DOES THE MORPHOLOGY OF PLEISTOCENE SPECIMENS OF *CROSSATA CALIFORNICA* (HINDS, 1843) ELUCIDATE EVOLUTIONARY PATTERNS?

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Near Playa del Rey, Los Angeles County, California, is a locality that yields fossils whose age is about 125,000 BP (Kennedy, 1973). Among this fauna are many "frog shells" formerly referred to the genus *Bursa* but now known as *Crossata californica* (Hinds, 1843). These shells display considerable variability of shape and sculpture. Especially notable is the variability among the smaller, less mature shells which is greater than among equivalent size and growth stage of Recent specimens. Relationship of *Crossata* to other bursids has been variously inferred by other workers (e.g., Vokes, 1973; Beu, 1988). Do these variations help unravel the phylogeny of *Crossata californica*, an eastern Pacific bursid?

Materials:

The locality is richly fossiliferous and in addition to the approximately 300 mollusk species reported by Willett (1937), crabs, bryozoans, barnacles, echinoids, fish and birds have been found. The frog shells are mostly complete and well preserved. The whole growth series from juveniles to adults is represented with a majority of specimens being of medium size (55-80 mm). Some specimens of *Crossata californica* display small round holes, doubtlessly drilled by naticid predators. A few frog shells had barnacles attached, and a very few were deformed. One hundred and fifty specimens were chosen for this study. Shells were selected for their similarity to geologically earlier species of bursids and ranellids. Many Pleistocene specimens repeat the morphological characteristics of Eocene through Recent species.

Ecology:

The Playa del Rey site (Figure 1) is about two miles inland from the present coast. The fossils are from lenticular beds of the Palos Verdes Sand of Woodring (1946). In addition to quartz grains the deposit includes sand-sized particles of broken shell and is typical of a deposit in an embayment (Fitch, 1964). The substrate consists of sand with a medium-sized cobble base, that was deposited on the outer periphery of an inland Pleistocene bay occupying part of the Los Angeles Basin. Completeness and fine preservation of the shells indicates lack of post-mortem transport. Analysis of the whole fauna has suggested that *Crossata californica* lived in warm water during an interglacial time at a depth of about 20-40 fm (Willett,1937; Valentine & Meade,1961). Ability of the bursids to lay abundant eggs and a long larval stage for the hatchlings may have helped to distribute the veligers throughout warm temperate and tropical seas (MacGinitie & MacGinitie, 1968). This gastropod feeds on echinoderms, ascidians, bivalves and also eats carrion.

The geologic range is from Pliocene to Recent. Grant & Gale (1931) reported a Pliocene specimen from the Puente Hills, "Fernando Formation", but Yerkes (1972) noted that *C. californica* of Puente Hills was in the Pleistocene, San Pedro Formation. Davis (1998) found a *C. crossata* specimen in the upper Pliocene "Fernando Formation" of Los Angeles, California (ARCO Towers area). Stadum (1984) reported *C. californica* from the Pliocene Niguel Formation, Laguna Hills, Orange County, California. Several San Diego Formation (Pliocene) Tijuana River border area localities, (LACMIP 305, 318 and 319), have yielded a number of *C. californica*. These are smaller than most Recent specimens and do not show much variation in shape but are similar to some of the Pleistocene Playa del Rey specimens (Figure 2). Also, from the San Diego Formation in Arroyo Drive Quarry, Balboa Park, San Diego (LACMIP locality 107), is a Pliocene *C.*

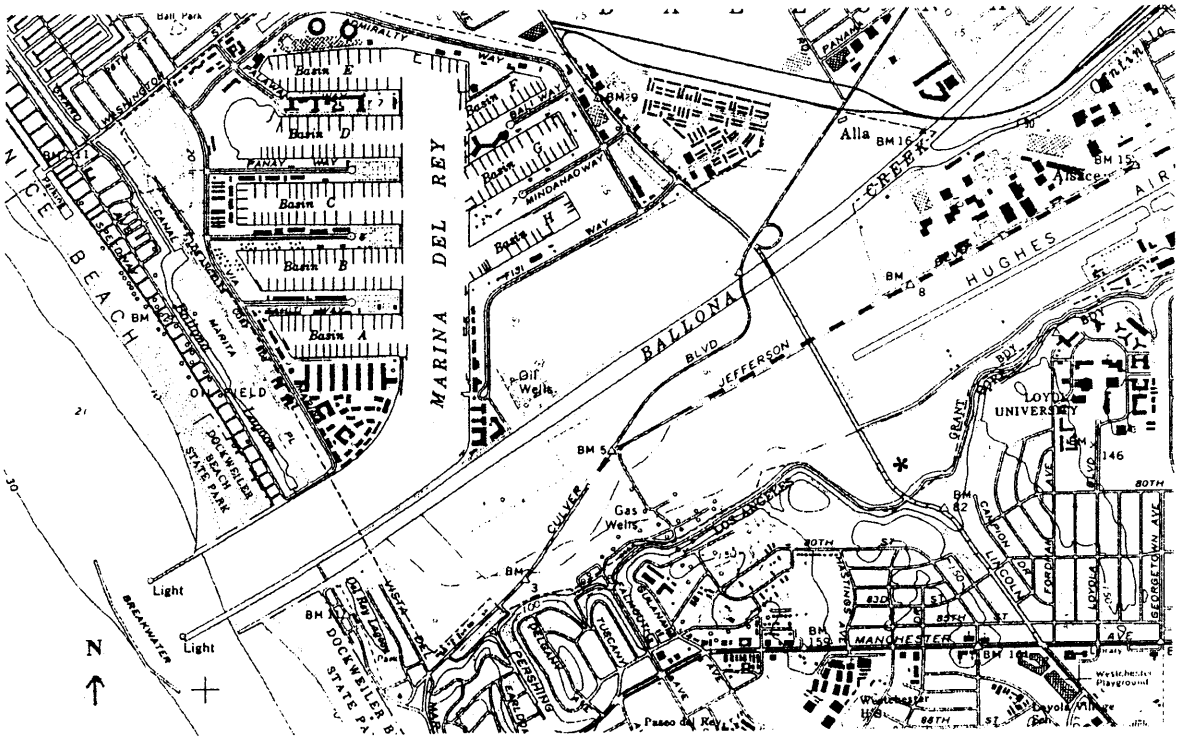


Figure 1. Map of site in Playa del Rey, Los Angeles County, California. Fossil site shown with an asterisk*.

