Title

Revision of northeast Pacific Paleogene cypraeoidean gastropods (Mollusca), including recognition of three new species: Implications for paleobiogeographic distribution and faunal turnover

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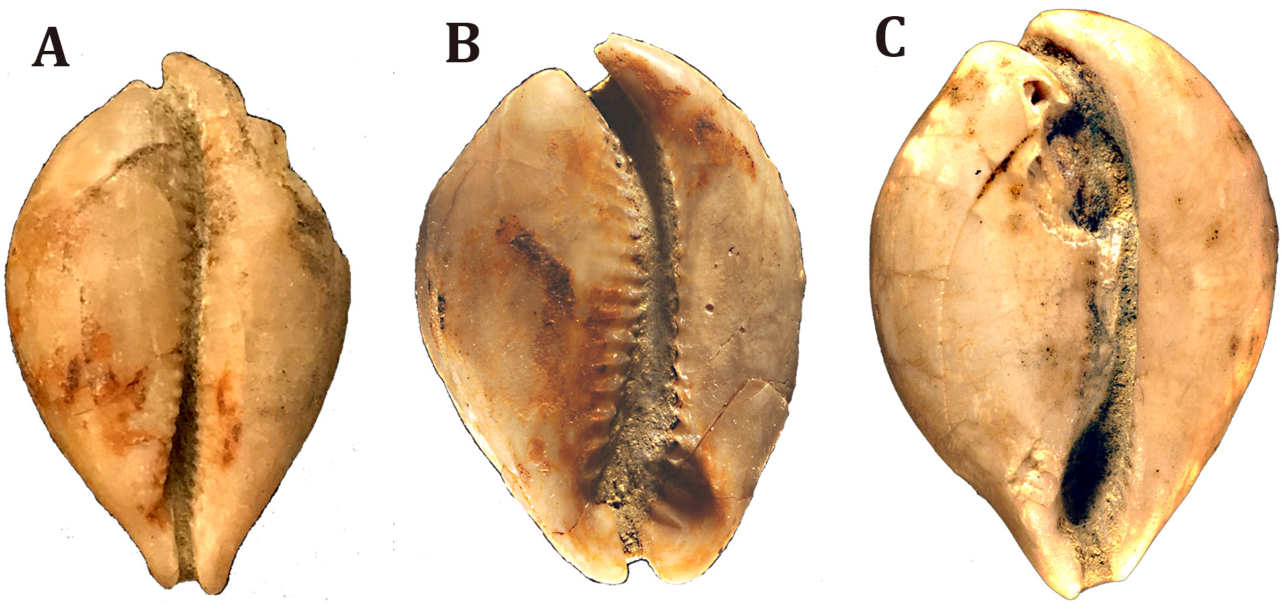

Lindsey T. GROVES & Richard L. SQUIRES (2023).

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Cover: New species of northeast Pacific Eocene cypraeoidians: A) *Subepona leahae* Squires and Groves in Groves and Squires n. sp., basal view, 2.7x, length 29.5 mm, width 13.9 mm, height 15.1 mm. B) *Bernaya kaylinae* Squires and Groves in Groves and Squires n. sp., basal view, 3.8x, length 25.6 mm, width 17.3 mm, height 12.9 mm. C) *Eocypraea judithsmithae* Groves and Squires n. sp., basal view, 2.4x, length 16.7 mm, width 18.3 mm, height 13.8 mm.

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Revision of northeast Pacific Paleogene cypraeoidean gastropods, including recognition of three new species: implications for paleobiogeographic distribution and faunal turnover

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The Paleogene cypraeoidean fauna of the northeast Pacific region (NEP), extending from Vancouver Island, British Columbia, Canada southward to Baja California Sur, México, consists of 12 genera, 20 named species (three of which are new), six open-nomenclature species, one Cypraeidae, indeterminate to genus and species, one cf. species, and four *nomina dubia*. All taxa are figured here. Species reassigned at the genus level are *Protocypraea*? *simiensis* (Nelson, 1925) and *Luponovula maniobraensis* (Squires and Advocate, 1986). Improved documentation of known NEP species include *Propustularia kemperae* (Nelson, 1925), *Grovesia castacensis* (Stewart, 1926) [1927]), *G. mathewsonii* (Gabb, 1864), and *Eratotrivia crescentensis* (Weaver and Palmer, 1922). The three new species, *Subepona leahae, Bernaya kaylinae*, and *Eocypraea judithsmithae* are from the upper lower Eocene Llajas Formation of Simi Valley, Ventura County and Devil Canyon, Los Angeles County, California. Six open-nomenclature species need better preserved material; they are: *Bernaya* sp., two *Protocypraea*? sp., *Gisortia* sp., *Eocypraea* sp., and *Cypraedia* sp., as does an indeterminate cypraeid from the Lodo Formation of central California. *Nomina dubia* are "*Bernaya*" *fresnoensis* (Anderson, 1905), "*Eocypraea*" *bayerquei* (Gabb, 1864), "*Sphaerocypraea*" *martini* (Dickerson, 1914), and "*Sulcocypraea*" *oakvillensis* (Van Winkle, 1918). *Eratotrivia mackini* (Durham, 1944) is herein reassigned to the synonymy of *Grovesia mathewsonii* (Gabb, 1869). The NEP Paleocene cypraeoidean fauna consists of four genera, a cypraeid of unknown generic affinity, and two *nomina dubia*. The early Eocene "Capay Stage" cypraeoidean fauna is comprised of eight genera and two *nomina dubia*. That was during the peak of NEP cypraeoidean biodiversity, which coincided with the "Early Eocene Climate Optimum" (EECO), the warmest time of the Paleogene. At the end of "Capay" time, biodiversity abruptly decreased, and this trend continued to the end of "Domengine Stage" time, when a faunal turnover took place. The cypraeoidean faunas in the subsequent "Tejon Stage" and Galvinian Stage continued to be diminished because of the ongoing cooling of the ocean waters. Continued global cooling eventually caused the disappearance of the thermophilic Paleogene NEP cypraeoideans before the beginning of the Oligocene. Most of the NEP cypraeoidean fauna is very similar morphologically to species found in the Tethys region of Europe, especially France, Italy, and Ukraine. These similar species are indicative that the introduction of most of the NEP cyraeoidean genera into the NEP region was via a westward-directed, warm-water current originating in the ancient Tethys Sea region of western Europe. The point of origin of the Paleocene *Propustularia* is unknown, and the late Eocene *Nuceolaria* most likely arrived in the NEP region via a Pacific Ocean route.

Keywords: Paleocene, Eocene, Gastropoda, Cypraeidae, Eocypraeidae, faunal changes

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INTRODUCTION

Cypraeoidean gastropods, popularly referred to as "cowrie shells," had a Late Jurassic origin in Sicily, Italy, and they have been widespread since the Cretaceous (Groves 1992, 1994c; Groves and Landau 2021), with their greatest abundance and diversity today in tropical to subtropical seas (Moretzsohn 2014, Lorenz, 2017). Cypraeoideans may be herbivorous, ominivorous, commensal, or predatory. Their dispersal is the result of having a preponderance of planktonic larvae (Scheltema 1986). Only seven known genera of modern cypraeoideans have direct development (i.e., lack of planktonic

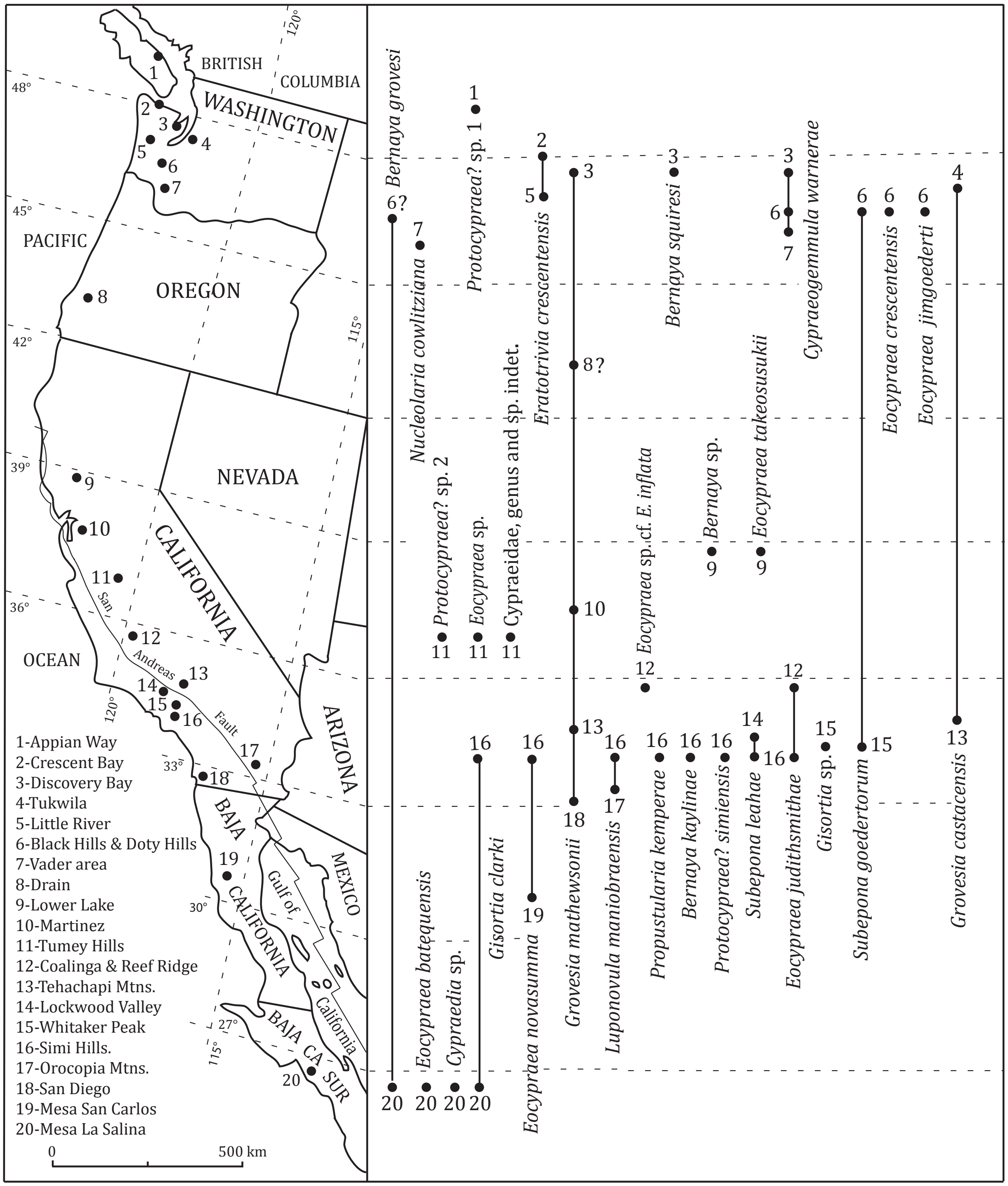

Figure 1. Index map of the northeast Pacific (NEP) region with latitudinal ranges of cypraeoidean species discussed in this present study, excluding *nomina dubia*.

larvae) (Paulay and Meyer 2006). Cypraeoideans are not common as fossils in the Northeast Pacific (NEP), and their original shell material (aragonite) normally has poor preservation. This is particularly evident in the NEP due to increased exposure to weathering associated with active tectonics throughout much of the region.

Stemming from the work by Gabb (1864), Paleogene (Paleocene and Eocene) cypraeoideans have been reported from shallow-marine strata in the northeastern Pacific region (NEP) extending from Vancouver Island, British Columbia, Canada to Baja California Sur, México (Fig. 1). Reports of Paleogene cypraeoideans from Oregon are meager and generally very poorly substantiated. Paleogene strata in the NEP region represent the most stratigraphically continuous record of data for nearshore-shelf conditions (i.e., suitable cypraeoidean habitats) found anywhere in the entire circum-Pacific area.

Perrilliat et al. (2003) documented a cypraeoidean fauna from the middle Eocene San Juan Formation near Tuxtla Gutiérrez, Chiapas, southern México. Although this fauna is not part of the NEP, and most of the specimens are poorly preserved internal molds, commentary on pertinent specimens are included.

The main purpose of this present paper is to comprehensively review and update the taxonomic composition of the NEP Paleogene cypraeoidean fauna. This information will help achieve a better understanding the paleoclimatic and paleobiogeographic implications of this fauna, as well as its evolutionary history.

MATERIALS AND METHODS

This study stems from many years of searching museum paleontological collections for cypraeoidean material to examine. The senior author used this procedure extensively searching though many of the invertebrate paleontology collections throughout the NEP region, as well as several other major museums elsewhere in the United States. Meanwhile an additional procedure was used extensively by R.L. Squires, who, in his collecting from NEP Paleogene outcrops from Washington to Baja California, was always looking for new cypraeoidean material. For example, the three newly detected species were collected in the 1980's in southern California Eocene strata by R. L. Squires, who recently gifted these specimens to the Natural History Museum of Los Angeles County. This study relied heavily on the restudy of type specimens. The authors borrowed and photographed most of the known species, however, in some cases, upon request, collection managers at various west-coast natural history museums photographed holotypes. Lateral

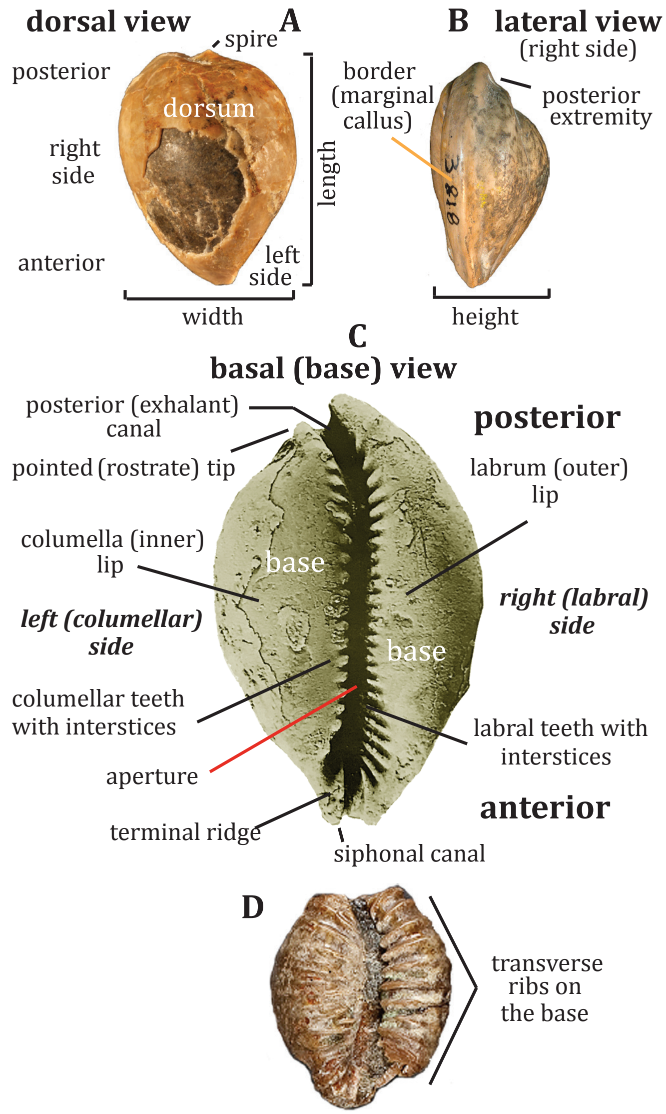

Figure 2. Illustrations of key morphologic terms used in describing cypraeoidean shells. **A**=*Bernaya* sp., hypotype LACMIP 22341.1, type 13644; **B** = *Protocypraea*? *simiensis* (Nelson, 1925), holotype UCMP 30498; **C** = *Subepona goedertorum* (Groves and Squires, 1995), holotype LACMIP 16655.23, type 12375; **D** = *Propustularia kemperae* (Nelson, 1925), holotype CASG 391.01.

views of many species are illustrated here for the first time. Although historically speaking lateral views have not been commonly used in the literature, lateral views can be critically important in identifying genera. Ingram (1942, 1947a, 1947b) illustrated many of the NEP type specimens, but he added very little new information to the cypraeoidean literature of the region. Descriptions of taxa treated here were mostly rewritten by the present authors in order to provide updated terminology and to show similarities and differences between similar species. Key terms used to describe the observed morphology of the studied specimens are illustrated in Figure 2. Measurement parameters are from Groves and Nielsen (2003: p. 351) and are defined as follows: length = greatest distance between anterior and posterior termini; width = greatest distance between lateral margins; and height = greatest distance between base and dorsum (Fig. 2). Size parameters used are the following: small size is 5 to 20 mm length, medium size is 21 to 50 mm length, and large size is >50 mm length.

