ture, and the body whorl can be almost straight-sided or strongly shouldered with a marked ramp. All of these variants are well illustrated by Nuttall (1990). *Loxotrema turritum* resembles only those specimens of *A. glabrum* that are smoothish and strongly shouldered (see Nuttall, 1990:figs. 286–287) and differs significantly from them by having a posterior notch in the aperture, a protruding (hoodlike) anterior portion of the outer lip rather than a slight concavity there, a weak siphonal fasciole, a sigmoidal growth line rather than a slightly sinuate one, shorter spire, tabulate spire whorls, beaded upper spire whorls, and a projecting and much thicker callus along the inner lip. In addition, *L. turritum* does not have a ramp associated with its strongly tabulate body whorl shoulder. In spite of the many differences between these two taxa, their overall similarilty does suggest a case of convergence.

Loxotrema turritum is only the second melanopsid recognized in the fossil record of the Pacific slope of North America. The other one is *Boggsia tenuis* (Gabb, 1864), known from the Upper Cretaceous (Campanian Stage) strata in northern California (Squires & Saul, 1997).

The name *Loxotrema* is a combination of *loxos* (Greek, slanting or crosswise) and the neuter noun *trema* (Greek, hole). Although early workers used the name "*turrita*," Fischer (1884) was correct in using the name "*turritum*" because *turritus* (Latin, with towers or castellated) is an adjective and its ending has to agree in gender with the genus.

STRATIGRAPHIC DISTRIBUTION AND DEPOSITIONAL ENVIRONMENTS

Introduction

Loxotrema turritum is known from numerous areas in California, two areas in Oregon, and one area in Washington (Figure 1). Its geologic range for each of these states is depicted in Figure 2. The formations in which it is found, as well as the associated inferred depositional environments, are given in Table 1.

"Meganos Stage"

The only known "Meganos Stage" record of *L. turritum* is new information. It is also the earliest record of this species, which was reported formerly by various workers (Table 1) to be no earlier than the "Capay Stage." The "Meganos Stage" record is based on a single worn specimen from a sandstone (UCMP loc. 3586) in the Kellogg Creek area of Contra Costa County in northern California. This sandstone was referred to as "division D of the Meganos Formation" by Clark & Woodford (1927), but modern workers use the name "Margaret Hamilton Sand" (Edmondson, 1984). Division D of the Meganos Formation is correlative with the middle of the CP9 Zone of the standard calcareous nannoplankton zonation (Almgren et al., 1988). This part of the CP9 Zone is correlative with the "Meganos Stage" (Squires, 1988a). Almgren (1978) reported the Margaret Hamilton Sand to contain benthic foraminifera indicative of a probable mid-neritic (shallow marine) environment of deposition. The mollusks found associated with *L. turritum* at UCMP loc. 3586 (Clark & Woodford, 1927:82–84) also indicate a shallow-marine environment. The broken and worn condition of the *L. turritum* specimen indicates that it was probably transported to the site.

"Capay Stage"

Only a single CSUN collection specimen was found in the "Capay Stage" Maniobra Formation of the Orocopia Mountains of Riverside County in southern California. This specimen, which is poorly preserved and worn, was tentatively identified (Squires, 1991b:pl. 1, fig. 16, table 1) as *L. turritum.* I now consider it to be *L. turritum.* This specimen is part of a relatively diverse and mostly shallow-marine megafossil assemblage that was interpreted as having lived in nearshore waters adjacent to a submarine canyon and was transported basinward into the bathyal depths of the submarine canyon (Advocate et al., 1988; Squires, 1991b).

Merriam & Turner (1937:table 2) reported *L. turritum* as part of a moderately diverse and mostly shallow-marine megafossil assemblage from the Capay Formation at the type section of the formation as Smith Canyon, Yolo County, northern California. I examined the UCMP collection specimens and found them to be poorly preserved. Redwine (1984) reported that the lower Eocene Capay Formation represents displaced material derived mostly from nearshore depths and deposited as turbidites in the lower part of the Princeton Submarine Valley system, whose length was approximately 265 km. These *L. turritum* specimens, therefore, probably underwent considerable postmortem transport.

