

subtruncate. Cardinal area bearing as many as five to six chevron-shaped, symmetrical, well-defined ligamental ridges/grooves. Hinge plate arched. Hinge bearing prominent taxodont teeth in two series, with anterior series longest; 12 teeth in anterior series and 10 in posterior series. Mesial teeth near beak thin and subvertical. Distal teeth thicker and more oblique. Concentric growth lines very numerous, growth checks can be common.

Etymology.—The new species is named for the Yolo Formation.

Types.—Holotype LACMIP 13600, paratype LACMIP 13601, and unfigured paratype LACMIP 13602, all three from LACMIP loc. 28757; paratype CASG 70694, CASG loc. 31918.

Occurrence.—Middle to upper Turonian lower Yolo Formation, Thompson Canyon, Yolo County, northern California (Area 15).

Discussion.—Four specimens were detected: three specimens from LACMIP loc. 28757, and one from CASG loc. 31918. Locality details are wanting for the latter locality, but based on lithology and associated identical-looking small fragments of rudistid bivalves, CASG loc. 31918 could be the same locality as LACMIP loc. 28757 or very near to it. According to LACMIP records, LACMIP loc. 28757 is in the Yolo Formation in Thompson Canyon. When plotted on Matsumoto's (1960, p. 38) geologic map of the area, this locality is in the lower part of the Yolo Formation, near the contact between the Yolo Formation and the underlying Venado Sandstone. Based on benthic foraminifera, Almgren (1986, table 2) assigned the lower Yolo Formation in the vicinity of Thompson Canyon to an early late Turonian age.

Also at LACMIP loc. 28757, five specimens of *G. pacifica* were detected. The new species resembles *G. pacifica*, but the new species differs by commonly having a subquadrate shape, more-inflated valves, steeper anterodorsal and posterodorsal slopes, more-inflated valves, posteriorly angulate umbones, and sulcate posterodorsal margin. In addition, one specimen (Fig. 5.8) of the new species has very narrow and widely spaced radial riblets.

Genus GLYCYMERITA Finlay and Marwick, 1937

Type species.—*Glycymeris concava* Marshall (1917, p. 459, pl. 36, fig. 42), by original designation; early Paleocene (Danian = Wangaloan), Boulder Hill, South Island, New Zealand. Marwick (1923, pl. 7, figs. 1, 4), Finlay and Marwick (1937, p. 22, pl. 2, figs. 1, 6), Fleming (1966, pl. 10, figs. 112, 113; pl. 11, fig. 121), and Beu and Maxwell (1990, p. 78, pl. 1, figs. e, h) also described and illustrated the type species.

Diagnosis.—Subquadrate to quadrate, rarely trigonal. Umbones wide and prominent, moderately inflated to well inflated, both sides strongly depressed and shouldered; valves can be produced posteriorly. Shell surface with many prominently raised radial ribs with well defined narrow interspaces. Radial striae rarely evident. Cardinal area symmetrical or nearly so. Cardinal-base area bearing numerous strong ligamental ridges/grooves. Hinge plate arched to strongly arched. Taxodont teeth stout.

Discussion.—Nearly all previous workers (e.g., Newell, 1969; Tashiro, 1971; Hayami, 1975) have treated *Glycymerita* as a subgenus of *Glycymeris*, but Beu and Maxwell (1990) used *Glycymerita* as a distinct genus, based on its strongly subquadrate shape and "relatively prominent sculpture." They recognized two subgenera: *Glycymerita sensu stricto* and *Manaia* Finlay and Marwick, 1937.

Finlay and Marwick (1937) did not discuss how *Glycymerita* differs from *Glycymeris*. Comparison between a borrowed GNS specimen of *Glycymerita concava* and several LACM specimens of *Glycymeris glycymeris*, as well as other specimens of extant species of *Glycymeris* stored in the LACM Collection, revealed that *Glycymerita* differs from *Glycymeris* by having a non-circular shape, sulcate posterodorsal slope, rectangular and prominently raised radial ribs, prominent interspaces between ribs (never linear), prominent ligamental ridges/grooves (base of cardinal area never smooth), and commonly a more arched hinge plate. The umbones of *Glycymerita* are commonly more prominent and commonly more inflated than on *Glycymeris*. In addition, *Glycymerita* can be slightly elongate posteroventrally. Although photographs of *Glycymeris* in the popular literature look like the specimens have radial ribs, these ribs are mostly demarcated by color change because the surfaces of these valves are nearly smooth. *Glycymerita* shells are up to a known maximum length of approximately 84 mm, whereas *Glycymeris* shells are up to a known maximum length of 100 mm.