Published refinements of biostratigraphic information (formations and ages) of most of the holotypes helped greatly also in this present study. The Paleocene and most of the Eocene NEP molluscan stages (Fig. 3) used in California are provincial and stem predominantly from work by Clark and Vokes (1936), Weaver (1942 [1943]), and Weaver et al., 1944). The chronostratigraphic California provincial stage names are in quotes because they are informal and also to distinguish them

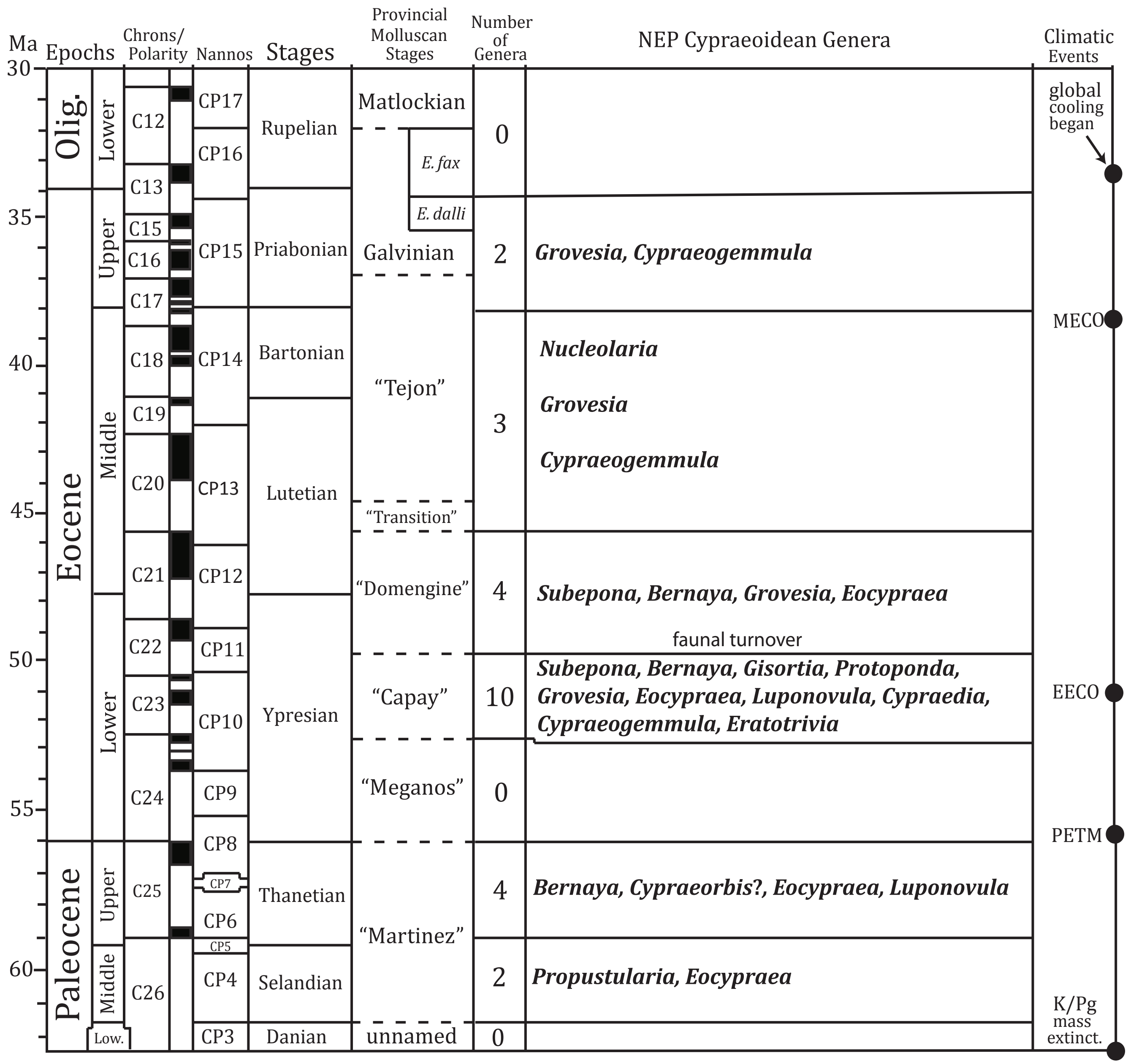

Figure 3. Chronostratigraphic diagram showing all the known NEP cypraeoidean genera, their key stratigraphic units, number of identifiable genera, and global-climate events. Geologic time scale, stage ages, chrons/polarity, nannofossil zones, and timing of global-climate events from Gradstein et al. (2012: fig. 28.11). Provincial-molluscan stages from Squires (2003: fig. 21.). Geologic age of "Stewart bed" from Squires (2022: fig. 3).

from similarly named lithostratigraphic units. Armentrout (1975) updated the out-of-date upper Eocene and lower Oligocene molluscan biostratigraphic "stages" of the Pacific Northwest by introducing and defining the Galvinian and Matlockian stages. The corresponding paleomagnetic chrons/polarity and nannofossil zones of all of these chronostratigraphic units, as well as their formalized European stage names are shown in Figure 3. In this present report, the European Paleocene Stage Danian is used for the NEP provincial "unnamed" stage, and the European Selandian and Thanetian stages are used in place of the NEP provincial and informal Paleocene "Martinez Stage," because the latter is very poorly defined and, therefore, is not amenable to being subdivided. Also in this present report, the NEP provincial and informal names for the various Eocene stages are used because of their common usage in the literature. Their equivalency to the corresponding European Eocene stages in shown in Figure 3.

Geologic time scale, stage ages, chrons/polarity, nannofossil zones, and timing of global-climate events ("Paleocene-Eocene Thermal Maximum" [= PETM], "Early Eocene Climatic Optimum" [= EECO], and "Middle Eocene Climatic Optimum" [= MECO]) utilized in this present report (Fig. 3) are discussed and illustrated in detail by Gradstein et al. (2012: pp. 884, 886, fig. 28.11).

Institutional abbreviations

ANSP, Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania; **CASG,** California Academy of Sciences, Invertebrate Zoology and Geology, San Francisco, California; **CDM,** Courtenay and District Museum and Palaeontology Centre, Courtenay, Vancouver Island, Bristish Columbia, Canada; **CGS**, Canadian Geological Survey, Vancouver, British Columbia; **CIT**, California Institute of Technology, Pasadena, California (collection now stored at LACMIP); **CSUN**, California State University Northridge, Department of Geological Sciences, Northridge, California (collection now stored at LACMIP); **IGM**, Instituto de Geología, Universidad Nacional Autónoma de México, México City; **IHN**, Instituto de Historia Natural y Ecología, Tuxtla Gutiérrez, Chiapas, México; **LACMIP**, Natural History Museum of Los Angeles County, Invertebrate Paleontology Department, Los Angeles, California; **LSJU**, Leland Stanford Jr., University, Stanford, California (collection now stored at CASG); **PU**, Purdue University, West Lafayette, Indiana. **SDSNH,** San Diego Society of Natural History, San Diego, California; **UCLA**, University of California, Los Angeles (collection now stored at LACMIP); **UCMP**, University of California, Museum of Paleontology, Berkeley, California; **UCR**, University of California, Department of Earth Sciences, Riverside, California; **UWBM,** University of Washington, Burke Museum of Natural History and Culture, Seattle, Washington.

SYSTEMATIC PALEONTOLOGY

MOLLUSCA Linnaeus, 1758
GASTROPODA Cuvier, 1797
CAENOGASTROPODA Cox, 1960
SORBEOCONCHA Ponder and Lindberg, 1997
HYPSOGASTROPODA Ponder and Lindberg, 1997
LATROGASTROPODA Riedel, 2000
CYPRAEOIDEA Rafinesque, 1815

Remarks—The classification and phylogenetic relationships of cypraeiodeans are currently in a state of flux. Schilder and Schilder (1971) developed a classification scheme based on radula, osphradium, and shell characteristics, much of which was published in Schilder (1936). The classification system used in the present report for the higher systematics (phylum to superfamily) are from Bouchet et al. (2017). The lower classification system (below superfamily level) is used, as follows: Cypraeidae from Lorenz (2017); Eocypraeidae from various sources including Dolin and Lozouet (2004), Dolin and Pacaud (2009), Lorenz and Fehse (2009), and Fehse (2021); and Eratoidae from Schilder and Schilder (1971). As noted by Groves (2019: p. 132) and Fehse (2021: p. 19), taxa within Cypraeoidea include the so-called true cowries (family Cypraeidae Rafinesque, 1815); egg and spindle cowries (family Ovulidae Fleming, 1822); pedicularias (family Pediculariidae Gray, 1853), eocypraeids (family Eocypraeidae Schilder, 1924a); false cowries (family Trividae Troschel, 1863), eratos (family Eratoidae Gill, 1871); and lamellarias (family Velutinidae Gray, 1840).

The genera in this present report are arranged (systematically), according to their present classification. The arrangement at the species level is, however, alphabetical for each genus (Table 1). Summaries of the synonyms (different names for the same species) and chresonyms (usages of any given scientific name), given in the "Systematic Paleontology" section for each species, represent combinations of synonomy and chresonomy. The latter term is used in the sense of Smith and Smith (1972).

CYPRAEIDAE Rafinesque, 1815

Remarks—These are the true cowries. Fossil cypraeids are a notoriously difficult group to work on, especially as a vast majority of specimens have lost their

Taxon	Location	NEP "stage"	standard stage
Cypraeidae			
Nucleolaria cowlitziana Groves, 1994	WA	upper "Tejon"	upper Bartonian
Propustularia kemperae (Nelson, 1925)	So CA	"Martinez"	Selandian
Subepona goedertorum (Groves and Squires, 1995)	WA, So CA	"Capay" to "Domengine"	mid to up Ypresian
Subepona leahae Squires and Groves, n. sp.	So CA	"Domengine"	up. Ypres.-low. Lut.
Bernaya grovesi Squires and Demetrion, 1992	WA?, BC Méx	"Capay"	middle Ypresian
Bernaya kaylinae Squires and Groves, n. sp.	So CA	"Domengine"	up. Ypres.-low. Lut.
Bernaya squiresi Groves, 2011	WA	"Capay"	middle Ypresian
Bernaya sp.	No CA	"Martinez"	Thanetian
Protocypraea? *simiensis* (Nelson, 1925) n. comb.	So CA	"Martinez"	Thanetian
Protocypraea? sp. 1	Van Is	"Martinez"?	Thanetian?
Protocypraea? sp. 2	No CA	"Martinez"	Thanetian
Gisortia clarki Ingram, 1940	CA, BCS Méx?	"Capay"	middle Ypresian
Gisortia sp.	So CA	"Capay"	middle Ypresian
Cypraeidae, gen. and sp. indeterminate	Mid CA	"Martinez"	Thanetian
Eocypraeidae			
Eocypraea batequensis Groves, 2011	BCS Méx	"Capay"	middle Ypresian
Eocypraea crescentensis Groves, 2011	WA	"Capay"	middle Ypresian
Eocypraea jimgoerderti Groves, 2011	WA	"Trans." to "Tejon"	middle Lutetian
Eocypraea judithsmithae Squires and Groves, n. sp.	So to mid CA	"Domengine."	up. Ypres.-low. Lut.
Eocypraea novasumma (Nelson, 1925)	So CA, BC Méx	"Martinez"	Selandian
Eocypraea takeosusukii Groves, 2011	No CA	"Martinez"	Thanetian
Eocypraea sp. cf. *E. inflata* (Lamarck, 1802)	So CA	"Domengine"	upper Ypresian
Eocypraea sp.	Mid CA	"Martinez"	Thanetian
Grovesia castacensis (Stewart, 1926 [1927]) n. comb.	WA, So CA	mid "Tejon" to Galvinian	Barton.-Priabonian
Grovesia mathewsonii (Gabb, 1869)	WA, OR, So CA	"Domeng." to Galvinian	up. Ypres.-Priabonian
Luponovula maniobraensis (Squires & Advocate, 1986) n. comb.	So CA	"Capay"	middle Ypresian
Pediculariinae			
Cypraedia sp.	BCS Méx	"Capay"	middle Ypresian
Cypraeogemmula warnerae Effinger, 1938	WA	"Capay" to Galvinian	up. Ypres.-Priabon.
Eratoidae			
Eratotrivia crescentensis (Weaver and Palmer, 1922)	WA	"Capay"	middle Ypresian
Nomina dubia			
"Bernaya" fresnoensis (Anderson, 1905)	mid CA	"Domengine"	up. Ypres.-low. Lut.
"Eocypraea" bayerquei (Gabb, 1864)	No CA	Martinez?	Paleocene
"*Sphaerocypraea" martini* (Dickerson, 1914)	No CA	"Martinez"	Thanetian
"*Sulcocypraea" oakvillensis* (Van Winkle, 1918)	WA	lower Galvinian	lower Priabonian

Table 1. Paleogene cypraeoideans from NEP, with author(s), families, subfamilies, geographic distribution, and stage range. Taxa arranged following Lorenz (2017) and Fehse (2021) and listed alphabetically under each genus. Van Is=Vancouver Island, British Columbia, WA=Washington, OR=Oregon, CA=California, BCS Méx=Baja California Sur, México. No=North, So=South, mid=middle, n. comb.=new combination, n. sp.=new species, sp.=species.

