "From 1964–2004, winter temperatures in the north central U.S. were never warm enough to allow adult *O. erosus* to successfully overwinter." Thus, the potential for establishment, and the biology, ecology, and impact of *O. erosus* in northern climates worldwide bears further scrutiny.

In its native and introduced range, *O. erosus* is considered to be a secondary pest that infests standing pine trees under some form of stress, or recently fallen trees, broken branches, or slash (Bevan 1984; Eglitis 2000a). One report from Zhejiang province in China suggests that it can colonize living, healthy pines and it is the primary colonizer and cause of death of these trees (Jiang et al. 1992). In this instance, a 20 % loss of standing *Pinus massoniana* Lambert was reported from the Zhejiang University Forest (Jiang et al. 1992). *Orthotomicus erosus* has a strong preference for portions of pine logs that are above the soil surface (Tribe 1992). In California we observed it to attack and develop in the stems of standing, declining trees (December 2004 in Fresno, Fresno Co., and July and August 2006 in Visalia, Tulare Co.), and have found galleries on dead branches (approx. 10 cm in diameter) removed from a standing live *P. brutia* (February 2005, near Kingsburg, Tulare Co.). In Israel, where its biology has been the most studied, outbreaks of *O. erosus* have occurred after thinning events, followed by winters with low rainfall or after fires in adjoining stands (Mendel and Halperin 1982; Halperin et al. 1983; Mendel 1983; Mendel et al. 1992). Interactions with fire or hail have also been reported in South Africa (Bevan 1984; Baylis et al. 1986; Tribe 1990; Zwolinski et al. 1995).

For example, Zwolinski et al. (1995) suggested that in South Africa, *O. erosus* has a higher rate of infestation in pines that were previously wounded by hail and infected with fungi through the wounds.

21.4.3.1 Biology and Community Ecology

In most locations throughout its native and introduced range, *O. erosus* has been observed to have two to four generations per year (Grüne 1979; Mendel 1983; Bevan 1984; Tribe 1990; Jiang et al. 1992; Eglitis 2000a). Based on developmental times taken during various seasons, Mendel (1983) estimated that *O. erosus* may have up to seven generations per year in Israel's coastal plain. This prediction has not been confirmed by observation anywhere in the distribution of *O. erosus*. In California, it appeared most active in flight in June and July based on the trapping survey records in Fresno and Kern Cos. Flight at these sites continued into mid-October in 2004 and 2005. Other trapping data from 2005 to 2006 suggested that flight begins in early February and continues into December in Fresno and Tulare Cos. (Lee et al. 2016). In our initial ground surveys in California, new galleries initiated by overwintering adults were first observed in March. First generation adult beetles from spring broods began emerging in June, whereas newly initiated galleries continued to be found in summer and fall to as late as early November. From these observations, *O. erosus* likely develops from egg to adult in 3 months in spring, and likely within 2 months in summer and fall. Given that beetle flight and brood activity were observed continuously from June to October, *O. erosus* likely completes three generations per year in California's Central Valley, possibly initiating a fourth generation in November that overwinters in the immature stages. As expected, the seasonal pattern of development that we have observed in California (three to four generations per year, active from February to November) is the inverse of the pattern for introduced populations in the Southern Hemisphere (Bevan 1984).

An analysis of the host range of *O. erosus* suggests that it can colonize all pines and a few nonpines (Appendix 21.I). Males construct a nuptial chamber, and emit an aggregation pheromone, which consists primarily of 2-methyl-3-buten-2-ol (Giesen et al. 1984; Seybold et al. 2006a, b; Lee et al. 2016). Two or three females mate with him; each female excavates an egg gallery in opposite directions laying 26–75 eggs. Larvae, white to cream-colored, legless grubs and up to approx. 3 mm long, mine away from the egg galleries in the phloem and can score the outer xylem. Thus, the nuptial chamber and egg galleries comprise the central tunnel; each is approximately 1.2–12.5 cm long with numerous larval tunnels extending outwards. Adults may initiate a new gallery in another location.

Interactions of *O. erosus* with various pathogenic and sapstaining fungi have been noted in South Africa (Zhou et al. 2001, 2002a, b) and Tunisia (Ben Jamaa et al. 2007), and some of the ophiostomoid fungi isolated from *O. erosus* may contribute to its impact on trees or wood products. For example, *Ophiostoma ips* (Rumb.) Nannf. [previously *Ceratocystis ips* Rumbold] was associated with 60 % of 665 samples of adult *O. erosus* or its galleries on trap logs of Mexican weeping pine, *P. patula*, and slash pine, *P. elliottii* (Zhou et al. 2001). Of six other fungi recovered in this study, none were present in more than 1.7 % of the samples. *Ophiostoma ips* was also isolated from *O. erosus* and from cambium associated with new bark beetle galleries in cut logs and standing trees of maritime pine, *Pinus pinaster* Ait., and *P. radiata*, both of which had been previously infected with the fungus *Verticladiella alacris* Wingfield & Marasas (Wingfield and Marasas 1980). *Orthotomicus erosus* has also been associated with several other fungal species including *Graphium pseudormiticum* M. Mouton & M.J. Wingfield, and *Leptographium lundbergii* Lagerb. & Melin (Wingfield and Marasas 1980; Mouton et al. 1994; Zhou et al. 2001). *Graphium pseudormiticum* was isolated from adult *O. erosus* recovered from *Pinus* sp. bait logs (tree species not reported); *L. lundbergii* was isolated from adult *O. erosus* or its galleries in *P. patula* and *P. elliottii* trap logs (Zhou et al. 2001). In South Africa, an analysis of resin exudation, sapwood discoloration, and lesion length in 2-year old pines (*P. radiata*, *P. elliottii*, and *P. elliottii x caribaea*) caused by inoculations of *O. ips*, *L. lundbergii*, and *Leptograpium serpens* (Goid.) M.J. Wingfield suggested that *O. ips* gave rise to longer lesions than the other two fungi, but that none of these fungi should be considered as serious pathogens of aboveground portions of young pines (Zhou et al. 2002a, b). In Spain a small proportion of a sample population of *O. erosus* were reported to carry the pitch canker fungus, *Fusarium circinatum* Nirenberg and O'Donnell (Romón et al. 2007). In California, the mycoflora of *O. erosus* overwintering in *P. canariensis* and *P. halepensis* was heavily dominated by *Ophiostoma ips* (S. Kim et al. unpublished data, Iowa State University), which agrees with phytopathological studies of *O. erosus* in South Africa (see above) and North Africa (Ben Jamaa et al. 2007).

A variety of natural enemies and subcortical competitors regulate the populations of *O. erosus* in its native and introduced range (Mendel and Halperin 1981; Mendel 1985, 1986). A life table analysis in *P. massoniana* in Guangxi province in China showed that mortality is distributed as egg (23 %), larvae (19 %), pupae (14 %) and adult (8 %), and natural enemies included spiders, staphylinids, mites, parasitoids, ants, and fungi (Chen et al. 1998). Yang (1996) listed *Rhopalicus tutela* (Walker), *Roptrocerus xylophagorum* (Ratzeburg), *Eurytoma blastophagi* Hedqvist, and *Metacolus unifasciatus* Förster as hymenopterous parasitoids of *O. erosus* in China. Kfir (1986) released Israeli populations of *Dendrosoter caenopachoides* Rusch. (Braconidae) and *Metacolus unifasciatus* Förster (Pteromalidae) in South Africa to enhance the biological control of *O. erosus*. Documented predators in the Mediterranean have included birds (Mendel 1985) and colydiid beetles (Mendel et al. 1990; Podoler et al. 1990). Several species of Histeridae and Tenebrionidae (both Coleoptera) may also feed on *O. erosus* (Mendel et al. 1990). Amezaga and Rodríguez (1998) have studied resource partitioning by *O. erosus* and three other scolytids in northern Spain. With cut stems of *P. radiata* and *P. sylvestris* (18–30 years old) they found that the pine shoot beetle, *Tomicus piniperda* L., generally flew earlier in the season than *O. erosus* and occupied a greater portion of the niche of *O. erosus* than vice versa. *Orthotomicus erosus* tended to colonize thinner barked portions of the cut stems and these authors suggested that bark thickness appeared to be a good segregation factor for the four species along the tree stems. In California, however, we have observed colonization by *O. erosus* in logs with a range of bark thicknesses, including extremely thick bark (e.g., in lower stem sections of *P. canariensis* and *P. pinea* from very large trees). In these instances the larvae and pupae may not reside immediately on the surface of the xylem, but may be found on the outer bark side of the phloem or almost in the outer bark itself.

