

VOLUTODERMINAE (GASTROPODA: VOLUTIDAE) OF CONIACIAN THROUGH MAASTRICHTIAN AGE FROM THE NORTH AMERICAN PACIFIC SLOPE

LOUELLA R. SAUL¹ AND RICHARD L. SQUIRES²

¹Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, <lousaul@earthlink.net>; ²Department of Geological Sciences, California State University, Northridge 91330-8266, <richard.squires@csun.edu>

ABSTRACT—Specimens of the large, shallow-marine, volutid gastropod *Volutoderma* Gabb, 1877, herein recognized only from strata of Late Cretaceous (Coniacian through early Maastrichtian) age in British Columbia, Washington, California, and Baja California have commonly been identified as *Volutoderma averillii* (Gabb, 1864). This review of available specimens assigns them to two genera: *Volutoderma* and *Longoconcha* Stephenson, 1941.

Twelve species, nine of them new, comprise three morphologic lineages of *Volutoderma*, i.e., 1) “Typical” includes *V. querna* n. sp., *V. averillii* (Gabb), *V. blakei* n. sp., *V. jalama* n. sp., *V. perissa* n. sp., and possibly *Volutoderma?* n. sp.; 2) “Angelica” includes *V. angelica* n. sp., *V. elderi* n. sp., and *V. ynezae* n. sp.; and 3) “Magna” includes *V. santana* Packard, *V. magna* Packard, and perhaps *V. antherena* n. sp. A new species of *Longoconcha*, *L. eumeka*, is the first Pacific Slope record of this genus, which has a Gulf Coast and Tethyan Old World distribution. A smaller volutid, *Retipirula* Dall, 1907 is endemic to the study area and was formerly known only from its type species *R. crassitesta* (Gabb, 1869) of Paleocene age. Two new *Retipirula* are reported: *R. calidula* of latest Maastrichtian age and *R. pinguis* of Paleocene age.

Only the *Volutoderma* lineage containing *V. averillii* has been found north of San Francisco. Recovery of rudist bivalves from formations yielding *Volutoderma* suggests that these volutes were warm-temperate to subtropical gastropods. Co-occurrences of these gastropods and rudistids may aid in placing the warm-temperate/subtropical boundary during the Late Cretaceous.

INTRODUCTION

SPECIMENS OF *Volutoderma* Gabb, 1877 are moderately common in Pacific Slope shelf deposits of Coniacian through early Maastrichtian age from British Columbia, Canada, to Baja California, Mexico. Gabb (1877) and subsequent early workers attributed to *Volutoderma* a nearly worldwide distribution in the Late Cretaceous, but only specimens from the Pacific Slope of North America are presently known to display characteristics of *Volutoderma*.

Material for this study includes type specimens of described taxa, additional collections from their type localities, and specimens from previously unreported localities (Fig. 1). Twelve species of *Volutoderma* are discussed, nine of them new. Their temporal ranges, as well as their three recognizable morphological lineages, are plotted on Figure 2. The “Typical” lineage ranged temporally from Coniacian to Maastrichtian, and geographically from British Columbia to Baja California (Fig. 1). The “Magna” and “Angelica” lineages are known only from the Campanian, and geographically might not have ranged north of southernmost California (Fig. 3 near 33°N). Specimens of these two lineages have been collected only west of the San Andreas Fault from terranes considered to have been transported northward.

Although this study focuses on *Volutoderma*, species of two other volutodermine genera, *Longoconcha* Stephenson, 1941 and *Retipirula* Dall, 1907, with morphological similarities to *Volutoderma* are included. *Longoconcha eumeka* n. sp. ranges from late Campanian into the Maastrichtian and has been recovered from north of Coalinga, Fresno County, California, southward to Arroyo Santa Catarina, Baja California, Mexico. Late Maastrichtian *Retipirula calidula* n. sp. and late early Paleocene *R. pinguis* n. sp. are known from southern California, but the early late Paleocene species *R. crassitesta* (Gabb, 1869) has been collected from near Clear Lake, Lake County, northern California, south to the vicinity of Arroyo Santa Catarina, Baja California, Mexico.

