ABSTRACT. Paleocene and Eocene oysters from the west coast of the United States, in the region extending from southwestern Washington to Southern California, are revised in terms of generic assignment, description, morphologic variability, geographic distribution, and biostratigraphy. Ecophenotypes and shell microstructures are described for the first time. The oysters lived in warm-temperate waters in environments that ranged from estuarine to offshore. Ten species, including four new species, are recognized: Acutostrea idriaensis (Gabb, 1869), Acutostrea griesensis (Effinger, 1938) comb. nov., Acutostrea gaviota sp. nov., Crassostrea tectonica sp. nov., Cubistreina californiana sp. nov., Gryphaeostrea avicusifornis (Anderson, 1905) comb. nov., Phygraea haleyi (Hertlein, 1933) comb. nov., Phygraea stewarti (Hanna, 1927) comb. nov., Phygraea badgeri sp. nov., and Phygraea lincolnensis (Weaver, 1916) comb. nov. Ostrea tayloriana Gabb, 1866 is determined to be a nomen dubium.

None of the oyster genera in the studied oyster fauna are endemic. Crassostrea, Cubistreina, Gryphaeostrea, and Phygraea sensu stricto are newly recognized, however, in Paleocene and/or Eocene strata of the study area. The closely timed extinctions of A. griesensis, A. gaviota, and P. lincolnensis coincided with arrival of cooler waters at the end of the Eocene.

The present-day positions of the Paleocene and Eocene oyster-bearing outcrops in coastal Southern California bear no resemblance to their original geographic position because of the effects of post-Paleogene clockwise tectonic rotation and northward translation over a few degrees of latitude.

INTRODUCTION

The Paleocene and Eocene oysters studied here are locally common in shallow-marine strata of the west coast of the United States, in a region extending from southwestern Washington to Southern California (Fig. 1). The original descriptions and illustrations of most of the previously named species are inadequate by moderate taxonomic standards because they rely on only the holotype and, rarely, a paratype. Some of the illustrations have poor resolution of critical details, like chomata, and there is no discussion of shell microstructure, which, as reported by Malchus (1990), is critical for classification purposes. Comments about variation in morphology, which is very common in oysters, are also wanted in most of the original descriptions by authors. Packard (1923) and Vokes (1935) commented subsequently, however, on the considerable variation in morphology of Ostrea idriaensis Gabb, 1869. Moore (1987) compiled the original descriptions, modified the nomenclature, and illustrated the previously named oyster species known to occur in California. The compilation included a review of Ostrea griesensis Effinger, 1938 and Ostrea lincolnensis Weaver, 1916, both of which are found only in Washington, but are included here.

The purposes of this present study are to provide 1) updated generic assignments, including recognition of genera new to the region, as well as new species; 2) better descriptions of the taxa, including, for the first time, shell-microstructure data; 3) improved illustration of diagnostic characters and species variability; 4) refinement of geologic ranges; and 5) better knowledge of stratigraphic and geographic distributions. Ancillary purposes are to provide 1) recognition, for the first time, of ecophenotypes; 2) reported depositional environments; 3) commentary on how tectonics affected the distribution of some species in Southern California; and 4) commentary on how the global cooling event at the end of the Eocene affected West Coast oysters. This study resulted in the recognition of some genera not previously known in the region, discovery of several new species, and the generic reassignment of some known species. These discoveries, as well as the revisions and refinements, allow for a more complete and accurate understanding of the diversity of the oyster fauna. It is a continuation of the work by Squires (2017) on Late Cretaceous oysters from this general region.

MATERIALS AND METHODS

The collection at the Natural History Museum of Los Angeles County, Invertebrate Paleontology (LACMIP) Department is the principal source of the studied material. In the last several decades, this collection has been augmented by the incorporation of other collections that used to be housed at Caltech (CIT), University of California at Los Angeles (UCLA), and California State University at Northridge (CSUN). Many of the specimens from the Santa Ynez Mountains were collected by W. Woodring and A. Clark and were originally part of the CIT collection. Nearly all of the Whitaker Peak area specimens were collected by Badger (1957) and were originally part of the UCLA collection. The photographed specimens used here of Acutostrea idriaensis from the Domengine Formation in the Vallecitos syncline area were originally part of the author’s personal collection and were donated, subsequent to this study, to the LACMIP collection.
being described. Shell-microstructure terms follow those as used by Jaitly et al. (2014). The term “mocret,” coined by Malchus (1990) and discussed by Vermeij (2014), refers to chalky deposits which can be found in the inner shell layers of some large-sized and thick-shelled oysters. Grain-size terms are from the following chart: https://pubs.usgs.gov/of/2006/1195/htmldocs/images/chart.pdf.

The term “ecophenotype” (= morphotype), which is used throughout this article, is a non-taxonomic term used for populations of organisms whose physical characteristics are subject to non-genetic adaptation to environmental conditions (Bayer et al., 1985); thus, each ecophenotype represents a specific environment. Ecophenotypic variation, which is very common in oysters, creates plasticity in shell forms, thereby causing much confusion in oyster taxonomy (Littlewood and Donovan, 1988). A single species can be represented by several ecophenotypes because of varying environmental conditions, which create morphological gradients. Intermediate forms between ecophenotypes are to be expected. Variations in the shapes of oysters represent adaptations to habitats ranging from estuarine to offshore marine, all of which are subject to changes in salinity, temperature, duration of subaerial exposure, growth space, rate of sedimentation (Haglund, 1998), changes in sediment grain size, water agitation, type of attachment to substrate, and growth stage (Machalski, 1988; Squires, 2017). In this present article, examples of each ecophenotype for each of the oyster species are illustrated in the accompanying figures, and labelled as such in the corresponding captions.

The provincial molluscan (gastropod) zones Echinophoria dalli Zone and Echinophoria fax Zone (Fig. 2) were proposed by Armentrout (1973) and formally described by Armentrout (1975). They are applicable to upper Eocene shallow-marine strata in Washington and Oregon.

The geologic ranges and occurrences in key formations of all the studied species are shown in Figure 2. Paleomagnetic studies summarized by Prothero (2001:fig. 2) were used to refine geologic ages of the following formations, listed in Figure 2 in ascending stratigraphic order: Domengine, Santiago, Coldwater, Cowlitz, Gaviota, Gries Ranch, lower Lincoln Creek, and lower Alegria. Paleomagnetic studies by Prothero (2009) were used to refine the geologic age of the Lookingglass Formation, and paleomagnetic studies by Prothero et al. (2009) were used to refine the geologic age of the Quimper Sandstone (Fig. 2) and the overlying Marrowstone Shale.

ABBREVIATIONS

CAS California Academy of Sciences, San Francisco, California
CIT California Institute of Technology, Pasadena, California (collections now housed at LACMIP)
CSUN California State University Northridge, Northridge, California (collections now housed at LACMIP; the number 40,000 is added to the old CSUN locality numbers)
LACMIP Natural History Museum of Los Angeles County, Invertebrate Paleontology Department, Los Angeles, California
MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
SDSNH San Diego Society of Natural History, San Diego, California
UCLA University of California Los Angeles, Los Angeles, California (collections now housed at LACMIP; the number 20,000 is added to the old UCLA locality numbers)
UCMP University of California Museum of Paleontology, Berkeley, California
UCR University of California, Riverside, California
UCSB University of California, Santa Barbara, California
UWBM University of Washington Burke Museum [¼ UW in older literature], Seattle, Washington

CITED LOCALITIES

Holotype localities are described in the “Systematics” for each new species. Locality information for other localities is given below in abbreviated format. Numbers in brackets refer to the “Area” numbers of Figure 1. Localities are listed in alphabetical order of institutions, in a north-to-south order of the “Areas.” More complete information can be accessed through the following website links:

LACMIP: https://nhm.org/site/research-collections/invertebrate-paleontology
SDNHM: www.sdnhm.org/science/paleontology/resources/collection-database
UCMP: http://ucmp.berkeley.edu

Domengine Formation, lower middle Eocene. [18] 66752.02. Santa Cruz Island, Santa Barbara County, Southern California, Pozo Formation, upper Paleocene.


Figure 2  Chronostratigraphic ranges of West Coast oyster Paleocene and Eocene species. Ages of epochs, chron (black = normal polarity, white = reversed polarity), nannofossil zones, and European standard stages from Gradstein et al. (2012). Boundaries of provincial West Coast molluscan stages (informal names in quotes) from Squires (2014:fig. 2). Age control of provincial stages and of associated gastropod zones Echinophoria dalli and Echinophoria fax was refined by paleomagnetic studies listed under “Materials and Methods.” Tick marks shown on “Species/ranges” correspond to presence of species in “Key stratigraphic units.”

Southern California, Llajas Formation, lower middle Eocene. [16]


SYSTEMATICS
Order Ostreida Férussac, 1822
Superfamily Ostreoidea Rafinesque, 1815
Family Ostreidae Rafinesque, 1815
Subfamily Crassotreinae Scarlato and Starobogatov, 1979
Tribe Crassostreini Scarlato and Starobogatov, 1979
Genus Acustorea Vialov, 1936

TYPE SPECIES. Ostrea acutirostris Nilsson, 1827, by original designation; late early Campanian, Sweden (Stenzel, 1971).

AGE AND DISTRIBUTION. Late Cretaceous (late early Campanian) to Oligocene (Stenzel, 1971). Widespread during the Late Cretaceous, including California and northern Baja California (Squires, 2017).

Acustorea idriaensis (Gabb, 1869)
Figures 3–42

Ostrea idriaensis Gabb, 1869:203, pl. 33, figs. 103b–d; pl. 34, figs. 103 [not 103a]; Arnold, 1907:pl. 9, fig. 2; Arnold, 1910:106, pl. 2, figs. 4, 5 (figs. repeated by Arnold and Anderson, 1910:70–71, pl. 24, figs. 4, 5); Hanna, 1927:276, pl. 30, fig. 1, fig. 2; pl. 31, figs. 3, 4; Stewart, 1930:126–127, pl. 8, fig. 3, pl. 17, fig. 1; Vokes, 1935:291–295, pl. 22, figs. 1–6 [not 7]; pl. 23, figs. 1–3 [not 4]; pl. 24, figs. 1–10; Turner, 1938:46, pl. 6, fig. 9; Vokes, 1939a:54; Weaver, 1942:78–79, pl. 15, fig. 5; Schenk and Keen, 1940:pl. 23, figs. 3, 4; Givens, 1974:44; Givens and Kennedy, 1979:tables 2, 4; Squires, 1984:45, fig. 101.

Ostrea fetkii Weaver, 1912:30, pl. 4, figs. 37, 39.
Ostrea columbiana Weaver and Palmer, 1922:13, pl. 8, figs. 15, 16.
Ostrea oregonensis Packard, 1923:4–6, pls. 1–4.
Ostrea cranadii Hanna, 1927:275–276, pl. 29, figs. 1, 2.
Ostrea n. sp.? Clark, 1938:693–694, pl. 1, fig. 23 [not figs. 16, 20].
Ostrea idriaensis Gabb var. fetkii Weaver. Vokes, 1939a:54–55, pl. 2, figs. 11, 13; Weaver, 1942:80, pl. 14, figs. 8, 10, 14, 15.
Ostrea cf. idriaensis var. fetkii Weaver. Durham, 1944:137 (unfig.).

