Gyrodes and *Biplica* are the only gastropods commonly found in abundance in these assemblages. Saul and Popenoe (1962, p. 323) suggested a shallow (7–40 m) water depth for these assemblages, and Saul (1973) reported that they inhabited inner sublittoral, current-disturbed, muddy sand substrates. The late Paleocene *Glycymerita major* is found with common to abundant shallow-marine bivalves (e.g., *Crassatella*, *Venericardia*) and common to abundant shallow-marine gastropods (e.g., *Turritella*).

The shallow-marine paleoenvironment of the studied species is in keeping with the environment of modern glycymeridids. Modern species burrow in sand and other sediments with large particles (Coan et al., 2000). They never live in brackish waters or in deep oceans. They are suspension feeders with large filibranch gills. Lacking siphons, their shells are normally just covered by the sediment, with their posterior-ventral margin exposed at the sediment surface. The interior margins of the valves of nearly all glycymeridids are crenulate (Boss, 1982), and, according to Stanley (1970), this morphologic feature is almost entirely restricted to shallow burrowers. Individuals of the glycymeridid *Tucetona pectinata* (Gmelin, 1791) have been observed leaving meandering furrows behind them as they crawl along the substratum in the process of trying to bury themselves. They burrow sluggishly with the commissure vertical, but their life orientation is such that they tend to lie on one valve or the other, probably in order to allow the anterior inhalent current to draw water through a minimum thickness of sediment. They keep the plane of commissure tilted sufficiently upward in order to keep the posterior current openings exposed at the sediment surface (Stanley, 1970). Despite its large foot, *Glycymeris glycymeris* is a mechanically inefficient and very sluggish burrower largely because its ligament is weak and unable to brace the shell firmly against the sediment. It occupies unstable sandy and gravelly habitats in water depths generally between 3 and 130 m, and, its habitats can be commonly swept by strong currents. This species is generally uncommon in depths less than 10 m (Thomas, 1975).

No epibiont boreholes and only nine predatory boreholes were seen on any of the study area specimens. All the boreholes are in valves of *Glycymerita veatchii*. Three of these specimens are Coniacian age (Member IV or V of the Redding Formation), one is of middle Campanian age (Chatsworth Formation), and five are of late middle Campanian age (Pleasants Sandstone Member of the Williams Formation). Most of these specimens were detected in lots consisting of 10 specimens or more. All of the boreholes are on small specimens between 11 and 19.5 mm in length. The boreholes occur on both left and right valves, and the locations of the boreholes occur 1) near the center of the umbones approximately one-third the shell height from the beak, 2) one-third the shell length from the medial-posterior region, or 3) near the ventral margin.

Warm-temperate conditions existed in the study area during the Late Cretaceous (Saul, 1986; Saul and Squires, 2008; Squires and Saul, 2009). In the Yolo Formation at LACMIP loc. 28757 and CASG loc. 31918, both in Thompson Canyon, the middle to late Turonian *Glycymeris pacifica* and *G. yoloensis* occur with fragments of rudistid bivalves. In the Gualala Formation, *Glycymerita banosensis* occurs with the rudistid-bivalve *Coralliochama orcutti* White. The presence of rudistids is palaeoclimatically significant because they serve as indicators of at least marginal tropicality based on their numerous low-latitude occurrences (Sohl, 1987). During the Paleocene, the climate in the study area was subtropical (Squires, 2003). These paleoclimates are in keeping with the climatic conditions of modern glycymeridids, which are mostly restricted to tropical and temperate waters, but, at least one species extends into boreal waters (Matsukuma, 1986; Coan et al., 2000).

PALEOBIOGEOGRAPHY OF THE STUDIED GLYCYMERIDIDS

Saul (1986, fig. 1) depicted the relative-ocean temperatures and the global cycles of sea-level changes for the northeast Pacific area during the Cretaceous. A warming trend and the high sea-level stand during the Turonian help explain the first occurrence of glycymeridids and the widespread distribution of *Glycymeris pacifica* in the study area during that time. The Coniacian and Santonian were cooler and associated with lower sea levels, thus probably accounting for the restriction of *Glycymerita veatchii* to just northern California during this interval. The Campanian and Maastrichtian were associated with a general warming trend and overall rising sea levels, thus providing excellent conditions for *Glycymerita* to spread.