Glycymerita differs from most *Glycymeris* by having a strongly shouldered shell that can be posteriorly truncate but never circular or subcircular. There are some large-sized modern species of *Glycymeris*, like *Glycymeris (G.) gigantea* (Reeve, 1843), *Glycymeris (G.) undata* (Linnaeus, 1758) from Venezuela, and *Glycymeris (G.) pilosa* (Linnaeus, 1767) from the Mediterranean Sea that have a strongly shouldered shell with a straight hinge and stout teeth, just like *Glycymerita*. The study area quadrate forms of *Glycymerita* differ from these species by having wider beaks, commonly more inflated shells, raised radial ribs, and less degenerate mesial teeth. In addition, these modern shells, which are smooth or nearly smooth, are covered by radial striae. Radial striae are only rarely preserved on the study area *Glycymerita*.

As discussed earlier in this present report, *Manaia* Finlay and Marwick (1937) and *Hanaia* Hayami, 1965 have been used as subgenera of *Glycymerita*, but both are treated herein as junior synonyms of *Glycymeris*. *Glycymerita* differs from both by having a much larger and more inflated shell, much stronger sculpture with much less common radial striae, more pronounced antero- and posterodorsal shoulders, thicker teeth inclined at a lower angle, and teeth more extended and closer to the periphery of the hinge plate.

At study area localities where at least 10 specimens were collected, the specimens of all the species of *Glycymerita* commonly show variation in the shape of the anterodorsal and posterodorsal slopes, resulting in both subquadrate and quadrate shapes, as well as, in some cases, intermediate shapes between these two forms. Each species will have a predominant form, however. The subquadrate form is predominant in the Cretaceous species, and the quadrate form is predominant in the Paleocene species (e.g., *G. concava*, *G. major*).

Although previous workers have reported that modern glycymeridids range in shape from subcircular to subtriangular (Newell, 1969; Boss, 1982), observations about any variability in shape among populations of species from the same lot are commonly not emphasized. Powell (1992), however, reported that *Glycymeris septentrionalis* (Middendorff, 1849) from the Pleistocene and Holocene of the northeastern Pacific is a very variable species and that specimens from a single locality show variability in the shell outline and size and shape of the hinge. He also reported that over the geographic range of the species, all the shell features vary considerably. Our cursory examination of the valves of

several modern glycymeridid species contained in the LACM collection revealed that even small populations (four to six specimens) of some species, like *Glycymeris glycymeris* (Linnaeus, 1758) from England, *Glycymeris pilosa* (Linnaeus, 1767) from the Mediterranean Sea, and *Glycymeris decussata* (Linnaeus, 1758) from Rio de Janeiro, Brazil show both variable shapes, even in the same lots.

Glycymerita resembles the genus *Tucetona* Iredale, 1931, in having raised radial ribs, but *Tucetona* differs by commonly having a subcircular to subtrigonal shape (i.e., fan shape), consistently lowly convex valves, fewer (approximately 25) and wider ribs that can be progressively nodulose ventrally, no radial striae, and broader crenulations on the shell interior. Tschudin (2001) reported that although *Tucetona* has a thin periostracum, it never has radial striae. He also reported that *Tucetona* is opisthogyrate, but that feature is very difficult to discern, even on Recent specimens.

GLYCYMERITA VEATCHII (Gabb, 1864)

Figure 3.1, 3.2; Figures 6–9, Table 1

- Axinaea veatchii* Gabb, 1864, p. 197, pl. 25, figs. 183, 183a.
Pectunculus veatchii (Gabb). Stanton, 1896, p. 1039–1040, pl. 64, fig. 1; Whiteaves, 1903, p. 391–392, pl. 47, figs. 3, 4.
Glycymeris veatchii (Gabb). Crandall, 1907, p. 43–44; Branner et al., 1909, sheet 2, fig. 4; Stewart, 1930, p. 70–71, text-fig. 1, pl. 1, fig. 7; Smith, 1945, p. 41–42, figs. 1, 9; Anderson, 1958, p. 96–97, unfig.; Saul, 1959, p. 68–70; Popenoe, 1973, pl. 3, fig. 30 [figure repeated in Stadum, 1973, pl. 2, fig. 5].
Glycymeris suciensis McLellan, 1927, p. 131, pl. 17, figs. 7, 8.
Cucullaea suciensis McLellan, 1927, p. 132, pl. 17, figs. 4–6.
Glycymeris veatchii var. *anae* Smith, 1945, p. 42, figs. 3, 7.
Glycymeris veatchii var. *reddingensis* Smith, 1945, p. 42, figs. 2, 4.
Glycymeris (*Glycymerita*) *veatchii* (Gabb). Nicol, 1950, text figs. 1a–c; fig. 1c repeated in pl. 21, fig. 12; pl. 22, fig. 16.
Glycymeris veatchii var. (Gabb). Popenoe, 1954, p. 19, fig. 4.6.
Glycymeris shastaensis Anderson, 1958, p. 97–98, pl. 18, figs. 8–10.
Glycymeris pentzana Anderson, 1958, p. 98, pl. 74, figs. 2, 2a.
Glycymeris suciensis McLellan. Dailey and Popenoe, 1966, fig. 3 (checklist).
Glycymeris apletos Dailey and Popenoe, 1966, p. 8, pl. 1, figs. 1, 5, 6.
Glycymeris (*Glycymerita*) *anae* Smith. Elder and Saul, 1993, pl. 1, fig. 3.
Glycymeris (*Glycymerita*) *apletos* Dailey and Popenoe. Elder and Saul, 1993, table 1, pl. 1, fig. 4.
Glycymeris (*Glycymerita*) *veatchii* (Gabb). Tashiro, 1971, pl. 27, figs. 33a, b.
Glycymeris (*Glycymerita*) aff. *apletos* Daily and Popenoe. Tashiro, 1971, pl. 27, figs. 34, 35.
Glycymerita veatchii (Gabb). Ludvigsen and Beard, 1994, p. 76, fig. 42 (views)—text and illustrations repeated in Ludvigsen and Beard, 1997, p. 98, fig. 52 (4 views).