Post-Turonian California volutodermine diversity was greatest during the middle to late Campanian (Fig. 2). Two lineages disappeared during latest Campanian, but diversity was partially maintained by the addition of *Longoconcha* to faunas of latest Campanian–early Maastrichtian age. Perhaps owing to unfavorable facies and restricted development of Maastrichtian deposits, late early and late Maastrichtian Volutoderminae are rare. Fewer

Pacific Slope Maastrichtian megafossils, especially from shallow-shelf habitats, have been collected, and those collected are, in general, not well preserved or studied.

All available Volutodermine specimens are incomplete. Their anterior siphon is rarely complete, and most larger specimens lack the early whorls. When present, the surface of the spire is usually abraded. Specimens from the Point Loma Formation near Carlsbad, San Diego County, especially of *Longoconcha* and *Volutoderma*, provide features not retained by specimens from elsewhere and have helped greatly toward identifying less-informative material.

The specimens studied are mainly from fine-grained, argillaceous sandstone and siltstone. The “Typical” lineage is most abundant in shallow-shelf deposits that probably accumulated at depths below wave base. Occurrences of “Angelica” and “Magna” lineages generally suggest more offshore or somewhat deeper water habitats. An association of a crepiduliform gastropod with the volutes may have developed in the late Campanian (Fig. 11.7, 11.8).

Despite the popularity of volute shells with shell collectors, little is known about the biology of the Volutidae, according to Darragh and Ponder (1998). They noted that although most live and burrow in sublittoral sands, modern volutes range from shallow-water, littoral habitats to abyssal depths. Volutids are carnivorous (C. S. Weaver and du Pont, 1970), and most feed on other mollusks, which they envelop with the foot (B. Morton, 1986), but some deepwater forms prey on echinoderms (Darragh and Ponder, 1998). The protoconch is generally smooth and is commonly of one to three whorls, but it is multiwhorled in some species. All modern volutes produce large eggs in capsules; most eggs develop directly into the crawling stage, and modern volutid hatchlings may exceed 10 mm (Darragh and Ponder, 1998). In contrast, earliest whorls found on *Volutoderma* are of less than half that size.

GEOLOGIC AGE CONSIDERATIONS

The present North American Pacific Slope biostratigraphic ammonite correlations, largely based on Matsumoto (1959a, 1959b; 1960), provide a framework for the chronologic ranges of the volutes plotted on Figure 2. The ammonites have been linked to the Geologic Time Scale of Gradstein et al. (2004) by geomagnetic polarity studies (e.g., Ward et al., 1983). The end of the long normal 34N is near the Santonian–Campanian boundary (Gradstein et al., 2004). This boundary and the reversal 34N–33R are

recognized in the Chico Formation along Chico Creek, (Area 6) where *Volutoderma querna* occurs below and *V. averillii* above the reversal. Although ammonite and *Turritella* ranges (Fig. 2) aid in defining the chronologic ranges of the studied species, some Pacific Slope ammonites, as noted by Matsumoto (1959b) regarding *Metaplacenteras* Spath, 1926, need revision. Matsumoto (1984) later referred *M. ? bowersi* Anderson, 1958 to *Hoplitoplacenteras*? Spath, 1926, but made no other revision. The occurrence of *V. blakei* with *H. ? bowersi* suggests that *H. ? bowersi* is older than *M. pacificum* (Smith, 1900) and may be younger than *H. vancouverense* (Meek, 1858).

Additionally, Figure 2 uses the *Eubaculites carinatus* Zone following Cobban and Kennedy (1995) who considered *E. ootacodensis* of Matsumoto (1959a) a synonym of *E. carinatus* (S. G. Morton, 1834). Figure 2 also reflects the recognition by Cobban and Kennedy (1995) of *Baculites lomaensis* Anderson, 1958 in the Prairie Bluff Chalk of Mississippi and Alabama, associated with ammonites of the *Discoscaphites iris* assemblage zone and thus suggesting an age as young as early late Maastrichtian.