As summarized by Saul and Squires (2008), most geologists agree that all Cretaceous rocks west of the San Andreas Fault in California (Fig. 1) have been moved tectonically northward 300 to 500 km in post-Cretaceous time. The present latitudinal location of approximately 49°30′N (i.e., Nanaimo Group, Vancouver Island, British Columbia) for deposits yielding *Glycymerita veatchii* (Fig. 1) is suggested to differ from the original latitudinal location because of the effects of terrane transport. Work on Cretaceous acilid bivalves (Squires and Saul, 2006), volutid gastropods (Saul and Squires, 2008), and opine bivalves (Squires and Saul, 2009) support the paleomagnetism and rudist-bivalve analyses by Kodama and Ward (2001) that the Nanaimo Group was 1) originally deposited no farther south than 40°N (i.e., northern California) and 2) tectonically displaced during post-Cretaceous time to its current position in the Vancouver Island area.

The present locations (Areas 1 and 2) of the lower Maastrichitan strata containing *Glycymerita aleuta* in Alaska differ from their original locations because of the effects of collision of allochthonous terranes with the North American continental margin. The Kaguyak Formation (Area 1) and the Matanuska Formation (Area 2), which contain the new species, plot in the Peninsular terrane that makes up the western half of the Wrangellia-composite terrance complex (see Plafker et al., 1994, fig. 2). This composite terrane was probably located just off the coast of southern Canada and isolated by a narrow seaway from older terranes to the east until accretion of the Peninsular terrane to North America took place in the latest Cretaceous time. Tectonic movements since the early Tertiary have caused counter-clockwise oroclinal rotation and northwestward displacement of the Peninsular terrane relative to the continental margin (Plafker et al., 1994, figs. 15c, d).

The geologically youngest specimens (late Campanian) of *Glycymerita veatchii* became geographically restricted to the Jalama Formation (Area 23) in what is now the Santa Barbara County area in the westernmost part of the Transverse Ranges, southern California. Based on paleomagnetic studies, this area was originally approximately 100 km south of its present location, and during the Neogene, it was tectonically rotated clockwise 90° to its present location (Hornafius, 1985).

EVOLUTIONARY TRENDS OF THE STUDIED SPECIES

The middle to late Turonian *Glycymeris yoloensis* is intermediate in morphology between *Glycymeris pacifica* and the earliest *Glycymertia veatchii*, and apparently *G. yoloensis* apparently represents some intermediate state between these two genera. *Glycymeris yoloensis* has the low ribs, well preserved radial striae, and, in a few cases, the subcircular shape of *G. pacifica* but also has a subquadrate shape (in most cases), moderately inflated valves, posteriorly angulate umbones, and sulcate-posterodorsal slope characteristic of *G. veatchii*. In addition, *G. yoloensis* can have some raised radial ribs, and raised radial ribs are a characteristic of *G. veatchii*.

Glycymeris veatchii shows more morphologic change over time of all the studied species. It lasted 19.5 million years (Fig. 2), and during this time it gradually increased nearly fivefold in size. Its shells acquired longer and much stronger hinge teeth, thicker walls, stronger marginal denticulations, and more truncate posterior dorsal margins. Its shells also commonly became more inflated, and the width of their radial ribs showed considerable morphologic variation. Radial ribs became narrower than usual on many specimens in the lower middle Campanian upper Holz Shale Member (Area 28) and in the upper middle Campanian Punta Baja Formation (Area 32), whereas radial ribs became wider than usual on many specimens in the upper Campanian Jalama Formation (Area 23). Using the observations of Stanley (1970) relating shell form to life habits of burrowing bivalves, it seems likely that the larger size, inflated valves with thick walls, and strong radial ribs served as stabilizers. In addition, the radial ribs could have facilitated burrowing by producing a serrated ventral margin. The strong hinge teeth and strong marginal crenulations would have prevented shearing of the valves parallel to the commissure plane. The truncate posterior dorsal margin would have been an advantage for feeding.

