LATE CRETACEOUS OYSTERS FROM THE PACIFIC SLOPE OF NORTH AMERICA: REVISION OF NAMED SPECIES AND DISCOVERY OF NEW SPECIES[1]

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ABSTRACT. Late Cretaceous oyster species are common faunal components in shallow-marine siliciclastic rocks on the Pacific slope of North America (PSNA), in a region extending southward from Vancouver Island, British Columbia, Canada, to Northern Baja California, Mexico. Seven species have been named, but they are poorly known. The purpose of this study is to better document these species by upgrading their morphologic, taxonomic, geographic, and stratigraphic data. In addition to the seven revised species, four new species, a questionable species, and an unnamed species were detected, resulting in a total of 13: *Oscillopha popenoei* sp. nov.; *Rastellum* sp., aff. *R. macropterum* (J.D.C. Sowerby, 1825); *Curvostrea crescentica* (Packard, 1922); *Curvostrea baia* sp. nov.; *Acutostrea taxidonta* (Packard, 1922); *Crassostrea brewerii* (Gabb, 1864); *Costagyra californica* (Packard, 1922); *Costagyra garza* sp. nov.; *Amphidonte parasitica* (Gabb, 1864) [assignment to this genus by Elder (1991) is confirmed]; ?*Amphidonte parasitica* (Gabb, 1864); *Pycnodonte (Pycnodonte) malleiformis* (Gabb, 1864); *Phygraea inornata* (Packard, 1922); and *Phygraea arida* sp. nov. Morphs most likely represent ecophenotypic responses to different water energies (e.g., *A. taxidonta*) or whether or not there was attachment (e.g., *P. inornata*). Growth stages were newly recognized for *A. parasitica*.

None of the detected oyster genera or subgenera are endemic to the warm-temperate PSNA region. Except for *Amphidonte*, none were previously recognized in the Cretaceous record of the PSNA region. The late Santonian *Oscillopha popenoei* is the first occurrence of this genus in North America. The highest biodiversity level of PSNA oyster species (five) coincided with the Turonian and late early to early late Maastrichtian (both warm times with high sea level), and the lowest biodiversity level (zero) coincided with the Coniacian (cooler time with lower sea level). In the PSNA region, there was a reoccurrence of the Turonian *Curvostrea-Costagyra-Phygraea* association in the late early to early late Maastrichtian.

INTRODUCTION

Oysters are common in Upper Cretaceous shallow-marine strata in the region extending from Vancouver Island, British Columbia, Canada, to Northern Baja California, Mexico (Fig. 1), referred to hereafter as PSNA (Pacific Slope of North America). Seven species have been named. Gabb (1864) named three, based on collecting in Northern California, and Packard (1922) named four, based on collecting in Southern California. Their descriptions are inadequate because they are too brief and rely on only the holotype. Their illustrations are commonly insufficient because they show only one view of a badly weathered holotype or show only its interior. In addition, Gabb's illustrations are idealized sketches. Subsequent workers encountered difficulty in trying to recognize these species and generally avoided using Gabb's and Packard's names, as evidenced by the short synonymies given here.

The purpose of this study is to improve on the fundamental paleontologic information concerning these previously named species. The improvements include 1) more detailed morphologic descriptions, including recognition of morphs and xenomorphism, 2) all the photographs necessary to document the observed morphologies, 3) integration of current concepts of familial classification of oysters, 4) integration of more comprehensive geographic and stratigraphic distributions, and 5) updated chronostratigraphic data. During the course of this study, four new species, one unnamed species, and one questionable species were also discovered. The revisions and these new discoveries have allowed, for the first time, meaningful biodiversity information concerning the oyster fauna to be inferred. The significance

of this contribution is that it establishes a modern foundation for future studies of Late Cretaceous PSNA oysters.

MATERIALS AND METHODS

The collection at the Natural History Museum of Los Angeles County, Invertebrate Paleontology (LACMIP) Department, is the principal source of material. Two of the core strengths of the collection's Cretaceous holdings are 1) Turonian through Campanian fossils collected by W.P. Popenoe and L.R. Saul in the Santa Ana Mountains, Orange County, California, and 2) Turonian fossils collected by W.P. Popenoe in the Redding area, Shasta County, California. The specimens they collected are critical for the revisions reported here. More recent additions of well preserved fossils to the LACMIP collection were essential in confirming and expanding the work of Elder (1991) on *Amphidonte parasitica* (Gabb, 1864).

Specimens from British Columbia, Canada, were the sources for supplemental material. Although Cretaceous strata are plentiful along the southeast side of Vancouver Island, British Columbia, oysters are not common in these strata, except at a few localities, like near Nanaimo (Ludvigsen and Beard, 1994, 1997) and on western Denman Island (R. Graham, personal communication, 2015). Raymond Graham facilitated the loan of some Nanaimo material collected by Graham Beard and now part of the Vancouver Island Paleontological Museum (VIPM) collection in Qualicum Beach, British Columbia. Raymond Graham photographed these specimens and provided detailed stratigraphic information. Raymond Graham also lent some western Denman Island specimens collected by him and Timon Bullard. Two of R. Graham's specimens and one of T. Bullard's specimens are used here as paratypes of *Phygraea arida* sp. nov. These three specimens are now part of the Royal British Columbia Museum (RBCM) collection in Victoria, British Columbia, Canada.

Upper Cenomanian oysters occur predominantly as internal casts, whereas Turonian through upper Maastrichtian oysters are generally
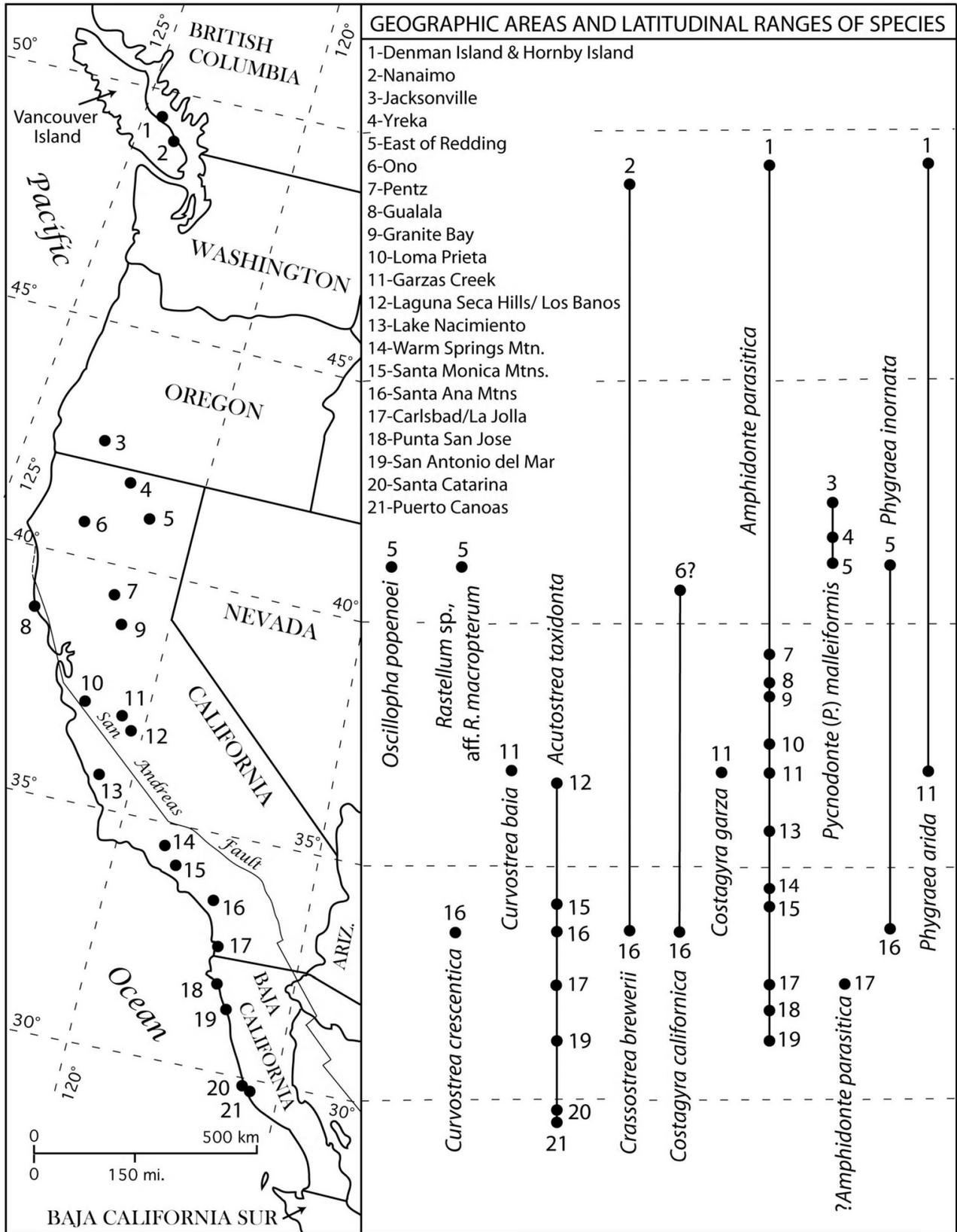
Figure 1 Geographic areas and latitudinal distribution of PSNA Late Cretaceous oyster species.

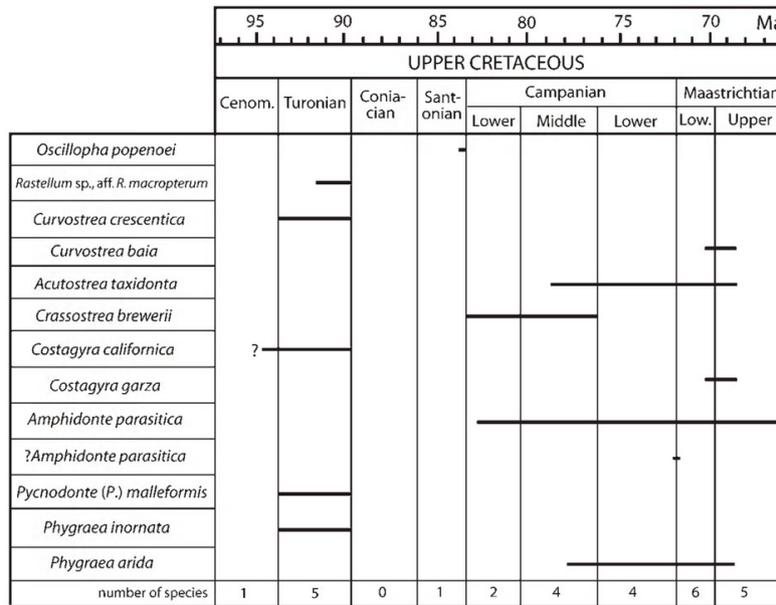|	Cenom.	Turonian	Conia-cian	Sant-onian	Campanian			Maastrichtian	
					Lower	Middle	Lower	Low.	Upper
Oscillopha popenoei									
Rastellum sp., aff. R. macropterum									
Curvostrea crescentica									
Curvostrea baia									
Acutostrea taxidonta									
Crassostrea brewerii									
Costagyra californica									
Costagyra garza									
Amphidonte parasitica									
?Amphidonte parasitica									
Pycnodonte (P.) malleformis									
Phygraea inornata									
Phygraea arida									
number of species	1	5	0	1	2	4	4	6	5

Figure 2 Chronostratigraphic ranges of PSNA Late Cretaceous oyster species and number of species per stage. Ages of stage boundaries from Gradstein et al. (2012).

well preserved. No confirmable Coniacian oysters were detected. Uppermost Maastrichtian oysters are poorly preserved.

The examined specimens are nearly all from shallow-marine siliciclastic deposits, consisting commonly of siltstone or silty fine-grained sandstone. In rare cases, the shallow-marine oysters experienced postmortem transport via turbidity currents into deeper environments. "Area" designations (see Fig. 1) for where the oysters were found are used throughout the text. Current summaries of the geological details of the formations and members containing the studied oysters are in the following papers (listed in ascending chronostratigraphic order): Budden Canyon Formation, Bald Hills Member (Squires and Saul, 2004) [Area 6]; Hornbrook Formation, Osburger Gulch Member (Squires and Saul, 2003a) [Area 4]; Redding Formation, Bellavista Sandstone Member, Frazier Siltstone Member, and Member VI (Squires and Saul, 2003b) [Area 5]; Ladd Formation, Baker Canyon Member (Saul and Squires, 2003) and Holz Shale Member (Squires and Saul, 2001) [Area 16]; Haslam Formation (Squires and Saul, 2001) [Area 2]; Chico Formation at Granite Bay (= Texas Flat) (Squires and Saul, 2009) [Area 9]; Chico Formation at Pentz (Squires and Saul, 2001) [Area 7]; Cedar District Formation, "White House" site, western Denman Island, off east coast of Vancouver Island, British Columbia, Canada (Squires and Saul, 2006a; Ward et al., 2015) [Area 1]; upper Tuna Canyon Formation (Squires and Saul, 2009) [Area 15]; unnamed formation, Loma Prieta (Elder, 1991) [Area 10]; Williams Formation, Pleasants Sandstone Member (Squires and Saul, 2001) [Area 16]; Point Loma Formation (Squires and Saul, 2001) [Area 17]; Rosario Formation (Squires and Saul, 2001; Ward et al., 2015) [Areas 18–21]; Northumberland Formation, Collishaw Point, Hornby Island, off the east coast of Vancouver Island, British Columbia, Canada (Squires and Saul, 2006a) [Area 1]; Gualala Formation, Anchor Bay Member (Elder et al., 1998) [Area 8]; Moreno Formation, Tierra Loma Shale Member, "Quinto Silt," informal member, and "Garzas Sand" informal member (Squires and Saul, 2003c) [Areas 11, 12]; El Piojo Formation (Squires and Saul, 2006b) [Area 14]; and basal San Francisquito Formation (Squires and Saul, 2006b) [Area 14].

The suprageneric classification of oysters has been in a state of flux during the last two decades. The most current classification scheme, and the one used here, is from Carter et al. (2011). Their scheme will be used for the pending revision of the "Treatise on Invertebrate Paleontology" volume on oysters. Standard morphologic terms are from Stenzel (1971), and those most commonly used here are illustrated in Figures 3–15. Shell-microstructure terms are chiefly from Malchus (1990) and Jaitly et al. (2014).

In compiling the species synonymies, references with accompanying illustrations were used almost exclusively. Nonillustrated references, such as a checklist, were used, but only if museum specimens of the species referred to were seen, thereby allowing for confirmation that the species occurs in beds relatable to the checklist.

To facilitate comparisons, photographs of each studied species were arranged in the following manner: left valve exterior; left valve interior; right valve exterior; and right valve interior. In some cases, anterior or posterior views of a single valve or of conjoined valves are shown, as well as the shell microstructure.

Information about the LACMIP localities is accessible through the website link http://ip.nhm.org/ipdatabase/locality_show. Information about the type localities of the Museum of Paleontology, Berkeley (UCMP), is accessible through the website link http://ucmpdb.berkeley.edu. Information about the Canadian localities is incorporated into the appropriate "Stratigraphic Distribution" sections.

ABBREVIATIONS

ANSP Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania
LACMIP Natural History Museum of Los Angeles County, Invertebrate Paleontology Department, Los Angeles, California
RBCM Royal British Columbia Museum, Victoria, Canada
UCMP University of California Museum of Paleontology, Berkeley, California
VIPM Vancouver Island Paleontological Museum, Qualicum Beach, British Columbia, Canada
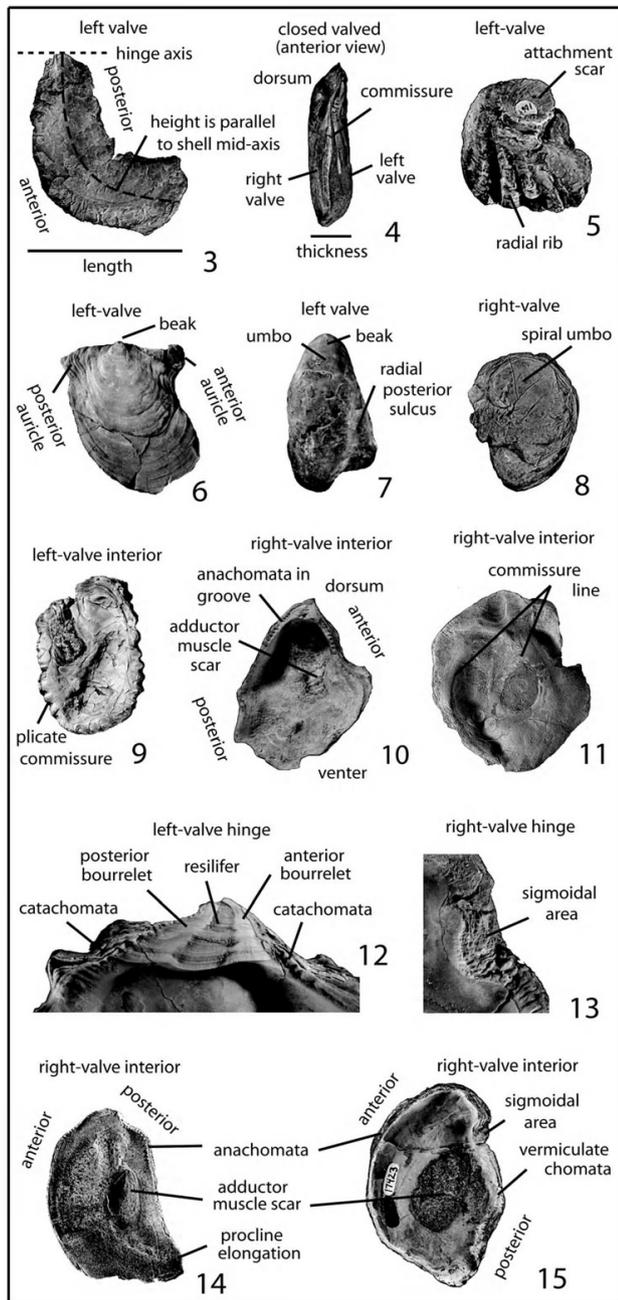
Figures 3–15 Key morphologic terms (after Stenzel, 1971) used in describing oyster shells. **3.** *Curvostrea crescentica*, hypotype LACMIP 14551. **4.** *Curvostrea crescentica*, hypotype LACMIP 14556. **5.** *Costagyra californica*, hypotype LACMIP 14590. **6.** *Pycnodonte* (*P.*) *malleiformis*, hypotype LACMIP 14618. **7.** *Phygraea inornata*, hypotype LACMIP 14626. **8.** *Amphidonte parasitica*, hypotype LACMIP 14612. **9.** *Rastellum* sp., aff. *R. macropterum*, hypotype LACMIP 14547. **10.** *Acutostrea taxidonta*, hypotype LACMIP 14570. **11.** *Phygraea arida*, paratype LACMIP 14640. **12.** *Acutostrea taxidonta*, hypotype LACMIP 14579. **13.** *Amphidonte parasitica*, hypotype LACMIP 14602. **14.** *Pycnodonte* (*P.*) *malleiformis*, hypotype LACMIP 14622. **15.** *Amphidonte parasitica*, hypotype LACMIP 14607.

SYSTEMATICS

Order Ostreida Férussac, 1822

Superfamily Ostreoidea Rafinesque, 1815

REMARKS. Fossil oysters are easily recognizable by their distinctive ligamental pit (resilifer), large adductor muscle scar, and, on certain species, well-developed chomata (denticulations on margins of the valves). Fossil oysters can be abundant, commonly well preserved, and their medium to large size allows for easy detection of the group, either in the field or in museum collections. Generic and specific identification of oysters, on the other hand, can be challenging. As mentioned by Koppa (2015:4–5), the main reasons for this are that they have relatively few unique characters, they likely exhibit significant morphologic variation due to their well-known ecophenotypic plasticity, and they display a distinct propensity for convergence.

