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Cover illustration: Eocene paleogeography and the amphiatlantic current system responsible that would have facilitated the influx of Old World Tethyan Realm mollusks into the CSWNA region.

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Revision of Eocene warm-water cassid gastropods from coastal southwestern North America: implications for paleobiogeographic distribution and faunal-turnover

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The warm-water (thermophilic) Eocene cassid gastropods reported previously from coastal southwestern North America (CSWNA), a region extending from the Olympic Peninsula, Washington to Baja California Sur, Mexico, are revised in terms of taxonomy, description, geographic distribution, and biostratigraphy. Five species of the cassine Galeodea and a single species of the phaline Echinophoria are recognized. Galeodea megalosensis, G. sutterensis, G. louella, G. californica and G. tuberculiformis are predominantly found in California and, collectively, range in age from early to middle Eocene. Echinophoria trituberculata of middle Eocene age in southern California and of earliest late Eocene age in southwestern Washington, is the earliest known record of this genus. Several poorly known supposed cassids are discussed. The pre-Oligocene global record of Galeodea is compiled for the first time. The first arrival of Galeodea in the CSWNA region occurred in the early Eocene just after the warmest peak and highest sea level of the Cenozoic. Some of the CSWNA Galeodea species are very similar morphologically to some found in the Tethys Realm of Western Europe, especially in England and France, and to some found in the Gulf Coast and Mexico (Nuevo León and Chiapas). These similar species are indicative that the migratory route of Galeodea into the CSWNA region was via a current system that emanated from the Old World, passed near southern Western Europe, the Gulf Coast of the United States, northern and southern Mexico, and eventually influenced the CSWNA region. Thermophilic CSWNA cassids radiated during the early Eocene but declined by the end of the middle Eocene, and, because of global cooling, disappeared near the beginning of the Oligocene.

Keywords: Cassid gastropods, Galeodea, Eocene, California, Washington, Tethyan Realm

INTRODUCTION

Cassid gastropods are popularly referred to as “helmet shells” or “bonnet shells.” They make up a relatively small group, in terms of the number of genera and species, but these predators of echinoderms have been widespread since the early Eocene in shallow, tropical to subtropical seas of the world. Their pre-Oligocene published species record, which is listed here for the first time, shows a poorly known Late Cretaceous record, very few Paleocene species, and a rich Eocene record. There are eight extant genera and about 70 extant species, which occur mostly in tropical Indo-West Pacific and Caribbean waters, from the low tide to a depth of about 100 m, but can be bathyal (Abbott 1968, Kreipl 1997, Verbinnen et al. 2016).

Stemming from the work by Conrad (1855) and Gabb (1864), cassids have been reported from Eocene shallow-marine strata in coastal southwestern North America (CSWNA), a region extending from the Olympic Peninsula, Washington to Baja California Sur, Mexico (Fig. 1). Their classification and geologic record have not been revised since Durham (1942) although there have been changes in their supraspecific categories (Beu 2008, 2010) and in their biostratigraphy (Squires 1984, 1987). There has been also new collecting in southern California (Squires and Advocate 1986) and Baja California, Mexico (Squires and Demetrion 1994). The chief goals of this present paper are to update the taxonomic and biostratigraphic records of the warm-water Eocene cassids in the CSWNA region, as well as to better understand
which are found in British Columbia, Washington, and Oregon in cool-, deep-water communities, including those fueled by chemosynthesis, originating within the accretionary wedge depositional setting of the Cascadia.

the paleobiogeographic and paleoclimatic implications of their record. With its tropical focus, this present paper does not address geologically younger cassid species of Echinophoria Sacco, 1890 and Liracassis Moore, 1963, which are found in British Columbia, Washington, and Oregon in cool-, deep-water communities, including those fueled by chemosynthesis, originating within the accretionary wedge depositional setting of the Cascadia.
forearc region. These cooler and deeper water cassids have been used effectively to refine Eocene-Miocene biostratigraphy and correlation in the Pacific Northwest (PNW). For modern revisions about the late Eocene to early Oligocene cassids in the PNW, see Moore (1963, 1984), Hickman (1980), and Nesbitt (2003).

MATERIAL AND METHODS

The clade-classification scheme of Bouchet and Rocroi (2017) is used for supra-generic categories. Modern updates in the taxonomy of cassids follow those of Beu (2008, 2010). Representative specimens of extant cassid shells, housed in the Department of Malacology collection at the Natural History Museum of Los Angeles County, were studied in order to better understand the morphologic distinctions among genera. The subheading “Primary Type Material” pertains to holotype, paratype, and lectotype specimens. Meanings of the terminology associated with the two kinds of shell varices (episodic and terminal) are taken from Webster and Vermeij (2017) and Hickman (2018). The boundaries of the informal provincial molluscan “stages” (“Martínez” through “Tejon”) are from Squires (2003), who discussed the history of their derivation, and Figure 2 shows their correlation to the European stages. The boundaries of the informal-molluscan biozones Echinophoria dalli through Licrassidae rex are from Nesbitt (2003). Magnetic stratigraphy studies by Prothero (2001, 2003) and Prothero et al. (2001) were used to augment the molluscan geologic age data for the cassid-bearing formations in the CSWNA region. Table 1, which lists published species of Late Cretaceous, Paleocene, and Eocene Galeodesa Link, 1807 from throughout the world, is based on a comprehensive but not an exhaustive literature search. The data are subject to imprecisely known geologic ages, poor preservation, inadequate illustrations of the species, and the possibility of synonyms.

Institutional Abbreviations—ANSP, Academy of Natural Sciences at Drexel University, Philadelphia, Pennsylvania; CASG, California Academy of Sciences, San Francisco; IGM, Instituto de Geología, Universidad Nacional Autónoma de México, México City. LACMIP, Los Angeles County Museum of Natural History, Invertebrate Paleontology Department, Los Angeles, California; UCMP, University of California, Berkeley; UWBM, University of Washington Burke Museum, Seattle.

Cited Localities—Information about the localities referred to in this paper can be accessed through the following website links:

LACMIP: https://nhm.org/site/research-collections/

invertebrate-paleontology

UCMP: http://ucmp.berkeley.edu. More detailed UCMP locality information is available to researchers by contacting the museum’s invertebrate collection manager.

SYSTEMATIC PALEONTOLOGY

GASTROPODA UNRANKED

CAENO GASTROPODA UNRANKED

TONNOIDEA SUTER, 1913

CASSIDAE LATREILLE, 1825

Strong et al. (2019) recognized two subfamilies of cassids. They are cassines and phaliines, and both are known in the CSWNA Eocene record. Strong et al. (2019: p. 26) reported, furthermore, that based on DNA studies, the cassines Galeodesa and Cassis Scopoli, 1777, as well as the phaliine Echinophoria Sacco, 1890 are supported as being monophyletic genera.

CASSIDAE LATREILLE, 1825

GALEODEA LINK, 1807

Type species—By monotypy, Buccinum echinophorum Linne, 1758 (=Morio echinophorum Linne, 1758). Pliocene to Recent, southern Europe to Mediterranean.

Geologic range—Late Cretaceous (Santonian to early Campanian) to Recent. Galeodesa is present in middle Miocene to early Pliocene strata, as well as rarely to uncommonly in the modern record; namely, in the Dominican Republic and elsewhere in the Caribbean Sea region (Beu 2010).

Differential diagnosis—Spire moderately low to moderately high, partially submerged or not. Radial ribs absent on spire. Last-whorl shoulder distinct, tabulate (common) or rounded, and bearing nodes strong (common) or weak. Anterior siphonal canal moderately short to long, twisted (leftward), and unnotched (therefore no siphonal fasciole). Canal reflected leftward and upward (dorsally). Aperture moderately wide; inner lip can have lirae or pustules; posterior end of inner canal can have parietal node and consequent restriction. Shell can have multiple episodic varices, and terminal varix weak to prominent; outer lip can be slightly flared and can bear denticles on its interior.

Remarks—Dall (1909: p. 64) gave a very detailed synonymy, up to the year 1909, of Galeodesa, and Beu (2010: p. 231) gave nine genus-group names. Beu (2008) demonstrated that Galeodesa belongs in the Cassinae. He commented that protoconchs of all the Recent Galeodesa species have almost no specific characters. They are like
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the protoconch of *G. echinophora*, the type species of *Galeodea*, in that they are all very small, blunt, and paucispiral (Beu 2008: figs. 11A, C, E). Some Eocene species of *Galeodea* have a long anterior canal (Gardner 1939), but other species do not.

**Galeodea meganosensis** Vokes, 1939

*Fig. 3A–D*

=Galeodea sutterensis* “Dickerson.” Clark and Woodford, 1927. p. 113; pl. 19, fig. 21 [misidentification].

*Galeodea sutterensis meganosensis* Vokes, 1939. p. 151; pl. 19, fig. 18.

*Galeodea (Gomphopages) meganosensis* Vokes.

*Galeodea aff. nodosa carinata* (Deshayes, 1835). Squires, 1988b. p. 13, figs. 30, 31.

**Primary Type Material**—Of *G. meganosensis* Vokes, 1939, holotype UCMP 31244, Locality UCMP 3152, Meganos Formation, Deer Valley, Mount Diablo area, Contra Costa County, northern California. Holotype = the specimen misidentified as *G. sutterensis* “Dickerson” Clark and Woodward.

