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Cretaceous Corbulid Bivalves of the Pacific Slope of North America

RICHARD L. SQUIRES

Department of Geological Sciences, California State University, Northridge, California 91330-8266, USA

AND

LOUELLA R. SAUL

Invertebrate Paleontology Section, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, USA

Abstract. This paper presents the first biostratigraphic study of Cretaceous corbulid bivalves from shallow-marine rocks along the Pacific slope of North America, with most of the outcrops in California and northwestern Baja California. Five genera, two of which are new, and 14 species, 11 of which are new, are represented: *Caryocorbula* ***coani***, sp. nov., *Caryocorbula* ***onoensis***, sp. nov., *Caryocorbula* ***vacca***, sp. nov., *Caryocorbula traskii* (Gabb, 1864), *Caryocorbula* ***lomana***, sp. nov., ***Excorbula coqua***, gen. et. sp. nov., ***Excorbula parkyi***, gen. et sp. nov., ***Excorbula shastana***, gen. et sp. nov., ***Panzacorbula*** *pozo* (Dailey & Popenoe, 1966), gen. nov., *Eoursivivas cultriformis* (Gabb, 1864), *Caestocorbula* ***cavus***, sp. nov., *Caestocorbula* ***attina***, sp. nov., *Caestocorbula* ***aura***, sp. nov., and *Caestocorbula*? ***allisoni***, sp. nov. The cumulative chronologic range of these 14 corbulid species is Early Cretaceous (latest Aptian) to Late Cretaceous (early late Maastrichtian), an interval of 40 m.y. Generic diversity of the study area corbulids is greatest during the Turonian and late Campanian to early late Maastrichtian.

Caryocorbula Gardner, 1926, and *Caestocorbula* Vincent, 1910, have been only provisionally reported before from Cretaceous rocks in the study area. *Eoursivivas cultriformis*, of late early to early late Maastrichtian age, is the youngest record of this genus and its first occurrence in the Western Hemisphere. *Eoursivivas* was previously known only from Lower Cretaceous (Valangian to Hauterivian) strata of Japan. ***Excorbula*** and ***Panzacorbula*** are apparently endemic to the study area.

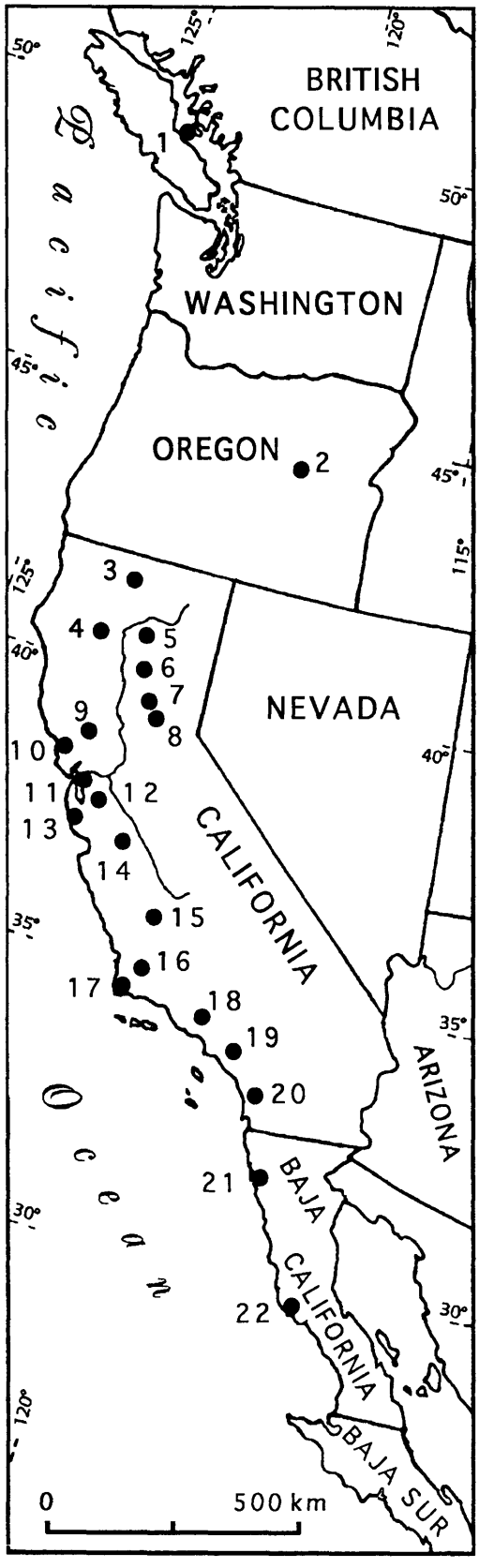
Caryocorbula ***onoensis***, of late early Albian age, is the earliest study area species to show evidence of predatory drilling.

INTRODUCTION

The earliest records of corbulids are of Middle Jurassic age from England (e.g., Morris & Lycett, 1854; Lycett, 1863; Cox & Arkell, 1948–1950; Duff, 1978; Harper et al., 2002); Africa (Cox, 1965); China (Yin & Fürsich, 1991; Yin & Fürsich, 1992); western India (Kanjilal, 1997; Singh & Rai, 1980; Fürsich et al., 2000); southern Mexico (Alencaster, 1963); Montana (Imlay, 1945, 1967), and Alberta, Canada (McLearn, 1924; Frebold, 1964). The majority of corbulid genera evolved during the Cretaceous and Eocene; the remainder radiated during the Miocene to Recent times (Lewy & Samtleben, 1979). Today, there are approximately 85 species (Coan et al., 2000), with most living in tropical and temperate waters of normal-marine salinities. Corbulids are sluggish burrowers, and most species live in nearshore, fine-grained sediments deposited in relatively low-energy environments. Some species range into the northern cold regions, and some species are euryhaline and live in normal marine to brackish waters. Some fossil corbulids are known to comprise monotypic shell beds associated with brackish-water conditions (Lewy & Samthleben, 1979).

Corbulids are widely distributed in Cretaceous shallow-marine faunas of the Pacific slope in British Columbia, Oregon, California, and northwestern Baja California, yet these small-sized fossils, which can be locally common, have been largely ignored by previous workers. Early paleontologists were mainly focused on ammonites, and studies of bivalves, as well as those of gastropods, were of secondary interest. If bivalves were investigated, then those consisting of large-sized specimens were favored. In recent years, we have been studying the fossil records of the more poorly known Cretaceous bivalves and gastropods from the region extending from Vancouver Island, British Columbia southward to Baja California, Mexico, in order to bring their biostratigraphic utility into the mainstream of geologic usage. This paper, which is one of these studies, is the first to record the stratigraphic succession of Cretaceous corbulids from the Pacific slope of North America.

The only other stratigraphic succession study on corbulids was done by Anderson (1996), who studied Neogene *Corbula* Bruguière, 1797, from the northern Dominican Republic. Coan (2002) studied the Recent eastern Pacific species of family Corbulidae Lamarck, 1818.



