New Late Cretaceous Mytilid and Tellinoidean Bivalves from California

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Abstract. One new subfamily, one new genus, and two new species of Late Cretaceous warm-water, shallow-marine bivalves from California are described and named. The mytilid *Xenomytilus fons*, gen. et sp. nov., from middle to uppermost Maastrichtian strata in central and southern California, represents the type genus of **Xenomytilinae**, subfamily nov. This new subfamily is comprised of *Lycettia* Cox, 1937, and *Xenomytilus*. *Lycettia* is an Old World Tethyan bivalve that ranges from the late Early Jurassic (Toarcian) to the Late Cretaceous (Campanian). **Xenomytilus** is known only from California, but future studies might reveal it to be more widespread.

Xenomytilus fons is from Maastrichtian strata in central and southern California and is locally moderately common. It inhabited siliciclastic nearshore, warm waters and most likely had an epifaunal mode of life, with attachment by byssus to hard substrate. Specimens were commonly transported by turbidity currents into deeper waters.

The other new species is the tellinoidean *Icanotia californica*, sp. nov., from the upper Turonian upper part of the Baker Canyon Member and lower part of the Holz Shale Member of the Ladd Formation in the Santa Ana Mountains, Orange County, southern California. It lived in inner shelf waters and was infaunal in silts and very fine sands. *Icanotia* is a relatively rare, warm temperate and Tethyan, Cretaceous (Valanginian to Maastrichtian) bivalve known predominantly from Europe. Rare dispersals of *Icanotia* into the New World were, most likely, by westward-flowing equatorial currents that coincided with high stands of sea level. Its occurrence in southern California is its only record on the Pacific slope of North America.

INTRODUCTION

This paper concerns the recognition of a new subfamily, genus, and species of mytilid bivalve, and a new species of tellinoidean bivalve. Both are warm-water taxa and occur in shallow-marine, Upper Cretaceous rocks in California. The new mytilid bivalve, *Xenomytilus fons*, gen. et sp. nov., is of Maastrichtian age and from central and southern California, whereas the new tellinoidean bivalve, *Icanotia californica*, sp. nov., is of late Turonian age and from southern California.

Although specimens of Cretaceous mytilid bivalves in the rock record of the Pacific slope of North America are usually not well preserved, they are moderately common. The mytilids and possible mytilids previously reported from Cretaceous strata in this area are listed in Table 1. Much work is needed to get all of the listed bivalve names tied to definite genera and to fully establish the chronologic and geographic ranges of the species. None of the previously named or reported mytilids or possible mytilids from Cretaceous strata in the study area belongs to the new genus of mytilid described here.

The following comments pertain to Table 1. Although

Stewart (1930:87) mentioned that the holotype of *Mytilus pauperculus* Gabb (1864) is from Martinez (perhaps indicating Maastrichian age), California, the University of California, Museum of Paleontology (Berkeley) label with this specimen says "Curry's," which would make the type Albian or Cenomanian in age. Whiteaves (1879: 167, 1903:394, unfig.) and White (1889:34, 38, unfig.) tentatively reported this species from Vancouver Island. For a discussion of the members of the lower Redding Formation, Members I–III, see Squires & Saul (2003a). For a discussion of the "Roof of Coal" stratigraphic unit, see Squires & Saul (2003b). *Lithodomus* Cuvier, 1817, is the junior synonym of *Lithophaga* Röding, 1798. Stewart (1930:103–104) reported that the holotype of the "*Crenella*" concentrica might be a crushed specimen of an astartid.

The modioliform "Modiolus" major Gabb (1869:191–192, pl. 32, fig. 88; Stanton, 1895:48, pl. 3, fig. 1) from Hauterivian and Albian strata in the Great Valley Group of northern California is not a mytilid, according to Stewart (1930:104, pl. 4, fig. 1), who placed this bivalve in the carditid genus Myoconcha J. de C. Sowerby, 1824. Campbell et al. (1993) reported that Gabb's species is part

Table 1

Mytilids and possible mytilids (names enclosed in parentheses) previously reported from Cretaceous strata of the north-eastern Pacific region.

Taxon	Age	Locale(s)
Mytilus pauperculus Gabb, 1864	Albian or Cenomanian	Mt. Diablo, Contra Costa Co., northern California and Vancouver Is., British Columbia
"Mytilus lanceolatus" Sowerby of White- eaves, 1884	Albian?	Shingle Bay, eastern Skidegate Inlet, Moresby Is., British Columbia
Modiolus persistens Whiteaves, 1900	Albian?	East end of Maude Is., Queen Charlotte Islands, British Columbia
"Lithodomus maudensis" Whiteaves, 1884	Albian?	East end of Maude Is., Queen Charlotte Islands, British Columbia
Modiolus siskiyouensis Gabb, 1864	Turonian?, Coniacian?, or Campanian?	Siskiyou Mountains, Jackson Co., southern Oregon
Lithophaga oviformis Gabb, 1864	Turonian	Lower Redding Fm., Members I-III, Cow Creek, Shasta Co., Calif.
Inoperna bellarugosa Popenoe, 1937	Late Turonian	Ladd Formation, lower Holz Shale Mbr., Orange Co., Calif.
Lithophaga sp. Ludvigsen & Beard, 1994 and 1997	Late Santonian or early	Haslam Formation, Nanaimo, Vancouver Is., British Columbia
Modiolus teleus Stewart, 1930	Late Santonian? and early Campanian	Chico Fm. at Tuscan Springs, Tehama Co. & at Pentz, Butte Co., California
Lithodomus nitidus Whiteaves, 1903	Early Campanian	Pender Fm. ("Roof of Coal," Nanaimo), Vancouver Is., British Columbia
Brachidontes bifurcatus Popenoe, 1937	Late middle Campanian	Ladd Formation, upper Holz Shale Member, Orange Co., Calif.
Mytilus? quadratus Gabb, 1869	Maastrichtian	"Chico Group" at Martinez, Contra Costa Co., northern Calif.
"Modiolus siskiyouensis" of Whiteaves 1903	Cretaceous	Nanaimo area, Vancouver Is., British Columbia
"Modiolus (Brachidontes)" sp. indet. of Whiteaves, 1903	Cretaceous	Hornby Is. and Sucia Is., British Columbia
"Mytilus" sp. indet. of Anderson, 1958	Cretaceous	Santa Ynez Mountains, Santa Barbara Co., California
"Crenella" concentrica Gabb, 1864	Cretaceous?	Martinez, Contra Costa Co., Northern California

of a chemosynthetic macroinvertebrate fauna in cold-seep limestones from the Great Valley Group at Wilbur Springs (Hauterivian) and at Cold Fork of Cottonwood Creek (Albian), northern California.

