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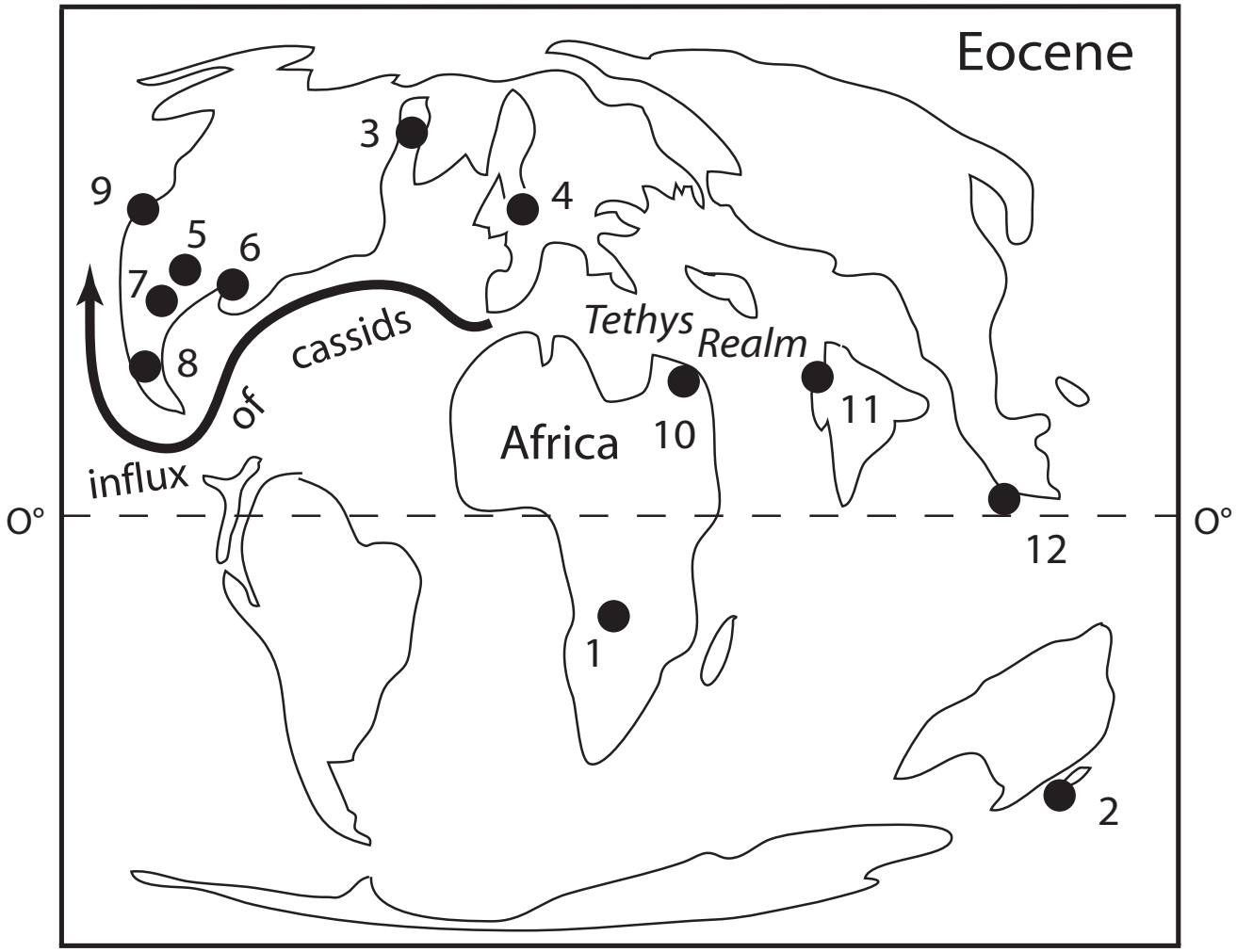

RICHARD L. SQUIRES (2019). Revision of Eocene warm-water cassid gastropods from coastal southwestern North America: implications for paleobiogeographic distribution and faunal-turnover.

