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REVIEW OF THE BIVALVE GENUS *PLICATULA* FROM CRETACEOUS AND LOWER CENOZOIC STRATA OF CALIFORNIA AND BAJA CALIFORNIA

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ABSTRACT—The Cretaceous and early Cenozoic species of the shallow-marine, warm-water bivalve *Plicatula* from California (United States) and Baja California (Mexico) are reviewed, and three new species are named. All of these species are representatives of *Plicatula* and not of the closely related taxon *Harpax*, which is associated with high-latitude and cool-water regions. The earliest-known Cretaceous species of *Plicatula* from the study area is *P. variata* Gabb, 1864, from Lower Cretaceous (Hauterivian Stage) strata in northern California, and our studies show it to be conspecific with *Plicatula onoensis* Anderson, 1958.

Plicatula allisoni new species is from Lower Cretaceous (Albian Stage) strata in Baja California, Mexico. *Plicatula modjeskaensis* new species is from Upper Cretaceous (Turonian Stage) strata in the Santa Ana Mountains, southern California. A possible new species from the same strata is also mentioned. A poorly preserved specimen of *Plicatula?* sp. is known from Upper Cretaceous (upper Campanian to lower Maastrichtian) strata in northern California.

The only Paleocene species of *Plicatula* from the study area is *P. ostreiformis* Stanton, 1896, from lower Paleocene strata of Lake County, northern California, and our studies show it to be conspecific with *Ostrea buwaldana* Dickerson, 1914. The only previously described Eocene species of *Plicatula* from the study area is *P. juncalensis* Squires, 1987, from lower middle Eocene ("Capay Stage") strata of Los Angeles County, southern California. *Plicatula surensis* new species is from middle lower Eocene ("Capay Stage") strata in Baja California Sur, Mexico. In addition, there is a *Plicatula?* sp. from Eocene strata of Baja California Sur, Mexico.

Although *Plicatula* is of uncommon occurrence north of Baja California, its thermophilic trait makes it useful in recognizing periods of warm climate.

INTRODUCTION

THE MARINE bivalve family Plicatulidae ranges from the Middle Triassic (Ladinian Stage) to Recent (Cox and Hertlein, 1969). Today, it is represented by only the genus *Plicatula* Lamarck, 1801, whose exact earliest appearance in the fossil record is not known. Cox and Hertlein (1969) reported its earliest record to be Middle Triassic (Ladinian), but their concept of genus *Plicatula* included *Harpax* Parkinson, 1811, as a junior synonym. Most modern workers now believe that *Harpax* is a valid taxon and is either a distinct genus, or possibly a subgenus of *Plicatula* (e.g., Poulton, 1991; Damborenea, 1993). *Harpax* has been reported from Upper Triassic strata in high-latitude areas in both the Northern and Southern Hemispheres, and its bipolar distribution is suggestive of climatic control (Damborenea, 1993).

Much work is needed to fully establish the relationship between *Harpax* and *Plicatula*, to document the place and time of origin of each taxon, and to reconstruct the paleobiogeographic distribution of each one.

The earliest record of *Plicatula* from the Pacific coast of North America is *P. perimbricata* Gabb, 1870, from the uppermost Triassic Modin Formation (Devils Canyon Member) of Shasta County, northern California (Sanborn, 1960, p. 25, pl. 2, figs. 26, 27) and from the uppermost Triassic Gabbs Formation, western Nevada (Laws, 1982). It is possible that this species might belong to *Harpax* because its peculiar oval shape, subdued sculpture, and projecting hinge area are similar to *Harpax* but are quite unlike the Cretaceous and Cenozoic *Plicatula* species reported on in this present study.