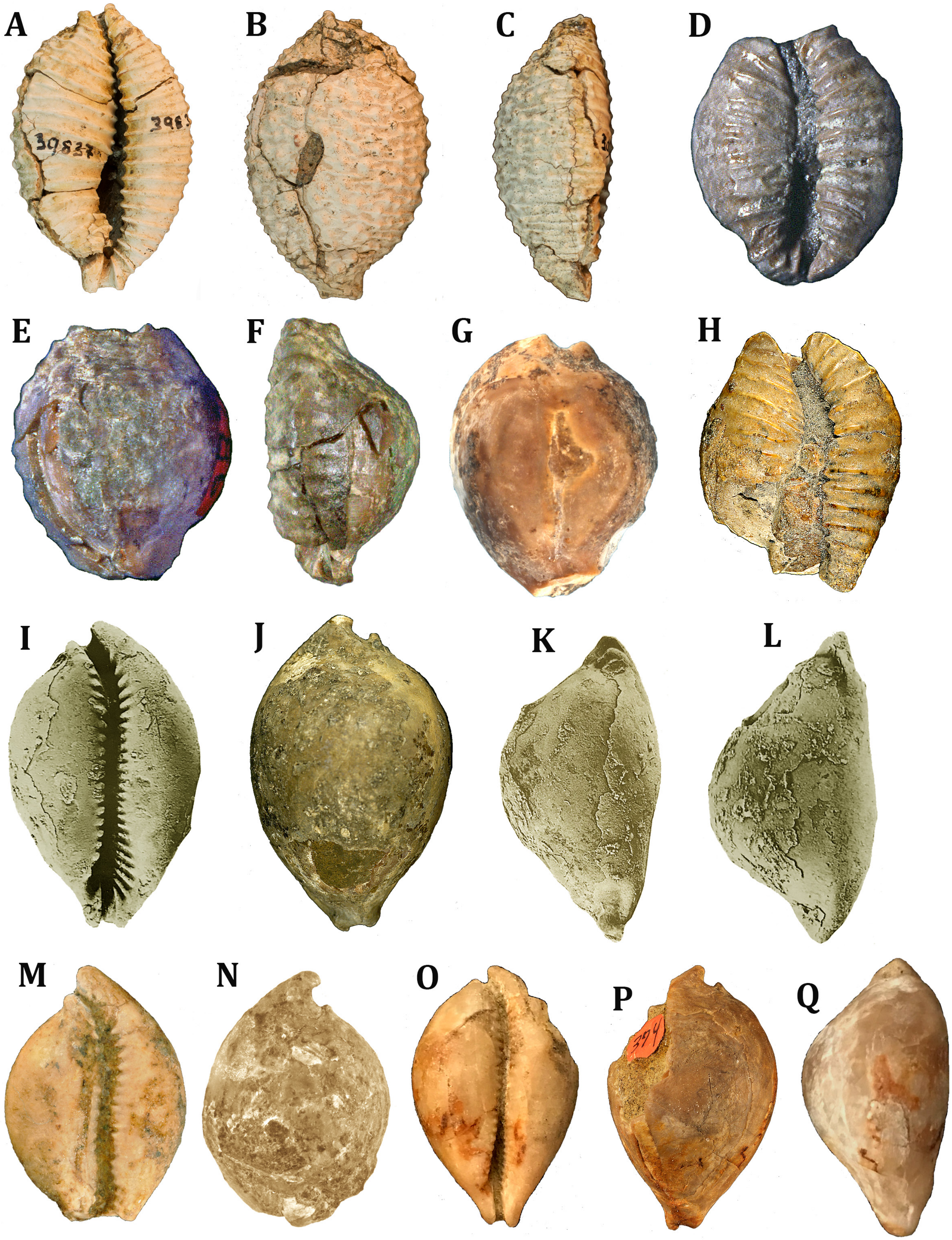
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Figure 4 (previous page). A–C. *Nucleolaria cowlitzensis* Groves, 1994, Cowlitz Formation (middle Eocene, upper "Tejon Stage"), Vader area, south-central Lewis County, Washington. Basal (**A**), dorsal (**B**), and left (columellar) side (**C**) views, 1.9x, length 27.2 mm, width 17.3 mm, height 11.3 mm, of holotype UCMP 39837, UCMP Locality D-8040. **D–H.** *Propustularia kemperae* (Nelson, 1925), Santa Susana Formation, (Paleocene, Selandian Stage), north side Simi Hills, Ventura County, southern California. Basal (**D**), dorsal (**E**), and right (labral) side (**F**), and views, 2.2x, length 21 mm, width 17.3, height 12 mm, of holotype CASG 391.01 [*ex* CASG 987], Locality CASG 391. Dorsal (**G**) view, 2.6x, length 18.2 mm, width 14.9, height 11.2 mm, of hypotype LACMIP 22307.6, LACMIP Type 14918 (LACMIP Locality 22307). Basal (**H**) view, 2.2x, length 21 mm, width 17.3, height 12 mm, of paratype UCMP 30541, UCMP Locality 3764. **I–N.** *Subepona goedertorum* (Groves and Squires, 1995), Crescent Formation (Eocene, "Capay Stage"), Black Hills, Thurston County, Washington. Basal (**I**), dorsal (**J**), left (columellar) lateral (**K**), and right (labral) (**L**) views, 2.8x, length 19.4 mm, width 12.3, height 10.8 mm, of holotype LACMIP 16655.23, LACMIP Type 12375, LACMIP Locality 16655 [=LACMIP Locality 41563; *ex* CSUN Locality 1563]. **M–N,** Juncal Formation, Canton Canyon, Whitaker Peak area, Ventura County, southern California. Basal (**M**) and dorsal (**N**) views, both 2.4x, length 19.4 mm, width 13.9, height 9.4 mm, of hypotype LACMIP 40807.1, LACMIP Type 14935 (LACMIP Locality 40807 [= LACMIP Locality 16191, *ex* CSUN Locality 807]). **O–Q,** *Subepona leahae* n. sp., Llajas Formation (Eocene, "Domengine Stage"), north side Simi Valley, Ventura County, southern California. Basal (**O**), dorsal (**P**), and left (labral) side (**Q**) views, 1.6x, length 29.5 mm, width 13.9, height 15.1 mm, of holotype LACMIP 40374.79, LACMIP Type 14936, (LACMIP Locality 40374).

color pattern, and many from the NEP are poorly preserved. Cypraeid systematics has been greatly enhanced by the works of Meyer (2003, 2004). Herein, lower level systematics below family follows that of Lorenz (2017).

EROSARIINAE Schilder, 1924a
NUCLEOLARIA Oyama, 1959

Type Species—*Cypraea nucleus* Linnaeus, 1758, by original designation (of Oyama, 1959: p. 361); Holocene, Indo-Pacific (Red Sea and east Africa to southern Japan, Australia, French Polynesia, and Hawai'i) (Groves 1994a).

Diagnosis—Shell small to medium in size; coarse to fine dorsal nodules with fine inter-nodular threads; prominent dorsal sulcus; coarse ribs on base of shell; fossula deep with strong dentition (Jousseaume, 1884: p. 98).

Geologic Range—Middle Eocene through Holocene (Groves 1994a).

Remarks—Jousseaume (1884: p. 98) originally described *Nuclearia* [*non-Nuclearia* Cienkowsky, 1865, a freshwater amoeboid].

Nucleolaria cowlitziana Groves, 1994a
Figs. 4A–C

Nucleolaria cowlitziana Groves, 1994a, p. 247–248, figs. 6, 7. Nesbitt, 1995. p. 1066. Groves, 1997. p. 7. Groves, 2000. p. 120. Dolin and Lozouet, 2004. p. 73. Lorenz, 2017. p. 220. Lorenz, 2018. p. 664, pl. 328, fig. 5.

Jenneria cowlitziana (Groves). Fehse, 2001. p. 37.

Holotype and Type Locality—UCMP 39837 (Figs. 4A–C), length 27.2 mm, width 17.3 mm, height 11.3 mm. UCMP Locality D-8040, Cowlitz Formation, south-central Lewis County, Washington.

Occurrence—Middle to upper Eocene ("Tejon Stage"), south-central Lewis County, Washington.

Etymology—Originally named for the Eocene Cowlitz Formation, Lewis County, southwest Washington.

Description—Shell of size medium size. Shape ovoid. Spire covered. Maximum height slightly posterior of midpoint. Dorsal groove faint; dorsal nodules smooth, circular, connected by fine threads that extend onto basal surface and form prominent denticulation. Marginal callus slight. Aperture curved slightly posteriorly toward columella. Denticulation prominent with smooth interstices, labial lip with 19 teeth, and columellar lip with 18 teeth. Fossula with strong denticulation. Anterior and posterior canals prominently lengthened by terminal teeth. (Groves 1994a: p. 247).

Remarks—The holotype of this Cowlitz Formation species is the only known record of this genus in the eastern Pacific. Fehse (2001: pp. 18, 37) assigned *N. cowlitziana* erroneously to the ovulid genus *Jenneria* Jousseaume, 1884, but later, following an examination of the holotype, Fehse acknowledged his error (personal communication, July 2004). Dolin and Lozouet (2004: p. 73) inexplicably questioned the provenance of this specimen and compared it to the living species *N. nucleus* (Linnaeus, 1758). In the same publication they described *Nucleolaria bezoyensis* and mistakenly claimed that their species (now reassigned to the genus *Naria* by Lorenz,

2017) was the earliest record of *Nucleolaria.* However, *N. cowlitziana* remains the earliest record of the genus and its provenance is certain.

This earliest known occurrence of *Nucleolaria* in the NEP region is an enigma. It is likely indicative of an eastward-directed faunistic influx during the Paleogene between the warm waters of the central Pacific Ocean and the NEP region. *Nucleolaria* today is a tropical Indo-Pacific genus. Like most other extant cypraeoideans, its larvae are planktonic (Groves 1994a). Emerson and Chaney (1995) documented 15 species of Indo-Pacific cypraeid species from the eastern Pacific, three of which are based on single specimens. Lorenz (2017) recognized only a single Indo-Pacific species established in the eastern Pacific. Lindberg et al. (1980) documented the only other fossil Indo-Pacific species [*Naria cernica* (G.B. Sowerby II,1870)] in the eastern Pacific from the Pleistocene of Isla de Guadalupe, Baja California, México.

PROPUSTULARIA Schilder, 1927

Type Species—*Cypraea surinamensis* Perry, 1811, by original designation (of Schilder, 1927: p. 104); Holocene, southern Florida to northern Brazil.

Diagnosis—Shell of medium size, moderately inflated to inflated, smooth. Basal margin of shell can have distinct border. Aperture widens anteriorly and strongly curves posteriorly to left. Outer lip can be somewhat swollen. Teeth strong on both lips and can have extensive lateral extent. Teeth on outer lip numerous and closely spaced, either approximately same strength as those on inner lip or stronger. Teeth on inner lip numerous and commonly weaker than those on outer lip. Inner lip crenulations can extend short distance across basal face and onto outer lip. Fossula can be prominent and moderately long. Terminal ridge, if present, narrow and sharp. Posterior terminations (rostrae) short and low, and generally equal (Schilder 1927: p. 103).

Geologic Range—Paleocene (Selandian) [herein] through Holocene; extant record based on a single extant species, which is the type species of the genus.

Remarks—Meyer's (2004: fig. 2) molecular work on cowries placed a clade, consisting of *Propustularia*, *Nesiocypraea* Azuma and Kurohara, 1967, and *Ipsa* Jousseaume, 1884, as basal to all cowries. Although the earliest known record of *Propustularia* is in the NEP region (lower upper Paleocene Selandian Stage) (new information), the place of origin of *Propustularia* has not been determined. Lorenz (2017: p. 211) reported that *Propustularia* is part of a lineage that encompasses the erosariines. Also according to him, the ancient genus *Propustularia* and its associated erosarine genera comprise a great variety of fossil taxa from America and Europe. These taxa are the genera *Subepona* Dolin and Lozouet, 2004, *Praerosaria* Dolin and Lozouet, 2004, and *Eopustularia* Fehse, 2010 [= *Subepona* Dolin and Lozouet, 2004].

Although this genus is extant, it is represented today only by its type species, *Propustularia surinamensis* (Perry, 1811), found only in the southern Florida to northern Brazil. It could be that *Propustularia* originated in the Caribbean area during the early to middle Paleocene and then spread into Baja California and southern California, both of which are known to have undergone considerable tectonic transport northward starting during the Miocene (Hornafius et al., 1986). This genus could have, however, originated in the Pacific Ocean region.

Propustularia kemperae (Nelson, 1925)
Figs. 4D–H

Cypraea kemperae Nelson, 1925. pp. 397, chart opposite 402, 424; pl. 56, figs. 9, 10; pl. 57, fig. 4. Ingram 1942. p. 104; pl. 9, figs. 8, 9. Keen and Bentson, 1944. p 152. Ingram, 1947a. p. 97; pl. 7, figs. 2, 3. Ingram, 1947b. p. 147. Zinsmeister and Paredes-Mejia, 1988. p. 12.

Propustularia kemperae (Nelson). Schilder, 1932. p. 158 [as *P. kemperae*]. Schilder, 1941. p. 89. Weaver, MS [1959]. p. 483; pl. 21, fig. 4. Schilder and Schilder, 1971. pp. 59, 125. Zinsmeister, 1974, p. 130; pl. 13 figs. 5–7 [as *kempera*]. Paredes-Mejia, 1989. p. 196–198; pl. 4, figs. 4, 5. Groves, 1992. p. 106. Groves, 1993. p. 11. Lorenz, 2017. p. 211. Groves and Squires, 2021. pp. 227 (as *Cypraea*), 286 (as *kempera*).

Propustularia kemperea [*sic*] (Nelson). Zinsmeister, 1983, pp. 64, 68, pl. 2, figs. 22–24 [as *kempera*].

Holotype and Type Locality—CASG 391.01 [*ex* CAS 987] (Figs. 4D–F), length 20.8 mm (anterior end missing), width 17.3 mm, height 11.9 mm. CASG Locality 391, Santa Susana Formation, between Runkle and Meier canyons, north side of Simi Hills, Ventura County, southern California.

Paratype—UCMP 30541 (Fig. 4H), length 21.0 mm (portion of anterior end missing), width 16.9 mm. height 11.7 mm, UCMP Locality 3764, in vicinity of the type locality of this species.

Referred Specimens—Hypotype LACMIP 22307.6, LACMIP Type 14918 (Fig. 4G), LACMIP Locality 22307 [*ex* UCLA Locality 2307], Santa Susana Formation, Meier Canyon, Simi Hills Ventura County, southern California. **Hypotype** (of Zinsmeister, 1974, 1983) UCR 4573/20.

Two additional specimens from UCMP Locality A6737, Simi Valley, Ventura County, California and one complete specimen (length 19.5 mm, width 14.8 mm and height 10.07) and four fragments CASG 391.03 (topotypes) from CASG Locality 391 are noted.

Occurrence—Selandian Stage: Lower part of Santa Susana Formation, north side of Simi Hills, Ventura County, southern California (Nelson, 1925) (see remarks below).

Etymology–Originally named for the late Mrs. Dorothy Kemper Palmer [1897-1947] (UCMP).

Description—Shell small size. Moderately inflated, dorsum mostly smooth. Base and adjacent rostrate margins heavily calloused with crenulations (elongated spiral ribs continuous with apertural teeth). Aperture generally straight or strongly curved anteriorly to left; aperture significantly widening anteriorly. Apertural crenulations prominent, numerous, long, and extending across both outer and inner lips and extending short distance onto both sides of last whorl. Approximately 12 strong crenulations on right-lateral side of base; approximately 21 weak to strong crenulations (seven of which on the medial area weakest and shorter) on left-lateral side of base; and crenulations on right-lateral side stronger than those on left-lateral side. Fossula prominent and moderately long. Posterior terminations somewhat extended on both sides of base. Anterior terminations less obvious.

Remarks—The 11 known specimens (see above) of *Propustularia kemperae* range in preservation from poor to moderately good. The holotype is figured in the present report with its anterior end complete. That is how is looked when the senior author photographed it. In recent years, however, the left side of the anterior end was broken off, and its whereabouts are unknown.

In the NEP region, *P. kemperae* is known only from the Santa Susana Formation in the Simi Hills of southern California. This species occurs only low in the Santa Susana Formation, and the type locality of this species is on a divide between Runkle and Meier canyons, where it co-occurs (Nelson 1925) with the gastropods *Mesalia martinezensis* (Gabb, 1869) and *Heteroterma trochoidea* Gabb, 1869. The geologic range of the former is late Danian to early Thanetian (Squires and Saul 2007), and the range of the latter is late Danian to early Selandian (Saul 1988). Based on the overlap of the geologic ranges of these two species, an early Selandian age is indicated for *P. kemperae*.

The hypotypes of Paredes-Mejia (1989: pp. 196–198, pl. 4, figs. 4, 5 [IGM4389]) and Perrilliat (2013: p. 133, figs. 3.41, 3.42 [IGM 4365]) are the same specimen, with different IGM hypotype numbers, of a so-called *Propustularia kemperae* from the Paleocene Sepultura Formation on the northwest flank of Mesa San Carlos, Baja California Sur, México. This specimen is very worn and/or weathered, and it cannot be identified with certainty.

Propustularia kemperae is similar to the middle Miocene *P. neugeboreni* (Hoernes and Auinger, 1880: pp. 58, 59, pl. 7, figs. 5, 6) from Lapugy (= Lăpugiu de Sus), Romania. Dolin and Lozouet (2004: p. 60, pl. 27, figs. 3a–3c, 4), Fehse (2009: pp. 14, 53, fig. 38, pl. 14, fig. 1), and Lorenz (2017: p. 211; 2018, pl. 328, fig. 2) also figured *P. neugeboreni*. *Propustularia kemperae* has much stronger and more laterally expansive sculpture on the base of its shell.

Lorenz (2017: p. 211) reported the geologic range of *Propustularia* to be Eocene to Holocene but based on new information concerning *Propustularia kemperae*, the earliest record of this genus is the Paleocene (Selandian Stage).

SUBEPONA Dolin and Lozouet, 2004

Type Species—*Subepona herrerensis* Dolin and Lozouet, 2004, by original designation (of Dolin and Lozouet, 2004: p. 59), Late Oligocene (Chattian) St. Paul-lès-Dax, Landes Department, France.