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 phaliine *Echinophoria* are recognized. *Galeodea meganosensis*, *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

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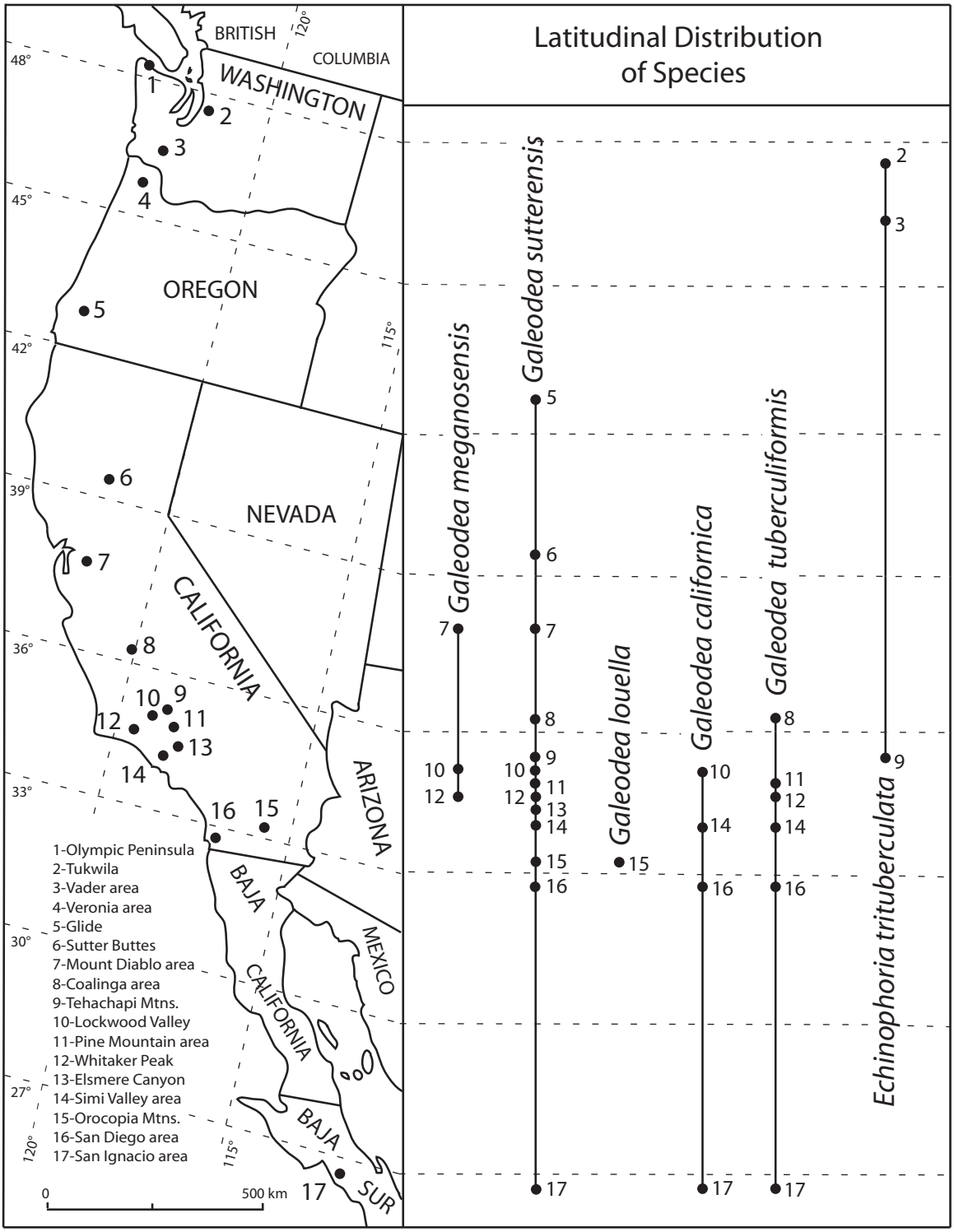

Figure 1. Index map of the coastal southwestern North America (CSWNA) region.

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 Deparment 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" ("Martinez" 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 *Liracassis 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 *Galeodea* 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 Geologîa, 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
CAENOGASTROPODA 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 *Galeodea* and *Cassis* Scopoli, 1777, as well as the phaliine *Echinophoria* Sacco, 1890 are supported as being monophyletic genera.