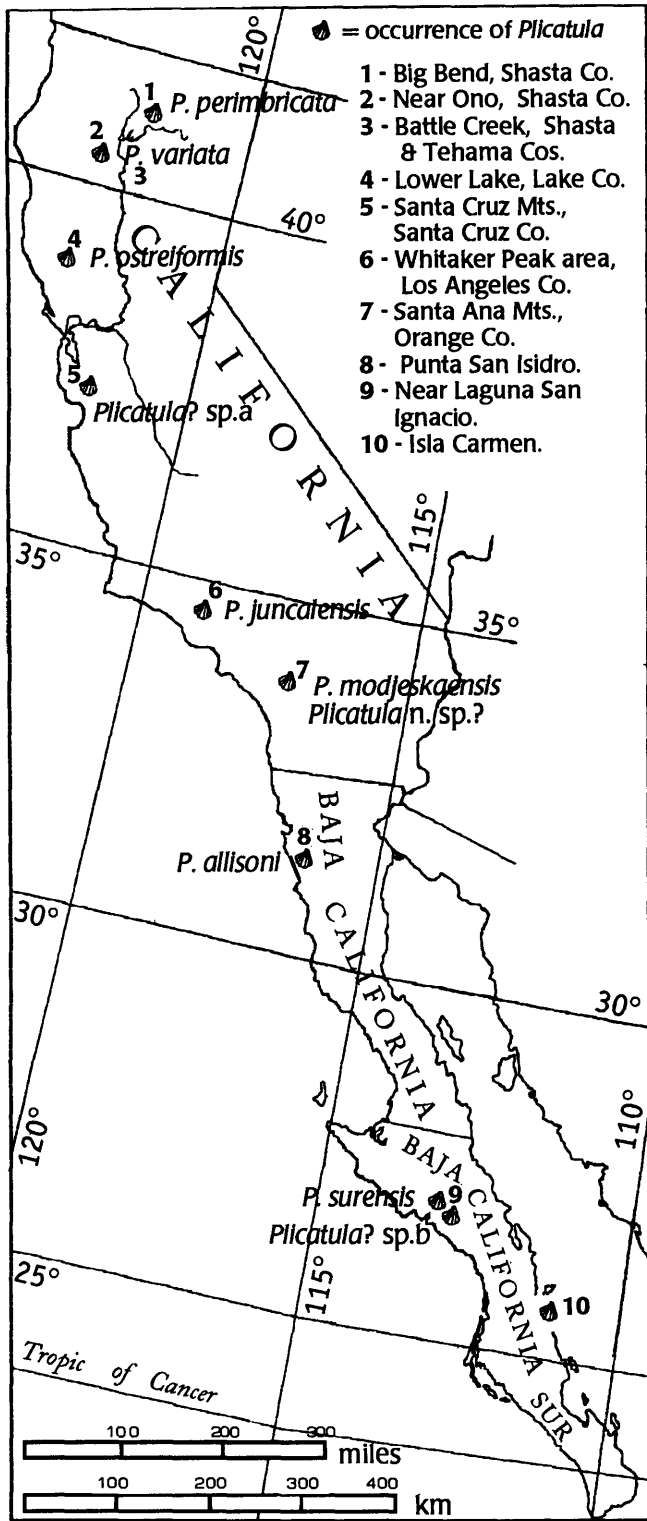


FIGURE 1—Index map for occurrences of *Plicatula* between northern California and southern Baja California Sur. *Plicatula* spp. near Isla Carmen (10) are *P. penicillata*, *P. spondyloopsis*, and *P. inezana*. Geologic ages of the *Plicatula* are plotted on Figure 2.

