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New Information on Morphology, Stratigraphy, and Paleoclimate Implications of the Eocene Brackish-Marine Gastropod *Loxotrema turritum* Gabb, 1868, from the West Coast of the United States

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Abstract. New morphologic information about the aperture of the brackish-marine Eocene gastropod *Loxotrema turritum* Gabb, 1868, allows for reassignment of this species from family Thiaridae to family Melanopsidae and shows that *L. turritum* is most closely related to the melanopsid *Faunus ater* Linnaeus, 1758, found today in the fully tropical Indo-West Pacific region near the mouths of rivers. New stratigraphic and geographic data show that the earliest record of *L. turritum* is in lowermost Eocene ("Meganos Stage") rocks in northern California, and that the species was most widespread during the middle lower Eocene ("Capay Stage") when it ranged from southern California to as far north as Crescent Bay, Washington. Most of these "Capay Stage" specimens underwent downslope postmortem transport, most likely from deltaic areas, into deeper waters and became mixed with shallow-marine mollusks. The "Domengine Stage" record of this species 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* lived in brackish-marine lagoons or bays within deltaic complexes in southern California. The last records of this species help confirm data from other disciplines that during the early middle Eocene there was a climate change from humid to drier conditions.

INTRODUCTION

The brackish-marine gastropod *Loxotrema turritum* Gabb, 1868, the only known species of genus *Loxotrema* Gabb, 1868, is confined to lower and lower middle Eocene rocks on the west coast of the United States. This article, which represents the first detailed study of any Eocene brackish-marine mollusk from the west coast of the United States, contains a thorough review of the stratigraphic occurrences and inferred depositional environments of this species. In addition, it contains the first discussion of the paleoclimatic implications of this species.

Loxotrema turritum is very distinctive due to its tabulate whorls and large cylindrical body whorl, but specimens are prone to poor preservation of the outer lip and the anterior end of the aperture, as evidenced by nearly all the published illustrations of this species. These features, which are critical in determining familial assignment, have not been used before by other workers, who, on the basis of general morphology, traditionally placed *Loxotrema* in the family Thiaridae. I examined nearly 300 specimens of *L. turritum,* most of which are stored at several museums on the west coast. I found only a single individual that shows the entire aperture and only two individuals that show some indication of protoconch morphology. This new morphological information reveals that *L. turritum* is most closely related to the extant melanopsid *Faunus ater* Linnaeus, 1758.

While examining museum collections, I found new stratigraphic and geographic occurrences of *L. turritum.* The known geologic range of this species is now lowered to the earliest Eocene, and its known geographic range is now extended northward to the Olympic Peninsula of southwestern Washington (Figures 1, 2).

Since the early paleontologic work by Arnold (1909) in the coal-bearing district of Coalinga in central California, *L. turritum* Gabb, 1868, has been recognized as a component of brackish-marine molluscan assemblages of Eocene rocks of California. Until this present article, however, there has been no attempt to evaluate all of its inferred depositional environments. As will be discussed herein, most of the early Eocene specimens of *L. turritum* were prone to displacement from coastal waters into much deeper waters, whereas middle Eocene specimens are usually found nearly *in situ* in deltaic settings. The species lived for 8.5 million years in humid, tropical to subtropical conditions. The disappearance of *L. turritum* from the fossil record during the early middle Eocene helps confirm data from other sources (paleosols, clay minerals, megaflora, palynomorphs, land-mammals, and land snails) that there was a change in climate at that time to drier conditions.

In this article, the term "shallow-marine" refers to unrestricted, nearshore waters of normal-ocean salinity seaward of beaches or barrier bars. The term "brackish-marine" refers to restricted waters with salinities lower than