CASSINAE Latreille, 1825
GALEODEA Link, 1807

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

Geologic range—Late Cretaceous (Santonian to early Campanian) to Recent. *Galeodea* 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 *Galeodea*, and Beu (2010: p. 231) gave nine genus-group names. Beu (2008) demonstrated that *Galeodea* belongs in the Cassinae. He commented that protoconchs of all the Recent *Galeodea* species have almost no specific characters. They are like

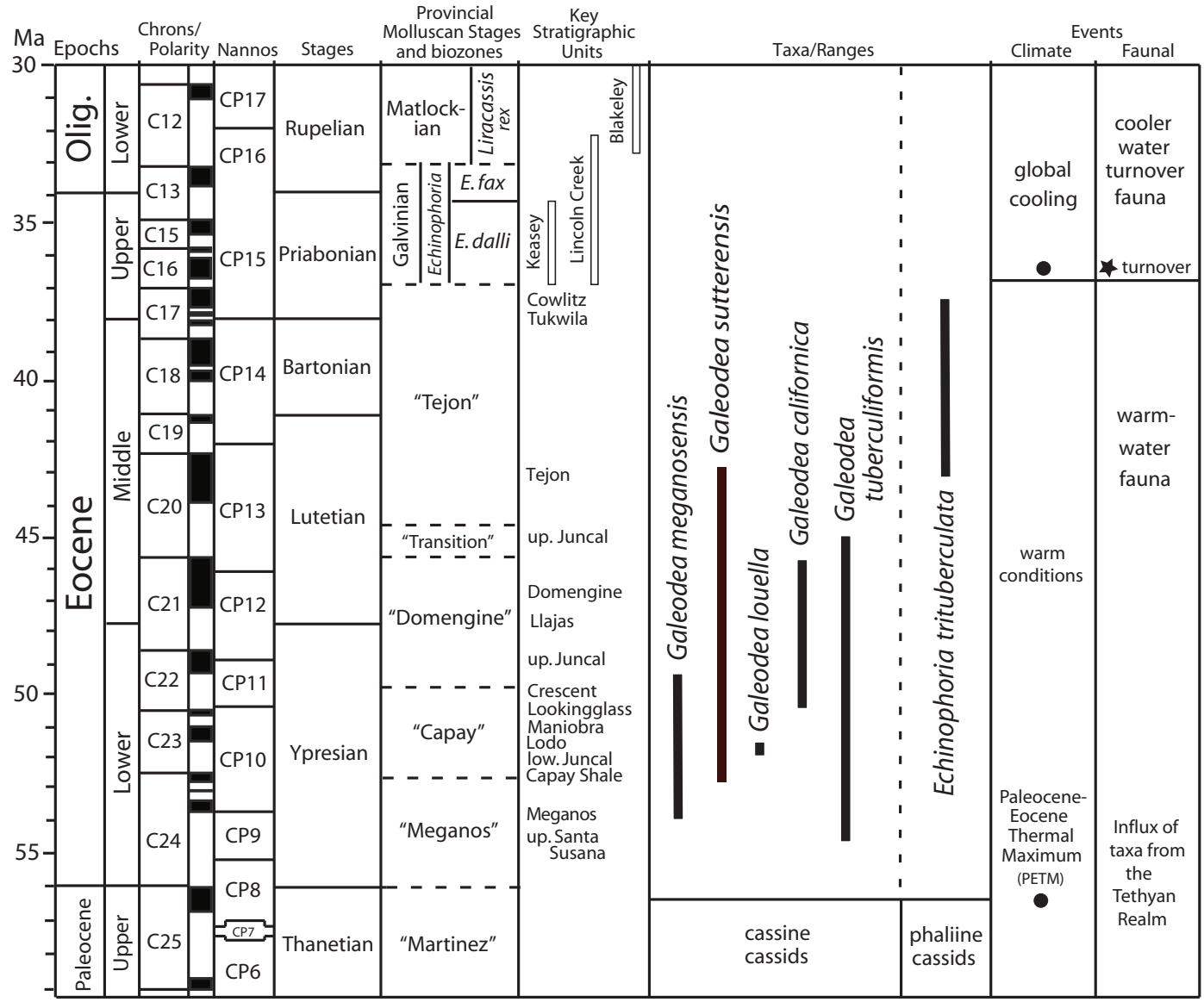

Figure 2. Chronostratigraphic diagram showing CSWNA Eocene cassid species and their geologic ranges. Geologic time scale, stage ages, chrons/polarity, nannofossil zones, and timing of global climate events from Gradstein et al. (2012: fig. 28.11). Provincial molluscan stages from Squires, (2003: fig. 2.1).