Acustorea idriaensis fetkii (Weaver). Moore, 1987:C30–C31, pl. 32, figs. 4, 6; pl. 33, figs. 1–3, 8.

Acustorea idriaensis idriaensis (Gabb), Moore, 1987:C31–C32, pl. 13, figs. 2, 3; pl. 14, fig. 6; pl. 16, fig. 3, [not pl. 29, fig. 4]; Lindberg and Squires, 1990:579; Squires, 1999:18–19, figs. 27, 28.

Acustorea idriaensis? Squires et al., 1988:185, pl. 1, fig. 6.

Ostrea sp. Squires, 2008:fig. 39.

[Not] Acustorea idriaensis fetkii (Weaver). Moore, 1987:pl. 30, fig. 5 [= Plicatula oestriforbus Stanton, 1896:1038, pl. 63, figs. 5, 6 = Ostrea buwaldana Dickerson, 1914:127, pl. 9, fig. 4], (see Squires and Saul, 1997:293).

EMENDED DESCRIPTION. Shell size (left valve) up to 119 mm in height, 80 mm in length. Most valves less than 60-mm height. Conjoined valves up to 51 mm total thickness. Shape quite variable with four ecophenotypes: falcate, spatulate, trigonal, and subcircular. Inequivalved. Falcate valves commonly thin and lightweight; trigonal, and subcircular valves moderately thick and heavy. Left valve moderately convex to highly arched, especially umbo region, and up to 48 mm thick; right valve evenly convex to flarish, rarely concavo-convex, and up to 25 mm thick. Both valves with growth squamae, strong and irregular in spacing or very closely spaced and resembling lineations (especially on right valve). Radial ribs, if present, mainly on left valve and weak to moderately strong, narrow to broad, dichotomous or not, and mainly on ventral half of valve. Ribs commonly weak or absent on right valve and restricted to ventral margin. Attachment scar small to moderately large. Beak pointed to blunt, can be slightly overhanging, narrow to wide, straight or opisthochine, and, at some localities, strongly opisthochine. Beak can be obscured or obliterated by attachment scar. Resilifer groove small but well developed, straight or opisthochine, and can be partially obscured by attachment scar. Bourrelets small but well developed. Base of hinge straight with corners upturned rarely. Adductor muscle scar small size, reniform, and postero-ventrally located. Chomata present mainly on small-sized specimens. Catachomata (left valve) abundant and in narrow groove on both sides, near hinge. Anachomata (right valve) common and can be present from hinge to half-way toward ventral margin. Shell microstructure prismatic/foliated, in thin lenses becoming thicker toward shell interior.

LECTOTYPE. MCZ 15048 [designated by Stewart, 1930:127 = specimen shown in Gabb, 1869:pl. 33, fig. 103d], partial left valve, 56-mm height, 51-mm length; Domengine Formation, near New Idria, San Benito County, central California.

GEOLOGIC RANGE. Early Eocene to early late Eocene.

GEOGRAPHIC RANGE. Southwestern Washington to Southern California.
STRATIGRAPHIC DISTRIBUTION. LOWER EOCENE (“Cappy Stage”): Lookingglass Formation, Douglas County, near Glide, southwestern Oregon (Turner, 1938); Goler Formation, El Paso Mountains, Kern County, Northern California (Squires et al., 1988; Cox and McDougall, 1988); lower Juncal Formation, Elsmere Canyon, Los Angeles County, Southern California (Squires, 2008). UPPER LOWER EOCENE TO LOWER MIDDLE EOCENE (“Domengine Stage”): Domengine Formation, Coal Mine Canyon, Fresno County, Northern California (Vokes, 1939a; Roush, 1986; Domengine Formation, Griswold Canyon and near New Idria, both in Vallecitos syncline area, San Benito County, Northern California (Vokes, 1939a; Schuelein, 1993); Matilija Sandstone, Cañada de Los Sauces Creek at LACMIP loc. 7291, Santa Ynez Mountains, Santa Barbara County, Southern California (new occurrence); Matilija Sandstone north of Jalama Creek and west of Los Amoles Creek at loc. LACMIP loc. 7203, Santa Ynez Mountains, Santa Barbara County, Southern California (new occurrence); Matilija Sandstone at Matilija Hot Springs, Ventura County, Southern California (Squires, 1999); Matilija Sandstone at Beartrap Creek, vicinity of Pine Mountain, Ventura County, Southern California (Squires, 1991a); Llajas Formation, Ventura and Los Angeles counties, Southern California (Squires, 1984); upper Juncal Formation, Elsmere Canyon, Los Angeles County, Southern California (Squires, 2008); Delmar Formation, Solana State Beach near city of Delmar, and Torrey Pines State Reserve, San Diego County, Southern California (Givens and Kennedy, 1979); unnamed formation, southwestern side of San Nicolas Island at LACMIP loc. 25210, Ventura County, Southern California (new occurrence), MIDDLE EOCENE (“Transition Stage”): upper Matilija Sandstone, Matilija Hot Springs, Ventura County, Southern California (Squires and Demere, 1991); MIDDLE EOCENE (“Tejon Stage”): Markley Formation, near Winters, Solano County, Northern California (Clark, 1938). UPPER MIDDLE EOCENE: Cowlitz Formation, Vader area, Lewis County and Coal Creek, Cowlitz County, southwestern Washington (Nebbitt, 1995); Tejon Formation, Edmonston Pumping Plant, Kern County, Southern California (Addicott in Nilsen, 1987; Lindberg and Squires, 1990).

REMARKS. Six hundred and twenty specimens were examined. Specimens can occur attached to one another in small clusters. This species is widespread, and its above-listed stratigraphic occurrences are not exhaustive. Preservation is good to excellent. The best-preserved and most abundant specimens are from the Big Bend locality (Fig. 1, Area 4) in the Cowlitz Formation, and the smallest examined specimens (2.5-mm height) are also from this locality. This is the type locality area of “Ostrea” fettkei Weaver, 1912, a junior synonym of *A. idriaensis*. The photographs provided by Weaver (1912:pl. 4, figs. 37, 39) of the type specimens of *fettkei* are not the same ones that supposedly are his type specimens illustrated by Weaver (1942:pl. 14, figs. 8, 9) and by Moore (1987:pl. 33, figs. 1, 2). The exterior of hypotype UWBM 24950 [Weaver’s UW 265] of *fettkei* is illustrated here for the time (Fig. 3). Weaver (1942:pl. 14, fig. 15) illustrated the interior of this specimen, but he erroneously referred to it as a “paratype.”

*Acutostrea idriaensis* is abundant in the Delmar Formation. At LACMIP loc. 199 in this formation, two of ecophenotypes are present. Most are falcate (Figs. 6, 9, 10), but some are subcircular (Figs. 25, 26). At LACMIP loc. 4899 in this same formation, conjoined specimens of the subcircular ecophenotype (Figs. 27–28) are present, as well as intermediates between trigonal and spatulate ecophenotypes (Figs. 30, 31).

*Acutostrea idriaensis* is also abundant in the Domengine Formation. At LACMIP loc. 41295 in the Vallecitos syncline area (Area 9), falcate (Figs. 18, 19, and 22–24 = a conjoined-valved specimen), trigonal (Figs. 32–33), and spatulate (Figs. 34–35) ecophenotypes are present. The largest specimens reported for this species are approximately 12 cm in height and are from the lower Eocene Lookingglass Formation in southwestern Oregon (Packard, 1923:table 1). Some of falcate specimens are gryphaeoid-like because the shell has a very strongly directed (posteriorly) opisthocline beak (Fig. 14), as well as a corresponding broad, shallow resilifer area (Fig. 15). Similar-looking specimens, from the middle Eocene Domengine Formation in the Vallecitos syncline area, central California, were illustrated by Vokes (1935:pl. 22, fig. 1; pl. 23, fig. 1). Many of the examined Lookingglass Formation specimens have been extensively micro-bored, and the boreholes are filled with sediment.

Large specimens of the falcate ecophenotype of *A. idriaensis* are found locally in the Cowlitz Formation at Coal Creek (Fig. 1, Area 5). A representative specimen (Figs. 16, 17) is 10.7 cm in height, but the valves are thin (6 mm on the umbalonic area and only 1 mm near the venter). Other similar-size Cowlitz specimens can have a strong opisthocline bending of the resilifer area and a flat or concavo-convex right valve.

Moore (1987) was the first to correctly identify *O. idriaensis* as *Acutostrea idriaensis*. She also provided a useful synonymy of this species but incorrectly, like Vokes (1939a), believed “Ostrea” haleyi Herzlet, 1933 to be a junior synonym of *A. idriaensis*.

Slodkewitsch (1938:106, pl. 13, figs. 4, 5; pl. 14, figs. 3a, 3b) and Devyatilova and Volobueva (1981:57, pl. 5, fig. 3) reported *Ostrea idriaensis* from Eocene strata in western Kamchatka, Russian Far East. These reports cannot be documented because the descriptions are inadequate and no interior views are illustrated. There are other Eocene oyster species, as well as Oligocene ones, from various formations in western Kamchatka (e.g., Slodkewitsch, 1938) and from the Aleutian Islands and coastal area of mainland Alaska (e.g., MacNeil, 1967:40).

*Acutostrea griesensis* (Effinger, 1938) comb. nov.

*Ostrea lincolnensis* Dickerson, 1917:160, pl. 28, fig. 1.

*Ostrea griesensis* Effinger, 1938:368, pl. 45, figs. 1, 8; Weaver, 1942:51, pl. 15, figs. 1, 2.

EMENDED DESCRIPTION. Shell size (right valve) up to 126 mm in height, 104 mm in length (same specimen). Shape variable with two ecophenotypes: falcate and trigonal. Inequivalved. Prominent flexure (sulcus) common on medial posterior shell margin of spatulate valves. Both valves lightweight. Left valve up to 11 mm thick. Right valve up to 5 mm thick. Falcate ecophenotype generally flattish (rarely strongly flexed); margins (especially anterior margins) can be vertical. Trigonal-shaped left valve inflated. Valve exterior irregular, wavy, and can be roughly lamellose with growth squamae; rarely smooth. Attachment scar not obvious, but some left valves can be completely cemented to hardground. Radial ribs absent. Beak pointed and straight to somewhat rounded on trigonal ecophenotype. Resilifer area best developed on juvenile trigonal ecophenotype and also on rare adults. Adult resilifer groove less obvious, wider, longer, and flatter. Rare, large-size trigonal ecophenotype individuals with groove height slightly less than body cavity height, and body cavity slowly bent relative to hinge. Base of hinge straight, without upturned corners. Right-valve hinge subduded, commonly not “tooth-like.” Adductor muscle scar large, reniform, and postero-ventrally located. Chomata can be absent. Catchomata (left valve), if present, occur as approximately 12 short depressions in narrow groove on posterior margin only near hinge. Anachomata (right valve), if present, occur as eight or so short denticles on posterior margin near hinge; denticles more widely...
spaced than corresponding chomata. Shell microstructure consisting of thin prismatic and foliated layers.

**HOLOTYPE.** UCMP 33510 (Fig. 46), left valve, 92-mm height, 60-mm length, 15 mm thick; Gries Ranch Formation, UCMP loc. 3607 (Gries Ranch) [= LACMIP loc. 10037], Lewis County, southwestern Washington. The holotype is completely cemented to a complete right valve of this same species.