**Material examined**—The ten specimens include: Plaster replica of holotype, hypotypes LACMIP 7474,
Table 1. Age and location of published species of *Galeodea* found in pre-Oligocene strata in the world.

| Species/Author(s)       | Age                  | Location                                  |
|-------------------------|----------------------|-------------------------------------------|
| aegyptiaca Oppenheim, 1906 | Lutetian             | Pakistan                                  |
| allani Finlay and Marwick, 1937 | Danian to Selandian | New Zealand                              |
| ambigua Solander, 1766 | early Bartonian to early Priabonian | England                                  |
| anderseni Schnetler and Heilman, 2011 | latest Ypresian to early Lutetian | Denmark                                  |
| angustana Wrigley, 1934 | Ypresian             | England                                   |
| anteniana Martin, 1931 | Bartonian or Priabonian | Java                                     |
| archiaci Cossmann and Pissarro, 1909 | earliest Ypresian | Pakistan                                  |
| boehmi Martin, 1931     | Bartonian or Priabonian | Java                                     |
| brevicastatum Conrad, 1834 | Lutetian             | Alab., Miss., Tex., Florida               |
| bullata Brown, 1839     | Ypresian             | England, Denmark                          |
| californica Clark, 1942 | late Ypresian to Lutetian | CSWNA                                    |
| cingulae Garvie, 2013   | middle Ypresian      | Texas                                     |
| coronata Deshayes, 1830 | Bartonian             | England, France                           |
| diadema Deshayes, 1835  | Ypresian             | England, France                           |
| douvillei O'Gorman, 1923 | Ypresian             | France                                    |
| dubia Aldrich, 1885     | early Ypresian       | Alabama, Texas                            |
| elongata Koenen, 1885   | latest Ypresian to early Lutetian | Denmark                                  |
| aff. elongata Koenen, 1885 | Danian to early Selandian | West Greenland; Denmark                   |
| enodis Deshayes, 1835   | Lutetian to early Bartonian | England, France                           |
| eurychilus Cossmann, 1889 | Bartonian             | France                                    |
| gallica Wrigley, 1934   | Ypresian             | England, France, Denmark                  |
| geminata Wrigley, 1934  | Lutetian             | England                                   |
| khaledi Abbass, 1967    | late Lutetian to Bartonian | Egypt                                     |
| klingeri Kiel and Bandel, 2004 | Santonian to early Campanian | South Africa                             |
| koureos Gardner, 1939  | late Paleocene to Ypresian | Alab., Tex., no and so. Mex.             |
| louella Squires and Advocate, 1986 | middle Ypresian | CSWNA                                    |
| marcus Garvie, 2013     | middle Lutetian      | Texas                                     |
| megalosensis Vokes, 1939 | middle Ypresian      | CSWNA                                    |
| millsapsi Sullivan and Gardner, 1939 | early Priabonian | Mississippi, no. Mexico                  |
| modesta Suter, 1917     | late Lutetian        | New Zealand                               |
| nodosa Solander, 1766   | Lutetian to Bartonian | England, France                           |
| petersoni Conrad, 1854  | early Priabonian     | Mississippi, Texas                        |
| planotecta Meyer and Aldrich, 1886 | early Priabonian | Alab., Miss., no. Mexico                 |
| planotecta jacksoni Palmer, 1937 | early Priabonian | Mississippi                               |
| pretiosa Deshayes, 1865 | Lutetian             | France                                    |
| reklawensis Garvie, 1996 | middle Ypresian      | Texas                                     |
| singularis Deshayes, 1865 | Bartonian             | France, Belgium                           |
| striata J. Sowerby, 1812 | Ypresian             | England                                   |
| sutterensis Dickerson, 1916 | Ypresian to middle Lutetian | CSWNA                                    |
| umbgrovei Martin, 1931  | Bartonian or Priabonian | Java                                     |
| taitii Conrad, 1834     | late Bartonian       | Alabama                                   |
| taitii johnsoni Palmer, 1947 | early Priabonian     | Mississippi, Lousiana                     |
| textiliosa Deshayes, 1835 | Lutetian             | France                                    |
| tuberculiformis Hanna, 1924 | early Ypresian to middle Lutetian | CSWNA                                    |
| turneri Gardner, 1939   | middle Ypresian to Lutetian | Texas                                     |
| unicoronata raricrenata O'Gorman, 1923 | late Ypresian        | France                                    |
Figure 3. See caption on the bottom of page 7.
Galeodea meganosensis

**Emended description**—Shell small to medium size (up to 33 mm height, incomplete). Shape globose with small spire and large subquadrate last whorl. Spire relatively high, last whorl with two carinae; carina on shoulder strongest with approximately 11 spinose tubercles; second carina noticeably weaker also with approximately 11 tubercles (rounded, not spinose) becoming weaker toward outer lip and unaligned relative to nodes on shoulder. Spiral thread with minute nodes can be present medially in interspace between carinae, and another spiral thread with minute nodes can be present anterior to second carina. Shell surface otherwise covered with very fine spiral threads, with cancellate patches. Anterior siphonal canal broken but shows twisting. Episodic varix uncommon but thick. Terminal varix narrowly thickened.

**Stratigraphic occurrence**—Lower Eocene, northern to southern California. "**Meganos Stage**": Meganos Formation, Deer Valley, north side of Mount Diablo, Contra Costa County, northern California (Vokes 1939, Clark and Woodward 1927). "**Capay Stage**": Lodo Formation, Cerros Shale Member [=new information: UCMP locality 1817; for locality details, see Squires (1988c)], Urrutia Canyon, north of Coalinga, Fresno County, northern California. Lower Juncal Formation, Whitaker Peak, Los Angeles County, southern California (Squires 1987). "**Domengine Stage**": Juncal Formation?, northern Lockwood Valley, Ventura County, southern California (Squires 1988b) [for age update, see Squires (2000)].

**Remarks**—Vokes (1939) recognized that Clark and Woodford (1927) misidentified a new gastropod as *Galeodea suttermensis* Dickerson, 1916. Vokes (1939) named this new gastropod *G. meganosensis* and regarded it to be a subspecies of *G. suttermensis*. Based on its less submerged spire, only two carinae (never three), more nodes, and shell covered otherwise with fine spiral threads, *G. meganosensis* is regarded herein a distinct species.

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SQUIRES—REVISION OF EOCENE WARM-WATER CASSID GASTROPODS FROM NORTH AMERICA

Galeodea susanae Dickerson, 1916

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**Fig. 3E–M**

Galeodea suttermensis Dickerson, 1916. p. 492; pl. 40, figs. 1a, 1b. Schenck, 1926. p. 84, figs. 1, 2 (both refigured from Dickerson 1916). Vokes, 1939. p. 150; pl. 19, fig. 15. Turner, 1938. p. 92; pl. 18, fig. 19. Schenck and Keen, 1940. p. 12, figs. 3, 4. Weaver, 1942. p. 402; pl. 78, figs. 6, 7.

Galeodea susanae Schenck, 1926. p. 85; pl. 15, figs. 3–7. Turner, 1938. p. 92; pl. 18, fig. 18. Schenck and Keen, 1940. p. 12, figs. 5, 6. Weaver, 1942. p. 402; pl. 78, figs. 2, 3.

Galeodea (Gomphopages) susanae Schenck. Durham, 1942. p. 184. Givens, 1974. p. 78; pl. 8, fig. 4. Squires, 1984. p. 27; fig. 7k.

Galeodea (Gomphopages) suttermensis Dickerson. Durham, 1942. p. 184; pl. 29, fig. 2. Givens, 1974. p. 78; pl. 8, fig. 4.

Galeodea cf. G. susanae Schenck. Givens and Kennedy, 1979. p. 86.

Galeodea sp. Squires and Demetrion, 1992. p. 32; fig. 85.

Galeodea (Mamabrina) [sic] susanae Dickerson. Squires, 2008. fig. 24.

[non] Galeodea suttermensis Dickerson. Clark and Woodford, 1927. pl. 19, fig. 21 [=Galeodea meganosensis].

**Primary Type Material**—Of *G. suttermensis*, holotype UCMP 11782, Locality UCMP 1853, Capay Shale, Sutter Buttes (=Marysville Buttes), Sutter County, northern California. Of *G. susanae*, holotype CASG 1753, Locality CASG 372, Llajas Formation, north side Simi Valley, southern California; paratypes CASG 1754, 1755, Llajas Formation; paratype CASG 1756, Lookingglass Formation, Glide, Douglas County, southwestern Oregon.

**Material examined**—The forty-two specimens include: Hypotypes LACMIP 13425, 14831-14833, and the following unfigured specimens: one from LACMIP Locality L1165, two from LACMIP Locality 2777, three from LACMIP Locality 7206, four from LACMIP Locality 7206.
Emended description—Shell small to medium size (up to 55 mm high, complete). Shape globose with small spire and large subquadrate last whorl. Protoconch small and smooth, naticoid, about three whors. Teleoconch about 3.5 large whors. Spire partly submerged. No sutureal cord. Penultimate whorl commonly unevenly submerged. Last whorl subquadrate, spiral sculpture much stronger than axial sculpture, with posterior two-thirds of whorl having widely spaced two or less commonly, three carinae (anteriormost carina can become obsolete toward the outer lip). Carinae bear tubercles, either spinose and long or less commonly, narrow; tubercles unaligned between rows; carina on shoulder with 7 to 12 nodes. Teleoconch covered by numerous, closely spaced fine spirals, not necessarily minutely cancellate; fine spirals can alternate in strength and can be strongest on last whorl neck. Inner lip and columellar lip callus merge, with resultant callus extensive, projecting laterally short distance, creating two false umbilici (one adjacent to neck and one adjacent to anterior end of canal). Neck constricted. Anterior canal long, slender, reflected sideways (laterally to the left) approximately 42°, and unnotched. Aperture moderately wide but constricted (grooved) at posterior end. Episodic varices normally lacking. Terminal varix narrow or plhnge-like reflection with exterior and interior smooth.

