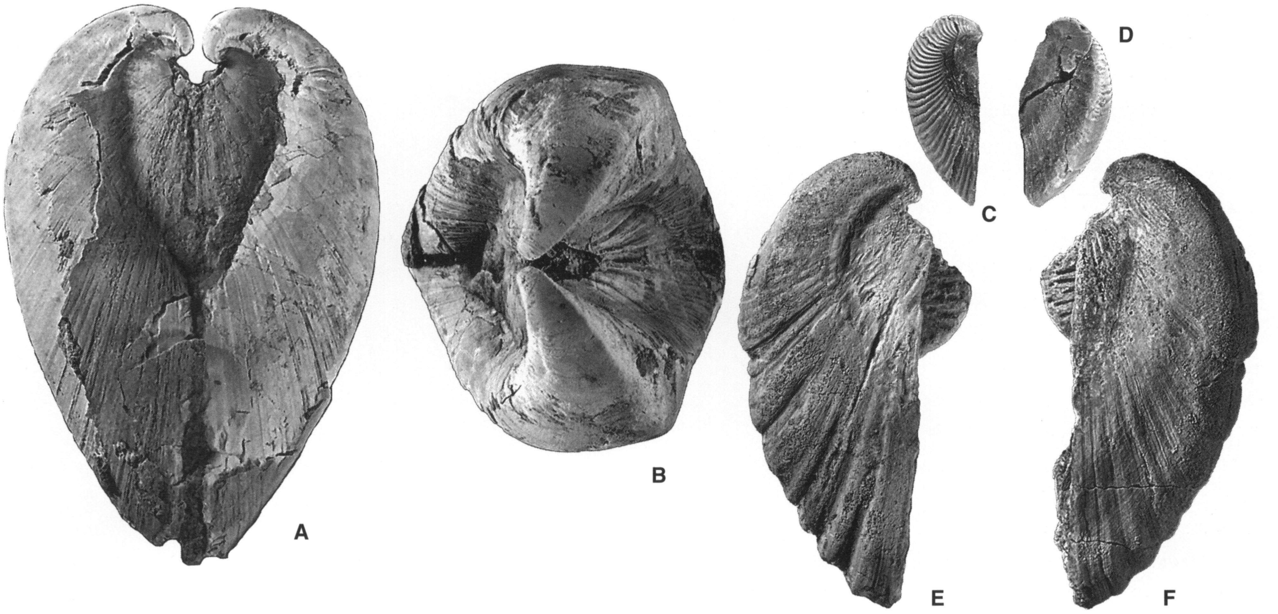


TEXT-FIG. 10. *Opis* (*Hesperopis*) *triangulata* (Cooper, 1894). All ×1. Specimens coated with ammonium chloride. A-B, hypotype, SDSNH 67148, SDSNH loc. 3403. A, lunule view. B, dorsal view. C–D, lectotype, CASG 624 from west base of Pt. Loma, San Diego, California, right valve. C, lunule view. D, escutcheon/corcelet view. E–F, hypotype, LACMIP 13544, LACMIP loc. 22661, right valve. E, lunule view. F, escutcheon/corcelet view.

Stephenson (1954) stated that this bivalve is a varietal form of *O.*? *elevata*.

Cretaceous undifferentiated

Meek (1864, p. 11) listed ?*Opis bicarinata* Conrad and ?*Opis bella* from the south-eastern United States. Stoliczka (1871) also listed *Opis bicarinata* and *O. bella* from Upper Cretaceous strata of Mississippi. *Opis bicarinata* Conrad (1858, p. 327, unfig.) and *Opis bella* Conrad (1858, p. 327, unfig.), both from Upper Cretaceous strata of Mississippi, were too briefly described by Conrad (1858) and not, as promised, subsequently figured. Their hinges are unknown. These two species are best considered to be *nomina dubia*.

Gabb (1861, p. 151) reported ?*Opis haleana* d'Orbigny from undifferentiated Cretaceous strata in Alabama, and Meek (1864, p. 11), included this name in his checklist of Cretaceous bivalves from the south-eastern United States. This record is poorly known, and Stanton (1895, p. 59) remarked that this species is a doubtful representative of *Opis* in America.

Palaeocene

Opis virginalis Waring (1917, p. 78, pl. 14, fig. 4), from the upper Palaeocene Santa Susana Formation, Ventura County, California (Keen and Bentson 1944, p. 74) is known only from the holotype, which is a small steinkern (16 mm in height). The specimen is trigoniform and appears to have a carinate-umbonal ridge. Observation of the holotype, however, revealed that the specimen has been crushed, which accentuated its trigonal shape and produced the apparent carinate-umbonal ridge. The beak area is missing, and the hinge is covered by rock matrix. The shell does not appear to have an escutcheon nor a corcelet ridge, and the lunule is not well delineated. This species is very likely not an *Opis*. If it were, it would be the youngest *Opis* and the only Cenozoic *Opis*.

Early Eocene

Isocardia conradi Gabb (1860, p. 392, pl. 68, figs 21–21a; Whitfield 1886, pp. 200–201, pl. 26, figs 3–4), is a venerid from the lower Eocene Vincentown Formation, New Jersey. Although this bivalve was mistakenly identified as an *Opis* by Gabb (1876, p. 311), Stanton (1895, p. 49, 59) stated that this species is not an *Opis*, and Palmer and Brann (1965, p. 150) concurred.

DISCUSSION

Life habits of Hesperopis

Hesperopis occurs in shallow-marine deposits, except for a few incomplete specimens that have obviously undergone post-mortem transport and are in bouldery submarine-fan turbidites. Specimens otherwise are found in siltstone or, less commonly, in fine sandstone. Some are doubled valved, thereby indicating they lived in non-turbulent waters (below effective-wave base) in moderate depths where shallow-marine silts and fine sands accumulated, most likely, in offshore shelfal areas.

The bulky shape of *Hesperopis* is strongly suggestive that this opine was a recliner that lived on, or partially settled into, the soft substrate. Its wide and flattish lunule side would have provided much stability for a juvenile or an adult specimen situated with its commissure perpendicular to the ocean floor. Having a vertical commissure would mean that both valves would have experienced the environment the same and, hence, would be equivalved, like what is observed for *Hesperopis.* In this position, the trigonal shape of the valves would have caused the wide, truncate posterior end of the corcelet side of the shell to project upward at an appreciable angle with respect to the horizontal. In the case of *O.* (*H.*) *popenoei*, for example, the posterior end of the shell would have projected upward at an angle of *c.* 55 degrees. The posterior umbonal ridge, corcelet ridge and corcelet furrow probably served as stabilizers, preventing any currents from disorienting the shells. Having an elevated posterior end of the shell would have also placed the incurrent–excurrent siphons well up into the water column. Modern astartids are all very shallow-infaunal filter feeders whose branchial and anal orifices are not produced into elongate siphons; instead they extend only about 2 mm beyond the shell (Boss 1982, p. 1137). It would have been critical for the siphons of *Hesperopis* not to have been covered by sediment.

The thick-walled, heavyweight shells, as well as the disproportionally large-sized hinges bearing sturdy and laterally serrated teeth, are also suggestive of an epifaunal, edgewise (i.e. vertical commissure) recliner life habit. The stout and serrated teeth would have provided resistance to shear forces produced by any currents or waves. Unlike the looser fit of most heterodont hinge teeth, which permit rocking movements that aid burrowing, the large teeth with interlocking lateral serrations that *Hesperopis* possesses would have prevented rocking of the valves.

It is pertinent to mention that the 'word' recliner is used in the sense of how Stanley (1970, p. 8) used the term. It means that a bivalve lived on or partially buried in the soft substrate, and that it lacked the capacity for attachment. *Hesperopis* was most likely a secondary soft-bottom dweller. Seilacher (1984, pp. 213–214) discussed that these types of bivalves, which are sessile, inherit the loss of the foot. They do not actively burrow but use the shell itself as an anchor in the sediment.

Through time, the shells of *Hesperopis* became larger, and the internal ligament became wider and longer. Within the *'holzana'* lineage, the shells also became broader, and the teeth became stouter. Within the *'anae'* lineage, the shells also became more elongate, and the teeth became longer. The larger shells, whether broader or more elongate, would have provided more stability for a recliner. The larger shells would have also placed the posterior end higher above the substrate. The larger shell size would have put more stress on the adductor muscles; hence, enlargement of the internal ligament would have aided the adductor muscles in opening the valves. The stouter and longer teeth would have provided better resistance to any shear forces.

Species within the *'holzana'* lineage have very subdued corcelet features, probably indicating that this lineage adapted to slightly deeper that is slightly quieter waters where the stabilizing effects of the corcelet features were not necessary.

One would expect to find encrusting epibionts (e.g. algae, bryozoans, serpulids) on the epifaunal valves of *Hesperopis.* There is, however, no evidence of epibiont activity made, while the specimens were alive. Modern astartids have a strong periostracum (Boss 1982), and it is conceivable that *Hesperopis* also had a thick or otherwise effective periostracum that prevented epibiont activity. Post-mortem epibiont drill-holes, presumably made by boring sponges or algae, however, are moderately common on the exteriors and interiors (including socket areas and cardinal teeth) of some adult left and right, single-valve specimens of *Hesperopis.* One of these specimens is shown on Plate 2, figures 6 and 10.

The thick shells, disproportionally large-sized hinge areas, and stout, serrated hinge teeth of *Hesperopis* would have provided defence against durophagous predators. The thick shells of *Hesperopis*, possibly covered by a strong periostracum, would have also offered resistance to predatory gastropods, whose drill-holes are rarely found on *Hesperopis.* Only two specimens with these kind of drill-holes were detected, and one of these is illustrated in Text-figure 5A. The rarity of predatory gastropod drill-holes on specimens of *Hesperopis* is similar to the rarity of predatory gastropod drill-holes that Squires and Saul (2004*b*) observed in Cretaceous shallow-burrowing corbulid bivalves from the study area. It might have been that gastropods capable of making drill-holes did not prefer the fine sediments inhabited by bivalves such as *Hesperopis* and corbulids.

Although *Hesperopis* is locally abundant, it is otherwise sparsely represented in the rock record. Specimens are also not commonly found associated with taxonomically diverse assemblages of burrowing bivalves. The localized occurrences of *Hesperopis* in low-diversity assemblages suggest that they thrived under specific circumstances. The presence of environmentally controlled, strong growth checks on some specimens of *O.* (*H.*) *triangulata* from the west side of the San Joaquin basin might be the result of these specimens having lived in a shallow embayment where temperature and salinity could have fluctuated.