**PARATYPE.** UCMP 33511 (Fig. 55), Gries Ranch Formation.

**GEOLOGIC RANGE.** Late Eocene.

**GEOGRAPHIC RANGE.** Southwestern Washington.

**STRATIGRAPHIC DISTRIBUTION.** UPPER EOCENE (Galvanian Stage: Echinophoria dalli Zone): Gries Ranch Formation, southwestern Washington (Effinger, 1938; Weaver, 1942).

**REMARKS.** Seventeen specimens were examined, and 11 are figured here. All but one are from the type locality. Specimens can occur in clusters, with two or three specimens entirely attached to one another. Preservation is good. *Acostrea griesensis* differs from *A. idriaensis* by having flatter valves, no subcircular shape, presence of prominent flexure (sulcus) on medial posterior shell margin of some spatulate forms, absence of radial ribs, only slightly curved or straight beaks, wider and less prominent hinge (on both valves), wider and shallower ligamental groove, much weaker bourrelets, no lateral projections, and absence of noticeable attachment scar on the beak area.

**Acostrea gaviota** sp. nov.

Figures 62–79

*Ostrea* n. sp.? Clark and Anderson, 1938:946, pl. 1, figs. 1, 9; pl. 2, fig. 5. *Ostrea* *tayloriana* Gabb, 1866. Weaver and Kleinpell, 1963:197, pl. 29, figs. 6, 8.

**DIAGNOSIS.** Shell size medium to large. Strongly inequivalved. Prominent flexure (sulcus) can be present on medial posterior shell margin of trivalve valves. Left valve moderately thick to thick, lightweight or heavy. Right valve thinner and moderately convex to flat. Radial ribs moderately abundant and can be both convex and concave. Resilifer groove short, with small bourrelets; base of hinge straight to slightly sinuous. Chomata moderately common and mainly indistinct. Adductor muscle scar reniform, somewhat postero-ventrally located.

**DESCRIPTION.** Shell size (left valve) up to 144.7 mm in height, 110.6 mm in length. Conjoined valves up to 68.7 mm total thickness. Shape variable with two ecophenotypes: trivalve and spatulate. Inequivalved. Prominent flexure (sulcus) can be present on medial posterior shell margin of spatulate and trivalve valves. Left valve normally moderately strongly convex and moderately thick (up to 24 mm). Right valve flat and relatively thin (up to 8.5 mm) and much thinner than accompanying left valve. Left valve with radial ribs common, few to many, narrow to broad, closely to widely spaced, and straight or dichotomous. Attachment scar can be either not obvious or can cover up to approximately 50% of left valve. Beak moderately straight or rounded. Resilifer groove short, straight, with weak or strong bourrelets. Base of hinge straight or, on some specimens, with upturned corners. Left-valve dorso-posterior interior margin can be flattened and wide. Adductor muscle scar reniform, postero-ventrally located or near center. Chomata rare, near hinge, and occur mainly as relics. Shell microstructure prismatic and foliated, with well differentiated lenses; thickest lenses near center of valves.

**HOLOTYPE.** LACMIP 14681 (Figs. 67–69), valves originally conjoined (total thickness 29.5 mm) but separated during cleaning process: left valve 129.2-mm height, length 107.8 mm, 17.5 mm thick; right valve 119.7-mm height, 100.9-mm length, 12 mm thick; LACMIP loc. 7289 [Area 12], upper Cuarta Canyon and next canyon west, stratigraphically highest oyster bed in Gaviota Formation in this area, 100 m stratigraphically below Vaqueros Formation, Santa Ynez Mountains; approximately lat. 34°29’30”N, long. 120°17’30”W, United States Geological Survey Sacate Quadrangle (7.5 minute), 1953, Santa Barbara County, Southern California.

**GEOLOGIC RANGE.** Late Eocene.

**GEOGRAPHIC RANGE.** Wheatland, Yuba County, Northern California and Santa Ynez Mountains, Santa Barbara County, Southern California.

**STRATIGRAPHIC DISTRIBUTION.** UPPER EOCENE (Galvanian Stage): Wheatland Formation, just north of Wheatland, Yuba County, Northern California (Clark and Anderson, 1938); Gaviota Formation, Santa Ynez Mountains, Santa Barbara County, Southern California (Dibblee, 1950, 1966 [probably as *Ostrea* *tayloriana*] and Weaver and Kleinpell (1963) [as *Ostrea* *tayloriana*]: lowermost Alegria Formation, Santa Ynez Mountains, Santa Barbara County Southern California (Dibble, 1950, 1966 [probably as *Ostrea* *tayloriannai*]).

**REMARKS.** Thirty-seven specimens were examined. Preservation is generally good. Many specimens have been weathered, and the radial ribs and attachment scar can be obscured to indistinct. The new species is most similar to *Crassostrea tectonica* sp. nov. (described below) but differs by having a smaller maximum size, more inequivalved shell, thinner to much thinner left valve, much thinner right valve, less convex right valve, much more common and more prominent radial ribs, attachment scar, sinus can be present on posterior medial part of both valves, much more abundant chomata (mostly indistinct), shorter ligamental groove, and no odontogyr-phase ecophenotype.

The new species differs from *A. griesensis* by having larger maximum size, thicker and heavier valves, more inflated left valve, radial ribs, much better development of resilifer groove, more sinuous base of resilifer groove, and much more prominent chomata.

The new species differs from *A. idriaensis* by having much larger maximum size, thicker and heavier valves, wider valves, more inflated left valve, mostly ovate (rarely falcate) and never subcircular, more
closely spaced radial ribs; attachment scar can be large, chomata are rare and only near hinge.

**ETYMOLOGY.** The new species name is derived from “gaviota” (Spanish, meaning “seagull”), in reference to the Gaviota Formation, where nearly all of the specimens were found.

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 Late Cretaceous, including California (Squires, 2017). *Crassostrea* is represented also by several species, some of them of very large size, in upper Oligocene, Miocene, and Pliocene deposits of California and Baja California, Mexico (Moore, 1987). The new species described and named here is the first Eocene report of *Crassostrea* in the West Coast region. This genus was overlooked previously in this region most likely because of inadequate description, poor illustrations, and overuse of the default name “*Ostrea tayloriana*” for large-sized oysters.

*Crassostrea tectonica* sp. nov.

Figures 80–111

*Ostrea idriaensis* Gabb, 1869:pl. 34, fig. 103a; Vokes, 1935:pl. 22, fig. 7; pl. 23, fig. 4.


*Acutostra idriaensis idriaensis* (Gabb). Moore, 1987:pl. 29, fig. 4.


*Steirostra* *tayloriana* (Gabb). Squires, 1994:table 4, pl. 3, fig. 1.

**DIAGNOSIS.** Shell size medium to large. Shape can be odontogryphaeate. Valves inflated, thick and heavy, especially left valve. Radial ribs rare and weak. Terebratuloid folds rare but strong. Flattened ventral surfaces of valves can be present. Resilifer groove short to long, with strong bourrelets, and, on some specimens, annular growth rings; base of hinge commonly curved with upturned corners. Chomata rare and mainly indistinct. Adductor muscle scar subcircular to subreniform; subcentral (slightly ventral).

**DESCRIPTION.** Shell size (left valve) up to 170 mm in height, 100 mm in length. Conjoined valves up to 70 mm total thickness. Shape variable with three ecophenotypes: falcate, trigonal, and odontogryphaeate. Subequivalved, or nearly equivalved; with the latter very rare. Left valve normally moderately strong convex and moderately thick to very thick (up to 60 mm). Right valve flat and moderately thick to thick (up to 34 mm), normally thinner than accompanying left valve but, rarely, can be same size. Both valves can have prominent dorso-posterior sulcus, wider on left valve. Right valve anterior side rarely sulcate. Exterior of valves smoothish, with lamellose and closely spaced irregular growth squamae. Radial ribs rare, weak, narrow, straight, closely to widely spaced, and mainly on ventral half of left valve. Terebratuloid fold can be present only on ventral area of both valves of odontogryphaeate phenotype; folds reciprocal (right valve ventral area reflected upward to fit into the arched area on corresponding left valve, and convex fold of left valve fitting into convave fold on corresponding right valve). Attachment scar not obvious. Beak moderately straight or rounded. Resilifer groove long, curved, or straight, strong bourrelets, and, on some specimens, with prominent annular growth layers. Base of hinge curved slightly and with upturned corners. Left-valve dorso-posterior interior margin can be flattened and wide. Adductor muscle scar subcircular to subreniform, subcentral (slightly ventral). Chomata very rare, near hinge, and occur mainly as relics. Shell microstructure prismatic and foliated, with well differentiated lenses; thickest lenses near center of valves.

**AGE AND DISTRIBUTION.** Middle Jurassic to Holocene and widespread during the Late Cretaceous, including California (Squires, 2017). This species is represented also by several species, some of them of very large size, in upper Oligocene, Miocene, and Pliocene deposits of California and Baja California, Mexico (Moore, 1987). The new species described and named here is the first Eocene report of *Crassostrea* in the West Coast region. This genus was overlooked previously in this region most likely because of inadequate description, poor illustrations, and overuse of the default name “*Ostrea tayloriana*” for large-sized oysters.

**HOLOTYPE.** LACMIP 14687 (Figs. 80–84), conjoined valves (total thickness 59.5 mm), but now separated: left valve 120-mm height, 88.4-mm length, 34 mm thick; right valve 109.2-mm height, 90.9-mm length, 25.5 mm thick; LACMIP loc. 40028 [= CSUN loc. 28] (see Squires, 1987:fig. 132) [Area 13], upper Matilija Sandstone; east of Blue Point Campground, Whitaker Peak area; lat. 34°31’38.98”N, lon. 118°44’53.25”W, at elevation 445 m (1460 ft.) on east side of small tributary to Piru Creek, SE ¼ of SE ¼ of section 10, T 5 S, R 18 W, United States Geological Survey Whitaker Peak Quadrangle (7.5 minute ), 1958, Los Angeles County, Southern California.

**PARATYPES.** LACMIP 14689 (formerly hypotype LACMIP 7515), valves conjoined; upper Matilija Sandstone; LACMIP 14699, Coldwater Formation.

**GEOLOGIC RANGE.** Middle Eocene.

**GEOGRAPHIC RANGE.** Central to Southern California.

**STRATIGRAPHIC DISTRIBUTION.** LOWER MIDDLE EO- CENE (“Domengine Stage”): Domengine Formation, Valleccitos Syncline, San Benito County, central California (Vokes, 1935), (“Tejon Stage”): Matilija Sandstone, upper Jalama Creek at LACMIP loc. 7203, Santa Barbara County, Southern California; upper Matilija Sandstone, Whitaker Peak area (between Piru Creek and Canton Canyon), Los Angeles County, Southern California (Squires, 1977; Squires, 1987).

UPPER MIDDLE EOCENE (“Tejon Stage”): Coldwater Formation, upper Sespe Creek, Ventura County, Southern California (Badger, 1957; Squires, 1994); Santiago Formation, probably upper part, Camp Pendleton Marine Corps Base (probably southwestern part), north San Diego County, Southern California.

**REMARKS.** One hundred and three specimens were examined. Preservation is good to excellent. Valves of *C. tectonica* rarely show chomata on their interior marginal edges. Relict chomata can be found on the sides of some unweathered valves, but, normally, the relict chomata are obscured by weathering. Also, no mocret was observed. All of the large and thick specimens were found directly on the surface of the ground and exposed to the effects of weathering, which would have obliterated any traces of mocret if it were originally present.