PALEO GEOGRAPHIC AND PALEOCLIMATIC IMPLICATIONS

The studied specimens have small multiwhorled protoconchs, in contrast to the larger pauciwhorled protoconchs characteristic of modern volutes. Fisher et al. (1964) inferred that a multiwhorled small protoconch in volutes is indicative of a relatively long pelagic stage and that decrease in protoconch whorl number in Paleocene and Eocene Gulf Coast volutes was recording shortening of the pelagic stage. A shorter pelagic stage could imply post-Cretaceous changes from planktotrophic larvae toward direct-developing juveniles. Cenozoic volutes having direct development have acquired an array of notably large, bulbous, odd, and secondary protoconchs. Direct development with "crawl-away larvae," as in Recent taxa, has resulted in many locally distinct volute populations (Darragh and Ponder, 1998).

Both Gabb (1877) and Dall (1907), in noting the wide paleogeographic distribution of early fossil volutes, suggested that it was facilitated by a lengthy pelagic stage. Dall (1907) especially noted the wide distribution of a considerable diversity of gastropod shells with volutid characteristics in the Cenomanian, among them being *Carota* Stephenson, 1952, which occurs in Europe, Middle East, India, North Africa, and North America and ranges probably into the Santonian. *Carota* is similar to *Volutoderma* and to *Longoconcha*. It preceded the latter two in the geologic record and was geographically more widespread. Our finding that *Volutoderma* had an east Pacific rather than global distribution perhaps indicates that even before reduction of protoconch whorl number, its planktotrophic larval stage had been reduced.

On the Pacific Slope, deposits yielding Late Cretaceous fossil volutes are at present found between latitudes 52°N to 29°30'N (Fig. 1). The Late Cretaceous paleomagnetic pole of Butler et al. (2001) is in northern Alaska, and Lund and Bottjer (1992) placed the western margin of the North American craton 11–15° north of its present position. Also, during the past quarter century post-mid-Cretaceous northward transport of up to 4,000 km with respect to the craton has been proposed for some terranes along the North American Cordilleran margin (Butler et al., 2001). Areas west of the San Andreas Fault are considered by most geologists to have been moved northward from 300 to 500 km (Fig. 1, Areas 8, 10, 12–22) in post-Cretaceous time, and additional travel distances have been proposed for individual terranes (especially Areas 8, 10, 15) (Dickinson and Butler, 1998, and references therein). The Baja British Columbia (Baja B.C.) hypothesis suggested transport of Nanaimo Basin deposits of southern British Columbia and northern Washington (Fig. 1, Areas 1 and 2), from a depositional latitude at near 25°N, northward for up to 3,500 ± 800 km (Ward et al., 1997, and additional references therein). An alternative interpretation of geophysical data by Butler et al. (2001) used only a northward translation of ~1,000 km. Using

compaction-corrected paleomagnetic paleolatitudes, Kodama and Ward (2001) suggested a lesser northward transport of up to 1,500 km for the Nanaimo Group from a depositional site not farther south than 40°N (i.e., northern California).

Co-occurrence of rudists and *Volutoderma* in the same formation (see Figs. 1 and 3) suggests that the studied *Volutoderminae* dwelt in subtropical to warm-temperate waters. Rudists serve as indicators of at least marginal tropicality because of their widely reported low-latitude occurrence (e.g., Sohl, 1987; Johnson, 1999). Kodama and Ward (2001) considered reef- and bank-forming rudists such as *Coralliochama* to be better indicators of tropical-water masses than other mollusks. Judging from their distributions in the strata, rudists and volutes were not inhabiting a common ecotope. Where rudists are especially abundant, as in the Rosario Formation at Punta Banda (Area 20), northern Baja California, volutes are extremely rare; at localities in the same formation which have a more diverse molluscan fauna, disarticulated and broken rudist valves are common to rare. Additionally, as distinctive rudist shell structure makes possible the recognition of rudist shell fragments that have been distributed postmortem, their latitudinal presence can be inferred beyond their ecologic niche.

