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CRETACEOUS OPINE BIVALVES FROM THE PACIFIC SLOPE OF NORTH AMERICA AND PALAEOBIOGEOGRAPHY OF SUBFAMILY OPINAE CHAVAN, 1969

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Abstract: Opines constitute a small subfamily of Mesozoic astartid bivalves that lived mostly in the Tethys Sea region. They first appeared in western Europe during the Middle Triassic, became most widespread during the Jurassic and had their first undoubted appearance in the New World during the Late Jurassic. Their Pacific slope of North America record is studied in detail for the first time. The earliest of the Pacific slope opines is *Opis californica* Stanton of Early Cretaceous (Hauterivian or Barremian) age. The other six opine species in the study area are of Late Cretaceous age (collectively Middle Turonian – early Late Maastrichtian), have hinges bearing two strong cardinal teeth in each valve, and are placed in the new subgenus *Hesperopsis*, which is the first astartid to have a partially internal ligament. These six species comprise two morphological lineages inferred to have evolved from *O.* (*H.*) *popenoei* sp. nov. The '*holzana*' lineage includes *O.* (*H.*) *holzana* sp. nov. and *O.* (*H.*) *rosarioensis* Anderson and Hanna. The '*anae*' lineage includes *O.* (*H.*) *anae* sp. nov., *O.* (*H.*) *vancouverensis* Whiteaves and *O.* (*H.*) *triangulata* (Cooper). *Hesperopis* lived in warm temperate waters in offshore shelfal areas. It had a vertical commissure and probably lived as an edgewise recliner. Through time, the species of both lineages became larger and either broader or more elongate. Neither *Opis shastalis* Anderson, of Aptian age, nor *Opis virginalis* Waring, of late Palaeocene age, are opines. A junior secondary homonym of *Opis trigonalis* (Sowerby) was detected and is renamed here as *Opis tamurai* nom nov.

Key words: Bivalvia, astartids, opines, *Hesperopis*, Cretaceous, palaeoecology, palaeogeography.

OPINE bivalves constitute a small subfamily of Mesozoic Astartidae placed by Chavan (1969) in the Opinae. They have distinctly carinated trigoniform shells with narrow umbones and incurved, high to very high beaks. Their hinges are short laterally, high to very high vertically, and bear notably elongate cardinal teeth. Anterior and posterior lateral teeth are obsolete. In spite of being widespread and distinctive, they have not received detailed systematic studies, other than preliminary work by Bigot (1895) and Chavan (1969), both of which focused on European species. The present article aims at establishing the first detailed, documentable, morphological and stratigraphical study of opines from the Pacific slope of North America, specifically from Vancouver Island, British Columbia southward to the north-western part of Baja California (Text-fig. 1). Seven species are recognized. One belongs to *Opis*, and the other six species, three of which are new, belong to a new subgenus, *Hesperopis*. Their latitudinal and temporal distributions are shown in Text-figures 1–2, respectively. Ancillary aims of the study are to (1) offer comments about the possible life habits of *Hesperopis*, (2) review the palaeoclimate of the study area during the Cretaceous and (3) present the first global overview of the geological history of opines. North American species erroneously or very questionably identified as opines are discussed. A junior secondary homonym was detected and renamed.

MATERIAL AND METHODS

A total of 253 specimens were studied. Material included type specimens of previously described species, additional collections from their type localities and specimens from previously unreported localities which were collected mainly by the late W. P. Popenoe. For most of the localities reported in this study, it was necessary to integrate current biostratigraphical information to determine proper stage position.

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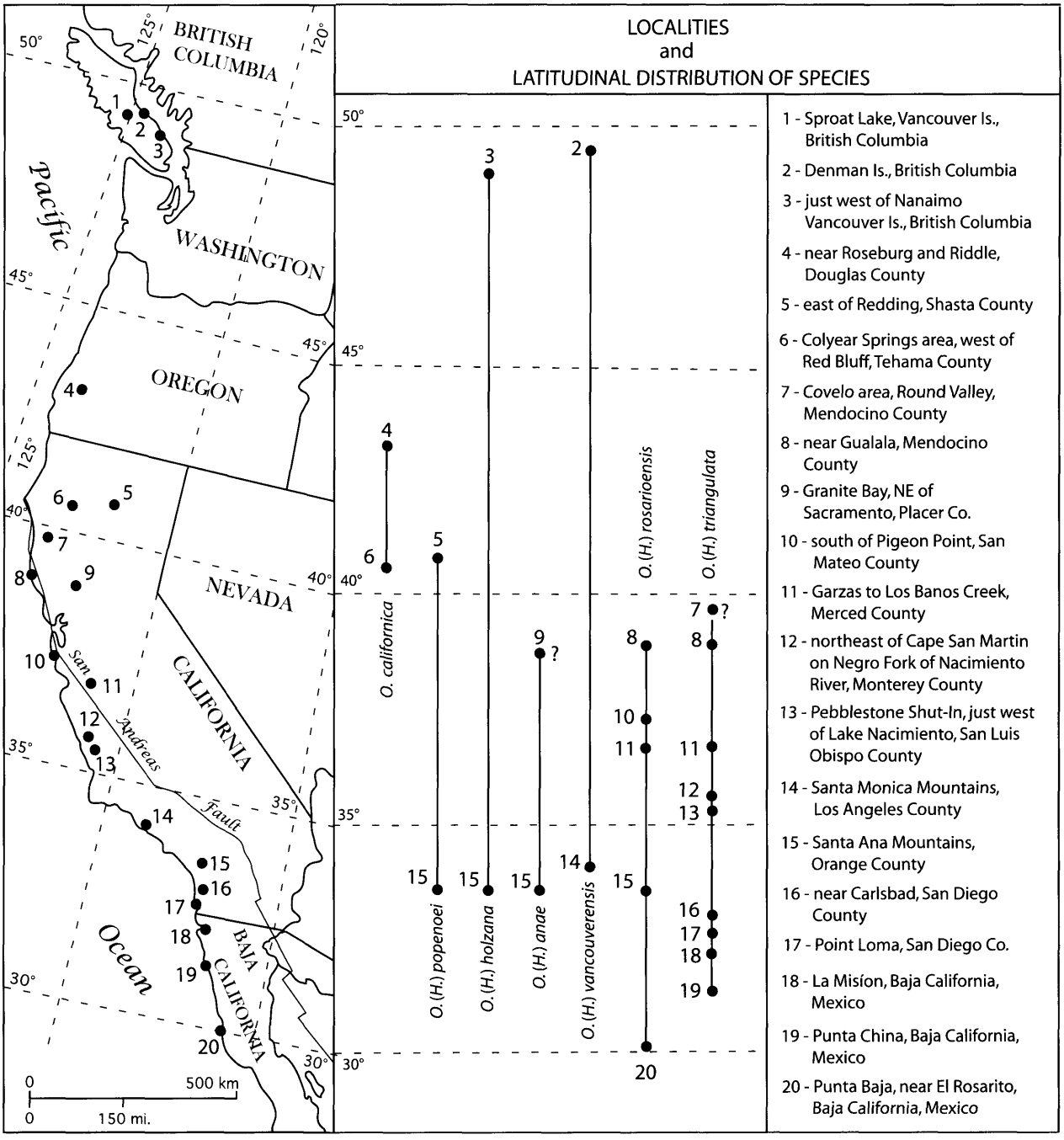
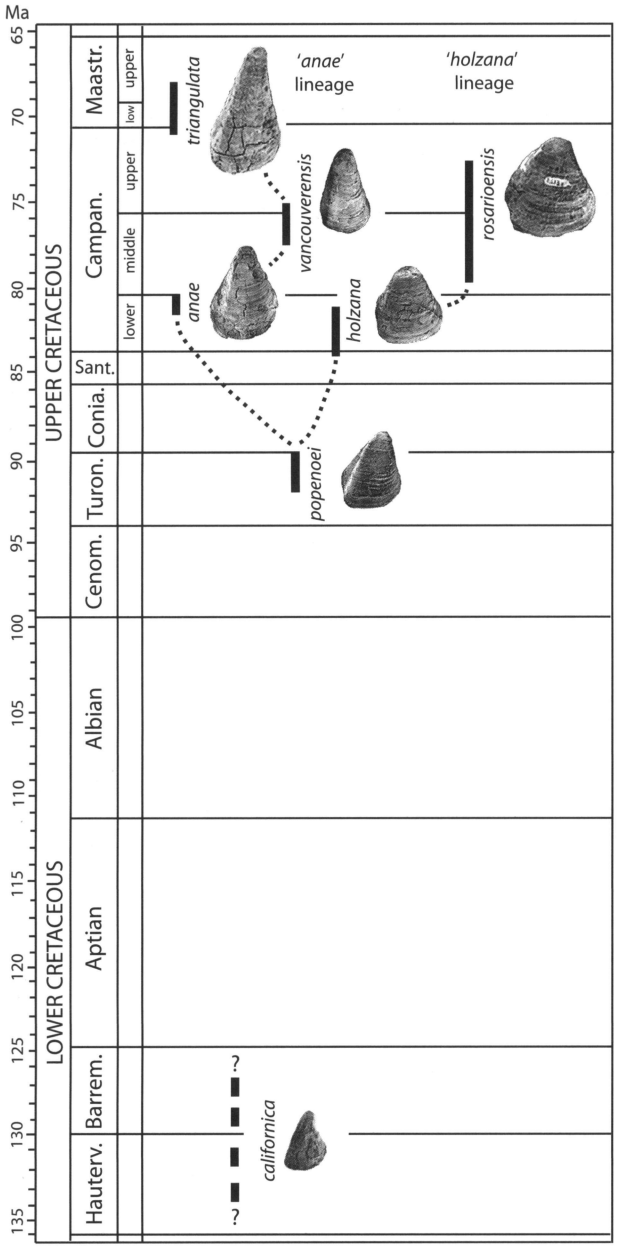


TEXT-FIG. 1. Localities map and latitudinal distribution of study area opine species. A question mark by a locality indicates that the specific identity of specimen(s) is uncertain.

Knowledge of the hinge and dentition of opines are critical in distinguishing genera, subgenera and species; therefore, it was necessary to excavate the hinges of many of the studied specimens from well-cemented matrix. This time-consuming and meticulous procedure, which, in large part, involved the use of a high-speed drill and diamond-coated grinding wheels, was carried out over a span of many years by the junior author.

STRATIGRAPHY

Current summaries of the geological details of most of the formations and members containing study area opines can be found in the following papers (listed in ascending chronostratigraphic order): Frazier Siltstone, Melton Sandstone and Bear Creek Sandstone members of the Redding Formation (Squires and Saul 2003*a*); upper



TEXT-FIG. 2. Geological ranges of the studied species. All the species belong to *Opis* (*Hesperopis*) subgen. nov., except *Opis californica*. Dotted lines connecting the species of *Hesperopis* indicate inferred lineages based on morphological similarity. Ages of stage boundaries from Gradstein *et al.* (2004).

Baker Canyon Member of the Ladd Formation (Squires and Saul 2003*c*); Holz Shale Member of the Ladd Formation (Saul 1982); Haslam Formation (i.e. see under 'Nanaimo Group) (Squires and Saul 2004*a*); Schulz Member of the Williams Formation (Filkorn 2007); Pigeon Point Formation (Squires and Saul 2003*b*); upper Cedar District Formation (Squires and Saul 2001; Squires and Saul 2006); Punta Baja Formation (Squires and Saul 2005); Gualala Formation (Squires and Saul 2004*b*); Point Loma Formation (Squires and Saul 2001) and 'Garzas Sand' and 'Quinto Silt' members of the Moreno Formation (Squires and Saul 2003*b*).

A few formations containing study area opines are discussed in the following, as they need a current summary of their geological details. The areas where the opines were collected are listed and plotted on Text-figure 1, and these area designations (e.g. Area 7) are used throughout the article.

Stony Creek Formation

This formation crops out in the north-western part of Sacramento Valley, northern California (Area 6). After a complicated history of changes in names, this formation is now known as the Stony Creek Formation of Dickinson and Rich (1972). It is the basal unit of the Great Valley Sequence, a 3750-m thick clastic wedge of forearc basin turbidites consisting mainly of dark grey to black mudstone containing lenses of sandstone and conglomerate. Based mainly on species of the bivalve *Buchia* [= *Aucella*], the formation ranges in age from the latest Jurassic (Tithonian) to the middle Early Cretaceous (Barremian) (Ingersoll and Dickinson 1990).

Tuna Canyon Formation

This formation crops out in the east central Santa Monica Mountains, southern California (Area 14), in an area of densely brush-covered, steep slopes that are complexly folded and faulted. The complex structure perhaps accounts for the differing estimates of thickness, ranging from 800 m near Tuna Canyon to over 3000 m in Rivas Canyon, approximately seven km to the east. The formation consists mostly of turbidite sandstone interbedded with siltstone and conglomerate and is disconformably overlain by lower Palaeocene deposits (Yerkes and Campbell 1979). Turonian ammonites have been recovered from the base of the formation (Alderson 1988) and early to late Campanian ammonites from upper beds (Saul 1983).

Chico Formation at Granite Bay

During recent grading for the 'Granite Bay' housing-tract subdivision in Placer County, east of Sacramento, northern California (Area 9), a section of the Chico Formation containing numerous molluscs and other fossils was found (Hilton and Antuzzi 1997). The bivalves and gastropods, however, are mainly partial casts with some

weathered bits of shell adhering, thereby making precise, specific identifications difficult. According to Hilton and Antuzzi (1997), the southern periphery of the 'Granite Bay' site coincides with Gabb's (1864, 1869) 'Texas Flat' locality, later called 'Rock Corral' by Turner (1894), but Gabb's fossils were said to have come from a mine shaft, at 12 m below the surface. Based on the work by Hilton and Antuzzi (1997), the section at Granite Bay consists of a basal conglomerate, of unknown thickness, overlain by 40 m of offshore marine fine-grained siliciclastics containing, in the upper part, a bouldery turbidite layer. They estimated that the lower part of the Granite Bay section is early Campanian age and the upper part is late Campanian. It is more likely that one of ammonites that they figured (Hilton and Antuzzi 1997, photo 3) is not a *Nowakites*. That specimen shows periodic constrictions throughout, and such constrictions continuing onto the phragmocone are characteristic of *Canadoceras* Spath, 1922. According to Matsumoto (1959*b*), several Campanian species of *Canadoceras* are present elsewhere in the Chico Formation. Furthermore, *Nowakites* Spath, 1922 is indicative of Coniacian or Santonian age and is not found in North America (Matsumoto 1959*b*; Wright *et al.* 1996).

Television sandstone

Although this sandstone remains an informal stratigraphical unit in the Panoche Group, it was mapped by Payne (1962) for a distance of approximately 129 km in the Panoche Hills along the west side of the San Joaquin Valley, central California (Area 11). It is a thin (up to 30 m thick) but persistent silty-to-fine–grained sandstone. Matsumoto (1960, p. 43, figs 10–11), who depicted the Television sandstone as 'unit KP-T' on his geological map and stratigraphical column, reported that beds directly below this sandstone contained Campanian ammonites, whereas beds above the sandstone contained Maastrichtian ammonites. Almgren (1986, table 2), using benthic foraminifera, correlated the Television sandstone to the lower part of the upper Campanian.

Cabrillo Formation

This formation, which is the uppermost unit of the Rosario Group, was mapped by Kennedy (1975) as conformable on the Point Loma Formation but with a more limited area of outcrop. Type sections for both formations are on Point Loma, San Diego, southern California (Area 17). Outcrops of Cabrillo Formation are in coastal bluffs and consist of massive medium-grained sandstone and cross-bedded cobble conglomerate. The formation consists of submarine-fan turbidites (Dawson 1978; Nilsen and Abbott 1981). Whereas the Point Loma Formation has provided a diverse fossil molluscan fauna of late Campanian to early Maastrichtian age (see Squires and Saul 2001; Saul and Squires 2008), the Cabrillo Formation has, with the exception of fossils from re-deposited boulders of Point Loma Formation, yielded a meagere fauna consisting almost entirely of the donacid *Adelodonax altus* (Gabb, 1864) of Maastrichtian age (Saul 1989). Based on the work by Matsumoto (1959*a*, p. 130) and Cobban and Kennedy (1995), specimens of the ammonite *Baculites lomaensis* Anderson, 1958 from the Point Loma Formation on Point Loma are also suggestive that both it and the overlying Cabrillo Formation are of Maastrichtian age. A fauna from a boulder collected by Dawson (1978) from the Cabrillo Formation is similar to the fauna collected from the Point Loma Formation near the Carlsbad Airport (Area 16) in northern San Diego County.