Xenomytilus fons, sp. nov. is locally abundant, and

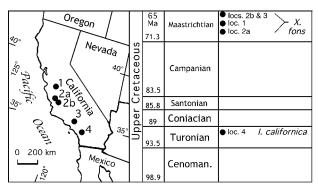


Figure 1. Index map showing locales of the new taxa. 1 = Garzas Creek. 2a = Cantinas Creek and north shore, Lake Nacimiento area. 2b = Dip Creek. 3 = Warm Springs Mountain. 4 = Santa Ana Mountains.

specimens are from moderately widespread locales in various formations (Figure 1). Although most of the specimens were collected by others and stored in museums, some of the specimens from Warm Springs Mountain and Lake Nacimiento area were collected by the authors. This new bivalve is unusual for a mytilid in that it possesses a strong tooth in either valve. It also possesses a sickle shape, a very sharp umbonal ridge that extends from the beak to the posterodorsal margin, abundant radial ribs, and a concave ventral margin. These external features are equivocal, and it is the hinge that is the most defining feature of this mytilid, which, so far, appears to be endemic to California. Xenomytilus is unusual among mytilids, so much so that it can be placed in its own subfamily, along with Lycettia Cox, 1937, an Old World Tethyan mytilid of Early Jurassic to Late Cretaceous age (see "Systematic Paleontology").

The occurrence of *Icanotia californica*, sp. nov., is the first documented record of this genus from the Pacific slope of North America. A total of 25 specimens was detected in museum collections. As will be discussed later in this paper, *Icanotia* is a warm-temperate and Tethyan

bivalve, whose geologic range is nearly the entire Cretaceous (Valanginian to Maastrichtian). It is predominantly known from Europe and Asia and is a relatively uncommon bivalve (Casey, 1961). Most of its species are based on only a few specimens (Dhondt & Dieni, 1993). Prior to this present study, the only other report of this genus in North America was a single specimen from the "Coon Creek fauna" in the Coon Creek Tongue at the base of the Ripley Formation, McNairy County, Tennessee (Wade, 1926:91–92). This fauna is of latest Campanian age (Cobban & Kennedy, 1995:2).

Abbreviations used for catalog and locality numbers are: CSUF, California State University, Fullerton; LAC-MIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; UCR, University of California, Riverside.

STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENTS OF THE NEW TAXA

The following stratigraphic units are listed from oldest to youngest.

Holz-Baker Transition of Ladd Formation

Specimens of Icanotia californica were found in the upper part of the Baker Canyon Member and in the immediately overlying, lowermost part of the Holz Shale Member of the Ladd Formation, Santa Ana Mountains, Orange County, southern California (Figure 1, locale 4). These two members are gradational in lithology, and this gradational zone, which is commonly referred to as the "Holz-Baker transition," constitutes the lowermost part of the Holz Shale. The Baker Canyon Member and the "Holz-Baker transition" are late Turonian in age, based on gastropods, bivalves, and ammonites (Saul, 1982). Sundberg (1980:text-fig. 2) provided a generalized Cretaceous stratigraphic column showing these two members. He also assigned fossils from this part of the Holz Shale Member to an Inoperna-Pterotrigonia association, which he reported as characteristic of a shallow-water, offshore environment that was above wave base. All but one of the specimens we were able to find of Icanotia californica are in siltstone; the one exception is in very fine sandstone. A few of the specimens found in siltstone are conjoined and one is "butterflied." We conclude that these specimens have undergone only minimal transport. Siltstone lithology is more consistent with an environment below wave base and more in keeping with a shelf environment of moderate depth, like the one Saul (1982: fig. 2) envisioned for the mollusks in the Holz-Baker transition.

Garzas Sand Member of Moreno Formation

The type locality of *Xenomytilus fons* is in the Garzas Sand Member of the Moreno Formation, Garzas Creek

area, Stanislaus County, central California (Figure 1, locale 1). This member has a complex nomenclatural history, but it has always had the term "Garzas" as part of its name. Regardless of how the term has been used, "Garzas" consistently refers to the uppermost Cretaceous sandstone that crops out north of the San Luis Reservoir/ Pacheco Pass area, Stanislaus and western Mecerd counties, along the western side of the northern San Joaquin Valley, central California (Bishop, 1970). This member contains an abundant molluscan fauna that is of late early Maastrichtian age (Saul, 1983:fig. 10), based primarily on turritellas (gastropods) and ammonites. The Garzas Sand Member was deposited in a nearshore shallow-water environment in the Garzas and Quinto creeks area, where specimens of the new mytilid species were found. More conjoined valves of the new species were found in this member than in the other stratigraphic units where this species occurs. Beyond the Garzas and Quinto creeks area, the Garzas Sand Member was deposited in deeper water (Bishop, 1970), and some of its fauna was probably transported downslope and offshore (Saul, 1983).

El Piojo Formation

Some specimens of Xenomytilus fons were found in this formation, which crops out at 1) Cantinas Canyon northwest of Lake Nacimiento in San Luis Obispo County, west-central California and 2) nearby, along the north and south shores of Lake Nacimiento (Figure 1, locales 2a & 2b). This formation, which is of early late Maastrichtian to earliest Paleocene age, based on turritellas (Saul, 1983, 1986; Squires & Saul, 1993), has not received detailed depositional-environment studies, but some of its mollusks are the same nearshore, warm-water ones found in other stratigraphic units that contain X. fons. Turritella chaneyi orienda Saul, 1983, is present in both the El Piojo Formation and the basal San Francisquito Formation (see below). Turritella webbi paynei Saul, 1983, and the bivalve Glycymeris (Glycymerita?) banosensis Anderson, 1958, are present in both the El Piojo Formation and the Garzas Sand Member. The strata that comprise what is now referred to as the El Piojo Formation were deposited by debris flows associated with turbidity currents (Grove, 1986). Saul (1983, 1986) also reported that, most likely, the shallow-marine mollusks found in the El Piojo Formation underwent some downslope movement into deeper water. No conjoined specimens of the new mytilid were found in the El Piojo Formation, but this is in keeping with its turbidite-influenced sedimentation. Specimens of the new mytilid from this formation are very unusual because they occur in pebbly sandstone.