Life habits of other opines

The life habits of most other opines are generally poorly known. During the Jurassic, most of them lived in muddy to silty environments, or in some cases, in fine sands (Liu 1995, appendix 2). Fürsich *et al.* (2000) reported, however, that some Middle Jurassic (Bathonian) opines belonging to *Coelopsis (Coelopsis)* and *Opis* (*Pachyopis*) from western India occur in carbonates with intercalations of coral meadows. The life habits of *Opisoma* are better known. Hallam (1977, p. 65) reported that in the European province during the Jurassic, *Opisoma* lived in coral-reef environments along with rudists and other hippuritoid bivalves. Lee (1983) reported that in Morocco, the shells of Early Jurassic *Opisoma menchikoffi* Dubar, 1948 formed *in situ* reef-like banks or mounds close to a shoreline characterized by tidal flats and channels. As mentioned earlier, however, *Opisoma* has a distinctive alatoform shape. Its entire shell is remarkably flattened in an antero-posterior direction, very much like the greatly compressed shell of the Recent cardiid genus *Corculum* Röding, 1798. The Indo-West Pacific *Corculum cardissa* (Linnaeus, 1758) is found living in strong sunshine in depths of approximately 0.5 m on sandy reef flats. This bivalve's very thin shell reclines in a roughly horizontal position with the commissure vertical. The shell is usually not attached, but there can be several short byssal threads. Its short siphons project very slightly into the water above. The upper valve has transparency, thereby allowing sunlight to reach endosymbiotic dinoflagellates (Kawaguti 1950; Farmer *et al.* 2001). Seilacher (1984, p. 224) noted that *Corculum* is an edgewise recliner, and Accorsi Benini (1981) reported a similar life habit for *Opisoma*. Yancey and Wilson (2006) reported that *Opisoma* was an edgewise recliner and that alatoform–bivalve radiations usually occurred during times of warm climates and reef development.

Review of palaeoclimate of study area during the Cretaceous

Saul (1986, fig. 1) depicted the relative ocean temperatures and the global cycles of sea level changes for the north-eastern Pacific area during the Cretaceous. A warming trend and a sea level rise during the Hauterivian/Barremian coincided with the first occurrence of opines in the study area in southern Oregon (Area 4) and northern California (Area 6). Aptian to Cenomanian opines are unknown in the study area, but a warming trend and a sea-level rise during the Turonian coincided with the first *Hesperopis* in the study area. During the Coniacian and Santonian, oceans were cooler and associated with lower sea levels, thus possibly accounting for the paucity of opines in the study area during this interval. The Campanian and Maastrichtian were associated with a general warming trend and overall rising sea levels, thus providing excellent conditions for *Hesperopis* to diversify.

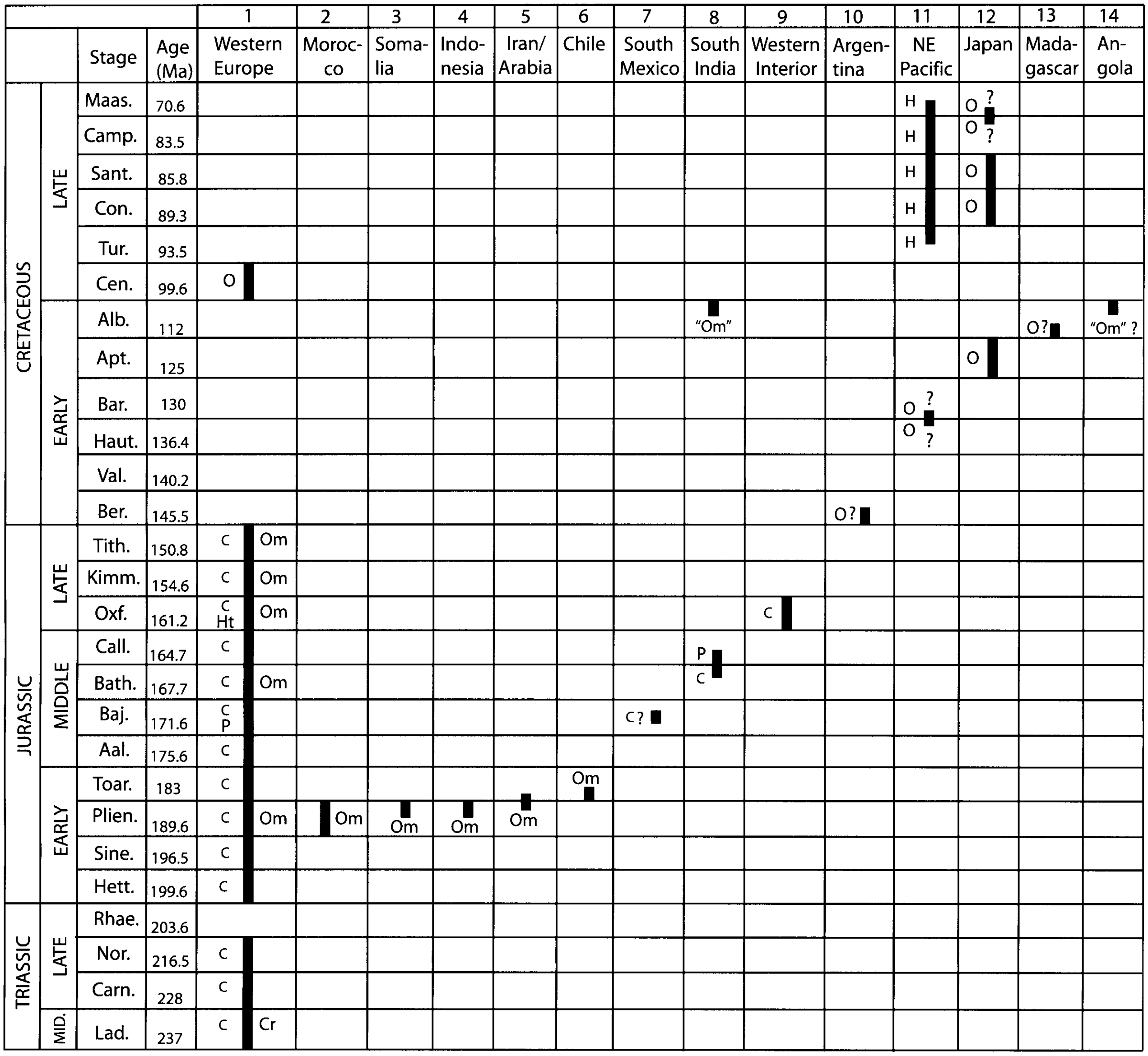
Localities with *Hesperopis* in Areas 4–7, 9 and 11 are especially useful for palaeoclimatical reasons, because they have not been tectonically displaced by the San Andreas Fault (Text-fig. 1). A comparison of the northernmost occurrences (Text-fig. 1) of the Turonian *O.* (*H.*) *popenoei*, the late early Campanian *O.* (*H.*) *anae* and the late Campanian to early late Maastrichtian *O.* (*H.*) *triangulata* shows that, over time, the marginally tropical waters shifted southward from 43°N to approximately 39°N. This pattern is similar to that reported by Saul and Squires (2008, fig. 3) for Turonian to late Maastrichtian volutodermine-gastropod specimens that also were not tectonically transported. These volutodermine data, which are more refined because of better distribution of specimens both numerically and spatially, show that the approximate position of the Late Cretaceous latitude of subtropical/warm temperate boundary shifted from 43°N in the Turonian to 36°N in the Campanian and Maastrichtian, with a slight northward expansion of warm waters during the middle Campanian.

Rocks west of the San Andreas Fault have been tectonically transported northward. Although the distance of offset is controversial (see Kodama and Ward 2001), most geologists believe that it was between 300 and 500 km since the end of the Cretaceous (Wentworth *et al.* 1998). In spite of this tectonic factor, palaeoclimatical implications of these rocks can be deciphered. At a few localities west of the San Andreas Fault, *Hesperopis* has been found in some of the same beds that contain rudist bivalves. Rudists have palaeoclimatical significance, because they have been found at numerous low-latitude occurrences and are indicators, at the very least, of marginal tropicality (e.g. Sohl 1987). Kodama and Ward (2001) reported that Late Cretaceous rudist bivalves in the study area were restricted to paleolatitudes between 40°N and 34°N. Localities that contain both *Hesperopis* and the rudist *Coralliochama orcutti* White, 1885 are the following: at least two localities in the Gualala Formation (Area 8) (see Elder *et al.* 1998); UCMP loc. A-3435 in the El Piojo Formation? (Area 12); LACMIP loc. 27199 in the Schulz Member of the Williams Formation (Area 15); and SDSNH loc. 3402 in the Point Loma Formation (Area 17). At LACMIP loc. 27199, *Hesperopis* has also been found with other genera of rudists (Filkorn 2007). At another locality, one in the Punta Baja Formation (Area 20), *Hesperopis* has been found in the same beds with rudists that are not *Coralliochama*, according to Kilmer (1963) and LACMIP collectors.

In summary, *Hesperopis* lived in warm-temperate waters, unlike its Old World tropical-water Jurassic predecessors. Elder and Saul (1993, p. 177) reported an *Opis*, herein identified as *O.* (*H.*) *rosarioensis*, to have been a warm-water, but not a 'Tethyan' (i.e. tropical) bivalve, and we concur.