El Piojo Formation west of Lake Nacimiento

Taliaferro (1944) used the name 'Asuncion Formation' for Upper Cretaceous rocks along the Nacimiento River drainage, Santa Lucia Range, central Coast Ranges, central California (Areas 12–13). Kodama and Ward (2001) used the name 'Ascunción Formation' for these rocks, and Grove (1986) referred to them as unnamed 'Upper Cretaceous strata.' Seiders (1989), mapping the Nacimiento vicinity in greater detail than Taliaferro, subdivided Taliaferro's Asuncion and named the part near Pebblestone Shut-In, western Lake Nacimiento (Area 13), as the El Piojo Formation. It consists mainly of proximal submarine-fan turbidites, and the most common rock type is very thick-bedded, pebbly to cobbly, graded sandstone containing few fossils. Calcareous nannofossils, agglutinated foraminifera and pollen from some of the mudstones in the formation are indicative of Maastrichtian age (Seiders, 1989). It is unclear whether this name can be used for an outcrop on Negro Fork of the Nacimiento River (Area 12), approximately 32 km north-west of Pebblestone Shut-In, although Seiders (1989) stated that this formation is exposed discontinuously from west of Lake Nacimiento westward towards the Cape San Martin area.

SYSTEMATIC PALAEONTOLOGY

Institutional abbreviations. CASG, California Academy of Sciences, Geology Section, San Francisco; CIT, California Institute of Technology (collections now housed at LACMIP); CSG, Geological Survey of Canada, Ottawa; CSMB, California State Mining Bureau (collection now mainly housed at UCMP); LACMIP,

Los Angeles County Museum of Natural History, Invertebrate Paleontology Section; SDSNH, San Diego Society of Natural History; RBCM, Royal British Columbia Museum, Victoria; UCLA, University of California, Los Angeles (collections now housed at LACMIP); UCMP, University of California, Berkeley, Museum of Paleontology; UCR, University of California, Riverside; USGS, United States Geological Survey, Menlo Park, California (collection now housed at UCMP); USNM, United States National Museum, Washington, DC; VIPM, Vancouver Island Paleontological Museum, Qualicum Beach.

Terms used

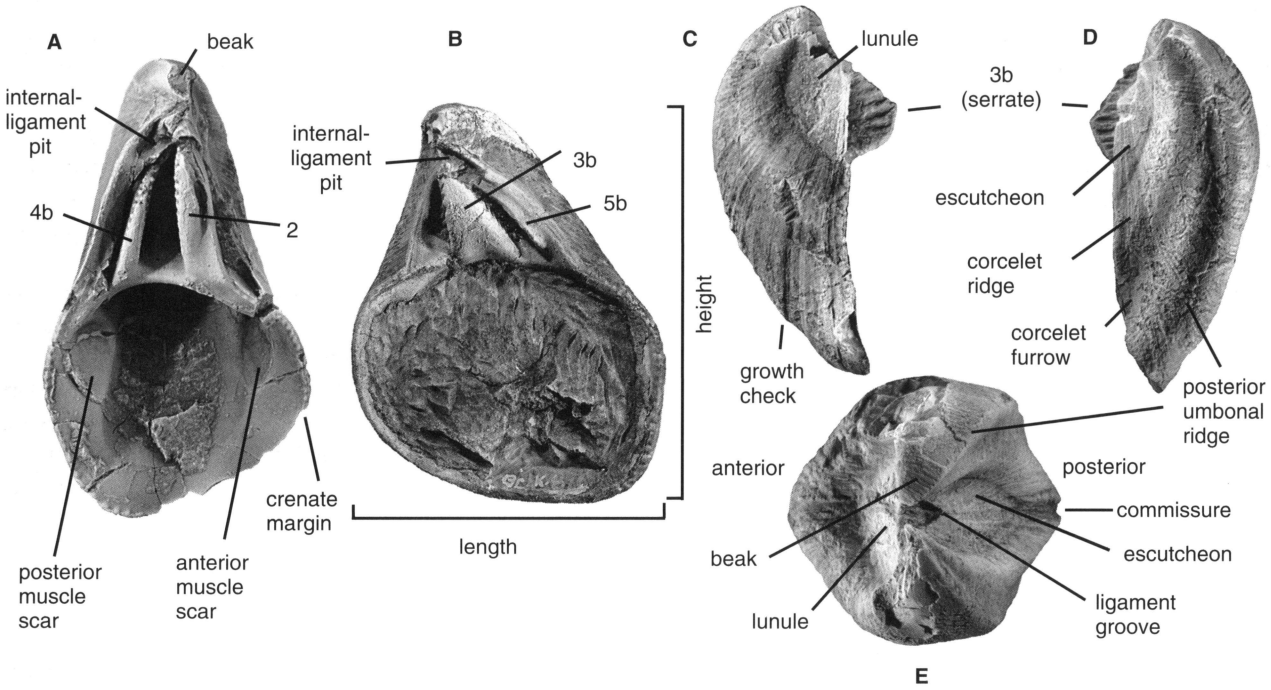
Most of the morphological terms used here are defined by Cox (1969), and key morphological terms are illustrated in Text-figure 3. The terms 'escutcheon' and 'corcelet' follow the usage of Carter (1967), who did not treat them as synonyms. As Carter (1967, p. 261) explained, the escutcheon corresponds to the track of the dentition on the external valve surfaces during growth, and the corcelet is a further differentiated area posterior to the umbones, outside of the escutcheon (Text-fig. 3).

The ligament in most opines is external and is located in a groove just beneath the beaks. In *Hesperopis*, the ligament has two parts: an external part and a submerged, internal part. In this report, the external part is referred to as the 'ligament groove,' and the internal part as the 'internal-ligament pit.' The notation for heterodont hinge tooth is derived from the system by Bernard (1895–1897) and implemented by him and fellow paleontologist E. Munier-Chalmas. Their system is summarized in Cox (1969, pp. N53–N56).

Illustrations of the specimens in the plates and text figures are arranged such that left valves precede right valves, in both exterior and interior views; all of which are arranged in increasing size. Additional views include double-valved specimens and views of single valves showing lunule and/or escutcheon/corcelet.

Phylum MOLLUSCA Linnaeus, 1758
Class BIVALVIA Linnaeus, 1758
Subclass HETERODONTA Neumayr, 1884
Order VENEROIDA H. Adams and A. Adams, 1856
Superfamily CRASSATELLOIDEA Férussac, 1822
Family ASTARTIDAE d'Orbigny, 1844

Remarks. Chavan (1969) placed family Astartidae in superfamily Crassatelloidea, but Coan *et al.* (2000) placed Astartidae in superfamily Astartoidea d'Orbigny, 1844. According to Coan *et al.* (2000, pp. 8–9), Astartidae is one of the groups of bivalves that has highest priority for a modern analysis, ideally with cladistic methodologies. Chavan (1969) reported that this family ranges from



TEXT-FIG. 3. Illustrated key of morphologic terms; all specimens ×1. A, *Opis* (*Hesperopis*) *vancouverensis*, hypotype, RBCM.EH2008.017.0001, left-valve interior. B, *O.* (*H.*) *holzana* sp. nov., paratype, RBCM RBCM.EH2008.016.0001, right-valve interior. C–D, *O.* (*H.*) *popenoei* sp. nov., paratype, LACMIP 13517, right valve. C, lunule view. D, escutcheon/corcelet view. E, ~~holotype~~ PARATYPE, LACMIP ~~9912~~ 13521, dorsal view.

Devonian–Recent, with questionable occurrence in the Middle Ordovician. Coan *et al.* (2000) reported that it ranges from the Early Devonian–Recent. Chavan (1969) recognized three subfamilies of astartids: Astartinae d'Orbigny, 1844; Eriphylinae Chavan, 1952; and Opinae Chavan, 1969. Gardner and Campbell (2002) erected the subfamily Trigonopinae.

Subfamily OPINAE Chavan, 1969

1952 Opisinae Chavan, p. 126.

Remarks. Chavan (1952, 1969) recognized seven genera in Opinae: *Prosocelus* Keferstein, 1857; *Opis* Defrance, 1825, with three subgenera *Opis*, *Pachyopis* Bigot, 1895 and *Trigonopis* Fischer, 1887; *Coelopis* Fischer, 1887, with two subgenera *Coelopis* and *Cryptocoelopis* Bittner, 1895; *Heteropis* Böhm, 1893; *Opisoma* Stoliczka, 1871; *Trigonastarte* Bigot, 1895; and *Seebachia* Holub and Neumayr, 1881. Several of these taxa are not Opinae and are discussed in the following paragraphs.

Prosocoelus, which is known only from the Devonian (Chavan 1969), belongs elsewhere based on its very oblique and very elongate cardinals, very small lunule and lack of the following: high beaks, sharp posterior umbonal ridge and well-developed posterior area.

Trigonopis was raised to genus level and placed in subfamily Trigonopinae, along with genus *Trigonastarte*, by Gardner and Campbell (2002) on the basis of mainly hinge characters of well-preserved specimens from Upper Jurassic (Kimmeridgian) strata of northern New Zealand. Gardner and Campbell (2002) reported, furthermore, that unlike opines, the anterior and posterior lateral teeth are functional in *Trigonopis*.

A new name for *Opis* (*Trigonopis*) *trigonalis* Tamura, 1959, which is a junior secondary homonym of *Astarte trigonalis* J. de C. Sowerby, 1823, is *Trigonopis tamurai nom.* nov. Both species are from the Jurassic. Sowerby's species is of Middle Jurassic (Bajocian) age from Dorset, England and western France (Anonymous 1967, pl. 15, figs 6, 7). Chavan (1969) moved Sowerby's species to *Trigonastarte trigonalis* (J. de C. Sowerby). *Opis* (*Trigonopis*) *trigonalis* Tamura, 1959 is of Late Jurassic age from Japan.

Heteropis is a genus based upon transposed hinges. It is comprised of only *H. carinata* (Quenstedt, 1858) and *H. raulinea* (Buvignier, 1852). According to Chavan (1969), both are of Late Jurassic age, from France and Germany, respectively. Illustrations in Chavan (1969, p. N573, fig. E72, 1b–1c) show a left valve of *H. raulinea* with a right-valve cardinal 3b, and a right valve of *H. carinata* with a left-valve cardinal 2. The latter illustration also shows a sinused pallial line, which is a rare morphological feature among opines. *Heteropis* also has anterior laterals partly developed, and future work might show that this genus is not an opine.

Seebachia of Early Cretaceous age was considered by Fürsich *et al.* (2000) to be better placed in the astartines on the basis of hinge characters and lack, in some species, of both an opine trigonal outline and a sharp posterior umbonal ridge.

With the removal of *Prosocelus*, *Seebachia*, *Trigonopis* and *Trigonastarte*, as well as possibly *Heteropis* from subfamily Opinae, opines are represented by *Coleopis* (*Coelopis*), *Coelopsis* (*Cryptocoelopis*), *Opisoma*, *Opis* (*Opis*), *Opis* (*Pachyopis*) and *Opis* (*Hesperopis*) subgen. nov. The type species of these opine genera/subgenera are the following: *Coelopis* (*Coelopis*) *lunulata* (J. Sowerby, 1818); *Coelopis* (*Cryptocoelopis*) *locularis* (Bittner, 1895); *Opisoma paradoxa* Buvignier, 1843; *Opis* (*Opis*) *cardissoides* (Lamarck, 1819); *Opis* (*Pachyopis*) *ponderosa* [based on a quotation by Eudes-Deslongchamps *in* Bigot (1895)]; and *Opis* (*Hesperopis*) *triangulata* (Cooper, 1894).

Opines can be distinguished from the other three subfamilies of astartids by having obsolete lateral teeth, as well as commonly having a carinated shell, high-to-very high and incurved beaks, and less pronounced commarginal sculpture. To this, we add the possible presence of a well-defined (but small) internal-ligament pit, which is present in the study area species of *Opis* (*Hesperopis*). Progressively through time, this pit encroaches upon cardinal 4b of the left valve and 5b of the right valve. Other opines do not have this small internal-ligament pit.

Ligamental areas of various opines have interesting diversity but are not adequately illustrated. *Coelopis* (*Coelopis*) *lunulata* (J. Sowerby, 1818) has a ligament of moderate length and low nymphs extending posteriorward from beneath the beaks. *Opis (Pachyopis) cordiformis* Lycett, 1857 has a longer ligament and lower nymphs. *Opisoma*, as illustrated by Buvignier (1852) and copied by Chavan (1969), appears to have high, relatively short external nymphs, but, as illustrated by Accorsi Benini (1981), *Opisoma* has a very elongate, very narrowly triangular ligament area paralleling posterior cardinals and extending, in some species, posteriorward of the teeth.

Opisoma is morphologically noticeably different from the other opines. The description provided by Stoliczka (1871, p. 276) for his genus *Opisoma* applies much better to his southern Indian species '*O.*' *geinitziana* than it does to the European species *Cardium paradoxa* Buvignier, 1843, which Stoliczka designated as the type species of *Opisoma*. Accorsi Benini (1981) noted that all subsequent authors dealing with Stoliczka's definition of *Opisoma* have altered his original diagnosis. Items being questioned are ligament position, left/right-valve designation, hinge formula and adductor-scar insertions. According to Ac-

corsi Benini (1981), *Opisoma* belongs to Opinae, and she reported that *Opisoma* has prosogyrous beaks, three cardinal teeth in both right and left valves [i.e. Chavan (1969) said 6b is appressed to the valve margin], a strong anteromedian carina and an unusual cardiiform shape. She reported also that the left and right valves of *Opisoma* are reversed in Dubar (1948) and in Chavan (1969) and that they incorrectly placed the ligament on the lunule. According to Accorsi Benini (1981), the captions for Chavan's (1969, p. N573, fig. E72, 4a–c) illustrations of the hinge are in error; figure E72, 4a–4b are right valves and 4c is a left valve. His description of *Opisoma* as having two teeth on the left valve and three on the right is, however, correct according to Accosi Benini, except for some species that have three cardinals in each valve (e.g. *O. menchikoffi* Dubar, 1948). *Opisoma* has a posteriorly-to-anteriorly very compressed shape, and Yancey and Wilson (2006) referred to *Opisoma*'s shape as being alatoform. This unusual shape strongly resembles that of the modern cardiid genus *Corculum* Röding, 1798.