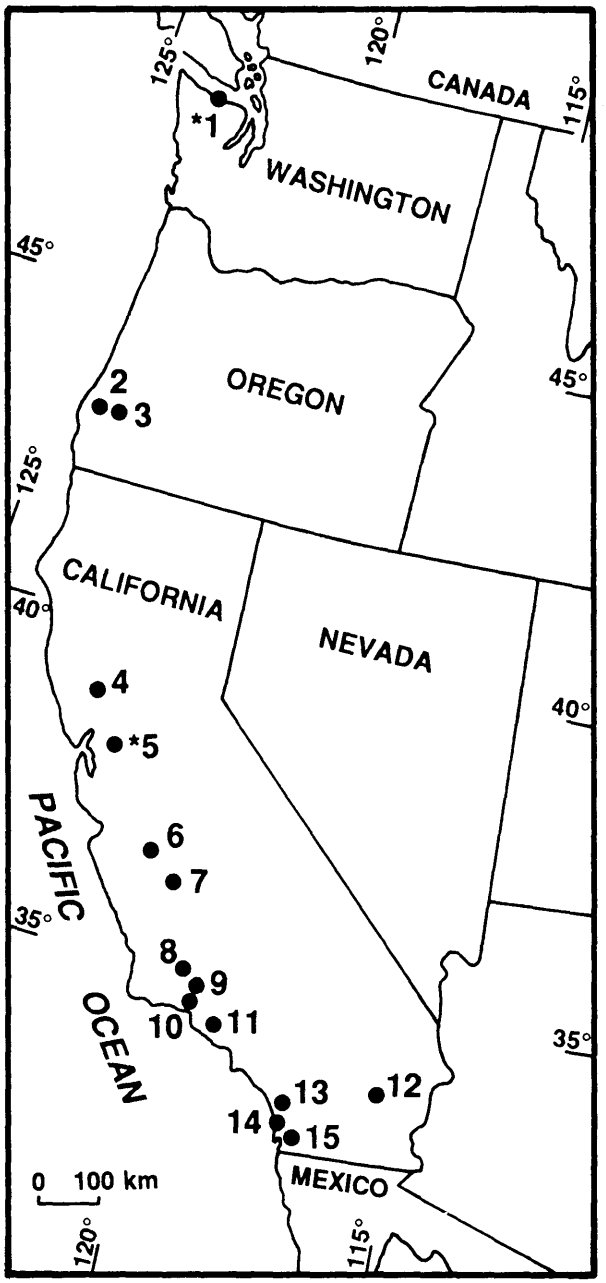


Figure 1

Index map showing geographic locations of *Loxotrema turritum* Gabb, 1868. Locations are numbered from north to south. (1) Crescent Bay. (2) West of Roseburg. (3) Glide. (4) Smith Canyon. (5) Kellogg Creek. (6) Griswold Canyon. (7) Coalmine Canyon. (8) Mouth of Alamo Creek and Beartrap Canyon areas. (9) Pine Mountain. (10) Matilija Hot Springs. (11) Simi Valley. (12) Orocopia Mountains. (13) Vista. (14) Torrey Pines State Reserve and Blacks Canyon areas. (15) Murphy Canyon. (* = New report).

those of normal-ocean waters. Furthermore, the term "brackish-marine" refers to waters landward of beaches or barrier bars but with some connection to the shallow-marine environment.

The following institutional acronyms are used: CAS, California Academy of Sciences, San Francisco; CSUN, California State University, Department of Geological Sciences, Northridge; LACM and LACMIP, Natural History Museum of Los Angeles County, Section of Malacology and Invertebrate Paleontology, Los Angeles, respectively; SDSNH, San Diego Society of Natural History; UCMP, University of California Museum of Paleontology, Berkeley; and UCR, University of California, Riverside.

SYSTEMATIC PALEONTOLOGY

Superorder CAENOGASTROPODA Cox, 1959

Order NEOTAENIOGLOSSA Haller, 1882

Superfamily CERITHIOIDEA Férussac, 1819

Family MELANOPSIDAE Adams & Adams, 1854

Discussion: The family Melanopsidae usually has been regarded as a subfamily of Thiaridae Troschel, 1857. In a cladistic analysis, Houbrick (1988) showed melanopsids to be distinct from thiarids and deserving of full familial status. In his analysis, the Melanopsidae is in a separate branch but relatively close to the branch supporting the Thiaridae.

Subfamily Melanopsinae Adams & Adams, 1854

Discussion: Houbrick (1988, 1991) confusingly assigned subfamily Melanopsinae to the family Thiaridae. Usage of this subfamily name with family Thiaridae, however, is not correct because Melanopsinae, by definition, has to be a subset of family Melanopsidae. It is in the latter sense, that the name Melanopsinae is used in this paper.

Genus *Loxotrema* Gabb, 1868

Original description: "Shell elongate, turrited, spire high; aperture with a very short canal in front; outer lip retreating above, sinuous below; inner lip heavily encrusted" (Gabb, 1868:147).

Type species: *Loxotrema turritum* Gabb, 1868, by original designation.