Figure 3 plots both modern latitude and probable Cretaceous latitude for the studied volutes, in order that a subtropical/warm temperate boundary can be inferred despite the left lateral, northward offset along the San Andreas Fault. Latitudinal changes of this boundary from north of 40° in the Turonian to less than 35° in the Campanian are suggested in Figure 3. Turonian rudists have been found as far north as southern Oregon in the lower Hornbrook Formation (Anderson, 1958). Although the apparent absence of rudists in the upper Hornbrook could result from incomplete collecting, their absence agrees with the restriction of rudists and of the Tethyan Realm subsequent to the Turonian that has been noted by Sohl (1987). Turonian is the youngest age during which rudist remains are known to have been deposited east of the San Andreas Fault in California sediments, whereas all North Pacific Slope Coniacian through Maastrichtian rudists have been recovered from west of the San Andreas Fault. Presence of rudists as far north as Gualala (Fig. 1, Area 8) in deposits of Campanian and Maastrichtian age registers the northward movement of the terranes west of the San Andreas Fault, but the inferred depositional latitude, derived from Dickinson and Butler (1998) for Area 8 on Figure 3, may indicate deposition too far north for elements of the fauna.

Various terrane transports cause offsets in an inferred subtropical/warm temperate boundary. Figure 3 attempts to remove the offsets and show paleotemperature changes. Work on Cretaceous mollusks by Squires and Saul (2006) supports the contention that the Nanaimo Group was deposited not any farther south than northern California. The diffuse tropic/warm temperate boundary of Figure 3 is based on data in the following discussions of the Coniacian through Maastrichtian volutes. Despite the gaps in the fossil record, there is a correspondence between the temperature highs and lows generated in Figure 3 and those recorded by Frakes (1999, p. 51, fig. 1).

Abbreviations.—The following institutional abbreviations are used: ANSP = Academy of Natural Sciences of Philadelphia; CASG = California Academy of Sciences, Geology; CIT = California Institute of Technology (collections at LACMIP); GSC = Geological Survey of Canada; LACMIP = Natural History Museum of Los Angeles County, Invertebrate Paleontology; RBCM = Royal British Columbia Museum, Victoria; SDNHM = San Diego Natural History Museum; UCLA = University of California, Los Angeles (collection at LACMIP); UCMP = University of California, Berkeley, Museum of Paleontology; USGS = United States Geological Survey, Menlo Park (collection now at UCMP); USNM = United States National Museum; VIPM = Vancouver Island Paleontological Museum in Qualicum Beach, Vancouver Island, British Columbia.