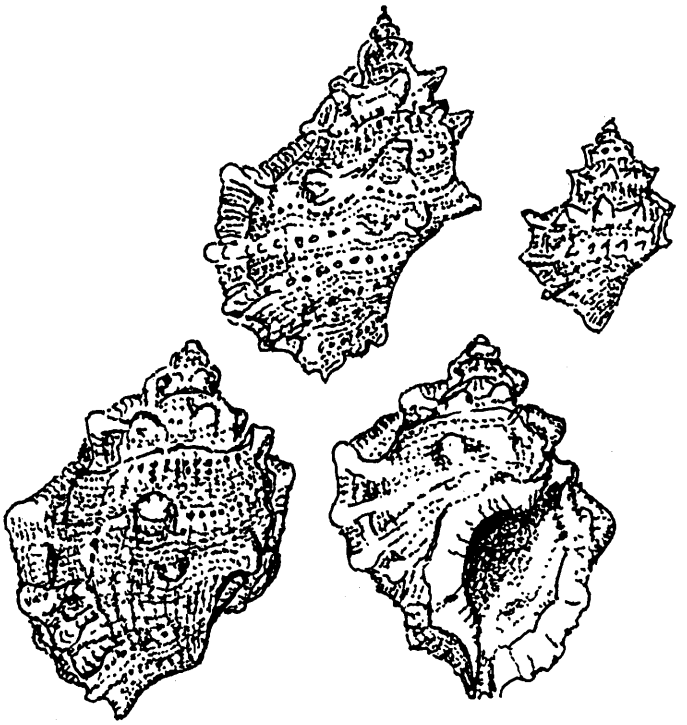


Figure 2. *Crossata californica* (Hinds, 1844). Palos Verdes Sand, Pleistocene, Playa del Rey, Los Angeles County, California. Figures 70% of actual size. Albi Collection.

californica.

Abbreviations used in this paper are LACMIP = Natural History Museum of Los Angeles County, Invertebrate Paleontology; BMNH = The Natural History Museum, London; USNM = National Museum of Natural History, Washington, DC; CAS = California Academy of Sciences, Menlo Park.

Systematics:

Phylum Mollusca Cuvier, 1797
Class Gastropoda Cuvier, 1797
Order Neotaenioglossa Haller, 1888
Superfamily Tonnoidea Suter, 1913
Family Bursidae Thiele, 1925

Genus *Crossata* Jousseaume, 1881
Type-species *Ranella ventricosa* Broderip, 1833, by original designation.

Crossata californica (Hinds, 1843)
Ranella californica Hinds, 1843: 255-256; Hinds, 1844:12, pl. 2, fig. 4; Gabb, 1869: 73; Keep, 1888: 44, fig. 24; Keep, 1892: 44; Williamson, 1892: 211; Arnold, 1903: 287; Rogers, 1908: 54, pl. 12.
Bursa (Lampas) californica (Hinds). Tryon, 1881: 40, pl. 22, fig. 42.
Bursa (Bufonaria) californica (Hinds). Dall, 1921: 141; Oldroyd, 1927: 241, pl. 33, figs.7, 8; Smith, 1948: 30, pl.10.
Bursa californica (Hinds). Jordan, 1924: 149; Jordan, 1926: 246; Grant & Gale, 1931: 731; Keen, 1958: 348; Dance, 1974: 115; McLean, 1978: 41, fig. 21.1.
Bursa (Crossata) californica (Hinds). Abbott, 1974: 167, color pl.7, fig. 1783.
Crossata californica (Hinds). Kaicher, 1982: 3260; Beu, 1988: 74; Parth, 1996: 133; Beu, 2001: 707.

Type Material: The holotype is apparently missing and Beu (personal communication, 2001) intends to designate a neotype from an authentic Hinds specimen at the BMNH.

Hypotype: USNM # 209567 collected 1904, 8.6 miles (13.8 km) north of Point Loma, San Diego, California. Recent.

Description:

Recent shells of *Crossata californica* (Figure 3) are commonly of medium size; a few are quite large. The shell has six whorls and is thick and heavy. The body whorl is corpulent with spiral bands of tubercles and with several blunt peripheral knobs (McLean, 1978). The spire is short and the protoconch is made up of 2½ smooth whorls. The aperture is longer than the spire and has well developed anterior and posterior siphonal canals that are similar in length. The outer lip