The "Capay Stage" specimens of *L. turritum* from Crescent Bay, Washington (UCMP locs. A-1547, A-1550) represent a new occurrence and extend, a distance of 580 km, this species' northernmost record, which was previously reported to be in southwestern Oregon (Turner, 1938). These Washington specimens differ from other "Capay Stage" specimens by having lived in coastal waters on the flank of a basalt volcano. These abundant and well-preserved UCMP collection specimens, all about 22 mm high and showing the delicate upper spire sculpture, were found in sedimentary interbeds in basalt flows of the Crescent Formation on the west side of Crescent Bay, Clallam County, Olympic Peninsula, southwestern Washington. Duncan (1982) proposed that this Crescent Formation basalt formed oceanic seamounts that became accreted, by means of subduction-zone tectonics, to the margin of the North American continent. More recently, Babcock et al. (1992) proposed that the basalt formed

Table 1

Formations containing *Loxotrema turritum* and their inferred depositional environments. Stages listed youngest to oldest, in descending order. [CA = California, OR = Oregon, WA = Washington, * = New occurrence].

Formation; location; literature sources	Inferred depositional environment; literature sources
"TEJON STAGE":	
Matilija Sandstone, Pine Mtn., Ventura Co., CA (Givens, 1974)	Mixed brackish-marine bays or lagoons & shallow marine at the seaward margin of a delta complex (Givens, 1974)
Matilija Sandstone, mouth of Alamo Creek, Ventura Co., CA (Givens, 1974)	Brackish-marine bays or lagoons on a delta complex (Givens, 1974)
Juncal Formation (sandstone facies), Pine Mtn., Ventura Co., CA (Givens, 1974)	Mixed brackish-marine bays or lagoons & shallow marine (beach & bar) at the seaward margin of a delta complex (Givens, 1974)
Matilija Sandstone, Beartrap Creek, Ventura Co., CA (Squires, 1991a)	Mixed brackish marine & nearshore marine (Squires, 1991a)
"TRANSITION STAGE":	
Matilija Sandstone, Matilija Hot Springs, Ventura Co., CA (Squires, 1991a)	Brackish-marine lagoon or bay in close association with beach-bar-barrier complexes (Link, 1975; Link & Welton, 1982; Squires, 1991a)
Juncal Formation (siltstone facies), NE of Pine Mtn., Ventura Co., CA (Givens, 1974)	Interdistributary bays or lagoons or prodelta at the seaward margin of a delta complex (Givens, 1974)
Scripps Formation, Murphy Canyon, San Diego Co, CA (Squires & Demere, 1991)	Nearshore shallow-marine with some transported brackish-marine lagoonal mollusks (Squires & Demere, 1991)
"DOMENGINE STAGE":	
*Ardath Shale, Blacks Canyon, San Diego Co., CA	Bathyal (600 to 1500 m depth) submarine-fan channel fill with reworked shallow-marine fossils (Lohmar et al., 1979; May & Warme, 1991)
Delmar Formation, Torrey Pines State Reserve, San Diego Co., CA (Hanna, 1927; Givens & Kennedy, 1979)	Marginal-marine oyster bioherms in a bay, estuary, or lagoon (Hanna, 1926; Lohmar et al., 1979; Warme, 1991; May & Warme, 1991)
Santiago Formation, Vista, Sand Diego Co., CA (Givens & Kennedy, 1976)	Marine or brackish marine, perhaps lagoon or estuary (Givens & Kennedy, 1976)
Domengine Formation, Vallecitos syncline, San Benito Co., CA (Vokes, 1939; Schulein, 1993)	Brackish-marine lagoon on a deltaic complex (Schulein, 1993)
Domengine Formation, Coalmine Canyon, Fresno Co., CA (Arnold, 1909; Arnold & Anderson, 1910; Vokes, 1939)	Swampy intertidal distributary bay on a delta complex (Roush, 1986)
"CAPAY STAGE"	
White Tail Ridge formation, Glide, Douglas Co., OR (Turner, 1938)	Mixed fluvial & shallow marine on a delta complex (Niem et al., 1992)
*Crescent Formation, Crescent Bay, Clallam Co., WA	Rift-zone? volcanic island in marine waters (Babcock et al., 1992)
Maniobra Formation, Orocopia Mtns., Riverside Co., CA (Squires, 1991b)	Bathyal submarine-canyon fill, very near a coastline (Advocate et al., 1988; Squires, 1991b).
Capay Formation, Smith Canyon, Yolo Co., CA (Merriam & Turner, 1937)	Bathyal (760 to 1830 m depth) submarine-valley fill (Redwine, 1984)
"MEGANOS STAGE"	
*Margaret Hamilton Sand, Kellogg Creek, Contra Costa Co., CA	Probable mid-neritic (shallow marine) (Almgren, 1978)