Basal San Francisquito Formation

Many specimens of *Xenomytilus fons* were found in the lowermost part of the basal San Francisquito Formation at Warm Springs Mountain, Los Angeles County, southern California (Figure 1, locale 3). Based on turritellas and ammonites (Saul, 1983), this formation ranges in age from late Maastrichtian to late Paleocene and represents a transgressive sequence that consists of nearshore, shallow-marine deposits grading upsection into deeper submarine-fan deposits (Kirby & Saul, 1995). Kirby & Saul (1995:text fig. 2) reported also that the Cretaceous part of this formation 1) conformably overlies the granite-gneiss basement rock, 2) is approximately 110 m thick, 3) was deposited in a transition-zone environment, and 4) contains storm-lag concentrations of fossils. Field work by the senior author of this present report revealed that specimens of the new mytilid occur in small lenses interbedded with thicker intervals of fine sandstone in the lowermost 15 m of this 110 m-thick stratigraphic unit. The lenses consist of poorly sorted, very fine to coarse sandstone, with scattered very angular granules and small pebbles of granite. In addition to Xenomytilus fons, other fossils in these lenses are Turritella, thick-shelled oysters, Glycymeris, and plant debris. Some of the lenses consist almost entirely of oyster coquinas, and others consist of very coarse grains of decomposed granite. Although the fossils in the lenses have been transported, the distance of transport was not great, based on the presence of a few conjoined valves of the mytilid. Based on the poor sorting of the deposits, the small lateral extent of the lenses, and the presence of coquinas, we interpret that the lowermost part of the San Francisquito Formation at Warm Springs Mountains was deposited in a nearshore environment that was either in the shoreface environment or at the interface between lower shoreface and the proximal part of the transition zone. A few meters stratigraphically above these Xenomytilus-bearing beds, specimens of the the warm-water bivalve Roudairia Munier-Chalmas, 1881, were found. Roudairia is a predominantly Tethyan genus, and its presence is suggestive that the basal part of the San Francisquito Formation was deposited in warm waters (Kirby & Saul, 1995).

MODE OF LIFE

Xenomytilus fons

Adult mytilids are byssate (Coan et al., 2000). Apparently the new mytilid rested on its ventral surface because conjoined specimens are stable in that position, much like those of the malleid bivalve *Nayadina* (*Exputens*) Clark, 1934, known from Eocene strata of North America and Mexico (Squires, 1990). *Nayadina* (*Exputens*), however, was a nestler, based on the wide variability in its morphology. The new mytilid does not show as much variability in its morphology.

Icanotia californica

The mode of life of *Icanotia* is difficult to fully document because icanotiids are extinct. *Icanotia* was un-

doubtedly infaunal, because Casey (1961) stated that it has a deep pallial sinus. According to Casey (1961), *Icanotia* does not have a posterior gape. Most of the conjoined specimens of *Icanotia californica* also do not show a gape. One conjoined specimen of *I. californica* (Figure 23), however, shows what appears to be a gape, but it is, most likely, the result of post-burial processes.

Sundberg (1980:text-fig. 8) depicted *Icantia* [sic] as a deeply infaunal, suspension feeder bivalve with separate, long siphons, like those found on Recent tellinids. In spite of what he stated, no one can be sure whether or not *Icanotia* was a suspension feeder. Most tellinoids (e.g., tellinids) are actually deposit feeders, although some tellinoids (e.g., psammobiids) are probably suspension feeders (Boss, 1982; Coan et al., 2000). Whereas modern tellinoids have separate siphons (Boss, 1982; Coal et al., 2000), no one can be sure of the morphology of the siphons of *Icanotia*.

PALEOBIOGEOGRAPHY OF THE STUDIED GENERA

Xenomytilus

Xenomytilus is known so far only from central and southern California. Although it is possible that it was endemic to this region, it seems likely that eventually it will be found elsewhere in the world. As mentioned under "Systematic Paleontology," there are similar age mytilids from central Asia and southern India, and careful cleaning of their hinges could reveal them to be the new genus.

Icanotia

Icanotia Stoliczka (1871) appears to be restricted to strata deposited in warm-temperate and tropical (Tethyan) seas in Europe, Africa, central Asia, and the Americas (Dhondt, 1987). The geologic occurrences of Icanotia that we are aware of are listed in Table 2 and summarized graphically in Figure 2. As can be seen, this genus ranges from Early Cretaceous (Valanginian) to Late Cretaceous (Maastrichtian). References heavily utilized in our study were Pictet & Campiche (1865), Wade (1926), Olsson (1934, 1944), Casey (1961), Dhondt (1987), and Dhondt & Dieni (1993). Among these workers, only Wade (1926) and Olsson (1934, 1944) included any mention of Icanotia from California.

Switzerland has the only known Valanginian and Hauterivian occurrences of *Icanotia* (Pictet & Campiche, 1865). No Barremian records are yet known, but the genus is presumed to have been present in the vicinity of Switzerland at that time, because Aptian records are known from there (Pictet & Renevier, 1855). Also during the Aptian, *Icanotia* migrated into England (Casey, 1961). The only Albian records are in upper Albian strata from England (Casey, 1961) and undifferentiated Albian strata in northern Peru (Olsson, 1934). This Peruvian occur-

Table 2
Stage and geographic distribution of species of *Icanotia*.

Stage	Species	Location
Valanginian	I. escheri (Pictet & Campiche, 1865)	Switzerland
Hauterivian	I. intermedia (Pictet & Campiche, 1865)	Switzerland
Barremian	None known	
Aptian	I. pennula Casey, 1961	England
	I. studeri (Pictet & Renevier, 1855)	Switzerland
Albian	I. peruviana Olsson, 1934	Northern Peru
	I. impar (Zittel, 1865)	England
Cenomanian	I. impar (Zittel, 1865)	France, Austria, Germany, England
	I. atlantica Dartevelle & Freneix, 1957	Cameroon & Congo, Central Africa
Turonian	I. californica, sp. nov.	Southern California
	I. discrepans (d'Orbigny, 1845)	France
	I. impar (Zittel, 1865)	France, Austria
	I. atlantica Dartevelle & Freneix, 1957	Cameroon & Congo, Central Africa
Coniacian	I. discrepans (d'Orbigny, 1845)	France
	I. impar (Zittel, 1865)	Austria, NE Italy
	probably I. atlantica Dartevelle & Freneix (1957)	Cameroon & Congo, Central Africa
Santonian	I. discrepans (d'Orbigny, 1845)	France
	I. impar (Zittel, 1865)	Austria, NE Italy
	probably I. atlantica Dartevelle & Freneix (1957)	Cameroon & Congo, Central Africa
Lowermost Camp. to uppermost Sant.	I. elicita Stoliczka, 1871	Southern India
Campanian	I. impar (Zittel, 1865)	Austria, Hungary, NE Italy, Central Asia
•	possibly I. discrepans (d'Orbigny, 1845)	France
Uppermost Camp.	I. pulchra Wade, 1926	Tennessee
Maastrichtian	I. pacifica Olsson, 1944	Peru

rence is associated with the gastropod *Sogdianella peruviana* (Olsson, 1934), which Olsson incorrectly placed in genus *Actaeonella* d'Orbigny, 1842, according to Sohl & Kollman (1985), who assigned this gastropod to the Albian. The arrival of *Icanotia* in Peru probably coincided with both a global trend of rising sea level (Haq et al., 1987) and with warm and equable surface waters that occurred during the Albian (Frakes, 1999). This migration into the New World was, most likely, via westward-flowing equatorial currents. This Peruvian occurrence represents the first known migration of this genus out of Europe, but the migration was rather limited, because during the Cenomanian, the genus is only known from Europe (d'Orbigny, 1845; Geinitz, 1871–1875; Woods, 1904–1913).