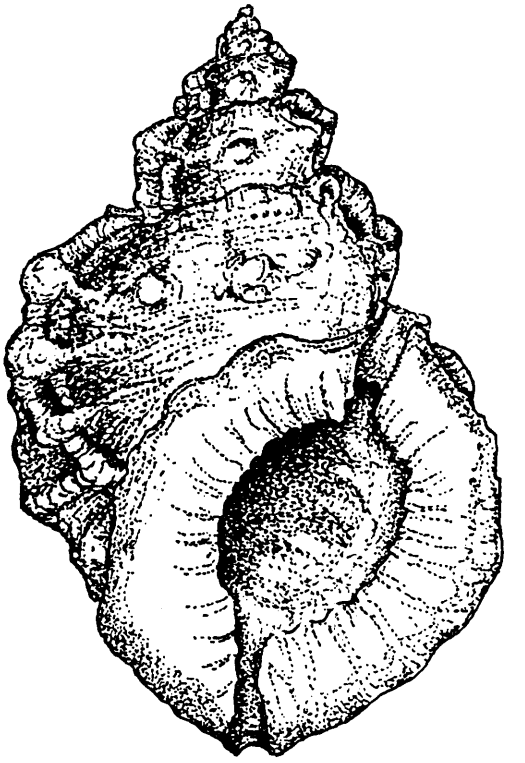


Figure 3. *Crossata californica* (Hinds, 1844). Recent. Palos Verdes, Los Angeles County, California. Figure 70% of actual size. Albi Collection.

is bedecked with a protruding varix that is not aligned with varices of previous whorls. Varices bear ridges and pointed or round nodes. Internally the outer lip displays grouped denticles. The inner lip is expanded and commonly stands out clearly from the whorl, its inner portion and the columella made plicate by the 10-16 lirae that cross the inner lip. Some specimens have fewer and less distinct plications. A large parietal plication borders the inner end of the posterior canal. The entire shell is commonly covered with a white chalky substance termed intriticalx. The shell is cream colored with tan lines, and a white aperture. On a few specimens a muddy, dark green borders the outer and inner lip. *Crossata californica* has a thin chitinous operculum (for terminology, see Figure 4).

Discussion:

Recent *C. californica* are epifuanal, now living on rocky substrates at depths of 20-91 m on rubble or reefs in outer harbors or, in some places, closer to shore (McConnaughey & McConnaughey, 1988). The shells of *C. californica* are less dorsoventrally compressed than many others in their family. The species has been

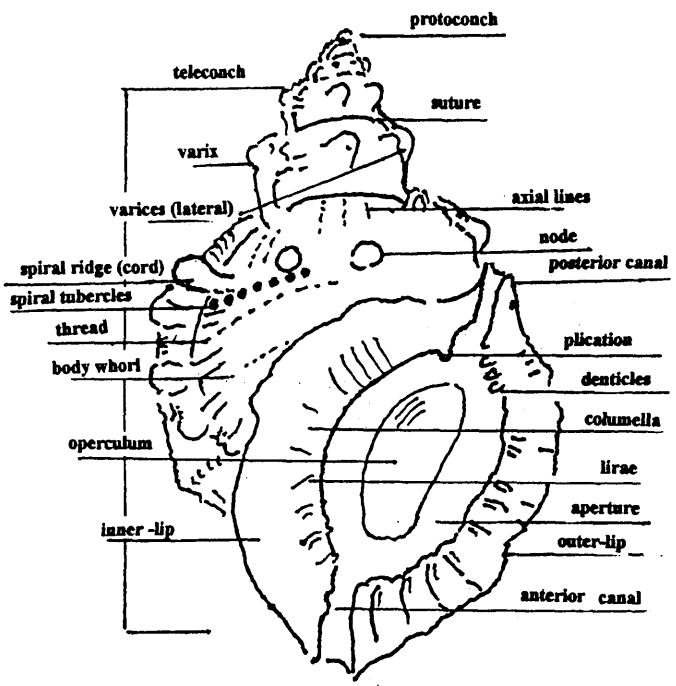


Figure 4. *Crossata* terminology.

reported from Monterey, California to the Golfo de California, México (Grant & Gale, 1931).

Pleistocene specimens of *Crossata californica* from Playa del Rey are commonly smaller and sturdier than Recent specimens and have greater variation in shell thickness. A few Pleistocene specimens are more flattened than Recent specimens (compressed anterior to posterior, a characteristic of many bursids) and have the anterior canal longer than the posterior canal. Some specimens have a smooth columella, others are very plicate, and in some the parietal plication is not prominent. The columella of some Pleistocene specimens is nearly straight; the outer lip of some patulous and frilled. Varices are moderately thick, and in most specimens slightly offset from those of the previous whorl. But in some few specimens varices are continuous with those of the previous whorl. Several specimens have varices with extremely sharp pointed nodes. The body whorl is large with dominant spiral sculpture consisting of moderately wide cords, beaded cords, and finer beaded threads, with spirally aligned nodes, and tubercles. The strength of these sculptural elements differs between specimens. Spire length varies slightly, and the total whorl number is six. The aperture is commonly longer than in Recent specimens. Some tan color is preserved on the fossil specimens, and a chalky intritacalx is often noticeable.

Crossata ventricosa (Broderip, 1833), the type species for *Crossata*, ranges from Perú to Chile and is moderately common. Cossignani (1994) discussed that *C. californica* could be a sub-species of *C. ventricosa*. Many characteristics of *C. ventricosa* are similar to those of Pleistocene specimens from Playa del Rey, but most *C. ventricosa* have a smooth columella, less prominent but broader varices, cords from the varices to the body whorl that are less obvious, a smaller shell overall and a body whorl that is more expanded anteriorly. *Crossata ventricosa* and Pleistocene *C. californica* (Figure 5), have similar sculpture and similar color patterns.

According to Beu (2001) and Parth (1996) *Crossata californica* and *Crossata ventricosa* belong to one intergrading species and *Bursa calcipicta* may be a deep-water link to the northern *C. californica* and southern *C. ventricosa* species.