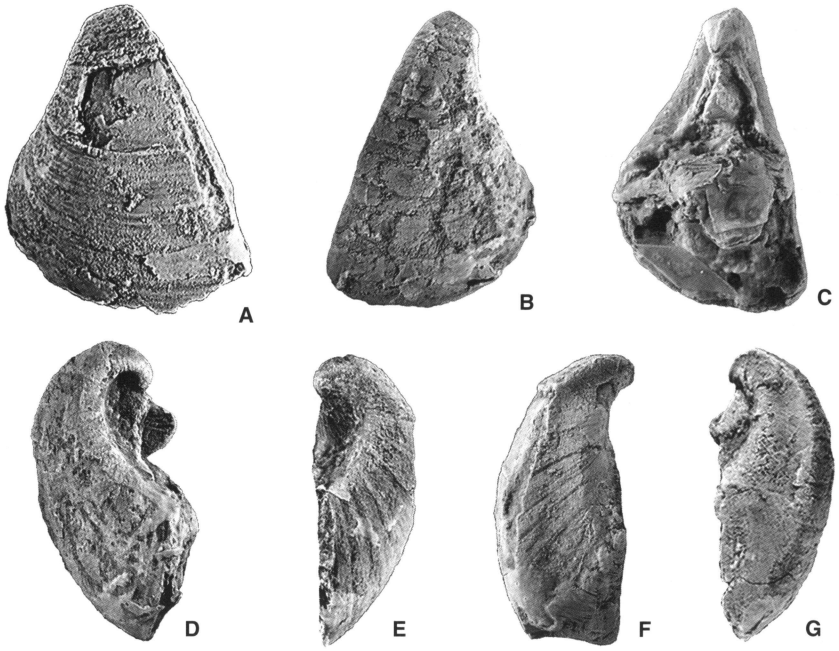
Our review of the literature revealed that *Opis sensu lato* is the taxonomic category used by authors for approximately 90 per cent of the reported opine species (approximately 120 named species, two-thirds of which were named before 1900). The names *Coelopis*, *Opisoma* and *Trigonopis* have been used in some cases, whereas the other available names are mainly used only by Chavan (1969). Supraspecific validity of the names collected from the literature is questionable in many cases, because the hinge characters are not known. In some cases, the type specimens are steinkerns. D'Orbigny (1850) named approximately 30 opine species (all of which he placed in genus *Opis*), but according to Cox and Arkell (1948–1950, p. 29) his names should be ignored because of poor characterization. In their opinion, his names come close to being *nomina nuda*. It is very likely that western European opine species have been overnamed and are in much need of clarification. To further complicate matters, opines can resemble certain arcticids (e.g. *Veniella* Stoliczka, 1871), certain inoceramids that have a noticeable curled-over beak (e.g. *Volviceramus* Stoliczka, 1871), and possibly certain trigoniids (e.g. *Trigonia* Bruguière, 1789).

In the present state of description and depiction of opine genera, subgenera and species, it is very difficult to propose evolutionary relationships among them. Before these relationships can be determined, it will be necessary for workers to re-evalutate their local opine taxa. This will involve procuring hard-to-find type specimens, making new collections in some cases, redefining the morphological aspects of the taxa, accurately identifying the taxa and documenting their stratigraphical distribution. The scope of that type of research is well beyond this present work, which deals with the details of only the study area opines.

Genus OPIS *sensu lato* Defrance, 1825

Type species. Trigonia cardissoides Lamarck, 1819, by monotypy, Cenomanian, Belgium (from Bigot 1895).

Remarks. Bigot (1895) indicated that *Opis* was erected by Defrance (1825) for a species described by Lamarck



TEXT-FIG. 4. *Opis californica* Stanton, 1895; from near Stephenson's, Cold Fork of Cottonwood Creek, Tehama Co., California. All ×1. Figs A, E–F. paralectotype, USNM 23055b, left valve. A, exterior. E, lunule view. F, escutcheon/corcelet view. B–D, G, lectotype, USNM 23055a, right valve. B, exterior. C, interior. D, lunule view. G, escutcheon/corcelet view.

(1819) under the name *Trigonia cardissoides*. Bigot (1895, p. 157) provided a synonymy for *Opis cardissoides* (Lamarck) and figured (pl. 9, figs 22, 22a–c) the specimen Defrance had used when describing the genus *Opis*. The specimen was found in the Defrance collection stored at the Faculty of Science of Caen. Three of the five illustrations of *Opis cardissoides* in the Treatise (Chavan 1969, fig. E71, 2b–d) are line drawings derived from more understandable photographs in Bigot (1895, pl. 9, figs 22a–22c) of different views of the same left valve. Treatise figures of some of Chavan's line drawings are mislabelled. His figure E71, 2b is a left valve, and his figure E71, 2d is posterior view (i.e. escutcheon/corselet view). The other two views of *O. cardissoides* in the Treatise (Chavan 1969, fig. E71, 2a and 2e) are based on specimens not illustrated by Bigot.

The Pacific slope opine species are externally similar to *Opis*. The hinge of the geologically oldest Pacific slope Cretaceous opine species, *Opis californica*, is poorly known; therefore, the species can only be generally assigned to genus *Opis*. The other six Pacific slope species are assigned to a new subgenus *Hesperopis*.

Opis californica Stanton, 1895
Text-figure 4

1895 *Opis californica* Stanton, pp. 58–59, pl. 7, figs 1–4.
1938 *Opis californica* Stanton; Anderson, p. 120 (unfig.).

Types. USNM lectotype 23055a (= Stanton's figs 1–3); USNM paralectotype 23055b (= Stanton's fig. 4); both types herein designated.

Type locality. Stanton (1895, p. 59) recorded the type locality of *O. californica* as being one km north-west of Stephenson Place, on Cold Fork of Cottonwood Creek, Colyear Springs area, west of Red Bluff, Tehama County, northern California (Area 6). He believed that the beds at the type locality were almost along strike with a *Buchia crassicollis* bed that crops out at Stephenson Place. *Buchia crassicollis* (Keyserling, 1864) would normally indicate *O. californica* as Valanginian in age, but works by Bailey and Jones (1973), Jones and Bailey (1973) and Jones *et al.* (1969) have shown that the area is complexly faulted, that there are no *Buchia* beds one km northwest of Stephenson Place and that the only beds containing *O. californica* in this area are either Hauterivian or Barremian in age. They reported an age range because of a lack of ammonites that would discriminate between the two ages. Stanton (1895) assigned the type locality to the upper part of the 'Knoxville beds,' but these beds are now known as the Stony Creek Formation.

Diagnosis. Small-sized and narrow *Opis*. Posterior umbonal ridge abruptly angulate, causing posterior third of shell to be scarcely visible, or not visible, in plan view. Corcelet flattish. Cardinal 3b equant.

Description. Shell size: up to 35 mm in height. Equivalved, inequilateral, inflated, triangular in plan view and cordate in profile. Beaks high, narrow and incurved. Umbones high, narrow to very narrow. Posterior umbonal ridge sharply angulate, causing posterior third of shell to be scarcely visible, or not visible, in plan view. Anterior and ventral margins regularly curved from lunule to end of angulation and form 80 degree angle with posterior margin. Corcelet furrow and corcelet ridge very weak to flattish. Lunule cordate, large and very deep, with narrowly rounded border. Escutcheon poorly differentiated, similar to lunule, but smaller and shallower. Surface marked by fine lines of growth and more distant, irregular, very closely spaced commarginal ribs. Left-valve hinge with two cardinals: 2 and 4b, both elongate and 2 fused to lunular shell margin. Right-valve hinge with one cardinal: 3b triangular, equant, serrated and larger but less elongate than left-valve cardinals.

Remarks. Stanton's (1895) figured specimens are small and similar to small specimens of *O.* (*H.*) *triangulata*, but in Stanton's illustrations of *O. californica* in plan view, his species has narrower umbones, a straighter posterior angulation and weaker but much less regular commarginal ribs than does *O.* (*H.*) *triangulata*. Stanton commented on variation in valve length of his species and figured a broad left valve (Stanton, 1895, figs 1–3) and a narrow right valve (Stanton 1895, figs 4–6), which he said is narrower than any of the other specimens. Although Stanton characterized his species as of medium size, the largest of his specimens (height 35 mm in height) is smaller than the average size of the other species in this present article. Although the hinge is very poorly preserved on the type specimens, Stanton's description of the hinge would seem to place his species in the typical subgenus. More specimens are needed to resolve the issue.

An *Opis* sp. was reported by Stanton (1895, p. 22) from a locality on Cow Creek, near its junction with the south fork of Umpqua River '...just below the bridge at Riddle and in the first low ridge east of the creek, a short distance above the town...' in Douglas County, south-western Oregon. Imlay (1960, p. 170), on the basis of ammonites, assigned the strata at the bridge to the middle Hauterivian. These strata belong to the Days Creek Formation (Imlay *et al.* 1959; Popenoe *et al.* 1960, chart 10e). Feldmann (1974) assigned the Cow Creek beds to the upper member of the Days Creek Formation. Stanton (1895) did not provide voucher specimens, and we were unable to confirm his report. Future work might show that it is another record of *Opis californica*.

Diller (1898, p. 2) reported some fossils identified by Stanton as *Opis californica* from a limestone lentil in the Myrtle Formation on Roberts Creek, south-east of Roseburg, south-western Oregon. Popenoe *et al.* (1960, p. 1531) commented that, based on ammonites, this particular lentil is of middle Portlandian (Late Jurassic) age. They also suggested, however, that the collections from this limestone

lentil are not in place and might have been derived from other strata. More work is needed to resolve the issue.

Although Anderson (1938, p. 120) did not figure any specimens of *Opis californica*, he based his comments on its type specimens, which were examined during the course of this present investigation.

Stratigraphical range. Lower Cretaceous (Hauterivian or Barremian).

Distribution. Stony Creek Formation on the tributary to Cold Fork of Cottonwood Creek, in the vicinity of Stephenson Place, Colyear Spings Quadrangle, west of Red Bluff, west side of Sacramento Valley, Tehama County, northern California (Area 6); probably in Day Creek Formation near Riddle, Douglas County, south-western Oregon (Area 4).

Subgenus HESPEROPIS subgen. nov.

Derivation of name. The new subgenus is a combination of *hesper*, Greek, meaning western and *Opis*, Greek, in reference to a nymph of the Greek goddess *Artemis*.

Type species. Corbula triangulata Cooper, 1894, late Campanian to early late Maastrichtian, California.

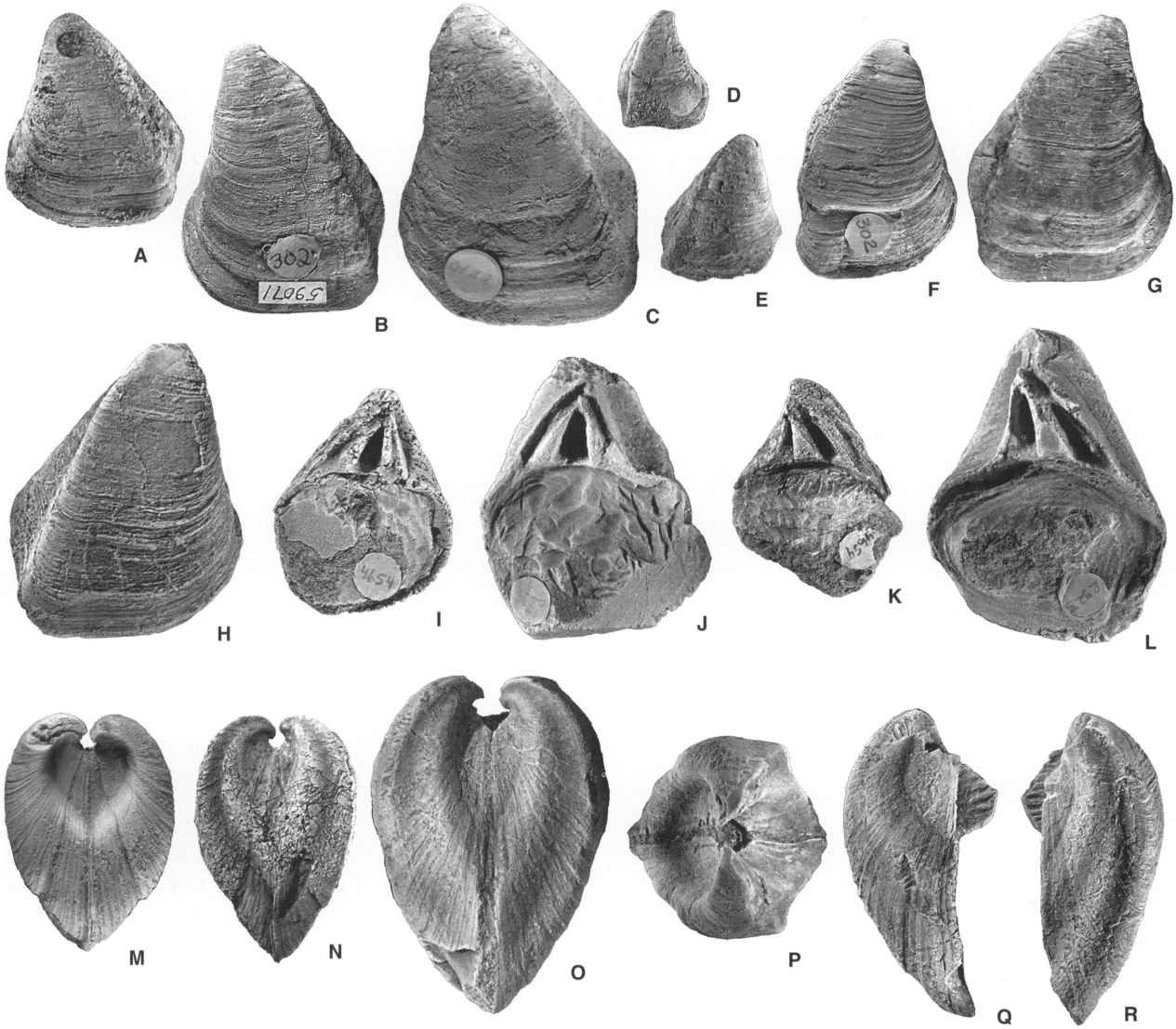
Other species. Listed in ascending stratigraphic order: *Opis* (*Hesperopis*) *popenoei* sp. nov.; *O.* (*H.*) *holzana* sp. nov.; *O.* (*H.*) *anae* sp. nov.; *O.* (*H.*) *rosarioensis* Anderson and Hanna, 1935; and *O.* (*H.*) *vancouverensis* Whiteaves, 1879.

Diagnosis. Shell moderately small to large sized, narrowly or broadly trigonal. Beaks high to very high. Posterior umbonal ridge weak to strong. Corcelet usually weak. Lunule cordiform and large. Commarginal ribbing absent to moderately strong. Hinge high to very high with two strong cardinal teeth in each valve. Ligament external beneath beaks and ventrally sunken as 'shoehorn'-shaped internal-ligament pit.

Description. Shell of moderately small to large size (up to 79 mm in height and 46.8 mm in length, same specimen); walls usually thick. Equivalved, inequilateral (higher than long), inflated, narrow or broad, trigonal to narrowly trigonal in plan view and cordate in profile. Corcelet side of shell posteriorly truncate; lunule side posteriorly rounded. Beaks high to very high, prosogryrous and can be strongly incurved. Umbones narrow or broad. Posterior umbonal ridge usually prominent, weak to strong. Corcelet furrow and ridge weak to strong. Lunule large, wide, cordiform and usually deeply sunken. Escutcheon weakly to moderately weakly delineated. Commarginal sculpture near beaks closely and uniformly spaced; rest of shell can be smoothish or bear commarginal rounded ribs of variable strength and spacing, with growth checks ranging from weak to very strong. Hinge high to very high. Left valve with two cardinals: 2 elongate and laterally serrate facing 3b; 4b stronger than 2 and serrate facing 3b and 5b. Right valve with two cardinals: 3b high, trigonal, usually narrow (but can be equant), moderately long to very long, with both sides serrate; 5b elongate, thin, appressed to margin and serrate facing 4b. Ligament elongate, in depression, external beneath beaks, more deeply submerged and covered ventrally in off-axis 'shoehorn'-shaped internal-ligament pit, extending from beneath beak to dorsal end of teeth 4b and 5b. Inner valve margins can be crenulate. Growth checks (i. e. environmentally controlled) can be present.

Remarks. Hesperopis resembles *Opis* (*Opis*) but differs in having large size, two cardinals in each valve (i.e. left valve 2 and 4b; right valve 3b with 5b appressed to margin), and in having an elongate, ventrally submerged, partially internal ligament that encroaches upon the dorsal ends of 4b and 5b. Chavan (1969) included *Pachyopis* Bigot, 1895 and *Trigonopis* Fischer, 1887 as subgenera of *Opis*. *Pachyopis* is more ventrally (rather than posteroventally) elongate, has a more oval outline, has a less strongly developed carina, and a shallower lunule than *Hesperopis*. In *Pachyopis*, furthermore, cardinal 2 of the left valve is rudimentary and the right valve lacks 5b, and there is no internal-ligament pit. *Trigonopis* is more strongly and regularly ribbed, has lower beaks with much less elongate cardinal teeth, lateral teeth, and a shallower lunule than *Hesperopis*. In addition, *Trigonopis* does not have an internal-ligament pit.