Malchus (1990) revised the classification of Mesozoic oysters considerably and restricted *Ostrea* Linnaeus, 1758, and *Lopha* Röding, 1798, to the "Tertiary," although these genera had been previously regarded as also occurring in older strata. Malchus' revisions are incorporated here.

Oysters range from Late Triassic to Holocene (Stenzel, 1971:N1051), but they did not become common faunal elements until the Jurassic. Depending on the species, they are indicative of shallow-marine or brackish-marine environments.

Family Arctostreidae Vialov, 1983

Subfamily Arctostreinae Vialov, 1983

Genus *Oscillopha* Malchus, 1990

TYPE SPECIES. *Oscillopha dichotoma* (Bayle, 1849), by original designation; Algeria, Santonian.

AGE AND DISTRIBUTION. Late Cenomanian to Maastrichtian and widespread (Malchus, 1990; Dhondt and Jaillard, 2005). The new species named below is the first record of *Oscillopha* in North America.

REMARKS. Malchus (1990) classified *Oscillopha* in his family Palaeolophidae. According to Carter et al. (2011), paleolophids are now classified in family Arctostreidae Vialov, 1983. *Oscillopha*, a plicate oyster with a large attachment scar, was an epifaunal oyster that abundantly encrusted hard surfaces in shallow seas (middle-shelf environments 20–50 m in depth) (El-Sabbagh, 2008). Its shell microstructure is foliated/homogeneous (Jaitly et al., 2014).

Oscillopha popenoei sp. nov.
Figures 16–25

DIAGNOSIS. Wide, oval, lowly wedge-shaped valves. Large attachment scar. Plicae closely spaced on both valves, 20–25 in number, moderately dichotomous.

DESCRIPTION. Shell size up to height 124 mm (incomplete). Shell oval, rectangular, or slightly crescent shape. Both valves wedge-shaped, with steep plicate wall on anterior margin and much lower plicate wall on posterior margin. Hinge wide, flat, with flat bourrelets and resilifer indistinguishable. Adductor muscle scar large, ovate, rimmed (especially on anterior side), posterodorsal, and not close to valve margin. Shell microstructure foliated, with lens-shaped layers. **Left valve:** Lowly convex with medium to large attachment area covering up to approximately 75% of valve. Plicae 20–25 in number (two per 7 mm, crest to crest), moderately dichotomous, strong, chevron-shaped, with slightly rounded tops. **Right valve:** Smooth and flat. Umbo reflected posteriorly.

HOLOTYPE. LACMIP 14542, height 92 mm, length 65 mm, LACMIP loc. 25392, Redding Formation, Member VI?, near Clover

Creek Falls on Clover Creek, east of Redding, Shasta County, Northern California.

PARATYPES. LACMIP 14543–14546, all from type locality.

GEOLOGIC AGE. Late Santonian.

GEOGRAPHIC RANGE. East of Redding, Shasta County, Northern California [Area 5].

STRATIGRAPHIC DISTRIBUTION. Redding Formation, Member VI?, near Clover Creek Falls on Clover Creek, east of Redding, Shasta County, Northern California.

REMARKS. Five specimens were examined: three left valves and two right valves. Although there are no complete valves, preservation is good, except for the hinge of the right valve. The hinge is missing on all the left valves.

The sculpture on the new species, especially on the paratype (Fig. 25), is similar to an unnamed variety of *Actinostreon dichotoma* (Bayle, 1849:365–366, pl. 18, figs. 17–18) from Tunisia, north Africa. Pervinquière (1912:pl. 14, fig. 21) illustrated this variety, which is of Coniacian age. Douvillé (1904:274–275, pl. 37, figs. 1a, 1b) figured *A. dichotoma* of Senonian age from Iran. The Redding Formation species differs from all these illustrations of *A. dichotoma* by having an obvious attachment scar and more closely spaced radial ribs, which are less dichotomous. The Tunisian and Iranian specimens have a posterior auricle that can be small to prominent, but it cannot be determined whether or not a posterior auricle was present on the Redding Formation specimens.

The only other record of *Oscillopha* in the Western Hemisphere is *Oscillopha syphax* (Coquand, 1862), which Dhondt and Jaillard (2005:pl. 1, figs. 6a, 6b) reported from upper Cenomanian strata in northern Peru. The new species differs from this Peruvian species by having half as many radial ribs.

ETYMOLOGY. The new species is named for molluscan paleontologist Willis Parkison ("Parky") Popenoe, who collected and donated many Late Cretaceous oyster specimens to the University of California Los Angeles invertebrate-fossil collection (now housed at LACMIP) and consistently provided detailed and reliable locality data.

Genus *Rastellum* Faujas-Saint-Fond, 1799

TYPE SPECIES. *Ostrea macroptera* J.D.C. Sowerby, 1825; by subsequent designation (Winkler, 1863); Maastrichtian, Netherlands.

AGE AND DISTRIBUTION. Late Middle Jurassic (Callovian) to Maastrichtian and widespread (except for polar seas) (Stenzel, 1971). The unnamed species described below is the first record of *Rastellum* in the PSNA region.

REMARKS. Some workers (e.g., Stenzel, 1971) have divided *Rastellum* into *Rastellum* (*Rastellum*) and *Rastellum* (*Arctostrea*) Pervinquière (1910). The morphologic and taxonomic distinctions between *Rastellum* and *Arctostrea* are uncertain, and Stenzel (1971:N1200–N1209) provided in-depth comments about these issues. Malchus et al. (1994) is followed here in treating *Arctostrea* as a hyote-spined "form" of *Rastellum* rather than as a subgenus.

Rastellum, a highly plicate oyster, was an epifaunal cementing oyster (Ayoub-Hannaa and Fürsich, 2012:125). Its shell microstructure is foliated/homogeneous (Jaitly et al., 2014).

Rastellum sp., aff. *Rastellum macropterum* (J.D.C. Sowerby, 1825)
Figures 9, 26–32

REMARKS. Three specimens were examined, and they are from the middle to upper Turonian Frazier Siltstone Member of the Redding Formation, east of Redding, Shasta County, Northern California [Area 5]. Two of the specimens are from LACMIP loc. 10745 and occur in the same hand specimen. One is a nearly complete left valve (height 75.2

mm) (Figs. 26–30), and the other is a fragment of a left valve (Fig. 32) attached to the larger specimen. The nearly complete left valve, which only shows its very concave interior, is strongly curved (crescentic), very arched with steep parallel flanks, and has a posterior auricle. Numerous angular and prominent radial plicae of uniform size are present along the valve margin and form a zigzag commissure. There are two plicae per centimeter. Most of the hinge of this valve is missing, but along its weathered anterior area there is much foliation of the shell layers. The adductor muscle scar is large, dorsoposterior, and very close to the posterior margin of the valve. The scar is filled with rock matrix and weathers quite differently from the rest of the shell (Fig. 27). On the partial left valve in the hand specimen (Fig. 32), the weathered hinge area consists of foliated shell with no distinct ligamental resilifer/bourrelets preserved, and the adductor muscle scar is crescent-shaped. There are no catachomata. The shell microstructure is foliated/homogeneous.

The third specimen of *Rastellum* sp. is a fragment of the interior of a dorsal surface of a valve from LACMIP loc. 24336 (Fig. 31). It shows the characteristic dorsal keel, as well as remnants of strong plicae.

The three specimens probably represent a new species of *Rastellum*, but it is not named because the specimens are so few and incomplete. They show the most affinity to *Rastellum macropterum* (J.D.C. Sowerby, 1825:105–106, pl. 68, figs. 2, 3), on the basis of the large posterior auricle and on shell size. Stenzel (1971:figs. J138, 1a, 1b) figured Sowerby's species, which is of Maastrichtian age from the Netherlands. The hinge of the PSNA species, however, is more similar to the hinge illustrated by Cooper (2002:fig. 1A) of the southeastern African *Rastellum allobrogensis* (Pictet and Roux, 1853:524–525, pl. 49, figs. 1a–1c) of Albian age.

Family Flemingostreidae Stenzel, 1971

Subfamily Flemingostreini Stenzel, 1971

Tribe Curvostreini Malchus, 1990

Genus *Curvostrea* Vialov, 1936

**TYPE SPECIES.** *Ostrea rediviva* Coquand, 1869, by original designation; Cenomanian, France.

AGE AND DISTRIBUTION. Early Cenomanian to Maastrichtian and widespread (Seeling and Bengtson, 1999). The species revised here and the new species named below are the first reports of *Curvostrea* in the PSNA region.

REMARKS. Although Stenzel (1971:N1168) regarded this genus to be of dubious taxonomic value, it has been recognized by numerous workers (e.g., Seeling and Bengtson, 1999:762; Ayoub-Hannaa and Fürsich, 2011:89–92, pl. 8, figs. 1–4, text figs. 3.9A, 3.9B). Cooper (1992) reported that *Curvostrea* is a homeomorph of the pycnodontine *Labostrea* Vialov, 1945, of Coniacian to Paleogene age in South Africa. *Curvostrea* differs from *Labostrea* by lacking vesicular shell structure, vermiform chomata, and a commissural shelf with a bordering curb.

Curvostrea was an epifaunal oyster whose cemented left valve is larger and thicker and has a higher preservation potential than its much thinner (lid-like) right valve, which was easily fragmented. This warm-water oyster lived in well-oxygenated, normal-marine conditions associated with a moderately soft substrate and preferred low to intermediate energy levels, with a low degree of environmental stress (Ayoub-Hannaa and Fürsich, 2012:111, 125). Its shell microstructure is prismatic/foliated (Malchus, 1990; Jaitly et al., 2014).

Curvostrea crescentica (Packard, 1922) comb. nov.
Figures 3, 4, 33–42

Ostrea crescentica Packard, 1922:420, pl. 26, fig. 3 [not fig. 4 = *Amphidonte parasitica* (Gabb, 1864)]; Sundberg, 1980:844, table 1, unfig.
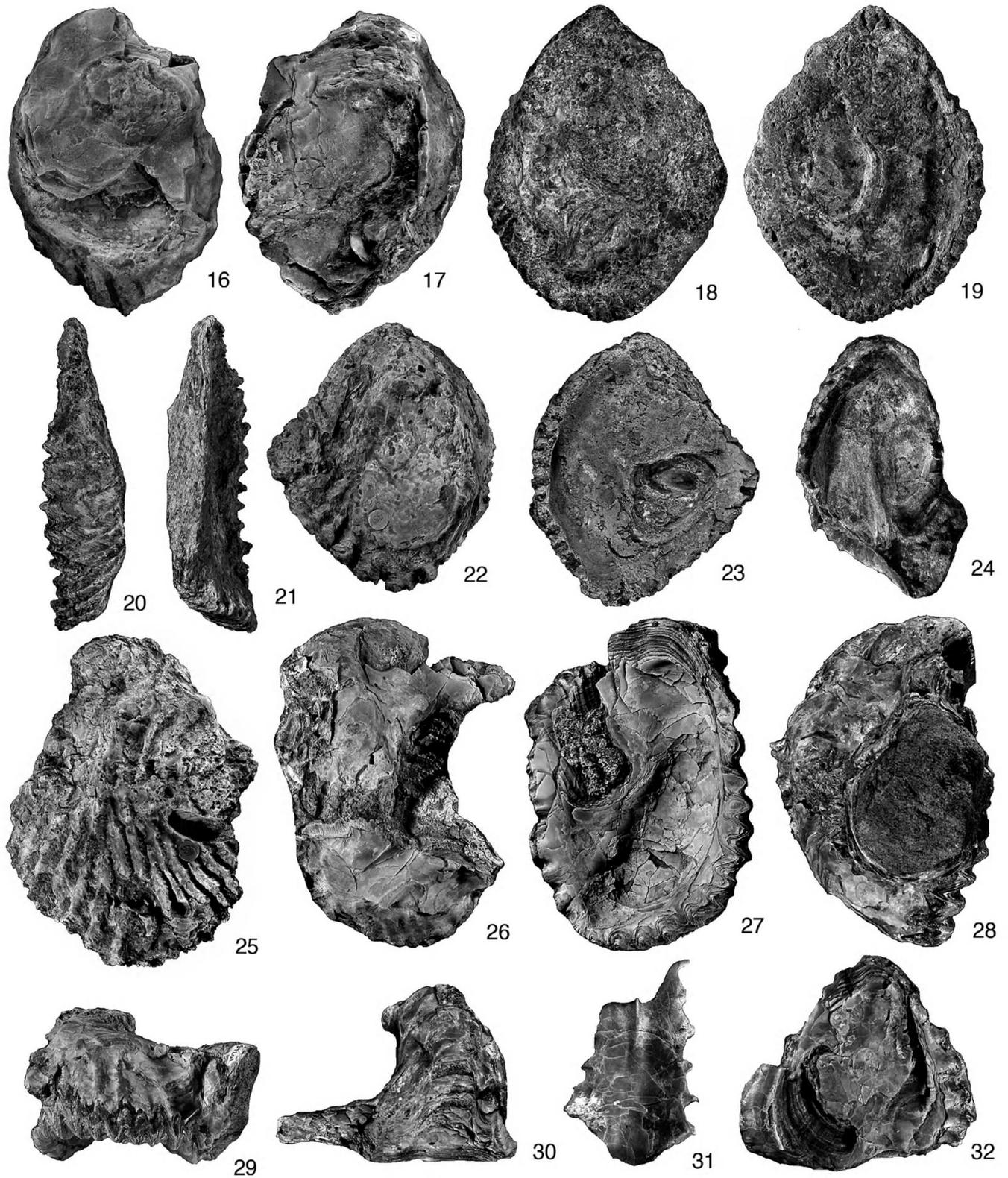
Figures 16–32 *Oscillopha* and *Rastellum*, Redding Formation [Area 5]. **16–25.** *Oscillopha popenoei* sp. nov., LACMIP loc. 25392, Redding Formation, Member VI?. **16–17.** Holotype LACMIP 14542, left valve, height 92 mm, ×0.6. **16.** Exterior. **17.** Interior. **18–21.** Paratype LACMIP 14543, left valve, height 124.4 mm, ×0.5. **18.**

EMENDED DESCRIPTION. Shell size up to height 68 mm. Shell thin, crescent-shaped, extended posteriorly. Inequivalved. Shell microstructure prismatic/foliated. **Left valve:** Lowly convex and with attachment scar (commonly very small) at dorsal end of valve. Commarginal striae very closely spaced, slightly crenulated or wavy, and forming bands of variable (but narrow) widths. Faint radial bands can be present toward ventral margin. Resilifer small but well defined. Catachomata simple and short but stout posterodorsally, fewer in number anterodorsally. Bourrelets narrow, anterior one slightly wider. Interior of posterior part of left valve can have narrow ridge paralleling shell margin. Adductor muscle scar round, located dorsal of center and near posterior shell margin. **Right valve:** Flattish (lid-like), can be slightly convex posteriorly near hinge. Faint radial striae can be present.

HOLOTYPE. UCMP 12318, height 68 mm, length 60 mm, UCMP loc. 2166, Ladd Formation, Silverado Canyon, Santa Ana Mountains, Orange County, Southern California.

GEOLOGIC AGE. Turonian.

GEOGRAPHIC RANGE. Santa Ana Mountains, Orange County, Southern California [Area 16].

STRATIGRAPHIC DISTRIBUTION. Ladd Formation, Baker Canyon Member and Holz Shale Member, Silverado Canyon, Santa Ana Mountains, Orange County, Southern California (Packard, 1922; Sundberg, 1980).

REMARKS. Thirty-two specimens were examined, and many are fragments. Preservation is poor, and exfoliation is common. The holotype, a right valve, has a worn exterior (Fig. 40). All the specimens are in siltstone. Six specimens at LACMIP loc. 8195 in the Baker Canyon Member are conjoined. At this locality, as well as at LACMIP locs. 8169, 10882, and 15738, all within the Baker Canyon Member, *C. crescentica* co-occurs with *Phygraea inornata* (Packard, 1922).

In his caption, Packard (1922:pl. 26, fig. 4) identified specimen UCMP 12319 as belonging to his *Ostrea crescentica*. In his write-up of this species (p. 420), however, he did not even mention this specimen. According to the UCMP records, specimen UCMIP 12319 is Packard's paratype of *O. crescentica*, but it is actually a hypotype of *A. parasitica* (Gabb, 1864).

Curvostrea baia sp. nov.
Figures 43–57

DIAGNOSIS. Shell size medium, shape narrow spatulate to subfalcate, posteroventral margins rarely with lateral flanges on both valves; left valve lowly convex, thick, very heavy, thins posteriorly and flattens ventrally, and with no attachment scar; right valve thin, lowly convex, covered with numerous fine, flat radial riblets crossed by commarginal lines, anterior margin beveled; left valve with well-developed, thick, prismatic/foliated microstructure.

DESCRIPTION. Shell size up to height 82 mm. Shape variable, with two morphs: narrow spatulate and subfalcate. Beaks small, poorly developed, ophistogyrate. Posteroventral margins of both valves rarely with lateral flanges. Adductor muscle scar size medium, elliptical, and located near shell margin just posterior of center of valve. Shell microstructure prismatic/foliated with several, thick, long, and lenticular layers of long (up to 4 mm) perpendicular calcite crystals, separated by

few, very thin nonprismatic layers. **Left valve:** Lowly convex, thin but heavy; valve thinning posteriorly and flattening ventrally. Valve can be slightly wedge shaped, with anterior wall higher than posterior margin. No attachment scar. **Right valve:** Juvenile subtrigonal, umbo inflated, commissure ventrally wavy, resilifer wide, bourrelets indistinct. Anachomata few, short, and extending ventrally from hinge along both margins for less than quarter of total height of valve. Commissural shelf prominent. Adult lowly convex, thin, and with beveled margins; distinct lip present on anterior side. Valve surface covered by many (approximately 15 per millimeter) fine, flat, radial riblets crossing bands of commarginal growth lines that can be raised slightly, thereby creating microscopic cancellate pattern; ribs variable width and can bifurcate; dorsal and medial parts of valve can have few irregular pustulose or lumpy radial ridges. Anachomata only along posterior margin, short and stout on dorsal half of margin but slit-like and more numerous on ventral half of margin. Posteroventral flanges with very weak cancellate lines. Ventral end of valve flattened, with wide border.

HOLOTYPE. LACMIP 14557, height 77 mm, length 36.6 mm, LACMIP loc. 26352, Moreno Formation, "Garzas Sand," Garzas Creek area, west side of San Joaquin Valley, Stanislaus County, Northern California.

PARATYPES. LACMIP 14558–14563. All from type locality or vicinity.

GEOLOGIC RANGE. Late early to early late Maastrichtian.

GEOGRAPHIC RANGE. Garzas Creek area, Stanislaus County, Northern California [Area 11].

STRATIGRAPHIC DISTRIBUTION. Moreno Formation, "Garzas Sand," Garzas Creek area, west side of San Joaquin Valley, Stanislaus County, Northern California.

REMARKS. Nine specimens were examined: one left valve and eight right valves. Preservation is excellent for the prismatic microstructure of the left valves and also for the exterior sculpture on a few of the right valves. Elsewhere, preservation is moderately poor. Several specimens are tightly conjoined, thereby making it difficult to discern the commissure. A few right valves have eroded remnants of the thick left valve. Some of these same specimens consist of a thin right valve and an associated thick internal cast of the left valve. These casts consist of tightly cemented, smooth, and shiny siltstone that resembles shell material. The two morphs are probably ecophenotypic responses to the environment, but they might be related to growth stage. More specimens are needed to confirm which of these differing suppositions is correct.

The hinge area of the left valve interior (Fig. 44) bears a cast of a wide, sideways U-shaped structure that could possibly be the impression of the bourrelets and resilifer of the right valve hinge. The sideways orientation would indicate that there was a sudden shift in the growth direction of the valves.