Crossata californica sonorana Berry, 1960, from Sonora, México, is so similar to *C. californica* that discriminating the subspecies from the species is very difficult. Additionally, their geographic ranges are not disjunct and the two may occur together. This Sonoran form is more often found in the Golfo de California. *Crossata californica sonorana*, according to Berry (1960), differs in having a broader spire, being smaller, and having a thinner shell with sharper nodules, but these characteristics are not adequately different to make the species and its subspecies readily separable. Any large assemblage of *C. californica* from a specific locality (e.g. near Guaymas, Sonora, México) may have morphological variations displaying the *C. sonorana* characteristics.

Early Tertiary bursids:

Many fossil bursids are known, but the origins of the family and of the genera are unclear (Beu, 1988). Among possible progenitors of *Crossata californica* is *Olequahia domenginica* (Vokes, 1939). This bursid had a geographic range from near San Diego to central California during the late early through early middle Eocene "Domengine" stage (Squires, 1984). A specimen from the Eocene Llajas Formation, on Runckle Ranch, Simi Valley, Ventura County, California, has well defined shoulders, two entire small varices per whorl, a row of small tubercles axially elongated on the body whorl, many spiral ridges and nodes, and a plication on the columella (Figure 6a).

Olequahia hornii (Gabb, 1864) of the late early

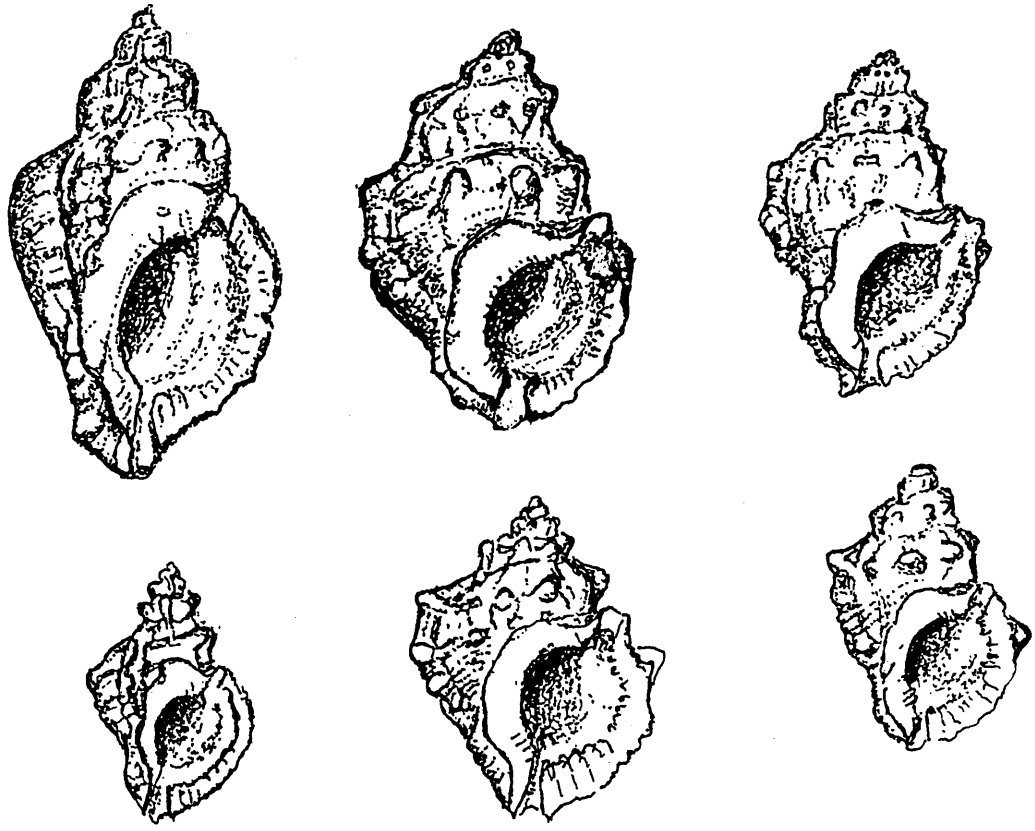


Figure 5 (top row). *Crossata ventricosa* (Broderip, 1833). Recent. Perú. Figures 70% of actual size. Albi collection. Figure 5 (bottom row). *Crossata californica* Pleistocene, Playa del Rey, a comparison. Figures 70% of actual size. Albi Collection.

through middle Eocene ("Tejon" stage); described originally from the Tejon Formation near, Fort Tejón, Tehachapi Mountains, Kern County, California, has been reported from other North Pacific deposits including some in easternmost Russia (Givens, 1974). Stewart (1926) indicated that *O. domenginica* might be a synonym of *O. hornii*, but Beu (1988) considered *O. hornii* to be more like *Olequahia washingtoniana* (Weaver, 1912). The shell of *O. hornii* is of medium size, and has a posterior canal and a straight columella. Whorls are faintly shouldered. The body whorl has noded spiral ribs and one varix. Two varices are present on the second whorl of the spire and minute axial ribs are on the third whorl. Specimens may appear to have had fewer varices as they are easily abraded.

The type species of *Olequahia* is *Cassidaria washingtoniana* Weaver, 1912, which was described from the Cowlitz Formation of early late Eocene age along Cowlitz River, Washington. *Olequahia washingtoniana* looks somewhat like a *Crossata* but lacks its strong varices. In *O. washingtoniana* varices are low and are present only on the first two or three whorls of the teleoconch (Beu, 1988). *Olequahia washingtoniana* has a medium-sized, thick shell, with strongly ornamented whorls that have an angulated profile and a short spire. The whorls are ornamented with spiral ribs, nodes and tubercles. The body whorl has nine axial ribs. The posterior canal is small, the outer lip crenulated, the columella straight, and the anterior canal straight. The protoconch is small, turban-like of 3.5 whorls. Beu (1988) considered *Olequahia* a possible direct ancestor of *Crossata*, or if not direct, that *Olequahia* branched from a lineage directly ancestral to *Crossata*.