With the exception of the late Turonian occurrence of *I. californica* in southern California, Europe continued to be the only area where this genus lived during the Turonian. The exceptional warming during the early Turonian (Frakes, 1999) most likely induced the spread of *Icanotia* into southern California. Additionally, there was a high-sea stand at this time, and the seaway across southern Mexico was apparently at its widest (Imlay, 1944; Alencaster, 1984). These conditions further enabled *Icanotia* to migrate. That this migration was via westwardflowing equatorial currents, rather than by way of the easternmost Tethys (Japan) and the northern Pacific gyre,

is suggested by the lack of this genus in Japan, British Columbia, Oregon, or northern California. If Icanotia had arrived onto the Pacific slope of the Americas via a northerly route, there should be some record of it in these higher latitude locales. The late Turonian New World occurrence in California, like the Albian New World occurrence in Peru, was relatively shortlived. During the Coniacian and Santonian, the genus is known to have lived only in Europe. During the Campanian, Icanotia was again present in Europe, but the genus migrated south to Cameroon and the Congo regions of central Africa, and east to central Asia and southern India (Stoliczka, 1871; Dartevelle & Freneix, 1957; Pojarkova, 1976). Again, these expansions into other regions did not persist very long. During the Maastrichtian, however, Icanotia was no longer present in the Old World, but was present only in the New World; namely, in Tennessee (Wade, 1926) and in Peru (Olsson, 1944). This Peruvian occurrence, which is based on Icanotia pacifica Olsson, 1944, is the youngest record for this genus. Olsson (1944: 217) assigned I. pacifica to his Baculites ammonite zone, which he believed to be of Maastrichtian age. He reported that this zone contains Baculites lyelli (d'Orbigny, 1847). For an updated synonymy of d'Orbigny's species, see Cobban & Kennedy (1995:26, 29), who stated that B. lyelli is a junior synonym of Eubaculites carinatus (Morton, 1834), which is a widely occurring baculitid of early to late Maastrichtian age.

SYSTEMATIC PALEONTOLOGY

Class Bivalvia Linnaeus, 1758
Order Mytiloida Férussac, 1822
Superfamily Mytiloidea Rafinesque, 1815
Family Mytilidae Rafinesque, 1815
Subfamily Xenomytilinae Squires & Saul, subfam. nov.

Type genus: *Xenomytilus*, gen. nov.; Maastrichtian, central and southern California.

Diagnosis: Small mytilid, smooth or ribbed, falcate (sickle shape), single tooth in either valve with socket in corresponding valve.

Included genera: Lycettia Cox, 1937, and Xenomytilus.

Discussion: Recognized subfamilies of Mytilidae in Soot-Ryen (1969) are: Mytilinae Rafinesque, 1815; Crenellinae Adams & Adams, 1857; Lithophaginae Adams & Adams, 1857; and Modiolinae Keen, 1958. Although the new subfamily has the pointed terminal beaks and falcate shape of some mytilines, the thickened anterior hinge margin of some crenellines, and the falcate shape of some modiolines, **Xenomytilinae** differs from all of these other subfamilies in having a single, strong tooth on either valve. The only other mytilid that has very similar dentition is *Lycettia* Cox, 1937, a genus considered to be a mytiline by Soot-Ryen (1969) but regarded by us to belong to the new subfamily.

Genus Xenomytilus Squires & Saul, gen. nov.

Type species: *Xenomytilus fons*, sp. nov.; Maastrichtian, central and southern California.

Diagnosis: Small mytilid, falcate, sharply carinate adajacent to ventral margin, radially ribbed, ventral surface concave, prominent strong tooth on either valve, deep socket on other valve, and chevron-like pits commonly present on valve margins near hinge area.

Discussion: The hinge of the new genus develops alternatively in either valve, with the single prominent tooth located between two sockets, the ventral one being the larger one. The new genus does not have true transposition, described by Popenoe & Findlay (1933), because the prominent tooth is variable in its location. The new genus is most similar in terms of dentition to *Lycettia* Cox, 1937, but the new genus differs by having ribs, more inflated valves, a sharp carina, a wider and more concave ventral surface, a more prominent tooth on the hinge, chevron-like pits posterior to the nymph, and a much

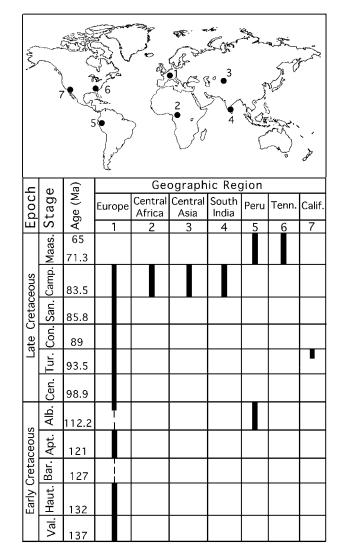


Figure 2. Global chronostratigraphic and geographic distribution of *Icanotia*. Dashed lines indicate presumed occurrence. 1 = France, Switzerland, Germany, Austria, Hungary, and England. 2 = Cameroon. 3 = Central Asia. 4 = Southern India. 5 = Northern Peru. 6 = Tennessee. 7 = Southern California. Geologic ages after Gradstein et al. (2004).

shorter and less distinct nymph. Cox (1937) illustrated only left valves of *Lycettia*, but Tashiro (1992:pl. 14, fig. 12) illustrated a right valve. Cox's (1937) description of the hinge of *Lycettia* is hard to make sense of, and his illustrations do not match his descriptions. His usage of the terms "above" and "below" are very confusing. He put too much emphasis on the ligamental ridge and did not provide enough information about the dentition.