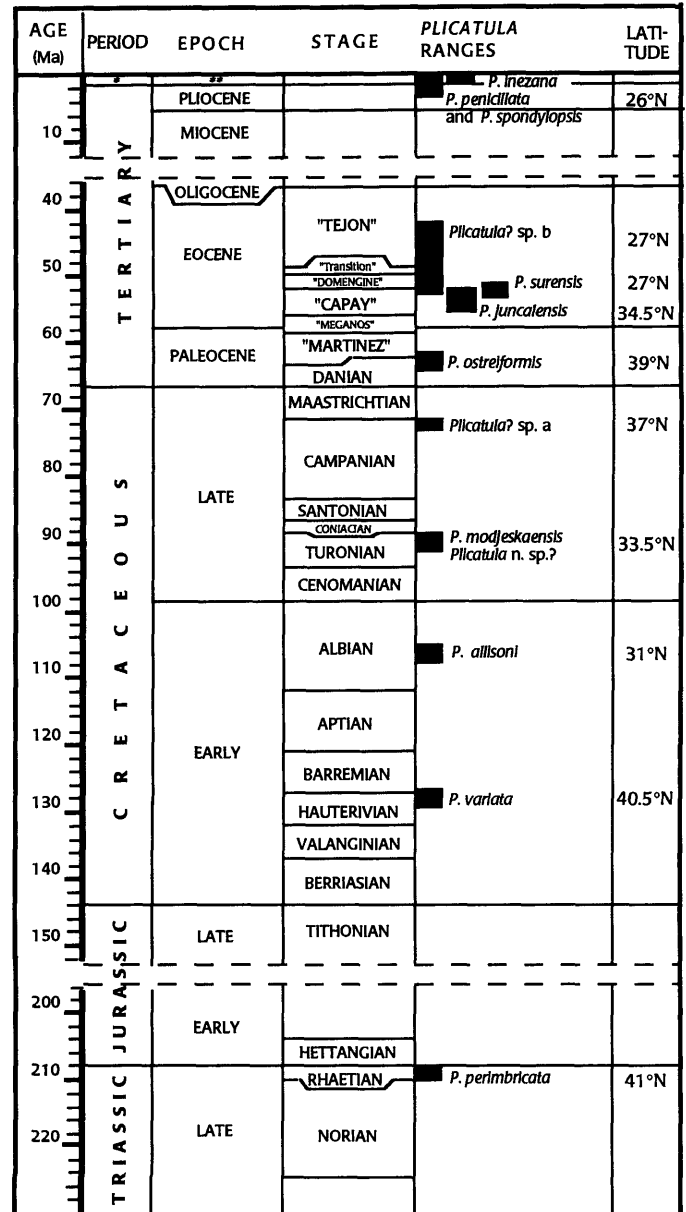


FIGURE 2—Time ranges of *Plicatula* in California and Baja California Sur. * = Quaternary; ** = Pleistocene. *Plicatula penicillata* and *P. spondyloopsis* range from Pliocene to Recent; *P. inezana* from Pleistocene to Recent. Latitudes given are approximate northernmost occurrences of each species.

Even though *Plicatula* was widespread during the Jurassic (Hallam, 1977), we know of no Jurassic occurrences of this bivalve in California and Baja California. Hallam (1977) reported, in a generalized checklist fashion, that Early Jurassic and Middle Jurassic *Plicatula* are present in his so-called "western margins of North America." He defined this area as including Alaska, British Columbia, Oregon, Nevada, and California, but he did not list any specifics regarding taxa or localities. *Plicatula* spp. have been reported, also in a checklist fashion, as present in Jurassic strata of the Arctic slope of northern Alaska (Imlay, 1955). It is likely that some of these species belong to genus *Harpax*, and a thorough study is needed.

During the Cretaceous, *Plicatula* was a widespread, warm-water bivalve (Kauffman, 1973). The earliest Cretaceous species

from the Pacific coast of North America is *P. variata* Gabb, 1864, from Lower Cretaceous strata (Hauterivian) of Shasta County, northern California (Figure 1). Occurrences of additional Cretaceous and Tertiary species of *Plicatula* from the Pacific coast of North America are plotted on Figure 1 and their age indicated on Figure 2. Three of these are new species, and one is a questionable new species. Two of the occurrences are questionable occurrences of genus *Plicatula*. None of these Cretaceous and Tertiary species included on Figure 2 is considered by us to represent the taxon *Harpax*.

The fossil record of *Plicatula* in California and Baja California is not continuous (Figure 2). The presence of confirmed *Plicatula* in this area includes the late Hauterivian, middle Albian, and Turonian. These times coincided with sea-level rises and the associated influx of warm-water, shallow-marine mollusks that show mainly a cosmopolitan and/or Tethyan aspect (Saul, 1986). Notable corresponding absences of species in the Cretaceous include the Berriasian through Valanginian, Barremian through early Albian, and Coniacian through early Campanian and Maastrichtian. These times in California and Baja California, as well as in the entire northeast Pacific region, coincided with lower sea levels, cooler water, and lower diversity of mollusks relative to the warm-water faunas (Saul, 1986).

The discontinuous aspect of the Cretaceous fossil record of *Plicatula* in California and Baja California also holds true for the Cenozoic record. The presence of *Plicatula* in this area includes the late Danian—"Martinez," "Capay," and most of the rest of the Eocene. The late Danian—"Martinez" coincided with a sea-level rise and the associated influx of warm-water, shallow-marine mollusks (Zinsmeister, 1983; Zinsmeister and Paredes-Mejia, 1988; Saul, 1986). The same is true for the "Capay," which was possibly the warmest time of the Cenozoic. During "Capay" time, the California and Baja California fossil record shows a very strong Tethyan aspect in the shallow-marine molluscan faunas (Squires, 1987; Squires and Demetron, 1992). Another pulse of warm-water mollusk immigration took place during the "Domengine Stage," but it was not as extensive as the earlier two of the early Cenozoic (Squires, 1984). From late Eocene through Miocene (Figure 2), there was a notable absence of any *Plicatula* in California and Baja California. This interval of time coincides to a worldwide deterioration of the greenhouse climate of earlier times and the beginning of a transition into an icehouse climate (Kennett, 1982).