Olequahia domenginica appears more similar to *Crossata* than do later *Olequahia* because its whorls consistently have varices, the varices are thicker and have a more rounded profile. *Olequahia washingtoniana* (Figure 6b) has more nodes on the central area of the body whorl, spiral and axial ridges are more prominent

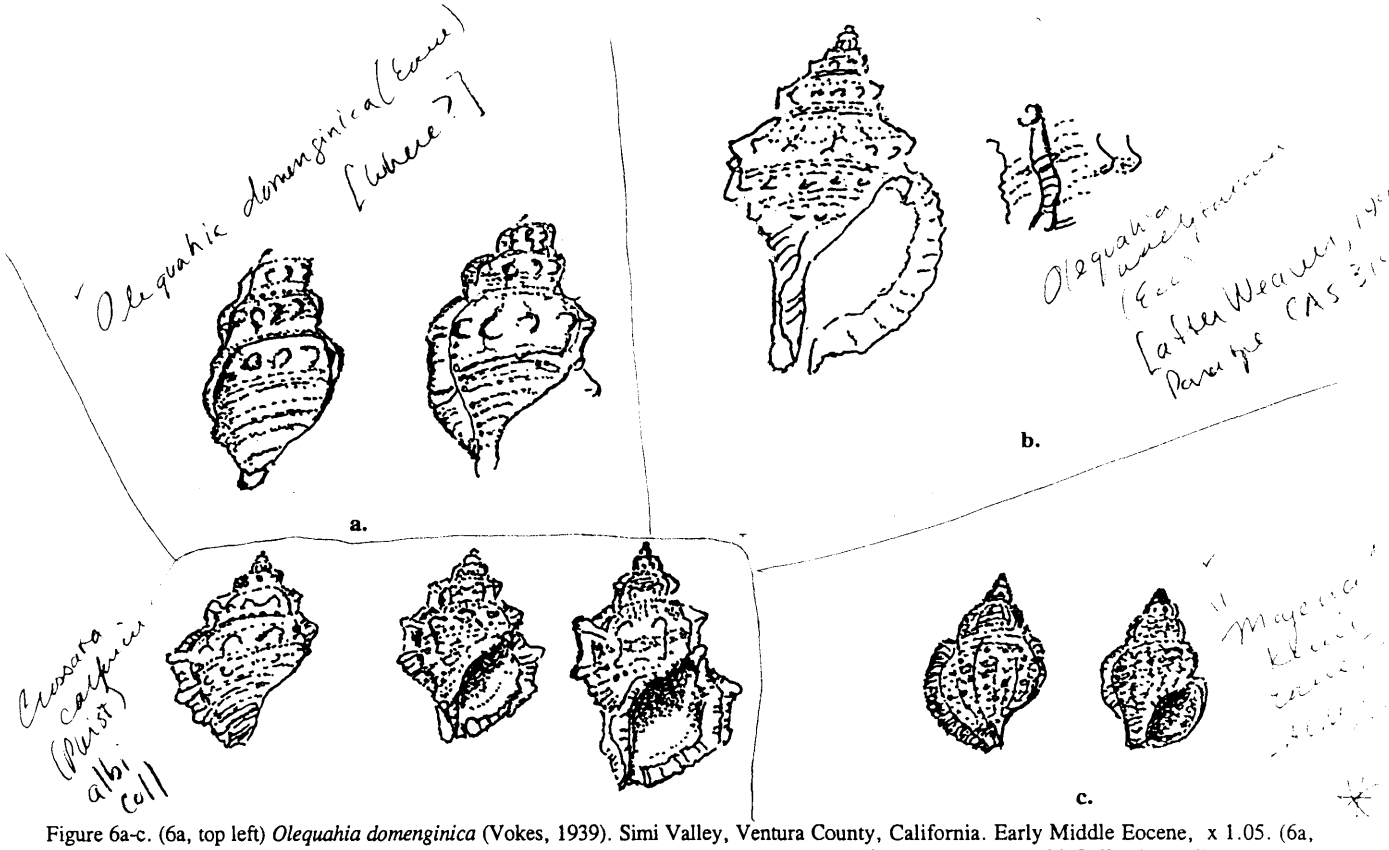


Figure 6a-c. (6a, top left) *Olequahia domenginica* (Vokes, 1939). Simi Valley, Ventura County, California. Early Middle Eocene, x 1.05. (6a, bottom left) Pleistocene *Crossata californica*. Playa del Rey, a comparison. Figures 70% of actual size. Albi Collection. (6b, top right) *Olequahia washingtoniana* (Weaver, 1912). Cowlitz Formation, Cowlitz River, Lewis County, Washington. Late Eocene (after Weaver, 1942). Reprint 1958, pl. 84, fig. 6, paratype (CAS 314). Compare with Pleistocene *Crossata californica*, Playa del Rey, bottom left. (6c bottom right) *"Mayena" kewi* (Dickerson, 1915). California Late Eocene, Tejon Formation, Grapevine Canyon, Kern County, California. (LACMIP 22340). Figures 70% of actual size.

than on *O. domenginica* and *Crossata*.

Olequahia schencki Durham, 1944, was described from specimens of late Eocene age from the Keasey Formation of Oregon. This specimen has no varices, but some specimens have a thickened outer lip. *Olequahia schencki* is most similar to *O. washingtoniana*.