Diagnosis—Shell ovoid, smooth, and somewhat lowly to considerably inflated. Aperture mostly straight with stout teeth on both lips. Fossula trigonal, slightly convave, smooth like the columellar area, weakly but regularly convex. Ends of shell protrude. Extremities on both sides of exhalant canal rostrate (can be beaklike), with labrum (outer lip) extremity large and more curved relative to shorter and straighter columellar extremity. Slight depression associated with submerged spire. Terminal fold long, thin, extended, and bladelike. Siphonal canal long, wide, deep and clearly distinct from curve of shell margin. Marginal border on shell sides weak (mainly near ends of shell) (Dolin and Lozouet 2004: p. 60).

Geologic Range—Lower Eocene (Ypresian) to upper Oligocene (Chattian) (Dolin and Lozouet, 2004: p. 60).

Remarks—Pacaud and Vicián, 2018 reported *Eopustularia* Fehse, 2010 to be an obvious subjective synonym of *Subepona*. A fairly well preserved specimen (SDSNH 169056) from the middle Eocene Scripps Formation, near Torrey Pines, San Diego County, California (SDSNH Locality 7895) could only be identified as *Subepona* sp. as critical features are obscured.

Subepona goedertorum (Groves and Squires, 1995)
Figs. 4I–N

Proadusta goedertorum Groves and Squires, 1995. pp. 113–116, figs. 2–5 [fig. 4 is a right-lateral view, not a left-lateral view as stated in the caption; fig. 5 is a left-lateral view, not a right-lateral view as stated in the caption]. Fehse, 2009. pp., 16, 19; fig. 32.

Subepona goedertorum (Groves and Squires). Dolin and Lozouet, 2004. p. 62. Pacaud, 2018a. p. 10 (table 2).

Eopustularia goedertorum (Groves and Squires). Fehse, 2010. p. 5 (as *Proadusta goedertorum*). Lorenz, 2017. p. 210. Lorenz, 2018. p. 662, pl. 327, fig. 11.

Holotype and Type Locality—LACMIP 16655.23, LACMIP Type 12375 (Figs. 4I–L), length 19.4 mm, width 12.3 mm, and height 10.8 mm. LACMIP Locality 16655 [= LACMIP Locality 41563; *ex* CSUN Locality 1563], upper part of Crescent Formation, Larch Mountain area, Black Hills, Thurston County, southwestern Washington.

Paratype—LACMIP 16655.24, LACMIP Type 12376, length 17.1 mm, width 10.4 mm, and height 8.9 mm. Locality same as holotype.

Referred Specimens—Hypotype LACMIP 40807.1, LACMIP Type 14935, (Figs. 4M, N), length 19.0 mm, width 13.8, and height 9.4 mm. LACMIP Locality 16191 [= LACMIP Locality 40807; *ex* CSUN Locality 807), Juncal Formation, Canton Canyon, Whitaker Peak area, Los Angeles County, southern California. A poorly preserved specimen from LACMIP Locality 16848 [*ex* CSUN Locality 1564], from the Rock Candy Mountain area, Thurston County, Washington, also exhibits original shell material. Two additional poorly preserved specimens, LACMIP 41599.1, from the Crescent Formation, LACMIP Locality 41599 (*ex* CSUN Locality 1599), Middle Fork Satsop River, Dry Lakes quadrangle, Mason County, Washington are noted.

Occurrence—Lower to late early Eocene, Washington to southern California. **"Capay Stage**": Upper part of Crescent Formation, Larch Mountain area, Black Hills, Thurston County, southwestern Washington (Groves and Squires 1995) at LACMIP Locality 16848 [*ex* CSUN Locality 1564], Thurston County, in the general vicinity of the type locality (for more details, see Groves and Squires 1995: p. 116). Juncal Formation, Canton Canyon, Whitaker Peak area, Ventura County, southern California at LACMIP Locality 40807 [= LACMIP Locality 16191; *ex* CSUN Locality 807] (new information). The Juncal Formation specimen, which is from the middle lower Eocene ("Capay Stage" = "*Turritella uvasana infera*" fauna) in the Juncal Formation, was originally believed by Squires (1987: p. 35, unfigured) to be a questionable (juvenile) specimen of *Gisortia clarki* Ingram, 1940.

Etymology—Originally named for colleagues James L. (Jim) and the late Gail H. Goedert [1940-2017] (Gig Harbor, Washington).

Description—Shell small to medium in size (holotype largest known specimen). Shell ovate, slightly elongate, smooth, dorsum medium to highly arched, maximum height near midpoint. Rostrate (can be beak-like) extremities present on both sides of exhalant canal, with labrial extremity large and more curved relative to much shorter and much straighter columellar extremity. Slight depression (shallow pit) can be present above submerged spire on more mature specimen. Marginal border on shell sides very weak but noticeable near ends of shell. Basal surface of shell wide and slightly convex to flattened (on less mature specimen). Aperture generally narrow and straight throughout most of its length but posteriorly labral side noticeably curved slightly toward columella. Mature specimen labial lip (outer lip) with 26 strong teeth. Mature specimen columellar lip with 17 slightly weaker teeth. Terminal fold (on each lip) long, thin, extended, and bladelike. Siphonal canal long, wide, deep and clearly distinct from curve of shell margin. Basal marginal callus (border) on both sides of shell but strongest on left side; callus produced at both extremities, especially on anterior extremity. (Groves and Squires, 1995: pp. 114, 115).

Remarks—This species is rare. The six known specimens of *Subepona goedertorum* range range in preservation from poor to excellent. It is characterized by its smooth shell, unequal-strength rostrate posterior terminae, inflated dorsum, presence of a slight depression in the submerged-spire area, strong but short dentition on both lips, and prominent terminal folds (one on each anterior end of shell). *Subpeona goedertorum* closely resembles *S. herrerensis* Dolin and Lozouet (2004: pl. 27, figs. 3a–3c), the type species of *Subepona* from France. The holotypes are near each other in size: the holotype of *S. goedertorum* is 19.4 mm length; the holotype of *S. herrerensis* is 14 mm.

Pacaud (2018a: table 2) listed *Subepona goedertorum* (Groves and Squires, 1995) as occurring in France, as well as the United States, and no geologic nor paleontologic details were provided. The "occurrence" of this species in France is likely a typographic error.

Subepona leahae Squires and Groves n. sp.
Figs. 4O–Q

Cypraea species indeterminate. Squires, 1988. p. 12, fig. 23. Groves and Squires, 2021. p. 227.

Eocypraea (*Eocypraea*) *castacensis* (Stewart, 1926 [1927]). Squires, 2000. p. 896.

Zoobank ID—LSID: urn:lsid:zoobank.org:act:363755AA-DB51-40D7-B996-A9EBA6EBBD85

Holotype and Type Locality—LACMIP 40374.79, LACMIP Type 14936 (Figs. 4O–Q), length 29.5 mm, width 13.9 mm, height 15.1 mm. LACMIP Locality 7242 [= LACMIP 40374; *ex* CSUN Locality 374], Llajas Formation, "Stewart bed," Las Llajas Canyon, north side of Simi Valley, Ventura County, southern California.

Paratype—LACMIP 16178.1, LACMIP Type 7704, length 23.2 mm, width 17.1 mm, height 13.8 mm, LACMIP Locality 16178 [= LACMIP Locality 40984; *ex* CSUN Locality 984) Lockwood Valley, Ventura County, California. This specimen was formerly hypotype LACMIP 7704 (of Squires, 1988: p. 12, fig. 23), of *Eocypraea castacensis* (Stewart, 1926 [1927]).

Occurrence—"Domengine Stage": Juncal Formation?, Lockwood Valley, Ventura County, southern California; Llajas Formation, Las Llajas Canyon ("Stewart bed," *ex* CSUN Locality 374), Ventura County, California.

Etymology—Named for Leah Rose Regan, granddaughter of R.L. Squires (who collected the type material).

Description—Shell medium size, moderately inflated, aperture fairly straight except for moderate bend posteriorly, fossula smooth, teeth numerous and small on entire lengths of both lips, with those on the outer lip becoming slightly coarser near anterior end of shell. Posterior end of shell with outer lip projecting out over the inner lip. Anterior end with an elongate, linear projection on each lip.

Remarks—The two known specimens of *Subepona leahae* have good preservation. The holotype is from the "Stewart bed" of the Llajas Formation, and the paratype is from the Juncal Formation?, Lockwood Valley, Ventura County, southern California.

Squires (1988: p. 12, fig. 23) reported a specimen (hypotype LACMIP 7704) of "*Cypraea* species indeterminate" [now identified as *Subepona leahae*] from LACMIP Locality 40984 [*ex* CSUN Locality 984] in the Juncal Formation? in Lockwood Valley, Ventura County, southern California. This locality is in the upper 100 m of the Juncal Formation, based on work by Squires (2000: p. 896), who identified this same specimen as *Eocypraea* (*Eocypraea*) *castacensis* and revised its age to the younger "Domengine Stage," instead of the previously reported (Squires 1988) "Capay Stage."

Subepona leahae differs from *S. goedertorum* by having much finer denticulation.

BERNAYINAE Schilder, 1927
BERNAYA sensu stricto Jousseaume, 1884

Type Species—*Cypraea media* Deshayes, 1835, by original designation (of Jousseaume, 1884: p. 88), upper middle Eocene (Bartonian Stage), northwest of Paris, France.

Diagnosis—Shell medium to large in size. Oval, sides inflated, rounded. Dorsum smooth. Spire of small to medium height and partially covered by successive whorls. Aperture wide. Anterior and posterior canals deep. Anterior end smooth, concave, and broad (Jousseaume 1884: p. 88).

Geologic Range—Paleocene (herein) to Oligocene (Lorenz, 2017).

Remarks—In the NEP region, a four-species lineage of *Bernaya* occurred and ranges from late Paleocene (Thanetian Stage) to the late early to early middle Eocene "Domengine Stage."

Bernaya grovesi Squires and Demetrion, 1992
Figs. 5A–C

Bernaya (*Protocypraea*) *grovesi* Squires and Demetrion, 1992. p. 31, figs. 74-76. Groves, 1993. p. 11. Groves, 1994b. p. 12. Groves, 1997. p. 7 [as *B.* (*Protocypraea*) *grovesi*].

Protocypraea grovesi (Squires and Demetrion). Lorenz, 2017. p. 205.

Holotype and Type Locality—IGM 5172 (Figs. 5A–C), length 17 mm, width 12 mm, height 7.8 mm. LACMIP Locality 41220b [*ex* CSUN Locality 1220b], Bateque Formation, near Laguna San Ignacio, Baja California Sur, México.

Paratype—IGM 5173, length 16 mm, width 10.5 mm, height 8 mm; same locality as the holotype.

Referred Specimen—A single, slightly crushed specimen (LACMIP 41653.6, LACMIP Type 14937) measuring length 14.3 mm, width 9.2 mm, height 5.8 mm from LACMIP Locality 16655 [= LACMIP Locality 41653; *ex* CSUN Locality 1563], Crescent Formation, lower Eocene ("Capay" Stage), Larch Mountain area, Black Hills, Thurston County, southwestern Washington that strongly resembles *B. grovesi* is here noted.

Occurrence—Lower to middle Eocene ("Capay

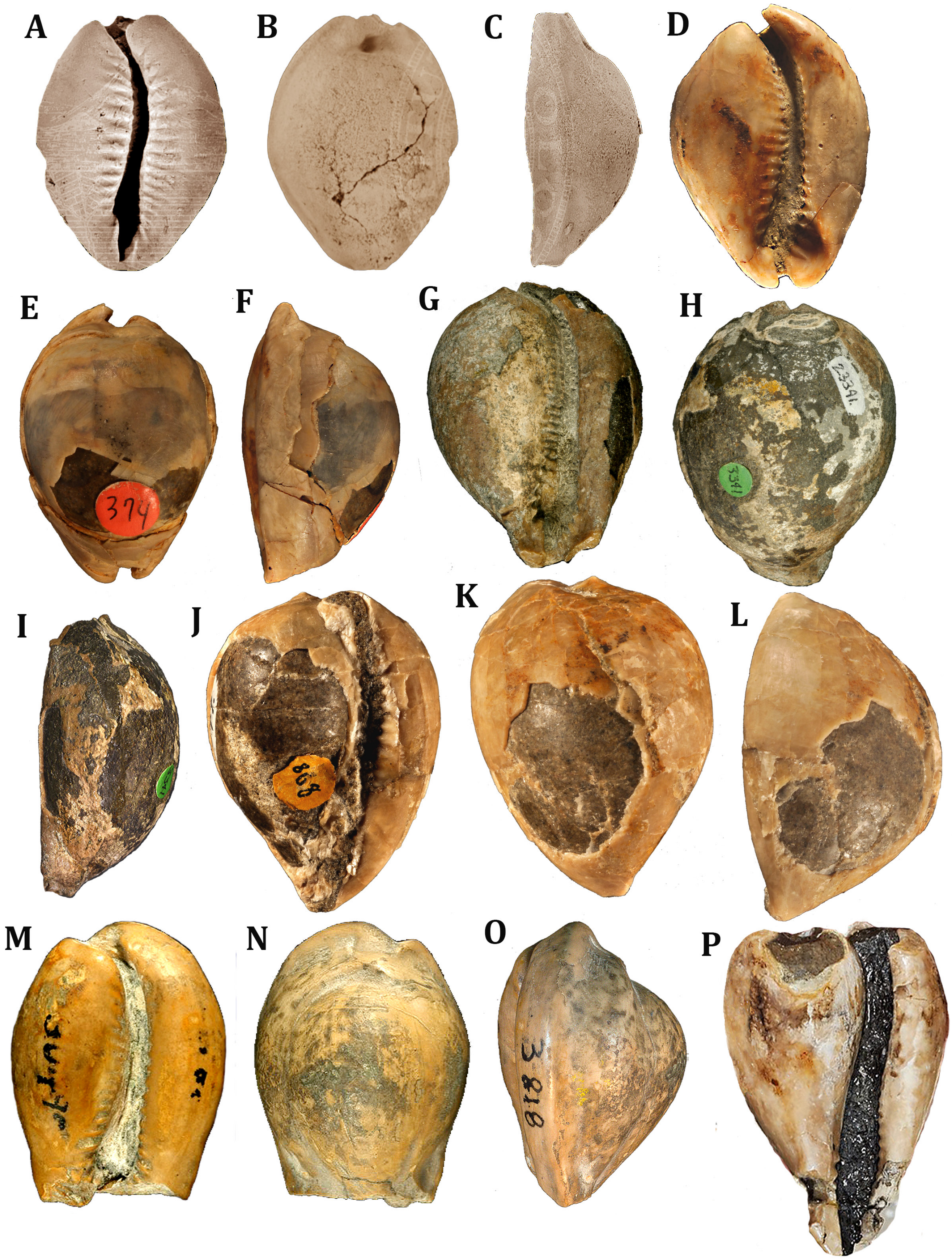
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Figure 5 (previous page) A–C. *Bernaya grovesi* Squires and Demetrion, 1992, Bateque Formation (Eocene, "Capay Stage"), Mesa La Salina, Baja California Sur, México. Basal (**A**), dorsal (**B**), and right (labral) (**C**) views, all 2.6x, length 17 mm, width 12 mm, height 7.7 mm, of holotype IGM 5172, LACMIP Locality 401220a (*ex* CSUN Locality 1220b). **D–F.** *Bernaya kaylinae* n. sp., Llajas Formation, (Eocene, "Domengine Stage"), Las Llajas Canyon, north side Simi Valley, Ventura County, southern California. Basal (**D**), dorsal (**E**), and right (labral) side (**F**) views, 3.8x, length 25.6 mm, width 17.3 mm, height 12.9 mm, of holotype, LACMIP 40374.80, LACMIP Type 14938 (LACMIP Locality 40374). **G–I.** *Bernaya squiresi* Groves, 2011, unnamed Eocene strata ("Capay Stage"), southwest end of Discovery Bay, Jefferson County, Washington. Basal (**G**), dorsal (**H**), and right (labral) side (**I**) views, 0.97x, length 52.7 mm, width 40 mm, height 26.3 mm, of holotype LACMIP 22341.1, LACMIP Type 13644, LACMIP Locality 22341. **J–L.** *Bernaya* sp., unnamed Paleocene strata (Thanetian Stage), near Lower Lake, Lake County, northern California. Basal (**J**), dorsal (**K**), and right (labral) side (**L**) views, 1.7x, length 33.8 mm, width 23 mm, height 18.3 mm, hypotype LACMIP 7047.72, LACMIP Type 14923 (LACMIP Locality 7047). **M–O.** *Protocypraea*? *simiensis* (Nelson, 1925), Santa Susana Formation (Thanetian Stage), Simi Hills, Ventura County, Paleocene, southern California. Basal (**M**), dorsal (**N**), and right (labral) side (**O**) views, 1.6x, length 32.3 mm, width 24.6 mm, height 17.3 mm, of holotype UCMP 30498, UCMP Locality 3818. **P.** *Protocypraea*? sp. 1, Oyster Bay Formation, Paleocene, Appian Way, Central Island District, Vancouver Island, British Columbia. Basal view, 1.8x, length 48.1 mm, width 31.4 mm, height 25.3 mm, of CDM 997.91.3, informal locality AP3.