The weak radial sculpture of the new species resembles the fine radial sculpture on the right valve of *Ostrea plumosa* Morton (1833:293, 1834:51, pl. 3, fig. 9; Stephenson, 1941:108, pl. 16, figs. 4–6; Akers and Akers, 2002:196, fig. 168, in part), a widespread oyster reportedly of Coniacian to Maastrichtian age in the Gulf and Atlantic coastal plains and in the Colorado-Wyoming-Utah region of the Western Interior of the United States. The new species differs markedly by having a larger

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← Exterior. **19.** Interior. **20.** Anterior side. **21.** Posterior side. **22–23.** Paratype LACMIP 14544, left valve, height 87.5 mm, ×0.6. **22.** Exterior. **23.** Interior. **24.** Paratype LACMIP 14545, right valve interior, height 67.5 mm, ×1. **25.** Paratype LACMIP 14546, right valve, height 101.7 mm, ×0.6. **26–32.** *Rastellum* sp., aff. *R. macropterum* (J.D.C. Sowerby, 1825), Redding Formation, Frazier Siltstone Member. **26–30.** Hypotype LACMIP 14547, LACMIP loc. 10745, left valve, height 76 mm, ×0.8 (unless otherwise indicated). **26.** Exterior. **27.** Interior. **28.** Posterior side. **29.** Edgewise view of venter, height 36.4 mm, ×7. **30.** Edgewise view of dorsum, ×0.6. **31.** Hypotype LACMIP 14548, LACMIP loc. 24336, left valve interior, height 32 mm, ×1.2. **32.** Hypotype LACMIP 14549 (attached to hypotype LACMIP 14547), left valve interior, height 45.3 mm, ×0.9.
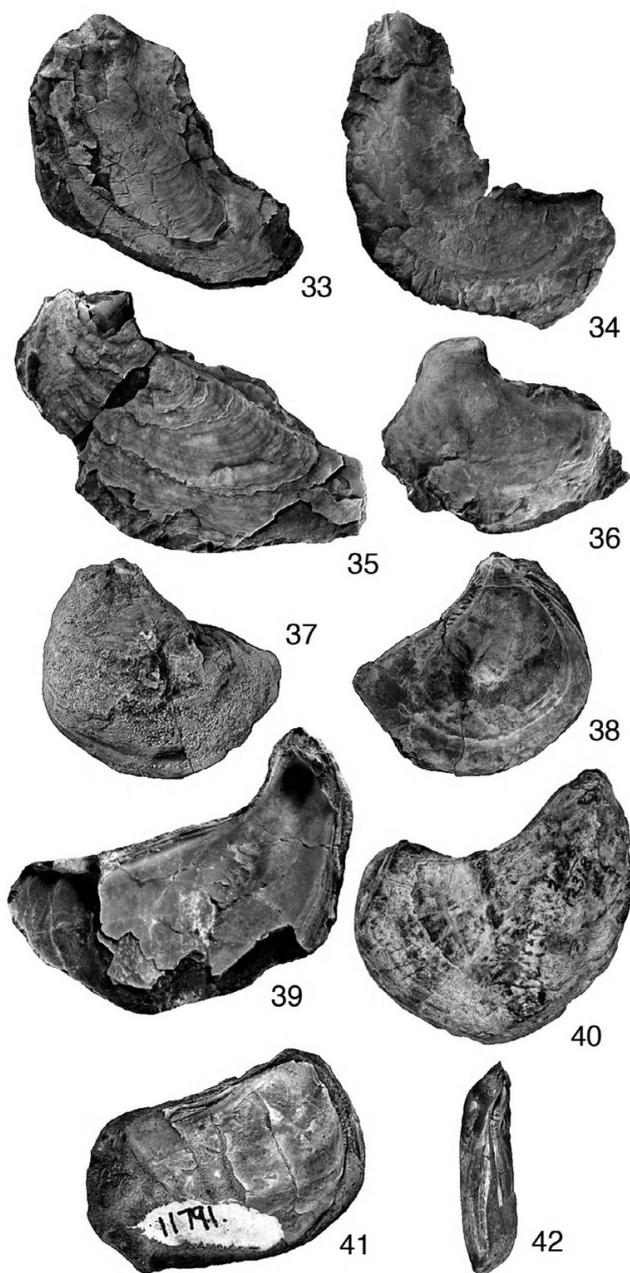
Figures 33–42 *Curvostrea crescentica* (Packard, 1922), Ladd Formation, Baker Canyon Member [Area 16], unless otherwise noted. **33.** Hypotype LACMIP 14550, LACMIP loc. 16860, left valve, height 51 mm, ×0.8. **34.** Hypotype LACMIP 14551, LACMIP loc. 8195, left valve, height 65 mm, ×0.8. **35.** Hypotype LACMIP 14552, LACMIP loc. 8195, left valve, height 58 mm, ×0.9. **36.** Hypotype LACMIP 14553, LACMIP loc. 8195, left valve, height 47 mm, ×0.6. **37–38.** Hypotype LACMIP 14554, LACMIP loc. 21529, Ladd Formation, Holz Shale Member [Area 16], left valve, height 16 mm, ×2.1. **37.** Exterior. **38.** Interior. **39.** Hypotype LACMIP 14555, LACMIP loc. 8195, left valve interior, height 34 mm, ×1.5. **40.** Holotype UCMP 12318, UCMP loc. 2166, height 74 mm, ×0.6. **41–42.** Hypotype LACMIP 14556, LACMIP loc. 11791, conjoined valves, height 28 mm, ×1.4. **41.** Right valve. **42.** Posterior side.

shell (twice as big); more crescentic shape; much flatter, much thicker, and heavier valves; hinge axis straighter; bumps and irregular ridges on the right valve exterior; and less well developed resilifer/bourrelets (not long and narrow). Unlike *C. baia*, the valves of "*O.*" *plumosa* are very thin (nearly eggshell thin) and easily broken.

The new species differs from *Ostrea crescentica* Packard, 1922, by larger size, narrow-spatulate morph, less falcate individuals, thicker and heavier shell, stronger radial sculpture, and much better development of prismatic layers.

The specimens of *C. baia* are in silty, very fine grained sandstone. The flattish to lowly convex, dense left valve, as well as the absence of an attachment scar, are indicative that *C. baia* was a recliner.

ETYMOLOGY. The new species name is derived from *baios* (Greek, meaning "little"), for the fine radial sculpture of the new species.

Subfamily Crassostreinae Scarlato and Starobogatov, 1979

Tribe Crassostreini Scarlato and Starobogatov, 1979

Genus *Acutostrea* Vialov, 1936

TYPE SPECIES. *Ostrea acutirostris* Nilsson, 1827, by original designation; late early Campanian *Belemnellocamax mammilatus* Zone, Sweden (Stenzel, 1971; Christensen, 1997).

AGE AND DISTRIBUTION. Late early Campanian to Oligocene and widespread during the Cretaceous (Cooper, 2002). The species revised here is the first report of Cretaceous *Acutostrea* in the PSNA region. *Acutostrea* is common and widespread in Eocene strata of the PSNA region (Moore, 1987).

REMARKS. *Acutostrea*, which has very variable morphology, was a cementing oyster and an abundant encruster (Wilson and Taylor, 2001:29). Its shell microstructure is prismatic/foliated (Malchus, 1990).
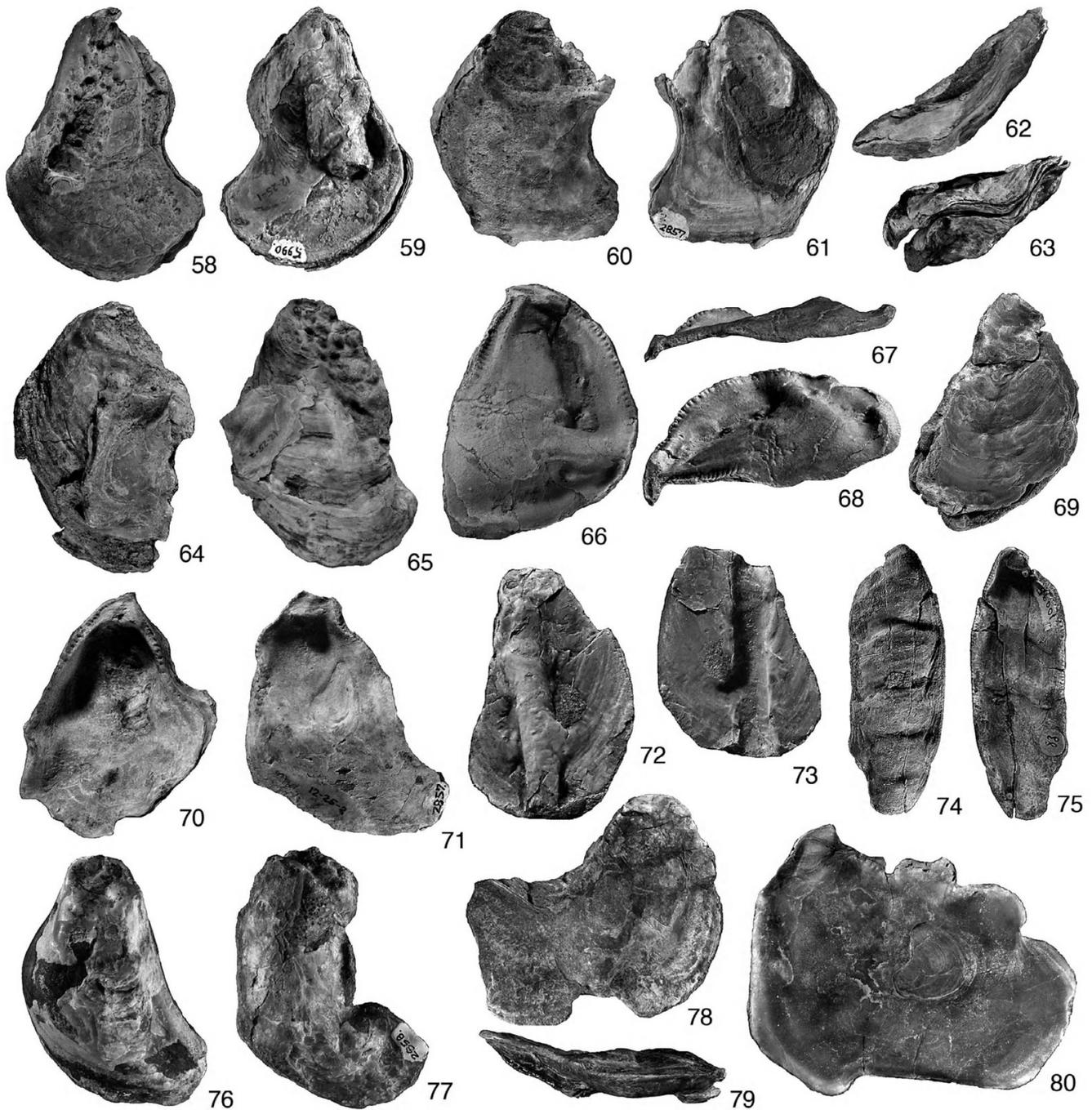
Acutostrea taxidonta (Packard, 1922) comb. nov.
Figures 10, 12, 58–97

Ostrea taxidonta Packard, 1922:420, pl. 26, fig. 2.

EMENDED DESCRIPTION. Shell size up to height 132 mm. Shape highly variable, with five morphs: trigonal, spatulate, suboval, falcate, and irregular. Trigonal and spatulate shapes most common, suboval and falcate shapes uncommon, irregular shapes rare. Trigonal morph mostly small in size but larger ones can be gradational in size and shape with spatulate or falcate morphs. Spatulate morph mostly medium in size but larger ones can be nearly as large as suboval ones (largest morph). Irregular shape small in size, rare, and can fill voids. Ventral half of both valves of all morphs, except irregular, geniculate (bent upward) approximately 40° and also having prominent flexure (sulcus) on medial posterior shell margin. Subequivalved. Resilifer well developed. Adductor muscle scar moderately large, reniform (with pointed end pointing toward hinge), and located near central-posterior margin. Shell microstructure prismatic/foliated. Xenomorphic structure common on left valve and can affect conjoined right valve, as well as interiors of both valves. **Left valve:** Low to moderately low convex. Beak can project beyond right valve beak. Catachomata commonly only on dorsal half of valve, including adjacent to bourrelets. Catachomata straight, those on posterior part of valve longer. Catachomata on larger valves only near hinge, few in number, and generally weak. Valve interior can have irregularities (bumps) near central and ventral regions. Attachment scar on trigonal specimens small to moderate in size, covering beak, and commonly shows outline of foreign matter (commonly long, straight groove with corresponding right valve exterior arched; interiors of valves also reversely affected). Attachment scar wide and large on spatulate specimens; large on suboval specimens, covering
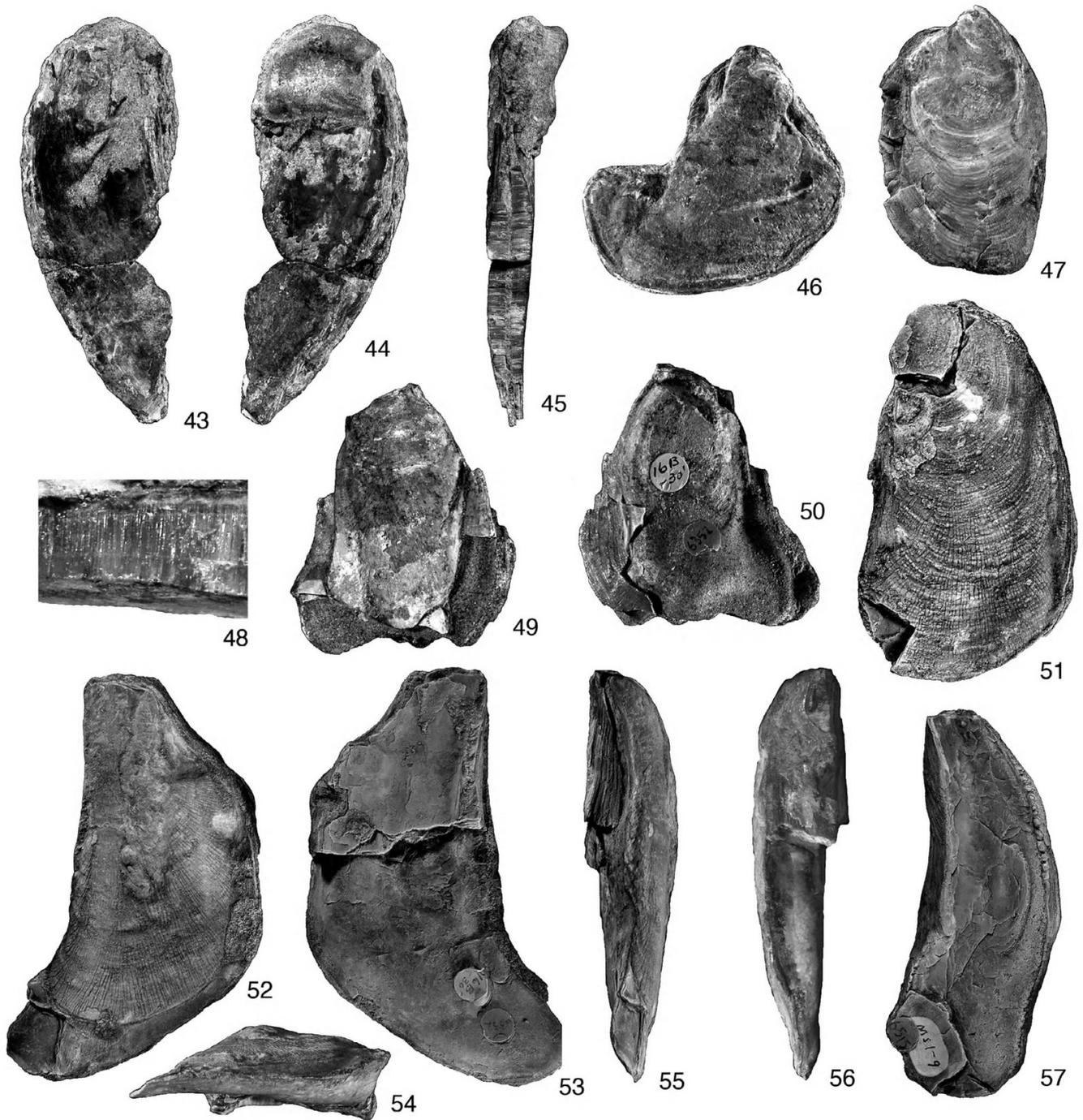
Figures 43–57 *Curvostrea baia* sp. nov., Moreno Formation [Area 11], LACMIP loc. 26352, unless otherwise noted. **43–45.** Paratype LACMIP 14558, left valve, height 83.5 mm, ×0.8. **43.** Exterior. **44.** Interior. **45.** Posterior side, showing predominantly prismatic shell structure. **46.** Paratype LACMIP 14559, right valve, height 32.2 mm, ×1.2. **47–48.** Paratype LACMIP 14560, right valve, height 36 mm, ×1.2. **47.** Exterior of an isolated specimen of three specimens of *A. parasitica* encrusting one another. **48.** Cross-section close-up of thick prismatic shell microstructure, posteroventral part of valve, height 2.5 mm, ×8.4. **49–50.** Paratype LACMIP 14561, conjoined valves, height 43.4 mm, ×1. **49.** Right valve exterior with lateral flanges. **50.** Internal cast of left valve, with remnant of posteroventral shell. **51.** Paratype LACMIP 14562, right valve, height 55.8 mm, ×.1.1. **52–56.** Holotype LACMIP 14557, right valve, height 77 mm , ×0.9. **52.** Exterior. **53.** Interior, with remnant of dorsal part of left valve. **54.** Ventral edge view, length 50 mm. **55.** Anterior view. **56.** Posterior view. **57.** Paratype LACMIP 14563, LACMIP loc. 26515, right valve interior, height 74.4 mm, ×0.9.

Figures 58–97 *Acutostrea taxidonta* (Packard, 1922), Rosario Formation [Area 20], unless otherwise noted. **58–59.** Hypotype LACMIP 14564, LACMIP loc. 5990, conjoined valves, height 64.3 mm, ×0.7 **58.** Left valve. **59.** Right valve. **60–62.** Hypotype LACMIP 14565, LACMIP loc. 2857, conjoined valves, height 59.4 mm, ×0.6. **60.** Left valve. **61.** Right valve. **62.** Posterior side. **63.** Hypotype LACMIP 14566, LACMIP loc. 23268, posterior side of conjoined valves, height 48.2 mm, thickness 22 mm, ×0.7. **64.** Hypotype LACMIP 14567, LACMIP loc. 23268, left valve, height, 63.5 mm, ×0.7. **65.** Hypotype LACMIP 14568, LACMIP loc. 2857, left valve, height 78.4 mm, ×0.6. **66–68.** Plastoholotype UCMP 12317, UCMP loc. 2167, Ladd Formation, uppermost Holz Shale Member [Area 16], left valve, height 35 mm, ×1.2. **66.** Interior. **67.** Posterior side. **68.** Oblique view. **69.** Hypotype LACMIP 14569, LACMIP loc. 11975, Tuna Canyon Formation [Area 16], left valve, height 59.1 mm, ×0.7. **70.** Hypotype LACMIP 14570, LACMIP loc. 2857, right valve interior, height 43 mm, ×0.9. **71.** Hypotype LACMIP 14571, LACMIP loc. 2857, attached to hypotype LACMIP 14563, right valve interior, height 64 mm, ×0.6. **72–73.** LACMIP loc. 11957, Tuna Canyon Formation [Area 15], originally conjoined valves. **72.** Hypotype LACMIP 14572, left valve interior (showing xenomorphic bulge), height 38.9 mm, ×0.9. **73.** Hypotype LACMIP 14573, right valve interior with corresponding xenomorphic groove, height 34.6 mm, ×1. **74–75.** Hypotype LACMIP 14574, LACMIP loc. 10095, Ladd Formation, Holz Shale Member [Area 16], right valve, height 57.8 mm, ×0.8. **74.** Exterior, showing xenomorphic replica of external mold of *Turritella* shell. **75.** Interior. **76.** Hypotype LACMIP 14575, LACMIP loc. 23268, left valve, height 65 mm, ×0.6. **77.** Hypotype LACMIP 14576, LACMIP loc. 2858, left valve, height 73 mm, ×0.7. **78–79.** Hypotype LACMIP 14577, LACMIP loc. 11975, Tuna Canyon Formation [Area 15], left valve, length 64 mm, ×0.6. **78.** Interior. **79.** Ventral-edge view. **80.** Hypotype LACMIP 14578, LACMIP loc. 23792, Rosario Formation [Area 19], right valve interior, length 89.1, ×0.6.

most of valve but not on beak; commonly small and covering beak and, rarely, half of valve on falcate specimens; attachment scar not obvious on irregular specimens. **Right valve:** Dorsal half commonly convex but can be flat, posterior half commonly concave to very concave. Exterior surface smooth on nearly all smaller specimens. Commarginal lamellae present on all large specimens but rare on small specimens. Exterior surface of valve can have xenomorphic-caused linear bulge, whereas interior surface can have corresponding hollow area. Valve concave medially. Anachomata short, simple, and present on entire posterior side of valve but becoming weaker and more widely spaced beyond midpoint of valve.