The largest specimens (17-cm height) of this species are in the Coldwater Formation. The examined specimens include clusters of several specimens in the upper Matilija Sandstone; at Whitaker Peak, Santiago Formation at Camp Pendleton, and in the Coldwater Formation in upper Sespe Creek. At UCMIP loc. A-1018 in the Domengine Formation, the new species co-occurs with *Acutostra idriaensis*, but the new species is uncommon in this formation.

A large fragment (90-mm height) of *C. tectonica* found at LACMIP loc. 40364 in the Whitaker Peak area has a long and wide ligamentary area and a thick (25-mm), massive shell with well-developed prismatic microstructure. This specimen was figured by Squires (1987:59, fig. 99), who reported it as having been collected from lower Eocene Juncal Formation. Locality 40364 is immediately adjacent to a fault (see Squires, 1987:fig. 133), and it is likely that the beds at this locality are part of a fault slier containing upper Matilija Sandstone? strata, rather than the Juncal Formation.

The odontogryphaeate ecophenotype is mostly found in the Coldwater Formation. Rare specimens of smaller-sized individuals (e.g., Figs. 105–106), which are gradational between the trigonal and odontogryphaeate ecophenotypes, occur in the upper Matilija Sandstone; in the Whitaker Peak area. The best developed specimens are in the Coldwater Formation, and the best one of these (Figs. 107–111) is extraordinary in that it resembles a giant-sized (120-mm height, 110-mm length, and 65-mm thickness of both valves combined) version of the late Paleocene to Eocene oyster *Odontogryphaea thirsae* (Gabb, 1861) from the Gulf Coast of the United States. Compared to *O. thirsae*, *C. tectonica* differs by having a much larger much size, no sharp beaks, an asymmetry to the
folds (i.e., they do not “line up”), and an absence of numerous chomata in a groove along both margins of both valves. The resemblance to *O. thyrat* is possibly because of homeomorphosis, and, as discussed under “Comments About Depositional Environments,” there is a commonality of the functional morphology of this shape in both of these oysters.

Odontotrephaeaceae specimens of *C. tectonica* somewhat resemble genus *Flemingostrea* Vredenburg, 1916, whose type species has a broadly folded valve commissure with a convex fold on the ventral part of left valve and a corresponding convave one on the ventral part of the right valve. The teretabuloid folds on *Flemingostrea* commonly develop only on mature specimens, and the strength of the folds varies from not obvious, to weak/broad, or to strong (Stenzel, 1971). The odontotrepheaceae ecophenotype of *C. tectonica* differs from *Flemingostrea* by having an arched shell rather than a flattish one, as well as much more strongly developed and much better delimited terebratuloid folds.

*C. tectonica* is somewhat similar to *Crasostrea* sp. Toulmin (1977:187, pl. 14, figs. 5, 6; pl. 15, figs. 1, 2) from the Tuscaloosa Sand (Greggs Landing Marl Member), of early Eocene age in Alabama. Like *C. tectonica*, *C. sp.* Toulmin is large (up to 200-mm height), has thick valves a prominent resilifer groove, and a horizontally expansile shell margin. Toulmin’s figure 2 shows many small chomata on the interior marginal edges near the hinge and extending toward the middle part of the posterior margin of the right valve. *Crasotella tectonica* differs by having valves lesser in height (only up to 170-mm height), no sinuosity in shell outline, and lack of a long spatulate, weakly falcate shape.

*Crasostrea tectonica* is also similar to *Crasostrea contracta* (Conrad, 1856), illustrated by Harris (1919:pl. 4, sole fig.) and of probable late Eocene age from southern Texas. In addition to sharing the large, massive shells of these species, *Crasostrea tectonica* has also a very similar long and well-developed ligamental groove with prominent bourrelets.

The new species differs by having a smaller shell size, narrower ligamental groove, and less development of valve flattening ventrally.

Two large specimens (height 200 mm) of *Ostrea sp.* cf. *O. contracta amichel* Gardner, 1945, which were found by Morales-Ortega et al. (2016:11–12, fig. 3,5–3,6) in the Eocene Bateque Formation in Baja California Sur, Mexico, might belong to *Crasostrea*, but more specimens and more study are needed to confirm this assertion. They differ from *C. tectonica* by having a much wider hinge, a much wider ligamental groove, straighter lateral margins, and a smaller muscle scar.

**ETYMOLOGY.** The new species name is derived from *tectonikos* (Greek, meaning “tectonic”), in reference to the tectonic rotation and translation that the Southern California outcrops containing the specimens have undergone.

**Genus Crasostrea** Sacco, 1897

**TYPE SPECIES.** *Ostrea cubitus* Deshayes, 1832, by original designation; late Eocene, France.

**AGE AND DISTRIBUTION.** Late Cretaceous (late Maastrichtian) to late Miocene; widespread in Paleogene rocks of North America, Europe, and South America; with the earliest and latest records in Argentina, South America (Griffin et al., 2015). The new species described and named here is the second occurrence of this genus along the west coast of North America. Squires and Dementron (1990, 1992) reported an Eocene species in Baja California Sur, Mexico.

**Crasostrea contracta** Squires, 1984:fig. 17) [Area 16], Llajas Formation, approximately 55 m stratigraphically below the “Stewart bed,” near head of and north side of Blind Canyon, north side of Simi Valley; lat. 34°18’46.9″N, long. 118°38’28.0″W, at elevation 791 m (2275 ft.), east side of section 27 (projected), T 3 N, R 17 W, United States Geological Survey, Santa Susana Quadrangle (7.5 minute), 1951 (photo revised 1969), Los Angeles County, Southern California.

**PARATYPES.** LACMIP 14700 (Figs. 112–113), left valve, 15.8-mm height, 10.3-mm length, 1.5 mm thick; LACMIP loc. 40485 (see Squires, 1984:fig. 17) [Area 16], Llajas Formation, approximately 55 m stratigraphically below the “Stewart bed,” near head of and north side of Blind Canyon, north side of Simi Valley; lat. 34°18’46.9″N, long. 118°38’28.0″W, at elevation 791 m (2275 ft.), east side of section 27 (projected), T 3 N, R 17 W, United States Geological Survey, Santa Susana Quadrangle (7.5 minute), 1951 (photo revised 1969), Los Angeles County, Southern California.

**HOLOTYPE.** LACMIP 14700, left valve, 15.8-mm height, 10.3-mm length, 1.5 mm thick; LACMIP loc. 40485 (see Squires, 1984:fig. 17). HEAD OF BLIND CANYON, north side of Simi Valley; lat. 34°18’46.9″N, long. 118°38’28.0″W, at elevation 791 m (2275 ft.), east side of section 27 (projected), T 3 N, R 17 W, United States Geological Survey, Santa Susana Quadrangle (7.5 minute), 1951 (photo revised 1969), Los Angeles County, Southern California.

**GEOLOGIC AGE.** Late early Eocene.

**GEOGRAPHIC RANGE.** Simi Valley to San Diego, Southern California.

**STRATIGRAPHIC DISTRIBUTION.** UPPPER LOWER EO- CENCE (“Dominge Stage”): Llajas Formation, north side of Blind Canyon, north side Simi Valley, Los Angeles County, Southern California; Ardath Shale, near mouth of San Clemente Canyon, San Diego area, San Diego County, Southern California.

**REMARKS.** The examined material consisted of 13 specimens: five, including the holotype, from a shallow-marine bed in the Llajas Formation, and eight from a bed in the Ardath Shale, San Diego area. Preservation is good to excellent, but many of the Ardath Shale specimens are broken. The Llajas Formation specimens are all small (less than 16.5-mm height). The San Diego area specimens are larger (up to 83.5-mm height), except for one juvenile (11-mm height). Two of the San Diego area specimens are small left valves, which are attached to the interior of a larger specimen. Two other San Diego area specimens are large fragments cemented together. All the specimens are well preserved in terms of their hinge and sculpture. A brachitellum is preserved only on an immature specimen of a left valve attached to the posterior margin of the interior of a mature right valve (Fig. 122).
The only other known occurrence of *Cubitostrea* in the Paleogene record of the West Coast is *Cubitostrea mezquitalensis* Squires and Demetrion, 1990 from the middle Eocene part of the Bateque Formation, Baja California Sur, Mexico. The new species differs from *C. mezquitalensis* by having much smaller size, flat valves, much weaker radial ribs, much less plicate valve margins, trigonal shape rather than crescentic to recurved, and much more weakly developed and fewer chomata.

*Cubitostrea californiana* resembles *Cubitostrea sanctiaugustini* Stenzel and Twining in Stenzel et al. (1957:91–95, pl. 10, figs. 1–7) and several species of *Cubitostrea* illustrated by Toumlin (1977:248–250, pls. 35–36) from middle Eocene strata in Texas and Alabama, respectively, but the new species differs by having much less curved valves, a tendency to have narrower and non-imbricating radial ribs, and flat valves (especially the right valve).

**ETYMOLOGY.** The new species is named for California.

Subfamily Crassotreinae Scarlato & Starobogatov, 1979
Genus indeterminate  
*Ostrea tayloriana* Gabb, 1866 *nomen dubium*

*Ostrea tayloriana* Gabb, 1866:34, pl. 12, figs. 60, 60a; Heilprin, 1884:313, pl. 67, figs. 1, 2.

*Striostrea tayloriana* (Gabb). Moore, 1987:C33, pl. 29, figs. 7, 8.

Not *Ostrea* tayloriana King, 1848, preoccupied. Not *Ostrea tayloriana* Jordan and Hertlein, 1926:428, pl. 33, fig. 3, preoccupied [= *Ostrea erici* Hertlein, 1929].

**HOLOTYPE.** UCMP 12005, San Marco Pass region, near Santa Barbara, Santa Ynez Mountains, Santa Barbara County, Southern California.

**REMARKS.** The name “*Ostrea tayloriana*” was used indiscriminately by Dibblee (1950, 1966) and Weaver and Kleinpell (1963) for any large-sized, late Eocene to early Oligocene oyster in the Gaviota and Alegría formations in the Santa Ynez Mountains, Southern California. Its holotype is a tightly cemented, paired-valved specimen with crassotreine-like layering of the sides of the valves. What is known about the exterior morphology of this specimen is not unique, and Gabb’s description is not adequate. The specimen could belong to any one of a number of crassotreine medium-sized oysters of Cenozoic age. “*Ostrea tayloriana*” is deemed here to be a *nomen dubium* because it represents a taxon that is not identifiable from the original description or from the type material. Also, there is no way to determine the location of its type locality.

Family Gryphaeidae Vialov, 1936  
Subfamily Gryphaeostreinae Stenzel, 1971  
Genus *Gryphaeostrea* Conrad, 1865

**TYPE SPECIES.** *Gryphaea evera* Melleville, 1843, by monotypy, late Paleocene (Thanetian), Paris Basin, France.

**AGE AND DISTRIBUTION.** Early Cretaceous (Albian) to Miocene; widespread, especially during the Cretaceous (Stenzel, 1971). The species mentioned below is one of two occurrences of this genus along the west coast of North America. Morales-Ortega et al. (2016) reported an Eocene species from Baja California Sur, Mexico.