Stage"), Baja California Sur, México.

Etymology—Originally named for Lindsey T. Groves (Natural History Museum of Los Angeles County, Malacology Department).

Description—Shell small (17 mm length), oval, highest at mid-point of dorsum. Base flattened with prominent concavity near anterior end. Spire covered, spire area coincident with small pit. Aperture straight, except for bending leftward in posterior region. Denticulation strong, outer lip with 16 teeth, inner lip with 12 teeth, sculpture extending halfway to shell margin, and ribs slightly stronger on inner lip. Outer lip callus prominent and with dorsal ring circumscribing entire shell (Squires and Demetrion 1992: p. 31).

Remarks—The two known specimens of *Bernaya grovesi* have good to excellent preservation.

Bernaya kaylinae Squires and Groves n. sp.
Figs. 5D–F

Eocypraea castacensis (Stewart, 1926 [1927]). Vokes, 1939. p. 26 [in part], 154 [in part], pl. 20, fig. 9 [not fig. 14, = *Eocypraea* (*Eocypraea*) sp. cf. *E.* (*E.*) *inflata* (Lamarck, 1802) of Groves, 2011]. Keen and Bentson, 1944. p. 154 [in part].

Cypraea castacensis Stewart, 1926 [1927]. Ingram, 1942. p. 103 [in part], pl. 8, fig. 5 [not fig. 6, = *Eocypraea* (*Eocypraea*) sp. cf. *E.* (*E.*) *inflata* (Lamarck) of Groves, 2011]. Squires, 1984. pp. 23, 24, fig. 7b. Groves and Squires, 2021. p. 226.

Zoobank ID—LSID: urn:lsid:zoobank.org:act:62DE473E-1DF7-45C0-B34A-80197B354555

Diagnosis—A *Bernaya* with medium-size shell, widest centrally, aperture moderately curving posteriorly, inner lip teeth moderately spaced and extending onto of left (columellar) side shell.

Holotype and Type Locality—LACMIP 40374.80, LACMIP Type 14938 (Figs. 5D–F), length 25.6 mm, width 17.3 mm, height 12.9 mm. LACMIP Locality 7242 [= LACMIP Locality 40374; *ex* CSUN Locality 374], "Stewart bed," middle part of Llajas Formation, Las Llajas Canyon, north side of Simi Valley, Ventura County, southern California.

Paratype—LACMIP 7242.7, LACMIP Type 6523, length 25.7 mm, width 17.2 mm, height 14.1 mm, LACMIP Locality 7242 [= LACMIP Locality 40374; *ex* CSUN Locality 374]. This specimen was formerly hypotype LACMIP 6523 (of Squires, 1984: pp. 23, 24, fig. 7b), of *Cypraea castacensis* Stewart, 1926 [1927] from the type locality ("Stewart bed," Llajas Formation).

Referred Specimens—Hypotype (of Vokes, 1939) UCMP 33808, UCMP Locality 3296 (Llajas Formation, Devil Canyon, formerly referred to as Aliso Canyon). One specimen each from LACMIP Locality 7474 [*ex* CIT Locality 559] (LACMIP 7474.1, LACMIP Type 14919), LACMIP Locality 11809 [*ex* CIT Locality 215] (LACMIP 11809.2, LACMIP Type 14920), LACMIP Locality 22312 [*ex* UCLA Locality 2312] (LACMIP 22312.47, LACMIP Type 14921), and LACMIP Locality 26619 [*ex* UCLA Locality 6619] (LACMIP 26619.1, LACMIP Type 14922), and three topotypic specimens, LACMIP 40374.81, LACMIP Type 14939 (LACMIP Locality 72421 [= LACMIP Locality 40374; *ex* CSUN Locality 374]), all Llajas Formation, Simi Valley, Ventura County, southern California.

Occurrence—Upper lower Eocene, lower part of

"Domengine Stage": "Stewart bed" north side of Simi Valley, and approximately 25 m stratigraphically below "Stewart bed," southwestern Santa Susana Mountains (Devil Canyon, [*ex* Aliso Canyon]), Ventura County, southern California. The depositional environment of the "Stewart bed" was revised by Squires (2022) as deposited in a subtropical, shallow-marine environment at the distal edge of a braided delta.

Etymology—Named for Kaylin Marie Solomon, granddaughter of R.L. Squires (who collected the holotype, paratype, and three non-type specimens of this species).

Description—Shell medium size, inflated, and smooth. Spire very low (normally covered by thin layer of shell). Aperture moderately straight (with moderate bend posteriorly), mostly narrow but widening significantly anteriorly into broad, concave depression. Outer lip with 18 to 19 teeth, confined to inner margin; most anteriorly located teeth (four to five) strongest and extend half way up lip and are coincident with thinning of outer wall. Remaining outer lip teeth weaker and extend only short distance and are coincident with nearly vertical surface. Inner lip with 15 to 16 teeth, moderately spaced and becoming slightly more closely spaced posteriorly; strongest and longest inner lip teeth located on medial part of inner lip and extend to lip margin. Anterior end smooth, concave, and broad. Anterior terminal ridge well developed. Anterior (siphonal) and posterior (exhalant) canals well developed and prominent.

Remarks—The ten known specimens of *Bernaya kaylinae* range in preservation from poor to good. *Bernaya kaylinae* differs from *Grovesia castacensis* by having a more inflated and non-tapered shell shape and much finer teeth. *Bernaya kaylinae* resembles a few specimens of *Grovesia mathewsonii* (Gabb, 1869) that were originally identified as *Cypraea kerniana* Anderson and Hanna, 1925 from the Tejon Formation in Grapevine Creek, Kern County, southern California. *Bernaya kaylinae* differs from them by having a much less tapered teleoconch, a rounded (not lop-sided) last whorl, shorter transverse ribs on the venter, and less numerous and more closely spaced teeth on the outer lip.

Bernaya kaylinae is very similar to *B. marcominii* Dolin and Aguerre (2016: pl. 2, figs. 1–3), of middle Ypresian age in the Oise region of France. *Bernaya kaylinae* differs by having a narrower and more curved posterior terminal of the outer lip, slightly more projected posterior terminal of the inner lip, and a wider anterior end of the aperture. *Bernaya kaylinae* is also similar to *B. sixi* Pacaud and Robert (2016: pl. 1, figs. 1, 2a, b), of middle Ypresian (Cuisian) age in the Oise region of France, in having a barely hidden spire. The new species differs from *B. sixi* by having coarser sculpture, a deeper notched posterior canal, a wide-concave depression at the anterior end of the shell, and no anterior terminal ridge.

Bernaya squiresi Groves. 2011
Figs. 5G–I

Bernaya (*Bernaya*) n. sp. Groves, 1997. p. 7 [as *B.* (*B.*) n. sp.].

Bernaya (*Bernaya*) *squiresi* Groves, 2011. p. 46, 47, figs. 1, 2.

Bernaya squiresi Groves. Lorenz, 2017. p. 208. Lorenz, 2018. p. 666, pl. 329, fig. 8.

Holotype and Type Locality—LACMIP 22341.1, LACMIP Type 13644 (Figs. 5G–I), length 52.7 mm, width 40.0 mm, height 26.3 mm. LACMIP Locality 22341 [*ex* UCLA Locality 2341], Crescent Formation, southwest end of Discovery Bay, Jefferson County, southwestern Washington.

Occurrence—Middle lower Eocene ("Capay Stage"), southwest end of Discovery Bay, Jefferson County, southwestern Washington.

Etymology—Originally named for Richard L. Squires (CSUN, Geological Sciences, professor emeritus).

Description—Shell of medium to large size, constricted on anterior end; maximum height near center of shell; maximum width slightly posterior of center; aperture wide, straight; dentition medium to coarse; labral (outer) lip with 24 teeth, columellar lip with 25 teeth; anterior terminal marginal callus (Groves 2011: p. 47).

Remarks—This species is known only from its holotype, which has moderately good preservation. Post-burial crushing damaged the anterior portion of the aperture and also dorso-basally distorted the holotype. Perrilliat et al. (2003: pl. 1, figs. 5, 6) figured a specimen identified as *Bernaya* (*Bernaya*) *obesa* (Deshayes, 1866) [hypotype IHN 5459] but is outwardly more similar to *B. squiresi*. Unfortunately, poor preservation prevents a positive identification. A poorly preserved outer lip fragment (LACMIP 41599.2), which could be *B. squiresi*, from the Crescent Formation, LACMIP Locality 41599 (*ex* CSUN Locality 1599), Middle Fork Satsop River, Dry Lakes quadrangle, Mason County, Washington is noted. *B. squiresi* represents the northernmost occurrence of the genus in Cenozoic strata and the only representative of the genus described from Washington.

Bernaya sp.
Figs. 5J–L

Hypotype—LACMIP 7047.72, LACMIP Type 14923 (Figs. 5J–L), length 33.8 mm, width 23 mm, height 18.3 mm.

Occurrence—LACMIP Locality 7047 [*ex* CIT Locality 868], Lower Lake area, Lake County, northern California, "Martinez Formation" strata containing *Turritella infragranulata* Gabb, 1864, in the Herndon Creek, Lower Lake, Lake County, northern California (Stanton 1896). Saul (1983: p. 102) confirmed Stanton's (1896) report of this turritellid and assigned it to the Thanetian Stage.

Remarks—This gastropod is represented by a single specimen, which has moderate preservation. It is similar to the only known specimen of *Bernaya squiresi* Groves, 2011 from the Crescent Formation (middle lower Eocene "Capay Stage"). Both specimens have similar shell shape, a small exposed spire, numerous strong teeth on the apertural lips, and are poorly preserved in the critically important anterior end. Three additional specimens of the Lower Lake taxon (LACMIP 7047.73), all from LACMIP Locality 7047 in the Lower Lake area, are likely the same genus but their preservation is too poor for confirmation. A single specimen from the Santa Susana Formation, Simi Valley, Ventura County, southern California (LACMIP 12481.1, LACMIP Type 14924) (LACMIP Locality 12481) may also be the same genus but is also too poorly preserved to make a positive identification.

PROTOCYPRAEA Schilder, 1927

Type Species—*Eocypraea orbignyana* Vredenburg, 1920 [non Grateloup, 1847], by original designation (of Schilder, 1927: p. 88), Late Cretaceous (Coniacian), Trichinopoly Group, Kullygoody, Tamilnadu District, India.

Diagnosis—Shell small to large in size. Moderately globular. Spire large, commonly projecting. Short and rounded posterior extremity. Anterior extremity with pointed or spatulate tips. Aperture narrow posteriorly curved, wide in the fossular section, constricted at the canal. Labrum narrow, spoon shapped, and sloping in front. Teeth usually weakly developed or absent. Fossula flat and smooth (Lorenz, 2017).

Geologic Range—Early Cretaceous (Barremian) to middle Eocene (Lutetian) (Groves, 1994).

Remarks—Schilder (1927) described *Protocypraea* as a subgenus of *Bernaya*. Vredenburg (1920) recognized similarities in illustrated specimens of Stoliczka (1867) identified as *Cypraea* (*Luponia*) *newboldi* Forbes, 1846 (pl. 4, figs. 2–3), *C.* (*Aricia*) *ficulina* Stoliczka, 1867 (pl. 4, fig. 11), and *C. kayei* Forbes, 1846 (pl. 4, fig. 7) and renamed them *Eocypraea orbignyana* [now = *Protocypraea orbignyana*].

Protocypraea? *simiensis* (Nelson 1925) n. comb.
Figs. 5M–O

Cypraea simiensis Nelson, 1925. p. 397, chart opposite p. 402, 425; pl. 57, figs. 3a–3c. Ingram, 1942. pp. 105, 106; pl. 9, fig. 18. Keen and Bentson, 1944. p. 152. Ingram, 1947a. p. 101; pl. 6, figs. 18, 19. Ingram 1947b:149.

Propustularia simiensis (Nelson). Schilder, 1932. p. 159 [as *P. simiensis*]. Schilder, 1941. p. 89. Weaver MS [1959]. p. 483, pl. 21, figs. 5, 6. Schilder and Schilder, 1971. pp. 59, 155. Groves, 1992. p. 106. Groves, 1993. p. 11. Groves, 1997. p. 7 [as *P. simiensis*]. Lorenz, 2017. p. 211. Groves and Squires, 2021. p. 227 [as *Cypraea*].

Propustularia simiensis (Nelson). Zinsmeister, 1974. pp. 130, 131, pl. 13, figs. 10, 11. Zinsmeister, 1983. p. 64, pl. 2, figs. 25, 26. Not *Protocypraea*? *simiensis* (Nelson).

Siphocypraea (*Muracypraea*) *koninckii* (Rouault, 1850). Dolin and Dolin, 1983. p. 46 (table). Not *Protocypraea*? *simiensis* (Nelson).

Propustularia cf. *P. simiensis* (Nelson). Paredes-Mejia, 1989. p. 198–200, pl. 4, figs. 17–19. Not *Protocypraea*? *simiensis* (Nelson, 1925).

Propustularia sp. cf. *P. simiensis* (Nelson). Perrilliat, 2013. p. 133, 134, fig. 4.1, 4.2. Not *Protocypraea*? *simiensis* (Nelson, 1925).

Holotype and Type Locality—UCMP 30498 (Figs. 5M–O), length 33.1 mm, width 24.5 mm, height 17.4 mm. UCMP Locality 3818, upper Santa Susana Formation, Runkle Canyon, Simi Hills, Ventura County, southern California.

Occurrence—Upper Paleocene (Thanetian Stage), Santa Susana Formation, north side of Simi Hills, Ventura County, southern California (Nelson 1925). *Protocypraea*? *simiensis* is known only with certainty from high in the stratigraphic section of the Santa Susana Formation in Runkle Canyon located on the north side of the Simi Hills, Ventura County, southern California. The type locality of *Protocypraea*? *simiensis* yielded just this species, and no other mollusks, Both of the other cypraoideans, *Propustularia kemperae* and *Eocypraea novasumma*, known from the Santa Susana Formation, occur much lower in the Paleocene stratigraphic section. Zinsmeister (1974: pp. 130, 131; pl. 13, figs. 10, 11, Zinsmeister, 1983: p. 64, pl. 2, figs. 25, 26. Zinsmeister and Paredes-Mejia, 1988: p.

13) reported *Propustularia simiensis* in the Santa Susana Formation from his so-called "Martinez marine member," but poor preservation prevents the identification of this specimen. Squires (1997: p. 851) noted that it was based predominantly on float material. In summary, based on its stratigraphic position, the Santa Susana Formation occurrence of *P.*? *simiensis* is reported here as of Thanetian Stage age.

Etymology—Originally named for Simi Valley, Ventura County, southern California.