Stratigraphic occurrence—Lower to middle Eocene, southwestern Oregon to Baja California Sur, Mexico. “Capay Stage”: Lookingglass Formation, Douglas County, southwestern Oregon (Turner 1938; Weaver 1942); Capay Shale, Sutter Buttes, Sutter County, northern California (Dickerson 1916); Lodo Formation, Cerros Shale Member, Urrutia Canyon, north of Coalinga, Fresno County, northern California (Vokes 1939) [UCMP Locality 1817, for updated locality details, see Squires (1988); Juncal Formation, Pine Mountain area, Ventura County, southern California (Givens 1974); Juncal Formation, Whitaker Peak (near basement contact), Los Angeles County, southern California (Squires 1987); Juncal Formation, Elsmere Canyon, Los Angeles County, southern California (Squires 2008). Maniobra Formation (near basement contact), Oroopia Mountains, Riverside County, southern California (Squires and Advocate 1986; Squires 1991); Bateque Formation, Baja California Sur, Mexico (Squires and Demetrion 1992). “Domengine Stage”: Domengine Formation, Coalinga area, San Benito County, northern California (Vokes 1939). Llajas Formation (shallow-marine [transgressive] facies), Devil Canyon, Santa Susana Mountains, just east of northern side of Simi Valley, Los Angeles County, southern California (Schenck 1926; Squires 1984). Ardath Shale, San Diego, San Diego County, southern California (Givens and Kennedy 1979). Juncal Formation?, northern Lockwood Valley, Ventura County, southern California (Squires 1988b) [for age update, see (Squires 2000)]. “Tejon Stage”: Tejon Fm, probably Liveoak Member [=including new information: LACMIP Locality 22340; for locality details, see Squires (1989: appendix)], Tehachapi Mountains, Kern County, southern California.

Remarks—Galeodea sutterensis and G. susanae are considered to be synonyms because of their closely similar morphology, which is not unique to either one. Galeodea sutterensis, which has been reported previously from lower Eocene (“Capay Stage”) strata, commonly has three rows of spiral nodes on the last whorl. Galeodea susanae, which has been reported previously from middle Eocene (“Capay/Domengine” boundary strata and “Domengine Stage”) strata, commonly has two rows of spiral nodes on the last whorl. Galeodea susanae, however, can have three spiral rows (Fig. 3K-M).

The anterior canal is broken on all known specimens of G. sutterensis, except for a single specimen from the middle Eocene Llajas Formation in northern Simi Valley, southern California. This specimen, which has retained its long anterior canal (Fig. 3H–J), is remarkably similar to Galeodea turneri Gardner (1939: p. 25, pl. 8, figs. 1, 4) from lower Eocene strata in Bastrop County, Texas. Galeodea sutterensis differs by having a less submerged spire and a ramp without weak to moderately weak axial ridges extending to each node on the shoulder of the last whorl.

Galeodea sutterensis is recognized herein for the first time in the Tejon Formation. It co-occurs there with the cassid Echinophora tri tubercula (Weaver, 1912) at LACMIP Locality 22340. The Tejon Formation G. sutterensis specimens are small-medium in size (up to 38 mm height) and can have good preservation, except they are incomplete and most consist of large fragments of the last whorl with widely spaced spines.

Galeodea louella (Squires and Advocate, 1986) Fig. 3N–P

Galeodea sp. cf. G. sutterensis Dickerson, Crowell and Susuki, 1959. p. 588; pl. 2, figs. 1, 4.
Phalium (Semicassis) louella Squires and Advocate, 1986. p. 858; fig. 2.11, 2.12. Squires, 1991. pl. 2, fig. 2.
Galeodea cf. G. gallica Wrigley, 1934. Squires and Advocate, 1986. p. 857; figs. 2.7, 2.8; Squires, 1991. pl. 2, fig. 1.
Phalium (Semicassis) louella Squires and Advocate. Squires and Demetrion, 1994. p. 130; figs. 10–11 [=Galeodea tuberculiformis Hanna, 1924].

**Primary Type Material**—Holotype LACMIP 7166 and paratype LACMIP 7167; both from Locality LACMIP 40665, Maniobra Formation, Orocopia Mountains, Riverside County, southern California.

**Material examined**—The four specimens include: Holotype, paratype, hypotype LACMIP 8836, and one unfigured specimen from LACMIP Locality 40662.

**Emended description**—Shell small to medium size (up to 25 mm height, incomplete). Shape ovate to sub-globose. Protoconch conical, paucispiral. Uppermost spire whorls rounded. Penultimate whorl partially submerged with carina bearing small, thin and narrow spinose nodes. Last whorl with three carinae; carinae evenly spaced, or second and third carinae can be closer spaced to each other. Carina on shoulder shoulder bearing 12 to 16 small, thin and narrow spinose nodes; second carina with much finer nodes; third carinae smooth. Shell covered otherwise by minute, non-cancellate spiral threads. Aperture narrow to moderately wide. Several spiral lirae on columella at the anterior end of aperture. Anterior canal region nearly entirely missing, except for short remnant of canal showing evidence of twisting. No varices observed.

**Stratigraphic occurrence**—Lower Eocene. Southern California to Baja California Sur, Mexico. "Capay Stage": Maniobra Formation, Orocopia Mountains, Riverside County, southern California (Squires and Advocate 1986; Squires 1991). Bateque Formation, eastern San Ignacio area, Baja California Sur, Mexico (Squires and Demetrion 1994).

**Remarks**—Preservation is moderately poor. Specimens are weathered, and the outer lip morphology cannot be determined. *Galeodea louella* is removed herein from *Phalium (Semicassis)* Mörch, 1852 and placed in *Galeodea* because of the overall *Galeodea* shape of the last whorl, several carinae with nodes, and absence of parietal columellar shield. The paratype (Fig. 3N) of *G. louella*, which is figured for the first time, shows better than its holotype how remarkably similar this species is to *Galeodea gallica* Wrigley, 1934 from England, France, and Denmark. *Galeodea louella* differs from it by having fewer small nodes on the shoulder of the last whorl.

*Galeodea californica* Clark. Givens and Kennedy, 1979. p. 86.

*Galeodea (Caliagaleodea) californica* Clark. Squires, 1984. p. 26; fig. 7j. Squires. 1988a. pl. 1, fig. 12; Squires. 1988b. p. 13, fig. 29. Squires and Demetrion, 1994. p. 130; fig. 9.

**Primary Type Material**—Holotype UCMP 34376 and paratype UCMP 34377, both from UCMP Locality UCMP 7004, Llajas Formation, north side Simi Valley, Ventura County, southern California.

**Material examined**—The thirty-one specimens include: Hypotypes LACMIP 6530, 14834, and 28 unfigured topotype specimens.

**Emended description**—Shell small to medium size (up to 33 mm height, incomplete), globose with thin shell. Spire very small, low, mostly submerged. Sutural “ramp” flat, between spire and last whorl. Callus thin to absent on parietal region of inner lip. Spiral ribs prominent, numerous, and smooth with wide interspaces, especially on most of last whorl. Spiral ribs on neck much thinner, very weak, and bearing closely spaced minute weak nodes. Interspaces on shell neck narrower and bearing three or four spiral threads. Anterior canal moderately long, twisted leftward (broken on nearly all specimens), and umbilicate. Episodic varices lacking. Terminal varix wide, flange-like, and reflected.

**Stratigraphic occurrence**—Lower Eocene to lower middle Eocene, southern California to Baja California Sur, Mexico. "Capay Stage": Bateque Formation, Baja California Sur, Mexico (Squires and Demetrion 1994); "Domengine Stage": Juncal Formation?, northern Lockwood Valley, Ventura County, southern California (Clark 1942; Squires 1984); lower Scripps Formation, San Diego, San Diego County, southern California (Givens and Kennedy 1979).

**Remarks**—Most of the specimens are internal molds or nearly so. The anterior canal is broken off on nearly all of them. Clark (1942) named Caliagaleodea as a subgenus of *Galeodea*. Beu (2008: p. 288) regarded *Caliagaleodea* as a synonym.

*Galeodea tuberculiformis* Hanna, 1924

Figs. 4D–H

*Morio (Sconsia) tuberculatus* Gabb, 1864. p. 104, pl. 19, fig. 57. Arnold, 1907. pl. 39, fig. 9.

*Phalium [sic] tuberculata* Risso, 1826. p. 186 (see Dall, 1909. p. 64).

*Cassadaria* [sic] (Phalium) tuberculata [sic] Dall, in
Figure 4. See caption on the bottom of page 11.
Diller (1896. p. 458).

Galeodea tuberculata (Gabb). Dickerson, 1916. pl. 42, fig. 2.

Galeodea (Morio) tuberculata (Gabb). Waring, 1917. pl. 15, fig. 17.

Galeodea tuberculiformis Hanna, 1924. p. 167. Anderson and Hanna, 1925. p 110. Schenck, 1926, p. 83; pl. 14, figs. 12–16. Stewart, 1927. p. 380; pl. 28, figs. 11. Vokes, 1939. p. 149; pl. 19, figs. 19, 21, 23–27.