Some species of *Hesperopis* (e.g. *O.* (*H.*) *vancouverensis*) resemble '*Opisoma*' *geinitziana* Stoliczka (1871, p. 288, pl. 10, figs 11a–b), from Cretaceous beds in southern India. Whiteaves (1879) commented upon the resemblance, and Anderson (1958, pp. 122–123) went so far as to assign *Opisoma vancouverensis* and *Opisoma pacifica* to the genus *Opisoma* Stoliczka, 1871. Neither species, however, has the very elongate ligament paralleling the posterior teeth, the three cardinal teeth in each valve that characterize Stolickza's genus, nor the alatoform shape of *Opisoma*. Stoliczka figured only a right valve of '*O.*' *geinitziana*, which clearly shows two similar elongate cardinals, rather than the three of *Opisoma*. He apparently did not have a specimen that allowed him to describe or illustrate the ligamental area. These two cardinals of '*O.*' *geinitziana* resemble those in the left valves of Pacific slope opines but not the large triangular 3b in right valves of *Opis* and *Hesperopis*. Stoliczka's placement of '*O.*' *geinitziana* in *Opisoma* appears to have been based on the similar shape of these two elongate cardinals to the cardinals in *Opisoma*, although he had noted that *Opisoma* has three cardinals in each valve. It is possible that Stolickza was misled by hinge transposition, because his illustrated right valve has the two cardinal teeth normally found on the left valve of *Opisoma*. Transposed hinges among crassatelloideans are relatively common (Popenoe and Findlay



TEXT-FIG. 5. *Opis* (*Hesperopis*) *popenoei* sp. nov. All ×1. Specimens coated with ammonium chloride. A, paratype, LACMIP 13512, LACMIP loc. 6026, Left valve showing drill-hole. B, G, P, holotype, LACMIP 9912, LACMIP loc. 10098. B, left valve. G, right valve. P, dorsal view. C, paratype, LACMIP 13513, LACMIP loc. 10098, left valve. D, paratype, LACMIP 13514, LACMIP loc. 10098, right valve. E, paratype, LACMIP 13515, LACMIP loc. 10135, right valve. F, M–N, paratype, LACMIP 13516, LACMIP loc. 10098. F, right-valve. M, lunule view. N, escutcheon/corcelet view. H, L, Q–R, paratype, LACMIP 13517, LACMIP loc. 22323, right valve. H, exterior. L, interior. Q, lunule view. R, escutcheon/corcelet view. I, paratype, LACMIP 13518, LACMIP loc. 24654, left-valve interior. J, paratype, LACMIP 13519, LACMIP loc. 22323, left-valve interior. K, paratype, LACMP 13520, LACMIP loc. 24654, right-valve interior. O, paratype, LACMIP 13521, LACMIP loc. 10098, escutcheon/corcelet view.

1933), as evidenced by the genus *Heteropis*, which is based on a transposed hinge.

Hesperopis differs from *Opisoma* by having an inflated trigonal shape, prosogyrous beaks, an internal-ligament pit, two cardinals on each valve, a strong posterior umbonal angulation and no nymph. We are inclined to place '*Opisoma*' *geinitziana* Stoliczka, 1871 in *Hesperopis*, but despite the considerable similarity, his species cannot be placed positively in, or excluded from, *Hesperopis* because his specimens apparently did not preserve the ligamental area. If Stoliczka's species does prove to belong to *Hesperopis*, it would be the earliest record of this subgenus. The type locality of '*Opisoma*' *geinitziana* is in the Ootatoor Group near Morarivatoor in southern India. Based on the update of Cretaceous biostratigraphy in southern India by Sundaram *et al.* (2001), Stoliczka's specimens possibly came for the upper Albian Dalmiapurpum Formation near Moruvattur [possibly = Moraviatoor].

The shape of the ligament groove of *Hesperopis* is commonly obscured by breakage, bending and/or poor preservation. Where the posterior margin beneath the beaks has not been too chipped, the margin has a triangular

space for a possible external ligament. A submerged ligament at the posterior end of the groove is indicated because the wider end of the groove ends below the valve margin. Dorsal views of double-valved specimens (Text-figs 3E, 5P and 10B) show the ligament groove on the posterior side of the beak; the anterior side shows no gap along the margin between the beaks.

Although juvenile shells (i.e. <28 mm in height) of the various species of *Hesperopis* have not been found for all its species, juveniles for those that have been found (i.e. *O.* (*H.*) *popenoei*, *O.* (*H.*) *anae* and *O.* (*H.*) *triangulata*) are very similar in having a short trigonal shape and usually having well-developed commarginal sculpture, even though the commarginal sculpture in the adult stage of each of these species can be either obsolete or moderately well developed.

Opis (*H.*) *popenoei* is intermediate in morphology between the following two morphological lineages of *Hesperopis*: (1) the '*holzana*' lineage, which includes *O.* (*H.*) *holzana* and *O.* (*H.*) *rosarioensis* Anderson and Hanna and (2) the '*anae*' lineage, which includes *O.* (*H.*) *anae*, *O.* (*H.*) *vancouverensis* Whiteaves and *O.* (*H.*) *triangulata* (Cooper). These two lineages are inferred to have evolved from *O.* (*H.*) *popenoei* (see Text-fig. 2). Although *Opis californica* resembles juveniles of *O.* (*H.*) *triangulata*, it is unknown whether *O. californica* was the ancestor of *Hesperopis*.

The main evolutionary trends of *Hesperopis* are that the species of both lineages became larger in size and that their internal ligament became better developed. The species within the '*Holzana*' lineage became slightly broader, and their teeth became stouter. The species within the '*Anae*' lineage became more elongate, as did their the teeth.

The beaks, umbones and hinges of the species of *Hesperopis* are unusually high for a bivalve and are disproportionate in size relative to the rest of the shell. For *O.* (*H.*) *popenoei* and the species of the '*holzana*' lineage, the height between the base of the hinge (i.e. directly beneath cardinal 3b) and the anterior end of the umbo is *c.* 40 per cent of the total shell height, and for the '*anae*' lineage it is *c.* 46 per cent.

Stratigraphical range. Middle Turonian to lower Upper Maastrichtian.

Distribution. Vancouver Island, British Columbia southward to north-western Baja California, Mexico; future work might show that *Hesperopis* also occurs in southern India.

Opis (*Hesperopis*) *popenoei* sp. nov.
Text-figures 3C–E, 5

1973 *Opis* sp. Popenoe, p. 18, pl. 1, fig. 14.

Derivation of name. The species is named after W. P. Popenoe, in honour of his many contributions to the morphological and biostratigraphical studies of Pacific slope Cretaceous molluscs.

Holotype. LACMIP 9912 (Text-figs 3E, 5B, G, P), LACMIP loc. 10098 [= hypotype, UCLA 59071 figured as *Opis* sp. by Popenoe (1973, pl. 1, fig. 14)].

Paratypes. LACMIP 13512–13521.

Material examined. Seventy-three specimens (22 left valves, 23 right valves and 28 double valves): 22 from east of Redding (Area 5), 51 from Santa Ana Mountains (Area 15).

Diagnosis. Moderately small-sized and somewhat equant *Hesperopis*. Umbonal posterior ridge strong. Corcelet strong. Cardinal 3b narrow and moderately long.

Description. Shell of moderately small size (up to 49 mm in height and 35 mm in length, same specimen); thick-walled. Equivalved, inequilateral (higher than long), inflated, trigonal and somewhat equant. Corcelet side of shell posteriorly truncate; lunule side posteriorly rounded. Beaks high, prosogyrous and incurved. Umbones narrow. Posterior umbonal ridge strong. Corcelet furrow and ridge strong. Lunule deep set, large and cordate. Escutcheon delineated by incised line; escutcheon lunule-like but narrower and shorter than lunule. Commarginal ribs weak to moderately weak and either closely spaced or irregularly spaced. Hinge high. Left-valve hinge with two cardinals: 2 shorter, somewhat closer to beak than 4b, and bordered by long-deep socket for 3b; 4b thin, elongate and located below sunken small, narrow internal-ligament pit. Right-valve hinge with two cardinals: 3b strongly trigonal, narrow, moderately long and serrate on both sides; 5b elongate, low, thin, serrate on anterior side and shorter than 3b. Growth checks moderately common, irregularly spaced, usually weak and rarely strong.

Remarks. Forty-three per cent of the examined specimens of this new species are of double valves. Juvenile specimens resemble *O. californica* in shape, but the new species has a posterior area slope that is partly inflated, rather than nearly straight sided. Mature specimens of *Opis* (*H.*) *popenoei* are most similar to some growth-checked specimens of *O.* (*H.*) *triangulata*, but *O.* (*H.*) *popenoei* differs by having a smaller size, more equant shape, sharper beaks that are less anteriorly directed, and a more projected corcelet ridge. In addition, growth checks are much less common and less regularly spaced on *O.* (*H.*) *popenoei*. Mature specimens of the new species are somewhat similar to *O.* (*H.*) *rosarioensis*, but *O.* (*H.*) *popenoei* differs by being smaller in size with a narrower umbo and a better developed escutcheon area. *Opis* (*H.*) *popenoei* is the smallest species of *Hesperopis*.

Popenoe (1942, pp. 178–179, fig. 4) listed *Opis* sp. cf. *triangulata* (Cooper) in his checklist of Upper Cretaceous strata in the Santa Ana Mountains, southern California

(Area 15). The specimens he analysed are stored in the LACMIP collection, and inspection of this material revealed that the so-called '*Opis* sp. cf. *triangulata*' from one locality (CIT loc. 302 = LACMIP loc. 10098) in the Holz-Baker transition is actually *O.* (*H.*) *popenoei*. The other specimens are *O.* (*H.*) *anae* and are from the upper Holz Shale Member. Saul (1982, p. 72) listed *Opis* cf. *O. triangulata* from the Holz-Baker transition and the lowermost Holz Shale Member in Area 15. The material she analysed is stored in the LACMIP collection, and inspection of this material revealed that these specimens are also *O.* (*H.*) *popenoei*.

The new species resembles *Opis* (*O.*) *hokkaidoensis* Ueda, 1963 from Campanian or Maastrichtian strata of Japan. Tashiro (1992, p. 198, pl. 58, fig. 2) also figured Ueda's species. The new species differs from Ueda's species by having weaker commarginal ribs, a deeper corcelet and a less truncate antero-ventral margin.

Opis (*H.*) *popenoei* is intermediate in morphology between the earliest members of the two lineages of *Hesperopis*. The somewhat equant shell, weak sculpture and width of cardinal 3b of *O.* (*H.*) *popenoei* are like *O.* (*H.*) *holzana*. The sharp beaks, strength of the posterior carina and corcelet and length of cardinal 3b of *O.* (*H.*) *popenoei* are like those of *O.* (*H.*) *anae*.

Stratigraphical range. Middle–Upper Turonian.

Distribution. Middle Turonian: Redding Formation, Frazier Siltstone Member; top of Frazier Siltstone Member or basal Bear Creek Sandstone, Shasta County, California (Area 5). Upper Turonian: Redding Formation, near top of Melton Sandstone Member, Shasta County, California (Area 5); Ladd Formation, upper Baker Canyon and lower Holz Shale members, Santa Ana Mountains, Orange County, California (Area 15).

Species of the *'holzana'* lineage

Diagnosis. Medium to moderately large-sized and broad *Hesperopis*. Beaks high. Posterior umbonal ridge rounded. Corcelet usually weak. Hinge high. Valves smoothish or with very weak to moderately strong commarginal ribs. Cardinal 3b moderately wide and long or equant.

Opis (*Hesperopis*) *holzana* sp. nov.
Text-figures 3B, 6

Derivation of name. The species is named after the Holz family whose members were hospitable and helpful to palaeontologists doing research in the Santa Ana Mountains.

Holotype. LACMIP 13524 (Text-fig. 6C, G–H, K), LACMIP loc. 21490.
24190

13523
Paratypes. LACMIP 13522–13524 and RBCM.EH2008.016.0001.

Material examined. Seven specimens (two left valves and five right valves): one from Nanaimo (Area 3); six from Santa Ana Mountains (Area 15).

Diagnosis. Medium-sized and broad *Hesperopis*. Posterior umbonal ridge weak. Corcelet weak to moderately weak. Cardinal 3b moderately wide and moderately long.

Description. Shell of medium size (up to 52 mm in height and 47 mm in length, same specimen); thick-walled. Equivalved, equilateral (only slightly higher than long) and inflated. Juveniles trigonal; adults subtrigonal, equant and broad. Corcelet side of shell posteriorly truncate; lunule side posteriorly rounded. Beaks high. Umbones high and broad. Posterior umbonal ridge weak. Corcelet furrow and ridge weak to moderately weak. Lunule large and cordate; lunular margin bulging towards valve margin to create pouch-like socket for 2b. Escutcheon area depressed, demarked by weak furrow and bordered posteriorly by low, broadly rounded radial ridge. Commarginal ribs very closely spaced, weak and of nonuniform strength; but valves can be nearly smooth. Hinge high. Left-valve hinge with two cardinals: 2 and 4b both long and moderately wide; socket for 3 broadly trigonal. Right-valve hinge with two cardinals: 3b broadly trigonal, strong, moderately wide and moderately long; 5b narrowly elongate and longer than 3b; socket for 2 as high as 3b; socket for 4b trigonal. Internal-ligament pit sunken, small and moderately narrow.

Remarks. The new species is most similar to *O.* (*H.*) *rosarioensis* but differs from the latter by being smaller in size, less broad, and having a slightly stronger posterior umbonal ridge and corcelet, deeper lunule, generally weaker sculpture, longer teeth, a narrower socket for 2 in right valve and a narrower internal-ligament pit.