Description—Shell of medium size. Smooth. Ovate, moderately inflated, dorsum can be elevated, especially posteriorly. Posterior end of shell wide, somewhat flattened, and projecting. Anterior end of shell missing (on holotype). Right-lateral margin, near base, with raised border (beveled basally). Dorsal posterior end if shell wide, flattened and projected (right side more than left side). Spire area (halfway between top of dorsal surface and posterior terminus of shell) covered with small but prominent protuberance (bump). Aperture narrow, moderately curved abaxially posteriorly, fairly straight medially, curved and widening anteriorly. Outer lip swollen with teeth numerous, small, and evenly spaced to at least mid-point of basal surface but becoming undetectable posterior of mid-point. Inner lip teeth few (approximately five near anterior end) to numerous, strong to moderately strong (strongest near anterior end), and can be restricted to anterior end of shell or present along most of aperture.

Remarks—Nelson's *Cypraea simiensis*, which does not fit into Schilder's (1927) description of *Propustularia*, is known only from the holotype. It has good preservation, but, unfortunately, its anterior end is missing, thereby only allowing questionable identification as to genus. Therefore, it is herein provisionally assigned to *Protocypraea* based on the partially exposed spire and weakly developed dentition.

Paredes-Mejia (1989: pp. 198–200, pl. 4, figs. 17–19) and Perrilliat (2013: p. 133, figs. 4.1, 4.2) illustrated the same specimen, with different hypotype numbers, of the so-called *Propustularia* cf. *P. simiensis* (Nelson) from the same locality in the Sepultura Formation in Baja California, México. Paredes-Mejia (1989) referred to this specimen as hypotype IGM 4390, PU Locality 1300-2, Sepultura Formation, San Carlos Mesa, northern Baja California. Perrilliat (2013) referred confusingly to this specimen as hypotype IGM 4366 [=hypotype 4390 of Paredes-Mejia (1989)], PU Locality 1300-2, Sepultura Formation, San Carlos Mesa, northern Baja California. This worn cypraeoidean specimen is too poorly preserved to positively identify as to genus and species.

Protocypraea? sp. 1
Figs. 5P, 6A–C

Eocypraea sp. Williams et al., 2018: unnumbered fig.

Hypotype—CDM 997.91.3 (figs. 5P, 6A–C), length 48.1 mm, width, 31.4 mm, height 25.3 mm, height. Informal locality AP3 (J.W. Haggart, personal communication, 2022).

Occurrence—Questionably late Paleocene (Thanetian Stage), central east coast of Vancouver Island, British Columbia, Canada. Oyster Bay Formation ("Appian Way beds"), approximately 45.5°N, intertidal area on east coast of Central Island District, Vancouver Island, British Columbia, Canada.

Description—Shell moderately large, smooth, turnip-shape, base narrow, aperture narrow, dentition relatively small size. Shell tapers rapidly anteriorly; anterior part of shell somewhat projected. Shell with maximum width posterior to center of shell, but very inflated posterior area incomplete showing only small depressed area (only base of spire present) with sunken sulcus area. Aperture is moderately wide and fairly straight, with some bending in posterior area. Outer lip shows numerous relatively small-sized teeth anteriorly. Inner lip similar, except for the teeth being smaller and not extensive.

Remarks—Only a single specimen (possibly a juvenile) is known. It is nearly complete, except for most of the broken-off posteriormost part of the shell, thus precluding the assignment of this unnamed specimen.

This specimen, which is the northernmost occurrence of a Paleogene cypraeoidean in the NEP region, is like no other NEP Paleogene cypraeoidean, nor like any NEP Late Cretaceous specimen. A manuscript currently in preparation by J.W. Haggart et al. will further document this so-called "Appian Way fauna" [presumably of late Paleocene age and contemporaneous with the "Oyster Bay Formation"], Central Island District, Vancouver Island, British Columbia, Canada. McLachlan and Pospelova (2021) presented dinoflagellate data for an early Paleocene age of the "Oyster Bay Formation," but that age is in contradiction to late Paleocene to middle Eocene ages variously based on plants, sporomorphs, marine mollusks, decapods, and shark teeth (see McLachlan and Pospelova 2021 for a review of this literature).

Protocypraea? sp. 2
Figs. 6D–G

Cypraea n. sp. Smith, 1975. p. 469, 479, pl. 2, fig. 10 [as *Cypraea* sp.]. Groves and Squires, 2021. p. 227.

Referred Specimens—Hypotype (of Smith, 1975)

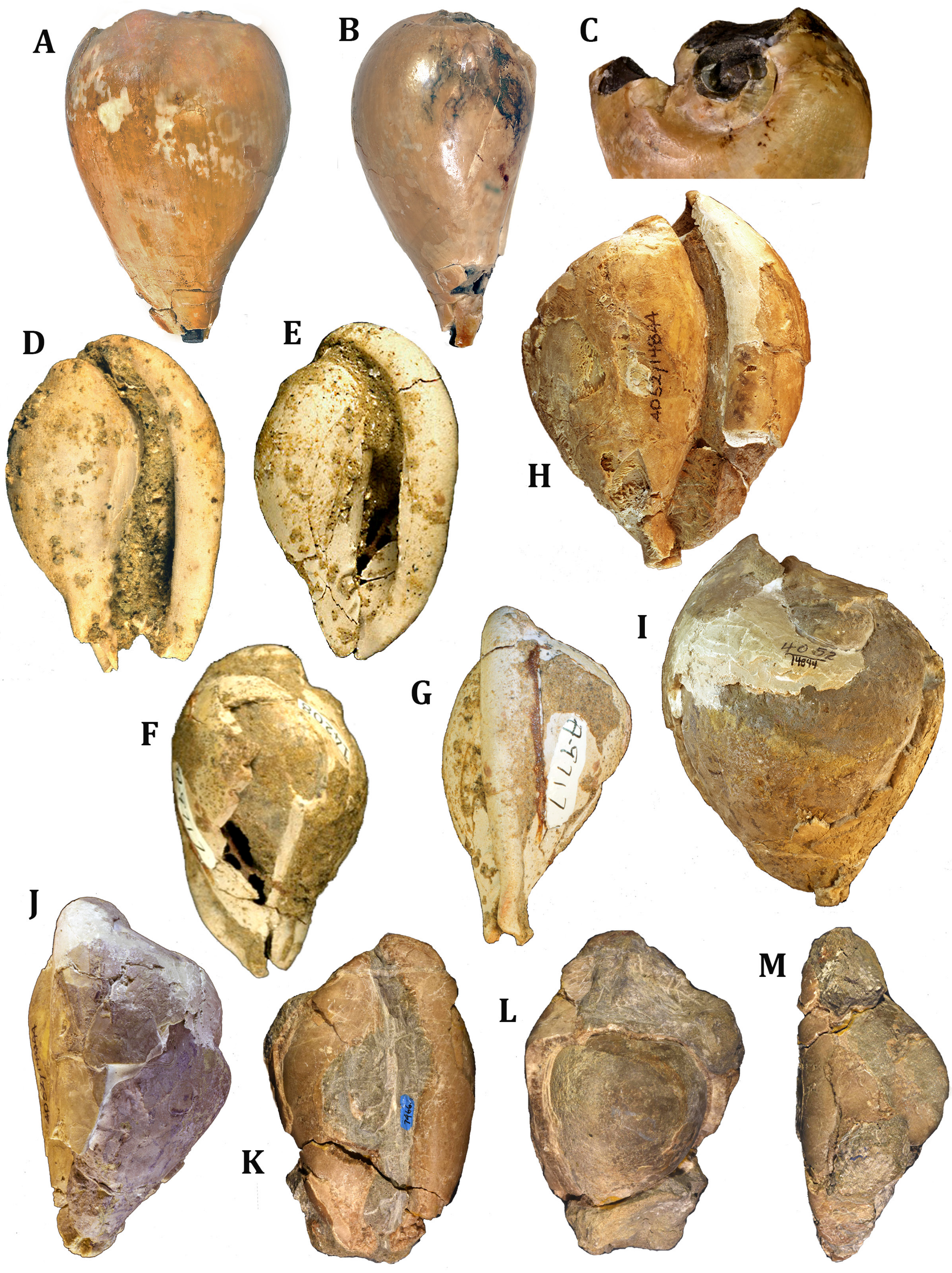
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Figure 6 (previous page) A–C. *Protocypraea*? sp. 1, Oyster Bay Formation, Paleocene, Appian Way, Central Island District, Vancouver Island, British Columbia, Canada. Dorsal (**A**) and (**B**) left (columellar) views, 1.8x, length 45.5 mm, width 29 mm, height 22 mm, of CDM 997.91.3, informal locality AP3. (**C**) Oblique view posterior incomplete end of shell showing sunken area encircling base of spire, width of field of vision 28.7 mm. **D–G.** *Protocypraea*? sp. 2, Lodo Formation (Paleocene, Thanetian Stage), Tumey Hills, Fresno County, central California, LACMIP Locality 26456 [*ex* UCLA Locality 6456]. Basal (**D**) view, 1.6x, length 42.2 mm, width 28.6 mm, height 18.5 mm, of hypotype LACMIP 26456.6, LACMIP Type 14925, Basal (**E**), dorsal (**F**), right (labral) (**G**) views, 1.44x**,** length 50 mm, width 28 mm, height 27 mm, of hypotype UCMP 14208, UCMP Locality A9717. **H–J.** *Gisortia clarki* Ingram, 1940, Llajas Formation (Eocene, "Capay Stage"), north side Simi Valley, Ventura County, southern California. Basal (**H**), dorsal (**I**), and right (labral) side (**J**) views, 0.5x, length 121.4 mm, width 96.4 mm, height 65.9 mm, of holotype UCMP 14844, UCMP Locality 4052. **K–M**. *Gisortia* sp., Juncal Formation (Eocene, "Capay Stage"), Whitaker Peak, Ventura County, southern California. Basal (**J**), dorsal (**K**), and right (labral) side (**M**) views, 0.5x, length 122 mm, width 75 mm, height 51 mm, of hypotype LACMIP 16243.1, LACMIP Type 7466, LACMIP Locality 40848 [*ex* CSUN Locality 848].

UCMP 14208 [= UCMP 6582] (Figs. 6E–G), UCMP Locality A-9717, length 50 mm, width 30 mm, height 25 mm. **Hypotype (herein)**, LACMIP 26456.6, LACMIP Type 14925 (Fig. 6D), measures length 42.7 mm, width 27.6 mm, height 16.8 mm, LACMIP Locality 26456 [= UCMP Locality A-917, *ex* UCLA Locality 6456].

Occurrence—Lodo Formation (basal part), Tumey Hills, Fresno County, California, late Paleocene (Thanetian Stage).

Remarks— Two specimens are known and their preservation is poor due to missing portions of the dorsum of both. They both outwardly resemble the hypotype of *Protocypraea gualalaensis* (Anderson, 1958) (SDSNH 33995) from the Upper Cretaceous (Campanian/Maastrichtian) Point Loma Formation, near Carlsbad, San Diego County, southern California (SDSNH Locality 3405) as figured by Groves (1990: figs. 25, 26) and Lorenz (2017: p. 205, unnumbered figure; 2018: pl. 329, fig. 2). Generic assignment of the basal Lodo Formation specimens is provisionally based on a partially exposed spire, poorly developed dentition, and flat, smooth fossula.

Smith (1975) reported that the cypraeoideans from UCMP Locality A-9717 in the basal Lodo Formation correlates to Mallory's (1959) California benthic foraminiferal Ynezian Stage. Almgren et al. (1988) updated Mallory's findings, and, with the use of calcareous nannofossils, equated the Ynezian Stage to the CP7 calcareous nannofossil biozone, of late Paleocene (Thanetian Stage) age. Saul (1983: pp. 99–102) reported the Thanetian index fossil *Turritella pachecoensis* Stanton, 1896 from the basal Lodo Formation.

GISORTIA Jousseaume, 1884

Type Species—*Ovula gisortiana* Passy, 1859, by original designation (of Jousseaume, 1884: p. 89), Eocene, France.

Diagnosis—Shell ovoid, irregularly rounded and can be tuberculous. Lips little or not toothed (Jousseaume, 1884: pp. 88, 89).

Geologic Range—Late Cretaceous (Maastrichtian) to late Eocene (Priabonian) (Groves 1994c).

Remarks—This genus is rare in the NEP Paleogene record.

Gisortia clarki Ingram, 1940
Figs. 6H–J

Gisortia n. sp. Clark and Vokes, 1936. pp. 861, 877, pl. 2, figs. 1, 3. Keen and Bentson, 1944. p. 164.

Gisortia clarki Ingram, 1940. p. 376, 377, fig. 1. Ingram, 1942. p. 109, pl. 11, fig. 1. Keen and Bentson, 1944. p. 164. Ingram, 1947a. p. 105, pl. 7, fig. 1. Ingram, 1947b. p. 150. Groves and Squires, 2021. p. 241, 242.

Gisortia (*Megalocypraea*) *californica* Schilder, 1941. p. 78 [*nomen nudum*].

Gisortia (*Megalocypraea*) *clarki* Ingram. Schilder and Schilder, 1971. p. 30, 105. Groves, 1992. p. 101, 102, 106, figs. 3a, 3b. Groves, 1993. p. 11. Groves, 1997. p. 7. Groves and Squires, 2021. p. 242.

Gisortia sp. cf. *G. clarki* Ingram. Smith, 1975. p. 469, 479, pl. 2, figs. 9, 13. Not *Gisortia clarki* Ingram, 1940.

Megalocypraea aff. *M. clarki* (Ingram). Woodring, 1982. p. 725, pl. 85, fig. 3, pl. 86, fig. 3. Not *Gisortia clarki* Ingram, 1940.

Gisortia (*Megalocypraea*) cf. *G.* (*M.*) *clarki* Ingram. Squires and Demetrion, 1994. pp. 129, 130, fig. 8. Not *Gisortia clarki* Ingram, 1940.

Holotype and Type Locality—UCMP 14844 (Figs. H–J), length 121.4 mm, width 96.4 mm, height 65.9 mm. UCMP Locality 4052, "Capay Stage," Llajas Formation, north side of Simi Valley, Ventura County, California.

Referred Specimens—Hypotype (of Squires and Demetrion, 1994: pp. 129–130) IGM 5953 from LACMIP Locality 401544a (*ex* CSUN Locality 1544a (internal mold)), lower Eocene ("Capay Stage"), Mesa La Salina and area just to the south, Baja California Sur, México. This specimen, which is significantly smaller than both the holotype of *Gisortia clarki* and the figured specimen of *Gisortia* sp. of Perrilliat (1996) (see below), is too poorly preserved to identify with certainty. Additional internal molds of this gastropod are also known from the Bateque Formation, Baja California Sur, México: two from LACMIP Locality 401544a (*ex* CSUN Locality 1544a), and one from LACMIP Locality 401220 (*ex* CSUN Locality 1220).

Occurrence—Lower to middle Eocene, California. "Capay Stage," Llajas Formation, north side of Simi Valley, Ventura County, southern California, and provisionally from the Bateque Formation, Baja California Sur, México.

Etymology—Originally named for the late Bruce L. Clark [1880-1945] (UCMP)

Description—Shell globose, heavy. Very wide medially. Spire almost totally submerged beneath shell, spire peak projecting (approximately 3.5 mm) above shell. Aperture curves to the left anteriorly and posteriorly. Labrum (outer) and columellar lips broadly rounded. Columella side of the anterior canal apparently compressed dorso-basally at its outermost extremity.

Remarks—*Gisortia clarki* is known with certainty only from the moderately well preserved holotype. The shell surface of the holotype is well preserved on the base, on the extreme posterior region, on the columellar lateral shell boundary, and on the posterior three-fourths of the outer lip. It is moderately eroded, however, on the dorsal surface, and the greater part of the dorsal convexity is represented by an intact internal mold. The aperture is filled with a matrix, which prohibits a description of the internal surfaces of the columellar and outer lips.

Smith (1975: pl. 2, figs. 9, 13) referred to a late Paleocene cypraeoidean specimen as *Gisortia* sp. cf. *G. clarki* from the basal Lodo Formation in the Tumey Hills of central California. This specimen, which has a very inflated dorsum, was mentioned by Squires (1987: p. 35) in his discussion on the distribution of *Gisortia* in the NEP region. This specimen, however, is recognized and described in this present paper as Cypraeidae, genus and species indeterminate.