volcanic islands within a rift zone along the margin of the continent, and this tectonic setting seems much more likely for *L. turritum* than one associated with oceanic seamounts. At UCMP loc. A-1547, *L. turritum* was found associated with a diverse shallow-marine, mega-invertebrate assemblage consisting of many species of mollusks and a species of colonial coral. Many of these same species of mollusks were reported by Arnold & Hannibal (1913:572) from the Crescent Formation near Tongue Point on the east side of Crescent Bay. At UCMP loc. A-1550, *L. turritum* was found associated with shallow-marine mollusks and some specimens of the gastropod *Potamides* (*Potamides*?) *carbonicola* Cooper, 1894. This potamidid has been reported by many workers (e.g., Arnold, 1909) as diagnostic of brackish-marine environments. The presence of it in the Crescent Formation is new information. Elsewhere in southwestern Washington, the upper part of the Crescent Formation has yielded mollusks and other megafossils that lived on the hard substrate formed where extrusion of basalt caused shoaling of marine waters. The megafaunas were subject to storm waves and were transported down steep slopes into shallow, subtidal depths where other mollusks lived (Squires et al., 1992; Squires & Goedert, 1994a, b, 1995, 1996). In all these previously studied areas, however, *L. turritum* has not been found, but at one locality in the Crescent Formation at Larch Mountain, Black Hills near Olympia, Squires & Goedert (1994a) reported the presence of the ellobiid *Ovatella* (*Myosotella*), a pulmonate (air-breathing) gastropod indicative of salt marshes and upper shores or estuaries. Evidently, the early Eocene volcanic island in the Crescent Bay region was associated with localized brackish-marine environments. The uniform size of the *L. turritum* specimens indicates sorting associated with postmortem transport, but the presence of delicate upper spire sculpture on these specimens indicates that the distance of transport was not great. Detailed paleo-environmental studies of the Crescent Formation in the Crescent Bay area are much needed.

The taphonomy of the specimens of *L. turritum* from the Maniobra, Capay, and Crescent formations is similar to that reported (Givens, 1994; Squires & Advocate, 1986; Squires, 1997) for some other early Eocene gastropods that lived in coastal waters along the tectonically active coast of California. Like *L. turritum,* they were subject to transport into deeper waters via turbidity currents.

Turner (1938) reported specimens of *L. turritum* in the Glide area of southwestern Oregon. The specimens are from the informal White Tail Ridge formation (A. Niem, personal communication, 1996), which is correlative to the upper Umpqua formation or the Lookingglass Formation, both of previous usage (Niem et al., 1992). The White Tail Ridge formation is assignable to the lower Eocene calcareous nannofossil CP11 Zone, which ranges from the upper part of the "Capay Stage" to the lower part of the "Domengine Stage" (Squires, 1988a). Givens & Kennedy (1976) believed that the rock unit at Glide might possibly be assignable to the "Domengine Stage," but the presence of *Turritella andersoni* Dickerson, 1916, a species diagnostic of the "Capay Stage" (Squires, 1988b), indicates that the rock unit is assignable to the "Capay Stage." It is likely that the Glide specimens are in rocks correlative to near the boundary between the "Capay Stage" and the "Domengine Stage." Although the White Tail Ridge formation consists of deltaic (mixed fluvial and shallow-marine) deposits (Niem et al., 1992), the actual beds containing the specimens of *L. turritum* have not been incorporated by any recent worker into a detailed depositional-model context. Several years ago, before I began this present investigation, I collected specimens of *L. turritum* from this formation in the Glide area at UCMP locs. A-661 and A-662. The specimens are in sandy lenses of transported fossils, and the lenses are about 15 to 20 m in lateral extent. The richest lens is at locality A-661, which is about 5 m stratigraphically below the lens at locality A-662. At locality A-661, there are abundant specimens of *L. turritum,* ranging in height from 17 to 40 mm (estimated). Many of them are nearly complete and are missing only the protoconch, the anterior end of the aperture, and the outer lip. The upper spire sculpture has been somewhat abraded, and although the specimens have undergone some postmortem transport they were not transported very far. Overall, the shells at this locality show better preservation than at any other locality where *L. turritum* has been found. There are also a few specimens of *Potamides* (*P.*?) *carbonicola* present at locality A-661.