Although there are no Pliocene and Pleistocene occurrences of *Plicatula* in California, there are species of this age in warm-water deposits of the Baja California region. The same is essentially true for the extant species. Today, four species of *Plicatula* live in the southern Gulf of California, two of which range into Ecuador (Keen, 1971). Two of these living species, *P. penicillafa* Carpenter, 1857, and *P. spondylopsis* Rochebrune, 1895, have a fossil record back to the Pliocene in Baja California Sur, Mexico (Moore, 1987), and *P. inezana* Durham, 1950, has a fossil record back to the Pleistocene (Durham, 1950; Keen, 1971). From early Paleocene to modern times, the northern limit of *Plicatula* from the Pacific slope of North America has been steadily shifting southward.

The noncontinuous distribution of *Plicatula* during the Cretaceous and Cenozoic in California and Baja California parallels that observed (Saul and Squires, in press) for thermophilic shallow-marine, neritic gastropods in this region.

Today, *Plicatula* comprises just a small number of living species, which are confined to tropical waters (Watson, 1930; Cox and Hertlein, 1969). They are oyster-like, with attachment to the substrate by means of the right valve. The gills of *Plicatula*, however, are more primitive than those in oysters, and this difference in gills may account, in part, for why *Plicatula* has

not been as successful as oysters during the Cenozoic (Watson, 1930).

Abbreviations used for catalog and/or locality numbers are: ANSP, Academy of Natural Sciences of Philadelphia; CASG, California Academy of Sciences, Geology Section, San Francisco; CIT, California Institute of Technology [collections now stored at LACMIP]; CSUN, California State University, Northridge; IGM, Instituto de Geología, Universidad Nacional Autónoma de México, Mexico City; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; UCMP, University of California, Museum of Paleontology, Berkeley; USGS, United States Geological Survey, Menlo Park, California; USNM, National Museum of Natural History, Washington, D. C.

SYSTEMATIC PALEONTOLOGY

Class BIVALVIA Linné, 1758

Family PLICATULIDAE Watson, 1930

Genus PLICATULA Lamarck, 1801

Discussion.—*Plicatula* is considered by most modern workers to be distinct from *Harpax* Parkinson, 1811. According to Poulton (1991), *Harpax* is an independent genus from *Plicatula* based on the fact that *Harpax* does not have a significant ligament pit and the teeth can be striate. Damborenea (1993) regarded *Harpax* as a subgenus of *Plicatula* based on the peculiar hinge and the peculiar scaly ornamentation of *Harpax*.

The species discussed below are considered by us to be representatives of *Plicatula* but not *Harpax*, based on the presence of a ligamental pit, absence of striae on the teeth, and/or the usual presence of well-developed radial ribbing.

Type species.—*Spondylus plicatus* Linné, 1758, by subsequent designation (Schmidt, 1818).

PLICATULA VARIATA Gabb, 1864

Figure 3.1–3.8

Plicatula variata GABB, 1864, p. 203, pl. 26, fig. 190; GABB, 1869, p. 252; STANTON, 1893, p. 251; DILLER AND STANTON, 1894, p. 443, 446; ANDERSON, 1902, p. 41–42; STEWART, 1930, p. 114–115, pl. 6, figs. 3–5; ANDERSON, 1938, p. 110; MURPHY, 1956, p. 2113, fig. 6; IMLAY, 1960, p. 179–180.

Plicatula onoensis ANDERSON, 1938, p. 111, pl. 4, figs. 1–3; IMLAY, 1960, p. 178.

Original description.—"Shell variable, usually somewhat curved. Lower valve attached by a portion of the surface, deep, radiately costate, ribs occasionally dichotomous. Upper valve flat or concave, plicate like the lower, but not so strongly, the ribs being sometimes obsolete. Hinge robust; muscular scar large; internal margin of the upper valve crenate; lower valve marked with pits corresponding with the teeth above. Average length, about .7 inch." [17.5 mm]. "This shell is extremely variable in outline and convexity; one of the commonest forms is illustrated in the figure" (Gabb, 1864, p. 203).

Supplemental description.—Shell medium (up to 27 mm high, most specimens about 16 mm high), semi-triangular, curved, subequilateral, very inequivalved, right valve strongly convex, left valve flattish to slightly concave with beak area usually protruding; right valve with small area of attachment in dorsal-posterior beak region; right valve with widely spaced primary radial ribs (interspaces about twice to 2.5 times as wide as the ribs), ribs in some cases bifurcated; rare specimens with single secondary radial riblet in interspaces, right valve with 8 to 14 (usually 8 to 9) primary radial ribs (including bifurcated ribs); radial ribs on unabraded specimens with valve profile broken by growth interruptions, radial ribs having node-like appearance with strongest "nodes" along anterior region of valve; left valve with closely spaced, wide primary radial ribs, bifurcation com-