Loxotrema turritum Gabb, 1868
(Figures 3–14)

Loxotrema turrita Gabb, 1868:147, pl. 14, fig. 21; 1869:168, 227, pl. 28, fig. 49. Cooper, 1894:61. Cossmann, 1904: 103. Arnold, 1909:14, pl. 4, fig. 17. Arnold & Anderson, 1910:71, pl. 26, fig. 17. Arnold & Hannibal, 1913: 572. Dickerson, 1913:285; 1914:115; 1916, 439, 450 (in

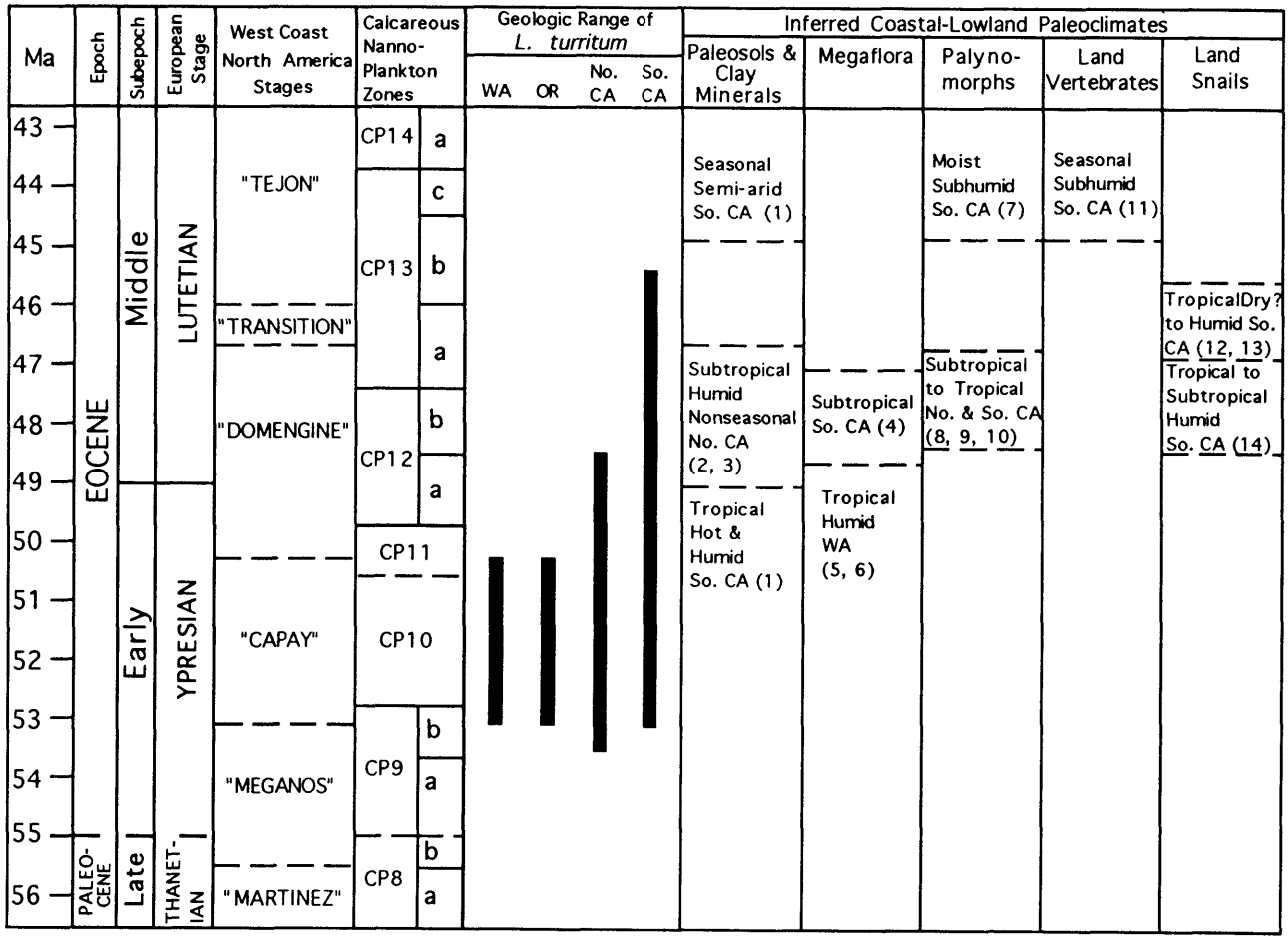


Figure 2

Geologic range of *Loxotrema turritum* Gabb, 1868, plotted against geochronologic time scale, European stages, standard calcareous nannoplankton zones (from Berggren et al., 1995), western North America stages (from Saul, 1983; Squires, 1988a), and inferred coastal-lowland paleoclimates. WA = Washington, OR = Oregon, No. CA = northern California, So. CA = southern California. Numbers in parentheses refer to the following literature sources: (1) Peterson & Abbott, 1979; (2) = Todd, 1968; (3) = Todd & Monroe, 1968; (4) = Meyers, 1991; (5) = Wolfe, 1968; (6) = Wolfe, 1994; (7) = Frederickson, 1991a; (8) = Elsik & Boyer, 1977; (9) = Lowe, 1974, quoted in Lillegraven, 1979; (10) = Schulein, 1993; (11) = Novacek & Lillegraven, 1979; (12) = Roth, 1988; (13) = Roth & Pearce, 1988; (14) = Roth, 1991.