Coalingodea tuberculiformis (Hanna). Durham, 1942. p. 186; pl. 29, figs. 5, 9. Givens, 1974. p. 78; pl. 8, fig. 7. Squires, 1977. page 1.

Cassis (Coalingodea) tuberculata (Gabb). Abbott, 1968. p. 59; pl. 34 (three views).

Phalium tuberculiformis (Hanna). Givens and Kennedy, 1979. pp. 86, 88.

Phalium (Semicassis) tuberculiformis (Hanna). Squires, 1984. p. 27; figs. 71. Squires, 1987, p. 40; fig. 50. Kappeler et al., 1984. page 2 on p. 17.

Phalium (Semicassis) louella Squires and Advocate. Squires and Demetrion, 1994. p. 130; figs. 10–11.

Phalium (Semicassis) tuberculiformis (Hanna). Squires, 1999. p. 19; fig. 37.

Primary Type Material—Lectotype ANSP 4343, designated by Stewart (1927: p. 380). Muir Sandstone, Bull’s Head Point, Martinez, north of Mount Diablo, Contra Costa County, northern California (Weaver 1953).

Material examined—The thirty-six specimens include: Hypotypes LACMIP 6532 and 14835, plaster replica of lectotype ANSP 4343, and the following unfugured specimens: eleven from LACMIP Locality 7180, two from LACMIP Locality 40371, nineteen from LACMIP Locality 40374, and one from LACMIP loc. 40764.

Emended description—Size moderately small, height up to 34.2 mm height. Immature shell fusiform, early adults can have moderately high spire and tabulate last whorl, whereas late adults can have lower spire and somewhat “rounded look” on periphery of last whorl or less, commonly, tabulate shoulder. Protoconch low (naticoid) or moderately high, 2.5 smooth whorls, with abrupt contact with earliest sculptured whorl. Teleoconch up to 3.5 whorls. Spire overall low, 0.23 to 0.24 of shell height, partially submerged. Radial ribs present on spire whorls. Suture impressed and somewhat wavy; bordered by sutural cord only on some upper spire whorls. Sutural ramp moderately inclined. Last whorl enlarged, posterior two-thirds of last whorl with widely spaced three (rarely four) carinae bearing spinose nodes (unaligned between carinae); anteriormost carina much weaker and with weaker nodes; carina on shoulder with 10 nodes. Sculpture on rest of shell (including short neck) consisting of many, closely spaced, spiral threads (visible to naked eye) crossed by growth lines and minutely cancellate, commonly producing “beaded” look on well preserved individuals. Parietal/columnar lip callus wide and well developed; separated from shell and forming umbilicus anteriorly. Siphonal canal moderately short, twisted, and unnotched; 7 to 8 transverse lirae on callused columnar lip with lirae becoming more closely spaced toward anterior end of aperture. Siphonal canal dorsally directed, with false umbilicus at posterior end. Episodic varix (or two varices) can be present (rarely none) but only on last whorl; location of varices variable. Terminal varix thick and with well developed denticles on inner edge of varix; posteriormost denticle can be prominent, thereby creating constriction in this region.

Stratigraphic occurrence—Lower to middle Eocene, southwestern Washington to San Diego, California. "Meganos Stage": Upper Santa Susana Formation, south side Simi Valley, Ventura County, southern California (Squires 1999). "Capay Stage": Batheque Formation, San Ignacio area, Baja California Sur, Mexico (Squires and Demetrion 1994). "Domengine Stage": Domengine Formation, Coalinga area, San Benito County, central California (Vokes 1939); Avenal Sandstone, Reef Ridge area, Kings County, central California (Kappeler et al. 1984). Muir Sandstone, Contra Costa County, northern California (Weaver 1953). Upper Juncal Formation, Pine Mountain area, Ventura County, southern California (Givens 1974). Upper Juncal Formation and Matilija Sandstone?, Whitaker Peak area, Las Lajas Canyon, north side Simi Valley, Ventura County, southern California. Apertural (A) and abapertural (B) views of hypotype LACMIP 6530, LACMIP Locality 7180, two from LACMIP Locality 40371, nineteen from LACMIP Locality 40374, and one from LACMIP loc. 40764.

Figure 4A–C. Galeodea californica Clark, 1942, Llajas Formation, (Eocene, "Domengine Stage"), Las Llajas Canyon, north side Simi Valley, Ventura County, southern California. Apertural (A) and abapertural (B) views of hypotype LACMIP 14834, LACMIP Locality 22312. D–H. Galeodea tuberculiformis Hanna, 1924, Llajas Formation, (Eocene, "Domengine Stage"), Devil Canyon, northern Simi Valley, Los Angeles County, southern California. Apertural (D), abapertural (E), left-lateral (F), and right-lateral (G) views of hypotype LACMIP 6532, LACMIP Locality 16115. H. Apertural view of hypotype LACMIP 14835, LACMIP Locality 40371. I–P. Echinophoria trituberculata (Weaver, 1912). Apertural (I) and abapertural (J) views of hypotype LACMIP 14836, LACMIP Locality 22340, Tejon Formation, (Eocene, "Tejon Stage"), Grapevine Canyon, Tehachapi Mountains, Kern County, southern California. Apertural (K), abapertural (L), and right-lateral (M) views of hypotype LACMIP 14837, LACMIP Locality 5654. Apertural (N), abapertural (O), and left-lateral (P) views of hypotype LACMIP 14838, LACMIP Locality 3125. K–P=Cowlitz Formation, (Eocene, "Tejon Stage"), Cowlitz River near Vader, Lewis County, southwestern Washington. Scale bars=10 mm.
Columella long, anterior siphonal canal strongly twisted, slightly to moderately notched, and fasciolate. Siphonal fasciole very distinct, with posterior edge of anterior canal noticeably producing two long “plica-like” spiral structures extending across ventral surface of siphonal canal and reaching notch area; siphonal fasciole separated from base of last whorl by distinct groove. Previous varices rare (on fossils), absent (on modern specimens). Episodic varices rare on fossils and very rare to absent on modern specimens. Terminal varix on outer lip thin to thickened and reflected (Beu 2010: p. 231).

Remarks—Beu (2010: p. 242) gave six genus-groups names of Echinophoria. The protoconch of Echinophoria is low-turbiniform, with a well-impressed suture and about three strongly inflated, smooth whorls. Beu (2008, 2010) opined that Echinophoria, with its prominent sculpture resembling that of Galeodea, is likely to have been the stem group of the Phaliinae, evolving from Galeodea late in Cretaceous time.

Durham (1942) was the first to recognize the presence of Echinophoria in the CSWNA region, and he used Echinophoria species to help establish a cassid-biostatigraphic zonation scheme for the Pacific Northwest (PNW). This zonation was developed further and expanded by Armentrout (1975: pp. 18–25). Moore (1984) used the phylogeny of the phaline genera Echinophoria and especially Liracassis for the purpose of also furthering the PNW cassid-biostatigraphic zones. Prothero and Armentrout (1985) used high-resolution, magnetostratigraphy for refining these zones, and this technique was utilized further by Prothero (2001: fig. 2), Prothero (2003: fig. 1.3), Nesbitt (2003: fig. 4.1), and Nesbitt et al. (2010) to update the cassid zonation. The Galeodea trituberculata zone, which includes the Cowlitz Formation and the tropical–Eocene fauna, is followed, in vertical stratigraphic succession, by the cooler water Echinophoria dalli, E. fax, and Liracassis zones (Fig. 2). Liracassis is one of several genera that diverged from Echinophoria during the Cenozoic but is now extinct (Beu 2008: p. 362). Echinophoria differs from Liracassis by having a smaller shell size, absence of strap-like spiral ribs, spiral ribbing never as dominant, nodes never as weak, longer and straighter anterior canal, and weaker development of longitudinal spiral cords on the anterior canal. 

Echinophoria trituberculata (Weaver, 1912)  
Fig. 4I–P

Morio tuberculatus var. trituberculatus Weaver, 1912. p. 39; pl. 3, fig. 35. 

Galeodea tuberculata (Gabb). Dickerson, 1915. pl. 6,
SQUIRES—REVISION OF EOCENE WARM-WATER CASSID GASTROPODS FROM NORTH AMERICA 13

figs. 3a, 3b.

Galeodea trituberculata (Weaver). Weaver and Palmer; 1922. p. 37; pl. 11, figs. 23, 27. Tegland, 1931; p. 408; pl. 59, fig. 1; pl. 60, figs. 1–4. Weaver, 1942. p. 404; pl. 78, figs. 10–15; pl. 79, figs. 1–4, 8. McWilliams, 1971. pl. 2, fig. 8. Moore, 1984. figs. A, D, E, G, H. Nesbitt, 1998. pl. 1, fig. 5.

Galeodea petrosa (Conrad, 1855). Schenck, 1926. p. 82; pl. 14, figs. 5–11.

Galeodea pretrosa [sic] (Conrad). Clark, 1929. pl. 14, figs. 1, 6.

Echinophoria trituberculata (Weaver). Durham, 1942. p. 184; pl. 29, fig. 10. Moore, 1984. figs. 4-A, D, E, G, H. Nesbitt, 1995. table 1.

“Galeodea” trituberculata [sic] (Weaver). Durham, 1944. p. 166.

Phalium (Echinophoria) trituberculatum (Weaver). Abbott, 1968. p. 109; pl. 93 (three views).

Echinophoria cf. E. trituberculata (Weaver). Givens, 1974. p. 79.

Primary Type Material—Holotype CASG 7612, UWBM Locality 232, north bank of Cowlitz River 2.4 km east of Vader, Cowlitz Formation, Lewis County, southwestern Washington.