Despite the cooler climate of the Oligocene, *Olequahia lorenzana* (Wagner & Schilling, 1923), originally described under the genus *Strepsidura*, occurs in considerable abundance at localities in the San Emigdio Formation in San Emigdio Canyon, southern San Joaquin Valley, Kern County, California. As with *O. schencki*, varices, an important characteristic of bursids, appear to be lacking in *O. lorenzana*. Shells are large; many incomplete specimens are 80 mm high and sturdy, sturdier than *O. washingtoniana*. *Olequahia lorenzana* has a small posterior canal, straight columella, and many nodes and cords on the whorls. It is the largest known *Olequahia* and differs by its more rotund body whorl.

Among other California early Tertiary species having some resemblance to *Crossata* is *"Mayena"(Nyctilocus) kewi* (Dickerson, 1915) (Figure 6c) from the late middle Eocene Tejon Formation on the west side of Grapevine Canyon, Kern County, California (Smith, 1970). Specimens are quite small, consist of 5½ whorls, and have two lateral varices per whorl. The suture is appressed, the earliest volutions have reticulate sculpture and the body whorl has spiral rows of coarse tubercles. Lirae are on the columella. *"Mayena" (Nyctilocus) kewi* resembles cymatiids in lacking the posterior siphon of bursids. *"Fusitriton"*

terrysmithae Hickman, 1980, also resembles *Bursa* somewhat and differs from most cymatiids, among which it has been classed, in having a posterior siphonal canal. The aperture of *"F." terrysmithae* has a denticulate outer lip and the columella is recurved. The shell is of medium size, and its sculpture is, unlike that of *Crossata,* predominantly axial. These specimens are of late Eocene age from the Keasey Formation of Oregon.

Peruvian and Ecuadorian Eocene and Oligocene bursids are, according to Vokes (1973) similar in ornamentation to *Bursa (Colubrellina) amphitrites* (Maury, 1917) (Figure 7), but a specimen (USNM 644042) from the late Pliocene age Esmeraldas beds of the Onzole Formation, Punta Gorda, Ecuador, that was referred to *Bursa (Colubrellina)* sp. by Olsson (1930; 1964) strongly resembles a small *C. californica*. *Bursa (C).* sp. of Olsson is larger than *B. (C.) amphitrites*, its lateral varices are slightly offset at the sutures, and it has two large medially placed nodes on the back of its body whorl, a similar more anteriorly placed set, and beaded spiral cordlets.

Bursa (Colubrellina) amphitrites Maury, 1917, has been recognized at a number of middle to late Miocene localities in the Caribbean faunal province. Middle Miocene occurrences include the type area of the Shoal River Formation of northwestern Florida, the Cerado and Gurabo Formations of the Dominican Republic, the Gatun Formation of Panamá and the late Miocene Gavilán Formation of Venezuela (Vokes, 1973). The shell of this species is small with finely beaded spiral sculpture and has about two stronger, more nodose cords. The anterior portion of the inner lip has thick raised lirae. Varices are virtually aligned on the spire whorls but to a varied extent offset on the body whorl (Woodring, 1959).

Bursa (C.) amphitrites has some resemblance to Recent *Bursa (Colubrellina) scrobilator* (Linnaeus, 1758) (= *Murex scrobilator* Linnaeus, 1758) of the Mediterranean and northwest Africa (Vokes, 1973). *Bursa scrobilator,* known as *B. scrobiculata* in some older texts, is sub-littoral and accepts lower water temperatures than most bursids.

Beu proposed in 1988 that the absence of Bursidae from the Tethyan warm-water faunas in which Ranellidae (notably *Sassia*, a cymatiid which is found in the Eocene of France and England) are so diverse, indicates that the Bursidae appeared first in the early Eocene, and probably first appeared in the eastern Pacific during the late early Eocene. The fossil record of *B. (C.) scrobilator* is unknown. With a long veliger stage *B. (C.) amphitrites*, which displays many similar characteristics with *Bursa (C.) scrobilator*, may have crossed the Atlantic eastward from the Caribbean to northwest Africa, on the nutrient rich surface current of the Tethys Sea (Ramsay, 1973).

The early Miocene fauna from the Chipola Formation yields *Bursa (Tutufa) pelouatensis* (Cossmann & Peyrot, 1923) (Figure 8), a species that is larger than *B. (C.) amphitrites* and has more ornate sculpture. The non-aligned varices of *B. (T.) pelouatensis* are similar to those of *Crossata*. Vokes (1973) indicated that this early appearance of non-aligned varices might be a random development and lacking in taxonomic significance. Conversely, these varices may be of greater specific importance. All bursids have varices, and bursid identification is facilitated by descriptions of placement and shape of the varices. *Bursa (T.) pelouatensis* is related to *Bursa (Colubrellina) caelata* Broderip, 1833 [now known as *Bursa (Colubrellina) corrugata corrugata* (Perry, 1811)] and is close to *Bursa (Bursa) rugosa* (Sowerby, 1835) (sometimes known as *Bursa (Bursa) calcipicta* Dall, 1908). *Bursa (T.) pelouatensis* was likened by Vokes (1973) to a common Recent Indo-Pacific bursid species *Tutufa (Tutufa) rubeta* (Linnaeus, 1758). *Tutufa (T.) rubeta* has a taller spire, lirae that extend into the aperture from the outer lip and more ornate sculpture.