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. Durham, 1942. p. 184. Squires, 1987. p. 39; fig. 49. Squires, 1988a. pl. 1, fig. 11.

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
*boehm*i Martin, 1931	Bartonian or Priabonian	Java
brevicostatum 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
marcusi Garvie, 2013	middle Lutetian	Texas
meganosensis 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

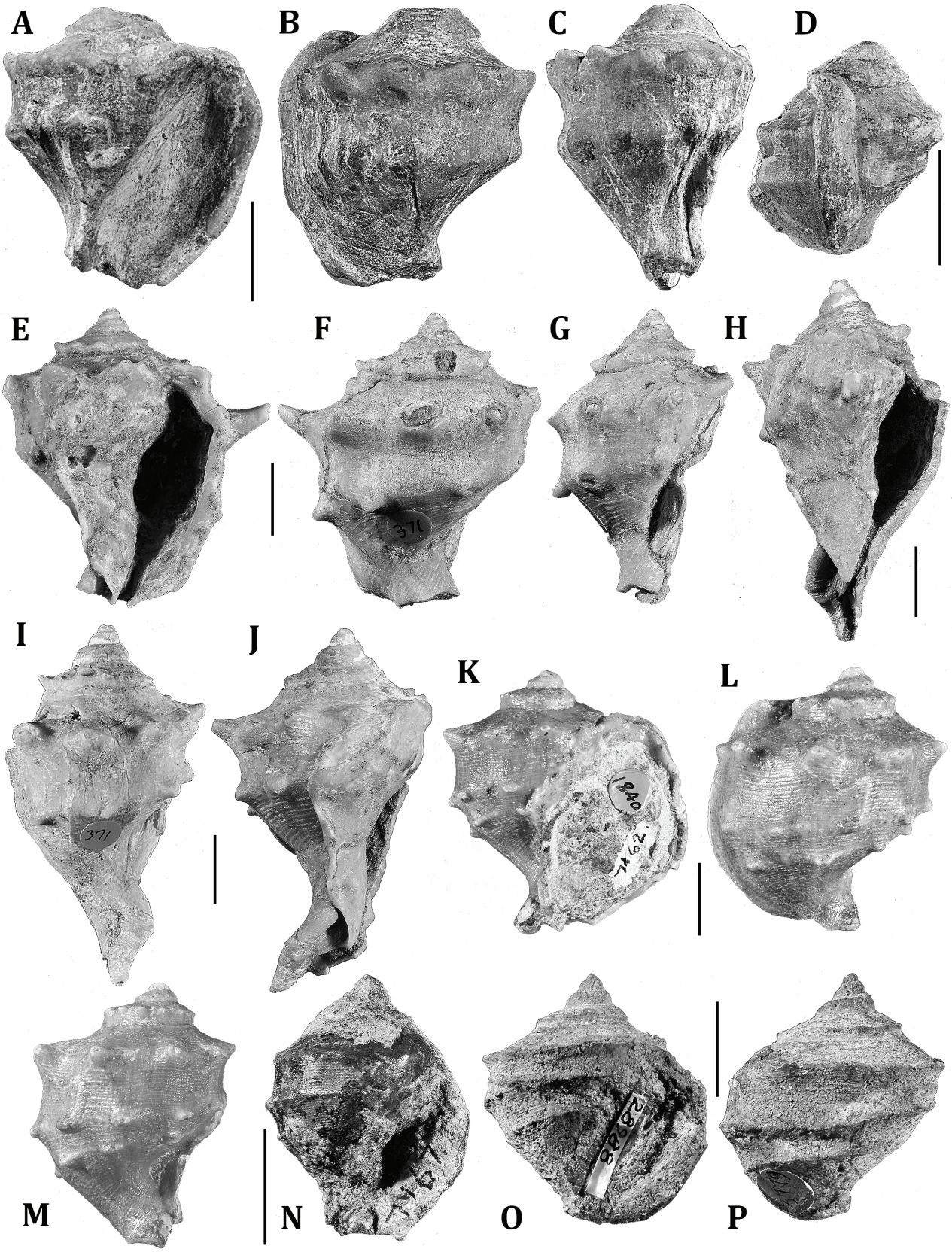

Figure 3. See caption on the bottom of page 7.