Material examined—The twenty-eight specimens include: Hypotypes (LACMIP 14836–14838) and 25 unfigured specimens: 15 from LACMIP Locality 22430 (Tejon Formation, Grapevine Canyon, Kern County, southern California, nine from LACMIP Locality 5654 (Cowlitz Formation, near Vader, Lewis County, southwestern Washington), one from LACMIP Locality 2777 (Llajas Formation, north side Simi Valley, Ventura County, southern California).

Emended description—Shell small to medium size (up to 60 mm height); transition at approximately 22 mm height from immature specimens (fusiform with apertural sculpture abundant) to mature specimens (globose quadrate shape with apertural sculpture absent). Spire medium high. Sutural cord can be present. Sutural ramp low. Last whorl with three carinae (anteriormost carina most strongly toward outer lip. Carina on shoulder with 11 widely spaced spinose tubercles; second carina with 11 nodes; third carina with nine nodes, but nodes can be essentially obsolete toward aperture. Shell surface mostly covered with minute spiral threads generally all same size, but finer threads can be irregularly and randomly present (i.e., not in a repeating pattern); base of last whorl with spiral ribs, becoming stronger anteriorly. Columellar callus moderately thick on immature specimens and bearing lirae in parietal area and bearing granules on posterior part of columella; columellar callus without sculpture and thin on mature specimens, with nodes showing through. Columella on mature specimens bearing faint spiral lines beneath callus. Columella long and overall straight, except at twisted anterior end. Peristome with moderate notch. Anterior siphonal canal with deep groove adjacent to twisted columellar end; fasciole well developed, especially over angulate adaxial side of canal. False umbilicus present. Outer lip on immature specimens thickened, with interior bearing numerous elongate denticles separated by deep grooves on immature specimens. Outer lip on mature specimens narrow, reflected, and with interior denticles or grooves becoming much less apparent with growth. Episodic varices rare. Terminal varix present.

Stratigraphic occurrence—Middle Eocene to lowermost upper Eocene, southwestern Washington to southern California. Lower part of “Tejon Stage”: Matilija Sandstone, Pine Mountain area, Ventura County (Givens 1974). Tejon Formation (Anderson and Hanna 1925), probably Liveoak Member, Kern County, southern California. Uppermost part of “Tejon Stage,” Cowlitz Formation, Lewis County, southwestern Washington; Tukwila Formation, King County, southwestern Washington (McWilliams 1971, Nesbitt 1998).

Remarks—Specimens from the Cowlitz Formation show the best preservation. Specimens from the Tejon Formation are commonly well preserved fragments, which are missing the anterior canal because of improper removal of the well-indurated rock matrix. Early workers assigned this species to genus Galeodea, and starting with Durham (1942), workers assigned it to genus Echinophoria. Well preserved specimens of Echinophoria are characterized by the presence of a longitudinal spiral cord on the anterior canal (Beu 2008: p. 287), as well as the development of a sutural cord. Development of both of these features on the CSWNA specimens of E. trituberculata can be absent, extremely faint (Tejon Formation specimens), or prominent (Cowlitz Formation specimens). These differences are probably the function of preservation.

Some specimens of Echinophoria trituberculata can resemble Galeodea tuberculiformis, but E. trituberculata differs by having a shell with a larger maximum size (up to 60 mm vs. 34 mm), its spire can be less submerged, ramp flatter, sutural cord present on all whorls, spirals stronger on the last whorl and with more spinose tubercles, spirals coarser on neck, fine sculpture not beaded and rarely cancellate or not at all, parietal shield
commonly not present or weaker. In addition, \textit{E. trituberculata} has its anterior siphon more twisted, left side of fasciole angulate (keeled) rather than rounded and with deeper channel, anterior canal notched, longer and also wider with a slight longitudinal indentation, and episodic varices not as common.

\textit{Echinophoria trituberculata} differs from the late Eocene to early Oligocene \textit{E. dalli} (Dickerson, 1917), found predominantly in the Keasey Formation in the Veronia area of northwest Oregon (Hickman 1980), in having weaker spiral sculpture between carinae, thicker parietal callus, and a thicker outer lip.

\textit{Echinophoria trituberculata} differs from the late Eocene to early Oligocene \textit{Echinophoria fax} (Tegland, 1931), found predominantly in the Lincoln Creek Formation in western Washington, by having no fourth carina, fewer (10 versus 14) nodes on shoulder of last whorl, noticeably finer less spiral sculpture between the carinae on the last whorl, and weaker spiral ribs on base of last whorl.

Weaver and Kleinpell (1963: p. 190, pl. 25, fig. 11) reported \textit{Echinophoria trituberculata} (Weaver) from the Matilija Sandstone (“Tejon Stage”) in the Pine Mountain area, Santa Barbara County, southern California. Their report is based on a poorly preserved single specimen whose anterior canal is missing, thus identification as to genus and/or species is not possible.

\textbf{FAMILY AND GENUS INDETERMINATE}

\textit{Galeodea? crescentensis} Weaver and Palmer, 1922

\textit{Galeodea tuberculata} (Gabb) var. \textit{crescentensis} Weaver and Palmer, 1922. p. 37; pl. 11, figs. 18, 20.

\textit{Galeodea crescentensis} (Weaver and Palmer, 1922). Tegland, 1931. p. 409, pl. 59, figs. 2, 3. Weaver, 1942. p. 403, pl. 78, figs. 4, 5. Durham, 1942. p. 186.

\textit{Cassis} (Coalingodea) \textit{crescentensis} (Weaver and Palmer). Abbott, 1968. p. 60.

? \textit{Galeodea crescentensis} (Weaver and Palmer, 1922). Schenck, 1926. p. 85, pl. 15, fig. 8.

\textbf{Primary Type Material}—Holotype CASG 7612-A, Crescent Formation, in sea cliff on west shore of Crescent Bay, Clallam County, Olympic Peninsula, Washington.

\textbf{Remarks}—This species is based on only its holotype, a specimen whose height is 16 mm. Tegland (1931) mentioned that the holotype has a close resemblance to a cassid from lower Oligocene deposits in Townsend Bay, Washington. Durham (1942: p. 186) commented that the holotype resembles \textit{G. tuberculiformis}, but the meager material available for \textit{crescentensis} prevents accurate taxonomic assignment of Weaver and Palmer’s gastropod. A partially crushed questionable specimen of \textit{G. crescentensis} (hypotype UCMP 31310), which was illustrated by Schenck (1926: p. 85, pl. 15, fig. 8) from the Crescent Formation in Washington, is morphologically very different in shape and sculpture from any other Eocene CSWNA cassid and also different from the holotype of \textit{G. crescentensis} illustrated by Weaver and Palmer, 1922 from the same formation. This questionable specimen, which is missing some of its shell, might not even be a cassid.

\textbf{”Stramonita” petrosa Conrad, 1855, nomen dubium}

\textit{Stramonita petrosa} Conrad, 1855. p. 17; 1857. p. 327; pl. 6, figs. 47, 47a.

\textbf{Remarks}—This species has been the source of considerable taxonomic confusion. Its two known specimens were found in a float boulder several kilometers from its supposed source, which was assumed to the Tejon Formation in the Grapevine Canyon area, Kern County, southern California. The specimens are very poorly preserved, and their smudged sketches are very inadequate. The curatorial details and whereabouts of these specimens are unknown. The anterior canal of this gastropod is not twisted, therefore it is not a cassid. It is also not the muricid \textit{Stramonita Schumacher}, 1817, but it might be a ficid. Based on the insufficient knowledge about \textit{Stramonita petrosa}, Conrad’s (1855) gastropod is regarded herein as a \textit{nomen dubium}.

On the basis of the above-mentioned two incomplete shells, Anderson and Hanna (1924: p. 108, pl. 10, figs. 2, 3 = hypotypes CASG 823 and 824) reported \textit{Galeodea petrosa} (Conrad, 1855) from Locality CASG 245 in the Tejon Formation, Grapevine Canyon, Kern County, southern California. These two specimens show no diagnostic morphologic characters, which would allow identification as to family, genus, or species.

Conrad’s use of the name \textit{“petrosa”} has been confused with \textit{Dolium petrosum} Conrad (1849), a Miocene cassid species from the Astoria Formation in Oregon. See Moore (1963) for illustrations and synonymy of this Miocene species, now referred to as \textit{Liracassis petrosa} (Conrad, 1849).

\textbf{”Galeodea” schencki Weaver and Kleinpell, 1963 nomen dubium}

\textit{Galeodea schencki} Weaver and Kleinpell, 1963. p. 189; pl. 25, figs. 15, 16.

\textbf{Primary Type Material}—Holotype CASG 70173 and paratype CASG 70174 are both from undifferentiated Sacate-Gaviota strata, Santa Barbara County, southern
California.

Remarks—The holotype is essentially an internal cast. The paratype does not look like a cassid and might be a cymatiid, based on the shell’s high spire, numerous spiral ribs, and narrow and sculptured terminal varix. The paratype is missing also its anterior end, and its aperture is not known. Both parts are needed for proper identification. This gastropod is regarded herein as a nomen dubium.

Weaver and Kleinpell (1963: p. 190, pl. 25, fig. 10) reported also a questionable Echinophoria dalli (Dickerson, 1917) from the undifferentiated Gaviota Formation ["Tejon Stage"] in Santa Barbara County, southern California. Their report is based, however, on a poorly preserved single specimen whose anterior canal is missing, thus detailed identification is not possible.