Lycettia is an Old World Tethyan bivalve that ranges from late Early Jurassic (Toarcian) to Late Cretaceous (late Campanian) (Tashiro, 1992). It is found in the upper Lower Jurassic of Spain (Gahr, 2002), the lower Middle

Jurassic (Aalenian to Bajocian) of England (Cox, 1937), the Middle Jurassic (Bathonian) of east Africa (Hallam, 1977), the Upper Jurassic of Portugal (Fürsich & Werner, 1987), the Upper Jurassic (Oxfordian to Kimmeridgian) to Lower Cretaceous of western China (Yin & Fürsich, 1991), and Lower Cretaceous (Berriasian to Valanginian) to Upper Cretaceous (upper Campanian) in southern Japan (Tashiro, 1992). It is tentatively known from the Middle Jurassic (Bathonian) of western China (Sha et al., 1998).

One species, *Lycettia tippana* (Conrad, 1858) has been reported by various workers (see Akers & Akers, 2002) to be in upper Campanian and Maastrichtian strata of southeastern and eastern United States, but this so-called "*Lycettia*" is *Cuneolus* Stephenson, 1941. Soot-Ryen (1969) regarded *Cuneolus* to be a synonym of *Lycettia*, but *Cuneolus* is edentulous.

In terms of the falcate shape and strong carina adjacent to the ventral margin, the new genus is similar to the Permian mytiline *Coxesia* Mendes, 1952; the Jurassic modioline *Falcimytilus* Cox, 1937, the Maastrichtian mytiline *Cuneolus*, and the Recent mytiline *Mytilaster* Monterosato, 1884. The new genus differs from the first three of these by having ribs and not being edentulous. The new genus differs from *Mytilaster* by having a dentition-bearing plate in the umbonal cavity, terminal beaks, more concave ventral surface, and chevron-like pits on the valve margins near the hinge area.

In terms of the overall shape and presence of ribs, *Xenomytilus* is similar to the Jurassic to Recent mytiline *Brachidontes* Swainson, 1840, but the new genus differs by having terminal rather than nearly always subterminal beaks, much more pointed beaks, an angulation rather than a rounded ridge between the beak and the posteroventral margin, a concave ventral surface, and a strong tooth or deep socket in each valve rather than a variable number of very small dysodont teeth with intervening shallow sockets.

In having chevrons along the dorso-posterior margin (see Olsson, 1961:pl. 12, fig. 5) and the possibility of only a single tooth on the hinge, *Xenomytilus* is also similar to *Aeidimytilus* Olsson, 1961, (type species: *Mytilus adamsiana* Dunker, 1857), a Recent mytilid from southern California to Ecuador (Coan et al., 2000). *Aeidimytilus* can have one to three central teeth. *Xenomytilus* differs from *Aeidimytilus* by having larger size, terminal beaks, falcate shape, much weaker and flatter ribbing, usually non-bifurcating ribs, and a much more concave ventral surface. Olsson (1961) opined that *Aeidimytilus* is a subgenus of *Scolimytilus* Olsson, 1961. Keen (1971) and Coan et al. (2000) opted for making *Aeidimytilus* and *Scolimytilus* synonyms of *Brachidontes*, because the soft parts do not differ.

Also, in terms of the general shape and presence of radial ribs, the new genus resembles the Triassic to Recent mytiline *Septifer* Récluz, 1848, *sensu stricto*, and the

Recent mytiline *Ischadium* (Jukes-Brown, 1905). The new genus differs from *Septifer* by having dentition instead of a septum. The new genus differs from *Ischadium* by having a narrower shell, an angulation between the disk and the concave ventral surface, and a single tooth in either valve. The hinge teeth of *Ischadium* are several in number (Soot-Ryen, 1955).

Etymology: The genus name is a combination of *xeno*, Greek for strange, and *mytilus*.

Xenomytilus fons Squires & Saul, sp. nov.

(Figures 3–17)

Brachidontes n. sp. Saul, 1986:26, 27. Brachidontes? n. sp. Kirby & Saul, 1995:24.

Diagnosis: Same as for genus.

Description: Shell small (most specimens approximately 30 mm in length and 15 mm in height, rare specimens up to 42.5 mm in length and 18 mm in height), longer than high, shell height/shell length ratio = usually 0.5 (largest specimen = 0.42). Falcate, inequilateral, equivalved, valves inflated. Anterior end acutely pointed. Hinge margin long with portion posterior to ligament bent in low angle. Beaks pointed and terminal at anterior end. Umbones terminal, acutely pointed. Umbonal ridge pronounced and sharp (angulate), extending from beak to postero-ventral margin. Disk moderately broad. Ventral margin of both valves concave. Valves ornamented with abundant radial ribs, varying in strength on different areas. Radial ribs of anterior area narrowest, slightly wider than interspaces but becoming approximately twice as wide as interspaces posteriorly. Radial ribs on disk flattish to lowly rounded. Radial ribs of anterior area diverging from ribs of flank along strong, arching beak-to-outer margin carina. Radial ribs on concave ventral margin narrow, closely spaced, and approximately three times as wide as interspaces. Hinge consisting of single, prominent tooth on either valve; tooth located between two sockets with the ventral socket larger. Tooth long and narrow, usually dorsal of center of hinge, but can be slightly ventral of center or extending diagonally across central area. Tooth bears microscopic striae on both sides, especially on ventral side. Valve not bearing tooth has deep socket. Ventral area of hinge with relatively inconspicous tooth and subordinate socket (notch) at hinge margin. Lunular area can be infolded to form very narrow channel for corresponding valve margin of other valve. Nymph moderately long, with thin extension of nymph not quite reaching apex of valve. Dorsal margin of valve, including ligamental area, can be pitted with chevron-like crenulations.

Dimensions of holotype: Conjoined valves, length 31.1 mm, height 16.5 mm, thickness 15.5 mm.

Holotype: LACMIP 13290.

Type locality: LACMIP loc. 10660, 37°13′41″N, 121°07′14″W.

Paratypes: LACMIP 13291-13299.

Geologic age: Middle to latest Maastrichtian.

Distribution: MIDDLE MAASTRICHTIAN: Moreno Formation, Garzas Sand Member, Garzas Creek, Stanislaus County, north-central California (type locality). LOWER UPPER MAASTRICHTIAN: El Piojo Formation, Cantinas Canyon northwest of Lake Nacimiento and north shore of Lake Nacimiento, San Luis Obispo County, west-central California. UPPERMOST MAASTRICHTIAN: El Piojo Formation, upper part, south shore of Lake Nacimiento, San Luis Obispo County, west-central California; San Francisquito Formation, basal part, Warm Springs Mountain, Los Angeles County, southern California.

Discussion: The above description is based on 71 specimens: 35 left valves, 27 right valves, and 9 conjoined valves. Several valves were carefully cleaned to expose the hinge. The chevron-like crenulations on the nymph and posterior to it are not preserved on all specimens.