The largest of the studied species are late middle Campanian to late Campanian *Glycymerita veatchii* (see Fig. 2), which commonly attained "giant size" (i.e., greater than 66 mm in length), with a maximum length of approximately 84 mm. They co-existed with some other large bivalves (e.g., *Calva*, *Crassatella*), as well as some large gastropods (e.g., *Volutoderma*). The "giant-sized" *Glycymerita veatchii* contradict Thomas' (1975) erroneous statement that Cretaceous glycymeridids are characterized by modest size, with heights, or lengths, rarely exceeding 25 mm.

Rare specimens of *Glycymerita veatchii* and especially some specimens of *G. banosensis* exhibit oblique posterior elongation. Purchon (1939) and Holme (1961) found that bivalves from quieter water tend to be more elongate posteriorly than those that from wave-swept water. Thomas (1975) suggested that elongation of the shell allows for slightly deeper burial. He also reported that living glycymeridids without a hairy periostracum (i.e., without radial striae) live in quieter waters.

The study area species of *Glycymerita* show a near constancy in number of adult hinge teeth (approx. 20). All the study area species of *Glycymerita* are subquadrate to quadrate in shape, except for *G. aleuta*, whose shape is trigonal to subquadrate. The subquadrate shape was most predominant during the Late Cretaceous, and the quadrate shape was most predominant during the Paleocene.

There is a nearly continuous record of *Glycymerita* in the study area. The only significant gap in its fossil record is coincident with the early Paleocene (Danian). Strata of this age are underrepresented in the study area because of tectonic uplift and associated erosion (see Zinsmeister, 1983). In the study area, the Maastrichtian/Paleocene boundary is not marked by a drastic change in glycymeridid morphology. The quadrate shape of *Glycymerita banosensis* is very similar morphologically to *Glycymerita major*. The latter species is also very similar morphologically to *Glycymerita concava* of early Paleocene age from New Zealand.

GLOBAL OVERVIEW OF CRETACEOUS AND PALEOCENE GLYCYMERIDINES

The global record of Late Cretaceous to Paleocene glycymeridids is not well known and the following summaries are, by no means, exhaustive. According to Nicol (1950), glycymeridids evolved probably during the Late Jurassic from another arcoid family, the cucullaeids, but Newell (1969) postulated that glycymeridids originated during the Early Cretaceous.

Although Stanton (1895) reported a pre-Aptian glycymeridid, *Glycymeris*? *ovatus* (Stanton, 1895, p. 51, pl. 6, figs. 9–10) from "near Stephensons, on the Cold fork of Cottonwood Creek," Tehama County, northern California, the identification and geologic age cannot be verified, even though Anderson (1938, p. 97–98, unfig.) stated that the hinge characters and sculpture of this species "leave little doubt as to its generic position." Squires and Saul (2009) reported that the rocks at this locality are Early Cretaceous (either Hauterivian or Barremian) in age. Both cotypes (UNSM 23046) of Stanton's species are illustrated photographically here for the first time (Fig. 12.2, 12.3). Only one (Fig. 12.3) of these shows what might be the cast of a hinge. Stanton's figure 10 is a line drawing that does not accurately depict the details; rather, it is an artistic enhancement that strongly favors a glycymeridid-like hinge. As can be seen in Figure 12.13, along one side of the dorsal margin there are approximately five, very minute indentations that seem to be too short and proportionally too small for teeth for a valve whose length is approximately 12 mm. They could instead represent casts of crenulations along the interior valve margin. In addition, along this same portion of the dorsal margin, there could be two oblique teeth nearer the beak. Along the other dorsal margin, there are approximately six long indentations that represent a portion of a taxodont hinge, but they could be part of a shell fragment that abuts up against the beak area. The rock containing Stanton's specimen is a coquina consisting mostly of closely packed, unabraded shell fragments. Stanton's other specimen does not show the hinge. The shape of this species resembles a cardiid bivalve, and the sculpture consisting of only 10 to 11 wide ribs with broad interspaces is unlike any known glycymeridid. Even Stanton stated that the shape and sculpture differ considerably from the common species of *Glycymeris*. One topotype was found in the LACMIP collection, but the specimen is missing its beak. In summary, we believe that Stanton's species is not a glycymeridid.