In multiple instances in California field surveys, active and old galleries in cut logs suggested extremely large populations of the insect without much evidence of either natural enemies or interspecific competition. Hand collecting and subsequent funnel trapping experiments with more targeted lures (Lee et al. 2016) have so far revealed only 11 species of Coleoptera and two species of Hymenoptera associated with *O. erosus*. One fairly common associate that is a likely predator of immature stages is *Microprius rufulus* (Motschulsky) (Coleoptera: Colydiidae), which is also apparently an exotic species to the USA, but has been well established in the desert areas of Southern California for at least 65 years (Ivie et al. 2001). We have observed this colydiid nearly ubiquitously in the galleries of *O. erosus* and caught it in *O. erosus* pheromone-baited flight traps in the southern Central Valley, which reflects a California range-extension for *M. rufulus* (Ivie et al. 2001). In several instances we have also found larvae of *T. chlorodia* (Trogositidae) beneath the bark in *O. erosus* galleries and have trapped adults in *O. erosus* pheromone-baited traps. These adult predators consumed adult *O. erosus* in the trap cups. We have not recovered any larvae or adults of predaceous checkered beetles (Cleridae) from beneath the bark of infested logs or from survey traps or pheromone-baited traps in the currently infested area. We have observed odorous house ants, *Tapinoma sessile* (Say) and thief ants, *Solenopsis molesta* (Say) (Hymenoptera: Formicidae) feeding on larvae of *O. erosus* beneath the bark of colonized logs that had been subjected to flooding in Tulare Co. Argentine ants, *Linepithema humile* (Mayr), which occur in sympatry with *O. erosus* both in the Mediterranean Basin and in California, did not appear to negatively impact the colonization success of *O. erosus* in Portugal (Henin and Paiva 2004). We have noted only two other scolytids beneath the bark in association with *O. erosus* in California: the California fivespined ips, *Ips paraconfusus* Lanier and *X. saxeseni*. Both of these associates were found in *P. halepensis*, but they have been rare in our rearings from *O. erosus*-infested logs. Late stage coleopteran associates of *O. erosus* include *Cossonus crenatus* Horn (Curculionidae) in old galleries (*P. brutia* and *P. pinea*); a bark anobiid, likely *Ernobius mollis* (L.) (Seybold and Tupy 1993), in *P. brutia* branches that were previously colonized and vacated by *O. erosus*; and a longhorned woodborer, *Eucrossus villicornis* LeConte (Cerambycidae), reared from *O. erosus*-infested *P. halepensis* logs. Interestingly, two stored products beetles, *Cryptolestes ferrugineus* (Stephens) and *Tribolium castaneum* (Herbst) have been collected both beneath the bark with *O. erosus* and in pheromone-baited flight traps. Sokoloff (1974) notes that *Tribolium* spp. are often found beneath the bark as semi-predators and scavengers, and that this may have been the ancestral habitat.

21.4.3.2 Chemical Ecology and Future Impacts of *O. erosus* in California

The pheromone system of *O. erosus* has been studied in Europe, Israel, and South Africa (reviewed in Seybold et al. 2006a). Males produce both ipsdienol and 2-methyl-3-buten-2-ol, which are active synergistically to elicit flight from both sexes. Research questions that needed to be addressed with the invasive population in California included (1) what are the optimal release rates of the two terpene alcohols?; (2) what is the optimal enantiomeric composition of the ipsdienol?; and (3) what is the effect, if any, of release rate and enantiomeric composition of host monoterpene co-attractants (e.g., α-pinene) on the flight response? (Seybold et al. 2006a; Lee et al. 2016). The answers to these questions were a necessary first step to improving the detection lure for *O. erosus*. The question of the co-attractant effect of monoterpenes was prompted by the relatively high catches of *O. erosus* at the original detection site in Fresno Co. to traps baited with the second detection lure (i.e., ethanol + α-pinene). The other two detection traps in the survey (neither of which contained α-pinene in the lure) only accounted for 10 % of the specimens. Thus, we hypothesized that α-pinene may play a role in the flight response of *O. erosus*.

An improved lure [2-methyl-3-buten-2-ol, (−)-ipsdienol, and α-pinene] was developed (Seybold and Downing 2009; Lee et al. 2016), and the host monoterpene co-attractant was very important to the ultimate efficacy of the lure. The release rate of the monoterpene appeared to be more important than its enantiomeric composition in the flight assays (Lee et al. 2016). Note that the enantiomeric composition of the ipsdienol was reported erroneously to be (+)-ipsdienol (Seybold and Downing 2009). The improved lure was used to both estimate the innate dispersal distance of *O. erosus* at two Central Valley locations and to install and monitor extensive trapping transects that penetrated the U.S. National Forest System in the Sierra Nevada and the Transverse Mountain Range (Seybold et al. 2008a, 2010). This work indicated dispersal distances of up to 10 km by a very small percentage of the released population and considerable invasion of the wild land forested area in California (Fig. 21.18). One specimen was even trapped in 2012 responding to (α)-pinene and ethanol at one of the entrances to Yosemite National Park in Tuolumne Co. (Fig. 21.17). Lee et al. (2008) provided an analysis of which native pines might be impacted by *O. erosus* once its populations expanded from their Central Valley point of introduction. Expansion of the range to the Sierra Nevada, Coastal, and Transverse mountain ranges would likely lead first to feeding and reproduction in native *Pinus sabiniana* Douglas *ex* D. Don*,* which encircles the Central Valley at foothill elevations (500–1000 m) (Griffin and Critchfield 1972). Lee et al. (2008) further speculated that at higher elevations, *O. erosus* could potentially reproduce in native populations of *P. contorta murrayana, P. jeffreyi, P. lambertiana,* and *P. ponderosa,* although harsher high elevation climates may restrain its invasion into these ecotones (Venette et al. 2009). These authors also predicted that *O. erosus* would spread easily to the Los Angeles Basin and Inland Empire regions of California where the weather is warm and exotic *Pinus* spp. are planted widely. Urban Las Vegas, Nevada (Clark Co.) has a comparable habitat and urban host type. Catches in trapping transects in 2009 and 2010 revealed that this expansion had already occurred as had expansions into the Antelope Valley area (Lancaster, Palmdale,