part). Kew, 1924:29. Clark, 1926:115; 1929:pl. 10, fig. 3. Hanna, 1927:312, pl. 50, figs. 5–8. Merriam & Turner, 1937:table 2. Vokes, 1939:159, pl. 20, figs. 15–19. Schenck & Keen, 1940:pl. 24, figs. 10–13. Weaver (1942 [1943]):374, pl. 75, figs. 1–3; pl. 103, fig. 18. Keen & Bentson, 1944:168.

Struthiolaria (*Loxotrema*) *turrita* (Gabb). Tryon, 1883:196, pl. 60, fig. 95; 1885:105.

"*Loxotrema turrita*" Gabb. Anderson & Hanna, 1925:44, 104.

Struthiolaria (*Loxotrema*) *turritum* Gabb. Fischer, 1884:678.

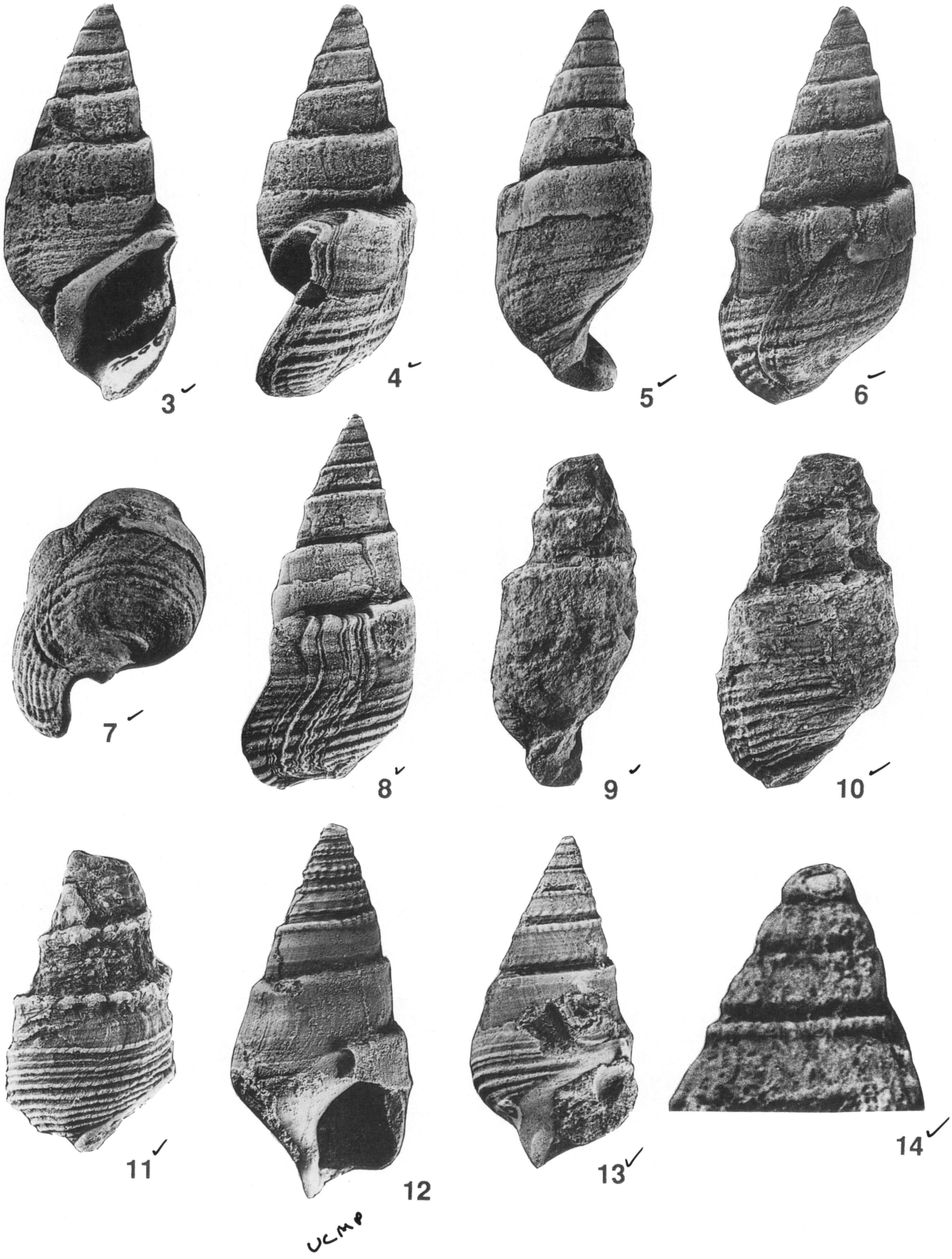
Loxotrema turritum Gabb. Stewart, 1927:347–348, pl. 26, figs. 3, 4. Turner, 1938:tables 2, 4, & 8, p. 81, pl. 17, figs. 12, 13. Givens, 1974:70, pl. 6, fig. 17. Givens & Kennedy, 1976:963, pl. 1, figs. 5–8; 1979:table on p. 87. Squires, 1991a:355. Squires & Demere, 1991:table 1.