A review of the literature revealed that the earliest known occurrences of definite glycymeridids are of Aptian age. *Glycymeris marullensis* (Leymerie, 1842) is known from lower to upper Aptian strata in France and England (Casey, 1961, p. 605). Nicol (1950) put Leymerie's species in *Glycymeris* (*Glycymerita*), but the small oval shape of this species and its short hinge with small, weak teeth would seem to place it in *Glycymeris* s.s. Although Gillet (1924, p. 20, table 3) reported this species from Valanginian strata in northern France, her work has been superceded by Casey (1961), who recognized an Albian age for these strata. *Glycymeris sublaevis* (Sowerby, 1823) is known from England and is of middle late Aptian to early Albian age (Casey, 1961, p. 605). *Glycymeris* (*Hanaia*) *haipensis* Hayami, 1965, is known from Aptian-Albian strata in Japan.

In Western Europe, glycymeridids have a continuous record from Aptian to Paleocene (Nicol, 1950; Casey, 1961; Dhondt and Dieni, 1993). In Japan, their record is Aptian to Campanian (Hayami, 1965, 1975; Tashiro, 1971). Henderson et al. (2000) reported "*Glycymeris*" from the Aptian in Australia. In southern India, the record of glycymeridids is Albian to Cenomanian and Campanian (Stoliczka, 1871). The South African record is confined to the late Santonian to early Campanian (Rennie, 1930). The New Zealand record is Cenomanian to Campanian to Paleocene (Fleming, 1966; Stilwell, 1998; Beu and Maxwell, 2000; Henderson et al., 2000). In the New World, glycymeridids are known only from the mid-Campanian to late Maastrichtian in Chile and Patagonia (Riccardi, 1988); late Campanian and Paleocene in the southeastern United States (Wade, 1926; Stephenson, 1941; Cvancara, 1966; Akers and Akers, 2002); Maastrichtian and Paleocene in the eastern United States (Palmer and Brann, 1965; Toulmin, 1977; Richards, 1958); Paleocene in Brazil (White, 1887). In the study area, their record spans the late Cenomanian through late Paleocene.

Prior to this paper, the time and place of the origin of *Glycymerita* had not been determined. It is shown here that the northern California middle to late Turonian specimens of *Glycymeris yoloensis* represent some intermediate state between *Glycymeris* and *Glycymerita*. *Glycymerita* persisted in the study area until the late Paleocene. The late Miocene *Glycymerita rangatira* (King, 1934) from New Zealand appears to be the youngest known species of this genus.

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APPENDIX

Type Localities of the New Species

LACMIP 28757.—Yolo Fm., middle to upper Turonian, North of Putah Creek, near mouth of small E-flowing ravine at its intersection with Thompson Canyon, 2,100 ft. E of Napa-Yolo Co. line and 2,700 ft. N to locality, SE 1/4 SE 1/4 of sec. 20, T. 8 N, R. 2 W, Monticello Dam Quadrangle (7.5′, 1959), Yolo Co., northern CA (Area 15). Collector: P. W. Reinhart.

USGS (Menlo Park) M6839.—Kaguyak Fm., lower Maastrichtian, elevation 2,000 ft., 2,500 ft. N, 700 ft. E of SW corner of sec. 31, T. 14 S, R. 28 W, Mt. Katmai (D-1) Quadrangle, Kamishak Hills, Mt. Douglas area, Alaska Peninsula, Alaska (Area 2). Latitude 58°55′14″N, longitude 154°0116″W. Coll.: L. B. Magoon, 1977.

Detailed information about the other cited localities is available via the following: LACMIP website: <http://ip.nhm.org/ipdatabase/locality_show>; UCMP website: <http://ucmpdb.Berkeley.edu/loc.html>; and CAS: contact the collections manager.