7711, 14829, 14830, and five unfigured specimens from LACMIP Locality 40827.

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)], Urruttia 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 sutterensis* Dickerson,1916. Vokes (1939) named this new gastropod *G. meganosensis* and regarded it to be a subspecies of *G. sutterensis*. 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.

GALEODEA SUTTERENSIS DICKERSON, 1916
FIG. 3E–M

Galeodea sutterensis 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. pl. 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. pl. 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*) *sutterensis* 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 sutterensis* Dickerson. Clark and Woodford, 1927. pl. 19, fig. 21 [=*Galeodea meganosensis*].

Primary Type Material—Of *G. sutterensis*, 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

Figure 3A–D. *Galeodea meganosensis* Vokes, 1939 , LACMIP Locality 40827, lower Juncal Formation (Eocene, "Capay Stage"), Whitaker Peak area, Los Angeles County, southern California). Apertural (**A**), abapertural (**B**), and left-lateral (**C**) views of hypotype, LACMIP 14829, Whitaker Peak area, Los Angeles County, southern California. **D.** Left-lateral view of hypotype, LACMIP 14830. **E–M.** *Galeodea sutterensis* Dickerson, 1916. Apertural (**E**), abapertural (**F**), and left-lateral (**G**) views of hypotype, LACMIP 14831, LACMIP Locality 40371, Llajas Formation (Eocene, "Domengine Stage"), Devil Canyon, northern Simi Valley, Los Angeles County, southern California. Apertural (**H**), abapertural (**I**), and left-lateral (**J**) views of hypotype, 14832, LACMIP Locality 40371, Llajas Formation (Eocene, "Domengine Stage"), Devil Canyon, northern Simi Valley, Los Angeles County, southern California. Apertural (**K**), abapertural (**L**), and left-lateral (**M**) views of hypotype, LACMIP 14833, LACMIP Locality 7162, Tejon Formation, (Eocene, "Tejon Stage"), Grapevine Canyon, Tehachapi Mountains, Kern County, southern California. **N–P.** *Galeodea louella* (Squires and Advocate, 1986), Maniobra Formation (Eocene, "Capay Stage"), Orocopia Mountains, Riverside County, southern California. Apertural (**N**) view of paratype LACMIP 7167. Locality 16335. Apertural (**O**) and abapertural (**P**) views of hypotype LACMIP 8836. LACMIP Locality 23799. Scale bars=10 mm.

7207, ten from LACMIP Locality 7210, three from LACMIP Locality 22362, and fifteen from LACMIP Locality 40371.

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 whorls. Teleoconch about 3.5 large whorls. Spire partly submerged. No sutural 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; tubercules 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 phlange-like refection 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, Urruttia Canyon, north of Coalinga, Fresno County, northern California (Vokes 1939) [UCMP Locality 1817, for updated locality details, see Squires (1988c)]; 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), Orocopia 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 *Echinophoria trituberculta* (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.

[*non*] *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 subglobose. Protoconch conial, 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 narrrow 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, 1942
Fig. 4A–C

Galeodea (*Caliagaleodea*) *californica* Clark, 1942. p. 118; pl. 19, figs. 15–19.

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 (Squires 1988c; [for age update, see Squires (2000)]. Llajas Formation, Simi 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.