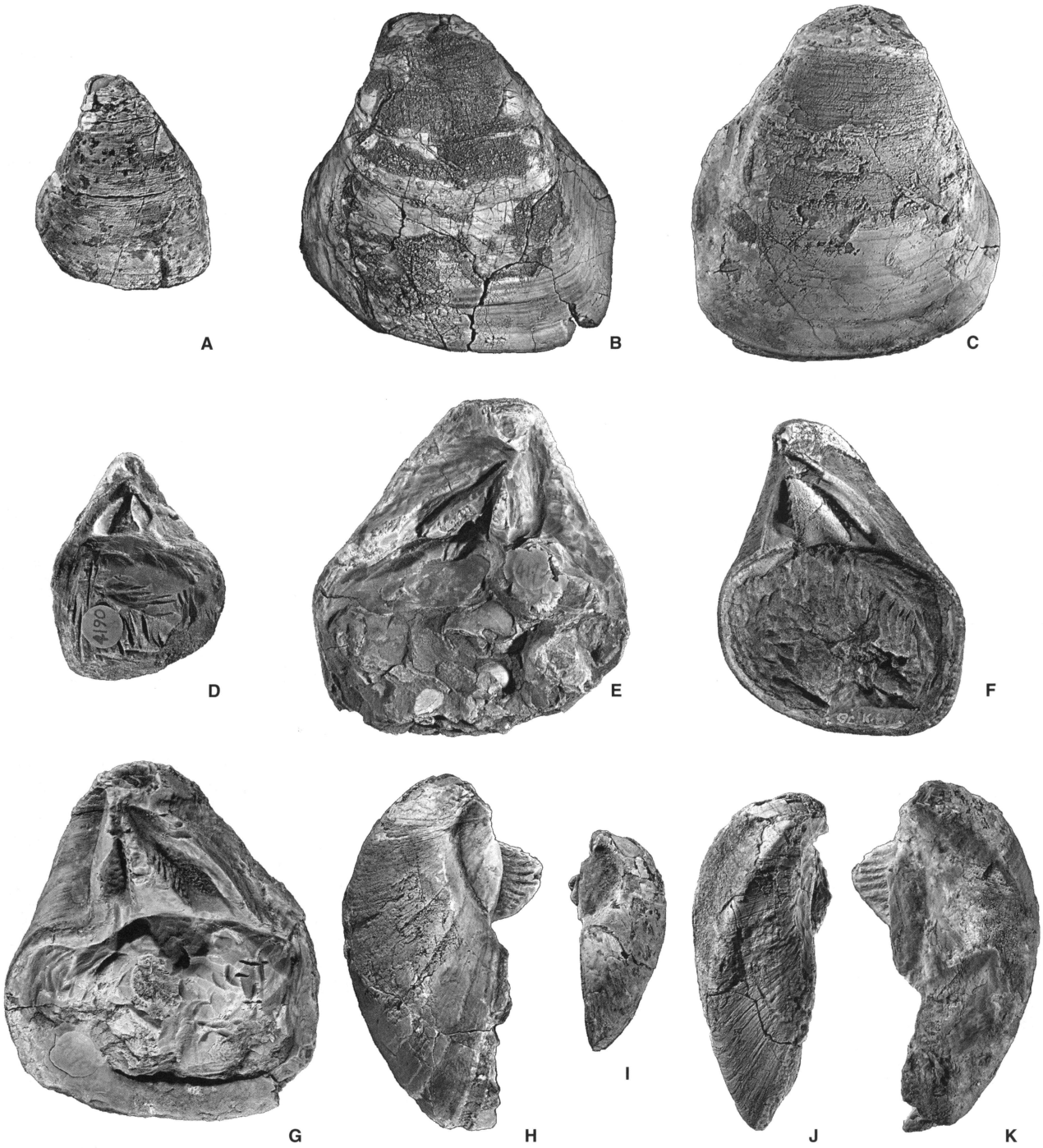
Ludvigsen and Beard (1997, p. 101) reported an unidentified species of *Opis* from the Haslam Formation, Vancouver Island, British Columbia (Area 3). This present study showed that all the known opine specimens (e.g. Text-figs 3B, 6F) examined from that formation are *O.* (*H.*) *holzana*.

Stratigraphical range. Uppermost Santonian – Lower Campanian.

Distribution. Uppermost Santonian: Haslam Formation, upper part, Lower Quarry site just west of Nanaimo, Vancouver Island, British Columbia (Area 3). Lower Campanian: Ladd Formation, lower upper Holz Shale Member, Santa Ana Mountains, Orange County, southern California (Area 15).

Opis (*Hesperopis*) *rosarioensis* Anderson and Hanna, 1935
Text-figure 7

1935 *Opis rosarioensis* Anderson and Hanna, p. 31, pl. 10, figs 2–3.



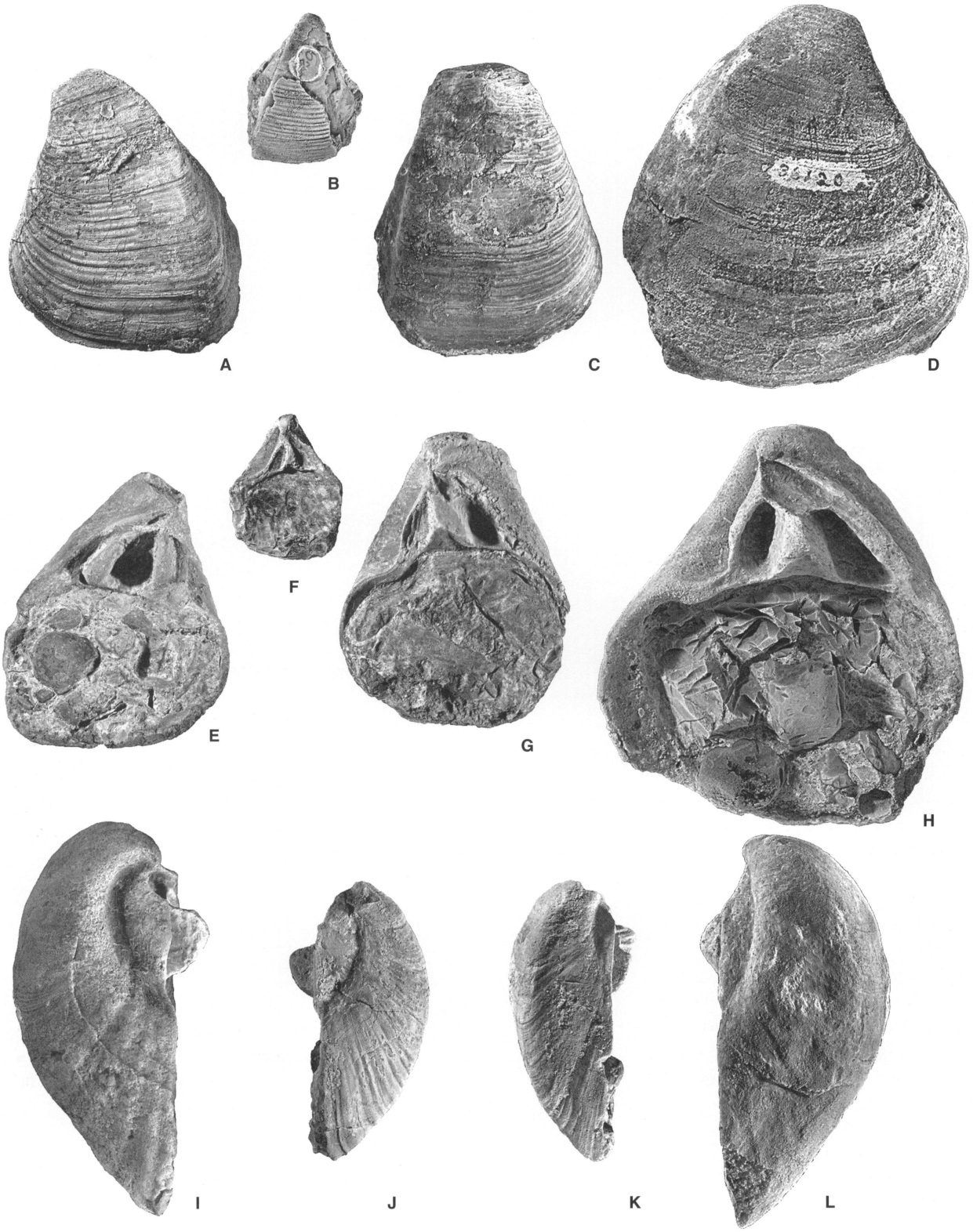
TEXT-FIG. 6. *Opis* (*Hesperopis*) *holzana* sp. nov. All specimens, unless otherwise noted, from LACMIP loc. 24190. All ×1. Specimens coated with ammonium chloride. A, D, I, paratype, LACMIP 13522, left valve. A, exterior. D, interior. I, lunule view. B, E, J, paratype, LACMIP 13523, left valve. B, exterior. E, interior. J, escutcheon/corcelet view. C, G–H, K, holotype, LACMIP 13524, right valve. C, exterior. G, interior. H, lunule view. K, escutcheon/corcelet view. F, paratype, RBCM.EH2008.016.0001, right-valve interior, CGS loc. 103851.

1989 *Opis rosarioensis* Anderson and Hanna; Perrilliat, p. 340, fig. 128h.

1993 *Opis* cf. *O. rosarioensis* Anderson and Hanna; Elder and Saul, p. 177, pl. 2, figs 12–13.

Holotype. UCMP 36120, UCMP loc. A-426.

Hypotypes. USNM 468584 [= specimen figured as *Opis* cf. *O. rosarioensis* by Elder and Saul (1993, pl. 2, fig. 12)]; LACMIP



TEXT-FIG. 7. *Opis* (*Hesperopis*) *rosarioensis* Anderson and Hanna, 1935. All ×1. Specimens coated with ammonium chloride. A, E, J–K, hypotype, LACMIP 13534, LACMIP loc. 26500, left valve. A, exterior. E, interior. J, lunule view. K, escutcheon/corcelet view. B, F, hypotype, LACMIP 13535, LACMIP loc. 27200, right valve. B, exterior. F, interior. C, G, hypotype, LACMIP 13536, LACMIP loc. 27199, right valve. C, exterior. G, interior. D, H–I, L, holotype, UCMP 36120, UCMP loc. A-426, right valve. D, exterior. H, interior. I, lunule view. L, escutcheon/corcelet view.

12129 [= specimen figured as *Opis* cf. *O. rosarioensis* by Elder and Saul (1993, pl. 2, fig. 13)]; and LACMIP 13534–13536.

Material examined. Five specimens (three left valves and two right valves): one from Pigeon Point (Area 10); one from the Garzas to Los Banos Creek region (Area 11); two from Santa Ana Mountains (Area 15); and one from Punta Baja (Area 20).

Diagnosis. Moderately large-sized, rather broad *Hesperopis*. Posterior umbonal ridge weak. Corcelet weak. Commarginal ribs weak, becoming obsolete on mature specimens. Cardinal 3b short and stout.

Description. Shell of moderately large size (up to 61 mm in height and 55 mm in length, same specimen); thick-walled. Equivalved, equilateral (only slightly higher than long) and inflated. Juveniles trigonal; adults subtrigonal, equant and broad. Corcelet side of shell posteriorly truncate; lunule side posteriorly rounded. Beaks high. Umbones broad. Posterior umbonal angulation weak. Corcelet furrow and ridge very weak. Lunule large, deep and cordate. Escutcheon area depressed, delineated by weak furrow and bordered posteriorly by low, broadly rounded radial ridge. Commarginal ribs very closely spaced, weak to moderately weak, and of nonuniform strength; ribs becoming obsolete on mature specimens. Left-valve hinge with two cardinals; socket for 3b widely trigonal and very broad. Right-valve hinge with two cardinals: 3b relatively short, stout and equant; sockets for 4b and 2 wide. Internal-ligament pit sunken, small and wide.

Remarks. The holotype is a mature specimen that is somewhat worn, especially about the beak, and only scant traces of commarginal sculpture remain there. The 3b cardinal of *O.* (*H.*) *rosarioensis* is noticeably shorter than the cardinal 3b of other species of *Hesperopis*.

In spite of its name, *O.* (*H.*) *rosarioensis* is not found in the Rosario Formation. The holotype is actually from the slightly older Punta Baja Formation at Punta Baja, northwestern Baja California, Mexico (Area 20). It was collected by T. Barrera and M. Santillán and deposited by them at UCMP during the early 1930s. Anderson (1958, p. 122) incorrectly reported the type locality as being near Rosario Landing, Baja California. He reported the age of the rocks near Rosario Landing to be Maastrichtian on the assumption that the *Opis* is from the same beds as a '*Parapachydiscus* sp.' from near San Antonio del Mar, more than 129 km to the north of Rosario. Perrilliat (1989) also incorrectly placed the type locality near the Rosario airport (influenced? by Anderson's Rosario Landing). She incorrectly inferred that the type was at the CASG because of F. M. Anderson's long association with that institution. The Rosario Formation does crop out at Punta Baja (Kilmer 1963), but the matrix filling the inside of the type specimen of *O.* (*H.*) *rosarioensis* is more similar to that found in the underlying Punta Baja Formation.

A nicely preserved specimen of *O.* (*H.*) *rosarioensis* is from LACMIP loc. 26500. On the geological map of Payne (1962), this locality plots in the Television sandstone in the Panoche Hills, Merced County, California (Area 11).

Filkorn (2007) reported an *Opis* sp. from conglomeratic beds at the base of the Schulz Member of the Ladd Formation. Inspection of his collection, which is stored at LACMIP, revealed that the specimens are *O.* (*H.*) *rosarioensis*. They were found associated with at least three species of rudist bivalves, other shallow-marine molluscs and colonial-scleractinian corals. Although the fauna is not *in situ*, the fossils apparently have not been reworked (Filkorn 2007).

Elder and Saul (1993, figs 2–3) reported *Opis* cf. *rosarioensis* from the upper middle Campanian lower part of the southern sequence of the Pigeon Point Formation south of Pigeon Point, San Mateo County, California (Area 10). The age of the beds there, however, is somewhat problematic because of limited exposures, faulting and a paucity of age-diagnostic fossils.

Elder *et al.* (1998, p. 165) reported *Opis rosarioensis* from the upper Campanian to the lower Maastrichtian Gualala Formation, Mendocino County, California (Area 8), but the material, which is missing, is probably *O.* (*H.*) *triangulata* (see 'Remarks' for *O.* (*H.*) *triangulata*).

Stratigraphical range. Lower Middle – middle Upper Campanian.

Distribution. Lower Middle Campanian: Williams Formation, Schulz Member, Santa Ana Mountains, Orange County, California (Area 15). Middle Upper Campanian: Panoche Group, Television sandstone, Panoche Hills, Merced County, California (Area 11); Pigeon Point Formation, San Mateo County, California (Area 10); Punta Baja Formation, Punta Baja, Baja California Sur, Mexico (Area 20).

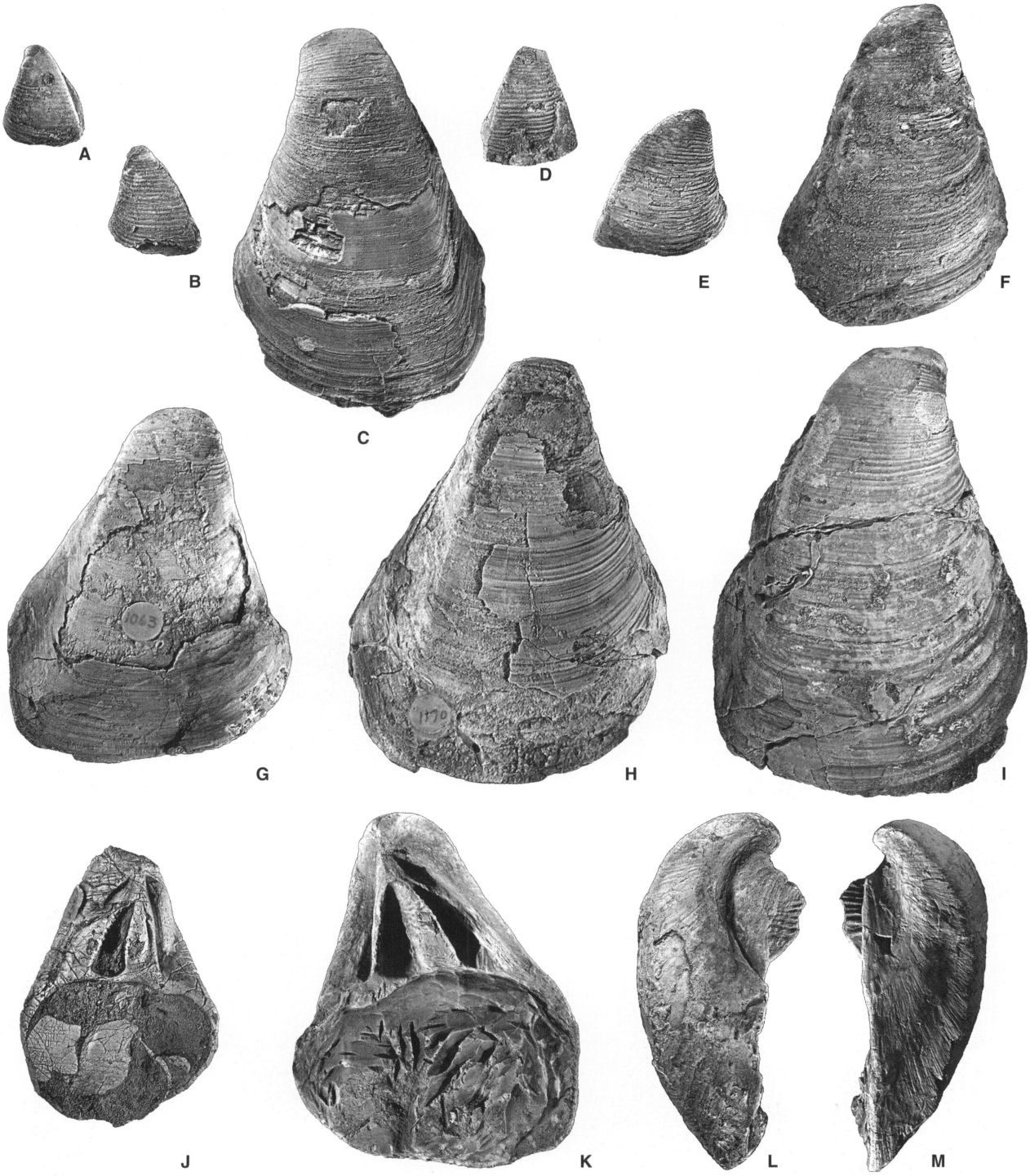
Species of the *'anae'* lineage

Diagnosis. Moderately large to large-sized, narrow and elongate *Hesperopis*. Beaks high to very high. Umbones anteriorly directed. Posterior umbonal ridge moderately strong. Corcelet moderately weak to weak. Commarginal ribs very weak to moderate strength; valves can be smoothish. Cardinal 3b narrow and moderately long to very long.