Saul (1986:26, 27) mentioned *Brachidontes*, n. sp. from Cantinas Creek area just northwest of Lake Nacimiento and from the north shore of Lake Nacimiento, west-central California, and this bivalve is synonymous with *Xenomytilus fons*. She also mentioned in this same article that a similar form of *Brachidontes*, n. sp. is from the Moreno Formation, and this bivalve is also synonymous with *X. fons*.

Kirby & Saul (1995:24) mentioned *Brachidontes*? n. sp. from the Warm Springs Mountain, southern California, and this bivalve is synonymous with *X. fons*.

Xenomytilus fons somewhat resembles Brachidontes fulpensis Stephenson (1952:84–85, figs. 10–13) from the lower Cenomanian Woodbine Formation of northeastern Texas but differs from this Texas species by having a terminal beak, a sharper angulation between the beak and the postero-ventral margin, a concave ventral surface, a sloping rather than a long and straight antero-dorsal margin, shorter nymph, and a single prominent tooth on either valve. The hinge of this Texas species has three or four, deep channels with intervening sharp teeth that are modifications of crenulations along the anterior margin.

The new bivalve is similar to *Septifer? ahaaralensis* Pojarkova (1976:92–93, pl. 47, figs. 8–9, pl. 48, figs. 6–

11) from lower Santonian to lower upper Campanian strata in central Asia. Although the new bivalve differs by having a more concave ventral surface and a narrower beak, some illustrated specimens of the central Asian species do approach the shape of *X. fons*.

The new bivalve is also similar to *Modiola annectans* Stoliczka (1871:380–381, pl. 23, figs. 8, 8a, 9, 9a) from the Ariyalur Group [= Arrialoor Group in Stoliczka] in the Vayalappadi [= Vylapauda in Stolickza] of the Cauvery Basin in southern India. Sastry et al. (1972) reported that these rocks at this locale are in the Sillakudi Formation. According to Sundaram et al. (2001), this formation is of Santonian to Campanian age. The new bivalve differs from Stoliczka's species by having much stronger ribs and a more sloping dorsal-anterior shell margin. No information is known about the hinge of Stoliczka's species.

Etymology: The new species is named for its occurrence on Warm Springs Mountain; Latin, *fons*, meaning of a spring.

Order Veneroida H. & A. Adams, 1856
Superfamily Tellinoidea de Blainville, 1814
Family Icanotiidae Casey, 1961
Genus *Icanotia* Stoliczka, 1871

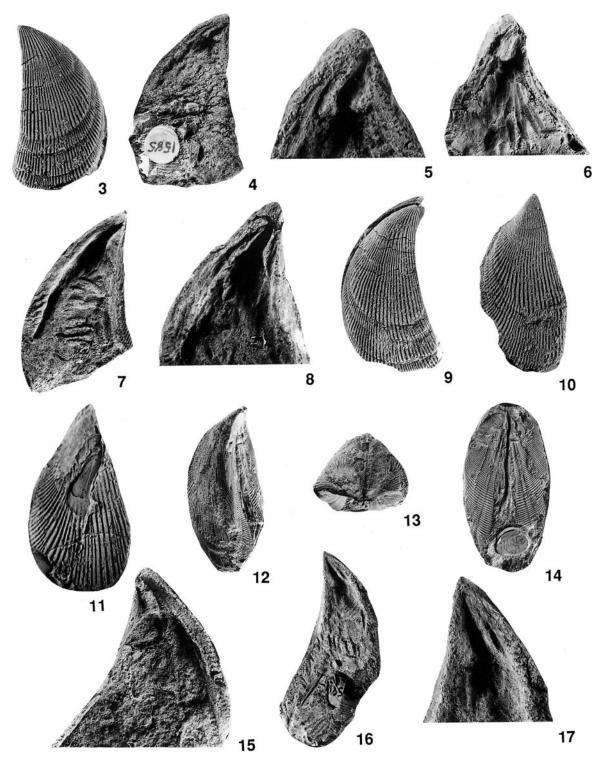
Type species: *Psammobia impar* Zittel, 1865, by original designation; Late Cretaceous (Cenomanian to Campanian), southern England, western and southeast France, Germany, Austria (Gosau), Hungary, northeast Italy, central Asia, and southern India. For an updated synonymy of this species, whose nomenclatural history has been very confusing, see Dhondt & Dieni (1993).

Discussion: Casey (1961) implied and Keen (1969) stated that *Icanotia* has two cardinal teeth in either valve. *Icanotia pulchra* Wade (1926:91, pl. 29, figs. 5, 6), from uppermost Campanian strata of Tennessee, however, has a single prominent cardinal tooth in the left valve, and this tooth is situated between a large socket posteriorly and a smaller socket anteriorly, just as in the new species described below. It is possible that *I. pulchra* and the new species constitute a new subgenus of *Icanotia* that is characterized by having only a single cardinal tooth, but more specimens of both species are needed in order to docu-

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Explanation of Figures 3 to 17

Figures 3–17. *Xenomytilus fons* Squires & Saul, genus et sp. nov., specimens coated with ammonium chloride. Figure 3. Holotype LACMIP 13290, LACMIP loc. 10660, left valve, ×1.6. Figures 4–5. Paratype LACMIP 13291, LACMIP loc. 10660, left-valve interior. Figure 4. ×1.5. Figure 5. Close-up of hinge shown in previous figure, ×4.6. Figure 6. Paratype LACMIP 13292, LACMIP loc. 9196, left-valve interior, ×3. Figure 7. Paratype LACMIP 13293, LACMIP loc. 10660, left-valve interior, ×1.8. Figure 8. Paratype LACMIP 13294, LACMIP loc. 10660, left-valve



interior, ×3. Figure 9. Holotype LACMIP 13290, LACMIP loc. 10660, right valve, ×1.6. Figure 10. Paratype LACMIP 13295, LACMIP loc. 26486, right valve, ×1.7. Figure 11. Paratype LACMIP 13296, LACMIP loc. 26526, right valve, ×1.5. Figures 12–14. Paratype LACMIP 13297, LACMIP loc. 26352. Figure 12. Apical view of beaks, ×1.6. Figure 13. Oblique ventral view, ×1.4. Figure 14. Ventral view, ×1.4. Figure 15. Paratype LACMIP 13298, LACMIP loc. 21193, rubber peel of right-valve interior, ×3.5. Figures 16–17. Paratype LACMIP 13299, LACMIP loc. 10660. Figure 16. Right-valve interior, ×1.4. Figure 17. Close-up of hinge shown in previous figure, ×3.7.

ment that this single tooth is a constant morphologic character.

