J. Paleont., 84(5), 2010, pp. 895-917 Copyright © 2010, The Paleontological Society 0022-3360/10/0084-0895\$03.00 Natural History Museum Of Los Angeles County Invertebrate Paleontology

NORTHEAST PACIFIC UPPER CRETACEOUS AND PALEOCENE GLYCYMERIDID BIVALVES

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ABSTRACT—The Late Cretaceous to late Paleocene record of glycymeridid bivalves in the region extending from the Alaska Peninsula, southward to Baja California, Mexico is studied in detail for the first time. *Glycymeris pacifica* (Anderson, 1902), of late Cenomanian to late Turonian age, is the earliest known glycymeridid in the study area. Very locally, it is found with the middle to late Turonian *Glycymeris yoloensis* n. sp. The latter apparently represents some intermediate state between genus *Glycymeris* da Costa, 1778 and genus *Glycymerita* Finlay and Marwick, 1937. In the study area, *Glycymerita* is represented by *Glycymerita veatchii* (Gabb, 1864), middle to late Turonian to late Campanian; *Glycymerita banosensis* (Anderson, 1958) new combination, late Campanian to latest Maastrichtian; *Glycymerita aleuta* n. sp., known only from Alaska and of early Maastrichtian age; and *Glycymerita major* (Stanton, 1896) new combination, Selandian to Thanetian. All the studied species lived in warm-temperate, shallow-marine waters and were shallow burrowers in fine-grained siliciclastic sediments. Variability in morphology is common in sizeable populations of the various species, especially *Glycymerita veatchii*, which increased nearly fivefold in size during its 19.5 million-year-long range and culminated in shells up to 84 mm in length.

INTRODUCTION

G LYCYMERIDID BIVALVES are common in northeast Pacific shallow-marine deposits of Late Cretaceous to late Paleocene age from the Alaska Peninsula southward to Baja California, Mexico (Fig. 1). Species have been overnamed because they can be confusingly similar-looking and can have considerable morphologic variation, even at a single locality. In spite of these problems, Popenoe (1942, fig. 4) and Saul (1982, figs. 2, 3) showed the biostratigraphic utility of glycymeridids in a portion of the Upper Cretaceous section of the Santa Ana Mountains, Orange County, southern California. They divided the molluscan fauna into two major units: the "Glycymeris pacificus" fauna and the "Glycymeris veatchit" fauna. This present study shows that their basic premise is valid and can be applied to the entire northeast Pacific region.

Four previously named species and two new species are recognized herein. Their combined temporal record nearly continuously spans the late Cenomanian to the end of the Paleocene, an interval of approximately 40 million years (Fig. 2). It is shown here that genus *Glycymerita* Finlay and Marwick, 1937 evolved from genus *Glycymeris* da Costa, 1778 in northern California during the middle to late Turonian. In addition to the systematic treatment of the glycymeridids, comments are provided about their paleoenvironments (including paleoclimate), paleobiogeography (including remarks about the tectonic transport of the rocks that contain some of them), and evolutionary trends. A global overview of Cretaceous and Paleocene glycymeridids is also given.

MATERIAL AND METHODS

A total of 1,665 specimens was studied. Most are from museum holdings but a few were collected by the author. The areas where these glycymeridids were collected are shown on Figure 1, and their designations (e.g., Area 15) are used throughout the paper.

Morphologic terms used in this report are those defined by Newell (1969), and the most commonly used ones are illustrated in Figure 3. The terms "ligamental ridges" and "ligamental grooves" refer to raised and incised areas, respectively, as part of the actual shell along the base of the cardinal area. A useful discussion of the criteria used for determining the orientation of glycymeridid valves is given by Nicol and Jones (1984).

Most of the previously named species had little or no hinge information, thus it was necessary to excavate hinges of representative specimens. Cleaning was done by means of a high-speed drill and diamond-coated grinding wheels, and/or by the use of hand-held, very sharp needles.

Differentiation of the studied species of *Glycymerita* was primarily based on the shape of the 1) shell, 2) posterodorsal margin, and 3) medial-posterior margin. These characters have to be used in combination with each other because they are variable and no one single character is reliable enough to distinguish a species. Juvenile specimens are especially difficult to identify as to species because they are so similar to each other.