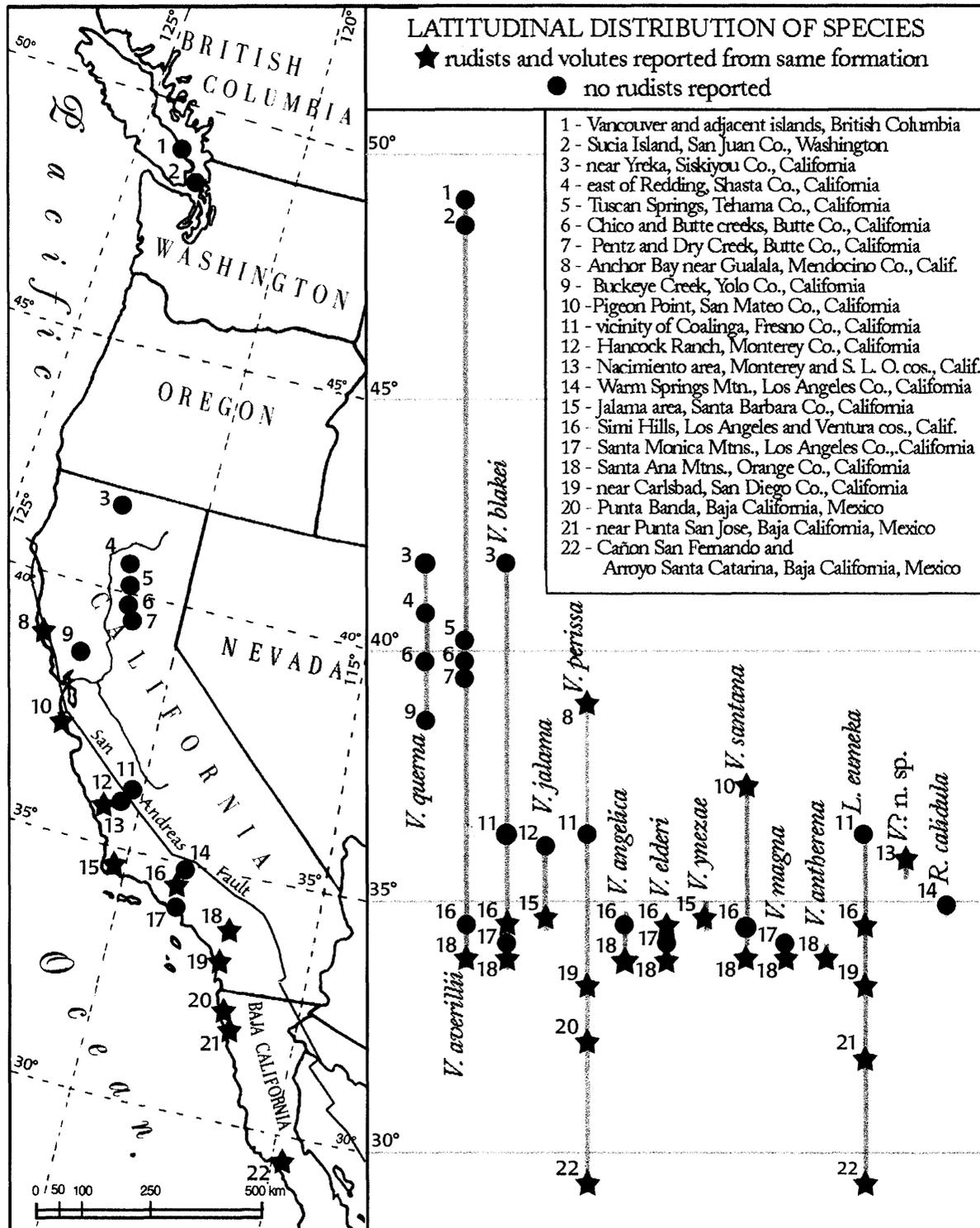


FIGURE 1—Index map with numbered areas from which studied specimens of Late Cretaceous volutes were collected. Map latitudes projected onto right-hand box of figure. Latitudinal range of species depicted by bars. Areas west of San Andreas Fault have been moved 300–500 km northward during post-Cretaceous time. Areas where rudists have been reported from the same formation that has yielded volutes marked by star; areas where rudists are not reported from the same formation marked by circles. See Figure 2 for age of species.

The photographs (Figs. 4–11) of the specimens are arranged in approximately ascending growth size and specimens were coated with ammonium chloride.

See Appendix for locality descriptions or LACMIP locality descriptions at ip.nhm.org or in the Supplemental archive of Journalofpaleontology.com.

SYSTEMATIC PALEONTOLOGY

Class GASTROPODA Cuvier, 1797
 Family VOLUTIDAE Rafinesque, 1815

Discussion.—In shell shape and columellar folds, *Volutoderma* spp. from the Pacific slope of North America display features