Diagnosis.—Shell size small to large. Subquadrate (most specimens) to quadrate. Shell height slightly greater than shell length and with well-inflated valves. Ribs raised, narrow to very wide, and narrowly to moderately widely spaced.

Description.—Shell size small to large, up to height 79.8 mm and length 82.8 mm (same specimen); commonly slightly higher than long, height/length ratio = 0.94–1.13. Subquadrate (most specimens) to quadrate; posteroventral margin very rarely slightly oblique; early specimens rarely subcircular. Subquadrate forms higher than long, strongly inflated (single-

valve convexity/height ratio = 0.45–0.54), posterodorsal slope truncate. Quadrate forms slightly longer than high, moderately inflated (single-valve convexity/height ratio = 0.31–0.48), both antero- and posterodorsal slopes truncate. Equivalved and slightly inequilateral. Sculpture consisting of 35–47 ribs, narrow to wide, and closely to moderately widely spaced; three to six ribs per 10 mm of distance, measured parallel to length at medial part of valve approximately 40 mm ventral of beak. Interspaces very narrow to moderately wide (up to one-half width of adjacent ribs). Ribs and interspaces commonly narrower on posterior side of valves. Superimposed radial striae very rarely preserved. Beaks central, prominent, incurved, and orthogyrate. Umbones commonly wide, posterior side bearing weak angulation with posterodorsal slope sulcate; umbones variable in degree of dorsal elongation. Posterodorsal margin subtruncate (rarely with small irregular protuberances on a few specimens) on subquadrate-shaped forms; posterodorsal margin looks similar to, but slightly flatter, than anterodorsal margin on quadrate-shaped forms. Cardinal area bearing up to nine to 10 symmetrical, chevron-shaped, well-defined ligamental ridges/grooves. Hinge plate strongly arched, can be bent nearly vertically at one or both margins. Hinge bearing prominent taxodont teeth in two series, with anterior series longer: up to 12 teeth in anterior series and 11 teeth in posterior series; anterior series commonly with one to three more teeth than posterior series, but both can have same number of teeth. Mesial teeth near beak thin and vertical. Distal teeth strong, thick, nearly vertical to nearly horizontal and straight, slightly curved or chevron-shaped (chevrons pointing toward beak). All teeth minutely serrate on both sides. Dimyarian, posterior adductor-muscle scar smaller and bearing small, raised myophoric flange along its anterior side. Pallial line entire. Interior shell margin with moderately strong, narrow crenulations. Concentric growth lines innumerable; growth checks can be common.

Types.—Of *Axinaea veatchii* Gabb, 1864, lectotype ANSP 4419, paralectotypes ANSP 4419a (both paralectotypes missing), Chico Formation, Tuscan Springs, Tehama County, California. Of *Glycymeris suciensis* McLellan, 1927, holotype UWBM 15008 and paratype UWBM 15009, Cedar District Formation, Sucia Island, San Juan County, Washington. Of *Cucullaea suciensis* McLellan, 1927, holotype UWBM 15010, Cedar District Formation, Sucia Island, San Juan County, Washington. Of *Glycymeris veatchii* var. *reddingensis* Smith, 1945, syntype LACMIP 4085 and syntype LACMIP 4086 (specimen missing); both from Redding Formation, Shasta County, California. Of *Glycymeris veatchii* var. *anae* Smith, 1945, holotype (designated here) LACMIP 4082, Ladd Formation, upper Holz Shale Member, Santa Ana Mountains, Orange County, California; and paratype (designated here) LACMIP 4081, Williams Formation, Pleasants Sandstone Member, Santa Ana Mountains, Orange County, California. Of *Glycymeris shastaensis* Anderson, 1958, holotype missing (CASG Collection), Redding Formation, Shasta County, California; paratype CASG 27830.02. Of *Glycymeris pentzana* Anderson, 1958, CASG holotype 61874.01, formation unknown. Of *Glycymeris apletos* Dailey and Popenoe, 1966, holotype LACMIP 89891, Jalama Formation, Santa Barbara County, California.

Occurrence.—Middle to upper Turonian to upper Campanian. MIDDLE TO UPPER TURONIAN: Redding Formation, lower Frazier Siltstone Member, east of Redding, Shasta County, California (Area 8). CONIACIAN: Hornbrook Formation, Osburger Gulch Sandstone Member, at Young