*Gryphaeostrea aviculiformis* (Anderson, 1905)  
Figures 129–136

*Ostrea aviculiformis* Anderson, 1905:166, 194–195, pl. 13, figs. 3–5; [questionably Arnold, 1910:50, pl. 2, fig. 12; fig. repeated by Arnold and Anderson, 1910:pl. 24, fig. 12]; Vokes, 1939a:55.

**EMENDED DESCRIPTION.** Shell small size (see “Holotype” below). Overall shape oblique, with left valve auricular dorsally and quadrate/irregular ventrally; right valve ovate. Strongly inequivalved, with left valve much larger than right valve. Valves thin. Left valve with fine growth squamae; right valve with thin, prominently raised, and widely spaced (regularly about 3 mm apart on ventral half of valve) commarginal ribs. Left valve convex and somewhat elongate, with beak pointed and overhanging, umbo considerably inflated, and posterior side of left valve with broad radial sulcus extending from beak to ventral margin of valve. Right valve operculiform and flatish but can be concave. Attachment scar not obvious. Resilifer groove short and wide; bourrelets weak, with best development along base of hinge line; posterior bourrelet stronger and more arched than anterior one; resilifer opisthogryate; base of hinge sinuous. Chomata absent. Shell microstructure of left valve recrystallized; commarginal ribs on right valve with well developed, prismatic microstructure.

**HOLOTYPE.** CAS 66747.01 [= old CAS no. 21] (Figs. 129–134, 135–136), both valves originally complete (height 27 mm) and conjoined; valves now separated and each consisting of only a fragment: left valve now 14 mm in height, 25.4 mm in length, 0.6 mm thick; right valve height now 9.5 mm in height, 12.7 mm in length, 2 mm thick; CAS loc. 66747 (see “Remarks” below), Domengine Formation, Alcalde Hills, just west of Coalinga, central California.

**GEOLOGIC AGE.** Early middle Eocene.

**GEOGRAPHIC OCCURRENCE.** Type locality only.

**STRATIGRAPHIC OCCURRENCE.** LOWER MIDDLE EOCENE: Domengine Formation, Alcalde Hills, west of Coalinga, Fresno County, central California.

**REMARKS.** This species is based entirely on its holotype, which was badly damaged after the earthquake-caused San Francisco fire in 1906 (Vokes, 1939a). Anderson’s (1905) original figures of this holotype are refuged here (Figs. 129–131). Only two fragments were saved, and, according to the label in the holotype box, Anderson “selected” them in 1921. They are the dorsal part of the left valve (Figs. 132–134) and presumably the ventral half of the right valve (Figs. 135–136). According to the label in the holotype box, however, it is not certain that the “selected” right valve is the actual right valve of the holotype. In addition, the “selected” right valve has more compressed raised oval-shaped commarginal ribs. These raised commarginal ribs are, nevertheless, diagnostic of a right valve of *Gryphaeostrea*. The rock matrix surrounding the holotype is fine-grained sandstone.

The type locality is in the NW ¼ of section 35, T 20 S, R 14 E (Anderson, 1905), which corresponds to the United States Geological Survey Alcalde Hills Quadrangle (7.5 minute), 1969, Fresno County, central California. The type-locality area is 1.6 km (1 mi.) south of Coalmine Canyon, where a useful stratigraphic section of the coal-bearing Domengine Formation is exposed (Roush, 1986). Anderson (1905) reported *O. aviculiformis* from the “Avenal Sands” at the type locality, but the “Avenal Sands,” now referred to as the Avenal Sandstone, crop out south of the Coalinga area (Kappeler et al., 1984).

The right valve of *Gryphaeostrea sanjuanicus* Morales-Ortega et al. (2016:11, fig. 3.3–3.4, fig. 4.1–4.5), from lower and upper middle Eocene strata in the Bateque Formation in Baja California Sur, Mexico, is similar to the right valve of *G. aviculiformis*. The limited and broken material available of *G. aviculiformis* and the absence of illustrations for the left valve of *G. sanjuanicus*, however, make comparisons difficult. Future collecting and study might reveal that they are conspecific.
EMENDED DESCRIPTION. Shell size (left valve) up to 93 mm in height, 54 mm in length (same specimen). Conjoined valves up to 17 mm total thickness. Shape variable with three ecophenotypes: falcate, elongate, and spatulate. Inequivalved (left valve larger than right valve). Valves smooth. Left valve lowly convex (elongate) to arched and thin (up to 3 mm thick). Right valve lid-like, flat and thin (up to 2 mm thick). Flange along anterior margin of falcate ecophenotype becoming wider ventrally. Attachment scar commonly not obvious on most ecophenotypes. Resilifer groove and bourrelets small but distinct; resilifer groove opisthogyrate; in-turning of beak can obscure apical part of resilifer groove. Hinge on right valve incompletely known, but resilifer groove area appears to be less prominent than on left valve. Falcate ecophenotype commonly with overhanging and/or twisted beak area on left valve. Spatulate ecophenotype with entire area beak truncated and/or flattened by large attachment scar; less-inflatedumbo and flange either not present or poorly developed. Elongate ecophenotype left-valve beak area pointed to somewhat rounded. Adductor muscle scar moderately large, circular to elliptical, posterodorsally to nearly centrally located. Chomata vermiculate and short. Catachomata (left valve) few in number, small, closely spaced, and located either anterior to hinge or along low shelf on antero-dorsal margin of umbal cavity and in alignment with anterior bourselet. Anachomata (right valve) immediately ventral of short auricles associated with hinge; anachomata extend farther along posterior side of valve (to medial area) than along anterior side of valve. These narrow ridges on both sides of interior of right valve fit into socket-like smooth grooves of corresponding left valve, especially on posterior side. Shell microstructure vesicular (“foamy”), in thin or moderately thick layers (up to 2 mm thick) very commonly recrystallized as massive, homogeneous calcite.

HOLOTYPE. CAS 5526 (Figs. 137–139), left valve, 45.5-mm height, 35.5-mm length, 15.1 mm thick; Pozo Formation, Cañada del Pozo, Santa Cruz Island, Santa Barbara County, Southern California.

PARATYPE. SDSNH 427, Pozo Formation.

GEOLOGIC RANGE. Late early Paleocene or early middle Paleocene to early Eocene.

STRATIGRAPHIC DISTRIBUTION. LOWER PALEOCENE (upper Danian Stage): lowermost Santa Susana Formation at LACMIP loc. 41691, near Mt. Sinai Memorial Park, north side Simi Valley, Ventura County, Southern California (new occurrence). MIDDLE PALEOCENE (lowermost Selandian Stage): lowermost Santa Susana Formation at LACMIP loc. 23109, south side Simi Hills, Ventura County, Southern California (new occurrence); lower to middle part of Santa Susana Formation, Simi Hills, Ventura County, Southern California (“Martinez Stage”) (Zinsmeister, 1983). UPPER PALEOCENE (Thanetian Stage): Pozo Formation, Cañada del Pozo, Santa Cruz Island, Santa Barbara County, Southern California (Hertlein, 1933). LOWER EOCENE (“Capay Stage”): lower Juncal Formation, Sespe Hot Springs, Ventura County, Southern California (Givens, 1974); Juncal Formation, Canton Creek, Whitaker Peak area, Los Angeles County, Southern California (Squires, 1987); Maniobra Formation, Orocopia Mountains, Riverside County, Southern California (Squires, 1991b).

REMARKS. Fifty-nine specimens were examined. Preservation is poor (especially Paleocene specimens) to rarely excellent. The interior of the left valve (Fig. 141) of this species was previously unknown, probably because the thin and delicate valves are encased commonly in very hard matrix. Separation of the valves of a conjoined-valved specimen (Figs. 142–144) revealed, for the first time, the morphology of the interior of the right valve (Fig. 143). At LACMIP loc. 23116 in the

Subfamily Pycnodontinae Stenzel, 1959
Tribe Pycnodontini Stenzel, 1959
Genus Phygraea Vialov, 1936

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

AGE AND DISTRIBUTION. Cretaceous to Miocene. Widespread (Stenzel, 1971), including the Cretaceous of California (Squires, 2017). Prior to this present paper, Paleocene and Eocene occurrences of Phygraea on the west coast of the United States were reported as various other genera. Early workers (e.g., Hertlein, 1933) commonly identified them as Ostrea, whereas post-1987 workers (e.g., Squires and Demetrion, 1990, 1992, 1994; Squires, 2001) mostly identified them as Pycnodonte (Phygraea).

Phygraea baleyi (Hertlein, 1933) comb. nov.

Figures 137–149

Gryphaea sp. Bremner, 1932:pl. 3, figs. 4, 5.
Ostrea baleyi Hertlein, 1933:277, pl. 18, figs. 5, 6; Squires, 1987:58, fig. 97; Squires, 1991b:table 1, pl. 2, fig. 18.
Odontogryphaea baleyi (Hertlein). Givens, 1974:45, pl. 1, figs. 11–13.
Ostrea simiensis Zinsmeister, 1983:1286–1287, fig. IE-G.
Acustrea simiensis (Zinsmeister). Moore, 1987:C30, pl. 34, fig. 4.
Ostrea idriaensis Gabb. Shapiro, 1998:table 1, pl. 1, fig. H.
At least eight small (approximately 20-mm height), flat, left valves of *Phygraea haleyi* are encrusting a single large (80-mm height) specimen of the gastropod *Saxituberosa titan* (Waring, 1917) found at LACMIP loc. 41691 in hard siltstone in the upper lower Paleocene (upper Danian) part of the lower Santa Susana Formation, near Mt. Sinai Memorial Park on the north side Simi Valley, Ventura County, Southern California. One of these specimens is shown in Figure 146. The abundant shallow-marine fossils at this locality underwent post-mortem transport, probably by turbidity currents emanating from shallower marine depths (Squires et al., in press). One of the encrusting oyster specimens at this locality has some of its left valve unattached, and the shape of that part is convex, like that normally found on specimens of *Phygraea haleyi*. Although one might be inclined to assign the encrusting, flat, left valves to a new species, it is more likely that the flatness is the result of just how “plastic” the morphology of pycnodonteines can be. Machalski (1988) reported similarly that the shape of a Danian pycnodonteine in Poland is ecologically controlled rather than taxonomically controlled, and that the mode of attachment and size of available substrates play a large role in determining the shape of these oysters. It is likely that the large gastropod was transported into the deeper waters where *P. haleyi* lived, and the young specimens took advantage of this rare hardground by colonizing it. The left valves grew very flat in order to provide secure attachment in an otherwise unstable environment, which was subject to the influx of storm waters. The presence of these encrusting specimens of *P. haleyi* in upper Danian strata on the north side of Simi Valley represents the earliest Cenozoic record of this genus in the West Coast strata. In stratigraphic position, it is slightly older than the occurrence of *P. haleyi* at LACMIP loc. 23109 in the lowermost Santa Susana Formation (lower Selandian) in the Simi Hills on the south side of Simi Valley (see Fantozzi, 1995).

Vokes (1935) believed that *Ostrea haleyi* Hertlein is a gryphaeoid variant of *Ostrea idriaensis* Gabb. Moore (1987) agreed but identified Hertlein’s species as *Acutostra idriaensis idriaensis* (Gabb). Givens (1974:45) believed that *haleyi* questionably belongs to genus *Odontogryphaea* (Ihering, 1903), but this species does not have any indication of a terebratuloid fold in the commissure, which is one of the main characteristics of *Odontogryphaea*.