This present study stems from a careful search for corbulid specimens in all the major museums that have extensive collections of Cretaceous fossils from the study area. We detected 113 lots (72 = LACMIP, 21 = CAS, 15 = UCMP, 5 = other) containing a total of 1547 specimens. We were able to recognize five genera and 14 species; two of the genera and 11 of the species are new. We also refined the paleontologic record of the three previously named species. Pacific slope of North America corbulids have a cumulative geologic range of late early Albian to early late Maastrichtian, a span of approximately 40 million years. The locales and stage occurrences of the studied species are shown on Figures 1 and 2, respectively.

This present report establishes the first record for *Eoursivivas* Ota, 1964, in the Western Hemisphere and its youngest species. In addition, this report is the first to document the Cretaceous occurrence of *Caryocorbula* Gardner, 1926, and *Caestocorbula* Vincent, 1910, in the study area. Allison (1974) had used the last two names in various faunal lists pertaining to the upper Aptian Alisitos Formation in Baja California, Mexico, but he did not photographically document his identifications, nor did he assign any museum-catalog numbers to his specimens. We used the specimens that he collected, but his identifications were inconsistent.

Predatory Drill Holes in Corbulid Shells

Late Cretaceous, Cenozoic, and modern corbulid shells are commonly bored by gastropods (Taylor et al., 1983; Kelley & Hansen, 1993), and the drill holes are usually assigned to naticids or muricids, although a few other types of gastropods are also capabable of making these holes (see Harper et al., 1998). Kase & Ishikawa (2003) reported the chronologic range of naticids to be Late Cretaceous (Campanian) to Recent and that earlier reports of Late Triassic to Early Cretaceous naticid boreholes are invalid. Furthermore, they reported that naticid drill holes became common only in Campanian and Maastrichtian shallow-marine environments. Sohl (1969) reported the chronologic range of muricids to be Early Cretaceous to Recent and that their boring activity is well represented only from the Late Cretaceous (Senonian) onward. There are predatory drill holes in late Albian corbulids and other bivalves of England (Taylor et al., 1983). In addition, in

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Figure 1. Index map showing locales mentioned in the text. 1 = Hornby Island. 2 = Dayville area. 3 = Yreka. 4 = Ono and Texas Springs. 5 = East of Redding. 6 = Tuscan Springs. 7 = Chico Creek. 8 = Pentz. 9 = Sites. 10 = Gualala. 11 = Martinez. 12 = Corral Hollow. 13 = Pigeon Point. 14 = Ortigalita Creek. 15 = Reef Ridge. 16 = Pozo. 17 = Jalama Creek. 18 = Simi Hills. 19 = Santa Ana Mountains. 20 = Carlsbad. 21 = Punta China. 22 = Arroyo Santa Catarina.

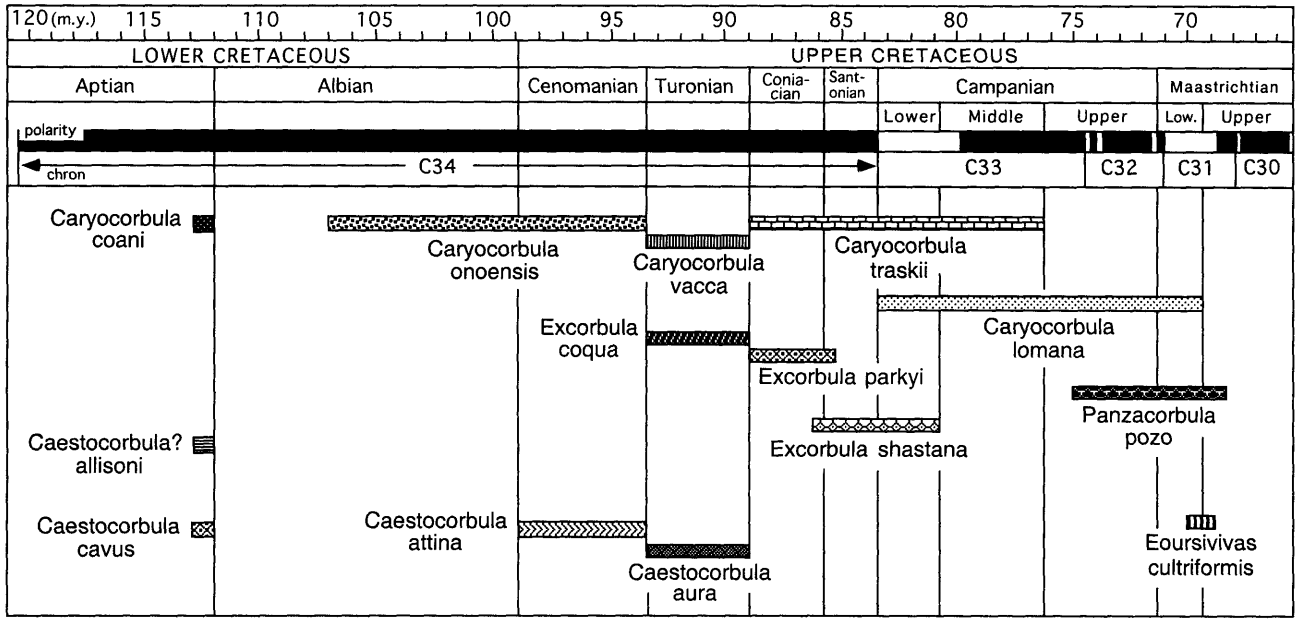

Figure 2. Chronostratigraphic positions of the new and restudied Cretaceous corbulids. Geologic ages, polarities, and chrons from Gradstein et al. (1994).

this present study, drill holes were found in a few valves of the late early Albian *Caryocorbula* ***onoensis***, sp. nov. This is the earliest corbulid species in the study area to show any evidence of drilling. Except for the late Aptian species and the Cenomanian *Caestocorbula* ***attina***, sp. nov., all the other study area species show drill holes, but, for the most part, these holes are rare to uncommon. Locally, however, drill holes are common only in the late Campanian to early Maastrichtian *Caryocorbula* ***lomana***, sp. nov. Details of drill-hole evidence are discussed for each species in "Systematic Paleontology."

Corbulids have discrete conchiolin (organic) layers within the microstructure of their valves (De Cauwer, 1985), and such layers are relatively rare in other marine bivalves (Taylor et al., 1973). As reviewed by Anderson (1992), it has been commonly reported that the conchiolin layers in corbulid shells inhibit predation by drilling gastropods. Anderson (1992), however, reported that other factors (e.g., variable shell thickness) are likely more important than presence of conchiolin.

