

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). *Hesperopsis* 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.

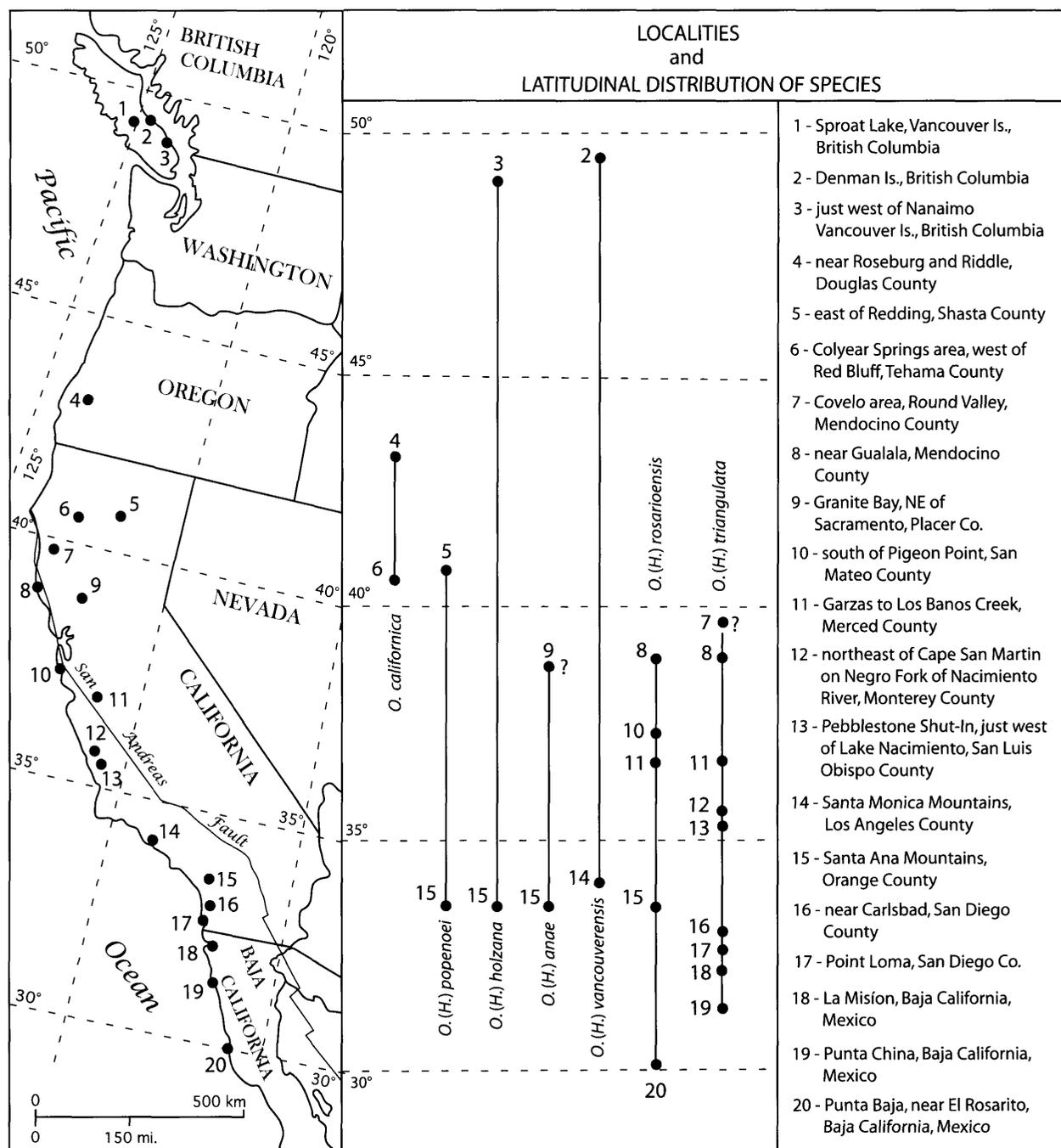
Key words: Bivalvia, astartids, opines, *Hesperopsis*, Cretaceous, palaeoecology, palaeogeography.

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, *Hesperopsis*. 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 *Hesperopsis*, (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.