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

Cassadaria [sic] (*Phalium*) *turberculata* [sic] Dall, in

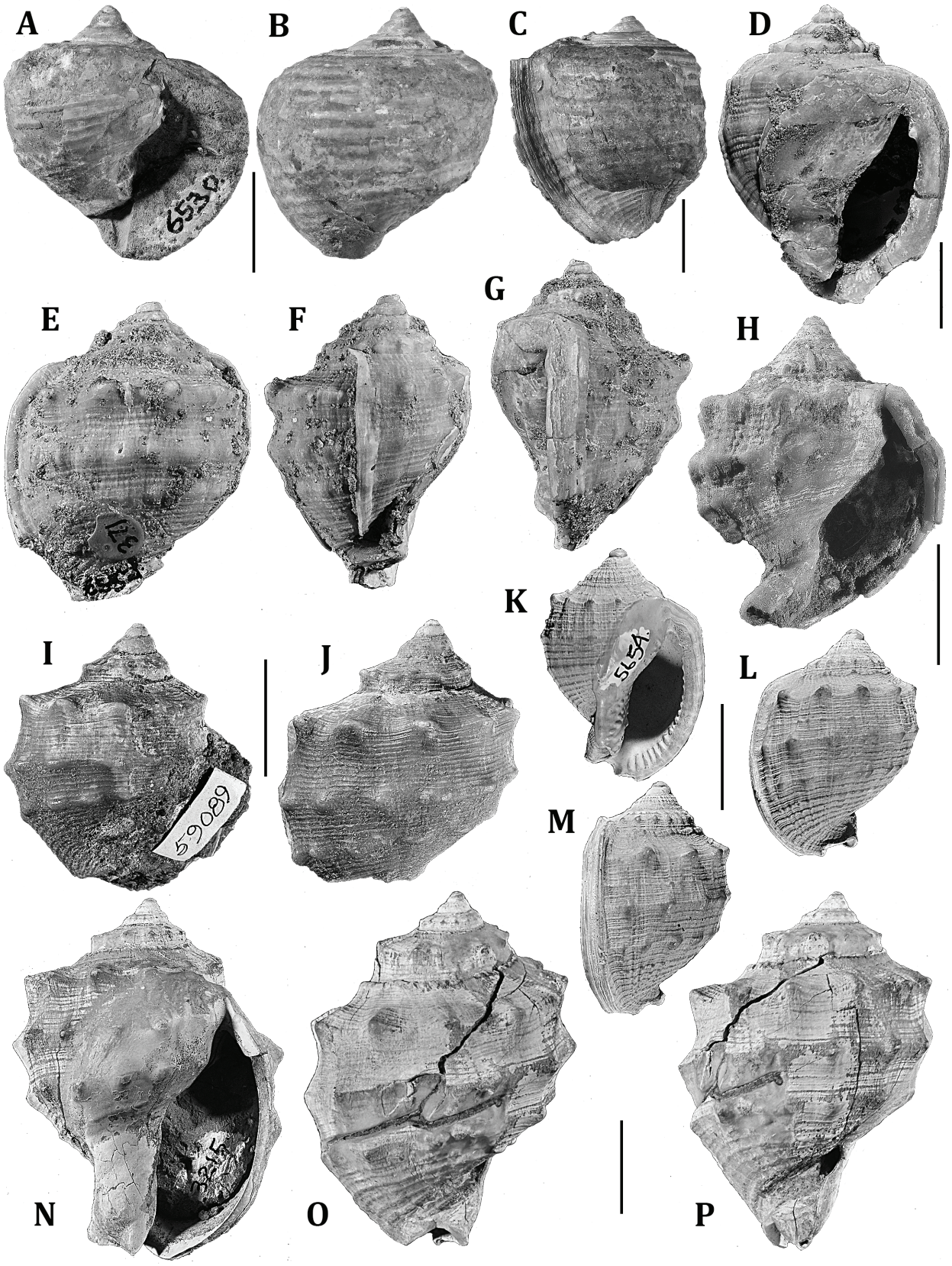

Figure 4. See caption on the bottom of page 11.

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. table 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. 7l. Squires, 1987, p. 40; fig. 50. Kappeler et al., 1984. table 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 unfigured 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/columellar 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 columellar 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**": Bateque 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,

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 6530, LACMIP Locality 7242. **C.** Abapertural (**C**) view 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.

Ventura County, southern California (Squires 1987). Llajas Formation, Ventura County, southern California (Squires 1984). Ardath Shale, San Diego County (Givens and Kennedy 1979).

Remarks—Figure 4D shows the prominent posteriormost denticle on the interior of the outer lip. Although the anterior siphonal canal is damaged or broken on most specimens, a few specimens from the Llajas Formation show that this canal is short, twisted, not notched (Fig. 4H), and with an angular left-lateral edge. At one locality in the Llajas Formation of Simi Valley, southern California, four out of 16 specimens of this species have an episodic varix, and one of these specimens has two episodic varices.