The suprafamilial classification system used here follows that of Keen (1969). Abbreviations used for catalog and locality numbers are: ANSP, Academy of Natural Sciences of Philadelphia; CAS, California Academy of Sciences, San Francisco; CIT, California Institute of Technology, Pasadena [collections now housed at LACMIP]; CGS, California Geological Survey [collections now housed mostly at UCMP and Academy of Natural Sciences, Philadelphia]; GSC, Geological Survey of Canada, Ottawa, Ontario; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; SDSNH, San Diego Society of Natural History, San Diego; 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, California) [collections now housed at UCMP].

STRATIGRAPHY

The geologic ages and depositional environments of most of the formations and members cited in this paper have been summarized in recent papers by Squires & Saul (2001, 2002, 2003a, b, c, in press). Stratigraphic information mentioned below concerns either those rock units not discussed in recent literature or additional pertinent biostratigraphic details. The following stratigraphic units are listed from oldest to youngest.

Cretaceous Rocks near Sites

The type locality of *Caryocorbula* ***onoensis***, sp. nov. is near Sites, west side of Sacramento Valley, Colusa County, northern California (Figure 1, locale 9). In this area, Brown & Rich (1961) reported that reworked megafossils of Albian age are found in submarine-slump blocks, depicted within unit 7 (Cenomanian age) on their geologic map. Fossils at LACMIP loc. 24285, the type locality of *C.* ***onoensis*** are from one of these submarine-slump blocks. A few additional specimens of the new species were found a few kilometers to the north of the type locality, in unit 7, at USGS locs. M-175, M-176, M-177, and M-178 in the Cenomanian Antelope Shale.

Panoche Formation at Reef Ridge

The type locality of *Caestocorbula* ***attina***, sp. nov. is in the Panoche Formation, Reef Ridge (Figure 1, locale 15), Kings County, central California. Campanian-age conglomerate beds at this locality, LACMIP 25526, contain reworked cobbles with shallow-marine mollusks, and the new species is one of these mollusks. Two reworked gastropods have been identified: ?*Natica allisoni* (Murphy & Rodda, 1960) of Cenomanian age (Popenoe et al., 1987) and *Latiala californicus* Saul, 1998, of ?late Albian/Cenomanian age (Saul, 1998).

Gas Point Member of Budden Canyon Formation

This member crops out in the Bald Hills area near Ono (Figure 1, locale 4), Shasta County, northern California. The ammonite *Mesopuzosia pacifica* Matsumoto, 1954 occurs in all parts of the member (Murphy et al., 1969) and is indicative of Turonian age (Matsumoto, 1959). *Caryocorbula* ***vacca,*** sp. nov. occurs in the fine-grained, lower part of the member.

Northumberland Formation, Northwest Side of Hornby Island

Whiteaves (1879) reported *Corbula traskii*? Gabb, 1864, and *Corbula minima* d'Orbigny, 1847, of Whiteaves, 1879, [considered herein to be synonymous with *C. traskii*] from "the northwest side of Hornby Island," off the east coast of Vancouver Island, British Columbia (Figure 1, locale 1). Unfortunately, Whiteaves' geographic information is inexact, but according to the geologic map of Katnick & Mustard (2001), the only rocks that crop out on the northwest side of Hornby Island belong to the mudstone of the Northumberland Formation of the Nanaimo Group. Pending on-going research (P. Ward, personal communication) on the age of the various formations of the Nanaimo Group, we believe it best to refer to the age of the Northumberland Formation as undifferentiated Campanian.

Anchor Bay Member of Gualala Formation

This formation, which crops out in southern Mendocino County, northern California (Figure 1, locale 10), is part of a sedimentary block that has been tectonically transported a considerable distance northward from its point of origin, which according to Elder et al. (1998), was probably as far south as southern California. The occurrence of ***Panzacorbula***, gen. nov. *pozo* (Dailey & Popenoe, 1966) at USGS loc. M8830 in the Anchor Bay Member of this formation, therefore, is geographically anomalous. Based on molluscan taxa, this member is late Campanian to early Maastrichtian age (Elder et al., 1998).

Unnamed Upper Cretaceous Formation, Pozo District

At its type locality LACMIP 23774, abundant specimens of ***Panzacorbula*** *pozo* (Dailey & Popenoe, 1966) make up an almost monotypic shell bed deposited under brackish-water-conditions in unnamed strata approximately 4 km northwest of the hamlet of Pozo (Figure 1, locale 16), east of Santa Margarita Lake, La Panza Range, west-central Coast Ranges, San Luis Obispo County, central California. The Upper Cretaceous rocks in this area have never been assigned to a formation. Dailey & Popenoe (1966:19) mentioned the type locality but did not assign an age to the rocks. Howell et al. (1977:fig. 12) provided a geologic map of the Pozo district and mapped the rocks in the immediate area of the locality (i.e., Toro Creek, section 7) as part of an unnamed Upper Cretaceous sandstone deposited in a shallow marine-canyon head. Vedder (1977:108) and Throckmorton (1988:220) provided faunal lists of mollusks found at this locality, and Vedder reported an age of late Campanian and/or early Maastrichtian for these mollusks.

Tesla Formation

This formation crops out as two sandstone members near Corral Hollow (Figure 1, locale 12) in the area between the cities of Livermore and Tracy in the eastern part of the central Diablo Range, western edge of the San Joaquin Valley, Alameda County, northern California. This formation ranges in age from Late Cretaceous into the middle Eocene, and possibly late Eocene. Specimens of ***Panzacorbula*** *pozo* are found near the base of the lower sandstone member, which was deposited in a brackish-water environment, and the reportedly early Maastrichtian molluscan assemblage in these rocks is very similar to that found at the above-mentioned type locality of this species in the Pozo district (Throckmorton, 1988).

PREVIOUS TAXA ASSIGNED TO *CORBULA* FROM THE STUDY AREA

Although previous workers loosely applied the name "*Corbula*" to nine "Cretaceous" species of the Pacific slope of North America, only four of these, *Corbula cultriformis* Gabb, 1864; *Corbula traskii* Gabb, 1864; *Corbula minima* d'Orbigny of Whiteaves, 1879 [considered herein to be synonymous with *C. traskii*]; and *Corbula pozo* Daily & Popenoe (1966) can be substantiated as being Cretaceous corbulids. They are discussed and illustrated in this paper. The other five species are discussed, in ascending stratigraphic order, in the following paragraphs.

Corbula concinna Whiteaves (1884:219, pl. 29, figs. 3, 3a) was originally reported from outcrops along the south side of Alliford Bay, Skidegate Inlet, Maude Island area in the Queen Charlotte Islands, British Columbia. These

outcrops are of the Yakoun Formation of Middle Jurassic (Bajocian) age (McLearn, 1949). *Corbula concinna* differs significantly from corbulids by having on both valves, especially the left valve, a very prominent and projecting beak and by having a trapedzoidal left valve. This species might be an astartid.