The traditional way of distinguishing the previously named studied species has been to count the number of ribs. This technique is unsatisfactory because the very small, very narrow, and very closely spaced ribs on the anterior and posterior dorsal sides of specimens, as well as immediately above the cardinal area, are especially prone to poor preservation, or not preserved at all. A better technique is to count the number of ribs present over a distance of 10 mm, measured parallel to length at the medial part of valve, approximately 40 mm ventral of the beak.

Other unsatisfactory ways that have been traditionally employed to differentiate the species include using rib width and rib-interspace width, number of ligamental ridges/ grooves, number of teeth, and comparing various biometric parameters (e.g., height/length ratios, length/height ratios, and height/convexity ratios). Rib width and interspace width are subject to considerable variation, especially for the post-early Campanian adult forms of *Glycymerita veatchii* (Gabb, 1864), and this variation will be discussed later. Using the number of ligamental ridges/grooves is hampered because the size of the cardinal area bearing these ridges/grooves increases with growth. In addition, in temporally long-ranging species, such as *G. veatchii*, the overall shell size increased significantly over time. Using the total number of teeth and/or the number of

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FIGURE 1-Localities map and latitudinal distribution of study area glycymeridid species.



FIGURE 2—Geological ranges of the studied species. Solid lines connecting the species indicate inferred lineage based on morphologic similarity. Ages of stage boundaries from Gradstein et al. (2004).

teeth in the anterior versus posterior dental series is similarly hampered because of the same two reasons. In addition, the mesial teeth below the beak area can be poorly preserved, as well as fused together or even partly resorbed during enlargement of the adjacent cardinal area, thereby making it difficult to determine where one series begins and the other ends. Compounding the problem, the distal-most tooth in each series can be inconsistently rudimentary and barely perceptible. The above-mentioned biometric parameters show little or no variation among the studied species, and any substantial variation is related to the intergrading subquadrate and quadrate forms found in each species. Apart from the elongation of their ligament and the increasing number of teeth from juvenile to adult stage, the adult proportions were established in most cases by the time their shells were approximately 5 mm in height. This observation is in keeping with what is known about modern glycymeridids, whose shell growth is largely isometric (Thomas, 1975).

The aragonite shell of glycymeridids does not lend itself to perfect preservation, and the sculpture on many specimens has been adversely affected because of etching caused by weathering of the aragonite.

Abbreviations used for catalog and locality numbers are: ANSP, Academy of Natural Sciences of Philadelphia; CASG, California Academy of Sciences, Geology Section, San Franciso; LACM, Natural History Museum of Los Angeles County, Malacology Section; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; GNS, Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand; RBCM, Royal British Columbia Museum, Victoria; UCLA, University of California, Los Angeles (collections now housed at LACMIP); UCMP, University of California Museum of Paleontology (Berkeley); USGS, United States Geological Survey (Menlo Park) (collections now housed at UCMP); USNM (Smithsonian Institution); and UWBM, University of Washington, Seattle.

SYSTEMATIC PALEONTOLOGY

Class BIVALVIA Linnaeus, 1758 Subclass PTERIOMORPHA Beurlen, 1944 Order ARCOIDA Stoliczka, 1871 Superfamily ARCOIDEA Lamarck, 1809 Family GLYCYMERIDIDAE Dall, 1908

Remarks.—Nicol (1945), Olsson (1961), Newell (1969), Boss (1982), and Coan et al. (2000, in press) provided succinct descriptions of the shell characteristics and anatomical features of Glycymerididae. Carter (1990) discussed the shell microstructure of members of this family.

There is no definitive modern classification available for glycymeridids. It is difficult to classify them mostly because of two underlying problems. One is that the essential morphologic features of this family were derived early in its history; hence, there are few known reliable morphologic differences that can be established to distinguish the named genera and subgenera. Some authors (e.g., Abbott, 1982) have resorted to only using the name *Glycymeris* sensu lato. The second problem is that the range of morphology for most glycymeridid taxa has not been established, and significant morpho-

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