The strength of the fine-beaded spiral sculpture on *G. tuberculiformis* is largely a function of how much a specimen is weathered. Beu (2008: p. 289) reported that *G. tuberculiformis* is more like a species of *Cassis*, but *Cassis* has a well developed siphonal notch, whereas *tuberculiformis* is unnotched.

Galeodea tuberculiformis has the most widespread latitudinal distribution of any of the cassids found in the CSWNA region (Fig. 1). It is found, therefore, in numerous formations, and it is likely the earliest cassid found in this region (Fig. 2). As noted by Durham (1942), it is very similar to *Galeodea coronota* (Deshayes, 1830) of middle Eocene (Lutetian) age in England and France (see Wrigley 1934: pl. 17, figs. 36–38).

For discussions regarding whether or not Hanna (1924) was justified in renaming Gabb's (1864) *tuberculatus*, see Schenck (1926), Stewart (1927), and Abbott (1968: p. 60). The renaming was necessary, however, because Dall (in Diller 1896: p. 458) used the name *Cassadaria* (*Phalium*) *turberculata* [sic] (Gabb), which created a secondary homonym of *Cassidaria tuberculata* Risso, 1826.

PHALIINAE Beu, 1981
ECHINOPHORIA Sacco, 1890

Type species—By subsequent designation (Dall, 1909), *Buccinum intermedium* Brocchi, 1814. Oligocene and Miocene of Italy (Abbott 1968: p. 96).

Geologic range—Middle Eocene to Recent. *Echinophoria* is present in middle Miocene to early Pliocene strata, as well as uncommonly in the modern record, in the Dominican Republic and elsewhere in the Caribbean Sea region (Beu 2010).

Differential diagnosis—Spire height moderately low. Inner lip callus thin or absent and columellar callus absent; no false umbilici created by calluses. Aperture wide. 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-biostratigraphic 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 phaliine genera *Echinophoria* and especially *Liracassis* for the purpose of also furthering the PNW cassid-biostratigraphic 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,

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*" *tritubreculata* [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 slightly weaker), all with nodes, which become progressively stronger 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 adajacent 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, *E. tritubercula* 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.

Echinophoria tritubercula differs from the late Eocene to early Oligocene *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.

Echinophoria tritubercula differs from the latest Eocene to early Oligocene *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 *Echinophoria tritubercula* (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.

FAMILY AND GENUS INDETERMINATE

Galeodea? *crescentensis* Weaver and Palmer, 1922 *nomen inquirendum*

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

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.

Cassis (*Coalingodea*) *crescentensis* (Weaver and Palmer). Abbott, 1968. p. 60.

? *Galeodea crescentensis* (Weaver and Palmer, 1922). Schenck, 1926. p. 85, pl. 15, fig. 8.

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

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 *G. tuberculiformis*, but the meager material available for *crescentensis* prevents accurate taxonomic assignment of Weaver and Palmer's gastropod. A partially crushed questionable specimen of *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 *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.

"*Stramonita*" *petrosa* Conrad, 1855, *nomen dubium*

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

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 *Stramonita* Schumacher, 1817, but it might be a ficid. Based on the insufficient knowledge about *Stramonita petrosa*, Conrad's (1855) gastropod is regarded herein as a *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 *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 "*petrosa*" has been confused with *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 *Liracassis petrosa* (Conrad, 1849).

"*Galeodea*" *schencki* Weaver and Kleinpell, 1963 *nomen dubium*

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

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 ficid 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. koureos* Gardner, 1939 from the Gulf Coast, northern Mexico (Nuevo León) (Gardner 1939), and the Isthmus of Tehuatepec 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