Corbula? *persulcata* Stanton (1895:61–62, pl. 11, fig. 3) was reported from limestone strata 5 km northwest of Paskenta, Tehama County, northern California. This limestone, which is part of the Stony Creek Formation of the Great Valley Series, is of latest Jurassic (Tithonian) age and contains in situ chemosynthetic mollusks that lived in a deep-marine setting dominated by turbidites (Campbell et al., 1993). It is not possible, with the available material, to positively assign Stanton's species to any family or genus because the species is known only from the holotype, and its dorsal posterior end is missing. *Corbula*? *persulcata,* however, differs from any known study area Cretaceous corbulid by having widely spaced commarginal furrows.

Corbula filosa Stanton (1895:62, pl. 11, figs. 1, 2) was originally reported from the Paskenta Group, Cold Fork of Cottonwood Creek, Tehama County, northern California. The age of these rocks is earliest Cretaceous (Berriasian) (Campbell et al., 1993). *Corbula filosa* does not appear to be a corbulid. Its projected to rounded anterior end, variable presence of an ill-defined posterior slope on the right valve, and an extremely broad posterior slope (when present) on the right valve suggest that it might be a venerid.

?*Corbula primorsa* Gabb (1864:148, pl. 22, figs. 120, 120a) was originally reported from probably Cretaceous rocks on the south side of Corral Hollow, just southeast of Tesla, Alameda County, north-central California, but the location information is inexact. Stewart (1930:7) reported that the type specimens of this species have been lost. Because it is not known what beds ?*Corbula primorsa* came from and because the types are lost, this species is deemed by us to be a *nomen dubium.*

Corbula parilis Gabb (1864:150, pl. 29, figs. 239, 239a) was originally reported as questionably of Cretaceous age and from Martinez, northern California. Although this species belongs to *Caryocorbula,* it is an Eocene one that ranges from San Diego, southern California through southwestern Oregon, in rocks of early ("Capay Stage") through middle ("Transition Stage") Eocene age (Squires, 1987).

SYSTEMATIC PALEONTOLOGY

Phylum MOLLUSCA Linnaeus, 1758

Class BIVALVIA Linnaeus, 1758

Order MYOIDA Stoliczka, 1870

Family CORBULIDAE Lamarck, 1818

Diagnosis: Shell small to medium, inequilateral, inequivalved to sub-inequivalved, aragonitic, with crossed-lamellar outer and complex crossed-lamellar inner layers. Ligament partly external, internal portion amphidetic. Right valve generally strongly inflated and larger than left valve, to a varying degree. Posterior end somewhat rostrate. Shell sculptured with commarginal ribs or smooth; radial ribs usually absent. Hinge simple with pit in left valve and corresponding anterior cardinal tooth in right valve. Chondrophore of left valve usually present, usually small, and variable in amount of projection. Muscle scars dimyarian. Pallial sinus small or absent (Vokes, 1945; Keen, 1969; Davies, 1971; Anderson, 1996; Coan, 2002).

Discussion: Corbulids have traditionally been placed in order Myoida, but molecular, conchological, and anatomical evidence suggests that corbulids might be more appropriately aligned to veneroids. Anderson & Roopnarine (2003) have summarized this evidence.

Dall (1898, 1900), Vokes (1945), and Keen (1969) did detailed systematic studies on Corbulidae. These bivalves have been largely split and grouped on shape and sculpture. Dentition, especially the shape of the chondrophore, and other shell features have been utilized, to some extent, as well. As indicated by Coan et al. (2000) and Coan (2002), inspection of the literature readily shows that early attempts to subdivide this family into subfamilies, genera, and subgenera were not successful. To date, however, there have been no rigorous morphology-based phylogenetic analyses of all the named genera, but Anderson & Roopnarine (2003) have done a rigorous phylogenetic analysis of Neogene genera and subgenera of the Corbulidae from tropical America.

In this present study, we endeavored to incorporate all available morphologic characters when assigning the species to the various genera. The key characters of these genera, as well as the study area species assigned to them, are given in Table 1. The biggest problem in working with Cretaceous corbulids, especially those from the study area, is the difficultly in cleaning the hinges of the small species (i.e., length less than 15 mm). They are almost always encased in well cemented matrix, and cleaning of the delicate chondrophore is very risky and can easily result in irreversible damage to the shell. For these particular species, a more effective technique is to inspect weathered specimens for those that show the dorsal surface of the chondrophore. In many of these cases, only minimal cleaning is required. At least the presence of the chondrophore can be determined, as well as whether or not it is projecting.

Subfamily CORBULINAE Lamarck, 1818

Diagnosis: Right valve slightly larger than left valve, valves more or less irregular in shape, from strongly inequivalve to subequivalve, posterior end somewhat rostrate. Ligament fitting into pit on hinge of left valve or onto expanded, usually projecting chondrophore (Keen, 1969; Coan et al., 2000).

Table 1

Check list of key morphologic characters used in differentiating the new taxa.

Taxa	Size	Left-valve sculpture	Right-valve sculpture	Other
Caryocorbula: elongate-ovate, valves tapered posteriorly, sculpture similar on both valves, single radial keel.				
*C. **coani***	medium	nearly smooth	nearly smooth	posterior keel very low
*C. **onoensis***	small	weak to medium	weak to medium	—
*C. **vacca***	small	very weak to weak	very weak to weak	minute radial threads possible
*C. **traskii***	medium	nearly smooth	very weak	—
*C. **lomana***	very small	very weak to weak	very weak to weak	quadrate shell, posterior slope squarish
Excorbula: trigonal, left valve smooth or nearly smooth, right valve initially smooth or with very weak ribs becoming stronger ventrally, right valve with two narrowly spaced keels.				
E. coqua	small	very weak	strong	—
E. parkyi	medium	smooth	strong	posterior slope groove-like
E. shastana	small	smooth	medium	posterior slope moderately wide
Panzacorbula: subpyriform, single keel obsolete on mature specimens.				
***P.** pozo*	medium	very weak to weak	strong	—
Eoursivivas: very elongate, subdued irregular bands on valves, keel weak.				
E. cultriformis	medium	weak	weak	—
Caestocorbula: left valve much smaller, less inflated, less rostrate, and with weaker ribs than right valve.				
*C. **cavus***	small	very weak	weak	—
*C. **attrina***	very small	very weak	very weak to weak	—
*C. **aura***	small	weak	weak	umbo of right valve smooth
*C.? **attisoni***	small	medium	weak to strong	both valves bulbous

Discussion: We agree with Coan (2002:50), who reported there are a "bewildering array of specific and generic taxa in this subfamily," but many of the species found in this present study readily can be shown to belong to *Caryocorbula.*

Genus *Caryocorbula* Gardner, 1926

Type species: *Corbula alabamiensis* Lea, 1833, by original designation; middle Eocene, southeastern United States.