Opis (*Hesperopis*) *anae* sp. nov.
Text-figure 8

1973 *Opis* sp. B. Popenoe, p. 20, pl. 2, fig. 25.

Derivation of name. The species is named after the Santa Ana Mountains, where it is locally abundant.



TEXT-FIG. 8. Figs 1–20. *Opis* (*Hesperopis*) *anae* sp. nov. All ×1. Specimens coated with ammonium chloride. A, paratype, LACMIP 13525, LACMIP loc. 10718, left valve. B, paratype, LACMIP 13526, LACMIP loc. 10724, left valve. C, paratype, LACMIP 13527, LACMIP loc. 22329, left valve. D, paratype, LACMIP 13528, LACMIP loc. 10724, right valve. E, paratype, LACMIP 13529, LACMIP loc. 10724, right valve. F, paratype, LACMIP 13530, LACMIP loc. 8173, right valve. G, K–M, holotype, LACMIP 13531, LACMIP loc. 10718, right valve. G, exterior. K, interior. L, lunule view. M, escutcheon/corcelet view. H, paratype, LACMIP 9917, LACMIP loc. 10084, right valve. I, paratype, LACMIP 13532, LACMIP loc. 22329, right valve. J, paratype, LACMIP 13533, LACMIP loc. 22329, left-valve interior.

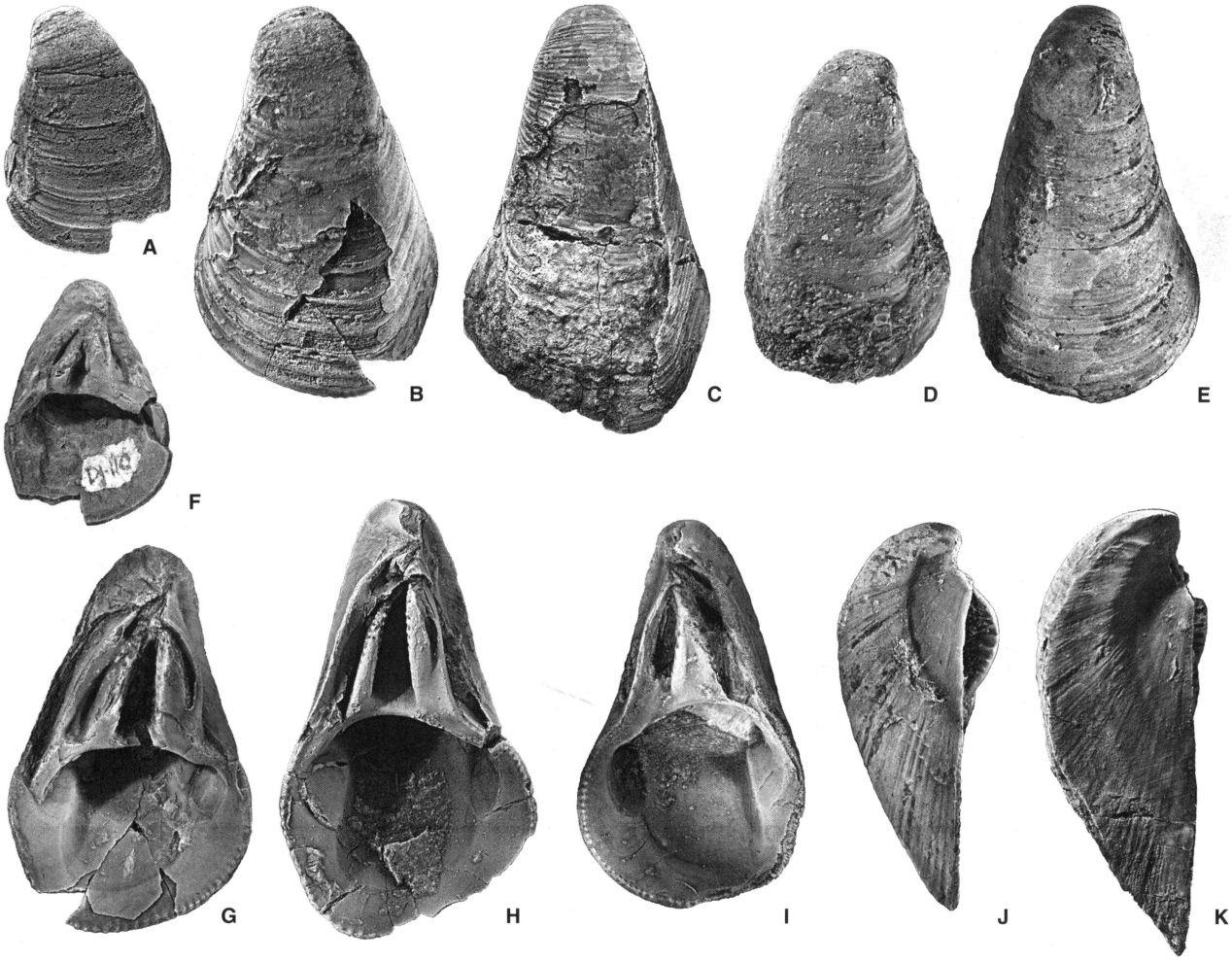
Holotype. LACMIP 13531 (Text-fig. 8G, K–M), LACMIP loc. 10084.

Paratypes. LACMIP 9917 [= specimen of *Opis* sp. B figured by Popenoe (1973, pl. 2, fig. 25)], 13525–13530 and 13532.-13533

Material examined. One hundred and ten specimens (43 left valves, 56 right valves and 11 double valves): one? from Granite Bay (Area 9); 109 from Santa Ana Mountains (Area 15).

Diagnosis. Moderately large-sized, moderately narrow and moderately elongate *Hesperopis*. Umbones anteriorly directed. Posterior umbonal ridge weak. Corcelet moderately weak. Commarginal ribs moderately strong but finer and more closely spaced on larger specimens. Cardinal 3b narrow and moderately long.

Description. Shell of moderately large size (up to 68 mm in height and 48 mm in length, same specimen); moderately thick-walled. Equivalved, inequilateral (higher than long), inflated and trigonal. Corcelet side of shell posteriorly truncate; lunule side posteriorly rounded. Beaks high and prosogyrous. Umbones narrow and directed anteriorly. Posterior umbonal angulation weak. Corcelet furrow and corcelet ridge moderately weak. Lunule deep set, large, wide and heart-shaped; lunular area bulges towards the valve margin creating a pouch-like socket for 2b. Escutcheon area with weak radial furrow, bordered posteriorly by weak to moderately weak radial ridge. Commarginal ribs moderately strong, close set and of uniform strength on juveniles (up to height 21 mm); commarginal ribs becoming much weaker, more closely spaced, and less uniform on larger specimens. Hinges high. Left-valve hinge with two nearly equally strong cardinals: 2 long but slightly shorter than 4b; 4b serrate on both sides; and 3b socket long. Right-valve



TEXT-FIG. 9. *Opis* (*Hesperopis*) *vancouverensis* Whiteaves, 1879. All specimens from Locality 1 (south-west Denman Island, British Columbia). All ×1. Specimens coated with ammonium chloride. A, F, hypotype, RBCM.EH2008.016.0002, left valve. A, exterior. F, interior. B, G, hypotype, RBCM.EH2008.016.0003, left valve. B, exterior. G, interior. C, H, K, hypotype, RBCM.EH2008.017.0001, left valve. C, exterior. H, interior. K, escutcheon/corcelet view. D, hypotype, RBCM.EH2008.016.0004, left valve. E, I–J, hypotype, RBCM.EH2008.016.0005, right valve. E, exterior. I, interior. J, lunule view.

hinge with two cardinals: 3b strongly trigonal, narrow, moderately long and serrate on both sides; 5b low and thin. Lunular margin deeply depressed. Internal-ligament pit sunken, narrow and situated dorsally of 5b and encroaching on its posterior end.

Remarks. Popenoe (1942, pp. 178–179, fig. 4) listed *Opis* sp. cf. *O. triangulata* (Cooper) in his checklist of Upper Cretaceous strata in the Santa Ana Mountains, southern California (Area 15). The specimens he used are stored in the LACMIP collection. Inspection of this material revealed that the specimens from all of his listed localities, except for CIT loc. 302 (= LACMIP loc. 10098) (see 'Remarks' on *O.* (*H.*) *popenoei*), are *O.* (*H.*) *anae* from the upper Holz Shale Member. One of these specimens of this species is designated herein as paratype, LACMIP 9917, and it is the same specimen (hypotype, UCLA 59072) figured by Popenoe (1973, p. 20, pl. 2, fig. 25) and identified by him as *Opis* sp. B from the Holz Shale Member. Saul (1982, p. 73, fig. 3) listed *Opis* aff. *O. triangulata* (Cooper) from the Holz Shale Member in Area 15. The material she used is stored in the LACMIP collection, and inspection of this material revealed that these specimens are *O.* (*H.*) *anae*.

Opis (*H.*) *anae* is similar to *O.* (*H.*) *vancouverensis* but differs from the latter by having a larger size, broader shape (especially posteriorly), less tendency to have obsolete commarginal ribbing, stronger corcelet ridge and slightly wider teeth. *Opis* (*H.*) *anae* is also similar to *O.* (*H.*) *triangulata* but differs from the latter by having smaller size, less tendency for anteriorly narrowing beaks, stronger commarginal ribbing, shorter teeth and absence of any strong growth checks.

An internal mould of what is probably *O.* (*H.*) *anae* from LACMIP loc. 17871 is the only known specimen of an opine from the Chico Formation in northern California.

Stratigraphical range. Upper Lower Campanian.

Distribution. Tentatively from Chico Formation at Granite Bay, east of Sacramento, Placer County, California (Area 9); Ladd Formation, uppermost Holz Shale Member, Santa Ana Mountains, Orange County, California (Area 15).

Opis (*Hesperopis*) *vancouverensis* Whiteaves, 1879
Text-figures 3A, 9

1879 *Opis vancouverensis* Whiteaves, 1879, p. 158, pl. 18, figs 4–4a.

1997 *Opis vancouverensis* Whiteaves; Ludvigsen and Beard, p. 101, fig. 55 (three views of a left valve, the two interior views of which are reverse images).

Holotype. CGS 5691 from west side of Denman Island (coll. Richardson in 1871), Strait of Georgia, British Columbia.

Hypotypes. RBCM.EH2008.016.0001 to RBCM.EH2008.016.00-05, and RBCM.EH2008.017.0001 [= VIPM 151 figured by Ludvigsen and Beard (1997, fig. 55)].

Material examined. Twelve specimens (six left valves, four right valves and two double valves): nine from Denman Island (Area 2); three from Santa Monica Mountains (Area 14).

Diagnosis. Medium-sized, narrowly trigonal and elongate *Hesperopis*. Beaks very high. Umbones anteriorly directed. Posterior umbonal ridge weak. Corcelet weak; strongest near beaks, otherwise flattish. Commarginal ribs very weak to moderately strong. Inner valve margins crenulate. Cardinal 3b very narrow and very long.

Description. Shell of medium size (up to 56 mm in height and 32 mm in length, same specimen); thick-walled. Equivalved, inequilateral, inflated and elongate trigonal. Corcelet side of shell posteriorly truncate; lunule side posteriorly rounded. Beaks very high, prosogyrous and incurved. Umbones narrow and directed anteriorly. Posterior umbonal carina moderately rounded. Corcelet furrow and corcelet ridge weak. Lunule deep set. Escutcheon weakly delimited by narrow raised area; escutcheon flattish but raised slightly near commissure. Commarginal ribs very weak to moderately strong, uniformly spaced on umbones; ribs becoming narrower and less uniformly spaced ventrally. Hinge very high. Left-valve hinge with two cardinals: 2 narrow, elongate, serrate on both sides, shorter and closer to beak than 4b, and bordered by longer deep socket for 3b; 4b serrate on both sides. Right-valve hinge with two cardinals: 3b moderately large, trigonal, very narrow, very long and serrate on both sides; 5b on anterior side appressed to valve margin. Ligament narrow beneath beaks; internal-ligament pit sunken, narrow, elongate, widening slightly ventrally and impinging on dorsal ends of 5a and 4b. Inner valve margins crenulate.

Remarks. Opis (*H.*) *vancouverensis* resembles *O.* (*H.*) *triangulata* in the elongation of the beaks, but *O.* (*H.*) *vancouverensis* differs by having a smaller shell size and weaker sculpture.

Three rather poor specimens of *O.* (*H.*) *vancouverensis* Whiteaves, 1879 have been recovered from the Tuna Canyon Formation in the Santa Monica Mountains (Area 14). Two of them are from LACMIP loc. 4818 in lower Santa Ynez Canyon. This locality yielded the ammonite *Metaplacenticeras pacificum* (Smith, 1900), but, unfortunately, collectors wandered about and collected from above and below the strata that yielded *M. pacificum*. According to J. Alderson (pers. comm. 2008), the *Opis* specimens are probably from underlying silty sandstone and, therefore, would be slightly older than the beds containing *M. pacificum*. This ammonite ranges from late

middle to early late Campanian age (Elder and Saul 1996), thus the *Opis* at locality 4818 is approximately middle Campanian in age. The third opine specimen from the Tuna Canyon Formation is tentatively identified as *O.* (*H.*) *vancouverensis*, because it is a poorly preserved left valve that shows of sculpture similar to that found in *O.* (*H.*) *vancouverensis*. This specimen is from LACMIP loc. 20215 in Rivas Canyon near Pacific Palisades, and the associated fossils also occur at a nearby locality that yielded abundant *M. pacificum*.

Anderson (1958, p. 123) reported '*Opisoma*' *vancouverensis* (Whiteaves) from the south-west side of Denman Island, which is just east of the coast of Vancouver Island, British Columbia. Ludvigsen and Beard (1997) reported *Opis vancouverensis* from the 'Trent River' Formation on the west side of Denman Island, but these outcrops were mapped as the Cedar District Formation by Katnick and Mustard (2001). According to Ludvigsen and Beard (1997), this opine is one of the rarest bivalves in Cretaceous rocks of Vancouver Island and vicinity.

Stratigraphical range. Middle–upper Middle Campanian.

Distribution. Cedar District Formation, upper part, west side Denman Island, British Columbia (Area 2); upper Tuna Canyon Formation, lower Santa Ynez Canyon and Rivas Canyon, Santa Monica Mountains, Los Angeles County, California (Area 14).

Opis (*Hesperopis*) *triangulata* (Cooper, 1894)
Plates 1–2, Text-figure 10

1894 *Corbula triangulata* Cooper, p. 49, 61, pl. 2, fig. 42 [not pl. 4 as stated].
1896 *Opis triangulata* (Cooper); Cooper, pp. 332–333, pl. 47, figs 7–9.
1958 *Opisoma pacifica* Anderson, pp. 122–123, pl. 26, figs 5–6.
1978 *Opis* cf. *O. triangulata* Dawson, pl. 1, fig. 18.