Pachychilus (*Loxotrema*) *turritum* (Gabb). Wenz, 1939:686, fig. 1968.

Loxotrema (no species designated). Baldwin, 1959:pl. 11, unnumbered figure. Fowkes, 1982:21, unnumbered figure.

?*Loxotrema turritum* Gabb. Squires, 1991b:table 1, pl. 1, fig. 16.

Original description: "Shell elongate, turreted, spire elevated, nearly twice the length of the aperture; whorls about six to six and a half, slightly convex on the sides, abruptly truncated and flat on the upper margin. Body whorl marked by eight or ten revolving lines on the anterior half, crossed by sinuous lines of growth; both sets of markings being very variable in distinctness in differ-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UCMP

ent specimens. Aperture obliquely subquadrate, bordered on the inner side by a raised lip, the top retreating upwards, and very obliquely backwards; outer lip thick above and below, very thin in the middle, and with a strongly sinuous margin, most prominent near the anterior end; inner lip thick, its margin somewhat raised above the surface of the body whorl; anterior extremity of aperture not notched, but produced, and slightly channelled" (Gabb, 1869:168).

Supplemental description: Medium in size (up to 45 mm high, estimated), turreted, approximately eight whorls (including protoconch); high-spired, spire about one-half of shell height; body whorl large and cylindrical. Suture in shallow groove, especially on body whorl. Protoconch approximately one whorl, low, smooth, and not well differentiated from teleoconch. Pleural angle approximately 40°. Upper spire whorls convex, remainder of teleoconch with tabulate whorls. Teleoconch sculpture changes from early whorls to later whorls. Uppermost spire whorls with two equal spiral ribs, increasing to three on middle part of spire, with posteriormost rib becoming the strongest. Spiral ribs with numerous, closely spaced small nodes; nodes strongest on posteriormost rib. Interspaces of spiral ribs with two to three very fine spiral threads forming a minute cancellate pattern with the intersecting growth lines. On lower spire and posterior part of body whorl, strength of spiral ribbing quite variable (moderately strong to smooth) and nodes obsolete except on tabulate shoulder, where nodes become very low and broadly spaced on older individuals. On anterior half of body whorl, spiral ribs strong, about eight to 20 in number; interspaces usually with a secondary spiral rib. Aperture obliquely subquadrate. Anterior end with a prominent notch. Siphonal fasciole usually weak, rarely moderately strong. Columella smooth, with a thick callus extending into parietal region and tabulate shoulder area. Posterior end of aperture (where parietal callus meets the tabulate shoulder) with a narrow notch. Outer lip sinuous, with a strong deflection medially. Outer lip projected at its anterior end and thick, thinning considerably toward the strong deflection area. Anteriormost part of outer lip crenulate, both externally and internally. Growth lines prosocline on upper spire, but opisthocline with a strong sigmoidal curve in region of the strong deflection area of the body whorl. Near suture, growth lines nearly straight to slightly opisthocline. Growth rugae commonly near outer lip on adult body whorl.

Lectotype: ANSP 4228 (designated by Stewart, 1927).

Type locality: "Tejon Group, ten miles west of Griswold's, between San Juan and New Idria" Gabb (1869:168). Vokes (1939:159) referred to topotypes of *L. turritum* from UCMP loc. A-1154, which is in the Domengine Formation, on the west side of Griswold Canyon, San Benito County, central California.

Geographic distribution: Crescent Bay, Olympic Peninsula, southwestern Washington to San Diego area, San Diego County, southern California.