Although *P. haleyi* can resemble gryphaeiform specimens of *A. idriaensis*, *P. haleyi* differs by having vesicular (“foamy”) shell microstructure (including the holotype), weak vermiculate chomata (rather than short, stout chomata), and a postero-lateral flange. Hertlein’s species, therefore, is a pycnodonteine oyster and is assigned here, for the first time, to genus *Phygraea*.

*Phygraea haleyi* somewhat resembles *Pycnodonte (Phygraea) pacifica* Squires and Demetrion comb. nov. (1990:386, fig. 3.1–3.4; Squires and Demetrion, 1992:39, fig. 113), from lower to middle Eocene strata (“Capay Stage” to “Tejon Stage”) in the Bateque and Tepetate formations in Baja California Sur, Mexico. *Phygraea haleyi* differs from *Phygraea pacifica* by having a smaller size, valves can be much narrower/

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**Figures 137–149** *Phygraea haleyi* (Hertlein, 1933), LACMIP loc. 7890, Pozo Formation [Area 18], unless otherwise indicated. 137–146. Falcate ecophenotypes. 137–139. Holotype CAS 5526, CAS loc. 6675.2. Left valve. 137. Exterior. 138. Interior. 140, 142–144. Hypotype LACMIP 14708, LACMIP loc. 7890, Left valve. 140. Exterior. 141. Interior. 142–144. Hypotype LACMIP 14709, LACMIP xloc. 41507, lower Juncal Formation [halfway between Areas 13 and 14], Santa Susana Formation, Simi Hills, left valves of both the elongate ecophenotype with a pointed beak (Fig. 147) and the elongate ecophenotype with a rounded beak (Fig. 148) co-occur.

*Squares: Paleocene and Eocene Oysters*
Pycnodonte

Ostrea

Gabb, 1869. Hanna, 1927:276, pl. 30, figs. 1, 2.

Ostrea idriaensis

Ostrea stewarti


California.

massive, homogeneous calcite.

microstructure vesicular ("posteriorly") to approximately 10 mm into valve interior. Shell extend inwardly from auricle-like shoulders (anteriorly and especially both valves of largest specimens of circular ecophenotype, chomata margins (especially posteriorly) on some circular ecophenotypes. Chomata abundant and can completely cover valve (most numerous posterior of hinge) on falcate and trigonal center of valve. Chomata vermiculate, sparse to moderately common large, circular, and located slightly posterior or slightly anterior of by circumferential curb, best developed on falcate ecophenotype and, straight. Commissural shelf barely discernible or delimited proximally shallow. Bourrelets prominent or weak. Base of hinge sinuous or groove straight to slightly opisthogyral, narrow or wide, deep or very rarely with trapezoidal shape (posterior side lowest). Resilifer falcate left valves. Hinge prominent or barely visible (rare), and hinge obscured by attachment scar on circular ecophenotype and most falcate left valves. Hinge prominent or barely visible (rare), and hinge very rarely with trapezoidal shape (posterior side lowest). Resilifer groove straight to slightly opisthogyral, narrow or wide, deep or shallow. Bourrelets prominent or weak. Base of hinge sinuous or straight. Commisural shelf barely discernible or delimited proximally by circumferential curb, best developed on falcate ecophenotype and, to a lesser degree, on circular ecophenotype. Adductor muscle scar large, circular, and located slightly posterior or slightly anterior of center of valve. Chomata vermucose, sparse to moderately common (most numerous posterior of hinge) on falcate and trigonal ecophenotypes. Chomata abundant and can completely cover valve margins (especially posteriorly) on some circular ecophenotypes. On both valves of largest specimens of circular ecophenotype, chomata extend inwardly from auricle-like shoulders (anteriorly and especially posteriorly) to approximately 10 mm into valve interior. Shell microstructure vesicular ("foamy") but commonly recrystallized as massive, homogeneous calcite.

HOLOTYPE. UCMP 30921 (Figs. 166–167), left valve, 128.5-mm height, 97.9-mm length; UCMP loc. 5062 [Area 22], from sea cliff at Torrey Pines State Reserve; probably from Delmar Formation, upper lower Eocene strata, San Diego area, San Diego County, Southern California.

PARATYPES. UCMP 30922 (two separate specimens), Delmar Formation.

GEOLOGIC RANGE. Middle early Eocene to late Eocene.

GEOGRAPHIC RANGE. Southwestern Washington to Southern California.

Squires: Paleocene and Eocene Oysters


REMARKS. Sixty-three ("in-hand") specimens were examined, in addition to as 31 digital images of well-preserved specimens provided by T. Deméré (personal communication, 2016). The homogeneous microstructure can have a granulated texture on weathered surfaces. Hanna's (1927:pl. 28, fig. 1) photograph of the interior of the holotype is superficially very similar to some specimens (e.g., Fig. 87) of Crassostrea tectonica sp. nov. His photograph does not show, however, the vermucose chomata (Fig. 166), nor did he mention the homogenous shell microstructure of stewarti. Both of these morphologic characters allow, with certainty, for the identification of this species as a pycnodonteine genus.

Phygaea stewarti is common in the Santiago Formation near Carlsbad, north of San Diego, and in the "Stewart bed" of the Llajas Formation on the north side of Simi Valley, Ventura County, Southern California. In the "Stewart bed" of the Llajas Formation at LACMIP loc. 22312, there is a partial growth series of the circular ecophenotype, with specimens ranging from 24 to 130 mm in height. One of the circular valves (Fig. 172) is a complete right valve 127 mm in height, and another circular valve (Fig. 173) is incomplete, with a 95.2-mm height. The valves of these two very large-sized, circular ecophenotypes are up to 10 mm thick. The ventral area can be reflected either upward or backward. A similar-sized and -shaped left valve was also found in the Delmar Formation (LACMIP loc. 5240) in San Diego County.

At LACMIPlocs. 22312 and 40458 in the "Stewart bed" of the Llajas Formation, P. stewarti co-occurs with a few specimens of the trigonal ecophenotype of A. idriaensis.

Vedder and Norris (1963:37, table 3) reported uncatalogued Ostrea aff. O. stewarti Hanna from two described localities (Vedder and Norris, 1963:58, table 8) in unit 10 of an unnamed Eocene formation, southwest side of San Nicolas Island, Ventura County, Southern California.

Phygaea badgeri sp. nov.

Figures 174–183

DIAGNOSIS. Shell size medium small to medium large. Valves thin to moderately thin. Both valves can be flat, with left valve bearing radial ribs crossed by growth bands producing cancellate pattern. Valve margins of valves not upturned. Commisural shelf can be obvious. Attachment area rarely obvious and chomata not obvious.

DESCRIPTION. Shell size (left valve) up to 97 mm in height, 84 mm in length (same specimen). Conjoined valves up to 18 mm total.
thickens. Shape variable with three ecophenotypes: falcate, trigonal, and spatulate. Development of posterior flange rare and radial sulcus on left valve absent. Valves thin to moderately thin. Nearly equivalved. Left valve slightly larger than right valve and more convex; left valve flattish to strongly arched, moderately thin (up to 10 mm). Right valve flat and lid-like, thin (up to 4 mm). Left valves rarely with concave umbo; right valves rarely concave ventrally. Left valve with radial ribs, narrow (widening somewhat ventrally), closely spaced, and can be dichotomous. Radial ribs crossed by widely spaced growth bands imparting cancellate pattern, with swellings (node-like) common, separated by small circular to elongate depression. Growth bands are more elevated on medial part of left valve than on ventral part, thereby imparting distinctive stair-step profile. Attachment scar not obvious on most specimens. Beak can be obliterated by scar on some specimens. Falcate left valve can be entirely attached to other individuals. Hinge straight (rarely upturned at very high angle) or moderately opisthogyrate. Resilifer groove, bourrelets, and annular layers wide. Commissural shelf moderately strong posteriorly and ventrally. Adductor muscle scar not seen. Chomata not seen. Shell microstructure preserved in patches consisting of laminae, where not recrystallized as massive homogeneous calcite.

**HOLOTYPE.** LACMIP 14731 (Figs. 175–176), conjoined valves, 74.6-mm height, 53.5-mm length, 16.2 mm thick; LACMIP loc. 23724 (see Squires, 1994:fig. 3) [Area 14], Coldwater Formation, upper Rock Creek on south flank of Pine Mountain, upper Sespe Creek area; lat. 34°35’33.09”N, long. 119°13’56.59”W, at elevation 1243 m (4087 ft.), NW ¼ of SE ¼ of section 20, T 6 N, R 22 W, United States Geological Survey, Lion Canyon Quadrangle (7.5 minute), 1943, Ventura County, Southern California.

**PARATYPES.** LACMIP 14732–14734, Coldwater Formation.

**GEOLOGIC RANGE.** Late middle Eocene to early late Eocene.

**GEOGRAPHIC RANGE.** Santa Ynez Mountains and upper Sespe Creek, Southern California.

**STRATIGRAPHIC RANGE.** UPPER MIDDLE EOCENE (middle part of “Tejon Stage”): Coldwater Formation, upper Sespe Creek, Ventura County, Southern California. LOWER UPPER EOCENE: Lower Gaviota Formation, Gaviota Pass region, Santa Ynez Mountains, Santa Barbara County, Southern California.

**REMARKS.** Twelve specimens were examined. Preservation is poor to good. In some beds, a few specimens are attached to one another, forming a cluster. In other beds, some specimens were stacked together by sedimentologic processes and subsequently somewhat crushed. Only the spicate ecophenotype occurs in the lower Gaviota Formation.

*Phygraea badgeri* differs from *P. baleyi* by having larger size, never elongate/narrow, radial/cancellate ribbing present, beak not in-turned, no radial sulcus, and flange not obvious. *Phygraea badgeri* differs from *P. steuerti* by having smaller size, no circular ecophenotype, radial ribs common (instead of being rare), cancellate sculpture can be present, no phalange, wider umbo, margins not upturned, adductor muscle scar much smaller, and chomata not obvious. *Phygraea badgeri* differs from *P. lincolnensis* by having larger size, thicker valves, radial ribs common, cancellate sculpture can be present, and chomata not obvious.

In terms of the presence of rounded radial ribs (plicae) on some specimens of the new species, *Phygraea badgeri* shows some similarity with *Hyotissa offernanae* Garvie (1996:32, pl. 4, figs. 5–9) from lower Eocene (Ypresian Stage) beds in the Gulf Coastal Plain. The new species differs in its larger size, flatter valves, and cancellate sculpture; radials that can be dichotomous; shell commissure margins that are not plicate; lack of scale-like extensions of radial ribs; attachment area that is not obvious; and chomata that are not obvious. On *H. offernanae*, the
attachment scar can cover 50% or more of the valve area, and chomata can occupy greater than 50% of the valve margins.

**ETYMOLOGY.** The species is named for R.L. Badger, who collected all the specimens of this species from the Coldwater Formation.

**Phygraea lincolnensis** (Weaver, 1916) comb. nov.

Figs. 184–215

*Ostrea lincolnensis* Weaver, 1916:36, pl. 1, figs. 5–6; Weaver, 1942:80, pl. 14, figs. 1–3; Durham, 1944:137 (unfig.); Armentrout, 1973:397, pl. 13, figs. 5, 6.