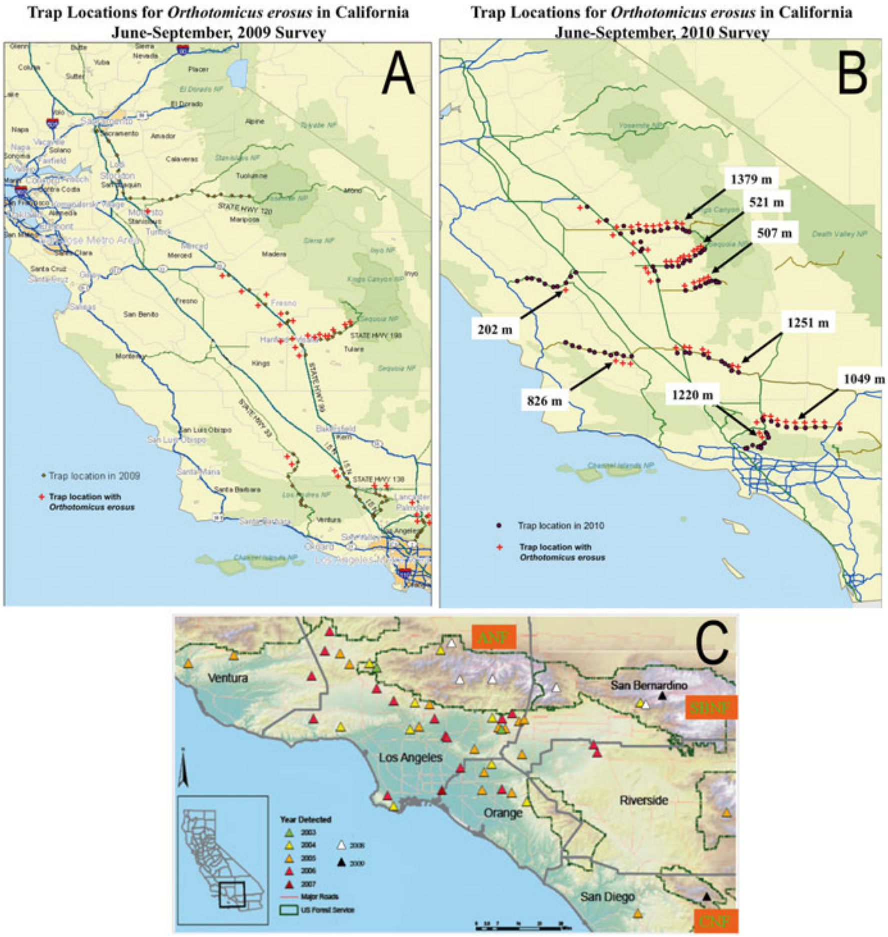


Fig. 21.18 Trap locations (*dots*) and detections (*red crosses*) of the Mediterranean pine engraver, *Orthtomicus* (*Ips*) *erosus* (Wollaston) from long transect surveys in 2009 (**a**) and 2010 (**b**) in California's Central Valley and surrounding foothill and mountane ecosystems (Seybold et al. 2008a). Elevations at the end of some transects are indicated because higher elevations are associated with California native conifers (Griffin and Critchfield 1972). (**c**) Similar survey for the red-haired pine bark beetle, *Hylurgus ligniperda* (F.) was carried out on U.S. National Forest Lands (Angeles, Cleveland, and San Bernardino) with positive detections in 2008 (*white triangles*) and 2009 (*black triangles*) (Seybold 2008)

Victorville) and into areas with native *P. monophylla* on the Tehachapi mountain range and adventive stands of *P. radiata* in the coastal locations to the west of the Central Valley (Fig. 21.18a, b). In all of these instances, collection of *O. erosus* in these California native hosts has not yet occurred and the impact of *O. erosus* on these trees in native forest areas has not been quantified.

The probability of introduction of *O. erosus* to California and Las Vegas, Nevada may have been enhanced by climate and by the ubiquitous plantings of exotic Mediterranean pines, which are familiar hosts for *O. erosus*. For example, Niemelä and Mattson (1996) noted a similar phenomenon with the successful introduction of the pine shoot beetle, *T. piniperda*, and the ornamental plantings of *P. sylvestris* and *Pinus nigra* in the lower Great Lakes region of North America. However, the ultimate success of *O. erosus* in California will depend on its capacity to co-occur with a rather dense pre-existing guild of subcortical insects in pines (Seybold et al. 2006a). In California's Central Valley, the Mediterranean pines tend not to be colonized frequently by native bark beetles (particularly obvious by its relative absence is *I. paraconfusus*), so newly introduced populations of *O. erosus* may have encountered an optimal scenario for establishment that included favorable climate, extremely suitable hosts, limited predation, and limited interspecific competition. In the various California native forest ecosystems, *O. erosus* will likely encounter anywhere from two to ten other pine-infested bark beetles or woodborers that also have a strong preference for the main stem of declining pines, and the allomonal effects of these competitors may limit the access of *O. erosus* to suitable phloem for feeding and reproduction. The redhaired pine bark beetle, *H. ligniperda* (see immediately below), will face the same crowded *niche* as it expands its invading populations into native California pines.

21.4.4 Redhaired Pine Bark Beetle, **Hylurgus ligniperda** *(Fabricius)*

The redhaired pine bark beetle, *H. ligniperda*, is a relatively long and narrow black beetle (Fig. 21.19a, b) about 6 mm long by 2 mm wide. Coarse, reddish to golden hairs are particularly noticeable on the posterior slope of the wing covers (elytra), and it lacks teeth, spines, or bumps on the posterior margins of the elytra (Fig. 21.19c) (Liu et al. 2007). It is unique morphologically among the California fauna and the only member of its genus in the State. Males and females can be differentiated by the morphology of the sixth and seventh abdominal tergites, which is likely related to the stridulation by the male (Liu et al. 2008).

The first established and overwintering population of *H. ligniperda* in North America was found in 2000 in Monroe County, New York near the city of Rochester (Petrice et al. 2004 and references therein). In 2001, the beetle was found in the two adjacent counties of Ontario and Wayne. In 2003, it was detected at two locations in Los Angeles County, California in multiple funnel traps; in 2005 and 2006 it was collected from stumps and woody debris from the frequently planted Mediterranean pines, *P. halepensis* and *P. canariensis* in the southern California urban landscape. It was especially abundant in cut logs in contact with the soil surface in and around green waste piles. When detected in survey traps, the majority of specimens responded to ethanol and (−)-α-pinene, which supports a survey of various baits conducted in New York (Petrice et al. 2004). The first detections in California occurred in 2003 at Bear Divide Guard Station, Angeles National Forest, and at the Frank G. Bonelli Regional County Park (both Los Angeles County) (Fig. 21.20, see red circles), which are both located near heavily urbanized areas. However,

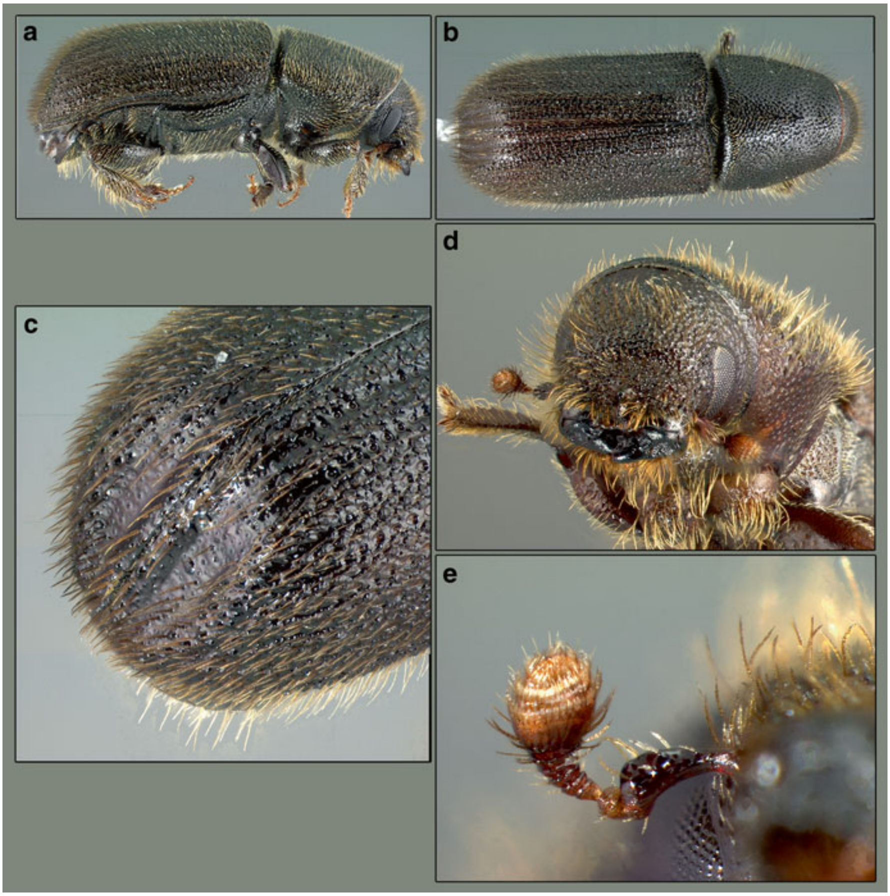


Fig. 21.19 Lateral (**a**) and dorsal (**b**) views of adult male redhaired pine bark beetle, *Hylurgus ligniperda* (F.). Dense, red setae on the elytral declivity (**c**) and longitudinal tubercle (projection) on the frons of the head (**d**). Male antennal club (**e**) (Photo credits, Dr. Anthony G. Gutierrez (Chief) and Danielle N. Thomas, Molecular Biology Lab, Entomological Sciences Program, U.S. Army CHPPM, Aberdeen Proving Ground, Maryland)