“Galeodea” sp. Bremner, 1932

Galeodea sp. Bremner, 1932. p. 17; pl. 2, fig. 9.

Remarks—Bremner (1932) reported this gastropod (hypotype CASG 5527) from upper Paleocene (Thanetian) beds in Pozo Canyon, Santa Cruz Island, Santa Barbara County, southern California. This specimen is poorly preserved, and its anterior end is missing. This specimen might be a cfid gastropod.

DISCUSSION

Paleobiogeographic Implications

The earliest known cassid occurrence consists of three specimens of Galeodea klingeri Kiel and Bandel, 2003 of Late Cretaceous (mid-Santonian to lower Campanian) age from the Umzamba Formation in South Africa. This species was identified originally as Galeodea (Taieria) klingeri, but Beu (2008: p. 288) reported Taieria Finlay and Marwick, 1937 to be a junior synonym of Galeodea. Other Late Cretaceous occurrences of cassids, which are only possible occurrences, have been mentioned by Dall (1909), Finlay and Marwick (1937), Riedel (1995), Kiel and Bandel (2004), and Strong et al. (2019). Haydenia impressa Gabb, 1864, of early Campanian age in northern California, is one of these “possible” occurrences, but well preserved specimens of it can have a plait, half-way up the columella. This is not, however, a characteristic of cassids.

The earliest reported Paleogene cassid is “Galeodea” aff. elongata Koenen (1885: p. 22, pl. 1, figs. 21a–c) of early through late Danian age in west Greenland (Rosenkrantz 1970: p. 427). Koenen (1885) originally referred to his species as Cassidaria? [now Galeodea?], but Schnetler (2001: table 4) removed the question mark and reported this cassid from middle Paleocene (Selandian) rocks in Denmark.

Galeodea allani (Finlay and Marwick, 1937: p. 68, pl. 9, figs. 17, 19, 20) [formerly Taieria allani] from southern New Zealand is another Danian cassid. The amphitropic distribution of Paleocene cassids in west Greenland/Denmark and New Zealand might be the result of them evolving from different lineages, which existed in these two disjunct areas during the Late Cretaceous. More research is needed to verify this assertion. These Paleocene Galeodea are not morphologically similar to the earliest known cassids in the CSWNA region.

By the early Eocene, Galeodea appeared, for the first time, in the CSWNA region (Fig. 5). Some Galeodea species found in the CSWNA region differ only slightly in morphology from certain species found in Western Europe and/or the Gulf Coast-Mexico region. Hickman (2003: p. 79) used the apt phrase “species pairs,” to refer to these congenera so similar in their morphology as to indicate close phylogenetic relationship. Five examples of cassid “species pairs” are the following: (1) Galeodea meganosensis and a form of G. nodosa Solander; 1766 from; (2) G. louella and G. gallica Wrigley, 1934 from France, England, and Denmark (Table 1); (3) G. louella and G. kourees Gardner, 1939 from the Gulf Coast, northern Mexico (Nuevo León) (Gardner 1939), and the Isthmus of Tehuantepec area (Chiapas) in southern Mexico (Perrilliat et al. 2006); (4) G. sutterensis and G. turneri Gardner; 1939 from Texas; and (5) as mentioned by Durham (1942), G. tuberculiformis and G. coronata (Deshayes, 1830) from England and France. All of these similar “species pairs” are indicative of a westward-directed amphiatlantic faunistic influx between Western Europe and North America (Fig. 5). As reviewed and discussed by Harzhauser et al. (2002), this influx has been recognized, on the basis of various gastropod and bivalve species, since the 1920’s (Cooke 1924, Gardner and Bowles 1934, Clark and Vokes 1936, Palmer 1967, and Squires 1987, 2003, 2013, 2014).

The long distance involved and the relatively short duration for the influx of Galeodea from the Old World into the CSWNA region would seem to dictate a planktotrophic larval stage, which is the norm for many living tonnoideans (Bandel et al. 1994). All Galeodea species, however, have a small, one-whorl, cap-shaped protoconch, which is not indicative of planktotrophy (Beu 2008). Hughes (1968a, 1968b) described, however, intracapsular development and secreted mucus-string “drogues” that enable Galeodea species to have wide distribution despite their lack of planktotrophy. Persistence
Figure 5. Eocene global paleogeographic distribution and temporal occurrences of *Galeodea* (plotted in order of first-appearance datum). Ages of climatic events from Gradstein et al. (2012: fig. 28.11). Maps modified from Smith et al. (1994) show land masses. Solid circles = *Galeodea* occurrences; thick vertical lines indicate *Galeodea* temporal ranges. Numbers at top of columns refer to geographic regions and primary sources of data derived from Table 1. PETM = Paleocene-Eocene Thermal Maximum.
of greenhouse conditions during the middle Eocene would have facilitated the northward expansion of warm-water cassids along the west coast of North America.

Echinophoria trituberculata is the earliest known Echinophoria. Kanno (1973: p. 225) reported the earliest Echinophoria to be from the warm-water, lower upper Eocene Cowitz Formation in southwestern Washington. He did not give the species name, but E. trituberculata is the Echinophoria found in this formation. It is found also in strata as old as middle Eocene in the lower part of the Tejon Formation in southern California (Fig. 2).

Faunal-turnover Implications

During Paleocene through early late Eocene time, global-warming (“greenhouse”) conditions existed (Gradstein et al. 2012). The Paleocene-Eocene Thermal Maximum (PETM) (Figs. 2, 5) occurred at the Paleocene-Eocene boundary, and there was 5 to 8°C of warming (Sluijs et al. 2007). In addition, sea level was at least 70 to 80 m higher during the PETM than at present (Sluijs et al. 2008). As a result, thermophilic faunas were more widespread than at present day and extended to higher latitudes (Adams et al. 1990). The PETM coincided with the radiation of thermophilic Galeoidea in Western Europe, the Gulf Coast, and Mexico. As mentioned above, thermophilic cassids arrived in the CSWNA region, for the first time, during the early Eocene, not long after the PETM.

Starting in the late Eocene-early Oligocene, there was globally a transition from the warm “greenhouse” state to a colder “icehouse” climate mode. The transition was linked to complex plate tectonic processes and complex paleo-oceanographic changes, including newly created pathways for oceanic circulation in the Southern Hemisphere and the accompanying onset of thermal stratification (Berggren 1982). The rapidly deteriorating climatic conditions associated with this transition caused the demise of the thermophilic Eocene fauna in the CSWNA region. From the end of the "Tejon Stage" and beginning of the Galvinian Stage (Fig. 2), there was a corresponding change in the taxonomic composition of marine gastropods, including cassids.

Smith (1910) was the first to mention the disappearance of tropical molluscan taxa at the end of the Eocene in the CSWNA region. Keen and Bentzon (1944: p. 9) and Durham (1950) provided additional comments. Addicott (1970: p. 7) recognized that this demise, now referred to as a “faunal turnover,” (i.e., a change in the composition of a biota), coincided with a distinct decline in biodiversity. Addicott’s conclusions were based, in large part, on the lower biodiversity of gastropods in the Galvinian Stage

upper Eocene San Emigdio Formation in the southern San Joaquin Valley of California (Wagner and Schilling 1923) in comparison to the higher biodiversity of gastropods in the underlying Tejon Formation, in the same area (Anderson and Hanna 1925). More recently, other workers (Nesbitt 2003, Hickman 2003, Oleinik and Marinovich 2003, Squires 2003, and Retallack et al. 2004) have further substantiated the faunal turnover at the beginning of the Galvinian Stage.

Most of the thermophilic CSWNA cassids had already disappeared before the turnover, except for Echinophoria trituberculata, which went extinct just before the turnover (Fig. 2). Afterward, CSWNA cassids were comprised of only Echinophoria and Liracassis and restricted to Oregon, Washington, and British Columbia, of the Pacific Northwest (PNW) area of the CSWNA region, and, in contrast to the thermophilic cassids, they lived in cooler and deeper water settings (Hickman 2003). The turnover coincided with the intensification of the latitudinal-thermal gradient, origination of regional endemic taxa, a shift from species-rich assemblages to species-dominant assemblages, abrupt decline in Turritella-dominated assemblages, appearance of the modern temperate-bathyal fauna, the beginning of a strong faunal connection between the PNW and Asia, and significant presence of chemosymbiotic mollusk communities (Hickman 2003), including Liracassis associated with Oligocene whale skeletons (Nesbitt 2005). This faunal turnover also affected some other shallow-marine gastropods of the CSWNA region; namely, certain stromboids (Squires 2013) and certain ficids (Squires 2014).

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LITERATURE CITED

Abbass, H.L. 1967. A monograph on the Egyptian Paleocene and Eocene gastropods. United Arab Republic, Geological Survey, Geological Museum, Palaeontological Series Monograph 4:1–154.

Abbott, R.T. 1968. The helmet shells of the world (Cassidae). Part 1. Indo-Pacific Mollusca, Vol. 2, pp. 15–202.

Adams, C.G., D.E. Lee, and B.R. Rosen. 1990. Conflicting isotopic and biotic evidence for tropical sea-surface temperatures during the Tertiary. Palaeogeography, Palaeoclimatology, and Palaeoecology 77:289–313.

Addicott, W.O. 1970. Tertiary paleoclimatic trends in the San Joaquin Basin, California. U.S. Geological Survey Professional Paper 644-D:1–19.

Aldrich, T.H. 1885. Notes on the Tertiary of Alabama and Mississippi, with descriptions of new species. The Journal of the Cincinnati Society of Natural History 8:145–155.