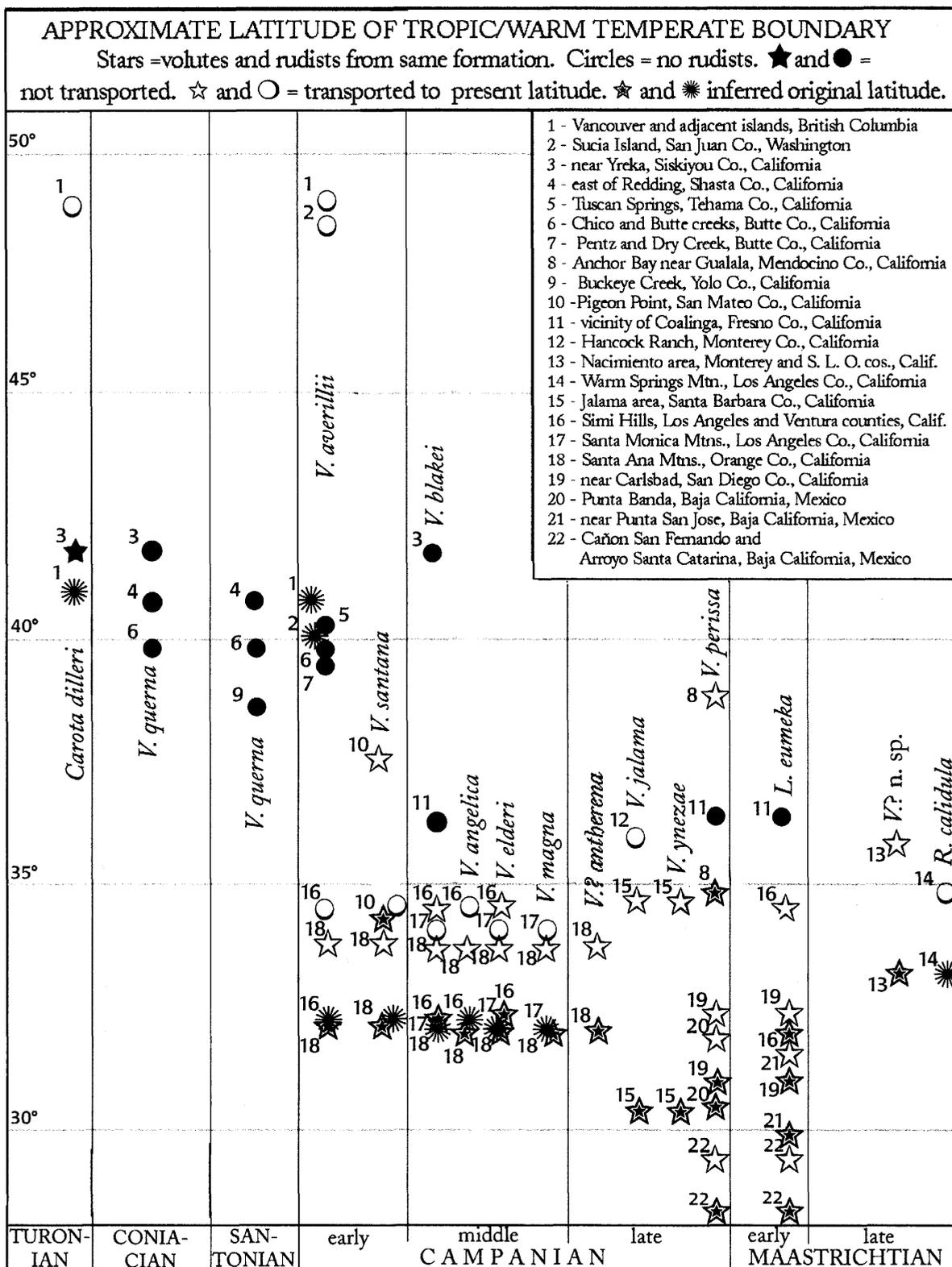


FIGURE 3—Approximate Late Cretaceous latitude of subtropic/warm-temperate boundary (grey bar) inferred from northern-most latitude provided by rudistid occurrence with a volutodermine species. Species plotted roughly within age but see Figure 2 for age range of species. Present latitude from Figure 1; inferred Cretaceous latitude from reconstructions of Dickinson and Butler (1998) and Kodama and Ward (2001). Pigeon Point Terrane with *V. santana* and Gualala Block with *V. perissa* n. sp. provide northward excursions of tropic boundary using these reconstructions. Turonian occurrence of rudists with *Carota dilleri* from lower Hornbrook Formation of northern California and southern Oregon but of *C. dilleri* without rudists from basal Nanaimo Group on Sidney Island, British Columbia, suggest possibility of Turonian subtropic boundary north of 40°. Late Campanian drop in subtropic boundary based on Jalama Formation occurrences is probably artifact of geologic record gaps. If rudist occurrences of El Piojo Formation are of late Campanian age, no drop would exist.