specimens have also been trapped on USDA National Forest lands in more remote locations in Los Angeles, Orange, Riverside, and San Bernardino Counties. Ground checking for this species on 10 March 2005, and 7 March and 13 April, 2006 at Bonelli Park and Descanso Gardens (Los Angeles Co.) revealed that *H. ligniperda* was frequently found in large dimensional (minimum 15–20 cm diameter) cut or broken logs of *P. halepensis* and *P. canariensis.* At these times the beetles were newly colonizing and ovipositing in this fresh host material. Egg galleries were about 6 cm in length. Most of the galleries were on the undersides of the logs that were in contact with soil or, in one case, concrete, and beetles often tunneled into the logs from the cut ends. Mating pairs of *H. ligniperda* were also collected on

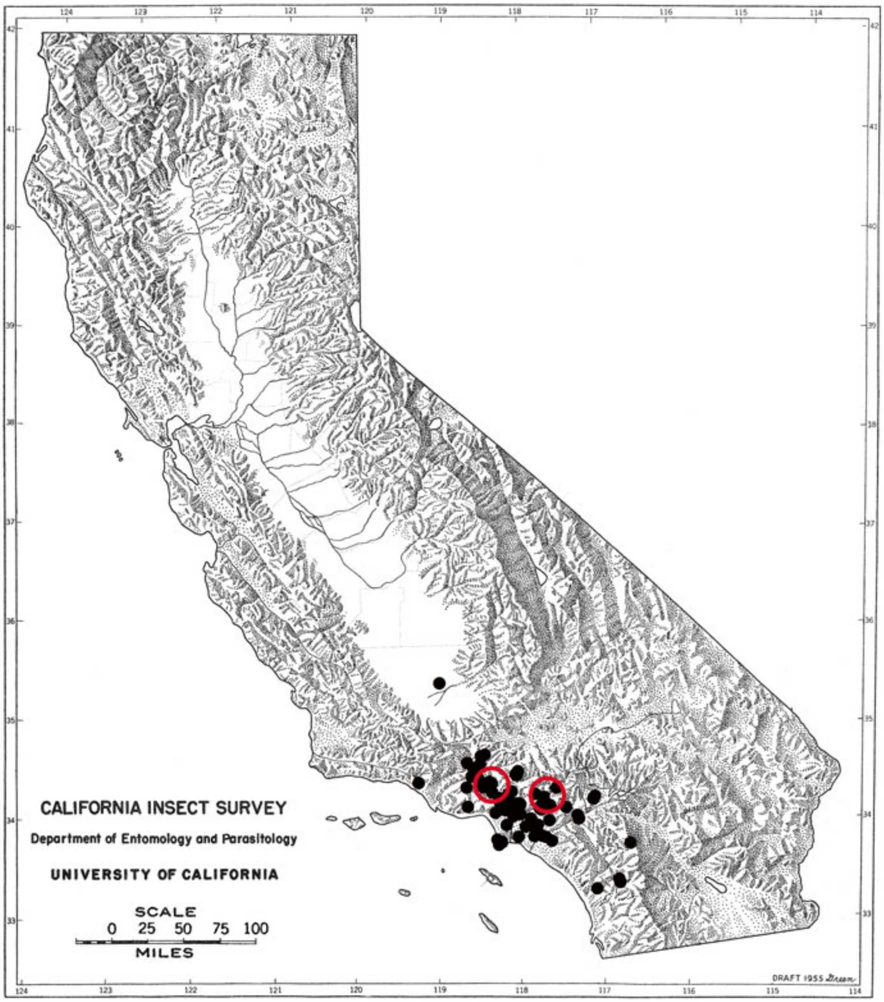


Fig. 21.20 Distribution of the redhaired pine bark beetle, *Hylurgus ligniperda* (F.), in California from field and museum survey by the authors (2003-present). The two initial Los Angeles Co. collection points are *circled* in *red* (VII-10-2003, F.G. Bonelli Regional Park, San Dimas and VIII-8-2003, Bear Divide Guard Station, Angeles National Forest)

10 March 2005 at Bonelli Park from a stump of a *P. halepensis* tree that had broken during a major storm on 27 December 2004. In the same logs and stumps, *H. ligniperda* were frequently found adjacent to larval mines of the invasive roundheaded woodborer, *Arhopalus syriacus*, and to more advanced galleries of *Ips paraconfusus* Lanier, which was generally absent from the undersides of the logs. In contrast to its near absence on Mediterranean pines in the southern Central Valley, *I. paraconfusus* is quite abundant in these pines planted in the Los Angeles Basin. Another native scolytid associated with *H. ligniperda*, *Carphoborus simplex* LeConte, was also

collected on several occasions in the Los Angeles Basin in smaller diameter logs and branches of *P. halepensis* and *P. canariensis*.

By May 2007, *H. ligniperda* had been collected by hand or in attractant-baited survey traps in six counties in southern California (Los Angeles, Orange, Riverside, San Bernardino, San Diego, and Ventura) (Fig. 21.20) Liu et al. 2007). The northernmost collection point at the time was near the community of Castaic in Los Angeles County on the southern base of the transverse Tehachapi Mountain Range. In August of 2009, *H. ligniperda* was detected in a survey trap near Lebec, California in southern Kern County, which represented a breach of the natural montane barrier (Penrose 2010). On the same date, survey entomologists collected a specimen of *H. ligniperda* in a funnel trap even further north near the Kern County Museum in Bakersfield (Penrose 2010). In 2009 and 2010, D.-G. Liu (UC Davis Department of Entomology) discovered that *H. ligniperda* was also established to the southeast of these locations in a native stand of singleleaf pinyon pine, *Pinus monophylla* Torr. & Frém., near the northern boundary of the Angeles National Forest and the southern edge of Lancaster/Palmdale and the Antelope Valley (Los Angeles County) (Fig. 21.18). The dispersal of the invasive population into native forest type, and particularly into *P. monophylla*, is significant because the primary concern in western North America is that *H. ligniperda* might become a highly effective vector of the pathogen for blackstain root disease, *Leptographium wageneri*, which is a serious native pest of conifers (Cobb 1988).

Specimens in the *CSCA* (Sacramento, California) indicated that *H. ligniperda* had been intercepted and collected at the Port of Oakland on several occasions on *P. radiata* lumber or dunnage from New Zealand (1995, 1996). In an assessment of pest risk associated with importation of *P. radiata* logs from Chile into the USA, *H. ligniperda* was considered to have the highest risk potential among ten insects in the analysis (USDA Forest Service 1993). In an analysis of national records from the Port Information Network, Haack (2001) reported 217 interceptions of *H. ligniperda* in the USA between 1985 and 2000. As was the case with *O. erosus*, California did not rank among the top five U.S. states for interception (11 records). These interceptions occurred at Long Beach (8), San Francisco (2) and San Diego (1), and they originated from Portugal (5), New Zealand (3), France (2), and Belgium (1) (RA Haack, pers. comm.). The population in New York has not appeared to have expanded beyond the area of the original discovery and has not dispersed into southern Canada as of December 2015 (Troy Kimoto, Canadian Food Inspection Agency, personal communication).