Diagnosis: Shell small to moderate, subquadrate to elongate ovate, inequilateral, right valve slightly larger and deeper than left. Posterior slope acutely set off by radial keel. Valves usually pointed (tapered) posteriorly. Umbones not inflated, nor set off by growth stages; beaks slightly prosogyrate. Lunule and escutcheon absent. Sculpture of weak to moderately strong commarginal ribs, similar on both valves; radial threads possibly present. Left-valve hinge with chondrophore and (posteriorly) adjoining deep pit. Chondrophore moderately broad, somewhat projecting and flattish, and bearing median ridge. Right-valve hinge with single, large triangular cardinal tooth (upcurved at tip) and adjoining deep, broad

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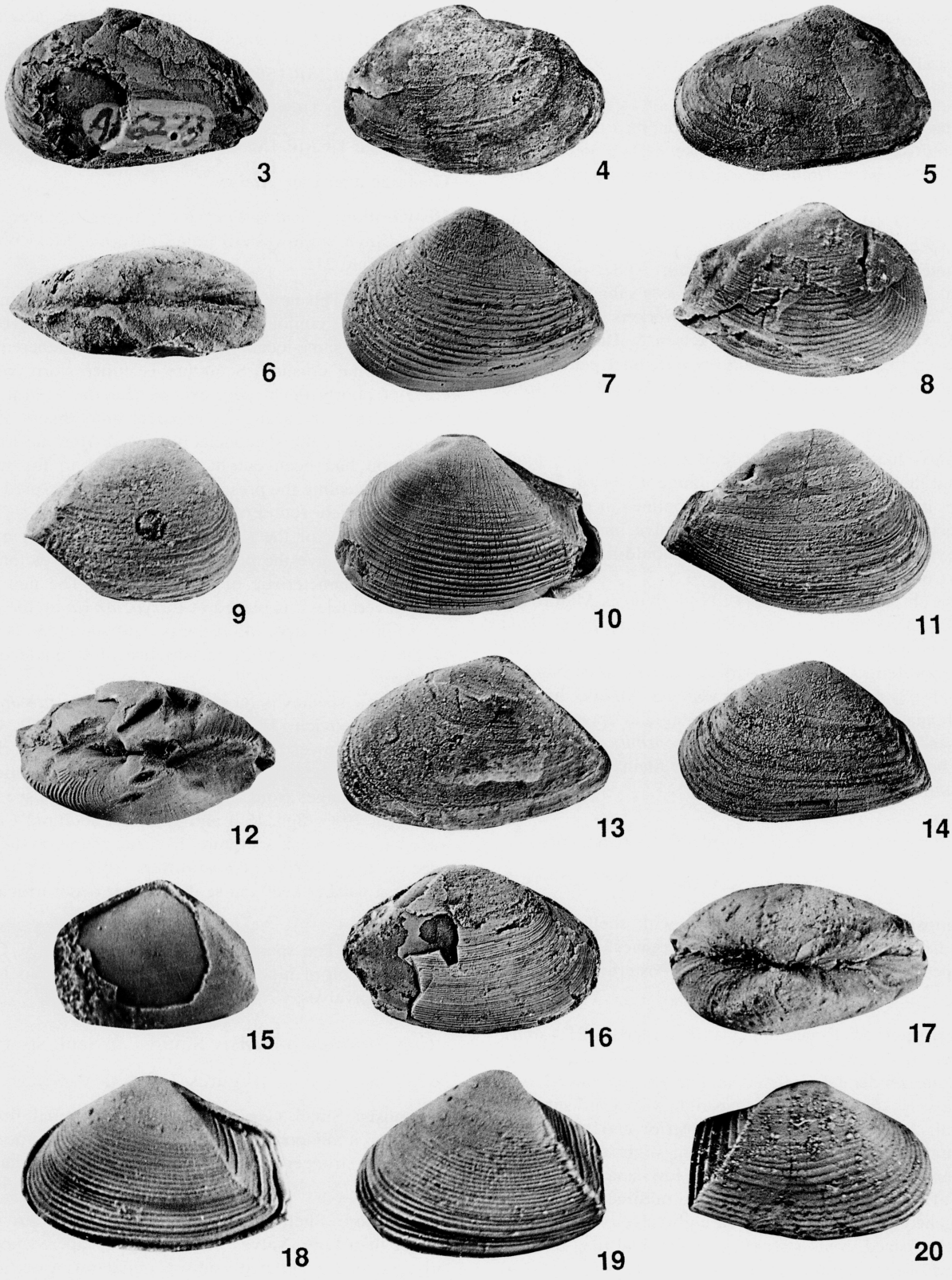
Figures 3–20. Specimens coated with ammonium chloride. Figures 3–6. *Caryocorbula **coani*** Squires & Saul, sp. nov., UCMP loc. A-6273. Figure 3. Paratype UCMP 155536, left valve, ×2.2. Figure 4. Paratype UCMP 155537, left valve, ×2.8. Figures 5, 6. Holotype UCMP 155535, ×2.3. Figure 5. Right view. Figure 6. Dorsal view. Figures 7–9. *Caryocorbula **ononensis*** Squires & Saul, sp. nov. Figure 7. Holotype LACMIP 13100, LACMIP loc. 24285, left valve, ×3.8. Figure 8. Paratype LACMIP 13101, loc. 29230, right valve, ×4.5. Figure 9. Paratype LACMIP 13102, LACMIP loc. 24285, right valve, showing predatory drill hole, ×3.3. Figures 10–12. *Caryocorbula **vacca*** Squires & Saul, sp. nov. Figure 10. Holotype LACMIP 13103, LACMIP loc. 24365, left valve, ×5. Figure 11. Paratype LACMIP 13104, LACMIP loc. 10764, right valve, ×4.5. Figure 12. Holotype LACMIP 13103, LACMIP loc. 24365, dorsal view, ×5.2. Figures 13–17. *Caryocorbula traskii* (Gabb, 1864). Figure 13. Lectotype UCMP 155538, CGS loc. 145, left valve, ×5.5. Figure 14. Hypotype LACMIP 13105, LACMIP loc. 22406, left valve, ×3.7. Figure 15. Hypotype GSC 5742, NW side Hornby Island, British Columbia, left valve, ×7.5. Figure 16. Hypotype LACMIP 13106, LACMIP loc. 22406, right valve, ×3.9. Figure 17. Hypotype LACMIP 13107, LACMIP loc. 10832, dorsal view, ×8. Figures 18–20. *Caryocorbula **lomana*** Squires & Saul, sp. nov. Figure 18. Holotype SDSNH 81140, SDSNH loc. 3387, left valve, ×11.5. Figure 19. Paratype SDSNH 81141, SDSNH loc. 3162-C, left valve, ×8.4. Figure 20. Paratype LACMIP 13108, LACMIP loc. 7792, right valve, ×8.2.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pit. Adductor scars prominent. Pallial sinus simple, short, nearly vertical, and shallow to absent (Vokes, 1945; Stenzel et al., 1957; Keen, 1969; Coan et al., 2000; Coan, 2002).