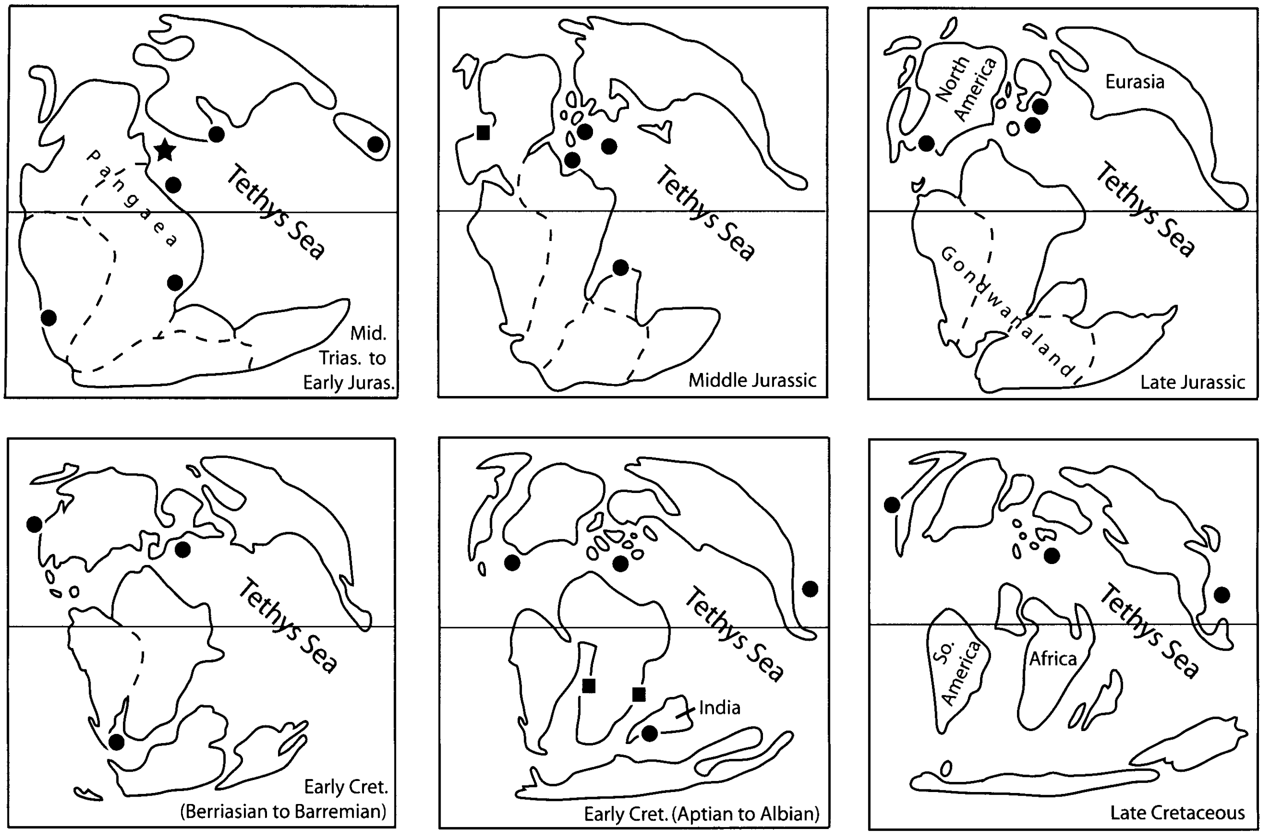
Overview of palaeobiogeography of opines

Introduction. To determine the global palaeogeographical distributions of opine genera/subgenera, a comprehensive but not exhaustive review of the literature was attempted. Precise distribution is not possible at present because of taxonomic inconsistencies and identification problems that exist in the literature, but the general trends are discussed and summarized in Text-figures 11–12.



				1	2	3	4	5	6	7	8	9	10	11	12	13	14
		Stage	Age (Ma)	Western Europe	Morocco	Somalia	Indonesia	Iran/ Arabia	Chile	South Mexico	South India	Western Interior	Argentina	NE Pacific	Japan	Madagascar	Angola
CRETACEOUS	LATE	Maas.	70.6											H █	O ? █		
		Camp.	83.5											H █	O █ ?		
		Sant.	85.8											H █	O █		
		Con.	89.3											H █	O █		
		Tur.	93.5											H █			
		Cen.	99.6	O █													
	EARLY	Alb.	112								█ "Om"					O? █	█ "Om" ?
		Apt.	125												O █		
		Bar.	130											O ? █			
		Haut.	136.4											O █ ?			
		Val.	140.2														
		Ber.	145.5										O? █				
JURASSIC	LATE	Tith.	150.8	C █ Om													
		Kimm.	154.6	C █ Om													
		Oxf.	161.2	C Ht █ Om								C █					
	MIDDLE	Call.	164.7	C █							P █						
		Bath.	167.7	C █ Om							C █						
		Baj.	171.6	C P █						C? █							
		Aal.	175.6	C █													
	EARLY	Toar.	183	C █					Om █								
		Plien.	189.6	C █ Om	█ Om	█ Om	█ Om	█ Om									
		Sine.	196.5	C █													
		Hett.	199.6	C █													
TRIASSIC	LATE	Rhae.	203.6														
		Nor.	216.5	C █													
		Carn.	228	C █													
	MID.	Lad.	237	C █ Cr													

TEXT-FIG. 11. Global palaeogeographical distribution of opine genera/subgenera (i.e. *Coelopis* (*Coelopis*) = C; *Coelopis* (*Cryptocoelopis*) = Cr; *Heteropis* = Ht; *Opisoma* = Om; *Opis* (*Opis*) = O; *Opis* (*Pachyopis*) = P; *Opis* (*Hesperopis*) = H), listed in the order of first-appearance datum (FAD). Thick vertical lines indicate opine occurrence. Numbers at top of columns refer to source(s) of data: 1, Marlière (1939), Chavan (1969), Hallam (1976, 1981, 1983), Liu (1995). 2, Hallam (1977, 1983), Accorsi Benini (1981). 3, Accorsi Benini (1981). 4, Accorsi Benini (1981). 5, Accorsi Benini (1981). 6, Accorsi Benini (1981). 7, Alencaster (1963). 8, Stoliczka (1871), Fürsich *et al.* (2000). 9, Imlay (1941). 10, Riccardi (1988). 11, This study. 12, Hayami (1975); Tashiro (1992). 13, Collignon (1949). 14, Mouta and Borgès (1926); Darteville and Freneix (1957).



TEXT-FIG. 12. Global palaeogeography of opines as a group, based on information (thick vertical lines) shown in Text-figure 11. Maps, modified from Smith *et al.* (1994), show land masses. Solid star = earliest known opine record; solid circles = opine occurrences; solid rectangles = possible opine occurrences.

Triassic and Jurassic opines. The earliest known opines are *Coelopis* (*Coelopis*) and the morphologically very similar *C.* (*Cryptocoelopis*) of late Middle Triassic age (Ladinian), and they have only been found in the western Tethys Sea (i.e. western Europe to Morocco) region (Chavan 1969; Hallam 1981). During the Jurassic, *Coelopis* (*Coelopis*) and *Opisoma* were the dominant opines in the world. As can be seen in Text-figure 11, *Coelopis* (*Coelopsis*) had a nearly continuous Jurassic record in western Europe. According to Liu (1995), the Early Jurassic was marked by *Opisoma*, whose distribution was basically confined to the Tethys Sea. Hallam (1977, p. 65) reported that *Opisoma* was stenothermal and restricted to a belt of warm waters 'within 30 degree of the Jurassic equator.' *Opisoma* reached its greatest specific diversity and largest size during the Early Jurassic, when there were some relatively short-lived dispersals of *Opisoma* into the eastern regions of the Tethys Sea and into Chile (Accorsi Benini 1981; Liu 1995). The presence of Early Jurassic *Opisoma* in Chile poses a special problem regarding its route of migration. Pangaea was nearly completely intact during this time, and it would seem that the most plausible route for *Opisoma* was around the eastern edge of Pangaea to reach Chile (Text-fig. 12). Hallam (1983, fig. 1) showed all possible marine migration routes between the continents during the Jurassic, including this easterly route. An alternative route of dispersal, however, might have been via the controversial 'Hispanic Corridor,' which was a postulated rift zone between eastern North America and north-western Gondwanaland. Its existence prior to the Late Jurassic is controversial, but Liu (1995, fig. 30) showed the 'Hispanic Corridor' as being open during the middle Early Jurassic (Pliensbachian). Sha (2002) reported that it first opened at the end of the Triassic or at the beginning of the Jurassic.

During the Middle Jurassic, there was also dispersal of western Tethys *Coelopis* (*Coelopis*) and *Opis* (*Pachyopis*) into western India (Fürsich *et al.* 2000). The 'Hispanic Corridor' route mentioned earlier conveniently explains a possible occurrence of a Middle Jurassic opine in Mexico. Alencaster (1963) and Perrilliat (2002) reported a western European species, *Opis* cf. *leckenbyi* Lycett, 1863, from the Middle Jurassic (upper Bajocian) Taberna Formation, Oaxaca, Mexico. Cox and Arkell (1948–1950, p. 29) placed Lycett's species in *Opis* (*Coleopsis*). Assignment of this Mexican specimen to *Opis* (*Coleopis*) is questionable because it is poorly preserved.

During the Late Jurassic, opines migrated to North America via the North Atlantic seaway, which was well established by that time (Smith *et al.* 1994). Imlay (1941) reported *Opis* (*Coelopis*) *americana* Imlay, 1941 of Late Jurassic age (Oxfordian) from the subsurface of Arkansas.

Overview of Early Cretaceous opines. During the Early Cretaceous (Neocomian), oceans cooled and Old World opines became more restricted in their distribution. According to Kauffman (1973, p. 359), *Opis* (*Opis*) became adapted to temperate conditions during the Cretaceous. During the early Berriasian, *Opis* occurred in southern Argentina (Riccardi 1988, table 6). This Argentinan occurrence coincides with the opening up of the South Atlantic as a new seaway by latest Jurassic or earliest Cretaceous time (Kauffman 1973, p. 372). *Opis californica* occurs in Hauterivian or Barremian strata in southern Oregon and northern California. No opines have been reported from the interval spanning the Middle Jurassic through the Valanginian on the Pacific slope of North America.

During the late Early Cretaceous (Aptian and Albian), opines are only known with certainty from southern India and Japan. '*Opisoma*' *geinitziana* is known from upper Albian strata in southern India (Stoliczka 1871), and *Opis* (*Opis*) is known from Aptian strata in Japan (Hayami 1975; Tashiro 1992). There are no Aptian nor Albian records of opines on the Pacific slope of North America, but bivalve faunas from these rocks are very incompletely studied.

During the late Early Cretaceous, there are several possible opines known from the Old World. Collignon (1949, p. 23, pl. 3, fig. 6) reported an *Opis* from the Ambarimaninga fauna strata in north-western Madagascar, but only a lunule view of a double-valved specimen is illustrated; thus, this report is very questionable. Kiel (2006) reported that the Ambarimaninga fauna is of early Albian age. A late Albian occurrence of '*Opisoma*' cf. *geinitziana* in Angola was noted by Mouta and Borgès (1926), and mention of this occurrence was repeated by Darteville and Freneix (1957).