Anderson, F.M., and G.D. Hanna. 1925. Fauna and stratigraphic relations of the Tejon Eocene at the type locality in Kern County, California. Occasional Papers of the California Academy of Sciences 11:1–249.

Armentrout, J.M. 1975. Mulluscan biostratigraphy of the Lincoln Creek Formation, southwest Washington. U.S. Geological Survey Professional Paper 644-D:1–18.

Berggren, W. 1982. Role of ocean gateways in climatic change. Pp. 118–125 in Climate Change in Earth History. National Academy Press, Washington, D.C.

Beu, A.G. 1981. Australian gastropods of the family Bursidae. Part 1. The families of Tonnacea, the genera of Bursidae, and revision of species previously assigned to Tutufa Joussenmume, 1881. Records of the Australian Museum 33:248–324.

Beu, A.G. 2008. Recent deep-water Cassidae of the world. A revision of Galeoidea, Occorys, Scosnia, Echinoporia and related taxa, with new genera and species (Mollusca, Gastropoda). In V. Héros, R.H. Cowie, and P. Bouchet [eds.]. Tropical Deep-Sea Benthos 25. Mémoires du Muséum national d’Histoire naturelle 196:269–387.

Beu, A.G. 2010. Neogene tonnoidean gastropods of tropical and South America: Contributions to the Dominican Republic and Panama paleontological projects and uplift of the Central American Isthmus. Bulletins of American Paleontology 377:1–499.

Bouchet, P., and J.-P. Rocroi. 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. Malacologia 61:1–526.

Brenner, C. St. J. 1932. Geology of Santa Cruz Island, Santa Barbara County, California. Santa Barbara Museum of Natural History Occasional Papers 1, 33 pp.

Broccoli, G.B. 1814. Conchologia fossile subappennine con osservazioni geologiche sugli Appennini. Stamperia Reale, Milano. 712 pp.

Brown, T. 1839. Illustrations of the fossil conchology of Great Britain and Ireland: with the description and localities of all the species. Ainsworth and Sons, Manchester, England. 273 pp.

Clark, B.L. 1929. Stratigraphy and faunal horizons of the Coast Ranges of California. With illustrations of index fossils of Tertiary horizons. Privately published, Berkeley, California. 30 pp. + 50 pls.

Clark, B.L. 1942. New middle Eocene gastropods from California. Journal of Paleontology 16:116–119.

Clark, B.L., and H.E. Vokes. 1936. Summary of marine Eocene sequence of western North America. Geological Society of America Bulletin 47:851–878.

Clark, B.L., and A.O. Woodford. 1927. The geology and paleontology of the type section of the Meganos Formation (lower middle Eocene) of California. University of California Publications Bulletin of the Department of Geological Sciences 17:63–142.

Conrad, T.A. 1834. Descriptions of new Tertiary fossils from the southern states. Appendix, pp. 130–157 in T.A. Conrad, Observations on the Tertiary and more recent formations of a portion of the southern states Journal of the Academy of Natural Sciences of Philadelphia 7:116–157.

Conrad, T.A. 1849. Fossils from northwestern America. Appendix, pp. 723–728 in Dana, J.D., Geology. U.S. Exploring Expedition, 1838–1842, under the command of Charles Wilkes. Philadelphia, vol. 10:723–728. [Reprinted by Dall, 1909, U.S. Geological Survey Professional Paper 59:152–157].

Conrad, T.A. 1854. Fossil Testacea of the Tertiary green-sand and marl-bed of Jackson, Mississippi. Determined and named by T.A. Conrad. P. 287 in B.L.C. Wailes. Report on the Agriculture and Geology of Mississippi embacing a sketch of the social and natural history of the state. Lippincott, Crambo. Mississippi. 371 pp.

Conrad, T.A. 1855. Descriptions of fossil shells from the Eocene and Miocene formations of California. House Doc. No. 129, July, 1855, pp. 9–20. Vol. 3, 33d Congress, 1st Session, 1855. Appendix to Preliminary Report by W.P. Blake. [Reprinted by Dall, 1909, U.S. Geological Survey Professional Paper 59:163–171].

Conrad, T.A. 1857. Report of explorations in California for Railroad Routes [Pacific R. R. Reports], U.S. 33d Congress, 2d Session, Senate Ex. Doc. 78 and House Ex. Doc. 91, vol. 5, pts. 2, app. Art 2, pp. 317–319, pls. 2–9.

Cooke, C.W. 1924. American and European Eocene and Oligocene mollusks. Bulletin of the Geological Society of America 35:851–856.

Cossman, A.E.M. 1889. Catalogue illustré des coquilles fossiles de l’Éocène des environs de Paris. Annales de la Société Royale Malacologique de Belgique 24:3–385.

Cossman, A.E.M., and G. Pissarro. 1909. The Mollusca of the Ranikot Series. Part 1. Cephalopoda and Gastropoda. Memoirs of the Geological Society of India, Palaeontologica Indica. New Series, volume 3, Memoir 1:1–82.

Crowell, J.C., and T. Susuki. 1959. Eocene stratigraphy and paleon, 1881. Reports on the Agriculture Palaeoecology during the Tertiary. Eocene gastropods. U.S. Geological Survey Professional Paper 59:163–171].
SQUIRES—REVISION OF EOCENE WARM-WATER CASSID GASTROPODS FROM NORTH AMERICA 19

Hanna, G.D. 1924. Rectifications of nomenclature. Proceedings of the California Academy of Sciences, Series 4, 13:151–186.

Harzhauser, M., W.E. Piller, and F.F. Steininger. 2002. Circum-Mediterranean Oligo-Miocene biogeographic evolution—the gastropods’ point of view. Palaeogeography, Palaeoclimatology, Palaeoecology 183:103–133.

Hickman, C.S. 1980. Paleogene marine gastropods of the Keasey Formation in Oregon. Bulletins of American Paleontology 78:1–112.

Hickman, C.S. 2003. Evidence for abrupt Eocene-Oligocene molluscan faunal change in the Pacific Northwest. Pp. 71–87 in D.R. Prothero, L.C. Ivan, and E.A. Nesbitt [eds.]. From Greenhouse to Icehouse, the Marine Eocene-Oligocene Transition. Columbia University Press, New York.

Hickman, C.S. 2018. A new Caliiovarica species (Seguenzioidae: Chilodontidae) from the Eocene of Oregon, USA: Persistence of a relict Mesozoic gastropod group in a unique forearc tectonic setting. PaleoBios 35:1–10.

Hughes, R.N. 1968a. Laboratory observations on the feeding behaviour, reproduction and morphology of Galeoea echnophora. Zoological Journal of the Linnean Society 86:355–356.

Hughes, R.N. 1968b. A functional morphology of marine gastropods. Croom Helm, London and Sydney. 245 pp.

Kanno, S. 1973. Japanese Tertiary cassidids (Gastropoda) and their related mollusks from the west coast of North America. Tohoku University Science Report, Series 2 (Geology), Special Volume 6 (Hatai Memorial Volume), pp. 217–233.

Kappeler, K.A., R.L. Squires, and A.E. Fritsche. 1984. Transgressive marginal-marine deposits of the Avenal Sandstone, Reef Ridge, central California. Pp. 9–27 in J.R. Blueford [ed.]. Kreyenhagen Formation and related rocks. Pacific Section, Society of Economic Paleontologists and Mineralogists, Los Angeles, California.

Keen, A.M., and H. Bentson. 1944. Check list of California Tertiary Mollusca. Geological Society of America Special Papers 20:1–280.

Kiel, S., and K. Bandel. 2003. New taxonomic data for the gastropod fauna of the Umzamba Formation (Santonian–Campanian, South Africa) based on newly collected material. Cretaceous Research 24:449–475.

Kiel, S., and K. Bandel. 2004. The Cenomanian Gastropoda of the Kassenberg quarry in Mülheim (Germany, Late Cretaceous). Paläontologische Zeitschrift 78, pp. 103–126.

Koenen, A. von. 1885. Über eine Paleocäne Fauna von Kopenhagen. Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Göttingen 32:1–128.

Kreipl, K. 1997. Recent Cassididae. Verlag Chrsta Hemmen, Wiesbaden, Germany. 151 pp.

Latreille, P.A. 1825. Familles naturelles du règne animal exposées succinctement et dans un ordre analytique, avec indication de leurs genres. Baillière, Paris. 570 pp.

Linné, C. von. 1758. Systema naturae per regna tria naturae. Genera animalia. Edition decima reformata, vol. 1. Laurentius Salvius, Stockholm. 245 pp.

McWilliams, R.G. 1971. Biostratigraphy of the marine Eocene near Seattle, Washington. Northwest Science 45:275–287.

Martin, K. 1931. Mollusken aus dem Obereocän von Nanggulan. Dienst van den Mijnbouw in Nederlandsch–Indië.
Prothero, D.R.. 2003. Pacific Coast Eocene-Oligocene marine chronostratigraphy: a review and an update. Pp. 1–13 in D.R. Prothero, L.C. Ivany, and E.A. Nesbitt [eds.]. From Greenhouse to Icehouse, the Marine Eocene-Oligocene Transition. Columbia University Press, New York.

Prothero, D.R., and J.M. Armentrout. 1985. Magneostratigraphic correlation of the Lincoln Creek Formation, Washington: implications for the age of the Eocene/Oligocene boundary. *Geology* 13:208–211.