Wood and Bright (1992) list Europe (including western Russia), the Mediterranean (including North Africa and associated Atlantic and Mediterranean Islands), and Asia (China) as the native range of *H. ligniperda*. Pfeffer (1994) notes that it is distributed in central and southern Europe, the Crimea, the Caucasus, Asia Minor, and Algeria. Whether the native distribution includes China is not substantiated elsewhere in the literature. Indeed, a review of the Chinese literature reveals that although it has been intercepted many times at Chinese ports, it is apparently not yet established in China (Wei and Shao 1991; Yang and An 2002; Liang et al. 2003; Hu et al. 2004; Wang et al. 2005). For example, Liang et al. (2003) specifically documented 65 records of interception in 2002 on Monterey pine, *Pinus radiata* D. Don, imported from New Zealand to Guangdong Province, China. *Hylurgus ligniperda* appears to have achieved an invasive distribution quite similar to *O. erosus*. Introduced locations include Australia, Japan, New Zealand (1974), St. Helena Island, Sri Lanka (=Ceylon), South Africa, South America (Brazil, Chile, Uruguay), Swaziland (Browne 1968; Bain 1977; Neumann 1979; Zondag 1979; MacKenzie 1992; Wood and Bright 1992), and the eastern USA (USDA Forest Service 2002). Like *O. erosus*, its presence in northern climates is questionable. Duffy (1953) reported *H. ligniperda* as neither "imported" nor "doubtfully indigenous," whereas Browne (1968) considered it "reported in Britain, but not as a breeding species." Recent collections have only involved interceptions at ports or from cargo without any further evidence of an established population (C Tilbury, Forest Research, UK Forestry Commission, Surrey, and MVL Barclay, BMNH, London, personal communication). There are no current records of indigenous or introduced populations in Norway (K Thunes, Norwegian Forest Research Institute, pers. comm.), and in Sweden it was detected on multiple pulpwood log shipments from Chile (10 of 14 shipments) and France (3 of 6 shipments), but is apparently not yet established (Schroeder 1990). Collection records from the Baltic countries of Estonia and Latvia (Bright and Skidmore 2002) are also likely not of established populations.

The beetle feeds in the phloem of the basal portion of pine stems, large roots, or woody debris on the soil surface. Throughout its native and introduced range, *H. ligniperda* infests fresh stumps, logging debris, the basal stems of standing trees, or large, exposed roots of unhealthy trees in the genus *Pinus*. Records of pine species colonized so far are listed in Appendix 21.I. It has a strong proclivity to colonize cut logs in association with soil (Tribe 1992; Mausel 2002; Mausel et al. 2007), even locating and colonizing logs buried 40 cm below the surface (Tribe 1992). Based on observations in Chile, Ciesla (1988, 1993) reported that it can also cause seedling mortality by feeding on root collars and roots. Similar observations were made in Australia (Victoria) in *P. radiata* nurseries and second rotation sites (Neumann 1979; Neumann and Marks 1990). In southeastern Australia, Neumann (1987) described mortality caused by *H. ligniperda* to *P. radiata* ranging in age from 4 to 14 years. In Spain, Garcia de Viedma (1966) reported that *H. ligniperda* colonized and killed only pines up to 15 cm diameter at the base and that adults overwintered in groups of 30 to 40 beneath the bark at the root collar and in the larger roots. However, in New Zealand, *H. ligniperda* does not appear to kill seedlings (MacKenzie 1992; Reay and Walsh 2001; Brownbridge et al. 2010). In South Africa, apparently *Hylastes angustatus* (Herbst) is considered more aggressive than *H. ligniperda* because it is *H. angustatus* (and by inference not *H. ligniperda*) that damages pine seedlings during maturation feeding (Zhou et al. 2002a, b). A similar situation pertains in New Zealand with *Hylastes ater* (Paykull) vs. *H. ligniperda* (Brownbridge et al. 2010). In South Africa *H. ligniperda* colonized *P. radiata* logs at greatest frequency during the fall months (April/May in the Southern Hemisphere), and, in contrast to *O. erosus*, was generally more active during the cooler months of the year (Tribe 1991a). Southern Hemisphere winter flight activity was also documented in mature *P. radiata* stands in Victoria (Neumann 1978), but was not observed in *P. radiata* plantations in Chile (Mausel 2002) or New Zealand (Reay and Walsh 2001).

The greatest impact of *H. ligniperda* in western North America may be as a vector of fungal pathogens or agents of sapstain (MacKenzie 1992; USDA Forest Service 1993). In New Zealand, *Leptographium truncatum* (= *L. lundbergii*) and *L. procerum* (W.B. Kendr.) M.J. Wingfield have been isolated from *H. ligniperda* (Wingfield et al. 1988; MacKenzie 1992). In South Africa 11 fungal species in various genera have been isolated from beetles or their galleries in *P. patula* and *P. elliottii* trap logs (Zhou et al. 2001), with 21.6 % of 199 samples carrying *L. lundbergii*, 21.1 % carrying *L. serpens*, and 12.6 % carrying *Ophiostoma ips* (Wingfield et al. 1985; Tribe 1991a, b; Zhou et al. 2001). In Chile, *O. ips*, *O. galeiformis* (Bakshi) Mathiesen-Käärik, *Ceratocystiopsis minuta* (Siemaszko) Upadhyay & Kendrick were isolated from 80 specimens of *H. ligniperda* or its galleries in felled *P. radiata* in log decks (Zhou et al. 2004). No relative frequencies of occurrence of the three fungi were provided in the latter study. In New York, *H. ligniperda* appears to be associated with a syndrome called white pine root decline (USDA Forest Service 2002), which involves *L. procerum* (Zhou et al. 2001), but to our knowledge this fungal species has not been reported from New York populations of the beetle. In the western USA, *L. wageneri* (Kendrick) M. J. Wingfield, which is the causal agent of black stain root disease (Cobb 1988), may become associated with *H. ligniperda*, with potentially negative consequences for western pines and perhaps other conifers. This disease is prevalent in the coniferous forests of the Tranverse (San Bernardino) Mountain Range (Wagener and Mielke 1961; Merrill 1997 and LD Merrill, pers. comm.), which overlaps with the current distribution of *H. ligniperda* in California (Figs. 21.18 and 21.20). An analysis of the fungal associates of specimens of *H. ligniperda* collected from Mediterranean pine logs at two locations in Los Angeles County revealed eight species of Ophiostomatales and seven unidentified species (Kim et al. 2011). The most frequently isolated species were *Ophiostoma ips* and *Grosmannia galeiforme*, which were isolated respectively from 31 % to 23 % of the 118 beetles. The other species isolated included *O. piceae* (isolated from 9 % of the beetles), *O. querci* (8 %) and *Leptographium tereforme* sp. nov. (6 %). *Grosmannia huntii*, *L. serpens*, three *Sporothrix* species, *O. floccosum*, *O. stenoceras*, two unidentified *Hyalorhinocladiella* sp. and a sterile fungus each were isolated from fewer then 5 % of beetles. Most of the identified species already were known in USA and have been found in association with *H. ligniperda* in other countries. However the new species, *L. tereforme*, and *G. galeiforme* were recorded from the USA for the first time, and this was the first report of *L. serpens* from western North America.