A few reports of late Early Cretaceous 'opines' from the Old World seem to be invalid. Whitfield (1891) reported *Opis megambona* Whitfield (1891, p. 398, pl. 5, figs 11–12) from the Abeih sandstone in Lebanon. According to Walley (1983), this sandstone is of early Aptian age. Based on the very narrow beaks and pronounced, widely spaced commarginal sculpture of this species, it seems like it belongs to *Trigonopis*. Stoliczka (1871) reported *Opis repleta* Stoliczka (1871, pl. 10, fig. 11) from possibly upper Albian rocks in southern India, but, based on the very narrow beaks of this species, its seems more like a *Trigonopis*.

Overview of Late Cretaceous opines. During the Late Cretaceous, opines are mainly known only from the Northern Hemisphere (Text-fig. 12). As far as it can be determined from the available literature, except for a Cenomanian occurrence of *Opis* (*Opis*) in Belgium (Bigot 1895; Marlière 1939), opines were expatriated from the western Tethys Sea area. *Opis* (*Opis*) was present in Japan from the Coniacian to possibly the early Maastrichtian (Hayami 1975; Tashiro 1992).

The only known Late Cretaceous record of opines in the study area is of *Hesperopis*. It most likely evolved from the middle Turonian *O.* (*H.*) *popenoei* rather than from the Hauterivian or Barremian *Opis californica* (see 'Remarks' for genus *Hesperopis*). *Hesperopis* appears to have been endemic to the Pacific slope of North America. It became most widespread in this area during the Campanian. Its early late Maastrichtian record is the youngest of any opine.

The present latitudinal range of 49°30′N–49°33′N (i.e. Nanaimo Group, Vancouver Island, British Columbia) for deposits yielding *O.* (*H.*) *holzana* and *O.* (*H.*) *vancouverensis* (Text-fig. 1) is suggested to differ from the original latitudinal range because of the effects of terrane transport. Works on Cretaceous acilid bivalves and volutid gastropods by Squires and Saul (2006) and Saul and Squires (2008), respectively, support the paleomagnetism and rudist-bivalve analyses by Kodama and Ward (2001) that the Nanaimo Group was (1) originally deposited no farther south than 40°N (i.e. northern California) and (2) tectonically displaced during post-Cretaceous time to its current position in the Vancouver Island area.

CONCLUSIONS

Opines first evolved during the late Middle Triassic (Ladinian) in the western Tethys Sea region. They were most widespread during the Middle and Late Jurassic, and *Coelopis* (*Coelopis*) and *Opisoma* were most dominant. *Opisoma* has a current-adapted shape and hinge and lived as an edgewise recliner in very shallow waters within coral-reef environments. The first undoubted appearance of opines (i.e. *Coelopis*) in the New World was during the Late Jurassic in Arkansas. *Opis* (*Opis*) was the most widespread opine during the Cretaceous, and arrival of opines onto the Pacific slope of North America is signalled by southern Oregon and northern California occurrences of the Early Cretaceous (Hauterivian or Barremian) *Opis californica* Stanton.

From Early Jurassic to Albian, *Opis* were small to medium size. Beginning in the Albian, the overall size of *Opis* increased by two to threefold. Whether or not opines inhabited the Pacific slope of North America during the Aptian through Cenomanian is unknown, because these faunas are very incompletely described, and the fossils can be poorly preserved.

From the Middle Turonian through early Late Maastrichtian, the record of opines in the study area is represented by six species of *Hesperopis* subgen. nov., which is, so far as known, endemic to the study area. It is unknown whether *Opis californica* was the ancestor of *Hesperopis*. *Hesperopis* is most similar to *Opis* (*Opis*), but the hinge of *Hesperopis* is unique. *Hesperopis* is the first astartid to have a partially internal ligament. *Hesperopis* is comprised of two morphological lineages that are inferred to have evolved from *O.* (*H.*) *popenoei* sp. nov. The '*holzana*' lineage, which is mainly characterized by broad shells, includes *O.* (*H.*) *holzana* sp. nov. and *O.* (*H.*) *rosarioensis* Anderson and Hanna. The '*anae*' lineage, which is mainly characterized by narrow shells, includes *O.* (*H.*) *anae* sp. nov., *O.* (*H.*) *vancouverensis* Whiteaves, and *O.* (*H.*) *triangulata* (Cooper).

Hesperopis reached its highest diversity during the Campanian, with nontectonically transported occurrences located as far north as northern California. Most of the species of *Hesperopis* had a relatively short chronologic range. Referring to Text-figure 2, *O.* (*H.*) *popenoei* has a range of at least 2 my; *O.* (*H.*) *holzana* of 3 my; *O.* (*H.*) *rosarioensis* of 10 my; *O.* (*H.*) *anae* of 1.5 my; *O.* (*H.*) *vancouverensis* of 3 my and *O.* (*H.*) *triangulata* of 3 my. With future collecting, more localities of these species are likely to be discovered, and thereby increasing the potential for the use of these species in biostratigraphical correlations. *Opis* (*H.*) *triangulata*, living as far north as central California during the early late Maastrichtian, represents the youngest known *Opis* in the world. Tectonic transport resulted in *Opis* (*H.*) *holzana* sp. nov. and *Opis* (*H.*) *vancouverensis* Whiteaves being found as far north as Vancouver Island.

Unlike its tropical water Jurassic predecessors, *Hesperopis* lived in warm temperate waters. It lived in non-turbulent waters where silty muds and fine sands accumulated, most likely, in moderate depths associated with offshore shelfal areas. *Hesperopis* had a vertical commissure and was most likely a sessile, edgewise recliner whose bulky and heavyweight shells lived on, or partially settled, into the soft substrate. The thick-walled shells and strong hinge teeth provided protection from predators, the lateral serrations on the teeth provided resistance to shear forces produced by any currents or waves, and the small internal ligament helped open the heavy valves. The posterior umbonal ridge and corcelet probably served as stabilizers, preventing any currents from disorienting the shells. Through time, *Hesperopis* became more adapted for a recliner life habit by evolving larger shells, broader or more elongate shells and stouter or longer teeth.

The study area '*Opis*' *shastalis* Anderson, 1938 of Aptian age is not an opine. The study area '*Opisoma*' sp. Ludvigsen and Beard (1994, 1997) of Early Jurassic age and '*Opis*' *virginalis* Waring, 1917 of late Palaeocene age are highly questionably identified as opines. Cretaceous and early Eocene 'opines' reported by various workers from south-eastern and eastern United States are either very poorly known, *nomina dubia*, or erroneously identified as opines.

A junior secondary homonym of *Opis trigonalis* (Sowerby) was detected in the literature and is renamed here as *Opis tamurai nom.* nov.

Acknowledgements. We are grateful for the permission given to us to examine the collections at CASG, LACMIP, SDSNH, UCMP and UCR. We thank the members of the Victoria Palaeontology Society, Victoria, Vancouver Island, British Columbia, for loaning us excellent specimens with good locality data from the Nanaimo Group. Dirk Nolf (Institut Royal des Sciences Naturelles de Belgique) and Jon Todd (British Museum of Natural History) tried very hard, but unsuccessfully, to find specimens of the type species of *Opis*, and we sincerely appreciate their efforts. Lindsey T. Groves (Los Angeles County Museum, Malacology Section) and Richard E. Petit, North Myrtle Beach, South Carolina, provided key information regarding some hard-to-find literature. The manuscript benefited by the comments of two anonymous reviewers.

REFERENCES

ACCORSI BENINI, C. 1981. *Opisoma* Stoliczka, 1871. Lamellibranco eterodonte della facies a 'Lithiotis' (Giurassico inf., Liassico). *Bolletino Della Società Paleontologica Italiana*, **20**, 197–228.

ADAMS, H. and ADAMS, A. 1854–1856. *The genera of Recent Mollusca arranged according to their organization*, Vol. 2. John Van Voorst, London, 1–661.

AKERS, R. E. and AKERS, T. J. 2002. Texas Cretaceous bivalves 2, descriptions and illustrations of all named Texas genera and species. *Houston Gem and Mineral Society, Paleontology Section, Texas Paleontology Series, Publication*, **7**, Houston, Texas, 516 pp.

ALDERSON, J. M. 1988. New age assignments for the lower part of the Cretaceous Tuna Canyon Formation, Santa Monica Mountains, California. *Abstracts with Programs of the Geological Society of America*, **20**, 139.

ALENCASTER, G. 1963. Pelicipodos del Jurásico medio del noroeste de Oxaxaca y noreste Guerrero. *Universidad Nacional Autónoma de México, Instituto de Geologia, Paleontologia Mexicana*, **15**, 1–52.

ALMGREN, A. A. 1986. Benthic foraminiferal zonation and correlations of Upper Cretaceous strata of the Great Valley of California – a modification. 137–152. *In* ABBOTT, P. L. (ed.). *Cretaceous stratigraphy western North America*, **46**. Pacific Section SEPM Book, Los Angeles, 239 pp.

ANDERSON, F. M. 1902. Cretaceous deposits of the Pacific coast. *Proceedings of the California Academy of Sciences, Series 3*, **2**, 1–154.

—— 1938. Lower Cretaceous deposits in California and Oregon. *Special Papers of the Geological Society of America*, **16**, 1–339.

—— 1958. Upper Cretaceous of the Pacific Coast. *Memoir of the Geological Society of America*, **71**, 1–378.

—— and HANNA, G. D. 1935. Cretaceous geology of Lower California. *Proceedings of the California Academy of Sciences, Series 4*, **23**, 1–34.

ANONYMOUS 1967. *British Mesozoic fossils, 1967*, Third edition. British Museum (Natural History), London, 207 pp.

BAILEY, E. H. and JONES, D. L. 1973. Preliminary lithostratigraphic map, Colyear Springs Quadrangle, California. *Miscellaneous Field Studies Map of the United States Geological Survey*, **MF-516**.

BERNARD, F. 1895–1897. Note sur le développement et la morphologie de la coquille chez les lamellibranches. *Bulletin de la Société Géologique de France, Series 3*, **23**, 104–154; **24**, 54–82, 416–449; **25**, 559–566.

BIGOT, A. P. D. 1895. Contributions á de la l'étude de la faune Jurassique de Normandie. Sur les *Opis*. *Mémoires de la Société Linnéenne de Normandie*, **18**, 153–191.

BITTNER, A. 1895. Lamellibranchiaten der Alpinen Trias. 1 Theil: Revision der Lamellibranchiaten von St. Cassian. *Geologische Reichsanstalt Abhandlungen*, **18**, 1–235.