HOLOTYPE. UCMP 12317, height 34.5 mm, length 25 mm, UCMP loc. 2167, Ladd Formation, uppermost Holz Shale Member, Williams Canyon, Santa Ana Mountains, Orange County, Southern California.

GEOLOGIC RANGE. Middle Campanian to late early to early late Maastrichtian.

GEOGRAPHIC RANGE. North end of Laguna Seca Hills, Merced County, Northern California [Area 12] to Puerto Canoas, Northern Baja California, Mexico [Area 21].

STRATIGRAPHIC DISTRIBUTION. MIDDLE CAMPANIAN: Ladd Formation, upper Holz Shale Member, Santa Ana Mountains, Orange County, Southern California (Packard, 1922). UPPER MIDDLE CAMPANIAN: Tuna Canyon Formation, South Fork of Garapito Creek, Santa Monica Mountains, Los Angeles County, Southern California (new occurrence). UPPER CAMPANIAN TO POSSIBLY LOWER MAASTRICHTIAN: Point Loma Formation, Carlsbad Research Center, northern San Diego County, Southern California (new occurrence); Rosario Formation (new occurrences) at 1) San Antonio del Mar and 2) "Ammonite Ravine," Santa Catarina and 3) Puerto Canoas, Northern Baja California, Mexico. UPPER LOWER TO LOWER UPPER MAASTRICHTIAN: Moreno Formation (new occurrence), "Quinto Silt," and "Garzas Sand," north end of Laguna Seca Hills, Merced County, Northern California.

REMARKS. One hundred and nine specimens were examined. Preservation is generally very good. Only a few, including the holotype, are known from the uppermost Holz Shale Member. The holotype (Figs. 66–68), a trigonal morph, is a left valve interior whose exterior is embedded in rock matrix. The ventral margin is not complete, but what is present shows incipient bending (Fig. 67). Specimens of this species are common and generally well preserved in the Rosario Formation, in Northern Baja California, in the San Antonio del Mar, Santa Catarina, and Puerto Canoas areas (Fig. 1). The largest specimens, which are from a single locality (LACMIP loc. 15388) in the Puerto Canoas area, have excellent preservation. Only a single specimen was detected from the Moreno Formation in Northern California.

The trigonal morph of *A. taxidonta* is abundant in siltstone in the Rosario Formation in the Santa Catarina area. The spatulate morph is mainly in very fine to fine-grained sandstones in the Rosario Formation in the San Antonio del Mar area. The suboval morph shape occurs in fine- to medium-grained sandstones in the Rosario Formation in the Punta Canoas area. At LACMIP locs. 22414 and 27263 in the San Antonio del Mar area and at LACMIP loc. 15388 in the Punta Canoas area, both the spatulate and suboval morphs coexist. *Acutostrea taxidonta* co-occurs with *A. parasitica* in the Rosario Formation at LACMIP loc. 27263.

The presence of several morphs of *A. taxidonta* in the Rosario Formation is not incompatible because the basal part of the formation, where specimens of this oyster are abundant, was deposited in a dynamic geologic setting. Miller and Abbott (1989), Lescinsky et al. (1991), and Johnson and Hayes (1993) reported that the basal conglomerate and sandstone units of the Rosario Formation were pervasive and deposited along a long coastline significantly shaped by subduction tectonism. The advancing (transgressive) sea eroded the margins of the coastline and created rocky shore habitats associated with agitated waters, where both the spatulate and suboval morphs of *A. taxidonta* occur. It is likely that both forms lived in agitated waters, but the suboval forms have a larger attachment surface area because of living in more agitated waters.

Upsection, the basal conglomerate and sandstone units of the Rosario Formation give way to relatively deeper shallow marine units. It is likely that the trigonal morph of *A. taxidonta*, which is found in siltstones in the Santa Catarina area, preferred these slightly deeper and less agitated waters than where the spatulate and suboval morphs lived. For these calmer water specimens, the attachment scar is smaller because of the lower energy water conditions.

Some specimens of the trigonal morph can be noticeably directed posteriorly (Fig. 71), so much so as to grade into the falcate morph (Fig. 77). This gradation occurs at several localities where a sufficient number of specimens (more than 10) were available for comparison (e.g., LACMIP locs. 2857 and 2858 [Rosario Formation, Santa Catarina] and LACMIP loc. 11975 [Tuna Canyon Formation]).

Acutostrea taxidonta is abundant in the Tuna Canyon Formation at LACMIP loc. 11975 in Garapito Canyon, Los Angeles County, Santa Monica Mountains, but preservation is poor because many of these specimens are encased in extremely hard sandstone concretions, and attempts to remove the sandstone matrix result in serious degradation of the shell material. Splitting of the concretions mostly revealed only very poorly preserved interior surfaces of trigonal morphs and a few falcate morphs. On the interior of several of the trigonal left valves is a linear xenomorphic bulge (e.g., Fig. 72). The accompanying right valve (e.g., Fig. 73), which was originally conjoined, has the same linear xenomorphic feature, but it occurs as a groove.

Some conjoined valves of the trigonal morph of *A. taxidonta*, especially from the Santa Catarina area, also show a grooved, linear xenomorphic attachment scar on the exterior surface of the left valve (e.g., Fig. 58) and a corresponding linear bulge on the exterior of the accompanying right valve (Fig. 59).

The irregular morph of *A. taxidonta* is represented by rare individuals attached to narrow gastropod shells. An example (Figs. 74, 75) from the Holz Shale Member of the Ladd Formation is a right valve whose exterior surface (Fig. 74), but not its interior surface (Fig. 75), shows the outline of the whorls and ribs of a *Turritella* gastropod. This oyster grew attached to the inside of an exterior mold of the *Turritella* specimen, thereby indicating a considerable interval of time between the preservation of the *Turritella* specimen and the formation of the oyster specimen.

In terms of its considerable morphologic variability, *A. taxidonta* is very similar to what Cooper (2002:39–43, figs. 6–9) observed for *Acutostrea incurva* (Nilsson, 1827) from upper Campanian to Maastrichtian strata of Europe, Algeria, Russia, and southeast Africa. Cooper (2002:39) stated that the range in morphology of *A. incurva* is "so variable that it almost defies description," and he concluded that this variability is dependent on the size of the attachment area.

Sundberg (1980:845, table 1) listed *Pseudoperna taxidonta* (Packard) as occurring in the Baker Canyon Sandstone Member of Turonian age in the Santa Ana Mountains, Orange County, Southern California. Packard's species, however, is not of Turonian age. In the Santa Ana Mountains, this species is only known from the upper Holz Shale Member of middle Campanian age. The so-called "*Pseudoperna taxidonta*" reported by Sundberg (1980) is most likely the truncated-spatulate morph of *Phygraea inornata* (Packard, 1922), known from the Baker Canyon Sandstone Member.
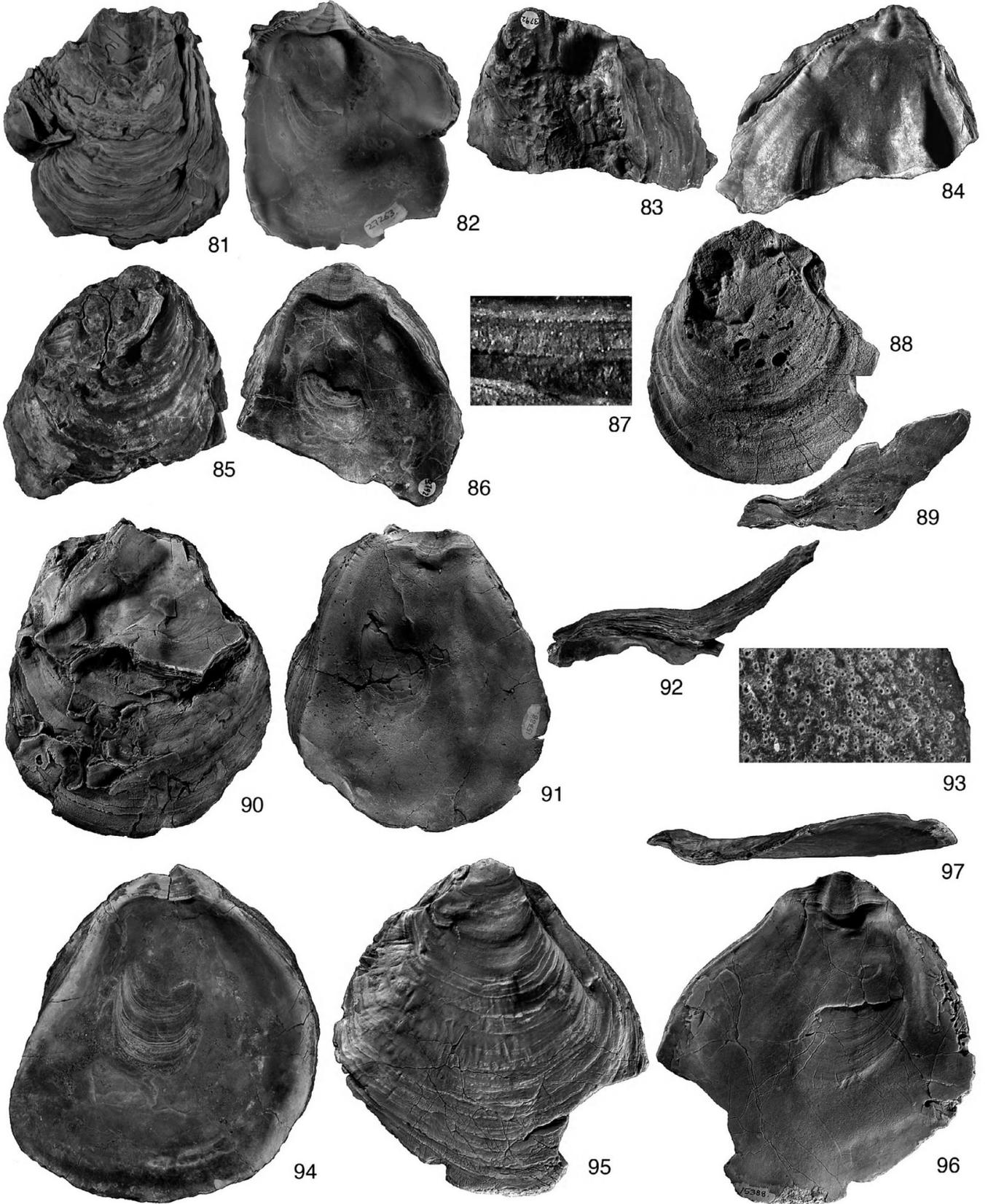
Genus *Crassostrea* Sacco, 1897

TYPE SPECIES. *Ostrea virginica* (Gmelin, 1791), by original designation; Holocene, Texas.

AGE AND DISTRIBUTION. Middle Jurassic to Holocene and widespread during the Cretaceous (Komatsu et al., 2002). The species revised here is the first Cretaceous report of *Crassostrea* in the PSNA region. *Crassostrea* is represented by several species, some of them of very large size, in Miocene and Pliocene deposits of California and Baja California (Moore, 1987).

REMARKS. This genus is morphologically highly variable, ranging from small size to very large size. Stenzel (1971) reported that *Crassostrea* is characterized by having no chomata. Sohl and Kauffman (1964:7) reported that Mesozoic *Crassostrea* species have chomata, whereas Tertiary species do not. Toulmin (1977) reported, however, Eocene *Crassostrea* with chomata.

Crassostrea, a soft-sediment recliner, is dominant in marginal marine environments but ranges into shallow, nearshore marine situations (Sohl and Owens, 1991:217). Komatsu et al. (2002) reported that this oyster lives today predominantly on muddy bottoms, where a firm basis for attachment is rare. They also reported that individuals of some species are known to have built large colonies to keep their position above the surface of the mud.

Crassostrea brewerii (Gabb, 1864) comb. nov.
Figures 98–113

Ostrea brewerii Gabb, 1864:204, pl. 26, fig. 191.
Odontogryphaea sp. Ludvigsen and Beard, 1994:79–80, fig. 45 (in part), 1997:101–102, fig. 56 (in part).

EMENDED DESCRIPTION. Shell size up to height 190 mm. Shell can be very thick, with left valve up to thickness 44 mm and right valve up to thickness 16.5 mm (not same individual). Shape variable with four morphs: subquadrate, narrow/elongate trigonal, subtrigonal, and rarely crescent. Inequivalved. Elongate posteroventrally. No attachment scar. Resilifer well developed, high and long (up to height 40 mm and length 25 mm), straight or curved (ophistocline). Bourrelets well developed and highly arched, especially ventrally; bourrelets can be equally wide or posterior bourrelet more arched and 2.5 times wider than anterior bourrelet. Adductor muscle scar large, oval with dorsal end "pointed," and posteroventrally located. Shell microstructure prismatic with numerous thick, long lenticular layers consisting of perpendicular large calcite crystals and separated by thinner, long lenticular layers filled with foliated and recrystallized material. **Left valve:** Convex, ranging from moderately to deeply convex. Valve generally straight-sided; largest specimen with very prominent horizontal, posteroventral bend in ventral region. Posterodorsal area commonly "hump" shaped. Overhang of shell can occur on anterodorsal region. Prominent groove extending along anterior side of valve and noticeable depressed areas just ventral of resilifer and bourrelets, with depression ventral of anterior bourrelets deeper. Chomata rare, near hinge. Large left valves can have chevron-shaped radial costae near ventral margin but not affecting commissure, except in minor way. **Right valve:** Flattish with upward low deflection on ventral area; valve smooth, moderately thick, with wide ligamental tooth.

HOLOTYPE. UCMP 31447, height 113.7 mm, length 72 mm, UCMP loc. 11381, "Chico Group, Cow Creek" (Stewart, 1930:131), southeast of Redding, Shasta County, Northern California.

GEOLOGIC RANGE. Early Campanian to late middle Campanian.

GEOGRAPHIC RANGE. Nanaimo, Vancouver Island, British Columbia, Canada [Area 2], to Santa Ana Mountains, Orange County, Southern California [Area 16].

STRATIGRAPHIC DISTRIBUTION. LOWER CAMPANIAN: Haslam Formation, Upper Quarry on Weigles Road near Brannan Lake, vicinity of Nanaimo, Vancouver Island, British Columbia, Canada (Ludvigsen and Beard, 1994, 1997); Redding Formation, most likely higher than Member VI, possibly South Cow Creek, east of Millville, Shasta County, Northern California (Gabb, 1864); Ladd Formation, Holz Shale Member, Santa Ana Mountains, Orange County, Southern California (new occurrence). UPPER MIDDLE CAMPANIAN: Williams Formation, Pleasants Sandstone Member, Santa Ana Mountains, Orange County, Southern California (new occurrence).

REMARKS. Twelve specimens were examined. Preservation is generally good, but most are large fragments of left valves. The four morphs of this species most likely represent ecophenotypic responses to changes in the environment, but more specimens are needed to confirm this supposition.

All the examined large-size, left-valve specimens from British Columbia and Southern California (Figs. 98, 100, 108) have a moderate to large size (up to diameter 33 mm), conjoined-valved specimen of the mytilid bivalve *Lithophaga* sp., which bored into the posterodorsal "hump" region in or near the umbo. These oyster valves also have small-diameter (up to 4 mm) boreholes, infilled with rock matrix, located elsewhere on them.

Gabb (1864:pl. 26, fig. 191) provided only a sketch of the interior of the left valve of the holotype of *brewerii*, and this sketch shows a projection on the right side of the figure. Stewart (1930:131) reported correctly that this projection is actually another valve, which is in the same hand specimen as the holotype and immediately adjacent to it. Gabb's holotype (Fig. 105) is shown here with the projection missing, and the immediately adjacent valve is shown separately (Fig. 104). The latter is a slender left valve with a narrow, tapered resilifer, which is a very common feature in *Crassostrea*.

Crassostrea brewerii is the largest and most thick walled Late Cretaceous oyster known from the PSNA region. This species is similar to *Crassostrea cusseta* Sohl and Kauffman (1964:pl.5, figs. 1–4) of Campanian age from the Gulf Coast of the United States, in terms of the following features: heavy, thick shell consisting of thick prismatic layers alternating with much thinner foliated layers, well-developed resilifer and strongly arched bourrelets with subcardinal cavities, rare chomata, and rough exterior surface. *Crassostrea brewerii* differs by being smaller (*C. cusseta* has an average shell height of 377 mm) and in having

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Figures 81–97 *Acutostrea taxidonta* (Packard, 1922), Rosario Formation [Area 19], unless otherwise noted. **81–82.** Hypotype LACMIP 14579, LACMIP loc. 27263, left valve, height 82 mm, ×0.5. **81.** Exterior. **82.** Interior. **83–84.** Hypotype LACMIP 14580, LACMIP loc. 23792, partial left valve, height 68 mm, ×0.5. **83.** Exterior. **84.** Interior. **85–87.** Hypotype LACMIP 14581, LACMIP loc. 23792, partial left valve, height 80 mm, ×0.5. **85.** Exterior. **86.** Interior. **87.** Cross section of prismatic/foliated shell microstructure, near hinge on anterodorsal margin of valve, width 4 mm, ×10. **88–89.** Hypotype LACMIP 14582, LACMIP loc. 15388, Rosario Formation [Area 21], left valve, height 104.3 mm, ×0.5. **88.** Exterior. **89.** Posterior side. **90–93.** Hypotype LACMIP 14583, LACMIP loc. 15388, Rosario Formation [Area 21], left valve, height 133 mm, ×0.4. **90.** Exterior. **91.** Interior. **92.** Posterior side. **93.** Close-up of pervasive microborings on interior of valve, near medial-anterior margin, height 2 mm, ×10. **94.** Hypotype LACMIP 14584, LACMIP loc. 15388, Rosario Formation [Area 21], left valve interior, height 131.5 mm, ×0.5. **95–97.** Hypotype LACMIP 14585, LACMIP loc. 15388, Rosario Formation [Area 21], right valve, height 129.6 mm, ×0.5. **95.** Exterior. **96.** Interior. **97.** Posterior side.
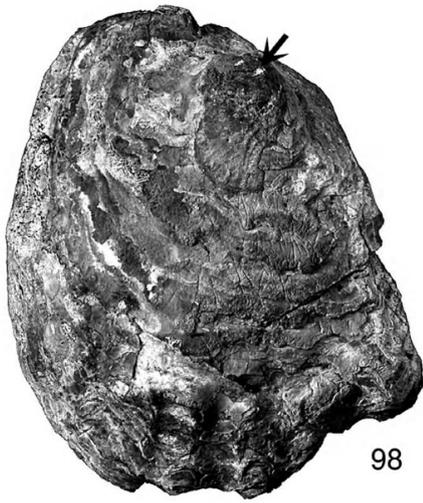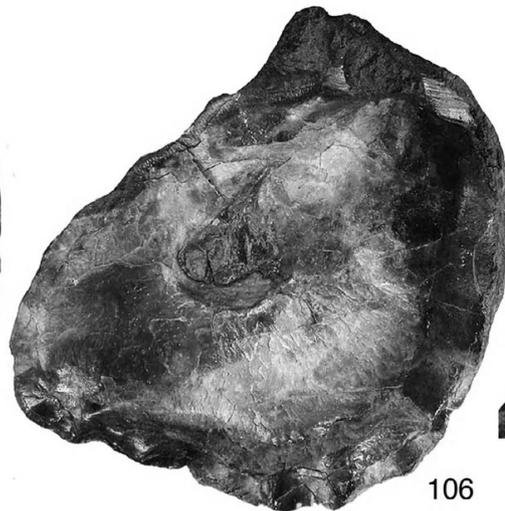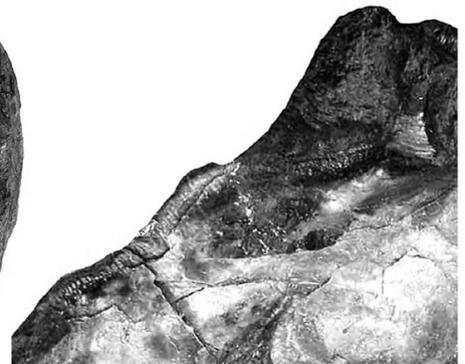
wide-spatulate rather than narrow-elongate shape, a shorter bend ventrally in the shell, and a better developed adductor muscle scar.