Concurrent with the Pleistocene *Crossata californica* is a southern species of bursid, *Gyrineum strongi* Jordan, 1936, from the Mulegé Formation near Mulegé, Baja California Sur, México. There is some resemblance to *C. crossata* but it differs in that it is smaller, less wide, with two lateral varices that are narrower, ornamented with tiny ribs and rows of small tubercles, one spiral row of larger nodes on each whorl, and sutures not very indented. Shell shape as in *Marsupina* Dall, 1904, a subgenus in the bursids, but narrower than most. *G. strongi* is extinct. Beu (2001) has placed this bursid in *Marsupina.*

The western Atlantic analog of Recent *Bursa (Bursa) calcipicta* Dall, 1908, is *Bursa (Bursa) rugosa* (G. B. Sowerby, 1835), which some malacologists consider to be a separate species. *B. calcipicta* (often covered with intritacalx) ranges from Jalisco, México, to Ecuador and the Islas Galápagos (Figure 9). It is in *Bursa* because of the consistent lateral parallel varices. It is small, with a pair of varices on each of five whorls, nearly continuous on the spire, and four large nodules on each varix. An angled anterior canal is observed

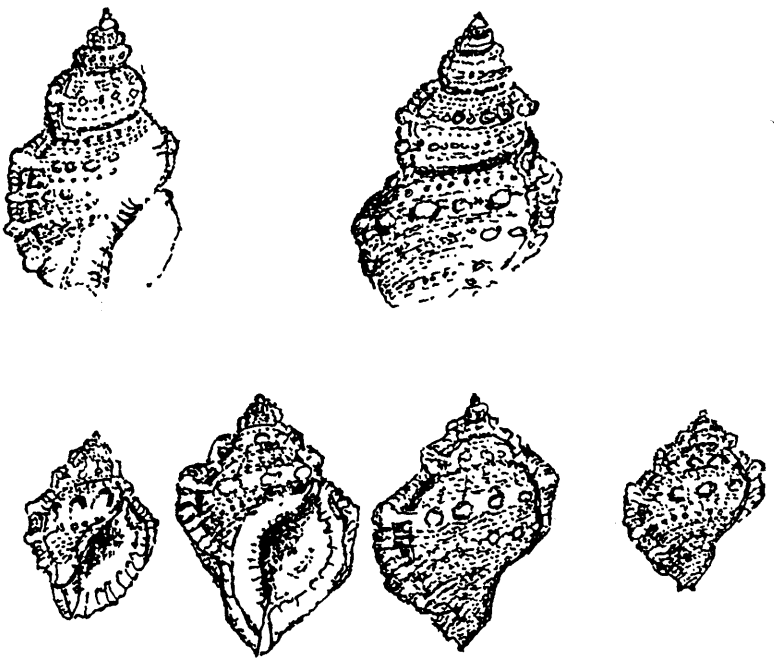
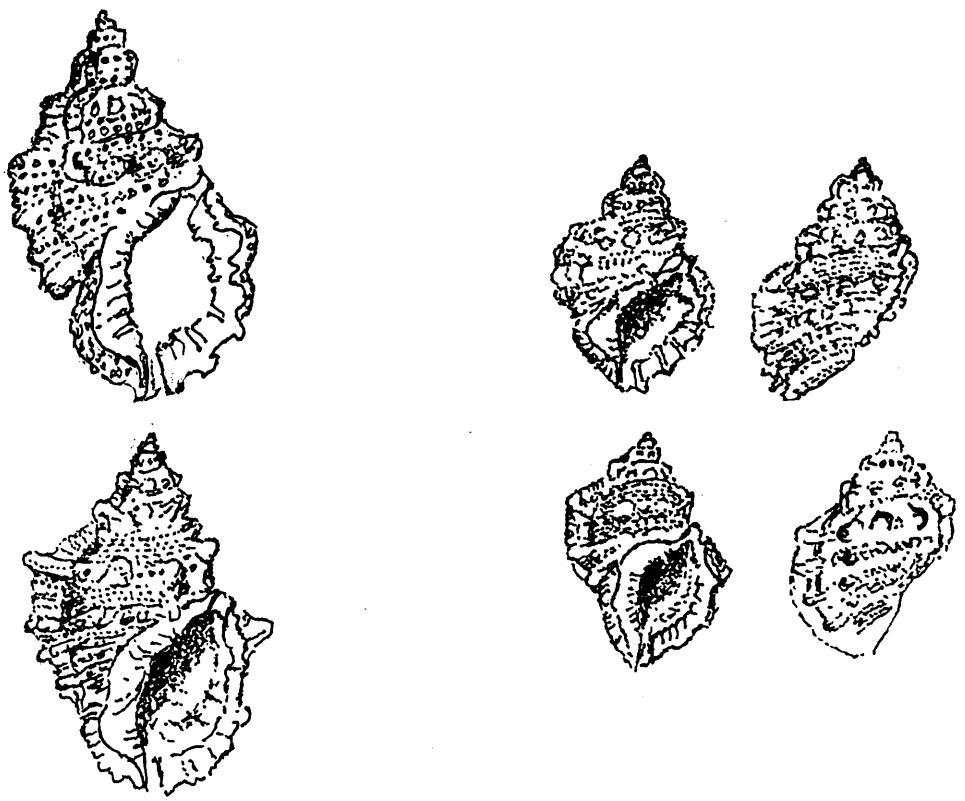


Figure 7. *Bursa amphitrites* Maury, 1917. (top row) Canal Zone, Pacific Panamá, Miocene, Gatun formation (LACMIP 17006), x 1.05. (Bottom row) Pleistocene *Crossata californica*. Playa del Rey, a comparison. Figures 70% of actual size.



Figures 8, 9. (8 top left)) *Bursa pelouatensis* (Cossmann & Peyrot, 1923), after E.H.Vokes (1973, Chipola Formation, Florida, Miocene (1973, fig. 2, USNM 647108). (8 bottom left) Pleistocene *Crossata californica*, Playa del Rey, a comparison.(9 top right) *Bursa calcipicta* Dall, 1908. Recent, México. (9 lower right) Pleistocene *Crossata californica*, Playa del Rey, a comparison. Albi Collection. All figures 70% of actual size.

dorsally, and is similar in shape to some of the small Pleistocene specimens of *Crossata* from Playa del Rey.