BÖHM, G. 1893. *Coelastarte* und *Heteropis*. *Berlichte Naturforschender Gesellschaft zu Freiburg*, **7**, 169–178.

BOSS, K. J. 1982. III. Mollusca. Vol. 1. 945–1166. *In* PARKER, S. P. (ed.). *Synopsis and classification of living organisms.* McGraw-Hill Book Company, New York, 222 pp.

BRUGUIÈRE, J. G. 1789. *Encylopédie méthodique. Histoire naturelle des Vers*, Vol. 1. Panckoucke, Paris, 785 pp.

BUVIGNIER, A. 1843. Sur quelques fossiles des départements de la Meuse et des Ardennes. *Mémoires de la Société Philomathematique du Verdun*, **2**, 225–252.

—— 1852. Description d'une partie des fossiles inédits ou peu connus recueillis dans les terrains du Département de la Meuse. *Statistique géologique, minéralogique, minérallurgique et paléontologique, du Département de la Meuse.* J. B. Bailliére, Paris, 52 pp.

CARTER, R. M. 1967. On the nature and definition of the lunule, escutcheon and corcelet in the Bivalvia. *Proceedings of the Malacological Society of London*, **37**, 243–263.

CHAVAN, A. 1952. Mélanges paléontologiques 3. Distinction et classement des astartidés. *Cahiers Géologiques du Thoiry*, **15**, 123–128.

—— 1969. Superfamily Crassatellacea Férussac, 1822. N562–N573. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part N. Vol. 2 (of 3), Mollusca 6, Bivalvia.* Geological Society of America, Boulder, Colorado and the University of Kansas Press, Lawrence, Kansas, 462 pp.

CLARK, S. G. 1940. Geology of the Covelo District, Mendocino County, California. *Bulletin of the Department of Geological Sciences, University of California Publications*, **25**, 119–142.

COAN, E. V. 1981. *James Graham Cooper, pioneer western naturalist.* University Press of Idaho, Moscow, Idaho, 255 pp.

—— SCOTT, P. V. and BERNARD, F. R. 2000. Bivalve seashells of western North America. Marine bivalve mollusks from arctic Alaska to Baja California. *Santa Barbara Museum of Natural History Monographs Number 2, Studies in Biodiversity*, **2**, 764 pp.

COBBAN, W. A. and KENNEDY, W. J. 1995. Maastrichtian ammonites chiefly from the Prairie Bluff Chalk in Alabama and Mississippi. *Memoir of the Paleontological Society*, **44** (*Journal of Paleontology*, **69**, no. 5 supplement III of III), 40 pp.

COLLIGNON, M. 1949. Recherches sur les faunes Albiennes de Madagascar. Part 1. L'Albien d'Ambarimaninga. *Annales Géologiques du Service des Mines*, **16**, 5–128.

CONRAD, T. A. 1858. Observations on a group of Cretaceous fossil shells, found in Tippah County, Miss., with descriptions of fifty-six new species. *Journal of the Academy of Natural Sciences of Philadelphia, Series 2*, **3**, 323–336.

COOPER, J. G. 1894. Catalogue of Californian fossils, parts 2–5. *Bulletin of the California State Mining Bureau*, **4**, 1–65.

—— 1896. On some new Cretaceous (and Eocene?) Mollusca of California. *Proceedings of the California Academy of Sciences, Series 2*, **6**, 330–337.

COX, L. R. 1969. General features of Bivalvia. N2–N129. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part N. Vol. 2 (of 3), Mollusca 6, Bivalvia.* Geological Society of America, Boulder, Colorado and the University of Kansas Press, Lawrence, Kansas, 952 pp.

—— and ARKELL, W. J. 1948–1950. A survey of the Mollusca of the British Great Oolite Series, primarily a nomenclatorial revision of the monograph by Morris & Lycett (1851–55), Lycett (1863) and Blake (1905–07). *Monograph of the Palaeontolographical Society of London*, 105 pp. + 43 pp. of revised captions.

CRAGIN, F. W. 1893. A contribution to the invertebrate paleontology of the Texas Cretaceous. *Annual Report of the Geological Survey of Texas*, **4**, 139–246.

DARTEVILLE, E. and FRENEIX, S. 1957. Mollusques fossiles du Crétacé de la Côte occidentale d'Afrique du Cameroun à l'Angola. II. Lamellibranches. *Annales du Musée Royal du Congo Belge Tervuren (Belgique), Sciences Géologiques*, **20**, 1–271.

DAWSON, M. K. 1978. The paleontology of the Cabrillo Formation. Unpublished MSc Thesis, San Diego State University, USA, 87 pp.

DEFRANCE, M. J. L. 1825. OKA–OSC. 219–220. *In* LEVRAULT, F. G. (ed.). *Dictionnaire des Sciences Naturelles*, Vol. **36**, Levrault, Strasbourg, 560 pp.

DICKINSON, W. R. and RICH, E. I. 1972. Petrologic intervals and petrofacies in the Great Valley Sequence, Sacramento Valley, California. *Bulletin of the Geological Society of America*, **83**, 3007–3024.

DILLER, J. S. 1898. Description of the Roseburg quadrangle. *Geological Atlas of the U. S. Geological Survey, Folio*, **49**.

DUBAR, G. 1948. La faune domérienne du Djebel Bou-Dahar. *Notes et Mémoires du Service Géologique*, **68**, 1–248.

ELDER, W. P. and SAUL, L. R. 1993. Paleogeographic implications of molluscan assemblages in the Upper Cretaceous (Campanian) Pigeon Point Formation, California. 171–186. *In*

DUNNE, G. and MCDOUGALL, K. (eds). *Mesozoic paleogeography of the western United States-II*, Vol. 71. Pacific Section SEPM Book, Los Angeles, 494 pp.

—— 1996. Taxonomy and biostratigraphy of Coniacian through Maastrichtian *Anchura* (Gastropoda: Aporrhaidae of the North American Pacific slope). *Journal of Paleontology*, **70**, 381–399.

—— and POWELL, C. L. II 1998. Late Cretaceous and Paleogene molluscan fossils of the Gualala block and their paleogeographic implications. 149–168. *In* ELDER, W. P. (ed.). *Geology and tectonics of the Gualala block, northern California*, Vol. 84. Pacific Section SEPM Book, Los Angeles, 222 pp.

FAIRBANKS, H. W. 1893. The validity of the so-called Wallala Beds as a division of the California Cretaceous. *American Journal of Science*, **45**, 473–478.

FARMER, M. A., FITT, W. K. and TRENCH, R. K. 2001. Morphology of the symbiosis between *Corculum cardissa* (Mollusca: Bivalvia) and *Symbiodinium corculorum* (Dinophyceae). *The Biological Bulletin*, **200**, 336–343.

FELDMANN, R. M. 1974. *Hoploparia riddlensis*, a new species of lobstser (Decapoda: Nephropidae) from the Days Creek Formation (Hauterivian, Lower Cretaceous) of Oregon. *Journal of Paleontology*, **48**, 586–593.

FÉRUSSAC, A. E. de 1822. *Tableau Systématiques des Animaux Mollusques Classés en Familles Naturelles*. J. B. Baillière, Paris, 111 pp.

FILKORN, H. F. 2007. Relict of a lost Pacific coast: Late Cretaceous (Campanian) reef fauna from the Black Star Canyon quadrangle, Santa Ana Mountains, southern California. *Abstracts with Programs of the Geological Society of America*, **39**, 417.

FISCHER, P. H. 1880–1887. *Manuel de conchyliologie et de paléontologie conchyliologique, ou histoire naturelle des mollusques vivants et fossils*. Librairie F. Savy, Paris, xxv + 1369 pp.

FÜRSICH, F. T., HEINZE, M. and JAITLY, A. K. 2000. Contributions to the Jurassic of Kachchh, western India. VIII. The bivalve fauna. Part IV. Subclass Heterodonta. *Beringeria*, **27**, 63–146.

GABB, W. M. 1860. Descriptions of new species of American Tertiary and Cretaceous fossils. *Journal of the Academy of Natural Sciences of Philadelphia, Series 2*, **4**, 299–305, 375–406.

—— 1861. *Synopsis of the Mollusca of the Cretaceous Formation, including the geographical and stratigraphical range and synonymy*. Privately published, 201 pp. [Reprinted by American Philosophical Society].

—— 1864. Description of the Cretaceous fossils. *California Geological Survey, Palaeontology*, **1**, 57–243.

—— 1866–1869. Cretaceous and Tertiary fossils. *California Geological Survey, Palaeontology*, **2**, 299 pp.

—— 1876. Notes on American Cretaceous fossils, with descriptions of some new species. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **4**, 276–324.

GARDNER, R. N. and CAMPBELL, H. J. 2002. Middle to Late Jurassic bivalves of the genera *Neocrassina* and *Trigonopis* from New Zealand. *New Zealand Journal of Geology and Geophysics*, **45**, 323–347.

GRADSTEIN, F., OGG, J. and SMITH, A. 2004. *A geologic time scale 2004*. Cambridge University Press, Cambridge, 589 pp.

GROVE, K. 1986. Depositional environments of Upper Cretaceous and lower Tertiary strata near Nacimiento Lake, central California Coast Ranges. 1–16. *In* GROVE, K. and GRAHAM, S. (eds). *Geology of Upper Cretaceous and lower Tertiary rocks near Lake Nacimiento, California*, Vol. 49. Pacific Section SEPM Book, Los Angeles, 63 pp.

HALLAM, A. 1976. Stratigraphic distribution and ecology of European Jurassic bivalves. *Lethaia*, **9**, 245–259.

—— 1977. Jurassic bivalve biogeography. *Paleobiology*, **3**, 58–73.

—— 1981. The end-Triassic bivalve extinction event. *Palaeogeography, palaeoclimatology, Palaeoecology*, **35**, 1–44.

—— 1983. Early and mid-Jurassic molluscan biogeography and the establishment of the central Atlantic seaway. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **43**, 181–193.

HAYAMI, I. 1975. A systematic survey of the Mesozoic Bivalvia from Japan. *Bulletin of the University Museum of the University of Tokyo*, **10**, 1–249.

HILTON, R. P. and ANTUZZI, P. J. 1997. Chico Formation yields clues to Late Cretaceous paleoenvironment in California. *California Geology*, **50**, 136–144.

HOLUB, E. and NEUMAYR, M. 1881. Über einige Fossilien aus der Uitenhage-Formation in Süd-Afrika. *Denschrift der köninglichen Akademie der Wissenschaften Wien*, **44**, 267–276.