Family Gryphaeidae Vialov, 1936

Subfamily Exogyrinae Vialov, 1936

Genus *Costagyra* Vialov, 1936

TYPE SPECIES. *Exogyra olisipoensis* Sharpe, 1850, by original designation; Cenomanian to Turonian, Portugal, Jordan, and Utah (Reeside, 1929; Malchus, 1990; Aqrabawi, 1993).

AGE AND DISTRIBUTION. Early Cenomanian to Maastrichtian and widespread (except in polar seas) (Reeside, 1929; Stenzel, 1971). The species revised here and the new species named below are the first reports of *Costagyra* in the PSNA region.

REMARKS. Early workers (e.g., Reeside, 1929; Stenzel, 1971) used *Costagyra* as a subgenus of *Exogyra* Say, 1820, although the radial ribs on *Costagyra* are fewer, stronger, and more widely spaced. Most modern workers (e.g., Dhondt et al., 1999; Dhondt and Jaillard, 2005; Ayoub-Hannaa and Fürsich, 2011; Hannaa, 2011) elevated *Costagyra* to the genus level, and their practice is followed here.

Costagyra juveniles were cemented to secondary hard substrate, whereas adults were adapted to a free, reclining mode of life on soft sediment. The thick shells of some species served to increase stabilization on the soft sediment and also helped to protect against predators (Ayoub-Hannaa and Fürsich, 2011). Variations in shell thickness and ornament of *Costagyra* were possibly related to water energy (Seeling and Bengtson, 1999:758). Its shell microstructure is predominantly prismatic, with some foliated layers (Jaitly et al., 2014).

Costagyra californica (Packard, 1922) comb. nov.
Figures 5, 114–120

Exogyra californica Packard, 1922:421, pl. 27, fig. 5.

EMENDED DESCRIPTION. Shell size up to height 55 mm. Shape rectangular to subfalcate. Inequivalved. Umbonal region tightly spirally coiled posteriorly. Shell microstructure predominantly prismatic with much thinner foliated layers. **Left valve:** Convex with medial axis coincident with broad, bumpy keel extending posteriorly from umbo to venter; keel can be continuous or with broad sulcus on medial part of valve. Posterior side of valve bearing nine to 10 ribs (can be dichotomous) which extend from umbo to venter and widen toward venter; radial ribs narrow to moderately wide and can be nearly hyote-like near venter; interspaces wide and concave. Attachment area present on small specimens. **Right valve:** Flat to slightly concave (near hinge) and smoothish, with overlapping spirally arranged growth lamellae. Radial ribs short (approximately eight) along anterior side of first whorl of spiraling umbo, with ribs becoming wider, more widely spaced, and less prominent with increasing size of whorl. Resilifer groove narrows posteriorly and can be nearly filled with shell deposit. Anterior bourrelet thin, coincident with sharp anterior edge of shell, and bearing many short anachomata. Posterior bourrelet forms short projecting ridge adjacent to concavity just ventral of hinge line. Adductor muscle scar large, reniform, and just posterior of central part of valve.

HOLOTYPE. UCMP 12320, UCMP loc. 2143, height 57 mm, length 60 mm, Ladd Formation, Baker Canyon Member, east side Silverado Canyon, Santa Ana Mountains, Orange County, Southern California.

GEOLOGIC AGE. Turonian.

GEOGRAPHIC RANGE. ?Ono area, Shasta County, Northern California [Area 6] to Santa Ana Mountains, Orange County, Southern California [Area 16].

STRATIGRAPHIC DISTRIBUTION. QUESTIONABLY UPPER CENOMANIAN: Budden Canyon Formation, Bald Hills Member, Ono area, Shasta County, Northern California (new occurrence). TURONIAN: Ladd Formation, Baker Canyon Member and Holz Shale Member, east side Silverado Canyon, Santa Ana Mountains, Orange County, Southern California (Packard, 1922).

REMARKS. Sixteen specimens were examined. Preservation is moderately poor, and the radial ribs are very faint on most specimens because of weathering, including the holotype (Fig. 114). Many of the specimens of this species are internal casts, including a questionable occurrence of this species from LACMIP loc. 10878 in the Budden Canyon Formation, Bald Hills Member, Ono area, Shasta County, Northern California. *Costagyra californica* co-occurs with *P. inornata* at LACMIP locs. 10887 (Baker Canyon Member) and 15894 (Holz Shale Member). A small left valve (Fig. 115) of *C. californica* from LACMIP loc. 8198 (Baker Canyon Member) shows a moderately large attachment scar.

Costagyra garza sp. nov.
Figures 121–127

Exogyra sp. Elder and Miller, 1993:table 3.

DIAGNOSIS. Shell size large, *Costagyra* with keeled left valve bearing 12 to 13 radial ribs.

DESCRIPTION. Shell size up to height 100 mm. Shape subfalcate to falcate. Very inequivalved, beaks spirally coiled. Shell microstructure predominately prismatic with some much thinner foliated layers. **Left valve:** Inflated greatly. Radial ribs 12 to 13, wide, can be dichotomous, and with moderately wide interspaces; ribs extend to umbo where partly covered by thin shell with rugose growth lines; ribs become wider ventrally and have development of some hyote-like raised areas; ribs obsolete on some large specimens. **Right valve:** Smooth, lid-like, thin; ventral half sunken, whereas dorsal half turns upward. Adductor muscle scar central.

HOLOTYPE. LACMIP 14594, height 92.8 mm, length 84.4 mm, LACMIP loc. 26517, Moreno Formation, "Garzas Sand," Garzas Creek, western side San Joaquin Valley, Stanislaus County, Northern California.
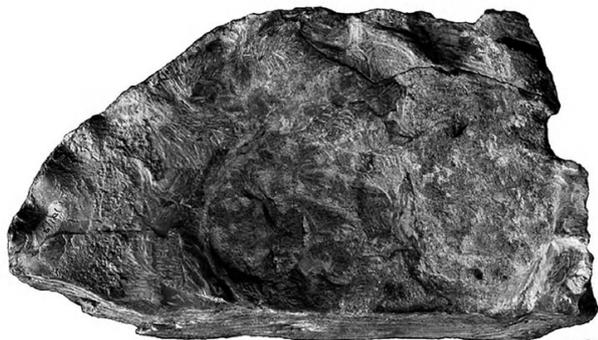
PARATYPES. LACMIP 14595–14597. All from vicinity of the holotype.

GEOLOGIC RANGE. Late early to early late Maastrichtian.

←

Figures 98–107 *Crassostrea brewerii* (Gabb, 1864), Ladd Formation, Holz Shale Member [Area 16], unless otherwise noted. **98–99.** Hypotype LACMIP 14586, LACMIP loc. 24190 left valve, height 133.3 mm, ×0.5. **98.** Exterior with boring bivalve *Lithophaga* sp. on posterodorsal umbo region (denoted by arrow). **99.** Interior. **100–103.** Hypotype LACMIP 14587, LACMIP loc. 10091, left valve, height 142.6. mm, ×0.5, unless otherwise noted. **100.** Exterior with boring bivalve *Lithophaga* sp. and encrusting annelid? tubes on posterodorsal umbo region. **101.** Interior. **102.** Close-up, ventral of hinge, of posterior shell margin bearing catachomata, height 40 mm, ×1.7. **103.** Posterior view. **104.** Plaster replica of left valve interior of specimen, height 100 mm, ×0.8, attached to anterior side of holotype of *C. brewerii*. **105.** Holotype UCMP 31447, UCMP loc. IP 11381, "Chico Group, Cow Creek" [Area 5], left valve interior, height 117 mm, ×0.6. **106–107.** Hypotype VIPM 017, Haslam Formation [Area 2], left valve interior. **106.** Height 140 mm, ×0.5. **107.** Close-up, ventral of hinge, of posterior shell margin bearing catachomata, height 23 mm, ×2.

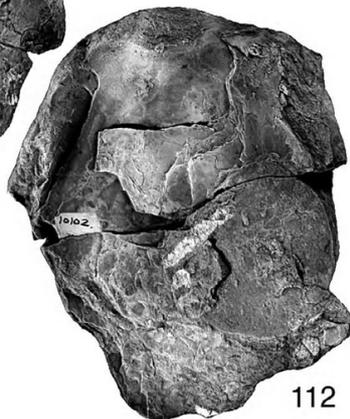**GEOGRAPHIC RANGE.** Garzas Creek area, Stanislaus County, Northern California [Area 11].

STRATIGRAPHIC DISTRIBUTION. Moreno Formation, "Garzas Sand," Garzas Creek, west side San Joaquin Valley, Stanislaus County, Northern California.

REMARKS. Seven specimens were examined. Preservation is moderately good. Two of the specimens are conjoined. *Costagyra garza* differs from *C. californica* by having a much larger size, nonrectangular shape, and more radial ribs. The new species is very similar to *Costagrya olisipoensis* illustrated by Malchus (1990:pl. 10, figs. 6a, 6b) and by Aqrabawi (1993:pl. 4, figs. 3–5, pl. 5, figs. 1, 2). The new species differs by having no hyote spines, a less prominent umbo (i.e., wide and projected), and no ribs on the right valve.

Elder and Miller (1993:table 3) reported *Exogyra* sp., of middle or approximately middle Maastrichtian age, from the Garzas Creek area, Stanislaus County, Northern California. The specimens they examined are the same ones examined for this present report: LACMIP locs. 6357 [now 26357], 6358 [now 26358], 10660, and 6517 [now 26517].

ETYMOLOGY. The new species is named for the "Garzas Sand."

Tribe Amphidonteini Vialov, 1983
Genus *Amphidonte* Fischer de Waldheim, 1829

TYPE SPECIES. *Amphidonte humboldtii* Fischer de Waldheim, 1829, by subsequent designation (Fischer, 1886); Late Cretaceous (Cenomanian), Russia.

AGE AND DISTRIBUTION. Early Cretaceous to late Maastrichtian and widespread (Aqrabawi, 1993). The species revised here is the first report of *Amphidonte* in Northern Baja California, Mexico.

REMARKS. Stenzel (1971) did not recognize any subgenera of *Amphidonte*, whereas many subsequent workers (e.g., Elder, 1991; Aqrabawi, 1993; Malchus et al., 1994; Seeling and Bengtson, 1999) recognized *Ceratostreon* Bayle, 1878, as a subgenus of *Amphidonte*.

Lazo (2007) reported *Amphidonte* to be a cementing, epifaunal bivalve, and LaBarbera (1981) reported it to be an epifaunal recliner, generally on soft sediment. Its shell microstructure is compact foliated with lens-shaped layers (Malchus, 1990).

Amphidonte parasitica (Gabb, 1864)
Figures 8, 13, 15, 128–155

Exogyra parasitica Gabb, 1864:205, pl. 26, figs. 192, 192a, 192b; pl. 31, figs. 273, 273a; Whiteaves, 1879:175, 1903:401, 409; White 1884:306, pl. 55, figs. 3, 4 (after Gabb); Stewart, 1930:132, pl. 1, fig. 1.

Ostrea washingtoni Coquand, 1869:63–64, pl. 33, figs. 5–9 (after Gabb); unnecessary new name for *Exogyra parasitica* Gabb. Not *Ostrea parasitica* Lindroth, 1788:17; not *Ostrea parasitica* Gmelin, 1791:3336.

Ostrea crescentica Packard, 1922:pl. 26, fig. 4 [not *Ostrea crescentica* Packard, 1922:420, pl. 26, fig. 3].

←

Figures **108–113** *Crassostrea brewerii* (Gabb, 1864), Williams Formation, Pleasants Sandstone Member [Area 16], unless otherwise noted. **108–110.** Hypotype LACMIP 14588, LACMIP loc. 10119, partial left valve, height 100 mm, ×0.5. **108.** Exterior, with partial specimen of boring bivalve *Lithophaga* sp. (denoted by arrow). **109.** Interior. **110.** Cross-section showing prismatic/foliated shell microstructure, middle part of ventral edge of valve, height 31 mm, ×1.1. **111–113.** Hypotype LACMIP 14589, LACMIP loc. 10102, Ladd Formation, Holz Shale Member [Area 16], right valve, height 107.6 mm, ×0.5. **111.** Exterior. **112.** Interior. **113.** Posterior view.

Amphidonte (Amphidonte) parasitica (Gabb). Elder, 1991:E11, pl. 4, figs. 9, 17–23.

Amphidonte sp. cf. *A. parasitica* (Gabb, 1864). Elder et al., 1998:pl. 1, fig. 14.

Amphidonte parasitica (Gabb). Kennedy et al., 2000:16.

?*Amphidonte (Amphidonte) parasitica* (Gabb). Elder, 1991:pl. 3, figs. 6, 10.

EMENDED DESCRIPTION. Shell size normally up to height 80 mm, rarely up to 100 mm. Shape variable with three morphs: auriform (ear-like), wedge, and short tube, listed in decreasing order of abundance. Auriform morph with shell height approximately 17–70 mm, wedge morph shell height approximately 53–100 mm, and short-tube morph shell height 20–60 mm. Auriform morph gradational in shape with wedge morph and, to lesser degree, with short-tube morph. Valve exteriors smooth, with only growth lamellae (if any). Adductor muscle scar size medium to large; scar shape oval on all morphs, and either central or off-center, near posterior wall. Umbo opisthogyral to various degrees. Hinge area commonly strongly coiled but can be poorly developed and wide. Resilifer not prominent on most specimens. Sigmoidal sinus (notch) can consist of infolded area where chomata bend abruptly in half-circle fashion, affecting both valves near posterior bourrelet, causing margin of the sinus to be wrinkled and forming small depression in left valve and corresponding slight bulge in right valve. Sigmoidal sinus can be "closed up" on some specimens. Ligamental area can remain obscure to weak or moderately strong. Chomata small, numerous and cover both interior margins of each valve or can be obscure. Shell microstructure foliated, with lens-shaped layers. **Left valve:** Attachment surface flat or slightly concave and commonly smoothish on all morphs. Smallest specimens (shell height 17 mm) crescent-shaped with wide umbo, hinge spirally coiled, and resilifer and sigmoidal sinus not obvious or poorly developed. Early adult to mature adult auriform-morph individuals (shell height normally 35-43 mm, but uncommonly can be up to 70 mm) with generally flattish valve, anterior wall slightly to moderately elevated with respect to posterior wall, umbo broad, hinge spirally coiled, resilifer obscure, sigmoidal sinus well developed, and chomata well developed. At approximate shell height 35 mm, auriform-morph anterior wall can become gradationally more elevated (increasing from 21 to 32 mm high, rarely up to 50 mm high), and also nearly vertical to vertical; posterior wall much lower (increasing from 5 to 13 mm high) and much thinner. At approximate shell height 50–58 mm, and continuing to shell height 80 mm, anterior wall elevated enough and thick enough to form wedge morphs. Distinction between specimens intermediate in shape between auriform and wedge morphs is arbitrary because change in the height of anterior wall relative to the posterior wall is gradational. Wedge morph has left valve sloping approximately 30° from highest point toward posterior margin; in addition, umbo spirals posterior and begins to "close up," as does sigmoidal sinus. Anterior wall normally smooth but can be broadly lumpy, with broad sulcus between two lumps. Short-tube morph only known from left valves, anterior wall thin (up to 14 mm high) and more elevated than posterior wall (up to 5 mm high), thereby producing overall partial wedge shape (depending on view). Short-tube morph flat bottomed (well cemented to hardground), resilifer small, sigmoidal sinus area generally obscured, and adductor muscle scar circular. **Right valve:** Auriform immature valves (less than shell height 20 mm) known only from right valves, flattish to lowly convex, with ligamental area very poorly developed (barely discernible), small indentation to accommodate spiraling of beak, and sigmoidal sinus absent. Auriform adult right valves flat (lid-like), smooth, thin but with some thickening anteriorly, especially on dorsoanterior region. As umbo spirals posterior, ligamental area can narrow and begin to "close up," as does sigmoidal sinus

(especially on wedge morphs). Ligamental area rarely very wide and obscure. On some auriform specimens (shell height 70 mm), right valve countersunk into groove of corresponding left valve, with numerous, short, and closely spaced anachomata on right valve margin meshing with chomata on overlapping left valve.

LECTOTYPE. ANSP 4429 (designated here), height 39.2 mm, length 26.3 mm, Chico Formation, Granite Bay [= Texas Flat], Amador County, Northern California. Gabb (1864) did not select a holotype of *E. parasitica*, nor did Stewart (1930), who re-examined Gabb's type specimens. Stewart (1930) suggested that ANSP 4429 might be a suitable lectotype but did not designate it as such. Specimen ANSP 4429 is designated here as the lectotype.

GEOLOGIC RANGE. Early Campanian to latest Maastrichtian.

GEOGRAPHIC RANGE. Denman Island and Hornby Island off east coast of Vancouver Island, British Columbia, Canada [Area 1], to San Antonio del Mar, Northern Baja California, Mexico [Area 19].