Limited studies have been conducted to identify attractants or pheromones for *H. ligniperda* (Reay and Walsh 2002; Mausel 2002; Petrice et al. 2004). Mausel (2002) did not find any evidence for an aggregation or sex pheromone in field studies, but Reay and Walsh (2002) and Petrice et al. (2004) found that host compounds such as α-pinene, β-pinene, and ethanol can affect flight behavior. Petrice et al. (2004) found that baits containing α- or β-pinene and ethanol were the most attractive to *H. ligniperda* among the four treatments of α-pinene (high release rate) plus ethanol, α-pinene (low release rate) plus ethanol, β-pinene (high release rate) plus ethanol, and α-pinene (low release rate) alone. Reay and Walsh (2002) reported that both α- and β-pinene were attractive to *H. ligniperda*, and ethanol had a synergistic effect on the attraction to α-pinene or β-pinene. Both studies had limitations of either not including appropriate controls or not reporting the enantiomeric composition of the monoterpenes.

A year-long field bioassay (2006–2007) of the flight response of both sexes of *H. ligniperda* in Los Angeles County by our lab group demonstrated that ethanol and (−)-α-pinene functioned synergistically for both sexes as an attractant (Liu et al. 2016). Ethanol was not attractive alone, but (−)-α-pinene was moderately attractive to both sexes. Seasonal flight activity data from the bioassay and from the statewide survey suggested that the flight of *H. ligniperda* occurred year round in Southern California with major peaks in the spring (March to early May) and summer (late July), but was relatively low from August to late January. A wide range of other subcortical Coleoptera from urban forests of Southern California were trapped in the experiment, i.e., 22 species of Scolytidae (including eight of the invasive species covered in this chapter), six species of Bostrichidae, three species of Colydiidae, and 5 species of Cerambycidae. *Xyleborinus saxeseni* and both sexes of three native species of false powderpost beetles [*Amphicerus cornutus*, *Scobicia declivis*, and *S. suturalis* (Horn) (Coleoptera: Bostrichidae)] responded significantly to either treatment containing ethanol. Both sexes of the invasive roundheaded borer, *Arhopalus syriacus*, and a native root-feeding bark beetle, *Hylastes tenuis* Eichhoff, responded to treatments similarly to *H. ligniperda*, i.e., with a significant and synergistic response to ethanol and α-pinene. Peak flight activities of these subcortical beetles were variable depending on localities and seasons. This study represented the first report of flight dynamics in California for *A. syriacus*, *Am. cornutus*, *H. tenuis*, *S. declivis*, *S. suturalis*, and *X. saxeseni*, as well as for *H. ligniperda*. The diversity of bark and woodboring beetles caught, and synergism of (−)-α-pinene and ethanol from the year-long flight bioassay confirmed the utility of including both (−)-α-pinene and ethanol in monitoring or early detection programs for invasive species (Rabaglia et al. 2008).

21.4.5 Miscellaneous Indigenous Exotic Species in California

The peach bark beetle, *Phloeotribus liminaris* (Harris), is an eastern North American species that was first collected on November 8, 2002 in Fullerton, California (Orange Co.) from a dying ornamental Catalina cherry tree, *Prunus licifolia* spp. *lyonii* (Eastw.) Raven. It has since been collected several times in funnel traps from sites in Los Angeles, San Bernardino, and San Diego Cos. This species, *Ips calligraphus* (Germar), and two ambrosia beetles previously reported in California, *Monarthrum mali* (Fitch) and *Xyleborus xylographus* Say (Wood 1982), are all examples of "indigenous" exotic bark and ambrosia beetle species (Dodds et al.

2010) that have likely come to California from eastern North America (Table 21.2). *Ips calligraphus* has not been reported from the State in many years, but at one time had a fairly substantial population in the central Sierra Nevada in ponderosa pine, *Pinus ponderosa* (Herbert 1916; Wood and Stark 1968; Connor and Wilkinson 1983; Lanier et al. 1991). Another subcortical species of note from eastern North America that is relatively new to California (Duckles and Švihra 1995; Dreistadt et al. 2004) and Nevada (Carlos et al. 2002) is the bronze birch borer, *Agrilus anxius* Gory, which is a flatheaded borer that attacks the main stem of ornamental birches. It was first detected in 1992 in Marin and Sonoma Counties in northern California (Dreistadt et al. 2004). Its distribution and current status in California need further attention. In 2003, one of us (RLP) also confirmed the presence of another eastern U.S. woodborer species in California: the redheaded ash borer, *Neoclytus acuminatus* (F.) (Coleoptera: Cerambycidae). As of late 2007, it was only known from Sacramento Co., but it was subsequently reared from *Juglans* (likely *J. regia*) in Tulare Co. (southern Central Valley) (Dennis Haines, CDFA, Tulare County, pers. comm., 10 April 2014) and trapped in July and August 2015 in surveys of the walnut twig beetle in *J. regia* orchards in Colusa, Solano, and Yolo Cos. (northern Central Valley).

21.5 Summary and Future Expectations

Over a decade of intensive survey has revealed a greater than 100 % increase in invasive Scolytidae in California (from 10 to 22 species) (Table 21.2), bringing the exotic species composition in the State to approx. 10 % of the native fauna. Five of the species are indigenous exotics from eastern North America or the desert Southwest. This increase in the number of invasive bark and ambrosia beetles is a reflection of both commitment of resources and research effort to the discovery and characterization of newly established populations of species as well as enhanced awareness of which "native" species may have been actually invasive (e.g., *C. bodoanum*, *H. eruditus*, *P. juglandis*, and *X. saxeseni*). The extra-continental invasive scolytids in California comprise nearly 30 % of the 58 documented invasive species in the USA (Haack 2001, 2006; Lee et al. 2007; Haack and Rabaglia 2013). Given the dictum that invasive species often re-associate themselves with their hosts of origin (i.e., in this case adventive populations of trees) in the invaded habitat (Mattson et al. 1992; Niemelä and Mattson 1996; Langor et al. 2009 for Canada), it is not surprising that some of the key invasive bark beetles are of Mediterranean origin (Mifsud and Knížek 2009). However, there is also a trend toward introduction and establishment of Asian invasive species in California (e.g., polyphagous shot hole borer and banded elm bark beetle, *Scolytus schevyrewi*). Invasive bark and ambrosia beetles present new management challenges for urban foresters and public and private land managers evoking a need for outreach and publicly accessible IPM literature (Dreistadt et al. 2004; Lee et al. 2005, 2006, 2007; Liu et al. 2007; Seybold et al. 2008b, 2013a, b; Flint et al. 2010; Coleman et al. 2013).

Southern California appears to have been a particularly fertile area for the introduction and establishment of exotic Scolytidae. Factors enhancing this immigration include favorable and diverse climate, diverse and exotic (tropical and temperate) vegetation, large human population centers and extreme ethnic diversity, poor air quality that stresses plants (Grulke et al. 2002), and high levels of commercial and military port traffic. The compatibility of California's Mediterranean climate with the native climate of some of these invaders cannot be overlooked. Despite a relatively even distribution of survey traps across the northern and southern portions of the state, the majority of the ten new records of Scolytidae reported here were exclusively or partially from southern California. We anticipate that this trend will continue.

Climate change is exerting a broad impact on the population biology of native scolytids in North America (Bentz et al. 2010), with the most obvious effects at higher elevations and latitudes. There also appears to be a trend whereby southern populations of indigenous exotic subcortical species are invading and expanding their populations generally northward. Examples of this include the Mexican pine beetle, *Dendroctonus mexicanus* Hopkins (Moser et al. 2005), the Mexican soapberry borer, *Agrilus prionurus* Chevrolat (Billings et al. 2014), the walnut twig beetle, *P. juglandis* (Rugman-Jones et al. 2015), the goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleman et al. 2015, see Chap. 22), and two other newly discovered flatheaded borers in California, *Chrysobothris analis* LeConte (Westcott et al. 2016) and *C. costifrons costifrons* Waterhouse (Basham et al. 2015). Whether or not this trend will continue to manifest itself in the urban, peri-urban, and wildland forests on the North American continent, and in California in particular, remains to be seen. As a counterexample to the south to north invasion trend, a historically significant southern outbreak of a defoliator was recently documented when Douglas-fir tussock moth, *Orgyia pseudotsugata*, for the first time in the forest entomological record, killed large numbers of white fir, *A. concolor*, trees in the San Bernardino Mountains (Coleman et al. 2014b).