IMLAY, R. W. 1941. Jurassic fossils from Arkansas, Louisiana, and eastern Texas. *Journal of Paleontology*, **15**, 256–277.

—— 1960. Ammonites of Early Cretaceous age (Valanginian and Hauterivian) from the Pacific coast states. *Professional Paper of the United States Geological Survey*, **334-F**, 167–228.

—— DOLE, H. M., WELLS, F. G. and PECK, D. 1959. Relations of certain Upper Jurassic and Lower Cretaceous formations, in southwestern Oregon. *Bulletin of the American Association of Petroleum Geologists*, **43**, 2770–2785.

INGERSOLL, R. V. and DICKINSON, W. R. 1990. Great Valley Group (Sequence), Sacramento Valley, California. 183–215. *In* INGERSOLL, R. V. and NILSEN, T. H. (eds). *Sacramento Valley Symposium and guidebook*, Vol. 65. Pacific Section SEPM Book, Los Angeles, 215 pp.

JONES, D. L. and BAILEY, E. H. 1973. Preliminary biostratigraphic map, Colyear Springs Quadrangle, California. *Miscellaneous Field Studies Map of the United States Geological Survey*, MF-517.

—— —— and IMLAY, R. W. 1969. Structural and stratigraphic significance of the *Buchia* zones in the Colyear Springs-Paskenta area, California. *Professional Paper of the United States Geological Survey*, **647-A**, A1–A24.

KATNICK, D. C. and MUSTARD, P. S. 2001. Geology of Denman and Hornby islands, British Columbia. *Geoscience Map of the British Columbia Geological Survey Branch*, **2001–3**.

KAUFFMAN, E. G. 1973. Cretaceous Bivalvia. 353–383. *In* HALLAM, A. (ed.). *Atlas of Palaeobiogeography*. Elsevier Scientific Publishing Company, Amsterdam, 543 pp.

KAWAGUTI, S. 1950. Observations on the heart cockle *Corculum cardissa* (L.) and its associated zooxanthellae. *Pacific Science*, **4**, 43–49.

KEEN, A. M. and BENTSON, H. 1944. Check list of California Tertiary marine Mollusca. *Special Papers of the Geological Society of America*, **56**, 1–280.

KEFERSTEIN, W. 1857. Ueber eininge deutsche devonische Conchiferen aus der Verwandtschaft der Trigoniaceen und Carditaceen. *Deutsche Geologische Gesellschaft, Zeitschrift*, **9**, 148–162.

KENNEDY, M. P. 1975. Geology of the San Diego metropolitan area, California. Section A. Western San Diego metropolitan area. *Bulletin of the California Division of Mines and Geology*, **200**, 1–39.

KEYSERLING, A. G. 1864. *Wissenschaftliche Beobachtung auf einer Reise in das Petschora-Land im Jahre 1843*. Cark Kay, St. Peterbourg, 465 pp., folio atlas of 22 pls.

KIEL, S. 2006. New and little-known gastropods fom the Albian of the Mahajanga basin, northwestern Madagascar. *Journal of Paleontology*, **80**, 455–476.

KILMER, F. H. 1963. Cretaceous and Cenozoic stratigraphy and paleontology, El Rosario area. Unpublished PhD dissertation, University of California, Berkeley, USA, 216 pp.

KIRBY, M. X. and SAUL, L. R. 1995. The Tethyan bivalve *Roudairia* from the Upper Cretaceous of California. *Palaeontology*, **38**, 23–38.

KODAMA, K. P. and WARD, P. D. 2001. Compaction-corrected paleomagnetic paleolatitudes for Late Cretaceous rudists along the Cretaceous California margin: Evidence for less than 1,500 km of post-Late Cretaceous offset for Baja British Columbia. *Bulletin of the Geological Society of America*, **113**, 1171–1178.

LAMARCK, J. B. P. A. 1818–1819. *Histoire Naturelle des Animaux sans Vertèbres*. Vol. 6, Longmans, Paris, 343 pp.

LEE, C. W. 1983. Bivalve mounds and reefs of the central High Atlas, Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **43**, 153–168.

LINNAEUS, C. 1758. *Systema Naturae per Regna Tria Naturae, Editio Decima Reformata, Tome 1. Regnum Animale*. Laurentii Salvii, Stockholm, 824 pp.

LIU, C. 1995. Jurassic bivalve paleobiogeography of the proto-Atlantic and the applications of multivariate analysis methods to paleobiogeography. *Beringeria*, **16**, 3–123.

LUDVIGSEN, R. and BEARD, G. 1994. *West coast fossils – a guide to the ancient life of Vancouver Island*. Whitecap Books, Vancouver, 194 pp.

—— 1997. *West coast fossils – a guide to the ancient life of Vancouver Island*. Harbour Publishing, Madeira Park, 216 pp.

LYCETT, J. 1857. *The Cotteswold Hills*. Piper, Stephenson, and Spence, London, 170 pp.

—— 1863. Supplementary mongraph on the Mollusca from the Stonesfield Slate, Great Oolite, Forest Marble, and Cornbash. *Palaeontolographical Society*, London, 129 pp.

MARLIÈRE, R. 1939. La transgression Albienne et Cénomanienne dans le Hainaut (études paléontologiques et stratigraphiques). *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, **89**, 1–401.

MATSUMOTO, T. 1959*a*. Upper Cretaceous ammonites of California, Part 1. *Memoirs of the Faculty of Science, Kyushu University, Series D, Geology*, **8**, 91–171.

—— 1959*b*. Upper Cretaceous ammonites of California, Part 2. *Memoirs of the Faculty of Science, Kyushu University, Series D, Geology*, **1**, 1–172.

—— 1960. Upper Cretaceous ammonites of California. Part 3. *Memoirs of the Faculty of Science, Kyushu University, Series D, Geology, Special Volume*, **2**, 1–204.

MEEK, F. B. 1864. Check list of the invertebrate fossils of North America. Cretaceous and Jurassic. *Smithsonian Miscellaneous Collections*, **177**, 1–40.

MOUTA, V. and BORGÈS, A. 1926. Sur le Crètacé du littoral de l'Angola (districts de Benguela et Mossamedes). *Boletim da Agência Geral das Colónias Lisboa*, **14–15**, 43 pp.

MURPHY, M. A., RODDA, P. U. and MORTON, D. M. 1969. Geology of the Ono Quadrangle, Shasta and Tehama counties, California. *Bulletin of the California Division of Mines and Geology*, **192**, 28 pp.

NEUMAYR, M. 1884. Zur Morphologie des Bivalvenschlosses. *Bayerische Akademie der Wissenschaften, Mathematisch-Physikalische Klasse, Abhandlungen, Sitzungsberichte, München*, **88**, 385–418.

NILSEN, T. H. and ABBOTT, P. L. 1981. Paleogeography and sedimentology of Upper Cretaceous turbidites, San Diego, California. *Bulletin of the American Association of Petroleum Geologists*, **65**, 1256–1284.

ORBIGNY, A. C. V. D. d' 1844. *Paléontologie Française. Terrains Crétacés. Volume 3, Lamellibranchs*. Arthus Bertrand, Paris, 807 pp.

—— 1850. *Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnés. Part 2*, Victor Masson, Paris, 428 pp.

PALMER, K. V. W. and BRANN, D. C. 1965. Catalogue of the Paleocene and Eocene Mollusca of the southern and eastern United States. Part 1. Pelecypoda, Amphineura, Pteropoda, Scaphopoda, and Cephalopoda. *Bulletins of American Paleontology*, **48**, 1–466.

PAYNE, M. B. 1962. Preliminary geologic map of the type Panoche Group (Upper Cretaceous) and overlying Moreno and Tertiary strata on the west side of the San Joaquin Valley. Plate 13. *In* BOWEN, O. E., JR (ed.). *Geologic guide to the gas and oil fields of northern California*, Vol. 181. Bulletin of the California Division of Mines and Geology, San Francisco, 412 pp.

PERRILLIAT, M. C. 1989. Mollusca. Bivalvia. 301–370. *In* PERRILLIAT, M. C. and CARREÑO, A. G. (eds). *Fosiles Tipo Mexicanos*, Universidad Nacional Autonoma de Mexico, Instituto de Geologia, Mexico, D. F., 531 pp.

—— 2002. Catálogo de Ejemplares Tipo de Invertebrados y Vertebrados Fósiles en la Colección de Paleontología del Instituto de Geología, UNAM, México. Parte 2. Universidad Nacional Autonoma de Mexico, Instituto de Geologia, Mexico, D. F., 106 pp.

POPENOE, W. P. 1942. Upper Cretaceous formations and faunas of southern California. *Bulletin of the American Association of Petroleum Geologists*, **26**, 162–187.

—— 1973. Southern California Cretaceous formations and faunas with especial reference to the Simi Hills and Santa Monica Mountains. 15–29. *In* FRITSCHE, A. E. (ed.). *Cretaceous stratigraphy of the Santa Monica Mountains and Simi Hills, Southern California*. Pacific Section SEPM, Geological Guidebook, Los Angeles, 93 pp.

—— and FINDLAY, W. A. 1933. Transposed hinge structures in lamellibranchs. *Transactions of the San Diego Society of Natural History*, **7**, 299–318.

—— IMLAY, R. W. and MURPHY, M. A. 1960. Correlation of the Cretaceous formations of the Pacific coast (United States and northwestern Mexico). *Bulletin of the Geological Society of America*, **71**, 1491–1540.

QUENSTEDT, F. A. 1856–1858. *Der Jura*. Laupp und Siebeck, Tübingen, 842 pp.

RICCARDI, A. C. 1988. The Cretaceous System of southern South America. *Memoir of the Geological Society of America*, **168**, i–v + 1–161.

RICHARDS, H. G. 1958. Pelecypoda. 59–226. *In The Cretaceous fossils of New Jersey. Part 1. Porifera, Coelenterata, Annelida, Echinoidea, Brachiopoda and Pelecypoda*. Paleontology Series, New Jersey Bureau of Geology and Topography, Trenton, 1–266.

RÖDING, P. F. 1798. *Museum Boltenianum*. Hamburg, J. C., Trappii, vii + 109 pp.

SAUL, L. R. 1982. Water depth indications from Late Cretaceous molluscs, Santa Ana Mountains, California. 69–76. *In* BOTTJER, D. J., COLBURN, I. P. and COOPER, J. D. (eds). *Late Cretaceous depositional environments and paleogeography, Santa Ana Mountains, southern California*. Pacific Section SEPM, Field Trip Volume and Guidebook, Los Angeles, 121 pp.