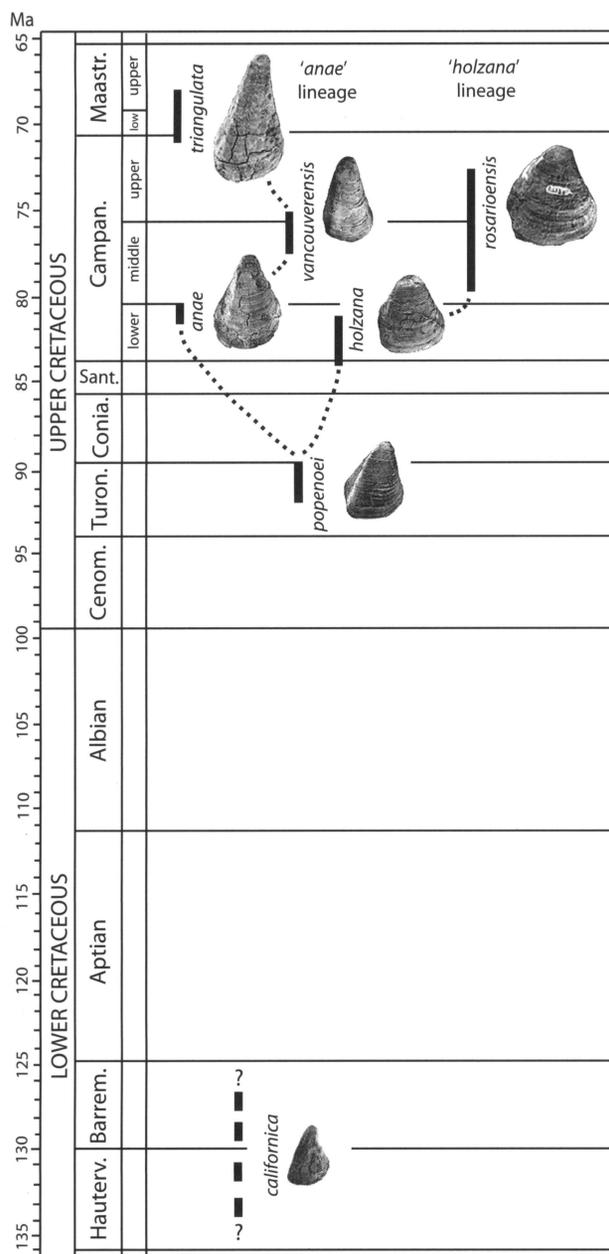


TEXT-FIG. 1. Localities map and latitudinal distribution of study area opine species. A question mark by a locality indicates that the specific identity of specimen(s) is uncertain.

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 2003a); 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 2003c); Holz Shale Member of the Ladd Formation (Saul 1982); Haslam Formation (i.e. see under 'Nanaimo Group') (Squires and Saul 2004a); Schulz Member of the Williams Formation (Filkorn 2007); Pigeon Point Formation (Squires and Saul 2003b); upper Cedar District Formation (Squires and Saul 2001; Squires and Saul 2006); Punta Baja Formation (Squires and Saul

2005); Gualala Formation (Squires and Saul 2004b); Point Loma Formation (Squires and Saul 2001) and 'Garzas Sand' and 'Quinto Silt' members of the Moreno Formation (Squires and Saul 2003b).

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 (1959b), 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 1959b; 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; Nilsson 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 meagre fauna consisting almost entirely of the donacid *Adelodonax altus* (Gabb, 1864) of Maastrichtian age (Saul 1989). Based on the work by Matsumoto (1959a, 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 PALAEOLOGY

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).

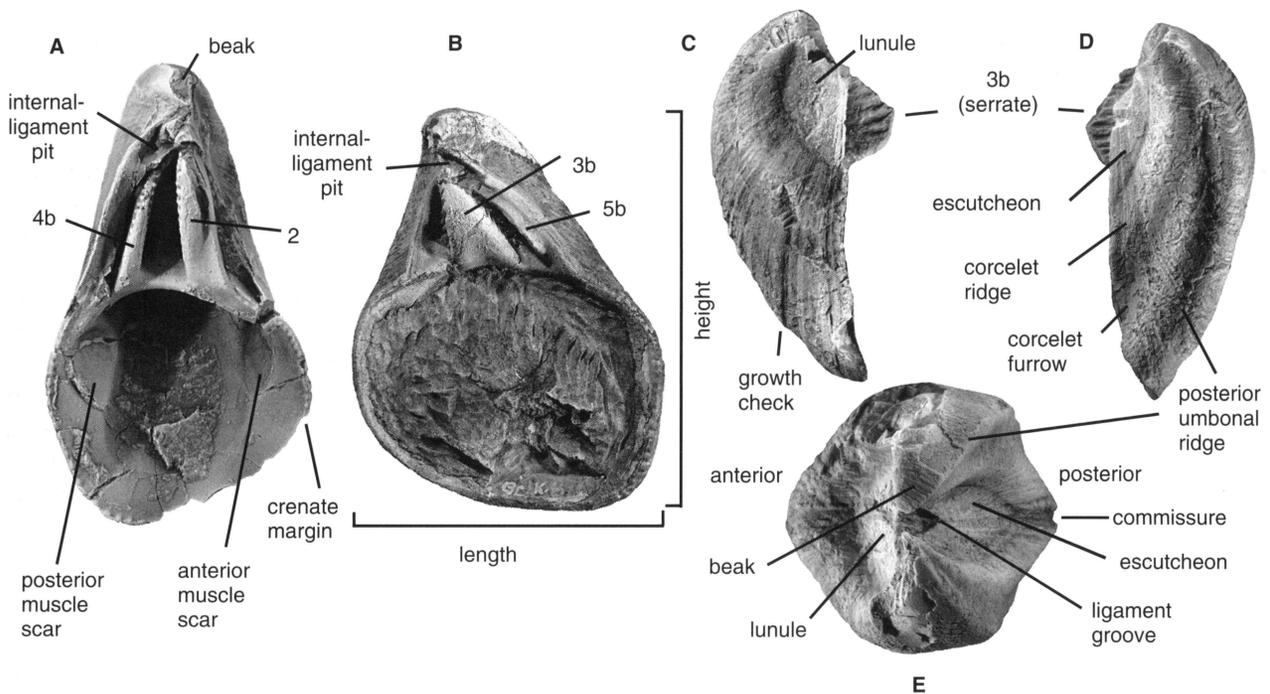
The ligament in most opines is external and is located in a groove just beneath the beaks. In *Hesperopis*, the ligament has two parts: an external part and a submerged, internal part. In this report, the external part is referred to as the 'ligament groove,' and the internal part as the

'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 $\times 1$. A, *Opes (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~~, LACMIP 9912, dorsal view. PARATYPE

13521

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; Eriphyliinae 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.

Prosocelus, 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 morpho-

logical 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 *Coelopis* (*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-