"Domengine Stage"

Arnold (1909) and Arnold & Anderson (1910) reported *L. turritum* from a section of middle Eocene rocks containing lignite and gypsiferous sandstone at Coalmine Canyon about 7 km northwest of Coalinga, central California, and they interpreted that these rocks were brackish marine. These rocks are now referred to as the Domengine Formation (Vokes, 1939:20). Roush (1986:81, figs. 5B, 25) studied the details of the depositional environment of the Domengine Formation at Coalmine Canyon, and although she found no *L. turritum,* she interpreted that the beds accumulated in an interdistributary bay on a river-dominated delta associated with a low-energy coastline where swamps were present.

Vokes (1939) reported *L. turritum* from the Domengine Formation in the Vallecitos syncline area between New Idria and Panoche, about 50 km north of Coalinga. In addition, he confirmed the presence of this species in the Domengine Formation at Coalmine Canyon. Vokes (1939:159) reported, furthermore, that *L. turritum* is a brackish-marine species and is always associated with *Acutostrea idriaensis idriaensis* (Gabb, 1869) and *Potamides* (*P.*?) *carbonicola.* He did not make it clear if he was referring to only the Vallecitos syncline area or to everywhere *L. turritum* is present. *Loxotrema turritum* is not always associated with these two species. Schulein (1993) studied the details of the depositional environment of the Domengine Formation in the Vallecitos syncline area. In the Griswold Canyon area in the central part of this syncline, he found *L. turritum,* usually associated with *P.* (*P.*?) *carbonicola* and *A. idriaensis idriaensis,* in lenses interbedded with carbonaceous claystone and siltstone. He interpreted the formation in this particular area as having been deposited on a deltaic complex and that these species represent nearly *in situ* brackish-marine lagoonal assemblages, or that they had undergone slight postmortem transport and accumulated at the seaward edge of a salt marsh.

Givens & Kennedy (1976) reported *L. turritum* from a small molluscan assemblage in middle Eocene ("Domengine Stage") strata near Vista in northern San Diego County, southern California. Although none of the specimens of this species is complete, they show good preservation and their depositional environment was interpreted (Givens & Kennedy, 1976) as having been "a low-energy, very shallow (0–30 m) marine or brackish-water environment, perhaps in a lagoon or estuary." These rocks are now assigned to the Santiago Formation (Eisenberg & Abbott, 1991).

Hanna (1926) reported *L. turritum* from the Delmar Formation near San Diego, and he interpreted the formation to be a brackish-marine deposit. Many sedimentological studies in recent years (e.g., Kennedy & Moore, 1971; Lohmar et al., 1979; Warme, 1991; May & Warme, 1991) have supported the interpretation that the Delmar Formation was deposited in a stream-mouth lagoonal setting.