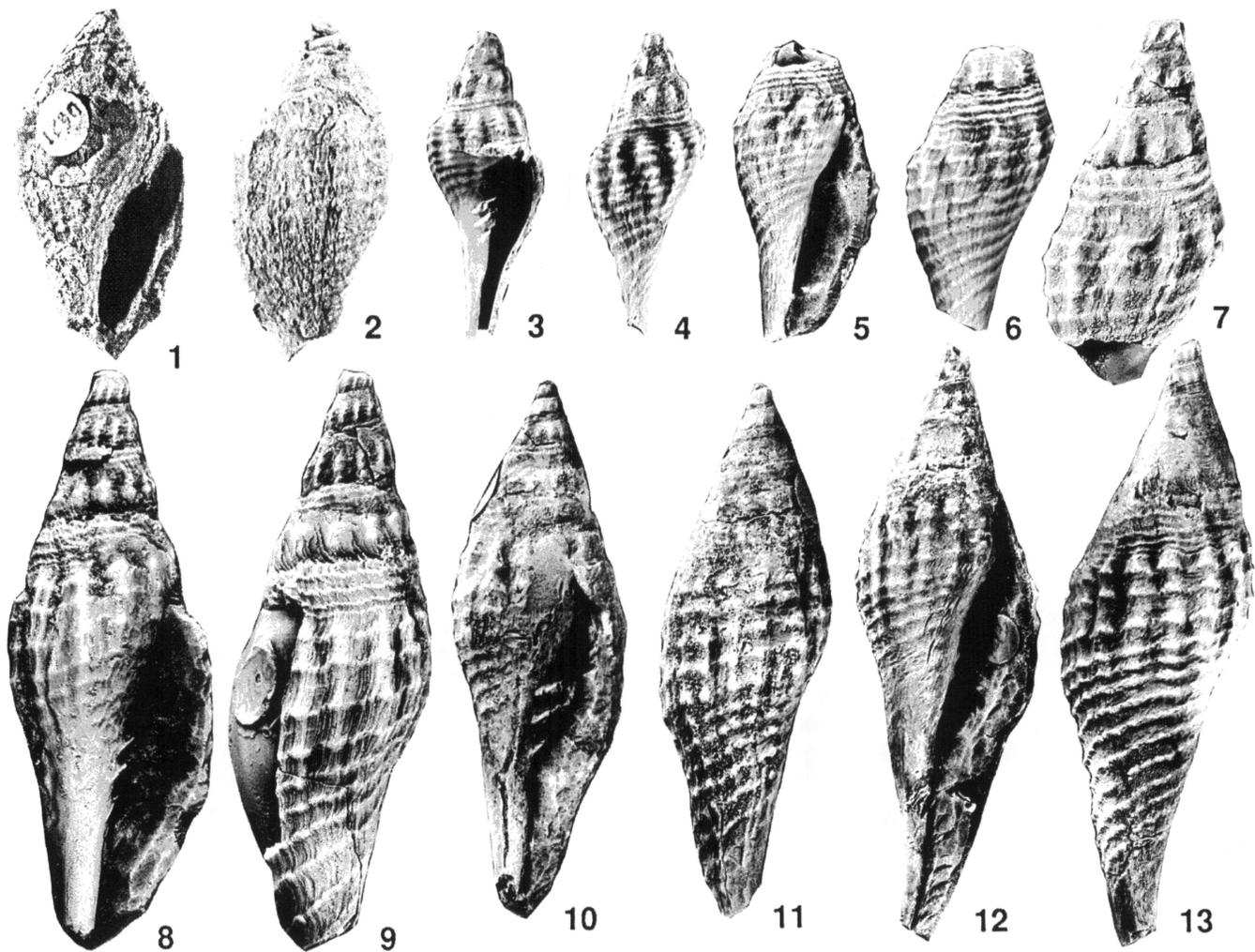


FIGURE 4—*Carota* cf. *C. dilleri* White, 1889 and *Volutoderma querna* n. sp. from Pacific Slope of North America. 1, 2, *Carota* cf. *C. dilleri*, LACMIP 13360 from LACMIP 10135, $\times 1$. 3–13, *Volutoderma querna* n. sp.; 3, 4, paratype, LACMIP 13155, $\times 1.8$; 5, 6, paratype, LACMIP 13162, $\times 2.2$; 7, paratype, LACMIP 13161, $\times 2.7$; 8, 9, paratype, LACMIP 13160, $\times 1.8$; 10, 11, paratype, LACMIP 13156, $\times 1.3$; 12, 13, holotype, LACMIP 13154, $\times 1.1$.

spiral cords; spiral cords commonly forming spirally elongate nodes on axial ribs; earliest whorls with strong distant axial costae and weaker spiral lines. Aperture elongate, outer lip commonly a little reflexed, especially posteriorly; inner lip callus well developed; parietal callus shield present, commonly expanded posteriorly across previous suture; three oblique columellar folds approximately medially placed on columella.

Occurrence.—Pacific Slope of North America, British Columbia to Baja California. Coniacian to late Maastrichtian.

Discussion.—Gabb (1877) indicated as type of *Volutoderma* the species from the lower Campanian Chico Formation at Tuscan Springs, which he had figured in 1864 as *Volutilithes navarroensis* Shumard, 1861. Stewart (1927) recognized that the specimen figured by Gabb is actually an adult of *Fusus averillii* Gabb, 1864, the type specimen of which is also from Tuscan Springs.

Despite Stewart's (1927) notation that the type of *Volutoderma* was by original designation of Gabb, the designation and the name of the type species have continued to be misunderstood (e.g., Anderson, 1958; Ludvigsen and Beard, 1994; Bandel,