It is highly likely that continued survey in the next few years will detect additional immigrant scolytid species in California. Based on available host type, climate, importation pathways, and geographic proximity, highly probable immigrant scolytid species to California include: *Gnathotrichus materiarius* (Fitch), *Hylastes opacus* Erichson, *Monarthrum fasciatum* (Say), *Xyleborinus alni* (Niisima), *Xylosandrus crassiusculus* (Motschulsky), and *Xyloterinus politus* Say (all introduced in neighboring Oregon, Mudge et al. 2001; LaBonte et al. 2005); *Hylurgopinus rufipes* (Eichhoff), *Hylurgops palliatus* (Gyllenhal), *Pityogenes bidentatus* (Herbst), *T. piniperda*, *Xyleborus glabratus* Eichhoff, and *Xylosandrus compactus* (Eichhoff) (all present in eastern North America); *Carphoborus minimus* F., *Crypturgus mediterraneus* Eichhoff, *Hylastes linearis* Erichson, *Hylurgus micklitzi* Wachtl., *Pityogenes calcaratus* Eichh., and *Tomicus destruens* (Woll.) (all associated with *O. erosus* in the Mediterranean, Mendel 1987; Mendel et al. 1991; Mifsud and Knížek 2009); *Hylastes angustatus* (Herbst) (associated with *H. ligniperda* in South Africa); and *Hylastes ater* (Paykull), *Ips duplicatus* (Sahlberg), *Ips sexdentatus* (Boerner), *Ips typographus*, *Pityogenes chalcographus* (L.), *Scolytus intricatus* (Ratzeburg), and *Scolytus scolytus* (Fab.) (major Eurasian pest species with frequent North American interception histories, Haack 2006). A Mediterranean cypress bark beetle, *Phloeosinus aubei* (Perris) (Mendel 1984, 1987; Bel Habib et al. 2007) has recently invaded Central Europe (Gabor Szocs, Plant Protection Institute CAR HAS, Budapest, Hungary, personal correspondence), and could represent a strong threat to California's many urban species and cultivars in the Cupressaceae as well as to the California endemics in the forested landscape. Another Mediterranean species, *Scolytus amygdali*, could already be present in California in crypsis with *S. rugulosus* (as was apparently the case in the Maltese Islands, Mifsud and Knížek 2009), which underscore the importance of investigating the complexity of populations of *S. rugulosus* in North America. Two final Eurasian species of concern because of their potential pest status are *Dendroctonus armandi* Tsai and Li and *D. micans* (Kugelann). Watchlists like this have merit when considering how to structure detection surveys, however, it has been the case that relatively obscure and unpredictable species [e.g., *S. schevyrewi*, the goldspotted oak borer, *A. auroguttatus*, or the Eucalyptus longhorned borers, *Phoracantha recurva* Newman and *P. semipunctata* (F.)] can also have relatively profound impacts on trees in the invaded habitat because of the lack of host resilience in the new environment. Also, the lists provide outreach specialists with a planning framework for the advent of key species through publications and presentations [e.g., Dreistadt et al. (2004) discussed the potential arrival of *X. crassiasculus* and its impact on California shade tree resources].

21.6 Acknowledgements

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Fig. 21.21 Richard Lynn Penrose (11 January, 1943–17 March 2011) at the California Department of Food and Agriculture Plant Health and Pest Prevention Services, Pest Exclusion Branch, Meadowview Field Office, circa 2009 (SJS photo)

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Appendix 21.I: Host Ranges of Selected Invasive Bark and Ambrosia Beetles in California Mediterranean Forest Systems

For more details on the host ranges of these species, the reader is referred to the World Catalog of the Scolytidae (Wood and Bright 1992) as well as to the three catalog supplements (Bright and Skidmore 1997, 2002; Bright 2014).

Fruit-Tree Pinhole Borer or Lesser Shothole Borer, Xyleborinus saxeseni *(Ratzeburg)*

Possibly no species is exempt from invasion (Bright and Stark 1973). Chamberlin (1939) only listed hardwoods (*Quercus*, *Fagus*, *Betula*, *Acer,* etc.), but Wood and Bright (1992) also list conifers such as *Abies*, *Chamaecyparis*, *Cryptomeria*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, and *Tsuga* among many other tree species. We have reared this species from *Alnus rhombifolia*, *Juglans californica*, *J. hindsii*, *J. mollis*, *J. regia*, *J. hindsii* x *nigra*, *J. hindsii* x *regia*, *Pinus radiata*, and *Prunus cerasifera* (SJS, unpublished data) and *Pterocarya fraxinifolia* (Hishinuma et al. 2015).

Spermophagous Bark Beetles, Coccotrypes *Eichhoff and* Dactylotrypes *Eggers*

Coccotrypes advena Blandford is thought to be native to Asia (Indonesia) and breeds in either bark or large seeds of a variety of tropical hosts (Wood 1977). Wood and Bright (1992) list these hosts, which include *Albizzia* sp., *Ficus bracteata*, *F. xylophylla*, *Pterocarpus indicus*, and *Theobroma cacao*. Bright and Skidmore (1997) listed four additional hosts: *Calophyllum brasiliense*, *Eugenia jambos*, *Pouteria multiflora*, and *Sloanea berteriana*, whereas Bright and Skidmore (2002) added the petioles of *Cecropia insignis* and *C. peltata* to the list. Bright (2014) cataloged references for seven new hosts, which included logs of *Pinus caribea* and *Sloanea berteroana*, as well as seeds of *Persea americana*.

Coccotrypes carpophagus (Hornung) likely originated in Africa, but was named for betel nuts from India (Wood 1977). Wood (1977) also suggest that it breeds in a wide variety of nuts and other large seeds, and Wood and Bright (1992) listed 27 genera or species of hosts. These included *Cassia grandis, Coccothrinix argentea, Diospyros spp., Neowashingtonia robusta, Phoenix dactylifera, Sabal palmetto, Theoborma cacao*, and *Washingtonia filifera*. Bright and Skidmore (1997) listed *Acacia mangium* and *Quercus variabilis*, whereas Bright and Skidmore (2002) listed four new host records, including *Washingtonia robusta* (presumably as a correction for *Neowashingtonia* in Wood and Bright 1992). Bright (2014) listed seeds of *Persea americana* and *Prestoea montana*, as well as fruits of *Dillenia indica* as additional host records.

Coccotrypes dactyliperda (F.) also likely originated in Africa, and frequently colonizes and breeds in date pits (Wood 1977). Wood (1977) also suggests that it "may breed in a wide variety of nuts, and buttons or other objects made from vegetable ivory." Wood and Bright (1992) listed 24 genera or species of hosts. This list overlaps with that of *C. carpophagus*, but also includes *Coccos* spp*., Olea europaea, Phoenix* spp., and *Persea gratissima.* Bright and Skidmore (1997); Bright and Skidmore (2002); and Bright (2014) provide summaries of only distributional records (including Hawaii, Malta, New Zealand), but no new host records.

Dactylotrypes longicollis (Wollaston) has been recorded from the following hosts (presumably on the seeds) in its native Atlantic Island distribution (or in invaded regions of France): *Butia eriospatha, Chamaerops humilis*, *Dracsena draco* (L.), *Phoenix canariensis*, *Phoenix pumila*, and *Trachycarpus excelsus* (Wood and Bright 1992). Bright and Skidmore (1997) reported an expanded distribution into Italy and Spain and added date palm, *Phoenix dactylifera* as a host. Whitehead et al. (2000) reported that it was collected in seeds of *P. canariensis* in Croatia and transported to Slovakia. It was found later in the Maltese Islands but no host of collection was reported (Mifsud and Colonnelli 2010). LaBonte and Takahashi (2012) report that it only attacks the seeds of palms and related plants; they found dead specimens of *D. longicollis* in the fallen seeds of Brazilian needle palm, *Trithrinax brasiliensis* Martius (Arecaceae) in a southern California arboretum (Fullerton, Orange Co.). It was collected in funnel traps at this site and at the Los Angeles County Arboretum.