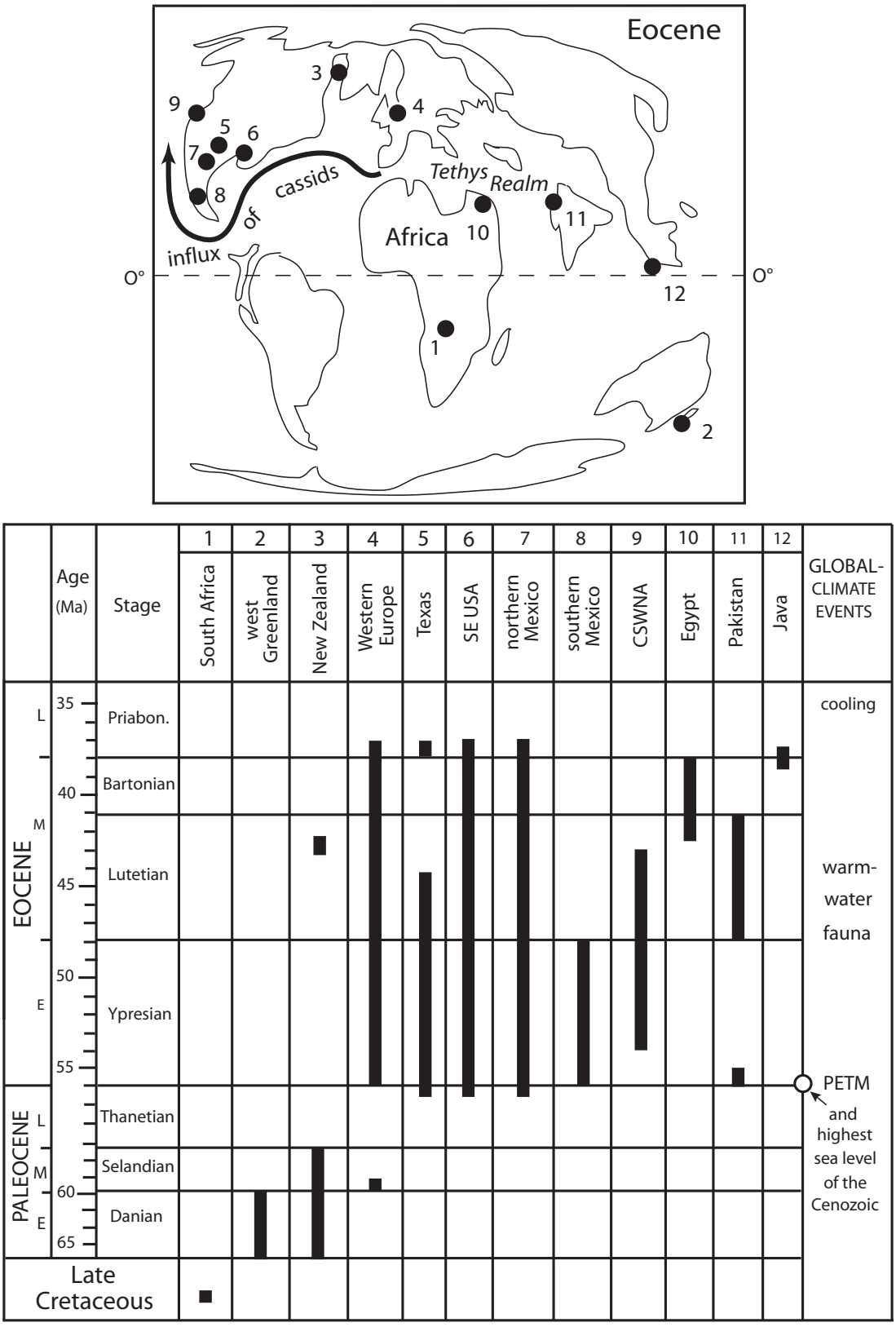

Figure 5. Eocene global paleogeographic distribution and temporal occurrences of *Galeodea* (plotted in order of first-appearance datum). Ages of climatic events from Gradstein et al. (2012: fig. 28.11). Maps modified from Smith et al. (1994) show land masses. Solid circles=*Galeodea* occurrences; thick 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 tritubercula*ta is the earliest known *Echinophoria*. Kanno (1973: p. 225) reported the earliest *Echinophoria* to be from the warm-water, lower upper Eocene Cowlitz Formation in southwestern Washington. He did not give the species name, but *E. tritubercula* 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 *Galeodea* 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 Bentson (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 Marincovich 2003, Squires 2003, and Retallack et al. 2004) have further substantiated the faunal turnover at the beginning of the Galvianian Stage.

Most of the thermophilic CSWNA cassids had already disappeared before the turnover, except for *Echinophoria tritubercula*, which went extinct just before the turnover (Fig. 2). Afterward, CSWNA cassids were comprised of only *Echinophoria* and *Lircassis* 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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