

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 antero-medial 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 Accorsi 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 *Coelopsis*, *Opisoma* and *Trigonopsis* 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).

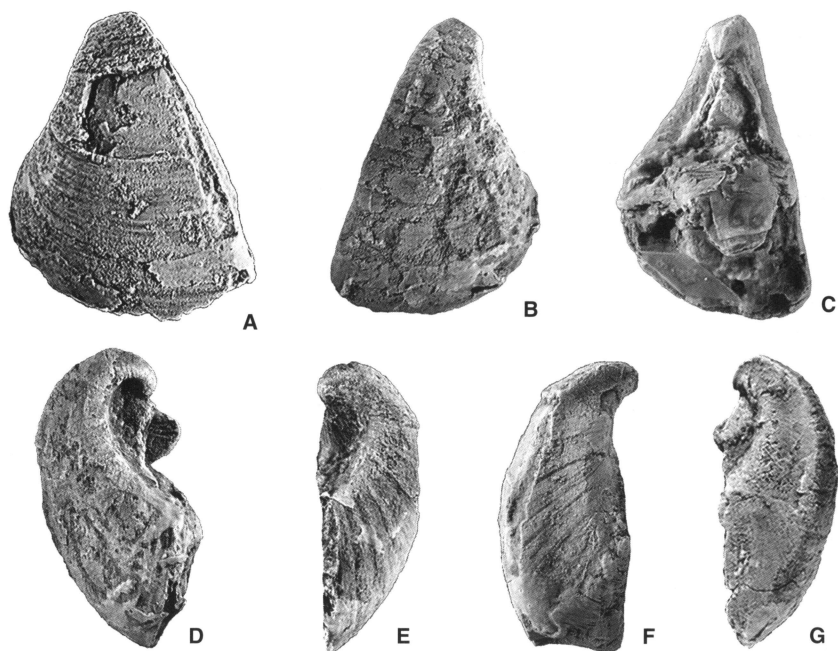
In the present state of description and depiction of opine genera, subgenera and species, it is very difficult to propose evolutionary relationships among them. Before these relationships can be determined, it will be necessary for workers to re-evaluate their local opine taxa. This will involve procuring 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 $\times 1$. Figs A, E-F, paralectotype, USNM 23055b, left valve. A, exterior. E, lunule view. F, escutcheon/corcellet view. B-D, G, lectotype, USNM 23055a, right valve. B, exterior. C, interior. D, lunule view. G, escutcheon/corcellet 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/corset 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 crassicolis* bed that crops out at Stephenson Place. *Buchia crassicolis* (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, southwestern 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, prosogyrous 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 cardi-

nals: 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 posteroventrally) 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 Stoliczka'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 Stoliczka 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