—— 1983. *Turritella* zonation across the Cretaceous-Tertiary bounday, California. *University of California Publications Geological Sciences*, **125**, i–x + 1–165.

—— 1986. Pacific west coast Cretaceous molluscan faunas: time and aspect of changes. 131–136. *In* ABBOTT, P. L. (ed.). *Cretaceous Stratigraphy of Western North America*, Vol. 46. Pacific Section SEPM, Book, Los Angeles, 233 pp.

—— 1989. California Late Cretaceous donaciform bivalves. *The Veliger*, **32**, 188–208.

—— and POPENOE, W. P. 1992. Pacific slope Cretaceous bivalves of the genus *Calva*. *Natural History Museum Contributions in Science*, **433**, 1–68.

—— and SQUIRES, R. L. 2008. Volutoderminae (Gastropoda: Volutidae) of Coniacian through Maastrichtian age from the North American Pacific slope. *Journal of Paleontology*, **82**, 213–237.

SEIDERS, V. M. 1989. Geologic map of the Burnett Peak Quadrangle, Monterey and San Luis Obispo counties, California. *Quadrangle Map Series of the United States Geological Survey*, **GQ-1658**.

SEILACHER, A. 1984. Constructional morphology of bivalves: Evolutionary pathways in primary versus secondarly soft-bottom dwellers. *Palaeontology*, **27**, 207–237.

SHA, J. 2002. Hispanic Corridor formed as early as Hettangian: On the basis of bivalve fossils. *Chinese Science Bulletin*, **47**, 414–417.

SMITH, A. G., SMITH, D. G. and FUNNELL, B. M. 1994. *Atlas of Mesozoic and Cenozoic coastlines*. Cambridge University Press, Cambridge, England, ix + 99 pp.

SMITH, J. P. 1900. The development and phylogeny of *Placenticeras*. *Proceedings of the California Academy of Sciences, Series 3*, **1**, 180–240.

SOHL, N. F. 1987. Cretaceous gastropods: Contrasts between Tethys and the temperate provinces. *Journal of Paleontology*, **61**, 1085–1111.

SOWERBY, J. 1818. *The mineral conchology of Great Britain*. 41–98. Published by the author, London, Vol. 3, 186 pp.

SOWERBY, J. de C. 1823. *The mineral conchology of Great Britain*. 65–138. Published by the author, London, Vol. 5, 171 pp.

SPATH, L. F. 1922. On the Senonian ammonite faunas of Pondoland. *Transactions of the Royal Society of South Africa*, **10**, 113–147.

SQUIRES, R. L. and SAUL, L. R. 2001. New Late Cretaceous gastropods from the Pacific slope of North America. *Journal of Paleontology*, **75**, 46–65.

—— 2003*a*. Additions to Late Cretaceous shallow-marine gastropods from California. *The Veliger*, **46**, 145–161.

—— 2003*b*. New Late Cretaceous (Campanian and Maastrichtian) marine gastropods from California. *Journal of Paleontology*, **77**, 50–63.

—— 2003*c*. New Cretaceous cerithiform gastropods from the Pacific slope of North America. *Journal of Paleontology*, **77**, 442–453.

—— 2004*a*. The pseudomelaniid gastropod *Paosia* from the marine Cretaceous of the Pacific slope of North America and a review of the age and paleobiogeography of the genus. *Journal of Paleontology*, **78**, 484–500.

—— 2004*b*. Cretaceous corbulid bivalves of the Pacific slope of North America. *The Veliger*, **47**, 103–129.

—— 2005. New Late Cretaceous (Santonian and Campanian) gastropods from California and Baja California, Mexico. *The Nautilus*, **119**, 133–148.

—— 2006. Cretaceous *Acila* (*Truncacila*) (Bivalvia. Nuculidae) from the Pacific slope of North America. *The Veliger*, **48**, 83–104.

STANLEY, S. M. 1970. Relation of shell form to life habits in the Bivalvia (Mollusca). *Memoir of the Geological Society of America*, **125**, 296 pp.

STANTON, T. W. 1895. Contributions to the Cretaceous paleontology of the Pacific Coast, the fauna of the Knoxville beds. *Bulletin of the United States Geological Survey*, **133**, 1–132.

STEPHENSON, L. W. 1952. Larger invertebrate fossils of the Woodbine Formation (Cenomanian) of Texas. *Professional Paper of the United States Geological Survey*, **242**, 1–226.

—— 1954. Additions to the fauna of the Raritan Formation (Cenomanian) of New Jersey. *United States Geological Survey, Professional Paper*, **264B**, iii + 25–43.

STOLICZKA, F. 1871. The Pelecypoda. *Memoirs of the Geological Survey of India, Palaeontologia Indica, Series 6*, Vol. 3. Cretaceous Fauna of Southern India, Calcutta, 537 pp.

SUNDARAM, R., HENDERSON, R. A., AYYASAMI, K. and STILWELL, J. D. 2001. A lithostratigraphic revision and palaeoenvironmental assessment of the Cretaceous System exposed in the onshore Cauvery Basin, southern India. *Cretaceous Research*, **22**, 743–762.

SUNDBERG, F. A. 1979. Upper Cretaceous macro-fossils of San Diego. 173–176. *In* ABBOTT, P. L. (ed.). *Geological excursions in the southern California area*. San Diego State

University, Department of Geological Sciences Guidebook, San Diego, 217 pp.

TALIAFERRO, N. L. 1944. Cretaceous and Paleocene of Santa Lucia Range, California. *Bulletin of the American Association of Petroleum Geologists*, **28**, 449–521.

TAMURA, M. 1959. Some pelecypods from the Upper Jurassic Sakamoto formation in central Kyushu, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, **35**, 53–65.

TASHIRO, M. 1992. *Illustrated book of fossils, bivalve fossils in Mesozoic (Cretaceous) Period in Japan.* Shirono Printing Co., Ltd. Kumamoto, Kyushu, 307 pp.

TURNER, H. W. 1894. The rocks of the Sierra Nevada. *United States Geological Survey, 14th Annual Report*, **2**, 435–495.

UEDA, Y. 1963. Two new species of *Opis* from the Cretaceous of Japan. *Transactions and Proceedings of the Palaentological Society of Japan, New Series*, **50**, 70–80.

WALLEY, C. D. 1983. A revision of the Lower Cretaceous stratigraphy of Lebanon. *Geologische Rundschau*, **72**, 377–388.

WARING, C. A. 1917. Stratigraphic and faunal relations of the Martinez to the Chico and Tejon of Southern California. *Proceedings of the California Academy of Sciences, Series 4*, **7**, 41–124.

WEAVER, C. W. 1944. Geology of the Cretaceous (Gualala Group) and Tertiary formations along the Pacifc Coast between Point Arena and Fort Ross, California. *University of Washington Publications in Geology*, **6**, 1–29.

WENTWORTH, C. M., JONES, D. L. and BRABB, E. E. 1998. Geology and regional correlation of the Cretaceous and Paleogene rocks of the Gualala block, California. 3–26. *In* ELDER, W. P. (ed.). *Geology and tectonics of the Gualala block, northern California*, Vol. 84. Pacific Section, SEPM Book, Los Angeles, 222 pp.

WHITE, C. A. 1885. New Cretaceous fossils from California. *Bulletin of the United States Geological Survey*, **22**, 25 pp.

WHITEAVES, J. F. 1879. On the fossils of the Cretaceous rocks of Vancouver and adjacent islands in the Strait of Georgia. *Geological Survey of Canada, Mesozoic Fossils*, **1**, 93–190.

WHITFIELD, R. P. 1886. Brachiopoda and Lamellibranchiata of the Raritan clays and Greensand marls of New Jersey. *Monograph of the United States Geological Survey*, **9** [= *Geological Survey of New Jersey series*, Volume **1**], 269 pp.

—— 1891. Observations on some Cretaceous fossils from the Beyút district of Syria, in the collection of the American Museum of Natural History, with descriptions of some new species. *Bulletin of the American Museum of Natural History*, **3**, 381–441.

WRIGHT, C. W., CALLOMAN, J. H. and HOWARTH, M. K. 1996. Cretaceous Ammonidea. *In* KAESLER, R. L. (ed.). *Treatise on invertebrate paleontology. Part L. Mollusca 4, revised.* Geological Society of America, Boulder, Colorado and University of Kansas Press, Lawrence, Kansas. 362 pp.

YANCEY, T. and WILSON, M. 2006. Alatoform edgewise reclining bivalves appear in the Triassic. 79–80. *In* MALCHUS, N. and PONS, J. M. (eds). *Scientific Program and Abstracts.* International Congress on Bivalvia, Universitat Autònoma de Barcelona, Bellaterra, Catalunya, Spain, 82 pp.

YERKES, R. F. and CAMPBELL, R. H. 1979. Stratigraphic nomenclature of the central Santa Monica Mountains, Los Angeles County, California. *Bulletin of the United States Geological Survey*, **1457-E**, E1–E31.

APPENDIX

Localities Cited

All quadrangle maps are United States Geological Survey maps.

Locality 1. 'White House Site,' intertidal bench 400 m north of Buckley Bay/Denman Island ferry terminal, west central shoreline of Denman Island, off east coast of Vancouver Island, British Columbia. Collectors: R. Graham and G. Beard, *c.* 2001. Cedar District Formation, upper part. Age: Late middle – early Late Campanian.

A-426 UCMP. Punta Baja [= Punta Abajo], north-western Baja California, Mexico. Collectors: T. Barrera and M. Santillan, 1928. Punta Baja Fm. Age: Middle Upper Campanian.

3384 SDSNH. Elevation 75 m, silty shell-hash mudstone discovered during mass grading (locality has since been graded away) of the Carlsbad Research Center and College Boulevard extension, San Luis Rey Quadrangle, 7.5 min, 1968 (photorevised 1975), Carlsbad, San Diego County, California. Collector: B. O. Riney, 16 January 1987. Point Loma Formation. Age: Latest Campanian – possibly early Maastrichtian.

3402 SDSNH. Elevation 49 m, at Carlsbad Research Center, in unweathered blue-gray siltstone in temporary exposure (locality has since been graded away), made during grading for the College Boulevard extension. San Luis Rey Quadrangle, 1968 (photorevised 1975), northern San Diego County, California. Collector: B. O. Riney, 23 April 1987. Point Loma Formation. Age: Latest Campanian – possibly early Maastrichtian.