Clark and Vokes (1936: p. 877) noted the morphologic similarities of their *Gisortia* n. sp. and *Gisortia tuberculosa* (Duclos, 1825) of Ypresian age in the Paris Basin, France. *Gisortia tuberculosa* has been reported as early Lutetian age in southern England (Pacaud and Canevet 2019).

Perrilliat (1996) reported a poorly preserved internal mold identified as *Gisortia* sp. (hypotype IGM 6761) from the late early Eocene Tepetate Formation near San Hilario, Baja California Sur, México (IGM Locality 2620). She noted that *Gisortia* sp. is larger than *G. clarki* and the spire displays five whorls, which are covered in *G. clarki*. Because of poor preservation it is difficult to make any positive comparison with *G. clarki*. The figured specimen of Woodring (1982) (USNM 647808) from the late Eocene Gatuncillo Formation of Panama is a large internal mold that is indeed a *Gisortia* but unlikely *G. clarki*.

Gisortia sp.
Figs. 6K–M

Gisortia clarki Ingram, 1940. Squires, 1987. p. 35, figs. 39–41 [as *Gisortia* new species? in caption]. Not *Gisortia clarki* Ingram, 1940.

Referred Specimen—Hypotype (of Squires, 1987) LACMIP 16243.1, LACMIP Type 7466 (Figs. 6K–M), LACMIP Locality 16243 [= Locality 40848 [*ex* CSUN Locality 848]), Juncal Formation, Canton Canyon, Ventura County, California.

Occurrence—Juncal Formation. "Capay Stage," *Turritella uvasana infera* fauna, LACMIP Localities 16156 [= LACMIP Locality 40837; *ex* CSUN Locality 837] and 16243 [= LACMIP Locality 40848; *ex* CSUN Locality 837], in an area just east of Sharps Canyon and southeastward toward Canton Canyon, Whitaker Peak area, Los Angeles County, southern California.

Description—Shell large, length 122 mm, width 75 mm, height 51 mm. Shell ovate. Anterior and posterior ends flattened somewhat and projecting. Aperture narrow, curving left posteriorly but becoming less curved anteriorly. Outer lip (anterior half) with several small teeth; presence of any dentition on rest of aperture is not known.

Remarks—A large complete specimen is known, but it is poorly preserved as a partial internal mold (steinkern). In addition, a large fragment (length 90 mm) was found in same-age rocks of the Juncal Formation approximately 0.5 km to the west in Sharps Canyon of the Whitaker Peak area (Squires 1987), LACMIP 40837.1, LACMIP Locality 16156 [= LACMIP Locality 40837; *ex* CSUN Locality 837]. Most of the dorsal shell convexity of the complete specimen is represented by an internal mold (steinkern),

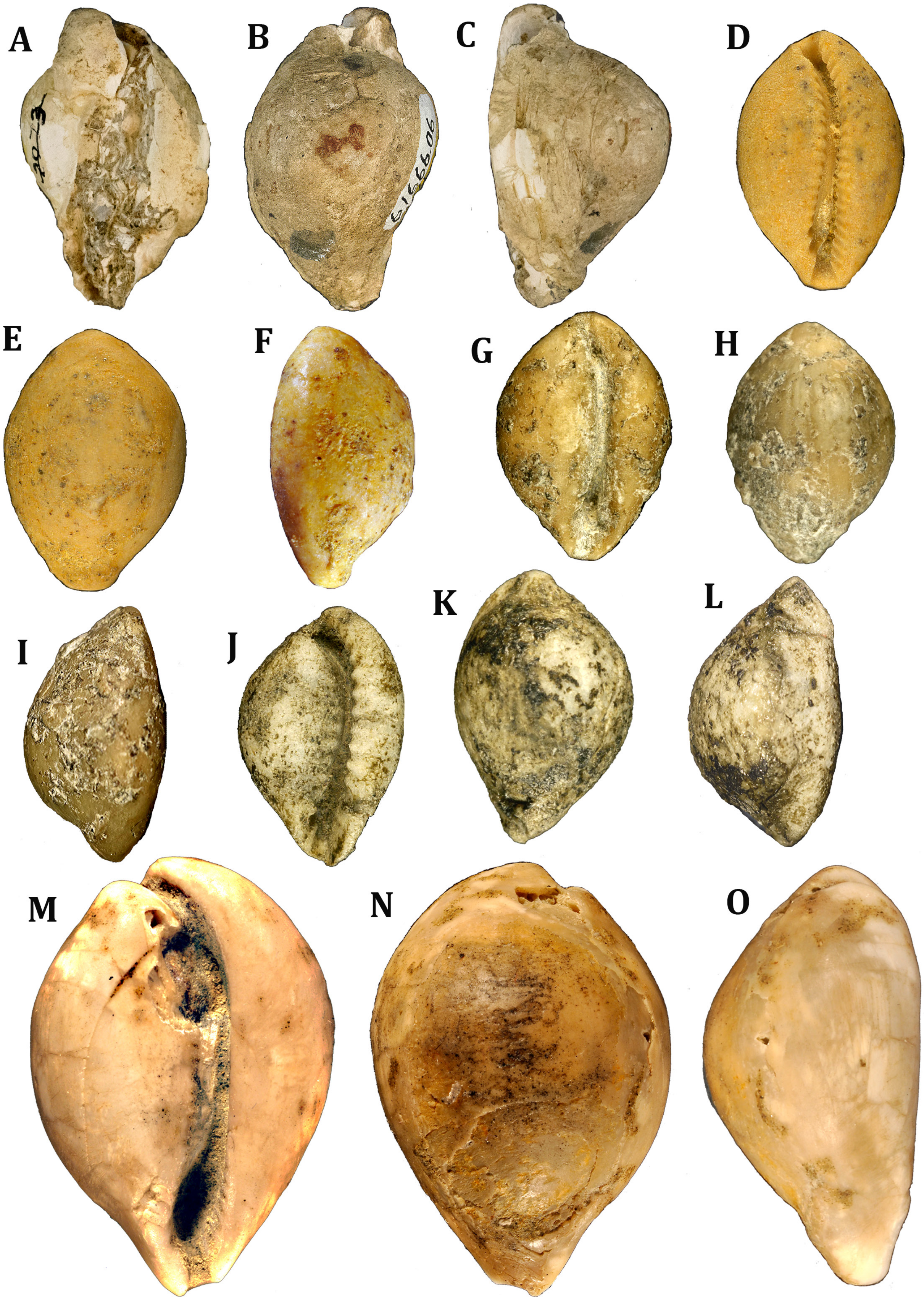
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Figure 7A–C. Cypraeidae, genus and species indeterminate, Lodo Formation (basal) (Paleocene, Seldanian Stage), Tumey Hills, Fresno County, central California. Basal (**A**), dorsal (**B**), and right (labral) (**C**) views, 1.3x, length 39 mm, width 25 mm, height 22 mm, of hypotype CASG 61666.06, CASG Locality 61666. **D–F.** *Eocypraea batequensis* (Groves, 2011), Bateque Formation (Eocene, "Capay Stage"), Mesa La Salina, Baja California Sur, México. Basal (**D**), dorsal (**E**), and right (labral) (**F**) views, 4.8x, length 9.4 mm, width 6.5 mm, height 5.1 mm, of holotype IGM 5174, LACMIP Locality 16951 [*ex* CSUN Locality1220b]. **G–I.** *Eocypraea crescentensis* (Groves, 2011), Crescent Formation (Eocene, "Capay Stage"), Larch Mountain, Black Hills area, Thurston County, Washington. Basal (**G**), dorsal (**H**), and left (columellar) (**I**) views, 3.9x, length 10.9 mm, width 7.6 mm, height 6.1 mm, of holotype LACMIP 16655.40, LACMIP Type 13646, LACMIP Locality 16655 [= LACMIP Locality 41563; *ex* CSUN Locality 1563]. **J–L.** *Eocypraea jimgoederti* (Groves, 2011), lower McIntosh Formation (middle Eocene, "Transition Stage" to "Tejon Stage"), Doty Hills, Lewis County, Washington. Basal (**J**), dorsal (**K**), and left (columellar) side (**L**) views, 3.5x, length 12.7 mm, width 8.2 mm, height 6.9 mm, of holotype LACMIP 41573.1, LACMIP Type 13647, LACMIP Locality 41573 [*ex* CSUN Locality 1573]. **M–O.** *Eocypraea judithsmithae* n. sp., Llajas Formation (Eocene, "Domengine Stage"), north side Simi Valley, Ventura County, southern California. Basal (**M**), dorsal (**N**), and left (labral) (**O**) views, 1.5x, length 26.6 mm, width 18.4 mm, height 12.6 mm, of holotype LACMIP 40372.1, LACMIP Type 14940 (LACMIP Locality 40732).

and its spire is obscured by matrix. The Juncal Formation specimen of *Gisortia* sp. differs from *Gisortia clarki* by having an ovate shell, a narrower shell, a narrower inner lip, and the presence of wide, flattened anterior and posterior margins.

The Juncal Formation specimens of *Gisortia* sp. are somewhat similar to a specimen of *Gisortia gigantea* Münster in Keferstein, 1828, from India as illustrated by Vredenburg (1927: p. 59, 60, pl. 13, fig. 2). *Gisortia gigantea*, which is of middle Eocene (Lutetian age) and known from France, England, and India, can have a wide range of variation in its posterior canal region owning to the absence or presence of elaborately shaped phlanges and/or wide spines. These variants usually have been assigned to subspecies of *Gisortia gigantea* or assigned a different species name. See Pacaud (2008) for clarifications. The Juncal Formation species of *Gisortia* differs from *G. gigantea* by having a more elongate shell shape with a posterior flattening of the shell and no evidence of any posterior phlanges.

CYPRAEIDAE, Genus and Species Indeterminate
Figs. 7A–C

Gisortia sp. cf. *G. clarki* Ingram, 1940. Smith, 1975. p. 469, 479, pl. 2, figs. 9, 13. Not *Gisortia clarki* Ingram, 1940.

Referred Specimens—Hypotype (of Smith, 1975) (Figs. 7A–C) CASG 61666.06 [*ex* LSJU 10235 of *Gisortia* sp. cf. *G. clarki*], length 39 mm length, width 25 mm width, height 22 mm, CASG Locality 61666 [*ex* LSJU Locality 2073, = UCMP Locality A-9717], Tumey Hills, Fresno County, middle California.

Occurrence— Basal Lodo Formation, Paleocene (Thanetian Stage).

Remarks—This medium-size gastropod is represented by a single specimen, which is too poorly preserved to be positively assigned to a genus or species. The specimen is an internal mold, is missing its right posterior end, and the aperture is filled with matrix. The general shape of this specimen resembles superficially the specimens of *Protocypraea*? sp. 2 also from the Lodo Formation.

EOCYPRAEIDAE Schilder, 1924a

Remarks—Based on protoconch, teloconch, and shell morphology, Fehse (2013, 2021) demonstrated that the Eocypraeidae should not be considered a subfamily within the Ovulidae. Eocypraeidae comprises the subfamilies Eocypraeinae and Sulcocypraeinae. The authors have chosen to adopt this classification scheme until additional, more conclusive data become available. Lorenz and Fehse (2009), Lorenz (2018), Pacaud (2018b), and Fehse (2021) all noted that this family is living today based on the presumption that *Sphaerocypraea incomparabilis* (Briano, 1993) [originally described as *Chimaeria incomparabilis*] is correctly placed. Indeed Briano's species outwardly resembles members of *Sphaerocypraea***,** but until conclusive molecular data and/or radular data can be obtained, thus affording correct systematic placement, it should be tentatively considered a living member of *Sphaerocypraea*.

EOCYPRAEINAE Schilder, 1924a

Type Species—*Cypraea inflata* Lamarck, 1802 by original designation (of Cossmann, 1903: p. 162), middle Eocene (Lutetian/Bartonian), Paris Basin, France.

Diagnosis—Inflated-pyriform shell of small to medium size; spire involute; elongate aperture; fossula broad, smooth, concave.

Geologic Range—Late Cretaceous (Cenomanian) to early Oligocene (Lattorfian) (Groves, 1994a, Fehse, 2021).

Remarks—*Eocypraea inflata* (Lamarck, 1802) resembles several NEP eocypraeid genera by having inflated-pyriform shells of medium size, involute spire, narrow elongate aperture, and reduced dentition on the inner lip.

Eocypraea batequensis Groves, 2011
Figs. 7D–F

Eocypraea? sp. Squires and Demetrion, 1992. p. 31, figs. 77–79.

Eocypraea (*Eocypraea*) n. sp. 1. Groves, 1997. p. 8 [*as E.* (*E.*) n. sp. 1].

Eocypraea (*Eocypraea*) *batequensis* Groves, 2011. p. 46 (table 1), 49, figs. 5, 6.

Grovesia batequensis (Groves). Fehse, 2021. p. 44.

Holotype and Type Locality—IGM 5174 (Figs. 7D–F), length 9.4 mm, width 6.5 mm, height 5.1 mm. LACMIP Locality 16951 [*ex* CSUN Locality 1220b], Bateque Formation, Mesa La Salina, Baja California Sur, México (Squires and Demetrion, 1992).

Occurrence—Lower Eocene. "Capay Stage," Baja California Sur, México.

Etymology—Originally named for the Eocene Bateque Formation, Baja California Sur, México.

Description—Shell small in size. Shell ovate, smooth, dorsal moderately inflated with central area flat. Spire covered. Aperture gently curved and moderately wide, opening anteriorly; denticulation well developed on both sides of aperture. Labial lip (outer lip) with approximately 30 teeth, strongest ones on central part of lip. Columellar lip (outer lip) with approximately 20 teeth, becoming smaller toward exhalant canal (posterior canal). Labial lip teeth slighty stronger than columellar lip teeth. Terminal ridge present on left side of columellar lip. Anterior end of shell slightly flattened out and projecting short distance. Posterior end of shell not projecting. Border on basal lateral margin of shell (Groves 2011: p. 49).

Remarks—*Eocypraea batequensis* is known only from its holotype.

Eocypraea crescentensis Groves, 2011
Figs. 7G–I

Eocypraea (*Eocypraea*) n. sp. 2 (in part). Groves, 1997. p. 7 [as *E.* (*E.*) n. sp. 2].

Eocypraea (*Eocypraea*) *crescentensis* Groves, 2011. p. 46 (table 1), 49, 50, figs. 7, 8.

Grovesia crescentensis (Groves). Fehse, 2021. p. 44.

Holotype and Type Locality—LACMIP 16655.40, LACMIP Type 13646 (Figs. 7G–I), 10.9 mm in length, 7.6 mm in width, and 6.1 mm in height. LACMIP Locality 16655 [= LACMIP Locality 41563; *ex* CSUN Locality 1563], Crescent Formation, Larch Mountain area, Black Hills, Thurston County, southwestern Washington.

Referred Specimens—A poorly preserved topotypic internal mold (7.8 mm in length, 5.6 mm in width, and 4.3 mm in height), and three small fragments [LACMIP Locality 16655] also exist.

Occurrence—Lower Eocene, "Capay Stage," southwestern Washington.

Etymology—Originally named for the Eocene Crescent Formation, Thurston County, western Washington.

Description—Shell small, moderately inflated, constricted anteriorly. Dorsal surface exhibits linear pattern which could represent growth lines. Aperture wide and very slightly s-shaped. Denticulation coarse with smooth interstices: outer lip with 14 teeth, inner lip with 6 teeth. Anterior and posterior canals shallow. Anterior and posterior basal ridges reduced forming a slight columellar basal callus; slight posterior spiral sulcus present; base rounded (Groves, 2011: p. 49).

Remarks—This rare species has finer dentition than the other NEP species of this genus and poorer preservation of its apertural area.

Eocypraea jimgoederti Groves, 2011
Figs. 7J–L

Eocypraea (*Eocypraea*) n. sp. 2 (in part). Groves, 1997. p. 8 [as *E.* (*E.*) n. sp. 2].

Eocypraea (*Eocypraea*) *jimgoederti* Groves, 2011. p. 46 (table 1), 50, figs. 9, 10.

Eocypraea jimgoederti Groves. Fehse, 2021. p. 42.