The geologic range of *Icanotia* is Valanginian to Maastrichtian, although it has been variously referred to as Aptian to Maastrichtian by Casey (1961), Hauterivian to Maastrichtian by Soot-Ryen (1969), and Valanginian to Maastrichtian by Dartevelle & Freneix (1957). Stoliczka (1871:168) reported *Icanotia elicita* Stoliczka, 1871, from the Aryialur Group [= Arrialoor Group in Stoliczka] north of Karappadi [= Karapaudy in Stoliczka] in the Cauvery Basin of southern India. Sastry et al. (1972) reported that the rocks at this locale are in the middle part of the Sillakkudi Formation. Sundaram et al. (2001) reported that this part of the formation is latest Santonian to earliest Campanian in age.

Lundgren (1894:50, pl. 2, figs. 12, 13) described *Icanotia? grosseplicata* Lundgren, 1894, of early late Campanian age from southernmost Sweden. We do not believe that Lundgren's species belongs in *Icanotia*, even tentatively, because the beak is located too far anteriorly, the ribs are much too strong, too widely spaced, too few, and the overall outline of the valves is too quadrate.

Icanotia californica Saul & Squires, sp. nov.

(Figures 18–29)

Icantia [sic] sp. Sundberg, 1980:table 1, text-fig. 8.

Diagnosis: A narrow, elongate *Icanotia* with low but distinct beaks and weak, closely spaced ribs confined to posterior slope.

Description: Shell medium, thin, narrow and compressed. Soleniform, narrow and elongate (up to 46 mm in length, with height of 13.5 mm), shell height/shell length ratio = 0.29. Equivalve and inequilateral. Dorsal margin long, straight, ventral margin essentially paralleling dorsal margin. Anterior end narrowly rounded, posterior end subtruncate. Lunule poorly developed or wanting. Escutcheon long and very narrow. Beaks low but distinct and prosogyrate. Beaks slightly less than onethird of distance fron anterior end, with maximum shell height at beaks. Shell sculpture confined to posterior slope, with ribs radiating from beak and covering sector about 20 to 25°, from beak to postero-ventral corner. Ribs 14 to 20 in number, narrow, closely spaced, and weak to moderately strong. Ribs strongest dorsally and posteriorly, with noticeable weakening ventrally. Anterior margin of shell with radial striae crossing incised growth lines and producing minute cancellate sulpture. Shell otherwise smoothish, with bands of growth lamellae. Hinge on left valve consisting of singular and prominent cardinal tooth perpendicular to hinge margin and situated between large socket posteriorly and small socket anteriorly. Ligament external and opisthodetic, seated on weakly developed nymph. Interior rib, very faint, extends from beak to half way toward postero-ventral corner. Musclescar pattern unknown.

Dimensions of holotype: Right valve, length 39.5 mm, height 12 mm.

Holotype: LACMIP 13300.

Type locality: LACMIP 10883, 33°43′12″N, 117°37′26″W.

Paratypes: LACMIP 13301–13306; UCR 4032/2.

Geologic age: Late Turonian.

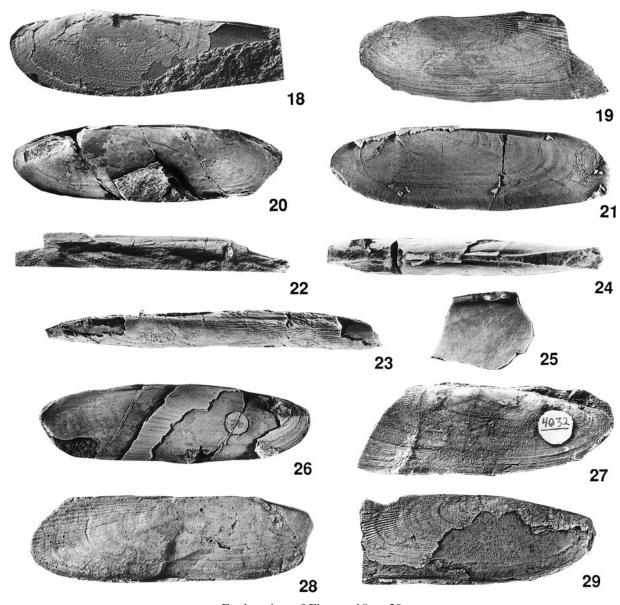
Distribution: Ladd Formation, upper part of Baker Canyon Member and Holz-Baker transition, Silverado Canyon, Santa Ana Mountains, Orange County, southern California.

Discussion: The new species is based on 25 specimens: 9 left valves, 11 left valves, and 5 conjoined valves. The largest specimen is 71 mm in length and 20 mm in height. Most of the specimens are internal molds, and most specimens are from the Holz-Baker transition; only a single specimen is from the Baker Canyon Member.

The new species is most similar to *Icanotia pacifica* Olsson (1944:55–56, pl. 5, fig. 6), known from a single specimen from Maastrichtian strata of northern Peru. The new species differs from *I. pacifica* by being smaller and having ribs that are less widely spaced and weaker throughout, ribs that do get weaker ventrally. In addition, the new species differs by having an umbo that is evident, rather than being nondistinct, and having the maximum height one-third from the anterior end, rather than at midlength.

The new species is the first fully documented report of *Icanotia* from the Pacific slope of North America. Sundberg (1980) listed the genus in a faunal list but misspelled the name. He also did not provide any type numbers nor any illustrations of this bivalve.

In addition to the new species, there are three other species of Icanotia known from the Turonian. These three all have long geologic ranges that encompass the Turonian, and they are the following: Icanotia impar (Zittel, 1865) of late Albian to Campanian age in Europe, central Asia, and southern India (Casey, 1961; Dhondt & Dieni, 1993); Icanotia discrepans (d'Orbigny, 1845) of Turonian to Campanian age in Europe (Dhondt & Dieni, 1993); and Icanotia atlantica (Dartevelle & Freneix, 1957) of Cenomanian to Senonian age (i.e., the latter term is undifferentiated as to Coniacian, Santonian, and Campanian) in central Africa (Dartevelle & Freneix, 1957). The new species differs from both I. impar and I. discrepans by being more elongate and with weaker and more closely spaced ribs. The new species is more similar to I. atlantica but differs from the central African species by being larger, having stronger and more widely spaced ribs on the posterior slope, absence of ribs along the ventral side and antero-ventral edge of the valves, and having commarginal bands on some specimens.