The presence of rare reworked specimens of *L. turritum* in the Ardath Shale at Blacks Canyon, San Diego County, southern California, represents the only post-"Capay Stage" record of this species in deep-marine rocks. This occurrence is new information. The specimens, which are from the upper 4 m of the Ardath Shale at UCR loc. 4930, have their apertures filled with clean, medium-grained sand matrix that is distinctly different from the surrounding siltstone, thereby indicating that the shells were transported prior to burial. The Ardath Shale consists of canyon fill deposited at depths between 600 and 1500 m. The submarine canyon incised into older shallow-water deposits of the Delmar Formation and other formations (Lohmar et al., 1979; May & Warme, 1991), and the Delmar Formation was most likely the source for the specimens of *L. turritum.*

"Transition Stage"

Roth (1988) and Squires & Demere (1991) reported *L. turritum* from SDSNH loc. 3278 in the Friars Formation at Murphy Canyon in the San Diego area. Walsh et al. (1996), however, reassigned the rocks at this locality to the laterally interfingering and subjacent upper part of the Scripps Formation. The *L. turritum* at this locality represents part of a transported and rare, but distinct, brackish-marine element of an otherwise moderately diverse nearshore, shallow-marine molluscan assemblage (Roth, 1988; Squires & Demere, 1991).

Givens (1974:table 1) reported *L. turritum,* along with *Potamides* (*P.*?) *carbonicola* and *Acutostrea idriaensis idriaensis,* at a single locality (UCR loc. 4696) in the *Ectinochilus supraplicatus* megafaunal biozone in the siltstone facies of the Juncal Formation about 2.5 km northeast of Pine Mountain, Ventura County, southern California. He also interpreted that the siltstone facies might have been deposited in interdistributary bays or lagoons or in the prodelta environment of the seaward edge of the deltaic complex.

The middle Eocene upper part of the Matilija Sandstone at Matilija Hot Springs in Ventura County, southern California contains numerous specimens of *L. turritum* within a 50 m-thick section of alternating sandstone and finer grained intervals consisting of complexly interbedded mudstone, fossiliferous mudstone, siltstone, and, in some cases, gypsum and limestone. Link (1975) and Link & Welton (1982) reported the section represents a restricted-coastal (paralic) environment, with three main subenvironments: beach-bar-channel complexes [= sandstone], lagoon or bay [= mudstone, fossiliferous mudstone, and siltstone], and coastal sabkha [= gypsum, limestone, mudcracks, and localized "red beds"]. Based on my own fieldwork, which is being incorporated into a detailed report of the molluscan fauna of these restricted-coastal rocks (Squires, in preparation), I found that *L. turritum* is present in several thin, silty mudstone beds immediately overlain by unfossiliferous mudstone or siltstone. Common associates are the gastropod *Potamides* (*Potamidopsis*) *californica* Squires, 1991a, the oyster *Acutostrea idriaensis idriaensis,* and corbiculid, tellinid, and venerid bivalves. The specimens of *L. turritum* and *P.* (*P.*) *californica* range in size from early juveniles to adults, show delicate sculpture, are mostly complete, and are randomly oriented. Many of the bivalve specimens are closed-valved. The distance of postmortem transport of any of these mollusks has been small, and the specimens have not been moved out of their original habitat. They represent nearly *in situ* brackish-marine individuals that lived in restricted-coastal waters. Some of the fossiliferous mudstones in this section contain lenses of gypsum and/or limestone. In comparison with the other fossiliferous mudstones, these mudstones directly associated with evaporites have a much lower taxonomic diversity of mollusks. Although *Potamides* (*Potamidopsis*) *californica* persists as a common faunal component in these mudstones associated with evaporites, *L. turritum* is never present, and its absence indicates that it did not tolerate evaporitic conditions.

"Tejon Stage"

Jestes (1963) and Squires (1991a) reported a storm-derived mixture of nearshore-marine and brackish-marine mollusks, including *L. turritum,* in the Matilija Sandstone in the vicinity of Beartrap Creek, just east of the mouth of Alamo Creek, Ventura County, southern California. Givens (1974) assigned the rocks in this part of the Matilija Sandstone to the "Tejon Stage."

Givens (1974:table 1) reported *L. turritum* from the *Ectinochilus canalifer* megafaunal biozone in the sandstone facies of the Juncal Formation just north of Pine Mountain, Ventura County, southern California. Some mollusks in this facies are indicative of the shallow-marine environment, possibly at the seaward margin of a delta complex, whereas others (oyster banks and *Potamides* (*P.*?) *carbonicola*) are indicative of brackish-water bays or lagoons (Givens, 1974).