STRATIGRAPHIC DISTRIBUTION. LOWER CAMPANIAN: Chico Formation, Pentz, Butte County, Northern California (Eric Göhre, personal communication, 2002); Chico Formation, Granite Bay [= Texas Flat], Amador County, Northern California (Gabb, 1864). UPPER MIDDLE CAMPANIAN [*Metaplacenticeras* cf. *pacificum* ammonite zone (see Ward et al., 2015:fig. 7)]: Upper Cedar District Formation, "White House" site, western Denman Island, off east coast of Vancouver Island, British Columbia, Canada (new occurrence); unnamed formation, Loma Prieta area, Santa Cruz Mountains, Santa Clara County, Northern California (Elder, 1991); Williams Formation, Pleasants Sandstone Member, Bee Canyon, Santa Ana Mountains, Orange County, Southern California (new occurrence). UPPER CAMPANIAN/LOWER MAASTRICHTIAN: Northumberland Formation, Collishaw Point, "shark tooth zone," Hornby Island, off east coast of Vancouver Island, British Columbia (new occurrence); Gualala Formation, Anchor Bay Member, west of Anchor Bay, Mendocino County, Northern California (Elder et al., 1998); an unnamed fault-bounded stratigraphic unit, Loma Prieta, Santa Cruz Mountains, Santa Clara County, Northern California (Elder, 1991); basal Point Loma Formation, Palmer Way, Carlsbad, San Diego County, Southern California (Kennedy et al. 2000); Point Loma Formation, La Jolla, San Diego County, Southern California (new occurrence); Rosario Formation (new occurrence), Punta San Jose and San Antonio Del Mar, Northern Baja California, Mexico. UPPER LOWER TO LOWER UPPER MAASTRICHTIAN: Moreno Formation, Tierra Loma Shale, north end of Laguna Seca Hills, Merced County, Northern California (new occurrence). UPPERMOST MAASTRICHTIAN: El Piojo Formation, Cantinas Creek and Dip Creek, Lake Nacimiento, San Luis Obispo County, Northern California (Saul, 1986a); San Francisquito Formation, Warm Springs Mountain, Los Angeles County, Southern California (Kirby, 1991).

REMARKS. Eighty-five specimens were examined. Preservation is best in the Point Loma Formation near Carlsbad, San Diego County; the Rosario Formation at San Antonio del Mar, Baja California, Mexico; and the Cedar District Formation on western Denman Island, British Columbia, Canada. Elsewhere, preservation is generally good. The short-tube morph (e.g., Figs. 141, 142) is only found in the Point Loma Formation in the Carlsbad area and in the upper Cedar District Formation on western Denman Island. The lectotype of *A. parasitica* is an early adult-auriform morph, and two views of a plaster cast of the lectotype are shown in Figures 131 and 132.

Elder (1991:E11, unfig.) reported the largest specimen of *A. parasitica* as having a shell height of 100 mm. It is from an unnamed fault-bounded stratigraphic rock unit near Loma Prieta [Area 11]. Elder (1991:pl. 4, figs. 9, 17–23) illustrated several morphs of *A. parasitica* found in this rock unit and referred to them as "typical" and "ovate"
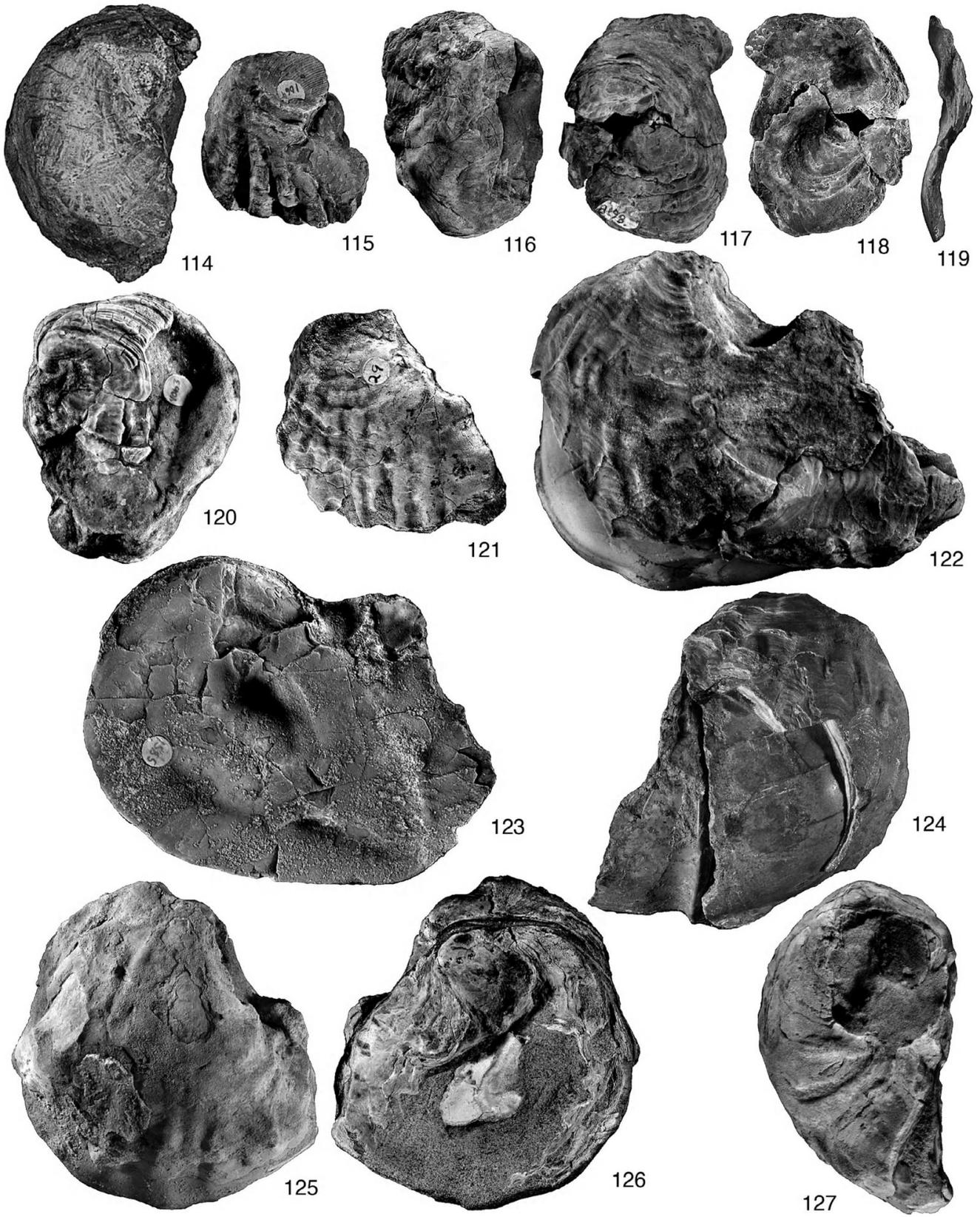
[both same as auriform here], "ovate with carinate umbilical ridge" [same as short tube here], and "elongate." Based on the low profile, robust shell, and large attachment surface of many of the oysters, they were adapted to a nearshore, high-energy environment. In the rock unit near Point Loma, they subsequently underwent transport downslope by turbidity currents and into deeper waters, where they accumulated as oyster coquinas (Elder, 1991).

A growth stage series of the auriform morph, ranging in height from 20 to 70.6 mm (Figs. 128–145), is best represented at LACMIP loc. 3966 in the Point Loma Formation, at Madonna Hill in the Carlsbad area, San Diego County [Area 17]. At this locality, the majority of the specimens represent the auriform morph, a few somewhat resemble the wedge morph, and a few are the short-tube morph. At other localities in the immediate vicinity, specimens are represented by the auriform and wedge morphs or by the auriform and those that resemble the wedge morphs. At nearby LACMIP loc. 17423, a large auriform morph (shell height 70 mm) with conjoined valves (Figs. 143–145) was collected.

The presence of growth stages and conjoined valves are strongly indicative that *A. parasitica* auriform morphs found in sandstones of the Point Loma Formation, Carlsbad area, San Diego County, are in situ or nearly so. Kennedy et al. (2000) interpreted the depositional environment at the Palmer Way localities in the Point Loma Formation to have been an intertidal? to a very shallow, nearshore marine, rocky bottom habitat. The common co-occurrence of auriform and the sturdier looking wedge morphs is suggestive that microenvironments (e.g., possibly protected habitats versus more exposed habitats, respectively) played a role in determining the morph shape. Detailed sedimentologic and paleoenvironmental studies, which might help to understand the variability of morph shapes found at these Carlsbad localities, cannot be made because the specimens were collected from temporary exposures of medium-grained (on average) sandstone at several localities (e.g., LACMIP 3966, 17423), just a few meters stratigraphically above a basal conglomerate. All these beds were destroyed in subsequent development.

In the Rosario Formation at LACMIP loc. 27263, in the San Antonio del Mar area, Baja California, Mexico [Area 19], both the auriform and wedge morphs are present, but the auriform morph (Fig. 146) is a minor component compared with the wedge morph (Figs. 147, 150). The specimens are robust and heavy, mostly free of sandstone matrix, and dark gray. Many of the specimens have large prominent "holes"(openings caused by dissolution) coincident with former position of the adductor muscle scar (Figs. 146, 147). One hand specimen (Fig. 147) contains three large specimens (height 60–82 mm) of *A. parasitica*, which solidly encrust one another. The specimen shown in Figure 147 is an auriform morph isolated from the hand specimen, whereas the other two specimens are more wedge shaped. Also at locality 27263, a left valve of a wedge morph of *A. parasitica* (Fig. 150) is totally cemented to a right valve of a trigonal morph of *A. taxidonta*. Sedimentologic and paleoenvironmental analyses are so far lacking for rocks at this locality.

Only the wedge morph (e.g., Figs. 148, 149, 151, 152) is known from LACMIP loc. 22415 in the Williams Formation, Pleasants Sandstone Member, Santa Ana Mountains, Orange County [Area 16]; specimens are not common. The left valves are thick and robust (i.e., sturdy looking). These Bee Canyon exposures are slightly younger than the Pleasants Sandstone Member found elsewhere and contain a shallow-marine fossil assemblage deposited in moderate depths (Saul, 1982:74). Detailed sedimentologic and paleoenvironmental studies are also lacking for this locality.

Saul (1986a:29) reported two fragments of a large thick-shelled ostreid from LACMIP loc. 26525 in the lower upper Maastrichtian El Piojo Formation in the vicinity of Lake Nacimiento [Area 13]. The largest fragment (height 68 mm) is a wedge morph. Its smooth exterior has been bored by bivalves, which is a common feature in specimens of *A. parasitica* found elsewhere. Kirby (1991:80, pl. 3, fig. 1) reported unidentifiable ostreid fragments from LACMIP loc. 14320 in a thin interval of uppermost Maastrichtian strata in the basal San Francisquito Formation in the Warm Springs Mountain area, Los Angeles County [Area 14]. Fossils in this part of the formation are generally not well preserved. He stated that one of the thin-shelled specimens might be a *Pycnodonte*, but it is *Amphidonte parasitica*.

Coquand (1869:63) believed that Gabb's *Exogyra parasitica* belonged in genus *Ostrea* and consequently a secondary homonym of *Ostrea parasitica* Gmelin, 1791. Coquand, incidentally, was not aware that the name *Ostrea parasitica* was first used by Lindroth, 1788. Gabb's species, however, does not belong in *Ostrea*; thus, Gabb's name is not a secondary homonym, and Stoliczka (1871:458) recognized this fact.

### ?*Amphidonte parasitica* (Gabb, 1864)
Figures 156, 157

REMARKS. A single and unusual left valve of ?*Amphidonte parasitica* (Figs. 156, 157) from LACMIP loc. 3966 in the Point Loma Formation, near Carlsbad, San Diego County, Southern California, is similar to the auriform morph of *A. parasitica* in terms of overall shape and adult size, anterior wall slightly higher than posterior wall, and large subcentral adductor muscle scar. This unusual specimen differs from *A. parasitica* by having prominent, angularly terminate wide plicae on the anterior wall, as well as obvious bourrelets, and catachomata present on only the dorsal half of both margins of the valve. In addition, the catachomata differ by being shorter, stronger, and similar shapes on both margins of the valve. This unusual specimen might represent another species. Although the presence of plicae on the ?*A. parasitica* specimen is indicative of placement in *Ceratostreon* Bayle, 1878, such a placement is unmerited because *Ceratostreon* has a much more spirally incurved ligamental area, as well as much weaker and longer catachomata.

Subfamily Pycnodonteinae Stenzel, 1959

Genus *Pycnodonte* Fischer de Waldheim, 1835

←

Figures 114–127   *Costagyra* spp., PSNA region. **114–120.** *Costagyra californica* (Packard, 1922), Ladd Formation, Baker Canyon Member [Area 16]. **114.** Holotype UCMP 12320, UCMP loc. 2143, left valve (very worn), height 57 mm, ×1. **115.** Hypotype LACMIP 14590, LACMIP loc. 8198, left valve, height 36.5 mm, ×0.9. **116–119.** Originally conjoined, LACMIP loc. 8198. **116.** Hypotype LACMIP 14591, left valve, height 52.6 mm, ×0.8. **117–119.** Hypotype LACMIP 14592, right valve, height 53.2 mm, ×0.8. **117.** Exterior. **118.** Interior. **119.** Posterior view. **120.** Hypotype LACMIP 14593, LACMIP loc 24063, right valve, height 52.7 mm, ×1. **121–127.** *Costagyra garza* sp. nov., Moreno Formation, "Garzas Sand" [Area 11]. **121.** Paratype LACMIP 14595, LACMIP loc. 26358, left valve, height 51.9 mm, ×0.8. **122–124.** LACMIP loc. 10660, originally conjoined valves. **122.** Paratype LACMIP 14596, left valve, height 80.4 mm, ×0.8. **123.** Right valve interior, height 74.2 mm, ×0.8 **124.** Anterior view of reunited conjoined valves, thickness 76 mm. **125–127.** Holotype LACMIP 14594, LACMIP loc. 26517, conjoined valves, height 92.8 mm, ×0.7. **125.** Left valve. **126.** Right valve interior. **127.** Left valve, posterior side, thickness 49.7 mm.
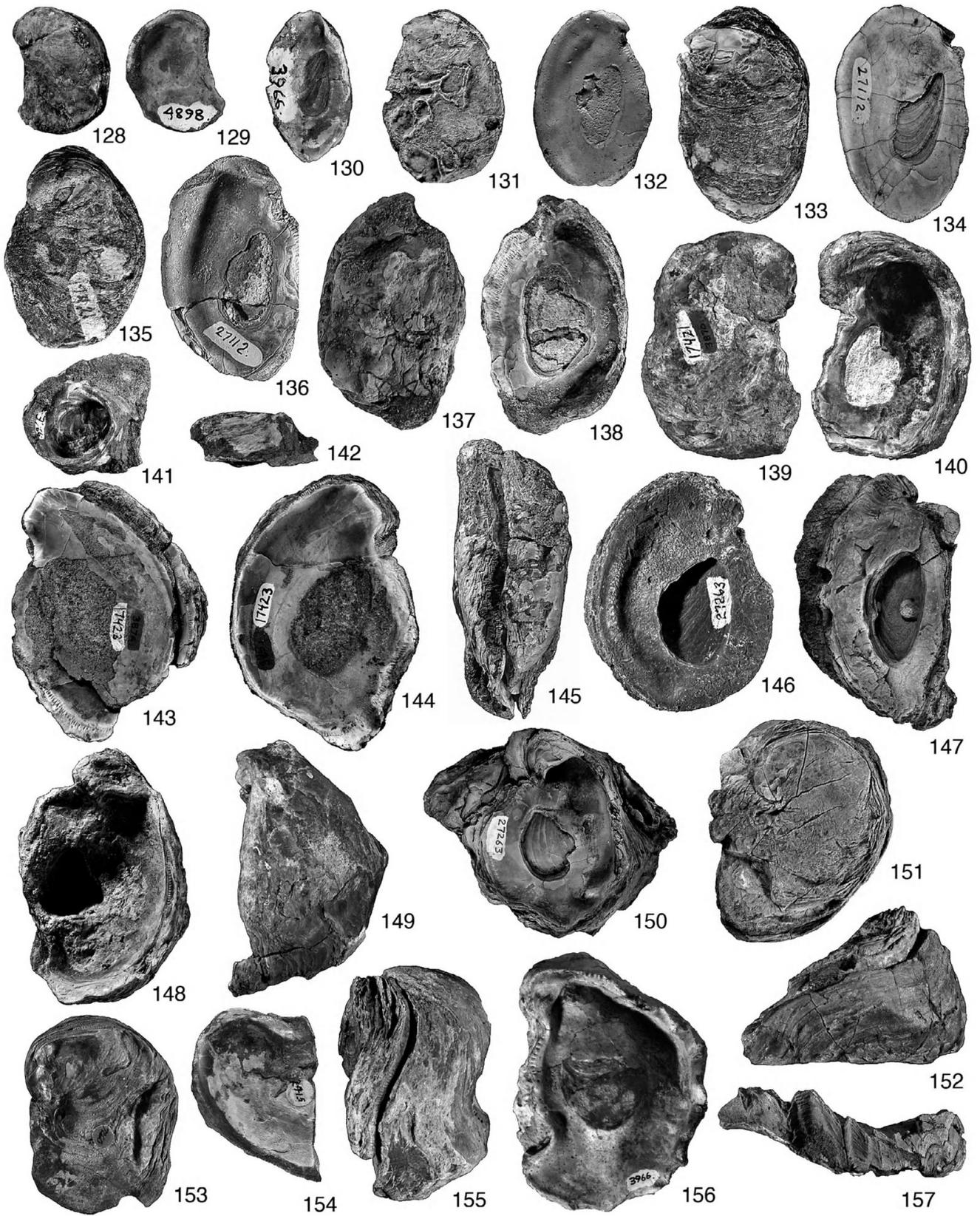
TYPE SPECIES. *Pycnodonte radiata* Fischer de Waldheim, 1835, by original designation; Late Cretaceous, Crimea.

AGE AND DISTRIBUTION. Cretaceous to Holocene, with modest post-Cretaceous record and at least one extant species (Hayami and Kase, 1992); and widespread (Stenzel, 1971). The PSNA species revised here is the earliest report of *Pycnodonte* s.s. in the PSNA region.

REMARKS. In addition to *Pycnodonte* s.s., Stenzel (1971) recognized three subgenera of genus *Pycnodonte*: *Costeina* Vialov, 1965; *Crenostrea* Marwick, 1931; and *Phygraea* Vialov, 1936. Since Stenzel's work, two other subgenera were added: *Eupycnodonte* Freneix, 1979, and *Pegma* Squires and Demetrion, 1990. The subgeneric division of *Pycnodonte* has historically been controversial and confusing. Hayami and Kase (1992) commented that much of this confusion stems from not considering intraspecific variation and different modes of life.

Pycnodonte has been reported as an epifaunal-cemented bivalve (Ayoub-Hannaa and Fürsich, 2012:125), but species can have adults that lived as free-living, "cup-shaped" recliners in silty substrate (Wilmsen and Voigt, 2006). Morphology can be very variable, with shell form and size of attachment area strongly dependent on ecologic factors, as well as on ontogenic factors (e.g., duration of fixation) (Machalski, 1998). Its shell microstructure is vesicular ("honeycomb") (Jaitly et al., 2014).

Subgenus *Pycnodonte* s.s.
Pycnodonte (*Pycnodonte*) *malleiformis* (Gabb, 1864) comb. nov.
Figures 6, 14, 158–168

Ostrea malleiformis Gabb, 1864:204, pl. 31, fig. 272; White, 1884:297, pl. 50, fig. 7 (after Gabb); Jones et al., 1978:XXII.9, unfig.
"*Ostrea*" *malleiformis* Gabb. Stewart, 1930:131, pl. 3, fig. 10; text-fig. 3.

EMENDED DESCRIPTION. Shell size up to height 27 mm. Shell paper-thin, brittle, and fragile. Shape variable with three morphs: auriculate, spatulate, and suboval. Valves flattish, oblique poster-oventrally, slightly inequivalved, and nearly equilateral. Dorsal margin normally long and straight but can be short. Beaks small but distinct. Adductor muscle scar small, elliptical, and located posterior of center of valve. Shell microstructure vesicular but obscure. **Left valve:** Auricles on both sides of hinge; anterior auricle more distinct, projecting, and can be concave medially. Umbo rising barely above long, straight dorsal margin. Exterior commonly smooth, but growth lines can occur in distinct commarginal bands, widely or closely spaced. Attachment scar not obvious. Catachomata sparse, located just anterior and posterior of resilifer; only faint pits along anterior margin of shell. Interior smooth; rarely with rimmed, large circular hollow area underneath umbo. **Right valve:** Fits within slightly larger left valve and is concave (sunken). Exterior smooth with extremely fine (microscopic) and closely spaced growth lines. Interior smooth. Anachomata very small, moderately spaced along most of posterior side up to hinge, and some on anterior side near hinge.