Explanation of Figures 18 to 29

Figures 18–29. *Icanotia californica* Squires & Saul, sp. nov., specimens coated with ammonium chloride. Figure 18. Paratype UCR 4032/2, UCR loc. 4032, left valve, ×1.3. Figure 19. Paratype LACMIP 13301, LACMIP loc. 10100, left valve, ×3.5. Figure 20. Paratype LACMIP 13302, LACMIP loc. 10100, left valve, ×1. Figure 21. Paratype LACMIP 13303, CSUF loc. 62–8, left valve, ×1.6. Figures 22–23. Paratype LACMIP 13304, LACMIP loc. 8198, left valve. Figure 22. Hinge, ×2.7. Figure 23. Dorsal view of hinge, ×2.8. Figure 24. Paratype LACMIP 13302, LACMIP loc. 10100, dorsal view, ×1. Figure 25. Paratype LACMIP 13305, LACMIP loc. 10100, right-valve interior, ×1.4. Figure 26. Paratype LACMIP 13302, LACMIP loc. 10100, right-valve, ×1.5 Figure 27. Paratype UCR 4032/2, UCR loc. 4032, right valve, ×1.3. Figure 28. Holotype LACMIP 13300, LACMIP loc. 10883, right valve, ×1.9. Figure 29. Paratype LACMIP 13306, CSUF loc. 44–24, right valve, ×0.8.

Etymology: The species is named for the state of California.

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APPENDIX

LOCALITIES CITED

CSUF 44-24 [= CSUF 62-8]. Approximately 260 m N and 10 m W of SE corner of section 7, T. 5 S, R. 7 W, El Toro Quadrangle (7.5 minute, 1949), Silverado Can-

- yon, Santa Ana Mountains, Orange County, southern California. Ladd Formation, lower part of Holz Shale Member. Age: Late Turonian. Collector: F. A Sundberg, circa 1978.
- LACMIP 8198. Section 16, T. 5 S, R. 7 W, Santiago Peak Quadrangle (7.5 minute, 1954), Santa Ana Mountains, Orange County, California. Ladd Formation, Baker Canyon Member. Age: Late Turonian. Collector: W. P. Popenoe, March 14, 1934.
- LACMIP 9196. Conglomerate cropping out on E side of Cantinas Creek approximately 30 m N of S line of section 5, T. 25 S, R. 9 E, Bryson Quadrangle (7.5 minute, 1948), San Luis Obispo County, west-central California. El Piojo Formation. Age: Early late Maastrichtian. Collectors: L. R. and R. B. Saul & V. M. Seiders, November 13, 1985.
- LACMIP 10100. Concretions in shale 30.5 m above stream bed and near fence on N side of canyon about 0.8 km N of road fork in Santiago Canyon, NW ¼ of NW ¼ of section 28, T. 5 S, R. 7 W, Santiago Peak Quadrangle (7.5 minute, 1973), Santa Ana Mountains, Orange County, California. Ladd Formation, Holz Shale Member. Age: Late Turonian. Collector: B. N. Moore, January 1, 1928.
- LACMIP 10660. In small gully, 59.5 m stratigraphically above base of Garzas Sand Member, 457 m E and 579 m S of NW corner of section 20, T. 8 S, R. 8 E, N side of Whitney Canyon, Howard Ranch Quadrangle (7.5 minute, 1953, photorevised, 1971), Stanislaus County, central California. Moreno Formation, Garzas Sand Member. Age: Early late Maastrichtian. Collectors: B. Adams & W. P. Popenoe, June 1, 1941.
- LACMIP 10883. Immediately above base of gray sandstones overlying gray basal conglomerate, NW ¼ of SW ¼ of section 21, T. 5 S, R. 7 W, Santiago Peak Quadrangle (7.5 minute, 1954), Santa Ana Mountains, Orange County, southern California. Ladd Formation, Baker Canyon Member. Age: Late Turonian. Collector: W. P. Popenoe, April 21, 1932.
- LACMIP 21193. At contact with gneiss-basement complex in ravine just S of NE ridge of Warm Springs Mountain, approximately 228 m N and 287 m E of Warm Springs Mountains, T. 6 N, R. 16 W, Warm Springs Mountain Quadrangle (7.5 minute, 1958, photorevised 1974), NW San Gabriel Mountains, Los Angeles County, southern California. San Francisquito Formation, basal part. Age: Latest Maastrichtian. Collectors: J. Elam & R. Webb, June 5, 1942.
- LACMIP 21599. Light brown, dirty sandstone, in trail cut between exposures of gneiss basement on SE slope NW side of ravine along Warm Springs trail, approximately 305 m E of junction with firebreak S from Warm Springs Mountain, 122 m S and 269 m E of Warm Springs Mountain, T. 6 N, R. 16 W, Warm Springs Mountain Quadrangle (7.5 minute, 1958, photorevised, 1974), NW San Gabriel Mountains, Los An-

- geles County, southern California. San Francisquito Formation, basal part. Age: Latest Maastrichtian. Collectors: R. W. Webb & E. H. Quayle, June 26, 1941.
- LACMIP 26352. West side San Joaquin Valley, approximately 1.2 km S of Garzas Creek, 671 m S, 84 m E of NW corner of section 20, T. 8 S, R. 8 E, Howard Ranch Quadrangle (7.5 minute, 1953, photorevised 1971), Stanislaus County, California. Moreno Formation, Garzas Sand Member. Age: Early late Maastrichtian. Collectors: R. B. Stewart & W. P. Popenoe, 1944.
- LACMIP 26486. North shore (at about water line) of Lake Nacimiento, 396 m N, 533 m E of SW corner of section 17, T. 25 S, R. 10 E, Bradley Quadrangle (15 minute, 1961), San Luis Obispo County, California. El Piojo Formation. Age: Early late Maastrichtian. Collectors: L. R. & R. B. Saul, November 25, 1977.
- LACMIP 26526. Poorly sorted conglomeratic sandstone, S side of Lake Nacimiento, E side of narrows of Dip Creek, elevation 225 m, 457 m S and 122 m W of NE

- corner of section 30, T. 25 S, R. 10 E, Lime Mountain Quadrangle (7.5 minute, 1948), San Luis Obispo County, California. Piojo Formation, upper part. Age: Latest Maastrichtian. Collectors: L. R. & R. B. Saul, December 31, 1977.
- LACMIP 30141. Fossils in pebbly sandstone, about 1.6 km N of Nacimiento River on E side of road (?Bee Rock Road) near quarter corner of section 18, T. 25 S, R. 10 E, and about 1.6 km N of Nacimiento River, Tierra Redonda Mountain Quadrangle (7.5 minute, 1949), San Luis Obispo County, west-central California. El Piojo Formation. Age: Early late Maastrichtian. Collector(s): unknown.
- UCR 4032. Approximately 260 m N and 10 m W of SE corner of section 7, T. 5 S, R. 7 W, El Toro Quadrangle (7.5 minute, 1949), Silverado Canyon, Santa Ana Mountains, Orange County, southern California. Ladd Canyon Formation, lower part of Holz Shale Member. Age: Late Turonian. Collector: unknown.