Prothero, D.R., E. Nesbitt, A.R. Niem, and D. Kleibacker. 2001. Magnetic stratigraphy and tectonic rotation of the upper middle Eocene Cowlitz and Hamlet formations, western Oregon and Washington. Pp. 75–95 in D.R. Prothero [ed.]. Magnetic stratigraphy of the Pacific Coast Cenozoic. Pacific Section SEPM (Society of Sedimentary Geology), Book 91. Los Angeles, California.

Rettelack, G.J., W.N. Orc; D.R. Prothero, R.A. Duncan, P.R. Kester, and C.P. Ambers. 2004. Eocene-Oligocene extinction and paleoclimatic change near Eugene, Oregon. *Geological Society of America Bulletin* 116:817–839.

Riedel, F. 1995. An outline of cassidoid phylogeny (Mollusca, Gastropoda). *Contributions to Tertiary and Quaternary Geology* 32:97–132.

Risso, A. 1826. *Histoire naturelle des principales productions de l’Europe méridionale et principalement de celles des environs de Nice et des Alpes Maritimes. Tome 4*, Mollusques. Levrault, Paris. vii + 439 pp.

Rosenkrantz, A. 1970. Marine Upper Cretaceous and overmost Tertiary deposits in west Greenland: investigations before and since 1939. *Bulletin of the Geological Society of Denmark* 19:406–453.

Sacco, F. 1890. I molluschi dei terreni terziarii del Piemonte e della Liguria. Parte 7: (Harpidae e Cassididae). *Bollettino dei Musei di Zoolo gia ed Anat omia Comparata della R. Università di Torino* 5:1–20.

Schenck, H.G. 1926. *Cassididae of western America. University of California Publications Bulletin of the Department of Geological Sciences* 16:69–98.

Schenck, H.G. and A.M. Keen. 1940. California Fossils for the Field Geologist. Preliminary edition. Stanford University, Palo Alto, California. 86 pp.

Schumacher, C.F. 1817. Essai d’un nouveau système des habitations des vers testacés. Schultz, Copenhagen. iv + 288 pp.

Schnetler, K.I. 2001. The Selandian (Paleocene) mollusc fauna from Copenhagen, Denmark: the Poul Harder 1920 collection. *Geology of Denmark Survey Bulletin* 37:7–85.

Schnetler, K.I., and C. Heilman-Clausen. 2011. The molluscan fauna of the Eocene Lillebaelt Clay, Denmark. *Cainozoic Research* 8:41–99.

Scopoli, G.A. 1777. *Introducito ad historianiaa nautreumz sisterns generae lapidum, plantrarum et animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges natureg. Prague*, 506 pp.

Sluijs, A., G.J. Bowen, H. Brinkhuis, L.J. Lounes, and E. Thomas. 2007. The Palaeocene-Eocene Thermal Maximum super greenhouse: biotic and geochemical signatures, age models and mechanisms of global change. Pp. 323–349 in M. Williams, A.M. Haywood, F.J. Gregory, and D.N. Schmidt [eds.]. *Deep-Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies*. The Micropalaeontological Society, Special Publications. The Geological Society, London.

Sluijs, A., H. Brinkhuis, E.M. Crouch, C.M. John, L. Handley, D.
Munsterman, S.M. Bohaty, J.C. Zachos, G.-J. Reichart, S. Schouten, R.D. Pancost, J.S. Sinninghe Damsté, N.L.D. Weters, A. F. Lotter, and G.R. Dickens. 2008. Eustatic variations during the Paleocene-Eocene greenhouse world. *Paleoceanography* 23, 18 electronic pages. [PA4216, doi:10.1029/2008PA001615]

Smith, A.G., D.G. Smith, and B.M. Funnel. 1994. Atlas of Mesozoic and Cenozoic Coasts. Cambridge University Press, Cambridge. 99 pp.

Smith, J.P. 1910. The geologic record of California. *Journal of Geology* 18:216–227.

Sowerby, J. 1812. The mineral conchology of Great Britain. Vol. 1. Self-published, London. 32 pp.

Squires, R.L. 1977. Middle Eocene molluscan assemblage and stratigraphy, lower Piru Creek, Transverse Ranges, California. *California Division of Mines and Geology, Special Report* 129:81–86.

Squires, R.L. 1984. Megapaleontology of the Eocene Llajas Formation, Simi Valley, California. *Contributions in Science* 350, 76 pp.

Squires, R.L. 1986b. Eocene macropaleontology of the Whiteraker Peak area, Los Angeles and Ventura counties, California. *Contributions in Science* 388, 93 pp.

Squires, R.L. 1988a. Geologic age refinements of West Coast Eocene molluscan mollusks. Pp. 107–112 in M.V. Filewicz and R.L. Squires [eds.]. Paleogene Stratigraphy, West Coast of North America. Pacific Section, Society of Economic Paleontologists and Mineralologists. Vol. 58. Los Angeles, California.

Squires, R.L. 1988b. Eocene macropaleontology of northern Lockwood Valley, Ventura County, California. *Contributions in Science* 398, 23 pp.

Squires, R.L. 1988c. Rediscovery of the type locality of *Turritella andersoni* and its geologic age implications for west coast Eocene strata. Pp. 203–208 in M.V. Filewicz and R.L. Squires [eds.]. Paleogene Stratigraphy, West Coast of North America. Pacific Section, Society of Economic Paleontologists and Mineralologists. Vol. 58. Los Angeles, California.

Squires, R.L. 1989. A new pseudolivine gastropod genus from coastal-western North America: phylogenetic and global paleobiogeographic implications. *Contributions in Science* 522:1–27.

Squires, R.L., and D.M. Advocate. 1986. New early Eocene mollusks from the Orocopia Mountains, southern California. *Journal of Paleontology* 60:851–864.

Squires, R.L., and R.A. Demetrion. 1992. Paleontology of the Eocene Bateque Formation, Baja California Sur, Mexico. *Contributions in Science* 434:1–55.

Squires, R.L., and R.A. Demetrion. 1994. New reports of Eocene mollusks from the Bateque Formation, Baja California Sur, Mexico. *The Veliger* 37:125–135.

Stewart, R.B. 1927. Gabb’s California fossil type gastropods. *Contributions in Science* 15:1–80.

Strong, E.E., N. Puillardre, A.G. Beu, M. Castelin, and P. Bouchet. 2019. Frogs and tuns and tritons—a molecular phylogeny and revised family classification of the predatory gastropod superfamily Tonnaeoida (Caenogastropoda). *Molecular Phylogenetics and Evolution* 130:18–34.

Sullivan, J.M., and J. Gardner. 1939. *Galeodea* (*Gomphopages*) *millsaspi* Sullivan and Gardner n. sp. Pp. 26–27 in J. Gardner. Notes on the fossils from the Eocene of the Gulf Province. *U.S. Geological Survey Professional Paper* 193–B:17–44.

Suter, H. 1913. Manual of the New Zealand Mollusca. Government Printer, Wellington xxiii + 1120 pp. [Atlas, 72 pls., published 1915].

Suter, H. 1917. Descriptions of new Tertiary Mollusca occurring in New Zealand, accompanied by a few notes on necessary changes in nomenclature. Part 1. *New Zealand Geological Survey Paleontological Bulletin* 5, 93 pp.

Tegland, N.M. 1931. The gastropod genus *Galeodea* in the Oligocene of Washington. *University of California Publications Bulletin of the Department of Geological Sciences* 19:397–434.

Turner, F.E. 1938. Stratigraphy and Mollusca of the Eocene of western Oregon. *Geological Society of America Special Papers* 10:1–130.

Verbinnen, G., I. Segers, F. Swinner, K. Kreipl, and D. Monsecour. 2016. Cassididae. An amazing family of seahells. ConchBooks, Harxheim, Germany. 251 pp.

Vokes, H.E. 1939. Molluscan faunas of the Domengine and Arroyo Hondo formations of the California Eocene. *Annals of the New York Academy of Sciences* 38:1–246.

Wagner, C.M., and K.H. Schilling. 1923. The San Lorenzo Group of the San Emigdio region, California. *University of California Publications Bulletin of the Department of Geological Sciences* 14:235–276.

Waring, C.A. 1917. Stratigraphic and faunal relations of the Martinez to the Chico and Tejon of southern California. *Proceedings of the California Academy of Sciences*, Series 4, 7:41–124.

Weaver, C.E. 1912. A preliminary report on the Tertiary paleontology of western Washington. *Washington Geological Survey Bulletin* 15:1–80.

Weaver, C.E. 1942. Paleontology of the marine Tertiary formations
of Oregon and Washington. *University of Washington Publications in Geology* 5:1–790.

Weaver, C.E. 1953. Eocene and Paleocene deposits at Martinez, California. *University of Washington Publications in Geology* 7:1–102.

Weaver, C.E., and K.V.W. Palmer. 1922. Fauna from the Eocene of Washington. *University of Washington Publications in Geology* 1:1–56.

Weaver, D.W., and R.M. Kleinpell. 1963. Oligocene biostratigraphy of the Santa Barbara embayment, California. Part 2. Mollusca from the *Turritella variata* zone. *University of California Publications in Geological Sciences* 43:81–161.

Webster, N.B., and G.J. Vermeij. 2017. The varix: evolution, distribution, and phylogenetic clumping of a repeated gastropod innovation. *Zoological Journal of the Linnean Society* 180:732–754.

Wrigley, A. 1934. English Eocene and Oligocene Cassididae, with notes on the nomenclature and morphology of the family. *Proceedings of the Malacological Society* 21:108–130.