3403 SDSNH. Carlsbad Research Center, San Diego County, Carlsbad, California. Collector: B. O. Riney, 26 April 1987. Point Loma Formation. Age: Latest Campanian – possibly early Maastrichtian.

A-3435 UCMP. Negro Fork of Nacimiento River near the northern boundary of the map, near the line between Sections 23 and 24, T22S, R5E, approximately 14 km north-east of Cape San Martin, Cape Martin Quadrangle (15-min, photoinspected 1972), Santa Lucia Range, central Coast Ranges, Santa Lucia Range, Monterey County, California. Collectors: H. G. Schenck, N. L. Taliaferro and B. L. Clark, June 13, 1940. El Piojo Formation? Age: Latest Campanian or earliest Maastrichtian.

4818 LACMIP. Steeply dipping massive light-brown sandstone with interbeds of shale and conglomerate, east side of road 2 km north on Palisades Drive from its junction with Sunset Blvd., lower Santa Ynez Canyon, Topanga Quadrangle, 7.5 min, 1952 (photorevised 1981), Santa Monica Mountains, Los Angeles County, California. Tuna Canyon Formation, upper part. Collector: E. Wilson, 1977. Age: Approximately middle Campanian.

6026 LACMIP. Upper Black Star Canyon, section 8.9 km upstream from junction of Santiago and Silverado Canyon roads, west side of canyon, 4 km south of Hidden Ranch; section comprises 175 m of slope from road down to stream bed, SE 1/4, SW 1/4, Sec. 19, T4S, R7W, Black Star Canyon Quadrangle, 7.5 min, 1949, Santa Ana Mountains, Orange County, California. Collectors: M. Webster and D. Williams, January–May 1965. Ladd Formation, Baker Canyon Sandstone Member. Age: Late Turonian.

8173 LACMIP. Elevation 557 m, upper Aliso Creek and at divide. Trabuco Oaks, Santa Ana Mountains, Orange County, California. Collector: C. R. Stauffer, 1 January 1945. Ladd Formation, uppermost Holz Shale Member. Age: Late Early Campanian.

10084 LACMIP [= CIT 1170]. North side Silverado Canyon, western edge of Holz Ranch, in shale about 15 m below basal Williams Fm., Schulz Member, 785 m south, 594 m west of north-east corner of Sec. 7, T5S, R7W, Black Star Canyon Quadrangle, 7.5 min, 1949, Santa Ana Mountains, Orange County, California. Collector: W. P. Popenoe, 17 May 1935. Ladd Formation, uppermost Holz Shale Member. Age: Late Early Campanian.

10098 LACMIP [= CIT 302]. North of Holz Ranch house, near spring on north side of Silverado Canyon, Black Star Canyon Quadrangle, 7.5 min, 1949, Santa Ana Mountains, Orange County, California. Ladd Formation, upper Baker Canyon Member. Age: Late Turonian.

10135 LACMIP [= LACMIP 24235 and CIT1290]. South side of prominent hill west of spring, about 457 m north of Holz Ranch house, Silverado Canyon, 792 m south, 61 m west of north-east corner of Sec. 7, T5S, R7W, Black Star Canyon Quadrangle, 7.5 min, 1949, Santa Ana Mountains, Orange County, California. Collectors: W. P. Popenoe, Henshal, Wells, Church and Fiedler, 6 April and 6 June 1937. Ladd Formation, Baker Canyon Member, near top. Age: Late Turonian.

10685 LACMIP [= CIT 1573]. Banos Creek, 975 m north, 549 m west of south-east corner of Sec. 12, T11S, R9E, Ortigalita Peak Quadrangle, 7.5 min, 1969 (photorevised 1984), Merced County, California. Collectors: Adams and W. P. Popenoe, 1942. [Locality now along edge of Los Banos Reservoir]. Moreno Formation, informal Quinto B member. Age: Late Early – early Late Maastrichtian.

10718 LACMIP [= CIT 1063]. North of Silverado Canyon, about 15 m below Schulz Member in Holz, about 701 m south and 594 m west of north-east corner of Sec. 7, T5S, R7W, Black Star Canyon Quadrangle, 7.5 min, 1949, Santa Ana Mountains, Orange County, California. Collector: W. P. Popenoe, 20 May 1934. Ladd Formation, uppermost Holz Shale Member. Age: Late Early Campanian.

10724 LACMIP [= CIT 1055]. Shale beds above conglomerate lens, crest of spur 1097 m north 25° east of juncture of Trabuco Canyon and El Toro-Santiago Creek roads, 2742 m south 18° east of dam in Harding Canyon, north-west corner of SE 1/4 of Sec. 33, T5S, R7W, Santiago Peak Quadrangle, 7.5 min, 1973, Santa Ana Mountains, Orange County, California. Collector: W. P. Popenoe, 10 October 1934. Ladd Formation, uppermost Holz Shale Member. Age: Late Early Campanian.

12245. LACMIP Single clast in conglomerate, on west bank of Nacimiento River, midway between Pebblestone Shut-In and Grizzly Bend at an elevation of about 229 m, 762 m south and 114 m east of north-west corner of Sec. 19, T25S, R9E, Pebblestone Shut-In Quadrangle, 7.5-min, 1959, western Lake Nacimiento, Santa Lucia Range, central Coast Ranges, San Luis Obispo County, California. Collector: V. M. Seiders, 1985. El Piojo Formation? Age: Probably early Maastrichtian.

17871 LACMIP. From spoil piles of Treelake Village subdivision, Granite Bay, approximately 1.02 km north of Placer-Sacramento County line, near 280-feet contour, SE 1/4, NE 1/4 of Sec. 16, T10N, R7E, Folsom Quadrangle, 1954, Placer County, California. Collector: Richard Hilton, 1996–1997. Chico Formation. Age: Early Campanian.

20215. LACMIP Rivas Canyon, Santa Monica Mountains, Los Angeles County, southern California. Collector: unknown. Upper Tuna Canyon Formation. Collector?: C. H. Crickmay. Age: Early? Late Campanian (*Metaplacenticeras pacificum* Zone).

22323 LACMIP. South end of low hill north of gully, about 792 m north of Holz Ranch house, 640 m south, 119 m west of north-east corner of Sec. 7, T5S, R7W, Black Star Canyon Quadrangle, Santa Ana Mountains, Orange County, California. Collector: W. P. Popenoe, 1946. Ladd Formation, sandstone at top of Baker Canyon Member. Age: Turonian.

22329 LACMIP. Outcrop on north side of small gully near head, at a point approximately 914 m north 40° west of the Holz Ranch House, NE 1/4 of Sec. 7, T5S, R7W, Black Star Canyon Quadrangle, 7.5 min, 1967. Collector: W. P. Popenoe, 5 May 1946. Ladd Formation, uppermost Holz Shale Member. Age: Late Early Campanian.

22661 LACMIP [= CIT 1573]. Conglomerate reef outcropping on north-west slope of Los Banos Creek, about 975 m north, 549 m west of south-east corner of Sec. 12, T11S, R9E, Ortigalita Peak Quadrangle, Merced County, California. Collector: Popenoe, Lian, McLain, Susuki, 28 April 1950. Moreno Formation, informal 'Quinto B' member. Age: Late Early – early Late Maastrichtian.

24190 LACMIP [= CIT 1162]. Crest of small north-south-trending spur north of Harding Canyon, about 762 m north 26° west of mouth of Harding Canyon, 1128 m east of south-west corner of Sec. 20, T5S, R7W, El Toro Quadrangle, Santa Ana Mountains, Orange County, California. Collector: W. P. Popenoe, 7 June 1934. Ladd Formation, lower upper Holz Shale Member. Age: Early Campanian.

24654 LACMIP. Bank of small southward-flowing tributary to Dry Creek, south of highway U.S. 299 and approximately 0.8 km nearly due west of Bella Vista, 620 m west and 396 m north of south-east corner of Sec. 8, T32N, R3W, Millville Quadrangle, 1953, Shasta County, California. Collector: W. P. Popenoe, 31 May 1961. Redding Formation, top of Frazier Silstone Member. Age: Middle Turonian.

26342 LACMIP. West side of San Joaquin Valley, conglomerate 'reef' bed cropping out on north-west slope of Los Banos Creek, about 975 m north, 549 m west of south-east corner of Sec. 12, T11S, R9E, Ortigalita Peak Quadrangle, Merced County, California. Collectors: R. B. Stewart and W. P. Popenoe, 1944. Moreno Formation, informal Quinto B member. Age: Late Early–early Late Maastrichtian. LACMIP

26500. Ridge midway between Garzas Creek and Mustang Creek, 297 m south and 305 m east of north-west corner of Sec. 29, T8S, R8E, Howard Ranch Quadrangle, 7.5 min, 1953 (photorevised 1971), Merced County, California. Collector: F. A. Schilling, before 7 February 1959. Panoche Group, Television Sandstone. Age: Early Late Campanian.

27199 LACMIP. Between Fremont Canyon and Oak Flat along a south fork of Fremont Canyon at about 567 m elevation, 107 m north and 317 m east of south-west corner of Sec. 7, T4S, R7W, Black Star Canyon Quadrangle, northern Santa Ana Mountains, Orange County, California. Collectors: W. P. Popenoe and J. E. Schoelhamer, 28 November 1951. Williams Formation, Schulz Member. Age: Early Middle Campanian.

27200 LACMIP. Between Fremont Canyon and Oak Flat along a south fork of Fremont Canyon at about 542 m elevation, 183 m north, 305 m east of south-west corner of Sec. 7, T4S, R7W, Black Star Canyon Quadrangle, northern Santa Ana Mountains, Orange County, California. Collectors: W. P. Popenoe and J. E. Schoelhamer, 28 November 1951. Williams Formation, Schulz Member. Age: Early Middle Campanian.

29118 CASG. Probably equivalent to locality 26500.

29120 CASG. On a knoll 91 m east and 549 m south of north-west corner of Sec. 19, T10S, R9E, Volta Quadrangle, 7.5 min, 1960 (photorevised 1971), Merced County, California. Collector: Unknown. Uhalde Formation, upper part. Age: Latest Campanian or earliest Maastrichtian.

103851 CGS. Moto 'X' track at Lower shale Quarry site on Doumont Road just west of Nanaimo, Vancouver Island, British Columbia (approximate coordinates 49°11′45″N, 124°06′00″W). Haslam Formation, upper part. Age: Latest Santonian. Collector: R. Graham, *c.* 1999.