Givens (1974:table 1) also reported *L. turritum* from the *Ectinochilus canalifer* biozone in the lower part of the Matilija Sandstone at the mouth of Alamo Creek, Ventura County, southern California. Associated mollusks (e.g., *Potamides* (*P.*?) *carbonicola* and *Acutostrea idriaensis idriaensis*) indicate that these rocks were probably deposited in brackish-water bays or lagoons (Givens, 1974).

Givens (1974:table 1), furthermore, reported a mixture of shallow-marine and brackish-marine mollusks, including *L. turritum,* in the *Ectinochilus canalifer* biozone in the Matilija Sandstone just east of Pine Mountain, Ventura County, southern California, and he interpreted the depositional environment of these mollusks to have been probably adjacent to a delta complex.

PALEOCLIMATE

Introduction

Inferred paleoclimatic conditions for the geologic range of *L. turritum* are summarized in Figure 2. Eocene rocks in San Diego County, southern California, are particularly useful for paleoclimate studies because of the complex intertonguing relationships between shallow-marine and nonmarine formations. These stratigraphic relationships span nearly the entire Eocene, and many types of geologic studies have been done on these rocks.

"Meganos Stage" and "Capay Stage"

Loxotrema turritum was most widespread (from Washington to southern California) during the time of the "Meganos Stage" and the "Capay Stage." This early Eocene time was the warmest interval of the Cenozoic, and tropical to subtropical conditions were widespread (Haq, 1981). On the west coast during this time, tropical and hot-humid conditions prevailed in coastal-lowland areas, as revealed by studies of a lateritic paleosol and of megafloral fossils (Figure 2). The paleosol study was done in the San Diego area, southern California, and in northwestern Baja California, Mexico (Peterson & Abbott, 1979). The megafloral study was done on the lower Eocene part of the Puget Group of southwestern Washington (Wolfe, 1968; 1994).

"Domengine Stage"

The "Domengine Stage" record of *L. turritum* is known only from California. From the middle part of this stage (lowermost middle Eocene) through the end of the geologic range of this species in the lower part of the "Tejon Stage" (lower middle Eocene), *L. turritum* is known only from southern California. During this same interval, tropical to subtropical conditions were prevalent in coastal-lowland areas, as revealed by studies of clay mineralogy, megafloral fossils, palynomorphs, and land snails (Figure 2). The clay mineralogy study was done on the Domengine Formation in northern California (Todd, 1968; Todd & Monroe, 1968), and the megafloral studies were done on the Torrey Sandstone in the San Diego area (Myers, 1991). This latter formation has been reported by many workers (e.g., May & Warme, 1991) as interdigitating laterally with both the marine Ardath Shale and the brackish-marine Delmar Formation. Palynomorph studies were done on the Ardath Shale (Lowe, 1974; quoted in Lillegraven, 1979), on the Delmar Formation (Elsik & Boyer, 1977), and on the Domengine Formation in the Vallecitos syncline area in northern California (Schulein, 1993). A land snail was studied from the Santiago Formation at Oceanside in northern San Diego County (Roth, 1991).

"Transition Stage"

The Scripps Formation record of *L. turritum* at Murphy Canyon (SDSNH loc. 3278) in the San Diego area is also associated with land snails. A study of camaenid land snails from the upper part of this formation indicated "forested land and a tropical climate with ample summer rainfall," and the land snails might have been living in a humid forest fringing a coastal lagoon (Roth, 1988). A single specimen of a transported helicinid land snail from elsewhere in the Scripps Formation could indicate tropical conditions, but paleoclimate inferences based on helicinids are somewhat inconclusive because modern members of this family range into xeric (dry) habitats (Roth & Pearce, 1988).

