



TEXT-FIG. 5. *Opis (Hesperopis) popenoei* sp. nov. All $\times 1$. 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, LACMIP 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 *Hesp-*

eropis, 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 Dalmiapurpurn 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 *Hesperopsis* 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 *Hesperopsis*: (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 *Hesperopsis*.

The main evolutionary trends of *Hesperopsis* 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 'Ane' lineage became more elongate, as did their the teeth.

The beaks, umbones and hinges of the species of *Hesperopsis* 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 Maastriichtian.

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

Opis (Hesperopsis) 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 *Hesperopsis*. 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 *Hesperopsis*.

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, demarcated 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.