NEOTYPE. ANSP 4433 (designated by Stewart, 1930:131), height 38 mm, length 27 mm, Cottonwood Creek, Siskiyou County, Northern California.

GEOLOGIC AGE. Turonian.

GEOGRAPHIC RANGE. Jacksonville, Jackson County, southwest Oregon [Area 3] to east of Redding, Northern California [Area 5].

STRATIGRAPHIC DISTRIBUTION. ?Hornbrook Formation: Jacksonville, Jackson County, southwest Oregon (Gabb, 1864); Yreka area, Siskiyou County, Northern California (Stewart, 1930); Redding Formation, Bella Vista Sandstone Member and Frazier Siltstone Member, Dry Creek, east of Redding, Shasta County, Northern California (Jones et al., 1978).

REMARKS. One hundred and twenty-eight specimens were examined. Both left and right valves are equally represented, and some are conjoined. Preservation of many specimens is excellent. The valves of *malleiformis* are most similar to those of the type species *Pycnodonte* (*P.*) *radiata*, as described by Stenzel (1971:N1107). The similarities are the left valve umbo rising barely above the long, straight dorsal margin; auricles present; radial ribs absent; and concentric puckers and welts absent. The valves of *malleiformis* differ by not being circular nor subcircular, and its chomata are not vermiculate.

Pycnodonte (*P.*) *malleiformis* is very similar in morphology to the extant *Pycnodonte* (*P.*) *taniguchii* Hayami and Kase (1992:1076–1082, figs. 2–7) from shallow depths (20–30 m) in several poorly lighted submarine caves (i.e., cryptic, sheltered habitat) of Miyako and Okinawa Islands, southern Japan. This oyster seems to adhere to cave walls via attachment of the left valve. According to Hayami and Kase (1992:1081), *P.* (*P.*) *taniguchii* is closely similar to *P.* (*P.*) *radiata*. *Pycnodonte* (*P.*) *malleiformis* differs from *P.* (*P.*) *taniguchii* by having a much smaller size, much flatter left valve, and absence of a well-defined commissural shelf.

Genus *Phygraea* Vialov, 1936

TYPE SPECIES. *Gryphaea pseudovesicularis* Gümbel, 1861, by original designation; late Paleocene, Austria.

Figures 128–157 *Amphidonte* and ?*Amphidonte*, Point Loma Formation [Area 17], unless otherwise noted. **128–154.** *Amphidonte parasitica* (Gabb, 1864). **128–129.** Hypotype LACMIP 14598, LACMIP loc. 4898, right valve, height 17 mm, ×1.4. **128.** Exterior. **129.** Interior. **130.** Hypotype LACMIP 14599, LACMIP loc. 3966, right valve interior, height 20 mm, ×1.4. **131–132.** Plastolectotype ANSP 4429, Chico Formation [Area 9], right valve, height 39.2 mm, ×0.8. **131.** Exterior. **132.** Interior. **133–134.** Hypotype LACMIP 14600, LACMIP loc. 27112, right valve, height 43 mm, ×0.9. **133.** Exterior. **134.** Interior. **135.** Hypotype LACMIP 14601, LACMIP loc. 17421, right valve, height 37.2 mm, ×1. **136.** Hypotype LACMIP 14602, LACMIP loc. 27112, right valve interior, height 43 mm, ×1. **137–138.** Hypotype LACMIP 14603, LACMIP loc. 3966, left valve, height 57.3 mm, ×0.8. **137.** Exterior. **138.** Interior. **139–140.** Hypotype LACMIP 14604, LACMIP loc. 17421, height 58.1 mm, ×0.7. **139.** Exterior. **140.** Interior. **141–142.** Hypotype LACMIP 14605, LACMIP loc. 3966, diameter 25.2, height 10.8, ×0.8. **141.** Top view. **142.** Side view. **143–145.** LACMIP loc. 17423, originally conjoined valves. **143.** Hypotype LACMIP 14606, left valve interior, height 65 mm, ×0.7. **144.** Hypotype LACMIP 14607, right valve interior, height 70 mm, ×0.7. **145.** Anterior view of previous two hypotypes shown conjoined, thickness 24 mm. **146.** Hypotype LACMIP 14608, LACMIP loc. 27263, Rosario Formation [Area 19], right valve interior, height 60.2 mm, ×0.7. **147.** Hypotype LACMIP 14609, LACMIP loc. 27263, Rosario Formation [Area 19], right valve interior, height 80.6 mm, ×0.6. **148–149.** Hypotype LACMIP 14610, LACMIP loc. 22415, Williams Formation, Pleasants Sandstone Member, Bee Canyon [Area 17], left valve, height 73.4 mm, ×0.6. **148.** Interior. **149.** Anterior view, thickness 43 mm. **150.** Hypotype LACMIP 14611, LACMIP loc. 27263, Rosario Formation [Area 20], left valve interior cemented to right valve exterior of *Acutostrea taxidonta*, height 63 mm, ×0.6. **151–152.** Hypotype LACMIP 14612, LACMIP loc. 22415, Williams Formation, Pleasants Sandstone Member, Bee Canyon [Area 16], conjoined valves, height 58.3 mm, ×0.7. **151.** Right valve. **152.** Anterior side of conjoined valves, thickness 32 mm. **153.** Hypotype LACMIP 14613, LACMIP loc. 27260, Rosario Formation [Area 19], right valve, height 57.2 mm, ×0.6. **154–155.** LACMIP loc. 22415, Williams Formation, Pleasants Sandstone Member, Bee Canyon [Area 16], originally conjoined valves. **154.** Hypotype LACMIP 14614, partial right valve interior, height 44.2 mm, ×0.8. **155.** Hypotype LACMIP 14615, anterior side of reunited conjoined valves, height 53.4 mm, thickness 34 mm, ×0.8. **156–157.** ?*Amphidonte parasitica* (Gabb, 1864), hypotype LACMIP 14616, LACMIP loc. 3966, left valve, height 58.8 mm, ×0.8. **156.** Interior. **157.** Anterior side.
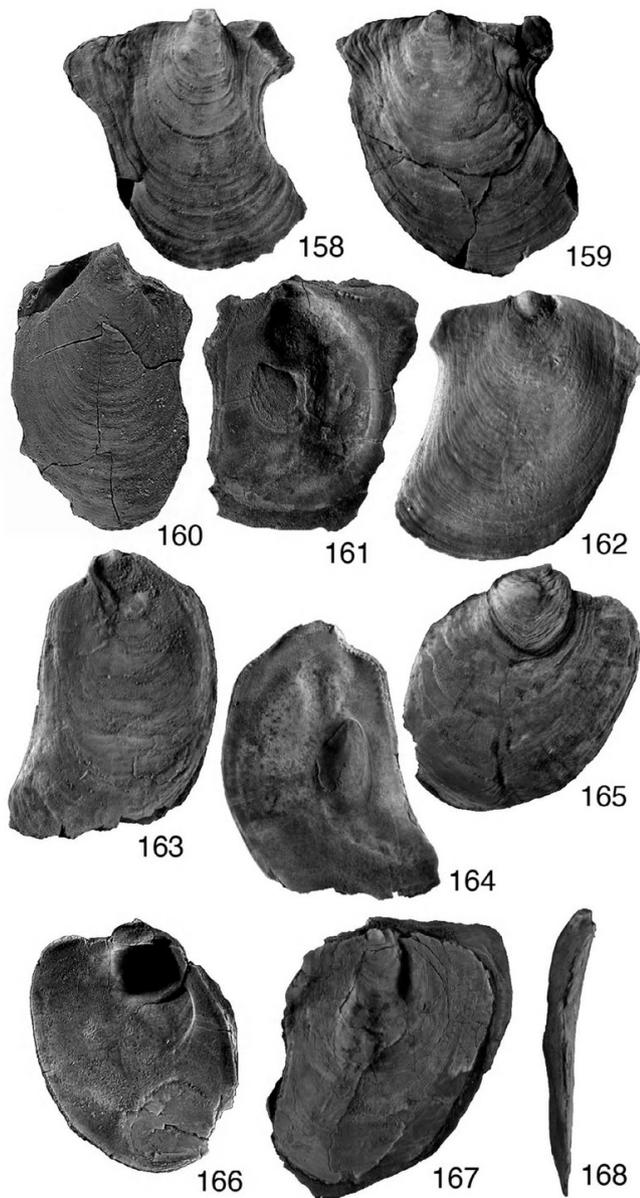
Figures 158–168 *Pycnodonte* (*Pycnodonte*) *malleiformis* (Gabb, 1864), Redding Formation, Frazier Siltstone Member [Area 5], unless otherwise noted. **158.** Hypotype LACMIP 14617, LACMIP loc. 24214, left valve, height 25.9 mm, ×1.4. **159.** Hypotype LACMIP 14618, LACMIP loc. 10730, Redding Formation, Bellavista Sandstone Member [Area 5], left valve, height 25.5 mm, ×1.4. **160.** Hypotype LACMIP 14619, LACMIP loc. 24214, left valve, height 29.2 mm, ×1.3. **161.** Hypotype LACMIP 14620, LACMIP loc. 24214, left valve interior, height 25.5 mm, ×1.4. **162.** Hypotype LACMIP 14621, LACMIP loc. 24214, right valve, height 22.1 mm, ×1.6. **163–164.** Hypotype LACMIP 14622, LACMIP loc. 24214, right valve, height 22.2, ×1.7. **163.** Exterior. **164.** Interior. **165–166.** Hypotype LACMIP 14623, LACMIP loc. 24214, right valve, height 27 mm, ×1.2. **165.** Exterior. **166.** Interior. **167–168.** Hypotype LACMIP 14624, LACMIP loc. 24214, conjoined valves, height 24.5 mm, ×1.5. **167.** Right valve. **168.** Posterior view, thickness 3.6 mm.

AGE AND DISTRIBUTION. Cretaceous to Miocene and widespread (Stenzel, 1971). The species revised here and the new species named below are the first reports of Cretaceous *Phygraea* in the PSNA region. *Phygraea* is represented by several species in Paleocene and lower Eocene strata in California (Squires and Demetrion, 1994).

REMARKS. As mentioned above, the subgeneric division of *Pycnodonte* has been controversial. It is especially confusing in regard to how *Pycnodonte* s.s. differs from *Phygraea*. Many modern workers (e.g., Malchus, 1990; Hayami and Kase, 1992; Malchus et al., 1994; Seeling and Bengtson, 1999; Wilmsen and Voigt, 2006) have followed the traditional view of Stenzel (1971) in placing *Phygraea* as a subgenus of *Pycnodonte*. Cooper (1992), Jaitly and Mishra (2001), and Jaitly et al. (2014), however, treated *Phygraea* as a distinct genus, and their practice is followed here.

The posteroventral flange of *Phygraea* most likely provided stability on soft sediments. Even at single localities there can be much morphologic variation, which represents polymorphic populations rather than allopatric or chronologic species/subspecies (Wilmsen and Voigt, 2006:23).

Phygraea inornata (Packard, 1922) comb. nov.
Figures 7, 169–187

Exogyra inornata Packard, 1922:420, pl. 27, fig. 1.

EMENDED DESCRIPTION. Shell size up to 66 mm height. Shell thin and smooth. Shape variable with three morphs: narrow, wide, and truncated spatulate. All strongly inequivalved. No auricles. Both valves smoothish. Adductor muscle scar small and off-center. Shell microstructure vesicular, in thin layers. **Left valve:** Juvenile and early adult specimens of narrow morph with umbo compressed, prominent, and tapered; beak straight, incurved (either anteriorly or posteriorly), and rising well above hinge. Adult narrow-morph specimens rarely have wide umbo, distinct posteroventral flange, and pseudo-auricle on anterodorsal region where attachment area intersects side of valve. Truncated-spatulate morph similar to narrow morph but with truncated umbo; umbo and beak replaced by small to large concavity (bowl-like) or flattened to bulging region representing attachment area on anterodorsal part of shell; ridgelets, welts, or puckers can be present adjacent to attachment area. Attachment scar not obvious. Catachomata on truncate-spatulate morph simple, short, and only on dorsal half of both shell margins. **Right valve:** Lowly concave to lid-like. Commarginal shelf can be present. Anachomata on both narrow and truncated-spatulate morphs short, vermiculate, and only on dorsal half of both shell margins.

HOLOTYPE. Holotype UCMP 12284, height 35 mm, length 33.8 mm, UCMP loc. 2143, Ladd Formation, Baker Canyon Member, Silverado Canyon, Santa Ana Mountains, Orange County, Southern California.

GEOLOGIC AGE. Turonian.

GEOGRAPHIC RANGE. East of Redding, Shasta County, Northern California [Area 5] to Santa Ana Mountains, Orange County, Southern California [Area 16].

STRATIGRAPHIC DISTRIBUTION. Redding Formation, Frazier Siltstone Member, tributary to Dry Creek, Shasta County, Northern California (new occurrence); Ladd Formation, Baker Canyon Member, Black Star Canyon and east side of Silverado Canyon, Santa Ana Mountains, Orange County, Southern California (Packard, 1922).

REMARKS. Three hundred and fifty specimens were examined. Nearly all of them are left valves, and their preservation is moderately good. Right valves and conjoined valves are scarce and poorly preserved. Specimens are encased in hard siltstone or in poorly sorted silty fine-
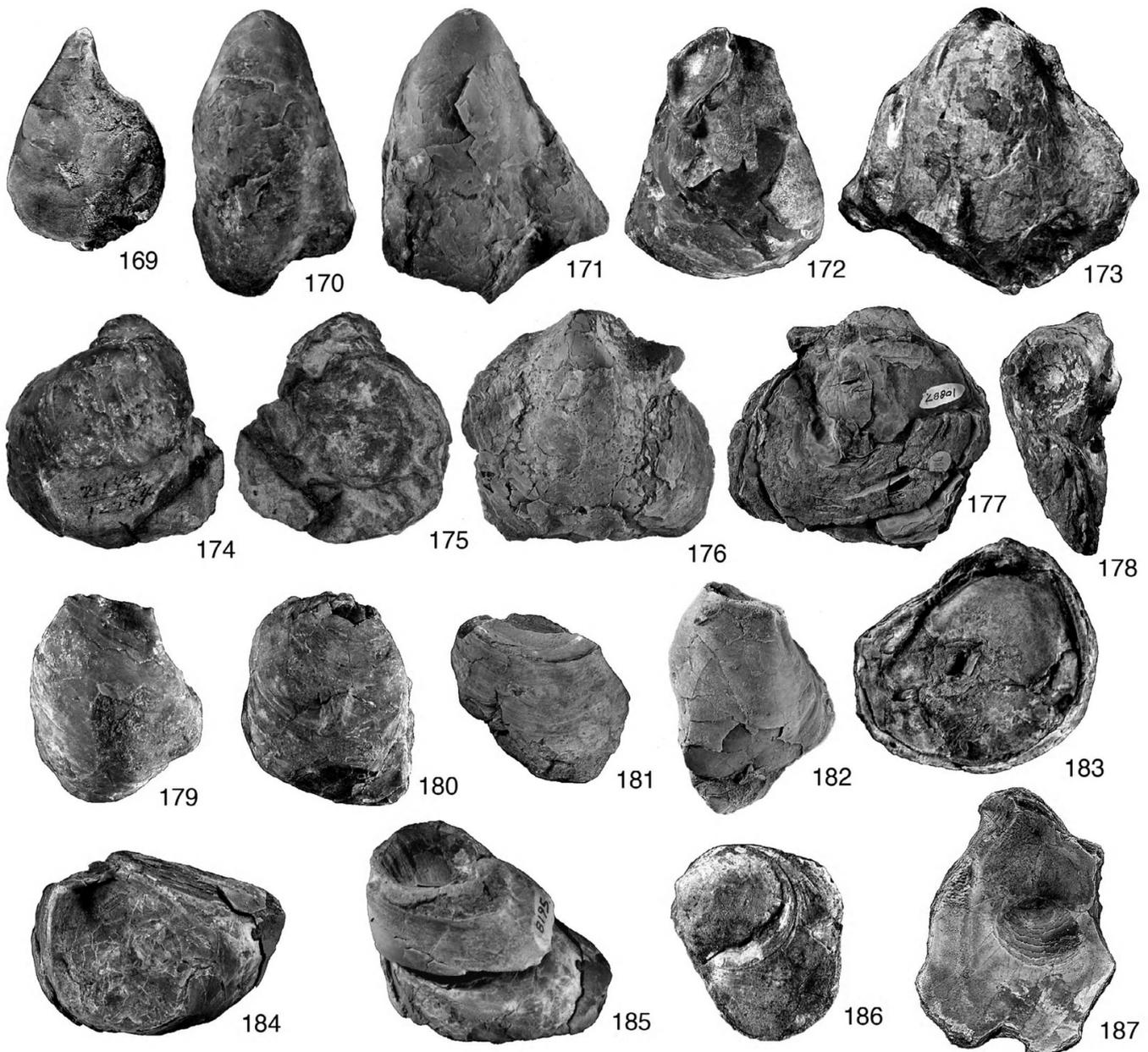
Figures 169–187 *Phygraea inornata* (Packard, 1922), Ladd Formation, Baker Canyon Member [Area 16], unless otherwise noted. **169.** Hypotype LACMIP 14625, LACMIP loc. 24654, Redding Formation, Frazier Siltstone Member [Area 5], left valve, height 21.1 mm, ×1.7. **170.** Hypotype LACMIP 14626, LACMIP loc. 8195, left valve, height 38.4 mm, ×1.2. **171.** Hypotype LACMIP 14627, LACMIP loc. 8195, left valve, height 42.4 mm, ×0.9. **172.** Hypotype LACMIP 14628, LACMIP loc. 8195, left valve, height 37 mm, ×1. **173.** Hypotype LACMIP 14629, LACMIP loc. 16857, left valve, height 55.6 mm, ×0.8. **174–175.** Holotype UCMP 12284, UCMP loc. 2143, left valve, height 35 mm, ×1. **174.** Exterior. **175.** Interior (mostly infilled with matrix). **176–178.** Hypotype LACMIP 14630, LACMIP loc. 10887, conjoined valves, height 59.5 mm, ×0.6. **176.** Left valve. **177.** Right valve. **178.** Posterior side, thickness 32.7 mm. **179.** Hypotype LACMIP 14631, LACMIP loc. 8195, left valve, height 26.3 mm, ×1.3. **180.** Hypotype LACMIP 14632, LACMIP loc. 8195, left valve, height 33.8 mm, ×1. **181.** Hypotype LACMIP 14633, LACMIP loc. 8195, left valve, height 38.9 mm, ×0.7. **182.** Hypotype LACMIP 14634, LACMIP loc. 8195, left valve, height 42.4 mm, ×0.9. **183–185.** LACMIP loc. 10959, originally conjoined valves. **183.** Hypotype LACMIP 14635, left valve interior, height 28.5 mm, ×1.3. **184.** Hypotype LACMIP 14636, right valve interior, height 28.4 mm, ×1. **185.** Oblique anterior view of previous two hypotypes shown conjoined, left valve above, right valve below, combined thickness of valves 25 mm, ×1.4. **186.** Hypotype LACMIP 14637, LACMIP loc. 24654, Redding Formation, Frazier Siltstone Member [Area 5], right valve, height 30.7 mm, ×1. **187.** Hypotype LACMIP 14638, LACMIP loc. 8195, right valve interior, height 25 mm, ×1.7.

grained sandstone, and the majority of them are from the Baker Canyon Member. Shell exteriors are decorticated on many specimens. Chomata are rarely preserved, and most are preserved on internal casts. The vesicular microstructure has been filled in with secondary calcite.