Lower Part of the "Tejon Stage"

In the San Diego area, the Scripps Formation laterally interfingers with and is partly subjacent to the chiefly nonmarine Friars Formation. Just upsection from the Friars Formation is the marine to nonmarine Mission Valley Formation. Neither of these two formations contains specimens of *L. turritum,* but both (especially the Mission Valley Formation) record a climatic change to less humid conditions (Peterson & Abbott, 1979). The Mission Valley Formation is correlative in time to just after the disappearance of *L. turritum* from the rock record. Frederickson (1991b) assigned this formation to the calcareous nannoplankton Subzone CP13c, but Walsh et al. (1996) suggested that it might be assignable to the slightly younger Subzone CP14a (equivalent to the lower part of the "Tejon Stage"). Caliche horizons, immature clay-mineral suites, and apparent salt crystallization from the Friars and Mission Valley formations have led to the conclusion that the paleoclimate during the deposition of these rock units was distinctly seasonal and arid (Peterson & Abbott, 1979). A study of over 100 species of land vertebrates from these same formations have led to the conclusion that the paleoclimate was seasonal and dry to moist subhumid (Novacek & Lillegraven, 1979). Frederickson (1991a) reported that the angiosperm-pollen flora from near the base of the Mission Valley Formation indicates that the climate was seasonal and no dryer than moist subhumid.

The synchronism between the disappearance of *Loxotrema turritum* and the change of climate from subtropical/tropical to seasonal semiarid strongly suggests that the extinction of this species was caused by climatic change. The species was adapted for humid, tropical conditions as evidenced by its widespread dispersal during the early Eocene. It is important to mention that the environment of *Faunus ater,* which is the closest living relative of *Loxotrema turritum,* is also confined to fully tropical conditions. *Faunus ater* is found today in the mouths and coastal reaches of freshwater rivers and streams, where there is some brackish influence, between 20°N and 20°S of the equator in southeast Asia, Sumatra, Java, Moluccas, Thailand, Sri Lanka (Ceylon), China, Philippines, New Guinea, Solomon Islands, and New Hebrides (Houbrick, 1991).

The presence of *L. turritum* in nearly *in situ* conditions in the upper part of the Matilija Sandstone at Matilija Hot Springs is especially revealing. As discussed earlier, it is present in fossiliferous mudstones not directly associated with evaporites, but it is always absent in fossiliferous mudstones containing lenses of evaporites. Although *Loxotrema turritum* was rather hardy because it lived in the brackish-marine environment, it could not tolerate arid conditions, and it is very likely that when the climate became too dry during the early middle Eocene the species went extinct.

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LOCALITIES CITED

CSUN 1450. About 225 m (836 ft.) W of junction of Highway 33 and a short, paved road that leads to Matilija Hot Springs, on S bank of North Fork Matilija Creek near W end of highway bridge that crosses the creek, NE ¼ of the SE ¼ of section 29, T. 5 N, R. 23 W, U.S. Geological Survey Matilija Quadrangle, 7.5-minute, 1952 (photorevised 1967), Ventura County, southern California. Matilija Sandstone. Age: Early middle Eocene ("Transition Stage"). Collector: R. L. Squires, 1990 and 1996.

LACMIP 7206. On E bank of Little River just S of highway bridge over the river at Glide, SE ¼ of the NW 14 of section 19, T. 26 S, R. 3 W, U.S. Geological Survey Glide Quadrangle, 15-minute, 1954, Douglas County, southwestern Oregon. White Tail Ridge formation (unknown member). Age: Middle early Eocene ("Capay Stage" but near the "Capay Stage"-"Domengine Stage" boundary). Collectors: D. W. Scharf & W. P. Popenoe, 3 September 1930; R. L. Squires, 10–11 July 1988. [= UCMP locs. A-661 & A-662].

LACMIP 24258. Approximately at sharp bend in a short, paved road that leads from Highway 33 to Matilija Hot Springs, NE ¼ of the SE ¼ of section 29, T. 5 N, R. 23 W, U.S. Geological Survey Matilija Quadrangle, 7.5-minute, 1952 (photorevised 1967), Ventura County, southern California. Matilija Sandstone. Age: Early middle Eocene ("Transition Stage"). Collectors: E. C. Jestes, 1963; R. L. Squires, 1990 and 1996.