Geologic age: Early Eocene ("Meganos Stage") to lower middle Eocene (lower part of "Tejon Stage").

Stratigraphic distribution: See Table 1.

Unsubstantiated stratigraphic reports: According to Anderson & Hanna (1925:104), Dickerson's (1916) report of *Loxotrema turritum* at the type section of the Tejon Formation in the southernmost part of the San Joaquin Valley, central California, is in error because there is no evidence whatsoever that it does occur there.

Turner (1938:tables 2, 8) reported *L. turritum* from the informal "lower Umpqua group" along the Middle Fork of Coquille River near Remote, southwest of Roseburg in southwestern Oregon. After a careful search, I was unable to find any of these specimens in the UCMP collection, where Turner deposited other specimens that he had collected from Eocene rocks of southwestern Oregon. Although no recent worker has assigned these reportedly *L. turritum*-bearing beds to any currently recognized stratigraphic units, the beds most likely belong to the lower Eocene undifferentiated and informal White Tail Ridge formation that has been recognized in this area by Niem et al. (1992). According to them, this formation in this area is mollusk-bearing and contains delta-front shallow-marine sandstone, as well as rare estuarine coals and mudstone. More work is needed to confirm the presence of *L. turritum* in these rocks.

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Explanation of Figures 3 to 14

Specimens coated with ammonium chloride.

Figures 3–14. *Loxotrema turritum* Gabb, 1868. Figures 3–7. Hypotype LACMIP 6449, LACMIP loc. 7206, height 37.3 mm, ×1.8. Figure 3. Apertural view. Figure 4. Right-lateral view. Figure 5. Left-lateral view. Figure 6. Abapertural view. Figure 7. Oblique anterior view. Figure 8. Hypotype LACMIP 6450, LACMIP loc. 7206, right-lateral view, height 34.6 mm, ×1.8. Figures 9–10. Hypotype LACMIP 7162, CSUN loc. 1450, height 28 mm, ×1.9. Figure 9. Left-lateral view. Figure 10. Abapertural view. Figure 11. Hypotype LACMIP 6451, LACMIP loc. 24258, abapertural view, height 20.2 mm, ×2.5. Figure 12. Hypotype UCMP 154003, UCMP loc. A-1550, apertural view, height 21.5 mm, ×2.9. Figures 13, 14. Hypotype LACMIP 6452, LACMIP loc. 7206, apertural view. Figure 13. Height 21.2 mm, ×2.6. Figure 14. Protoconch (some shell missing) and uppermost teleoconch, height 3.5 mm, ×12.

Published reports of *L. turritum* in the Llajas Formation of Simi Valley, Ventura County, southern California are unsubstantiated because of indefinite geologic and geographic information. Kew (1924:29) listed *L. turritum* as one of the mollusks from a locality (UCMP loc. 3311) on the south side of Simi Valley. Using the locality information given by Kew, the locality does not plot in bedrock, rather it plots in the streambed of the modern Simi Arroyo. Information in the UCMP locality records is even less informative, with the locality cited only as Simi Valley. Clark (1921:155) was the original collector of the mollusks from this locality, but he did not include any details as to its location. He listed nearly the same mollusks from this locality that Kew did, but, for some reason, Clark did not include *L. turritum.* I was able to find a specimen of *L. turritum* from UCMP loc. 3311 in the UCMP collection, but the associated mollusks were totally different from those listed by Clark (1921) and Kew (1924) and are ones normally found in the shallow-marine part of the Llajas Formation that crops out on both the north and south sides of Simi Valley. This formation, which was named many years after the work of Clark (1921) and Kew (1924), is an obvious candidate for the stratigraphic position of UCMP loc. 3311. Turner (1938: table 8) even reported, by means of a checklist, that *L. turritum* is present in the "lower Llajas Formation," but he did not provide any other stratigraphic or geographic details. In my monographic study (Squires, 1984) of the megafossils of the Llajas Formation, I found no *L. turritum* anywhere in the formation. I also did a careful search at LACMIP, which has an extensive collection from the Llajas Formation, without finding any specimens of *L. turritum.* I did find several other specimens of *L. turritum* from the Llajas Formation in the collections at UCMP, CAS, and UCR, but the locality data are very indefinite.

Discussion: A total of 297 specimens of *L. turritum* was studied. Most are worn, and the upper spire sculpture usually has been nearly obliterated. The anterior notch and siphonal fasciole are best developed on adult specimens, but even these show variability as to strength of the siphonal fasciole. A weak siphonal fasciole is illustrated in Figure 5, whereas a much stronger one is illustrated in Figures 9 and 10.