Conclusion:

Are morphological traits from ancestral species recognizable in descendant species? The many specimens of *C. californica* from the Pleistocene of Playa del Rey provide an opportunity to check for apparent atavism in the species. Characteristics of three distinct middle Eocene and Miocene species are as follows: 1) *O. domenginica* — large nodes, paired lateral varices on all whorls, and small tubercles 2) *B. (C.) amphitrites* — cords from the varices to whorls, fine spiral tubercles, and node placement 3) *B. (T.) pelouatensis* — large shell and nonaligned varices — may be considered atavistic in *C. californica* specimens (Figures 6a, 7, and 8). The difficulty in deciding which characteristics are most important is apparent in the efforts of Vokes (1973) and Beu (1988). Both thoroughly explored available facets of the ancestry of *Crossata* and *Bursa*. Beu tended to view as most reasonable, an ancestral lineage for *Crossata* that passed through *Olequahia washingtoniana* but Vokes considered *Bursa (C.) amphitrites* a more likely progenitor.

The Oligocene species *O. lorenzana* attains the largest size for the genus. Its large size is suggestive of *Crossata*, but it lacks varices, and a Miocene descendant is not known. A ranellid from the Imperial Formation of late Miocene to early Pliocene age in Imperial County, California, tentatively referred to *Charonia* sp., is large and flattened, has nodes and disconnected varices, and may be derived from the Tethyan fauna (Figure 10).

Though Willett (1937) stated all Pleistocene fossils from Playa del Rey were exactly the same as their Recent counterparts, variations are apparent. These *C. californica* are polymorphic with respect to strength of nodes, whorl profile, strength of lirae about the aperture and varix placement; all of these corroborate their Pleistocene diversity.

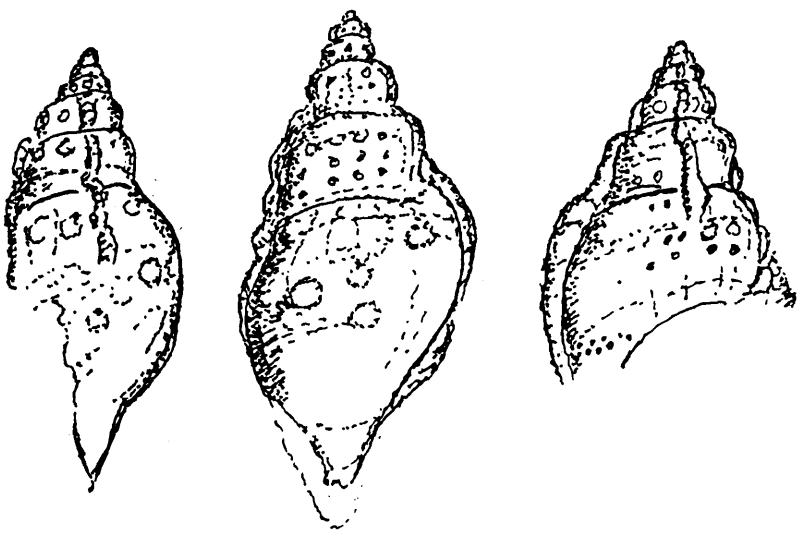


Figure 10. Ranellid, possibly *Charonia* sp. Imperial Formation, Imperial County, California, late Miocene. Figures 70% of actual size. June Maxwell Collection. (now at LACMIP) Loc. 17740 Fossil Canyon (Alverson Gp) Coyote Mtns.

ACKNOWLEDGMENTS

Many thanks to the Invertebrate Paleontology Section staff of the Natural History Museum of Los Angeles County (LouElla Saul and Lindsey Groves) for their helpful loan of specimens, literature, comments and review of the paper. Richard Squires (California State University, Northridge) was of assistance suggesting some of the bursids to be examined. Nancy Schneider of Poway, California, kindly provided a specimen and information on *Gyrinium strongi*. Also, I am indebted to James H. McLean (LACM, malacology) for use of his extensive library, the opportunity to view the Recent bursids and a wonderful comprehensive learning experience concerning mollusks.

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THE 35th ANNUAL WESTERN SOCIETY OF MALACOLOGISTS CONFERENCE

During July 20-24, 2002, the 35th annual Western Society of Malacologists Conference will return to the Asilomar Conference Center on the Monterey Peninsula, California, USA, as in years past. It is a pleasant 3-minute walk to rocky and sandy shores and each dawn will offer a negative 0.3-m low tide there! Cal State University Hayward and San Francisco Bay Wildlife Society are hosting the conference.

WSM conferences feature molluscan ecology, behavior, physiology, genetics, systematics, paleontology, and close-up/underwater photography. This will be one of only two North American, international molluscan meetings for 2002 (following the Vienna Conference during 2001), with the American Malacological Society (AMS) in the midwest this year.

Dr. Cynthia Trowbridge (trowbric@ucs.orst.edu) has organized a symposium on community and population ecology of mollusks for this meeting. There are many exciting ecological topics being investigated by west-coast researchers. This ecology symposium will include talks on consumer-prey interactions, interspecific competition, recruitment, larval biology, environmental stress topics, and invasion ecology.

Other molluscan symposia are also planned — on Biogeography and Photographic Documentation or Paleontology.

At Asilomar, only rooms with meals will be available, or participants can arrange on their own to stay off site. An evening is planned at the Monterey Bay Aquarium, hosted largely by them. Members registered for the whole conference receive free Aquarium admission to the Monterey Bay Aquarium.

For those interested in presenting a paper, a 250-word abstract will be due by April 10, 2002.

For further information, contact either Treasurer Cynthia D. Trowbridge" <trowbric@onid.orst.edu> or, WSM President Chris Kitting <ckitting@csuhayward.edu>