**EMENDED DESCRIPTION.** Shell size (left valve) up to 69.5 mm in height, 55.7 mm in length (same specimen). Conjoined valves up to 28 mm total thickness. Shape variable, with three ecophenotypes: falcate, trigonal, and spatulate. Inequivalved. Valves thin (commonly 2.5 to 3.5 mm thick), somewhat fragile, and flattish. Left valve slightly convex and moderately thin (10 mm); right valve slightly thick and thin (up to 7.4 mm), with umbo rarely inflated (on spatulate ecophenotype). Valves smooth, left valve of spatulate ecophenotype with approximately 20 radial ribs, becoming more distinct near ventral margin of valve. Right valve of trigonal ecophenotype commonly with prominent growth lamellae. Attachment scar not obvious, except on spatulate ecophenotype where scar can be moderately large. Beak well developed only on trigonal ecophenotype. Hinge prominent, widest on trigonal ecophenotype. Resilifier groove straight or somewhat opisthogyral, moderately short, and shallow to moderately deep. Bourelets prominent. Shelf commissure commonly prominent; commarginal shelf can be wide, especially posteriorly. Adductor muscle scar small and prominent. Shelf commissure-shelf margins. Catachomata especially pustulate on left-ventral attachment scar can cover 50% or more of the valve area, and chomata can occupy greater than 50% of the valve margins.

**EMENDED DESCRIPTION.** Shell size (left valve) up to 69.5 mm in height, 55.7 mm in length (same specimen). Conjoined valves up to 28 mm total thickness. Shape variable, with three ecophenotypes: falcate, trigonal, and spatulate. Inequivalved. Valves thin (commonly 2.5 to 3.5 mm thick), somewhat fragile, and flattish. Left valve slightly convex and moderately thin (10 mm); right valve slightly thick and thin (up to 7.4 mm), with umbo rarely inflated (on spatulate ecophenotype). Valves smooth, left valve of spatulate ecophenotype with approximately 20 radial ribs, becoming more distinct near ventral margin of valve. Right valve of trigonal ecophenotype commonly with prominent growth lamellae. Attachment scar not obvious, except on spatulate ecophenotype where scar can be moderately large. Beak well developed only on trigonal ecophenotype. Hinge prominent, widest on trigonal ecophenotype. Resilifier groove straight or somewhat opisthogyral, moderately short, and shallow to moderately deep. Bourelets prominent. Shelf commissure commonly prominent; commarginal shelf can be wide, especially posteriorly. Adductor muscle scar small and circular, located slightly dorso-posterior of center of valve. Chomata vermiculate, ranging from short to moderately long, straight to irregular, and lenticular to pustulate. Chomata commonly occur near hinge on commissure-shelf margins. Catachomata especially pustulate on left-valve posterior, where pustules occur in single or double rows or as irregularly spaced squiggles. Anachomata fewer in number to sparse or not obvious; mostly with short vermiculate shapes (can be in two rows), but longer shapes to irregular shapes can be present, especially ventrally. Shelf microstructure vesicular (foamy) and recrystallized homogeneous with recti wavy wisps of laminae caused by growth squamae.

**HOLOTYPE.** CAS 453 [= UW 88], (Figs. 205–207), left valve, 57-mm height, 41-mm length, 2.5 mm thick; 1.6 km (1 mi.) north of Galvin Station, Lewis County, southwestern Washington.

**GEOLOGIC RANGE.** Latest Eocene to early Oligocene.

**GEOGRAPHIC RANGE.** West coast of Washington State.


**REMARKS.** Twelve specimens were examined, along with two fragments. Preservation is excellent. Two of the specimens are conjoined. Most of the examined specimens are from the lower Lincoln Creek Formation, at the type section at Galvin, southwestern Washington. Although Weaver (1942) mentioned a paratype of *O. lincolnensis*, Weaver (1916) never indicated a paratype of his species. The only type specimen is the holotype, which is illustrated here (Figs. 205–207). Specimens from the Quimper Sandstone and Marrowstone Shale are all fragments, and many are of small size (E. Nesbitt, personal communication, 2017). Specimens from the Cowlitz Formation are rare. The one figured here (Fig. 213) has a few serpulid worm tubes attached to it.

According to Armentrout (1975:22–25), the geographic range of *Ostrea lincolnensis* is latest Eocene * [Echinophoria dalii Zone] to early Oligocene *[Echinophoria fax Zone]*. Age-control data provided by paleomagnetic studies of strata (e.g., Quimper Formation, lower Lincoln Creek Formation) (see Fig. 2), which contain this oyster in southwestern Washington, are supportive of this age range for *O. lincolnensis*.

**Phygraea lincolnensis** is similar to “*Ostrea* kochae Gardner (1935:140–141, pl. 8, figs. 1–5). Gardner’s species, which is from the Tetchucana member of the Kinaid formation in Medina County, Texas, has vesicular microstructure (C.L. Garvie, personal communication, 2017). Gardner did not mention the word “vesicular,” but she did note that the margin of the valves of this species are “strongly plicate." **Phygraea lincolnensis** differs from Gardner’s species by having a larger size, falcate shape, beak never elongate, and plications can be present on rare specimens.

**COMMENTS ABOUT DEPOSITIONAL ENVIRONMENTS**

Depositional environments of the studied oysters are indicated in Figure 216. *Acustotrea idriaensis* lived most commonly along delta shores with soft-bottom embayments (lagoons or bays) (Nesbitt, 1995) and/or sand flats, whose tidal and subtidal facies are in close proximity to each other, and whose boundaries could shift rapidly and intergrade (Warme, 1991). In the Delmar Formation at Solana Beach, north of San Diego [Area 22], Warme (1991) reported in situ growth series of conjoined-valve specimens of *A. idriaensis* on intertidal and adjacent shallow-subtidal sand flats between tidal channels, as well as on tidal-channel floors. He did not describe the oysters or use ecophenotype terminology, but trigonal and a few falcate ecophenotypes are recognizable in Warme’s (1991:fig. 7) illustration of one of these in situ oyster beds. These same facies/environments, in association with abundant specimens of *A. idriaensis*, occur also in outcrops of the Delmar Formation at Torrey Pines State Reserve, about 10 km (6.2 mi.) south of Solana Beach, (Lohmar et al., 1979).

Trigonal-ecophenotype specimens of *Acustotrea idriaensis* can also be found, but uncommonly, in shelfal-subtidal deposits. In the Lajas Formation of Simi Valley, they co-occur with specimens of **Phygraea** *stewarti*, another oyster that could live intertidally or subtidally. Both are discussed more fully below.

Vokes (1939a:54, 1939b:605) reported that brackish water conditions were responsible for the diminished size of *A. idriaensis* in beds of the Domengine Formation near Coalinga. He did not specify the shell characteristics of the specimens to which he was referring, nor did he figure any specimens. Although detailed sedimentologic studies are needed to prove his assertion, most of the specimens examined from this formation near Coalinga are less than 34 mm in height, whereas, in other formations, specimens commonly exceed this height. Many of these specimens from near Coalinga are broken and occur as coquinas. Some specimens from the Domengine Formation in the Vallecitos syncline area [Area 9] can be of small size, but not all. At LACMIP loc. 41295 [Area 9], three ecophenotypes were found: falcate (some with conjoined valves), trigonal, and spatulate. This locality is the same as Schulien’s (1993) locality 12395, and he assigned the environment at this locality to brackish marine.

The valves of the only known specimen of **Gryphaeostrea aviculiformis** are very thin, and they have some silty, very fine-grained sandstone
adhering to them. The specimen is from the Domengine Formation in the Alcalde Hills area west of Coalinga [Area 10]. This formation was deposited there in a relatively low-energy, fluvial-dominated delta with marsh areas and an interdistributary bay (Roush, 1986). It is likely, therefore, that this species lived in such a calm-water area.

Acostastra griesensis is only known from its type locality in the Gries Formation in southwestern Washington. The depositional environments of this formation are very poorly known, with a range from nearshore (or littoral) to offshore (Eifinger, 1938). Mollusks found co-occurring with A. griesensis at its type locality include mostly subtidal-subfossiliferous dwellers (e.g., bivalves Nuculana and Pitar, gastropods Conus, Exilia, Molopophorus, Scaphander, and Terebellum). These taxa are common components of similar environments found elsewhere in Eocene-age strata on the West Coast (e.g., Squires, 1984; Moore, 1976). Pending future research on the depositional environments of this formation, a shelfal-subtidal environment can only be assigned questionably to A. griesensis.

The depositional environment for specimens recognized here as Acostastra gaviota sp. nov. from the Santa Ynez Mountains [Area 12] is not well known but is generally lower shoreface (Sgriccia and Fritsche, 2001).

Although some fossil species of Crassiostra inhabited subtidal shallow-marine environments where they produced large and heavy shells, like C. tectonica sp. nov., other fossil species of Crassiostra lived in the estuarine environment, which probably served as a refuge from marine predation, competition, and erosion (Kirby 2000, 2001). Exant Crassiostra are restricted primarily to brackish, hypersaline, and intertidal environments (e.g., estuaries and lagoons) where they produce smaller and thinner shells with no chomata (Stenzel, 1971; Kirby, 2001).

The most commonly reported depositional environment for specimens recognized here as Acostastra tectonica is lower shoreface (Fig. 216), which is associated with agitated waters and normal salinity conditions. Most specimens occur in fine- to medium-grained sandstone, which locally can be coarse grained with angular fragments and moderately poor sorting. Using the rationale of Campbell (2010) for how shape in oysters can be dictated by habitat, it is possible that large, thick, and heavy valves (with thick prismatic shell structure), like those of C. tectonica, as well as like those of A. gaviota, provided stability in the substrate and also protection against predation. In contrast, the odontogyriforme ecophenotype of C. tectonica occurs in fine-grained sandstone. As mentioned earlier, this ecophenotype resembles the Paleogene Gulf Coast Odontogyriforme thrauma (Gabb) in having a strong terebratuloid fold of the left (lower) valve. According to Glawe et al. (2011), such a strong fold on O. thrauma might have functioned as a keel, which would help to prevent this unusual-shaped oyster shell from tipping over onto its side the shifting sands of soft substrate. The strong fold on the odontogyriforme specimens of C. tectonica likely acted as a keel, as well.

The very thin and fragile valves of specimens recognized here as Cubitostrea californiana sp. nov. occur in beds reported as being of shallow-marine origin in both the Llajas Formation in Simi Valley (Squires, 1981, 1984) and the Ardath Shale north of San Diego (Givens and Kennedy, 1979). This oyster would have been suited for relatively quieter-water conditions in the shelfal-subtidal environment and could not have survived in highly agitated waters.

Phygraea stewarti is most common in very fine- to fine-grained sandstone. North of San Diego [Area 22], falcate ecophenotypes of this oyster are commonly found in marine-estuarine beds of member C of the Santiago Formation and in similar facies in the Friars Formation, although sparse specimens occur in shallow-marine deposits of the Mission Valley Formation and Scripps Formation (T. Deméré, personal communication, 2016). Falcate, trigonal, and circular ecophenotypes of P. stewarti, a few of which have conjoined valves (Figs. 152–153), co-occur with a few disarticulated specimens of the smooth and thick-shelled trigonal ecophenotype of Acostastra idriaensis, in the “Stewart bed” (e.g., LACMIP loc. 22312) in the Llajas Formation, Simi Valley [Area 16]. This bed, which consists of silty to granular glauconitic sandstone with rare large pebbles, caps a thick section of shallow-marine facies consisting of alternating laminated (storm-related) and bioturbated (fair-weather related) very fine- to fine-grained sandstones with scattered fossiliferous beds, and the “Stewart bed” is immediately overlain by a section of slope to outer shelf silstone (Squires, 1981, 1984). The silt content at locality 22312 was most likely conducive for P. stewarti. It is possible that the “Stewart bed” had a slow depositional rate and represents a time-averaged deposit. Based on the evidence, the depositional environments of P. stewarti include both deltaic and shelfal-subtidal depths.