SDSNH 3278. At 4760 Murphy Canyon Road, at elevation of 104 m (340 ft.) on W side of Murphy Canyon, 5746 m (18,850 ft.) S and 610 m (2000 ft.) E of NW corner of La Mesa Quadrangle, U.S. Geological Survey La Mesa Quadrangale, 7.5-minute, 1967, San Diego County, southern California. Upper part of Scripps Formation. Age: Early middle Eocene ("Transition Stage"). Collector: B. O. Riney, 23, February 1985. [A retaining wall now covers the collecting site].

UCMP 3311. Information from Kew (1924:29): On point of ridge at edge of Simi Valley, south side of Simi Valley, 1.6 km (1 mi.) N and O .13 km (0.08 mi.) W of SE corner of Piru quadrangle, Ventura County, southern California. Collector: B. L. Clark. Information from UCMP locality registry: Simi Hills, Simi Valley, Ventura County, southern California.

UCMP 3586. At elevation of 99 m (325 ft.), on ridge immediately SE of Kellogg Creek, 302 m (990 ft.) N of NE corner of section 12, T. 1 S, R. 2 E, U.S. Geological Survey Byron Hot Springs Quadrangle, 7.5-minute, 1953 (photorevised 1968), Contra Costa County, northern California. Margaret Hamilton Sand [= division D of Meganos Formation as used by Clark & Woodford (1927)]. Age: Early Eocene ("Meganos Stage"). Collector: A. O. Woodford, circa 1920s.

UCMP A-661. See LACMIP loc. 7206.

UCMP A-662. Five meters stratigraphically higher than UCMP loc. A-661.

UCMP A-1154. At elevation of 671 m (2200 ft.), on NE face of ridge marked by prominent red-sandstone capping on W side of Griswold Canyon, near center of W edge of section 23, T. 16 S, R. 10 E, U.S. Geological Survey Panoche Quadrangle, 7.5-minute, 1969, San Benito County, central California. Domengine Formation. Age: Late early to early middle Eocene ("Domengine Stage"). Collector: H. E. Vokes, 1930s.

UCMP A-1547. Dark sandstone interbedded with basalt at base of sea cliff on small point about 183 m (600 ft.) due N of hill 108 on W side of Crescent Bay, approximately center of section 20, T. 31 N, R. 8 W, U.S. Geological Survey Joyce Quadrangle, 7.5-minute, 1950 (photorevised 1979), Clallam County, Olympic Peninsula, southwestern Washington. Crescent Formation. Age: Middle early Eocene ("Capay Stage"). Collectors: S. A. Berthiaume & Mr. Bramkamp, 1935. [= UCMP loc. A-1548 (approximately) and UCMP loc. A-3212].

UCMP A-1550. About 30 m (100 ft.) S of small cove on W side of Crescent Bay and about 183 m (600 ft.) due E of hill 108 on W side of Crescent Bay, east central part of section 20, T. 31 N, R. 8 W, U.S. Geological Survey Joyce Quadrangle, 7.5-minute, 1950 (photorevised 1979), Clallam County, Olympic Peninsula, southwestern Washington. Crescent Formation. Age: Middle early Eocene ("Capay Stage"). Collectors: S. A. Berthiaume & Mr. Bramkamp, 1935.

UCR 4696. On U.S. Forest Service hiking trail from Fishbowls Campground to Pine Mountain Lodge, 396 m (1300 ft.) S and 122 m (400 ft.) W of NE corner of section 12, T. 6 N, R. 22 W, U.S. Geological Survey San Guillermo Quadrangle, 7.5-minute, 1943, Ventura County, southern California (Givens, 1974:97). Uppermost tongue of siltstone facies of Juncal Formation. Age: Early middle Eocene ("Transition Stage"). Collector: C. R. Givens, circa late 1960s.

UCR 4930. Light gray siltstone containing scattered pebbles and small cobbles, near base of sea cliff 120 m (394 ft.) S of end of beach access road in Blacks Canyon, 3.74 km (2.32 mi.) N, 7.66 km (4.75 mi.) E in zone 11 of UTM grid system, U.S. Geological Survey Del Mar Quadrangle, 7.5-minute, 1967, San Diego County, southern California. Ardath Shale. Age: Late early to early middle Eocene ("Domengine Stage"). Collector(s): Unknown.