Primary types. Of *Corbula triangulata* Cooper, 1894, lectotype CASG 624 (ex CSMB 13752), designated by Stanton (1895), Point Loma Formation at Point Loma, San Diego County, California (Area 17). Of *Opisoma pacifica* Anderson, 1958, holotype CASG 29118.03, CASG loc. 29118, Moreno Formation, Merced County, California (Area 11).

Hypotypes. LACMIP 13537–13544; SDSNH 33989–33990, 67147–67148; and CASG 29120.02.

Material examined. Forty-seven specimens (14 left valves, 23 right valves and 8 double valves): one from Gualala (Area 8); 28 from Garzas to Los Banos Creek (Area 11); two from north-east of Cape San Martin (Area 12); two from Pebblestone Shut-In (Area 13); five from Carlsbad (Area 16); three from Pt. Loma (Area 17); two from La Misíon (Area 18); and four from Punta China (Area 19).

Diagnosis. Large-sized, narrowly trigonal and elongate *Hesperopis*. Beaks very high. Umbones directly anteriorly. Posterior umbonal carina weak to moderately strong. Corcelet weak to moderately weak. Shell smoothish to weakly sculptured with commarginal ribs. Growth checks can be very strong. Cardinal 3b very narrow and very long. Internal-ligament pit moderately broad.

Description. Shell of large size (up to 88 mm in height and 48 mm in length, same specimen); moderately thin-walled to thick-walled. Equivalved, inequilateral, inflated, narrowly trigonal and elongate. Corcelet side of shell posteriorly truncate; lunule side posteriorly rounded. Beaks very high, prosogyrous and incurved. Umbones narrow. Posterior umbonal carina broadly rounded to moderately prominent. Corcelet furrow weak, corcelet ridge moderately weak. Lunule deep set, very wide, smoothish and gently convex. Escutcheon weakly delimited by narrow raised area; escutcheon long, smoothish and gently convex. Commarginal ribs on juveniles moderately strong, closely and uniformly spaced; adult shell smoothish (showing only growth lines) or with irregularly spaced growth checks, becoming especially strong ventrally on some specimens. Left-valve hinge with two cardinals: 2 closer to beak than 4b, and 2 bordered by long deep socket for 3b; 4b elongate, thin and serrate on both sides. Right-valve hinge with two cardinals: 3b trigonal, strong, very narrow, very long and serrate on both sides; 5b low and thin. Internal-ligament pit sunken, moderately broad and situated dorsal to 4b.

Remarks. Opis (*H.*) *triangulata* is most similar to *O.* (*H.*) *vancouverensis*, but *Opis* (*H.*) *triangulata* differs by having a much larger shell size and stronger sculpture. Cooper (1894) described *Opis* (*H.*) *triangulata* based on two specimens collected by Fairbanks (1893), who reported that the fossiliferous sandstone, from which these specimens were taken, crops out at the base of the cliffs on the outer (western) side of Point Loma and also occurs as re-deposited boulders in the overlying conglomerate. Cooper (1894) did not designate a type specimen, but Stanton (1895), who requested Cooper's Point Loma material from the CSMB, observed material that consisted of Cooper's figured specimen and a second, much larger but broken specimen. Stanton (1895, p. 59) recognized both specimens as belonging to the genus *Opis*, and he indicated that the specimen figured by Cooper (1894, pl. 2, fig. 42) was the 'type.' Stanton, thus, designated the lectotype although Anderson (1958) referred to this specimen as the holotype. In 1896, Cooper wrote that when describing the species, he had not seen the larger specimen mentioned by Stanton in 1895, and had referred his species to *Corbula* because of a

smaller broken specimen that revealed a single, large median tooth. Both this small broken specimen (a syntype because Cooper indicated its use in describing the hinge) and the larger, later figured specimen (Cooper, 1896, pl. 47, fig. 7) appear to be lost. Coan (1981) indicated that CSMB 13752 was a syntype. Even though Coan (1981, p. 155) used Cooper's original generic assignment for the species, Coan was aware that Stanton had placed Cooper's species in the genus *Opis*. Unfortunately, the lectotype is a juvenile (Text-fig. 10C–D), but well-preserved conspecific specimens from the Point Loma Formation near Carlsbad (Area 16) have been used to help describe the adult characteristics of this species. Anderson (1958, p. 122) restated some of Cooper's (1894) comments and some of Stanton's (1895) comments regarding *Opis triangulata* but did not figure any specimens.

Fifty-three per cent of the examined specimens of this species are double valves, which is the highest percentage for the studied species of *Hesperopis*. All of the double valves are from the San Diego area. No growth checks (i.e. environmentally caused) were found on any of the specimens from the San Diego area.

Sundberg (1979, table 1) reported *Opis* cf. *O. triangulata* (Cooper) from the Cabrillo Formation on the east side of Point Loma, San Diego County, southern California (Area 17). Inspection of his collection, which is stored at California State University Fullerton, revealed that the specimens are *O.* (*H.*) *triangulata*. A few specimens of *O.* (*H.*) *triangulata* (Cooper, 1894) were recovered by Dawson (1978) from the same area where Sundberg collected his fossils.

All the specimens of *O.* (*H.*) *triangulata* from the west side of the San Joaquin Valley (Area 11) are single valves. Most are covered with growth checks although some have them only on the adult part. Some specimens from a single locality have them, whereas other specimens from the same locality do not. All the studied specimens from LACMIP loc. 22661, however, have strong growth checks. At both LACMIP locs 10685 and 26342, some of the specimens have growth checks, whereas and others do not.

Opis (*H.*) *triangulata* was detected at two localities in the El Piojo Formation in the Lake Nacimiento area, San Luis Obispo County, California (Areas 12–13). The locality with the better preserved fossils (LACMIP loc. 12245) is a reworked fossiliferous boulder from a conglomerate that crops out just west of Pebblestone Shut-In, western Lake Nacimiento, San Luis Obispo County (Area 13). The age of this boulder that contains *Opis triangulata* is probably early Maastrichtian, based on the presence of the bivalve *Calva* (*Penecallista*) *marina* Saul and Popenoe, 1992, whose geological age range is latest Campanian? and early Maastrichtian.

The other Nacimiento River drainage locality (UCMP loc. A-3435) is on Negro Fork of the Nacimiento River, approximately 32 km north-west of the other locality and 14 km north-east of Cape San Martin, Monterey County (Area 12). Preservation is very poor and species identifications of the fossils at this locality are tentative. Saul (1986, p. 26) mentioned that the rudist *Coralliochama* cf. *C. orcutti* White, 1885 occurs at the locality. Locality UCMP A-3435 is most likely the locality from which Taliaferro (1944) *Opus* [*sic*] *triangulata* was collected. Saul (1986, p. 26) erred in suggesting that might it have come from a boulder in a conglomerate that crops out just west of Pebblestone Shut-In.

Weaver (1944) included *Opis triangulata* in a faunal list of fossils from the Gualala Formation near Gualala, Mendocino County, California (Area 8). Anderson (1958, p. 69) noted Weaver's list and followed it by another list of Gualala species, including *Opis* (*Opisoma*) aff. *O. vancouverensis*, based on specimens, which were collected by S. G. Clark. During this present investigation, Clark's specimens could not be found at either UCMP or CASG. Elder *et al.* (1998) reported *Opis rosarioensis* from the Anchor Bay Member of the Gualala Formation, and this material is also missing. During this present investigation, a specimen of an opine from this formation was studied. It is poorly preserved, but its narrowness resembles *O.* (*H.*) *triangulata*. It is tentatively concluded here that all the Gualala Formation reports of opines are *O.* (*H.*) *triangulata*.

There are potential opine specimens at UCMP from five Cretaceous localities in the Covelo district, western part of Round Valley, Mendocino County, California (Area 7). A bivalve? impression is labelled *Opis*?, but the impression is too indefinite for even identification to a family. If *O. triangulata* were correctly identified from this area, they

EXPLANATION OF PLATE 1

Figs 1–9. *Opis* (*Hesperopis*) *triangulata* (Cooper, 1894). All ×1. All left valves. Specimens coated with ammonium chloride. 1, LACMIP hypotype 13537, LACMIP loc. 10685, exterior. 2, LACMIP hypotype 13538, LACMIP loc. 10685, exterior. 3, LACMIP hypotype 13539, LACMIP loc. 10685, exterior. 4. SDSNH hypotype 67148, SDSNH loc. 3403, exterior. 5, LACMIP hypotype 13540, LACMIP loc. 26342, exterior. 6, 9. SDSNH hypotype 67147, SDSNH loc. 3869. 6, exterior. 9, interior. 7, SDSNH hypotype 33989, SDSNH loc. 3384, exterior. 8, LACMIP hypotype 13541, LACMIP loc. 22611, interior.

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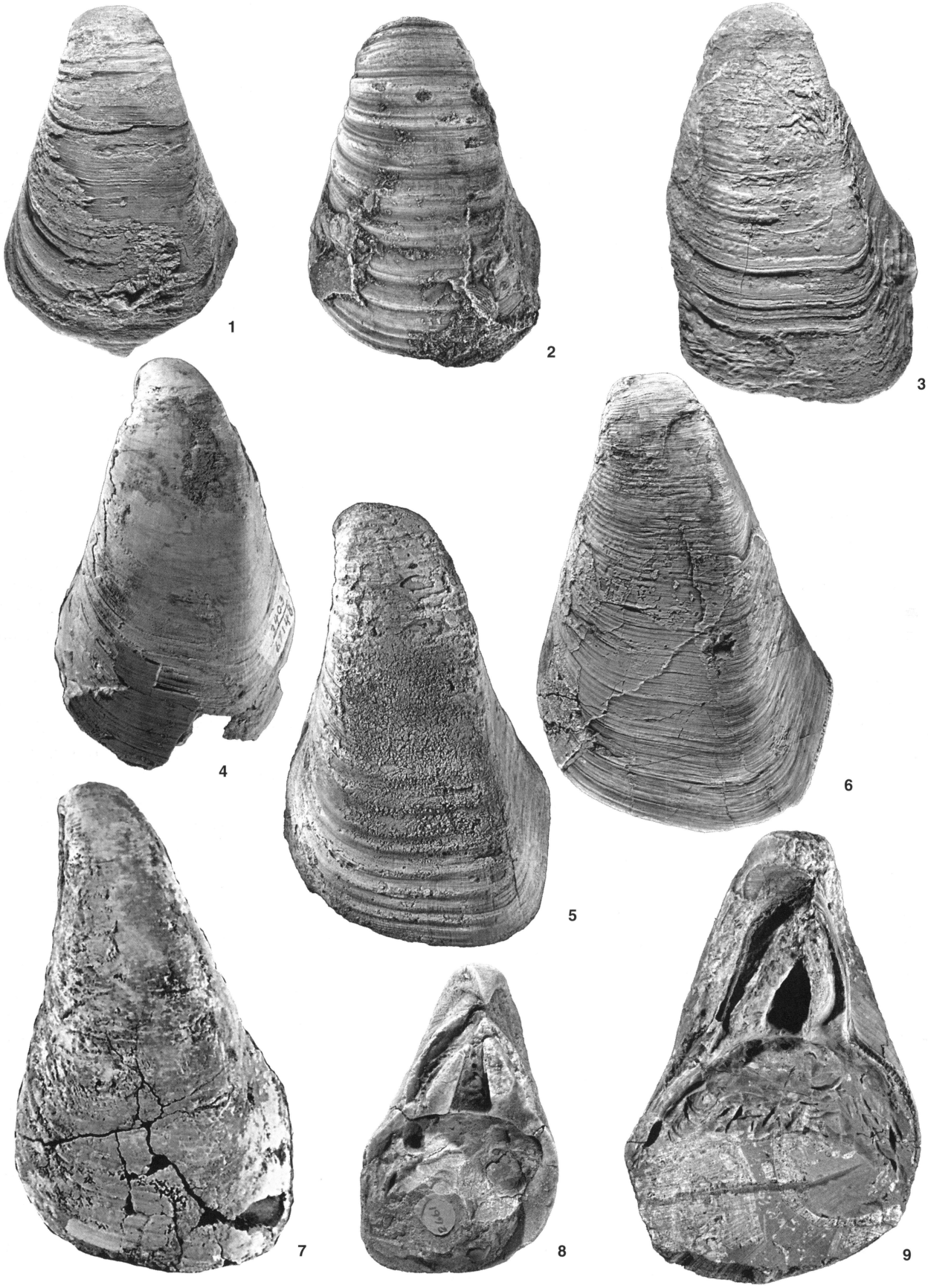


SQUIRES AND SAUL, *Opis (Hesperopis) triangulata*

would represent the northernmost known occurrence of this species. Clark (1940) mapped this area and listed fossil localities, but he did not provide any faunal lists. Anderson (1958, p. 70) provided two short lists of a few Cretaceous mollusc species collected by Clark from the Covelo district. Anderson's lists did not include *Opis*.

Stratigraphical range. Upper Campanian – lower Upper Maastrichtian.

Distribution. Upper Campanian to Lower Maastrichtian: probably in the Gualala Formation, Anchor Bay Member, Mendocino County, California (Area 8); Uhalde Formation, upper part, Volta area, Merced County, California (Area 11); Point Loma Formation near Carlsbad, San Diego County (Area 16); Point Loma Formation and re-deposited Point Loma Formation specimens in the Cabrillo Formation, Point Loma, San Diego County, California (Area 17); Rosario Formation near La Misíon (Area 18) and south of Punta China, Baja California, Mexico (Area 19). Upper lower to lower upper Maastrichtian: possibly from unnamed Upper Cretaceous strata, Covelo district, Round Valley, Mendocino County, California (Area 7); Moreno Formation, informal 'Garzas Sand' and informal 'Quinto Silt' members, Merced County, west side of San Joaquin Valley, California (Area 11); El Piojo Formation?, Negro Fork of Nacimiento River, north-east of Cape Martin, southern Santa Lucia Range, Monterey County (Area 12); El Piojo Formation, Pebblestone Shut-In west of Lake Nacimiento area, southern Santa Lucia Range, San Luis Obispo County, California (Area 13).

NORTH AMERICAN SPECIES ERRONEOUSLY OR VERY QUESTIONABLY IDENTIFIED AS OPINES

Early Jurassic

A bivalve reportedly of Early Jurassic (Pleinsbachian) age from the Bonzana Group south of Sproat Lake, Vancouver Island, British Columbia (Area 1), was figured as *Opisoma* sp. by Ludvigsen and Beard (1994, p. 64, figs 25, in part; 1997, p. 81, fig. 33, in part). No hinge information is available for this rather digitate bivalve that does not resemble any published figures of *Opisoma*. It is most likely not an *Opisoma*.

Early Cretaceous

Opis shastalis Anderson (1938, p. 121, pl. 4, figs 4–5) from the Budden Canyon Formation, probably the Huling Member, Ono area, Shasta County, California is a small bivalve (17 mm in height, 17 mm in length) described as being smooth, polished and pearly. The pearly shell indicates that this species does not belong to Crassatelloidea. Anderson (1938, p. 65) reported that the type specimen was found associated with the ammonite *Lytoceras* (*Gabbioceras*) *angulatum* Anderson, 1902 and the belemnite *Acroteuthis aboriginalis* Anderson, 1958. According to Murphy *et al.* (1969), these cephalopods are indicative of Aptian age.