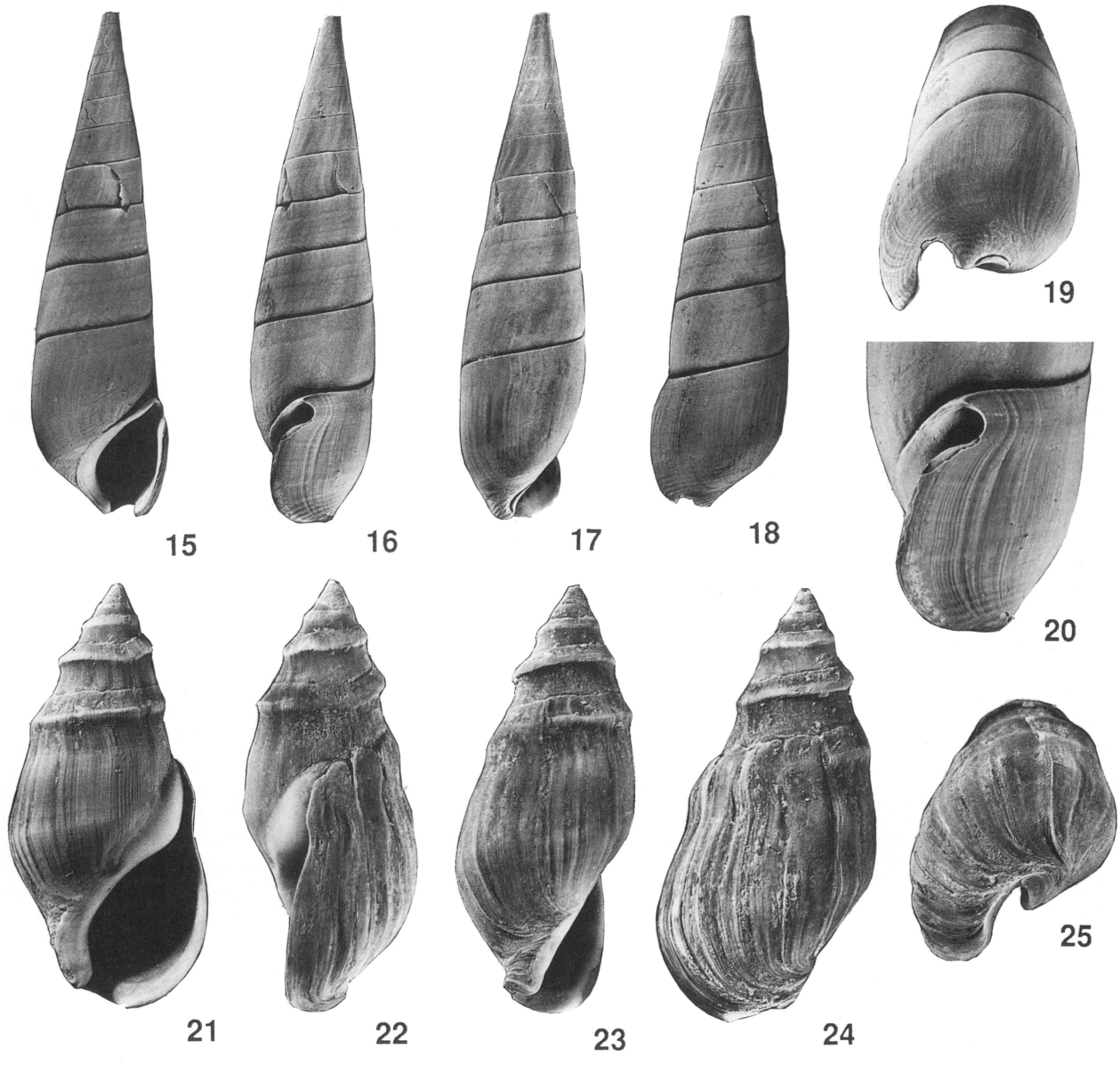
The most numerous specimens were found in the Crescent Formation at Crescent Bay, Washington. Nearly all of these are early adults and show very well the sculpture on the upper spire. One of these specimens is illustrated in Figure 12. Some specimens from the upper part of the Matilija Sandstone at Matilija Hot Springs show nodes on the shoulder of the adult body whorl. One of these specimens is illustrated in Figure 11.