Hypothenemus eruditus *Westwood*

The host range is enormous (Wood and Bright 1992; Bright and Skidmore 1997, 2002; Bright 2014). Wood (2007) noted that "hundreds of host species have been recorded including fungal fruiting bodies, twigs, weeds, pods, seeds, and other unexpected places." "The original series was removed from active tunnels in the cover of an old book."

Shothole Borer, Scolytus rugulosus *(Müller)*

Scolytus rugulosus has been described as cosmopolitan and occurring wherever the hosts (*Malus* spp., *Prunus* spp., *Pyrus* sp., and less frequently *Crataegus* spp., *Cydonia* sp., *Ulmus* sp., etc.) are cultivated (Wood 1982) or as "occurring in most fruit-growing areas of the United States and Canada" (Furniss and Carolin 1977). The latter authors also list mountain mahogany (*Cercocarpus*) amongst the hosts. Michalski (1973), Wood and Bright (1992), and Bright and Skidmore (1997) provide much more comprehensive host lists, which include species of significance to urban and wild land forestry, such as *Acer*, *Betula*, *Castanea*, *Fagus*, *Taxus*, *Tilia*, *Ulmus* (*carpinifolia*), as well as *Amelanchier*, *Celtis*, *Corylus*, *Cotoneaster*, *Morus*, *Sorbus*, *Juglans regia* L., and many others. Whether these are truly developmental hosts or just chance collections on these plants or plant misidentifications needs to be verified. The primary hosts noted by Furniss and Carolin (1977) and Wood (1982) appear to be the only confirmed hosts so far in California, as Dreistadt et al. (2004) list English laurel, fruit trees, and hawthorn as hosts. In our museum survey, we found specimens with host labels that included *Cupressus* (Santa Clara Co., V-1985, *SDMC*, doubtful developmental host record); *Pyracantha* spp. (Rosaceae, Contra Costa Co., VI-1953, *EMEC*); and loquat, *Eriobotrya japonica* (Rosaceae, Orange Co., IV-1915, *EMEC*).

European Elm Bark Beetle, Scolytus multistriatus *(Marsham)*

Wood and Bright (1992) note that this species colonizes *Ulmus* spp. as hosts and is rare in other hosts. Baker (1972) reports that *S. multistriatus* attacks and colonizes all native and introduced species of elms (*Ulmus* spp., slippery, American, English, Japanese, etc.) in North America as well as the related Japanese zelkova, *Zelkova serrata* (Thunb.) Makino.

Banded Elm Bark Beetle, Scolytus schevyrewi *Semenov*

Scolytus schevyrewi has been reported to colonize elms (*Ulmus* spp., American, big fruit, chalked bark, English, European white, field, Japanese, rock, Siberian, smooth-leaved, winged); various trees in the rose family (Rosaceae, almond, apricot, cherry, paradise apple, peach, pear, other *Prunus* spp.); Oleaster (Elaeagnaceae); pea shrub (Fabaceae); Russian olive; and weeping willow (Salicaceae) (Latin names provided in Negrón et al. 2005 and host range summarized in Lee et al. 2007). However, in North America, the only confirmed hosts are in the *Ulmus*. In the laboratory, *S. schevyrewi* readily colonized bolts of American elm, *Ulmus americana* L., but not Chinese elm, *Ulmus parvifolia* Jacq.; Siberian peashrub, *Caragana arborescens* Lam.; a cherry, *Prunus fontanesiana* (Spach) C. K. Schneid.; or Russian olive, *Elaeagnus angustifolia* L. (2011).

Walnut Twig Beetle, Pityophthorus juglandis *Blackman*

Pityophthorus juglandis colonizes all species of *Juglans* (walnuts, butternuts, and their hybrids) as well as several species of *Pterocarya* (wingnut) (reviewed in Hishinuma et al. 2015).

Mediterranean Pine Engraver, Orthotomicus *(*Ips*)* erosus *(Wollaston)*

The principal species of pines colonized by *O. erosus* in its native range are *Pinus armandii* Franchet, *P. brutia*, *P. canariensis*, *P. halepensis*, *P. kesiya* Royle ex Gordon var. *langbianensis* (Chevalier) Cheng & Fu, *P. massoniana*, *P. nigra* Arnold, *P. pinaster* (= *P. maritima* Ait.), *P. pinea*, *P. sylvestris*, *P. tabuliformis* Carrière, and *P. yunnanensis* Franchet (Yin et al. 1984; Jiang et al. 1992; Wood and Bright 1992; Yin and Huang 1992; Bright and Skidmore 1997, 2002; Chen et al. 1998; Eglitis 2000a). In introduced areas it has colonized *P. caribaea* Morelet, *P. echinata* Mill., *P. elliottii* Engelmann, *P. patula* Scheide & Deppe, *P. radiata*, and *P. taeda* L. (Bevan 1984; Eglitis 2000a). Reports of *O. erosus* in Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, spruce, *Picea* spp., fir, *Abies* spp., cypress, *Cupressus* spp., and cedar, *Cedrus* spp. (Grüne 1979; Mendel and Halperin 1982; Wood and Bright 1992; Bright and Skidmore 1997, 2002; Eglitis 2000a) are considered by us in most cases to likely be instances of maturation feeding, collection from adult overwintering sites, or accidental associations rather than developmental records (Chararas and M'Sadda 1970). This hypothesis has been substantiated in part by a laboratory no-choice physiological host range study with the introduced California population where, Lee et al. (2008) identified potentially vulnerable native and adventive hosts in North America among 22 conifer species. The beetle reproduced on four pines from its native Eurasian range: Aleppo, Canary Island, Italian stone, and Scots pines; 11 native North American pines: eastern white, gray, jack, Jeffrey, loblolly, Monterey, ponderosa, red, Sierra lodgepole, singleleaf pinyon, and sugar pines; and four native nonpines: Douglas-fir, black and white spruce, and tamarack. Among nonpines, fewer progeny developed and they were of smaller size on Douglas-fir and tamarack, but sex ratios of progeny were nearly 1:1 on all hosts. Beetles did not develop on white fir, incense cedar, or coast redwood (Lee et al. 2008). With loblolly pine, the first new adults emerged 42 days after parental females were introduced into host logs at temperatures of 20–33 °C and 523.5 or 334.7 accumulated degree-days based on lower development thresholds of 13.6 °C or 18 °C, respectively. Laboratory studies of walking and boring behavior as a prelude to host selection (Walter et al. 2010a, b) showed slightly broader ranges of suitability or short-range acceptability, with the angiosperm non-host *Betula papyrifera* Marsh eliciting a higher walking response than would be expected by chance (Walter et al. 2010b) and extracts of the marginal host tamarack, *Larix laricina* (Du Roi) Koch, eliciting an increase in the initiation and extent of boring by *O. erosus* on a filter paper substrate (Walter et al. 2010a).

Redhaired Pine Bark Beetle, Hylurgus ligniperda *(Fabricius)*

Pine species colonized by *H. ligniperda* include *P. brutia, P. canariensis, P. elliottii, P. halepensis, P. montezumae* Lamb*., P. nigra, P. patula, P. pinaster, P. pinea, P. radiata, P. strobus* L.*,* and *P. sylvestris* (Browne 1968; Bain 1977; Pfeffer 1994; Bright and Skidmore 1997; Eglitis 2000b; USDA Forest Service 2002). Its host range may extend to other species in the Pinaceae (USDA Forest Service 2002), but we could not confirm this in the primary literature or on the ground in California.

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