Two views of the holotype are figured here (Figs. 174, 175). Packard (1922) mentioned a "cotype" of his species but did not assign a catalog number. The whereabouts of this "cotype" are unknown. Representative interiors of the valves of *P. inornata* are shown here for the first time (Figs. 183, 184, 187).

The morphs of *P. inornata* are not restricted geographically nor stratigraphically, and this information is strongly suggestive that they are the result of ecophenotypic factors rather than evolution (i.e., separate species). For example, these polymorphic populations occur in the Redding Formation, Shasta County, Northern California (LACMIP loc. 24654), and in the Baker Canyon Member, Orange County, Southern California (LACMIP loc. 8195). The relative abundance of each morph, however, can differ from locality to locality. Most of the narrow-morph specimens of *P. inornata* show no attachment scar, but a rare specimen from locality 8195 (Fig. 172) has a small shell attached to its umbo. Also, most of the wide-morph specimens do not show an attachment scar. A particularly wide specimen (Figs. 176–178) from LACMIP loc. 10887 in the Baker Canyon Member has a moderately large attachment scar creating a pseudo-auricle. The truncated-spatulate morph specimens all show attachment scars on the left valve. The shape of *P. inornata*, therefore, was largely controlled by whether there was attachment to a foreign object.

As mentioned earlier, *P. inornata* co-occurs with *C. crescentica* and *C. californica* at various localities in the Baker Canyon Member of the Ladd Formation, Santa Ana Mountains, Orange County, Southern California.

Phygraea arida sp. nov.
Figures 11, 188–199

DIAGNOSIS. Shell size large. Shape variable but predominantly circular. Shell smooth, flattish, moderately thick, and heavy. Left valve with slight genticulation posterior to umbo region and with tongue-like flange extending from posterocentral region. Right valve low convex anteriorly, concave posteriorly, with well-developed commissural shelf.

DESCRIPTION. Shell size up to height 95 mm. Shell moderately thick and heavy. Shape variable with three morphs: circular, truncated spatulate, and subtrigonal. Circular morph common, other morphs rare. Umbo and beak mostly improminent, except projected beak on subtrigonal morph. Dorsal margin long, rarely short. Valves smooth (no radial ribs). Adductor muscle scar moderate size, circular, nearly central but somewhat near hinge. Catachomata and anachomata only near hinge and vermiculate (lath-like). Commissural shelf prominent, delimited proximally by circumferential curb. Shell microstructure vesicular ("foamy") with several thin to thick layers (individually up to 8 mm thick) separated from each other by thin horizontal lamellae. **Left valve:** Juvenile shell area of circular morph inflated; adult circular morph with prominent tongue-like flange extending from posterocentral region, and anteroventral part of interior of valve concave; commissural shelf on larger specimens close to muscle scar and to prominently raised posterior of muscle scar. **Right valve:** Lowly convex (inflated) along anterior side and concave posteroventrally; umbo area can be swollen. Adductor muscle scar near posterior, anachomata along dorsal anterior and dorsal posterior regions. Commissural shelf occurs as raised narrow curb along anterior margin and occurs as much broader swollen area along most of posterior side, including posterior side of adductor muscle scar.

HOLOTYPE. Holotype LACMIP 14639, height 81.3 mm, length 89.2 mm, LACMIP loc. 10685, Los Banos Creek, Moreno Formation, "Quinto Silt," Los Banos Creek, Merced County, Northern California.

PARATYPES. LACMIP 14640–14642; RBCM.EH2016.001. 0001.001, RBCM EH.2016.001.0002.001, and RBCM.EH2016.002. 0001.001.

GEOLOGIC RANGE. Late middle Campanian to late early to early late Maastrichtian.

GEOGRAPHIC RANGE. Denman Island, Vancouver Island, British Columbia, Canada [Area 1], to Garzas Creek, Merced County, Northern California [Area 11].

STRATIGRAPHIC DISTRIBUTION. UPPER MIDDLE CAMPANIAN: Upper Cedar District Formation, "White House" site, western Denman Island, off east coast of Vancouver Island, British Columbia, Canada [*Metaplacenticeras* cf. *pacificum* ammonite zone (see Ward et al., 2015:fig. 7)]. UPPER LOWER TO LOWER UPPER MAASTRICHTIAN: Moreno Formation, Tierra Loma Shale, "Garzas Sand," and "Quinto Silt," Garzas Creek, Merced County, west side of San Joaquin Valley, Northern California.

REMARKS. Thirty specimens were examined, including one conjoined-valved specimen. Preservation is generally excellent. Some of the Moreno Formation specimens are fragments. All the specimens (10) from the upper Cedar District Formation are small size, whereas those from California are much larger. *Phygraea arida* co-occurs with *A. parasitica* in the Cedar District Formation at the "White House" site on western Denman Island, British Columbia, Canada.

Most specimens of *P. arida* were probably soft-sediment recliners, based on absence of any attachment scar. A small-sized, single left valve from the upper Cedar District Formation, however, is strongly cemented to an echinoid spine (Fig. 199).

The new species differs from *P. inornata* by having a much larger and heavier shell, well developed commissural shelf on many specimens, discernible "foamy" texture, orbicular shape on most specimens, stronger vermiculate chomata, no overhanging or twisted beaks, and no radial sulcus.

The new species is very similar to the *Pycnodonte (Pycnodonte) gigantica* (Solander, 1766:36, fig. 88). Solander's species was originally named *Ostrea gigantica* and was the type species of *Gigantostrea* Sacco (1897:14, pl. 4) from Eocene strata in Italy. The new species differs from *P. (P.) gigantica* by having a tongue-like flange extending centroposteriorly from the left valve. Stenzel (1971) equated *Gigantostrea* with *Pycnodonte (Pycnodonte)*, but his usage is not followed here.

ETYMOLOGY. The new species name is derived from *aridus* (Latin, dry), in reference to Laguna Seca (Spanish, dry lake) Creek.

PALEOGEOGRAPHY AND PALEOCLIMATE COMMENTS

The PSNA region makes up a large part of Kauffman's (1973:fig. 1) Cretaceous bivalve-based "Northeast Pacific Subprovince" of the "North Pacific Province," which was part of the "North Temperate Realm." A temperate realm for this area has been corroborated by faunal studies of a wide array of mollusk groups (Saul, 1986b; Kiel, 2002), including neritid and cypraeoidean gastropods (Squires et al., 2001), nerineid gastropods (Saul and Squires, 1998; Saul and Squires, 2002), volute gastropods (Saul and Squires, 2008), and opine bivalves (Squires and Saul, 2009). These studies provide ample evidence that the "Northeast Pacific Subprovince," in the area of this present report, experienced warm-temperate waters during much of the Late Cretaceous. In addition, *Coralliochama orcutti*, a warm-water rudist bivalve (Saul, 1986b), co-occurs with *A. parasitica* in four formations in PSNA: 1) Gualala Formation, Anchor Bay Member, Mendocino County (Elder et al., 1998); 2) Williams Formation, Pleasants Sandstone Member (LACMIP loc. 22415, Bee Canyon, Santa Ana Mountains, Orange County); 3) basal Point Loma Formation (vicinity of LACMIP loc. 17421, Carlsbad, San Diego County); and 4) Rosario Formation (LACMIP loc. 27263,

San Antonio del Mar, Baja California, Mexico). The warm-temperate *A. parasitica* is one of most common PSNA oysters of Campanian to Maastrichtian age and has the widest geographic range, from British Columbia to Northern Baja California. In Europe, *Amphidonte* is also a warm-temperate oyster and not reported from Tethyan (tropical) locales in that region (Aqrabawi, 1993).

None of the PSNA Late Cretaceous oyster genera are endemic to the "Northeast Pacific Subprovince." They are all widespread genera, and, using Kauffman's (1973:359) bivalve categories, *Rastellum* [= *Arctostrea*], *Crassostrea*, and *Pycnodonte* are "truly cosmopolitan forms." Although Stenzel (1971:N1107) reported the geographic distribution of *Pycnodonte* (*Pycnodonte*) to be worldwide, Hayami and Kase (1992:1076) noted that Cretaceous, as well as Paleogene, species of this oyster are known almost exclusively from low–middle latitudinal regions; namely, western Europe, Crimea, north and west Africa, south India, and Gulf Coast regions. The PSNA region can now be added to this list. *Phygraea* was widely distributed in both temperate and tropical (Tethyan) waters, and this oyster has diminished value for paleogeographic purposes (Aqrabawi, 1993).

BIODIVERSITY COMMENTS

During Late Cretaceous time, the world experienced greenhouse climate conditions, and the late Cenomanian and early Turonian interval coincided with the Cretaceous thermal maximum and highest sea levels. The Turonian-Coniacian turnover event, which coincided with a global drop in sea level, was a cool time that persisted during Coniacian time. Although there was a modest warming in early Santonian time, cool-water conditions returned during the late Santonian. During Campanian time, there were fluctuations in sea surface temperatures and sea level, but there was an overall warming trend and a sea level rise that culminated during early Maastrichtian time (Forster et al., 2007:fig. 2; Miller et al., 2011:fig. 4; Linnert et al., 2014:fig. 2).

The PSNA Late Cretaceous oyster fauna (Fig. 2) had a high biodiversity level (five species) during Turonian time. This was followed by a dramatic drop (zero species) during the Coniacian, a low level (one species) near the end of the Santonian, and a mostly gradual buildup during the Campanian. The highest biodiversity level (six species) occurred in the late early to early late Maastrichtian, followed by a continuing high level (five species) during the late Maastrichtian. This overall biodiversity pattern is very similar to that of Late Cretaceous neritid and cypraeoidean gastropods in the PSNA region (Squires et al., 2001).

A rigorous analysis of the causes of the observed biodiversity pattern in the PSNA Late Cretaceous oysters is beyond the scope of this paper. Some possible explanations include 1) global changes in ocean surface water temperatures, 2) global changes in sea level, 3) closure of seaways, 4) tectonic influences associated with the active plate margin that existed in the PSNA region, and 5) collecting/sampling artifacts. The available evidence is indicative, however, that warm surface waters during the Turonian, Campanian, and Maastrichtian would have favored the thermophilic oysters, and the accompanying high sea levels would have provided more habitats and the best potential for burial of the nearshore oysters. The abrupt drop of diversity at the end of the Turonian was most likely related to the influx of cooler waters. The cooler surface waters, reduced potential for habitats, and pervasive on-going erosion of nearshore deposits associated with the lower sea levels during the Coniacian and Santonian could have been responsible for the paucity of oyster taxa. The PSNA oyster species that originated during the Campanian went extinct at various times, thereby indicating more gradual and short-lived changes in temperature.

In the PSNA region, there was a reoccurrence of the warm-water Turonian *Curvostrea-Costagyra-Phygraea* association in the late early to early late Maastrichtian. This reoccurrence is very strongly indicative that warm temperature and high sea level were largely responsible for the highest diversities of PSNA oysters.

In his work on Late Cretaceous oysters in Jordan, Aqrabawi (1993) reported a biodiversity pattern similar to that of the PSNA region, in that there are no oyster taxa of Coniacian age and there is low biodiversity in the Santonian, in contrast to much higher biodiversity before and after these times. He also reported a similar pattern for Late Cretaceous oysters from northwest Europe. For both areas, he provided no evidence as to what caused the observed patterns, although he did mention, for northwest Europe, that transgressions and regressions were responsible.

CONCLUSIONS

During the course of revising the seven previously named oyster species from the warm-temperate Late Cretaceous "Northeast Pacific Subprovince," four new, one unnamed, and one questionable species were recognized, thereby resulting in a total of 13 species. All seven of the previously named species belong to genera different from those Gabb (1864) and Packard (1922) assigned. The revised identifications are: *Curvostrea crescentica* (Packard, 1922); *Acutostrea taxidonta* (Packard, 1922); *Crassostrea brewerii* (Gabb, 1864); *Costagyra californica* (Packard, 1922); *Amphidonte parasitica* (Gabb, 1864); *Pycnodonte* (*P.*) *malleiformis* (Gabb, 1864); and *Phygraea inornata* (Packard, 1922). The *Amphidonte parasitica* (Gabb) identification was recognized previously by Elder (1991) and is confirmed here. An unusual specimen of ?*Amphidonte parasitica* is mentioned and figured here because it might represent another species.

The four new species are *Oscillopha popenoei*, *Curvostrea baia*, *Costagyra garza*, and *Phygraea arida*. The one unnamed species is *Rastellum* sp., aff. *R. macropterum* (J.D.C. Sowerby, 1825). *Oscillopha popenoei* is the first known occurrence of this genus in North America, and *Rastellum* is the first known occurrence of this genus in the PSNA region.

Genera represented by a single species are *Oscillopha*, *Rastellum*, *Acutostrea*, *Crassostrea*, and *Pycnodonte* (*Pycnodonte*). Those represented by two species are *Curvostrea*, *Costagyra*, possibly *Amphidonte*, and *Phygraea*. All the oyster genera were globally widespread, and none were endemic to the PSNA region.

Amphidonte has the longest geologic range in the PSNA region, from early Campanian to questionably latest Maastrichtian. The species of *Oscillopha*, *Rastellum*, *Curvostrea*, *Acutostrea*, *Crassostrea*, *Costagyra*, and *Phygraea* were relatively short lived. *Phygraea inornata* is the most abundant Late Cretaceous PSNA oyster. *Crassostrea brewerii* is the largest species, with its thick and heavy large specimens, which were commonly bored by large specimens of the bivalve *Lithophaga*. The PSNA Turonian species of *Curvostrea*, *Costagyra*, and *Phygraea* are much smaller than their early Maastrichtian species.

Nearly every Late Cretaceous PSNA oyster species has several morphs, which are most likely ecophenotypic responses related to changes in the paleoenvironments or related to the presence or absence of an attachment scar. In the case of *A. taxidonta*, the outline of its shell is dependent on the size of the attachment scar. Trigonal specimens have a small attachment scar, spatulate specimens have a large attachment scar, and oval specimens have an even larger attachment scar. It is likely that the larger the size of the attachment scar, the more agitated the waters were that the specimens lived in. In the case of *P. inornata*, whether or not there was attachment to a foreign object directly affected the shape of the individuals. Other species (e.g., *Crassostrea brewerii*) might also be represented by ecophenotypes, but the number of

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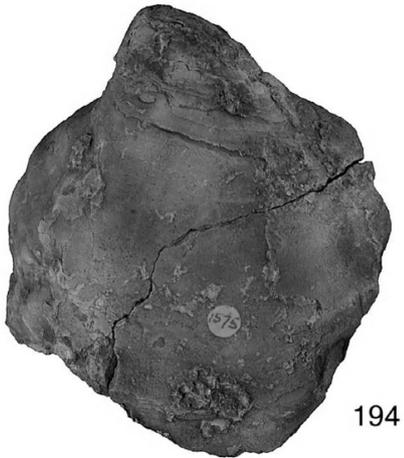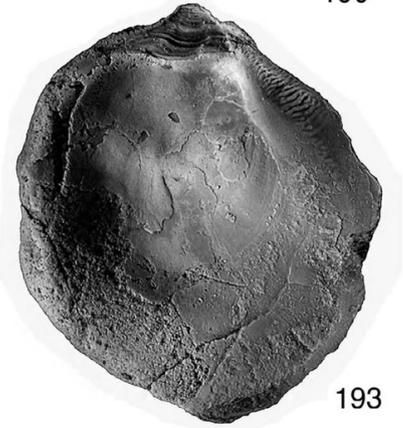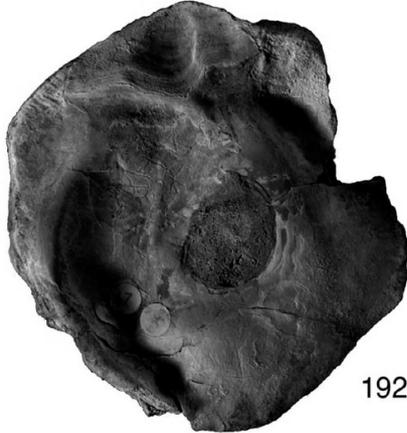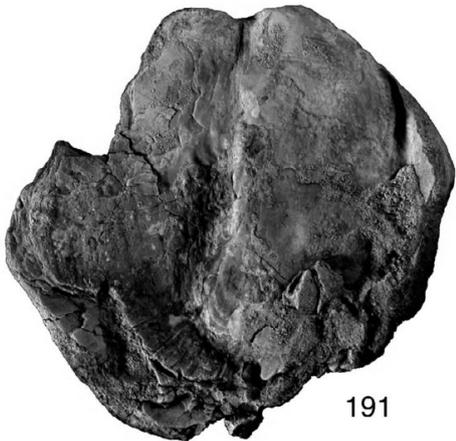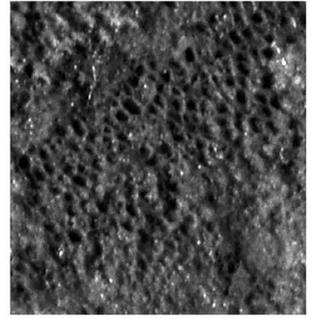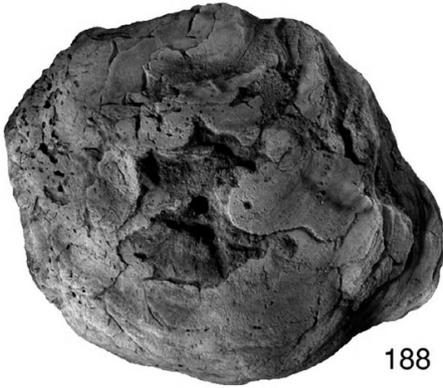
specimens is too low to confirm this. Xenomorphism was most commonly observed in valves of *Acutostrea taxidonta*. A growth series was detected for *A. parasitica*.

The highest biodiversity levels of PSNA oysters (five to six species), which occurred during warm-temperate times and high sea levels (Turonian and late early to early late Maastrichtian), stand in stark contrast to a much lower biodiversity level (either no species or only one) during cooler times (Coniacian and Santonian, respectively). In the PSNA region, there was a reoccurrence of the Turonian warm-water *Curvostrea-Costagyra-Phygraea* association during the warm-water times of the late early to early late Maastrichtian. The PSNA oyster biodiversity pattern needs further study, but the available evidence is strongly indicative that global fluctuations in surface water temperature and contemporaneous sea level changes were most likely the controlling forces.

ACKNOWLEDGMENTS

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Figures 188–199 *Phygraea arida* sp. nov., Moreno Formation [Area 11], unless otherwise noted. **188–190.** Holotype LACMIP 14639, LACMIP 10685, left valve, height 81.3 mm. **188.** Exterior, ×0.6. **189.** Interior, ×0.6. **190.** Close-up of vesicular shell microstructure, posteroventral edge of valve, height 18.5 mm, ×10. **191–192.** Paratype LACMIP 14640, LACMIP loc. 26349, right valve, height 83.8 mm, ×07. **191.** Exterior. **192.** Interior. **193.** Paratype RBCM.EH.2016.001.0001.001, upper Cedar District Formation [Area 1], right valve interior, height 30.6 mm, ×1.9. **194.** Paratype LACMIP 14641, LACMIP loc. 10677, right valve, height 90.3 mm, ×0.7. **195–196.** Paratype LACMIP 14642, LACMIP loc. 22588, partial right valve, height 80.4 mm, ×0.7. **195.** Exterior. **196.** Interior. **197–198.** Paratype RBCM.EH.2016.001.0002.001, upper Cedar District Formation [Area 1], right valve, height 12.3 mm, ×2.9. **197.** Exterior. **198.** Interior. **199.** Paratype RBCM.EH2016.002.0001.001, upper Cedar District Formation [Area 1], right valve attached to echinoid spine, valve height 27 mm, ×1.1.

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