In terms of the apertural notches and outline of the outer lip, *L. turritum* most closely resembles *Faunus ater* Linnaeus, 1758, the type species and only living species of *Faunus.* Houbrick (1991:figs. 1–18) reported *F. ater* from freshwater to slightly brackish-marine habitats in the Indo-West Pacific. Utilizing LACM specimens (lot number 107993) for comparison, both genera have a subquadrate apertural shape, a well-developed anterior notch, a posterior notch, a projected anterior end of the aperture, a sinuous outer lip, and a siphonal fasciole. A specimen of *F. ater* is illustrated in Figures 15–20. The aperture of *Loxtrema* differs only in minor ways by having shallower anterior and posterior notches, a much narrower posterior notch, usually a weaker siphonal fasciole, and a crenulated anterior end of the outer lip. In terms of the rest of the shell, *Loxotrema* differs by having a much lower spire, tabulate whorls, presence of shell sculpture, no subsutural band on the adult body whorl, and deflection of the outer lip-area ophisthocline growth lines nearer the suture.

After a detailed anatomical study of *F. ater,* Houbrick (1991) assigned *Faunus* to subfamily Melanopsinae and reported that *F. ater* has certain unusual anatomical features that unite *Faunus* to the melanopsid *Melanopsis* and to the thiarid *Melanatria* Bowdich, 1822. Houbrick (1991) also discussed how the classification of *Faunus* is still very provisional and that much work is needed to clarify its exact phylogenetic relationship with the thirarid group, a large and poorly defined family of freshwater prosobranchs in need of major revision.

Loxotrema turritum closely resembles the living species *Melanopsis* (*Lyrcaea*) *dufouri* Férussac, 1823, the type species of *Lyracea. Melanopsis* (*L.*) *dufouri* was illustrated by Wenz (1939:691, fig. 1987), who reported it from Valencia, Spain. Subgenus *Lyrcaea* is generally smoothish, ranges from Eocene to Recent, and its fossil record is in Europe, North Africa, and Asia. Today it is confined to the Mediterranean region (Wenz, 1939). Comparison with LACM specimens (lot number 108173) of *M.* (*L.*) *dufouri,* from a floodplain-river system near Sevilla, Spain, revealed that *Loxotrema turritum* differs from this species by having a higher spire, shorter body whorl, spiral ribbing on the whorls rather than just a swollen spiral rib at the whorl shoulder, an oblique posterior notch rather than a vertical one, usually a much weaker siphonal fasciole, and a more sigmoidal growth line on the body whorl. A specimen of *M.* (*L.*) *dufouri* is illustrated in Figures 21–25.

Loxotrema turritum is also somewhat similar to *Cerithium? macarum* Olsson (1931:183–184, pl. 28, fig. 3) in terms of general shape, upper spire ornamentation, and growth-line shape on the body whorl. *Cerithium? macarum,* which has been found in the Oligocene Mancora Formation of Peru, is known from only a single specimen, and it lacks the aperture and the tip of the spire. *Loxotrema turritum* differs from this species by having a longer body whorl, much shorter spire, more inflated body whorl, more prominent spiral ribs on body whorl, more tabulate and nodose shoulder on the whorls, and no in-



Explanation of Figures 15–25

Specimens coated with ammonium chloride.

Figures 15–20. *Faunus ater* Linnaeus, 1758, hypotype LACM 107993, Recent, Sri Lanka (Ceylon), height 63 mm, ×1.2 Figure 15. Apertural view. Figure 16. Right-lateral view. Figure 17. Left-lateral view. Figure 18. Abapertural view. Figure 19. Oblique anterior view. Figure 20. Enlarged right-lateral view of body whorl. Figures 21–25. *Melanopsis* (*Lyrcaea*) *dufouri* Férussac, 1823, hypotype LACM 108173, Recent, Sevilla, Spain, height 25.4 mm, ×2.4. Figure 21. Apertural view. Figure 22. Right-lateral view. Figure 23. Left-lateral view. Figure 24. Abapertural view. Figure 25. Oblique anterior view.

dication of varices. Until better material is found for Olsson's species, its generic assignment is open to question.

Loxotrema turritum generally resembles the living species *Aylacostoma glabrum* Spix, 1827 (in Spix & Wagner, 1827), which is the type species of *Aylacostoma. Aylacostoma glabrum* was recently described and illustrated by Nuttall (1990:259, 261, figs. 286–291), who reported it from a freshwater habitat in eastern Brazil. This genus belongs to family Thiaridae and subfamily Hemisininae Thiele, 1928. The only other known species of this genus is *Aylacostoma* sp., which is based on poorly preserved specimens of Miocene age from Ecuador (Nuttall, 1990). *Aylacostoma glabrum* shows considerable variation in morphology. It can be smooth or have rather strong sculp-