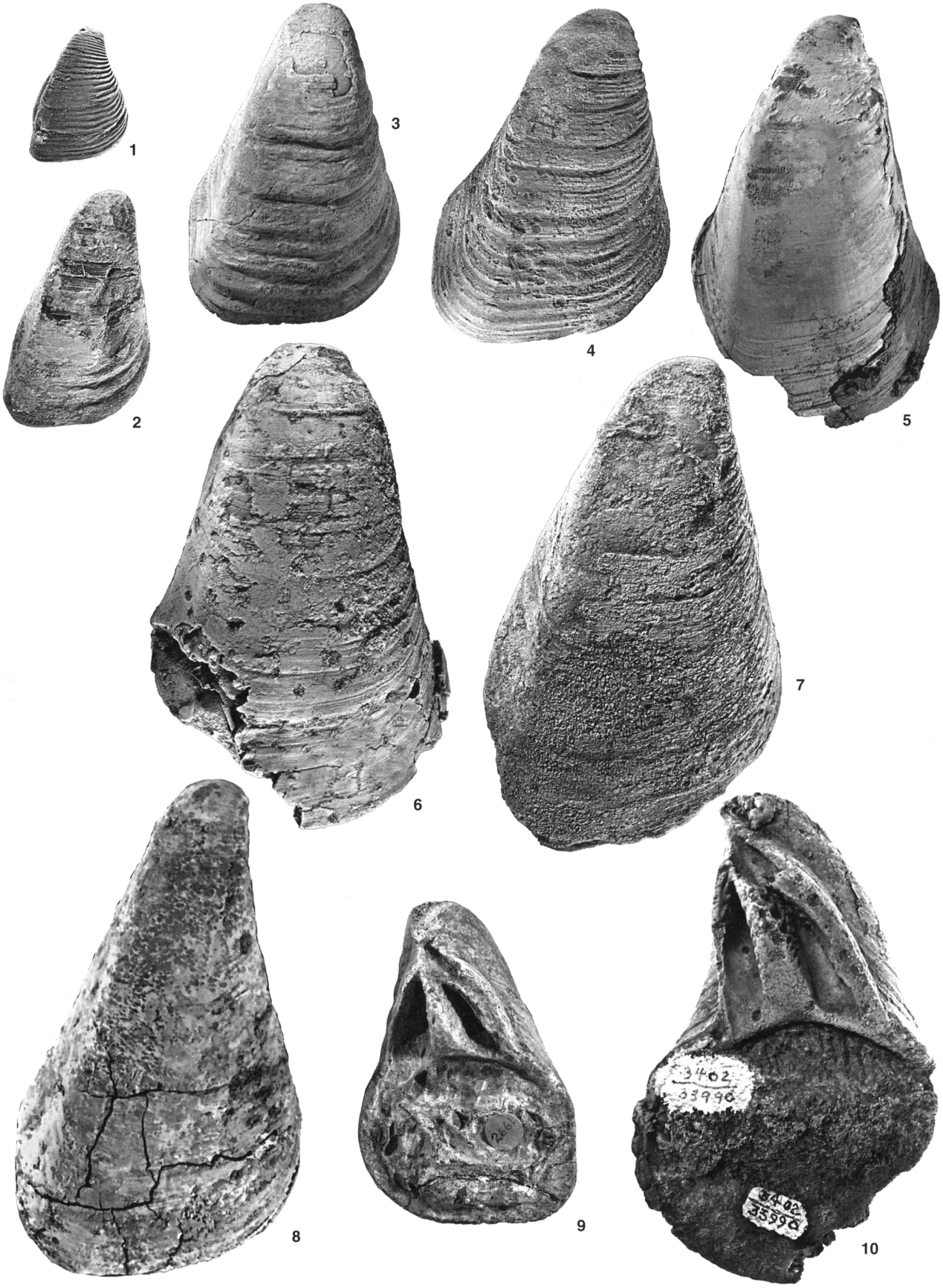
Opis texana Cragin, 1893 from the Albian Fredericksburg Group, Tom Green County, Texas (Akers and Akers 2002, p. 244), is based on a steinkern specimen. The hinge is unknown, and the species has never been figured.

Opis? *elevata* Stephenson (1952, p. 96, pl. 22, figs 2–6; Akers and Akers 2002, p. 244, fig. 217) from the Cenomanian Woodbine Formation, Templeton member, Grayson and Lamar counties, north-eastern Texas, is based on only five specimens, some of which are internal moulds. Overall shell shape of *Opis*? *elevata* resembles an *Opis*, but in Stephenson's (1952, pl. 22, fig. 14) illustration and in his description, the right-valve hinge of this species has two cardinals, whereas the right valve of *Opis* has one large cardinal (Chavan 1969). Possibly, the figured valve has a transposed hinge, but the teeth of *O.*? *elevata* appear tipped forward of the beak as in *Veniella* Stoliczka, 1871 (see Kirby and Saul 1995, pl. 2, fig. 2) rather than pointing more directly as the beak as in *Opis*. Additionally, *O.*? *elevata* is described as having both the lunule and escutcheon poorly delineated, whereas both *Opis* and *Hesperopis* have a well-delineated lunule and escutcheon.

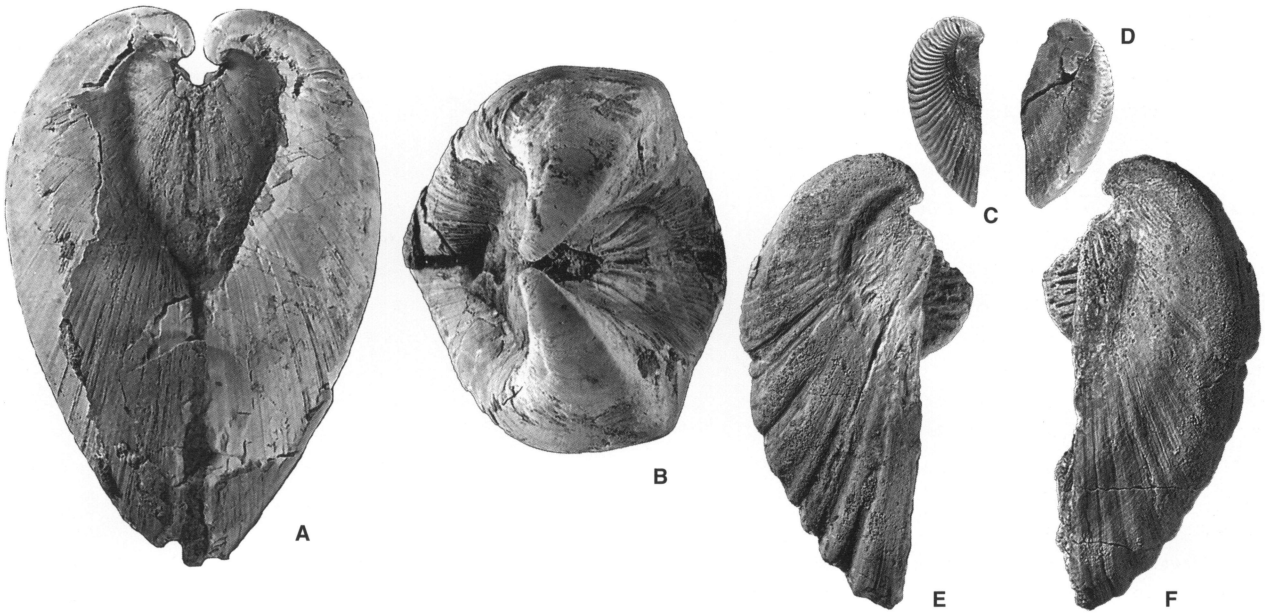
Opis? *elevata biangulata* Stephenson (1954, pp. 32–33, pl. 7, figs 15–16; Richards 1958, pp. 181–182, pl. 42, fig. 9) from the Cenomanian Raritan Formation near Sayreville, New Jersey is represented by three small and incomplete internal moulds. The hinge is unknown.

EXPLANATION OF PLATE 2

Figs 1–10. *Opis* (*Hesperopis*) *triangulata* (Cooper, 1894). All ×1. All right valves. Specimens coated with ammonium chloride. 1, lectotype, CASG 624 from west base of Pt. Loma, San Diego County, California. 2, hypotype, LACMIP 13542, LACMIP loc. 22661, exterior. 3, 9, hypotype, LACMIP 13543, LACMIP loc. 22661. 3, exterior. 9, interior. 4, holotype, CASG 29118.03, CASG loc. 29118, exterior. 5, hypotype, SDSNH 67148, SDSNH loc. 3403, exterior. 6, 10, hypotype SDSNH 33990, SDSNH loc. 3402. 6, exterior. 10, interior. 7, hypotype, CASG 29120.02, CASG loc. 29120, exterior. 8, hypotype, SDSNH 33989, SDSNH loc. 3384, exterior.



SQUIRES AND SAUL, *Opis (Hesperopis) triangulata*



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.

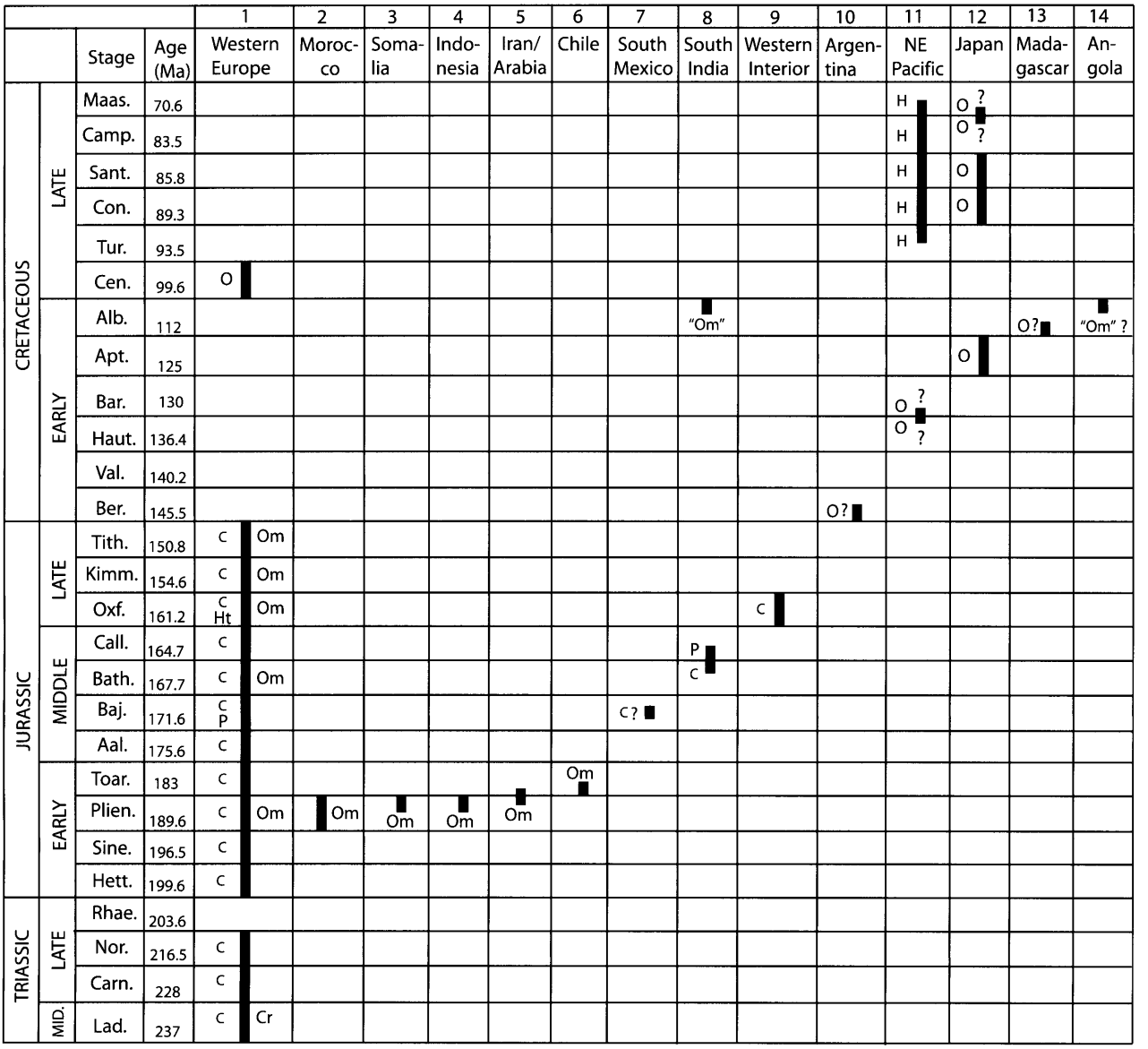
Rocks west of the San Andreas Fault have been tectonically transported northward. Although the distance of offset is controversial (see Kodama and Ward 2001), most geologists believe that it was between 300 and 500 km since the end of the Cretaceous (Wentworth *et al.* 1998). In spite of this tectonic 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.

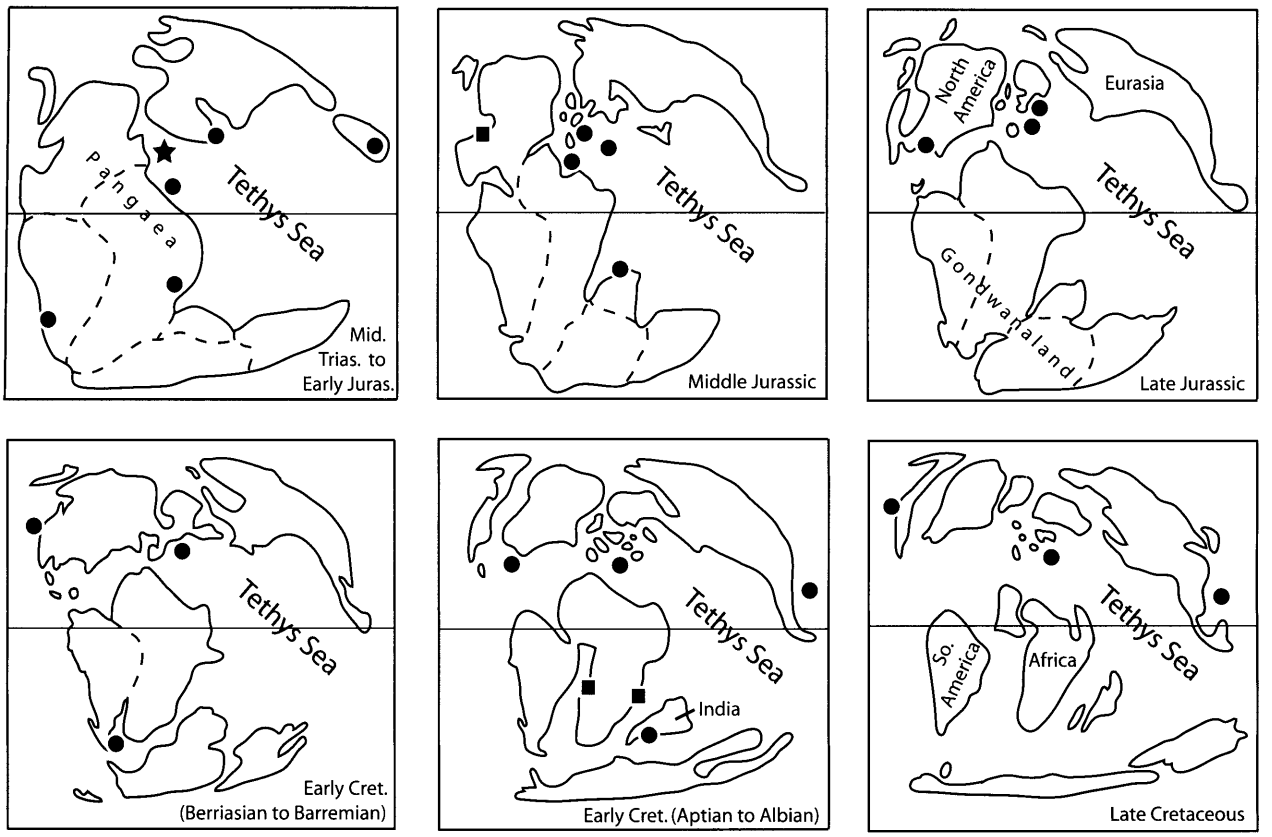
In summary, *Hesperopis* lived in warm-temperate waters, unlike its Old World tropical-water Jurassic predecessors. Elder and Saul (1993, p. 177) reported an *Opis*, herein identified as *O.* (*H.*) *rosarioensis*, to have been a warm-water, but not a 'Tethyan' (i.e. tropical) bivalve, and we concur.

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.



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.

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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, photo-inspected 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. 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. 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.