2000). Gabb (1864) identified specimens from Tuscan Springs, Tehama County, California as *Volutilithes navarroensis* Shumard, and figured one of them on plate 19, figure 56. In 1869, Gabb listed the California specimens as *V. navarroensis*, Shum.? and indicated that he was questioning his earlier identification. Gabb (1877, p. 289), cited his 1864 figure, and established the genus *Volutoderma* on “*V. navarroensis* Shum., Gabb, Palæontology of California, vol. i, pl. 19, fig. 6” (fig. 6 = error for 56). Because Gabb questioned his 1864 identification and cited his plate 19, figure 56 as typical of *Volutoderma*, this citation involves three articles of the ICZN (1999) code: Article 67.2.1, the species cited is eligible for type fixation; Article 67.13, the misidentified species so fixed becomes a new nominal species; and Article 69.2.4, the species thus designated *Volutoderma navarroensis* (Gabb) is the nominal species (and *Volutilithes navarroensis* Shumard is not). *Volutoderma navarroensis* (Gabb, 1877) is a junior synonym of *Fusus averillii* Gabb, 1864.

Of the pre-Coniacian Pacific Slope volutes, the one most similar to *Volutoderma* is *Carota*, which differs from *Volutoderma*

FIGURE 5—*Volutoderma averillii* (Gabb, 1864) from Pacific Slope of North America. 1, 2, hypotype, LACMIP 13170, $\times 1.9$; 3, hypotype, LACMIP 13169, $\times 1.75$; 4, 5, hypotype, RBCM.EH2004.013.0001, $\times 1.8$; 6, hypotype, LACMIP 13172, $\times 1$; 7, hypotype, LACMIP 13171, $\times 1$; 8, hypotype, LACMIP 13168, $\times 1$; 9, hypotype, LACMIP 13173, $\times 1.01$; 10, paralectotype of *Volutoderma suciana* Dall, 1907, GSC 5786d from Sucia Island, $\times 0.92$; 11, 12, lectotype of *Volutoderma suciana*, GSC 5786c from Sucia Island, $\times 0.93$; 13, 14, hypotype, UCR 3435/1, $\times 0.73$.