Phygraea haleyi is found in silty sand and silstone. At its type locality on Santa Cruz Island, it is associated with mollusks (e.g., Turritella (large sized), Crassatella, and Cuculales) and benthic foraminifera, but no planktic foraminifera (Doerner, 1969). The mollusks are common components of the shelfal-subtidal environment gradational with offshore conditions found elsewhere in Paleocene and Eocene strata on the West Coast (e.g., Doerner, 1969; Squires, 1984), and the benthic foraminifera are indicative of the central or outer shelf (Doerner, 1969).

Phygraea badgeri co-occurs with mollusks (e.g., Turritella, Pachy-crommium, Fiopis, Venericardia (Pacificor), Callista, and Crassatella) in the Coldwater Sandstone at LACMIP loc. 20581 [Area 14] in upper Sespe Creek. Squires (1994) reported that the fauna, which includes some articulated specimens of these bivalves, which constitute a Turritella–Venericardia–Crassatella paleocommunity, that lived between nearshore and the shelf break.

The depositional environment of Phygraea lincolnensis is very poorly known. Based on the very fragile thin valves of most of its specimens and also on their occurrence in silstone or silty sandstone, the depositional environment was in a calm environment. Pending future research, a shelfal-subtidal environment, gradational with offshore conditions, is assigned questionably to this species.

**EFFECTS OF TECTONICS ON THE DISTRIBUTION OF PALEOGENE OYSTERS IN SOUTHERN CALIFORNIA**

The present-day positions of the oyster-bearing outcrops in Southern California bear no resemblance to their original geographic positions. This is because of complex tectonism and associated rotation, which began about 18 million years ago (early Miocene), when the Pacific...
and North American plates first made contact with each other. The San Andreas Fault system began to form at the common boundary between these plates, with the Pacific Plate moving northwest in relation to the North American Plate, and this movement continues to the present day. The palinspastic reconstructions and back-rotation histories of the Southern California tectonic blocks involved in this complex movement have been depicted by Fritsche (1998:figs. 1–10), who showed in his figure 3 that the Santa Ynez Mountains, which contain the Acustostrea gaviota–bearing Gaviota Formation, was initially submerged and located offshore opposite the San Diego region, which was at that time in the northern part of Sonora, Mexico (Abbott, 1999:fig. 5.15). The Pozo Formation, which contains the type locality of Phygraea haleyi, on Santa Cruz Island [Area 18] in the Channel Islands, was initially located offshore north of Camp Pendleton [Area 21] (Fritsche, 1998:fig. 3).

Figure 216  Ecophenotypes of the studied oyster species versus their depositional environments, associated lithologies, grain sizes (VF = very fine, F = fine, M = medium, C = coarse), and key references for depositional environments. Dashed vertical lines indicate gradational boundaries.
Between about 18 and 5 million years ago, the tectonic blocks containing the Gaviota and Pozo formations broke loose, pivoted along the edge of the North American Plate, rotated clockwise about 60°, and underwent northward translation. Since then, an additional 30° of rotation has taken place, along with additional northward translation (Hornafius et al., 1986).

In sum, the outcrops containing the Gaviota Formation in the Santa Ynez Mountains and the outcrops containing the Pozo Formation in the Channel Islands have undergone a total of 90° of clockwise rotation (Onderdonk, 2005). They both had an east–west trend, and the Gaviota Formation outcrops have been sutured to a large triangular-shaped tectonic block (Fritsch, 1998, fig. 3), which contains C. tectonica in the Coldwater Formation in upper Sespe Creek [Area 14], and, farther east, in the upper Matilija Sandstone? in the Whitaker Peak area [Area 13]. The upper Sespe Creek and Whitaker Peak areas were near the pivot point of rotation and therefore underwent less rotation. The San Nicolas Island [Area 20] was part of another area involved also in this complex history of assimilation of disjunct tectonic blocks (Kamerling and Luyendyk, 1985).

**PALEOClimATE IMPLICATIONS**

The west coast of the United States during the Paleocene and Eocene was a warm-temperate region characterized by thermophilic mollusks (Squires, 2003:29). As discussed in the previous section, the Southern California areas of deposition were farther south (about 2.5° of latitude) and hence in slightly warmer waters than would be expected just by plotting locales on present-day maps. Gradstein et al. (2012:884–886:fig. 28.11) discussed the timing of the four major global paleoclimatic events of the Paleogene. These were the global warming during the Paleogene–Eocene Thermal Event [=PETM], the short-lived but warmest time of the Paleogene during the Early Eocene Climatic Optimum [=EECO], the MId-Eocene Climatic Optimum [=MECO], and the subsequent cooling trend near the end of the Eocene (see Fig. 2). Miller et al. (2011:fig. 4) graphically depicted the global sea-level rise that occurred during the Paleocene and reached its highest stand for the entire Cenozoic during the early Eocene EECO through the early middle Eocene. They also depicted the sharp drop in sea level at the end of the Eocene.

The combination of warm temperatures and rising sea level during most of the Paleogene would have greatly facilitated the dispersal of warm-water molluscan taxa from the Old World Tethys Sea province into the West Coast region, and this influx of taxa was reported on by Squires (1987). Additional faunal components of this influx include *Cubitostrea* and *Gryphaeostrea*. Most of the genera of oysters found in Paleogene strata in the West Coast region were possibly reintroductions. *Acustostrea*, *Crassostrea*, and *Phygraea* were present, for example, also in the West Coast region during the Late Cretaceous (Squires, 2017). Of these three, *Phygraea* showed up again in the Paleocene, whereas *Acutostrea* and *Crassostrea* do not show up until the Eocene. *Cubitostrea* was known prior to the present report only in lower Eocene rocks in Baja Sur, Mexico, and its presence in middle Eocene rocks in Southern California probably coincides with northward migration of this genus.

Worldwide ocean-cooling–associated drops in sea level were caused by the beginning of glaciation in Antarctica that began near the end of the Eocene (Gradstein et al., 2012), and there were several faunal turnovers that affected thermophilic shallow-marine mollusks (Squires, 2003; Nesbitt, 2003; Hickman, 2003); as well as terrestrial organisms of the west coast of the United States (Retallack et al., 2004). The faunal turnover near the Eocene–Oligocene boundary especially affected oyster taxa, based on the extinction of *A. grieensis*, *A. gaviota*, and *P. linocolenis*. Jarrett et al., (2009) noted that fossil bivalves, including late Eocene *Crassostrea gigantissima* in the Gulf Coastal Plain of the United States were impacted also by a cooling event during the late Eocene.

**CONCLUSIONS**

The Paleocene and Eocene oyster fauna in the region extending from southwestern Washington to California consists of 10 species, four of which are new. Although all the previously named species were either originally assigned to *Ostrea*, or rarely to *Gryphaea*, none belong to these genera. Instead they belong to *Acutostrea*, *Gryphaeostrea*, and *Phygraea*. The new species belong to *Acutostrea*, *Phygraea*, *Crassatella*, and *Cubitostrea*. The last-mentioned two genera were not previously recognized in the fauna. The name “*Ostrea* tayloriana” Gabb, which has long been used for large-sized oysters of Eocene age, especially in the Santa Ynez Mountains of Southern California, is a *nomen dubium*.

Populations of the species, except those represented by only a few specimens, are made up of newly recognized ecophenotypes, which represent non-genetic adaptations to living in different water energies, ranging from estuarine to offshore environments.

Three species of *Acutostrea* are recognized. *Acutostrea idriaensis* (Gabb, 1869) is widespread, with occurrences in California, Oregon, and southwestern Washington. It ranges from early Eocene to late middle Eocene age. Its falcate and trigonal ecophenotypes, with their thin valves, lived in silty intertidal areas, whereas its subcircular and trigonal ecophenotypes, with their thicker and smoother valves, inhabited tidal and subtidal sand-flat areas. *Acutostrea grieensis* (Effinger, 1938) is found only in southwestern Washington, is of late Eocene age, and is questionably known from shelfal-subtidal deposits at its type locality. *Acutostrea gaviota* sp. nov. is almost entirely confined to Southern California and is of late Eocene age. Its ecophenotypes, with their relatively large and thick valves, lived just seaward of the lower shoreface environment.

*Crassostrea* is reported for the first time in the Eocene record of the west coast of the United States. Except for a rare occurrence in central California, its occurrences are in Southern California, especially in the Whitaker Peak area. *Crassostrea tectonica* sp. nov. is of middle Eocene age. Its falcate and trigonal ecophenotypes, with their very large, thick, and heavy valves, lived in the sandy lower shoreface environment. Its odontogryphaeate ecophenotype has an unusual large teretabratuloid fold, which probably functioned as a keel, for anchoring purposes in fine sands.

*Crassostrea californiensis* sp. nov. represents the first record of this genus in California. It is of late early Eocene age and known only from rare and very thin-valved specimens in shelfal-subtidal deposits of the Llajas Formation and Ardhsh Shale in Southern California.

*Gryphaeostrea avicularis* (Anderson, 1905), known only from its holotype from central California, is early middle in age. It lived in a calm-water environment in an upper delta setting.

*Phygraea haleyi* (Hertlein, 1933), which is the senior synonym of *Ostrea simiensis* Zinsmeister, 1983, is only known from Southern California, including Santa Cruz Island. This oyster ranges from early Paleocene to early Eocene age. Its ecophenotypes, with their thin valves, lived in a silty shelfal-subtidal environment gradational with offshore conditions.

*Phygraea stewartii* (Hanna, 1927) is known predominantly from Southern California but is found also in southwestern Washington. This oyster ranges from middle early to late Eocene age. Its varied ecophenotypes lived in lagoons, sand flats, or shelfal-subtidal areas.
Phygraea badgeri sp. nov. is found only in the Santa Ynez Mountains and upper Sespe Creek, Southern California. It ranges from late middle to early late Eocene age. Its varied ecophenotypes lived between nearshore and the shelf break.

Phygraea lincolnensis (Weaver, 1916) is found only in southwestern Washington and is of late Eocene age. It lived in calm-water deposits, in questionably the shelfal-subtidal environment gradational with offshore conditions.

During the Paleocene and Eocene, oyster-bearing deposits in the Santa Ynez Mountains and Channel Islands were originally opposite mainland Southern California in the San Diego area, which was located in the northern part of Sonora, Mexico. Post-Paleogene clockwise tectonic rotation of 90° and northward translation over a few degrees of latitude have moved these coastal Southern California outcrops to their present-day locations.

Warm-water and high-sea-level times existed in the West Coast region during the Paleocene and nearly all of the Eocene, when many mollusks migrated into the region or were possibly reintroduced. Global cooling during the late Eocene and earliest Oligocene coincided with the closely timed extinctions of A. griesensis, A. gaviota, and P. lincolnensis.

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