Discussion: Coan (2002) gave taxonomic details concerning *Caryocorbula,* whereas Vokes (1945) and Stenzel et al. (1957) gave detailed descriptions of the type species of *Caryocorbula.* Stenzel et al. (1957) also provided a very useful, labelled drawing of the hinge features of the type species.

Some workers (e.g., Keen, 1969; Anderson, 1996; Coan, 2002) included *Caryocorbula* as a subgenus of genus *Corbula* Bruguière, 1797. Other workers (e.g., Vokes, 1945; Stenzel et al., 1957; Mikkelsen & Bieler, 2001), however, treated *Caryocorbula* as a distinct genus. It is important to emphasize that *Caryocorbula* differs from *Corbula* sensu stricto (type species *Corbula sulcata* Lamarck, 1801) by having a projecting chondrophore on the left-valve hinge and an absence of a small posterior tooth behind the pit on the right-valve hinge. *Corbula,* furthermore, is also unlike most other corbulines in not have a projecting chondropore on the left-valve hinge. We believe, therefore, that *Caryocorbula* should not be a subgenus of *Corbula.*

The chronologic range of *Caryocorbula* is Middle Jurassic to Recent. Its earliest record is apparently *Corbula tanganyicensis* Cox (1965) from Middle Jurassic (Bajocian?) of Tanganyika, east Africa. *Corbula attenuata* Lycett (1863) from the slightly younger Middle Jurassic (Bathonian) Great Oolite beds of England appears to be the second earliest species of *Caryocorbula.* We believe that both of these species have the main characters of *Caryocorbula.*

Caryocorbula ***coani*** Squires & Saul, sp. nov.

(Figures 3–6)

Diagnosis: Medium *Caryocorbula* with shell subquadrate. Commarginal ribs on both valves weak, poorly developed; valves overall smoothish. Posterior keel very low.

Description: Shell medium (maximum length 21.4 mm), longer than high. Valves subquadrate to somewhat ovate-elongate, moderately inflated, and nearly equivalved. Left valve very slightly smaller than right valve and subequilateral. Anterior end rounded. Posterior end variable in amount of elongation, ranging from slight to moderate. Posterior keel very low. Umbones low, anterior to midline of valves; beaks just anterior to midline. Lunule and escutcheon absent. Sculpture on both valves consisting of closely spaced, weak strength commarginal ribs, best developed near ventral margin and anteriorly becoming less tangential to ventral margin. Right-valve hinge with single, large cardinal tooth; adjoining pit deep.

Dimensions of holotype: Conjoined valves, height 13 mm, length 19.9, thickness 8.6 mm.

Holotype: UCMP 155535.

Type locality: UCMP loc. A-6273, 31°31′N, 116°41′W.

Paratypes: UCMP 155536 and 155537.

Geologic age: Late Aptian.

Distribution: Alisitos Formation, upper member, near Punta China, northwestern Baja California, Mexico (Figure 1, locale 21).

Discussion: This new species is based on nine specimens: eight pairs of conjoined valves and one right valve. All are from the same locality. Most are badly weathered and/or somewhat crushed. Sculpture is either worn, weathered, or poorly developed, except near the ventral margins, thereby imparting an apparent smoothness to the valves. One of the specimens borrowed from the UCMP collection had been cut in half, parallel to the hinge, thereby revealing the presence of this tooth. No predatory drill holes were found on any of the specimens.

Only a few of the specimens (e.g., Figure 3) of the new species have the posteriorly tapered valves that are normally characteristic of *Caryocorbula.* The new species, nevertheless, is placed in *Caryocorbula* on the basis of similarity in size, inflatedness, and sculpture of both of the valves, as well as an absence of a lunule or escutcheon.

The new species is most similar to *Caryocorbula betsyae* Marincovich (1993:23, 26, figs. 13.1–13.20, 14.1–14.6), from lower Cenozoic (Danian) strata in northern Alaska. Like the new species, the posterior elongation of *C. betsyae* ranges from slight to moderate (e.g., see Marincovich, 1993, figs. 13.3 and 13.6). In addition, *C. betsyae* has very weak sculpture, like that found on the new species. *Caryocorbula* ***coani*** differs from *C. betsyae* by having a weaker keel and sculpture that is not irregularly rugose.

Etymology: The species is named for Eugene V. Coan, in recognition of his many valuable contributions to the study of bivalves.

Caryocorbula ***onoensis*** Squires & Saul, sp. nov.

(Figures 7–9)

Diagnosis: Small *Caryocorbula.* Commarginal ribs on both valves moderately closely spaced, weak to medium, becoming stronger ventrally. Posterior keel moderately low.

Description: Shell small (maximum length 11.6 mm), longer than high. Valves trigonal ovate, tapered posteriorly, moderately inflated, and subequilateral. Anterior end rounded. Posterior end subtruncate. Posterior slope on both valves subvertical, with growth lines only, and set

off by moderately low, straight keel. Umbones moderately high, at midline of valves; beaks prosogyrate, just anterior to midline. Lunule and escutcheon absent. Sculpture on both valves consisting of moderately closely spaced, weak to medium strength commarginal ribs, and overlapping shinglelike. Sculpture on each valve, strongest ventrally, especially on left valve. Ribs on left valve also becoming more widely spaced ventrally and showing prominent growth lines. Right-valve umbo can be smooth (worn?). Left-valve hinge with projecting chondrophore; adjoining pit deep.

Dimensions of holotype: Left valve, 7.9 mm in height, 11.4 mm in length.

Holotype: LACMIP 13100.

Type locality: LACMIP loc. 24285, 39°16′40″N, 122°19′52″W.

Paratypes: LACMIP 13101 and 13102.

Geologic age: Late early Albian to Cenomanian.

Distribution: UPPER LOWER ALBIAN: Budden Canyon Formation, Chickabally Member, Texas Springs, Shasta County, northern California (Figure 1, locale 4). CENOMANIAN: Great Valley Series, in lower part of informal Antelope Shale at "Peterson Ranch," north of Sites, Colusa County, northern California (type locality) (Figure 1, locale 9). UPPER ALBIAN TO UNDIFFERENTIATED CENOMANIAN: Budden Canyon Formation, Bald Hills Member, Bald Hills near Ono, Shasta County, northern California (Figure 1, locale 4).

Discussion: This new species is based on 38 specimens: 25 right vales and 13 left valves. No conjoined valves were found. Specimen are most abundant at LACMIP loc. 29230, located at Texas Springs, near Ono, northern California. The holotype and paratype are somewhat worn, but they are most complete specimens available. Only a single specimen (Figure 9) shows a predatory drill hole.

The new species is similar to *Corbula tanganyicensis* Cox (1965:122, pl. 19, figs. 9a, 9b, 12a–d) from Middle Jurassic (Bajocian?) of Tanganyika, East Africa. The new species differs by being larger and having a more elongate right valve. The new species is also similar to *Corbula attenuata* Lycett (1863:62–63, pl. 37, figs. 6, 6a) from the Middle Jurassic (Bathonian) Great Oolite of England, but the new species differs by having slightly stronger sculpture and a less pronounced keel on the left valve.

The new species resembles *Corbula lineata* Müller (1847:26, pl. 2, figs. 6; Holzapfel, 1889:146–147, pl. 10, figs, 16–19) from the Greensand beds of Vaals and Aachen, Germany, which are of earliest Campanian age (Albers, 1976). We believe that Müller's species has all the characteristics of a *Caryocorbula.* The new species differs from *Caryocorbula lineata* by having fewer commarginal ribs with deeper interspaces, and a somewhat more rostrate right valve.

Etymology: The new species is named for Ono, California.

Caryocorbula ***vacca*** Squires & Saul, sp. nov.

(Figures 10–12)

Diagnosis: Small *Caryocorbula.* Commarginal ribs on both valves very closely spaced and very weak (mainly) to weak strength, occasionally crossed by minute radial threads, posterior keel low to moderately strong. Posterior end with short rostrum.

Description: Shell small (maximum length 9.6 mm), longer than high. Valves trigonal ovate, tapered posteriorly, moderately inflated, and subequilateral. Left valve slightly smaller than right valve. Anterior end rounded. Posterior end projected into short rostrum. Posterior slope wide, flattish, at moderate angle and set off by low to moderately strong, straight keel; rostrum short, truncate. Umbones moderately high, at midline of valves; beaks prosogyrate, just anterior to midline. Sculpture similar on both valves and consisting of closely spaced (6 to 10 ribs/mm) very weak (mainly) to weak strength commarginal ribs; occasionally intersected, on both valves, by minute radial threads (especially on umbones). Commarginal ribs continue onto posterior slope. On some specimens, ventral parts of both valves curl hingeward with growth, causing change in slope of disk; ribs on curled part becoming slightly stronger, wavy, and with deep interspaces. Left-valve hinge with slightly projecting chondrophore; adjoining pit wide and deep. Right-valve hinge with single, large cardinal tooth; adjoining pit deep. Pallial line simple, well developed, not indented.

Dimensions of holotype: Conjoined valves, 6 mm in height, 9.5 mm in length, 4.5 mm in thickness.

Holotype: LACMIP 13103.

Type locality: LACMIP loc. 24365, 40°39′10″N, 122°6′25″W.

Paratype: LACMIP 13104.

Geologic age: Turonian.

Distribution: Hornbrook Formation, Osburger Gulch Member, Yreka area, Siskiyou County, northern California (Figure 1, locale 3); Redding Formation, Bellavista Sandstone and Frazier Siltstone (type locality) members, east of Redding, Shasta County, northern California (Figure 1, locale 5); Budden Canyon Formation, lower part of Gas Point Member, near Ono, Shasta County, northern California (Figure 1, locale 4); Ladd Formation, Baker Canyon Member, Santa Ana Mountains, Orange County, southern California (Figure 1, locale 19).

Discussion: This new species is based on 98 specimens:

57 right valves, 34 left valves, and seven pairs of conjoined-valves. Only one valve (right valve) has a predatory drill hole. At LACMIP loc. 10079 in the Baker Canyon Member, the new species co-occurs with ***Excorbula coqua***, gen. et sp. nov.

The new species is similar to *Corbula truncata* Sowerby (1836:240, 341, pl. 16, fig. 8; Woods, 1908:215, pl. 34, figs. 17–22) from the upper Albian Upper Greensand in England but differs from *C. truncata* by having radial riblets, slightly stronger commarginal ribs, and on the left valve, a weaker rostrum. We believe that Sowerby's species belongs to *Caryocorbula.*

Caryocorbula ***vacca*** is intermediate in morphology between *C.* ***onoensis*** and *C. traskii. Caryocorbula* ***vacca*** differs from *C.* ***onoensis*** by having weaker and more closely spaced ribs, and *C.* ***vacca*** differs from *C. traskii* by having much more prominent ribs on the left valve and stronger and more widely spaced ribs on the right valve.

Etymology: The species is named for its occurrence in Little Cow Creek Valley, east of Redding, Shasta County; Latin, *vacca* meaning cow.

Caryocorbula traskii (Gabb, 1864)

(Figures 13–17)

Corbula traskii Gabb, 1864:149, pl. 22, figs. 121, 121a.
Corbula minima d'Orbigny. Whiteaves, 1879:138, pl. 17, figs. 4, 4a.
Corbula traskii? Gabb. Whiteaves, 1879:138, pl. 17, fig. 3.

Diagnosis: Medium *Caryocorbula* with left valve nearly smooth. Commarginal ribs on right valve very closely spaced and very weak. Posterior keel very low on both valves.

Description: Shell medium (maximum length 15 mm), longer than high. Valves trigonal ovate, tapered posteriorly, moderately inflated, subequilateral, and nearly equivalved. Left valve very slightly smaller and slightly less inflated than right valve. Anterior end rounded. Posterior end somewhat truncate. Posterior keel very low on both valves. Umbones moderately low, at midline of valves; beaks prosogyrate, just anterior to midline. Lunule and escutcheon absent. Left valve with very weak commarginal ribs to nearly smooth. Right valve with very closely spaced (approximately 11 ribs/mm on adult), very weak strength commarginal ribs; rarely becoming somewhat wavy ventrally. Left-valve hinge with projecting chondrophore separated into two parts by shallow groove, widening posteriorly.

Dimensions of lectotype: Left valve, 5.3 mm in height, 8.3 mm in length.

Lectotype: UCMP 155538 [= CGS 145], designated here.

Type locality: Exact location unknown, Pentz, Butte County, northern California.

Geologic age: Coniacian to middle Campanian.

Distribution: CONIACIAN: Chico Formation, Ponderosa Way Member, Chico Creek, Butte County, northern California (Figure 1, locale 7). SANTONIAN: Redding Formation, Member V, east of Redding, Shasta County, northern California (Figure 1, locale 5); Chico Formation, Musty Buck Member, Chico Creek, Butte County, northern California (Figure 1, locale 7). LOWER CAMPANIAN: Chico Formation, Ten Mile Member, Chico Creek, Butte County, northern California (Figure 1, locale 7); Chico Formation, Pentz Road member (informal), Butte County, northern California (type locality) (Figure 1, locale 8); Chico Formation, ?Tuscan Springs, Tehama County, northern California (Figure 1, locale 6); Ladd Formation, Holz Shale Member (upper part), Santa Ana Mountains, Orange County, southern California (Figure 1, locale 19); Williams Formation, Schulz Member, Santa Ana Mountains, Orange County, southern California (Figure 1, locale 19). MIDDLE CAMPANIAN: Pigeon Point Formation, south of San Francisco, San Mateo County, northern California (Figure 1, locale 13); Chatsworth Formation, Bell and Dayton canyons, Simi Hills, Ventura County, southern California (Figure 1, locale 18). UNDIFFERENTIATED CAMPANIAN: Northumberland Formation, northwest side of Hornby Island, east side of Vancouver Island, British Columbia (Figure 1, locale 1).

Discussion: This study of Gabb's species is based on 511 specimens (including Gabb's original material): 295 right valves, 127 left valves, and 89 pairs of conjoined valves. Five specimens (all right valves) show predatory drill holes.

Corbula traskii Gabb (1864:149, pl. 22, figs. 121, 121a) was originally reported from Texas Flat, Placer County; Tuscan Springs, Tehama County; and Pentz [= Pence's Ranch], Butte County, northern California. According to Stewart (1930:289), UCMP has a number of specimens which are presumably the original material upon which Gabb based his species. Our search of the UCMP collection resulted in the discovery of two cabinets containing original material formerly stored under the auspices of the old California Geological Survey collection. A box labelled "CGS no. 145, original material," contains several specimens of *Corbula* and possibly several other genera of bivalves. Because Gabb did not designate a holotype, we selected the best preserved specimen (Figure 14) to serve as the lectotype. It has labels glued to it that identify the specimen as *Corbula traskii* Gabb and as CGS 145. This specimen is indistinguishable in morphology from the other specimens of this species from Pentz.

A poorly preserved specimen questionably labelled as from Tuscan Springs is also among the original material

of Gabb's stored at UCMP. No original material was found from Texas Flat, thus this occurrence could not be verified.

Whiteaves (1879:138, pl. 17, fig. 3.) reported *C. traskii*? from the northwest side of Hornby Island, but, according to him, the specimens are too poorly preserved for positive specific identification. His illustrated specimen appears to be an internal mold. There are no GSC numbers for any of these specimens mentioned by Whiteaves, and they were not found by Bolton (1965).

Whiteaves (1879:138, pl. 17, figs. 4, 4a) also reported *Corbula minima* d'Orbigny, 1847, from the northwest side of Hornby Island, east side of Vancouver Island, British Columbia. Whiteaves (1879) illustrated a left and a right valve, but only the left valve (GSC hypotype 5742) was detected by Bolton (1965:99). Examination of the left-valve specimen (GSC hypotype 5742) revealed that it is *Caryocorbula traskii*, and an illustration (Figure 15) is provided here.

Caryocorbula traskii is similar to *Corbula broggii* Olsson (1944:65–66, pl. 6, figs. 1–3) from Maastrichtian strata in the Paita region of northern Peru, and even Olsson remarked on the similarity. *Caryocorbula traskii* differs from the Peruvian species by having more inflated valves and finer ribs.

Caryocorbula ***lomana*** Squires & Saul, sp. nov.

(Figures 18–22)

Diagnosis: Very small *Caryocorbula* with shell usually quadrate. Commarginal ribs on both valves very weak to weak. Posterior slope usually squarish, bearing ribs more widely spaced and more prominent than elsewhere.

Description: Shell very small (maximum length 6 mm), longer than high. Valves usually quadrate, rarely trigonal, lowly inflated, and inequilateral. Left valve slightly smaller than right valve. Anterior end rounded. Posterior end truncate. Posterior dorsal margin of right valve ridged and parallel or subparallel to hinge. Posterior keel sharp on both valves. Posterior slope wide and tall. Umbones low, at midline of valves; beaks prosogyrate, just anterior to midline. Lunule and escutcheon absent. Sculpture on both valves usually consisting of very weak to weak, closely spaced commarginal ribs; some variability in rib strength, ranging from moderately weak to moderately strong. Posterior slope on both valves with fewer ribs, but more widely spaced and usually more prominent than elsewhere. Left valve with microscopic radials in interspaces between ribs and minute, raised radial threads on anterior or posterior part of valve. Left-valve hinge with projecting chondrophore, flattish with median groove; adjoining pit narrow and deep. Right-valve hinge with small cardinal tooth; adjoining pit wide and deep. Right-valve interior grooved for reception of margin of left valve. Posterior ends of both valves flattened and somewhat projected, with extreme postero-ventral margin bluntly pointed where keel meets ventral margin. Pallial line simple, nearly vertical posteriorly, with slight indentation. Adductor muscle scars prominent, posterior one larger.

Dimensions of holotype: Conjoined valves, 3 mm in height, 4.6 mm in length, 2 mm in thickness.

Holotype: SDSNH 81140.

Type locality: SDSNH loc. 3387, 33°8′22N, 117°17′0″W.

Paratypes: SDSNH 81141 and 81142; LACMIP 13108 and 13109.

Geologic age: Campanian to early Maastrichtian.

Distribution: LOWER CAMPANIAN: Chico Formation, Ten Mile Member, Chico Creek, Butte County, northern California (Figure 1, locale 7). MIDDLE CAMPANIAN: Chatsworth Formation, Simi Hills, Ventura County, southern California (Figure 1, locale 18). UPPER CAMPANIAN TO LOWER MAASTRICHTIAN: Point Loma Formation, Carlsbad area, San Diego County, southern California (type locality) (Figure 1, locale 20); Rosario Formation, Arroyo Santa Catarina, northwestern Baja California, Mexico (Figure 1, locale 22).

Discussion: This new species is based on 289 specimens: 119 right valves, 60 left valves, and 110 pairs of conjoined valves. Preservation is excellent for specimens from the Point Loma Formation, and specimens were particularly abundant from that stratigraphic unit at SDSNH loc. 3387. This locality yielded 239 specimens: 85 left valves, 51 right valves, and 103 pairs of conjoined valves. Thirty-six of these 239 specimens show predatory drill holes: 14 on left valves and 19 on right valves.

The new species resembles *Corbula swedesboroensis* Weller (1907:644–645, pl. 72, figs. 33–36) from Campanian strata of New Jersey but differs from Weller's species by having a more quadrate rostrum with stronger and more widely spaced commarginal ribs. The left valve of Weller's species is not known.

The usually squarish rostrum on the new species resembles that found on *Tenuicorbula tenuis* (Sowerby, 1833:36; Olsson, 1961:434, pl. 77, figs. 3, 3a), the type species of the Miocene to Recent *Tenuicorbula* Olsson, 1932, known from Central and South America. The new species differs from *T. tenuis* by having smaller size, much less elongate shell, ribs more widely spaced on rostrum, only a single rather than a double keel on both valves, and a straighter keel.

Etymology: The species is named for the Point Loma Formation, San Diego County, southern California.

Genus ***Excorbula*** Squires & Saul, gen. nov.

Type species: ***Excorbula parkyi***, sp. nov.; Late Cretaceous (Turonian to Santonian), California.