Holotype and Type Locality—LACMIP 41573.1, LACMIP Type 13647 (Figs. 7J–L), length 12.7 mm, width 8.2 mm, height 6.9 mm. LACMIP Locality 41573 (*ex* CSUN Locality 1573), Crescent Formation, Doty Hills, Lewis County, Washington. The type locality of this species occurs in the lower McIntosh Formation, northern Doty Hills, Lewis County, southwestern Washington, and not, as stated in Groves (2011: p. 50) as in the Crescent Formation. The lower McIntosh Formation is middle Eocene in age (Squires and Goedert 1995).

Occurrence—Middle Eocene, "Transition Stage" to

"Tejon Stage," Lewis County, southwestern Washington.

Etymology—Originally named for colleague James L. (Jim) Goedert (Gig Harbor, Washington).

Description—Shell small and slightly inflated. Dorsum highly arched with maximum height slightly posterior of center; maximum width nearly centered. Spire covered. Aperture wide for size Denticulation coarse with smooth interstices; outer lip with 14 teeth, inner lip with 12 teeth. Anterior canal shallow. Posterior columella area moderately inflated. Anterior ridges prominent. Posterior ridges slightly reduced. Posterior canal deep. Basal marginal callus moderate on outer lip; base rounded (Groves, 2011: p, 50).

Eocypraea judithsmithae Groves and Squires n. sp.
Figs. 7M–O

Zoobank ID—LSID: urn:lsid:zoobank.org:act:515D4573-172F-457E-AAB9-BD37AC242CD9

Diagnosis—Inflated-pyriform shell of small to medium size; spire involute; narrow elongate aperture; fossula broad, smooth, concave.

Holotype and Type Locality—LACMIP 40372.1, LACMIP Type 14940 (Figs. 7M–O), length 26.7 mm, width 18.3 mm, height 13.8 mm. LACMIP Locality 40372 [*ex* CSUN Locality 372], Llajas Formation, approximately 25 m stratigraphically below "Stewart bed," Devil Canyon (formerly known as Aliso Canyon), southwestern Santa Susana Mountains, Los Angeles County, California.

Paratype—LACMIP 7171.1, LACMIP type 14926, length 24.8 mm, width 18.4 mm. height 13.3 mm, LACMIP Locality 7171 [*ex* CIT Locality 1074], Domengine Formation, Domengine Ranch, Fresno County, California. The paratype is worn but has a well preserved labial lip.

Occurrence—Llajas Formation, upper lower Eocene, Devil Canyon (formerly Aliso Canyon), southwestern Santa Susana Mountains, Los Angeles County, southern California and Eocene Domengine Formation, Fresno County, California.

Etymology— Named in honor of friend and colleague Judith T. Smith (USNM, Paleobiology) for her numerous contributions to molluscan paleontology.

Description—Shell of medium size, noticeably inflated and smooth. Constricted anteriorly , spire completely covered, dorsum highly arched, maximum height slightly posterior of center, maximum width nearly center, aperture slightly s-shaped, curves towards columella posteriorly, denticulation semi-coarse, outer lip with 18 teeth, inner lip with 13 teeth (tooth count incomplete due to missing posterior portion of inner lip), fossula smooth and wide, anterior and posterior canals deep, anterior terminal ridges short, base rounded, very slight basal callus on outer lip.

Remarks—The holotype has good preservation and the paratype has moderately good preservation. This new species resembles closely the middle Eocene *Eocypraea inflata* (Lamarck, 1802), known from France, but the new species differs by having being less globular in shell shape and having weaker denticulations on both lips of the aperture. Two additional specimens (LACMIP 7171.2) from the paratype locality (LACMIP Locality 7171 [*ex* CIT Locality 1074] are poorly preserved specimens with little original shell material.

Eocypraea novasumma (Nelson, 1925)
Figs. 8A–C

Ovula novasumma Nelson, 1925. p. 398, chart opposite p. 402, 425; pl. 57, fig. 2. Keen and Bentson, 1944. p. 183. Zinsmeister and Paredes-Mejia, 1988. p. 12.

Eocypraea (*Eocypraea*) *novasumma* (Nelson). Schilder, 1932. p. 214 [as *E.* (*E.*) *novasumma*]. Schilder, 1941. p. 102. Weaver, MS [1959]. p. 480; pl. 21, figs. 1, 2. Groves, 1992. p. 106. Groves, 1993. p. 11. Groves, 1997. p. 7. Groves, 2011. p. 46 (table 1).

Cypraea novasuma [*sic*] (Nelson). Ingram, 1947a. p. 60, 98, pl. 3, fig. 9. Ingram, 1947b. p. 147.

Eocypraea (*Eocypraea*) *sabuloviridis* (Whitfield, 1892). Schilder and Schilder, 1971. pp. 66, 137. Not *Eocypraea sabuloviridis* (Whitfield, 1892).

Eocypraea novasumma (Nelson). Zinsmeister, 1974. p. 129; pl. 13 [not pl. 8 as in text], figs. 8, 9; Zinsmeister, 1983. pp. 64, 69, pl. 3, figs. 1, 2. Groves and Squires, 2021. p. 227 (as *Cypraea*), 232. Fehse, 2021. p. 42.

Eocypraea novasumma (Nelson). Paredes-Mejia, 1989. p. 195, 196, pl. 4, figs. 8–10. Perrilliat, 2013. p. 134, figs. 4.3, 4.4. Not *Eocypraea novasumma* (Nelson, 1925).

Holotype and Type Locality—UCMP 30499 (Figs. 8A–C), length 15.8 mm, width 11.9, height 9.3 mm. UCMP Locality 3776, north side Meier Canyon, south side of Simi Valley, Ventura County, southern California.

Referred Specimens—Hypotype (of Zinsmeister, 1974, 1983) UCR 6871/13 (not UCR 3776/1), UCR Locality 6871, from the Santa Susana Formation on the north side of Simi Hills, Simi Valley, Ventura County, southern California. **Hypotype** (of Paredes-Mejia, 1989) IGM 4388, PU Locality 1334, Mesa San Carlos, Baja California, México (= hypotype IGM 4367 of Perrilliat, 2013).

Occurrence—Middle Paleocene, southern California to northern Baja California, México. **Selandian Stage:**

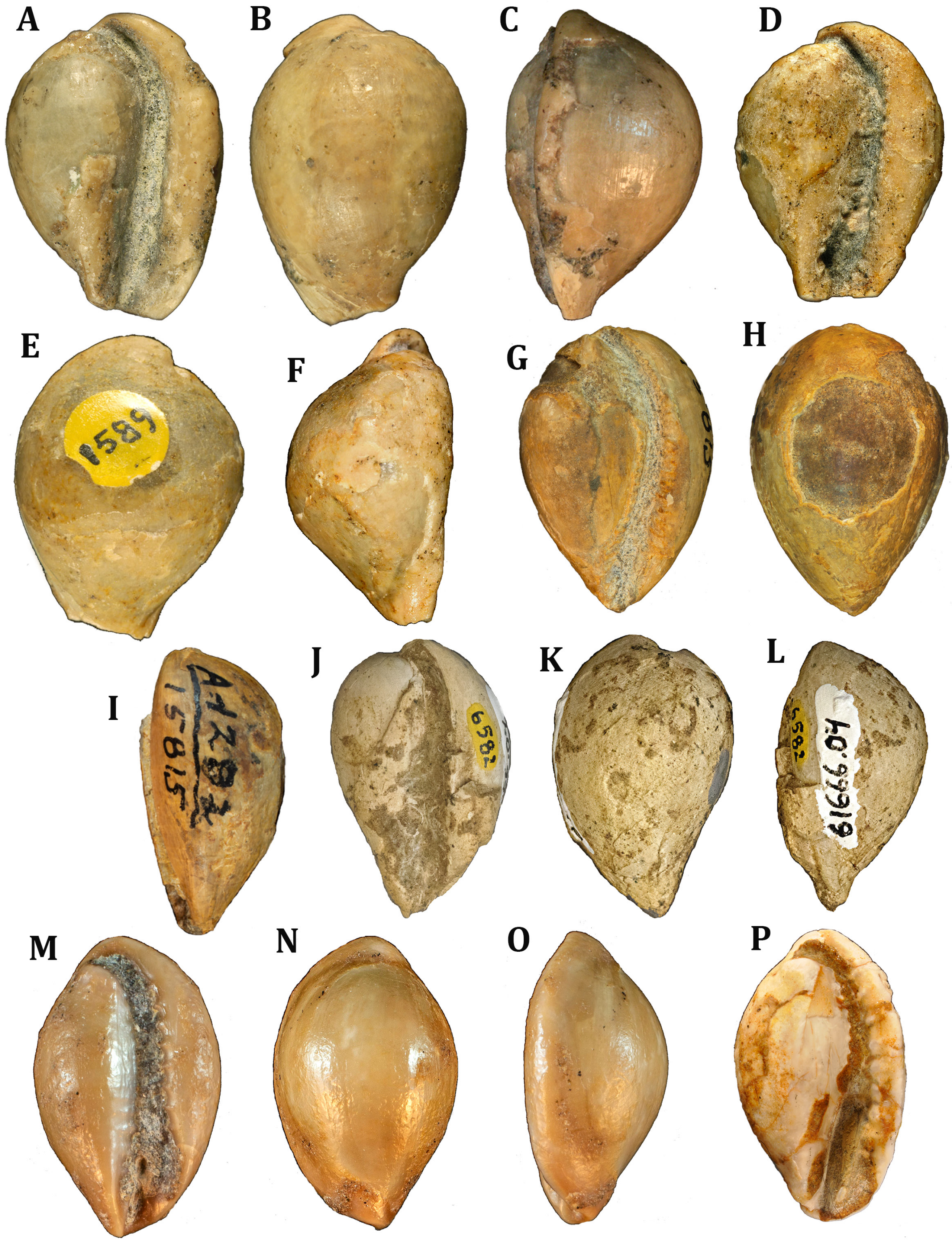
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Figure 8A–C. *Eocypraea novasumma* (Nelson, 1925), Santa Susana Formation (Paleocene, Thanetian Stage), Runkle Canyon, north side Simi Hills, Ventura County, southern California. Basal **(A)**, dorsal **(B)**, and right-labral **(C)** views, 3.2x, length 17 mm, width 11.6 mm, height 9.3 mm, of holotype UCMP 30499, UCMP Locality 4776. **D–F.** *Eocypraea takeosusukii* Groves, 2011, "Martinez" Formation (Paleocene, Thanetian), Lower Lake area, Lake County, northern California. Basal (**D**), dorsal (**E**), and left-lateral (columellar) views, 2.6x, length 18.8 mm, width 14.4 mm, height 11.2 mm, of holotype LACMIP 7045.1, LACMIP Type 13645, LACMIP Locality 7045 [*ex* CIT Locality 1580]. **G–I.** *Eocypraea* sp., cf. *E. inflata* (Lamarck, 1802), "Domengine Formation" (Eocene, "Domengine Stage"), Reef Ridge, Kings County, central California. Basal (**G**), dorsal (**H**), and right (labral) (**I**) views, 1.8x, length 26 mm, width 17.7 mm, height 13 mm, of hypotype UCMP 15815, Locality UCMP A-1282. **J–L.** *Eocypraea* sp. Lodo Formation (basal part) (Paleocene, Thanetian Stage), Tumey Hills, Fresno County, central California. Basal (**J**), dorsal (**K**), and right (labral) (**L**) views, 1.5x, length 33 mm, width 21.5 mm, height 19 mm, of hypotype CASG 61666.04 [*ex* LSJU 10236], CASG Locality 61666 [*ex* LSJU Locality 2073; = UCMP Locality A-9717]. **M–P.** *Grovesia castacensis* (Stewart, 1926 [1927]), Tejon Formation (Eocene, "Tejon Stage"), Tehachapi Mountains, Kern County, southern California. Basal **(M)**, dorsal **(N),** and left (columellar) **(O)** views, 4.5x, length 12.2 mm, width 7.8 mm, height 5.9 mm, of holotype UCMP 11690, Grapevine Canyon, UCMP Locality 452. Basal (**P**) view, 3.4x, length 15.5 mm, width 9.1 mm, height 6.9 mm, of hypotype LACMIP 41206.2, LACMIP Type 14941, base of Metralla Sandstone Member, Live Oak Canyon, LACMIP Locality 41206.

Santa Susana Formation (lower part), north side Simi Valley, Ventura County, southern California (Zinsmeister 1974, 1983; Groves 1992, 1993, 1997, 2011).

Etymology—Originally from Latin *novasumma* 'new ones' … a new species.

Description—Shell small and smooth; inflated; left-lateral side more inflated than right-lateral side (thereby producing moderate "lop-sided" shape. Shell widest medially. Basal surface slightly inflated. Left-lateral posterior side of shell lowly protruding. Spire covered (involute?). Aperture straight, widens anteriorly, and prominently curved posteriorly adxially (to the left). Outer lip broad, flattish and with very subdued small teeth. Inner lip teeth also subdued and apparently more numerous and more closely spaced than those on outer lip.

Remarks—Preservation of the holotype of this species' dentition is very poor. The anteriormost end of the holotype is missing. Only a few specimens are known of the small-sized species. In the Simi Hills, *E. novasumma* occurs only low in the Santa Susana Formation in Runkle and Meier canyons, where its type locality is in the vicinity of the type locality of *Propusularia kemperae*, whose geologic age was discussed earlier in this present paper and is of Selandian age. A poorly preserved specimen from the Santa Susana Formation, Quarry Canyon area, Santa Monica Mountains, Los Angeles County, California (LACMIP 11677.1, LACMIP Type 14927), LACMIP Locality 11677, may be *E. novasumma.* An additional poorly preserved internal mold from the Sepultura Formation, Santa Catarina, Baja California, México (LACMIP 6364.1, Type LACMIP 14928) (LACMIP Locality 6364) may also be *E. novasumma*.

Schilder and Schilder (1971) listed *E. novasumma* as a synonym of *E. sabuloviridis* (Whitfield, 1892, pp. 223, 224, pl. 32, figs. 20–22), of the Eocene Greensand Marls of New Jersey but they offered no explanation for this assignment. The holotype of *E. sabuloviridis* is a poorly preserved internal mold, which does not resemble *E. novasumma*.

In the Sepultura Formation, Mesa San Carlos, Baja California, México, *Eocypraea novasumma* has been reported from the same area as where specimens of *Propustularia kemperae* (Paredes-Mejia 1989: p. 503; Perrilliat 2013: p. 29) were reported. However, the specimen, with different IGM hypotype numbers, reported by both Paredes-Mejia (1989) and Perrilliat (2013) is poorly preserved and does not favorably compare to the holotype and is likely another species.

Eocypraea takeosusukii Groves, 2011
Figs. 8D–F

Eocypraea (*Eocypraea*) n. sp. Groves, 1997. p. 7 [as *E.* (*E.*) n. sp.].

Eocypraea (*Eocypraea*) *takeosusukii* Groves, 2011. p. 46 (Table 1), 48, 49, figs. 3, 4. Groves and Squires, 2021. p. 232.

Eocypraea takeosusukii Groves. Fehse, 2021. p. 42.

Holotype and Type Locality—LACMIP 7045.1, LACMIP Type 13645 (Figs. 8D–F), length 18.8 mm, width 14.4 mm, height 11.2 mm. LACMIP Locality 7045 (ex CIT Locality 1589), "Martinez Formation" (Thanetian Stage), east end of Lower Lake, Lake County, northern California.

Occurrence—Late Paleocene, "Martinez Formation," Lower Lake area, Lake County, northern California.

Etymology—Originally named for the late Takeo Susuki [1920-2006] (UCLA, Earth and Space Sciences Department).

Description—Shell small/medium size. Shell constricted anteriorly. Dorsum highly arched, maximum height and maximum width near center. Aperture slightly s-shaped, widens anteriorly, curves sharply toward columella posteriorly. Denticulation semi-coarse with smooth interstices: outer lip with 16 teeth, inner lip with 11 teeth. Fossula smooth, wide. Posterior columella highly inflated. Anterior canal missing. Posterior canal deep. Anterior and posterior basal ridges slight and do not form basal calluses. Base rounded. (Groves 2011: p. 49).

Remarks—The holotype is the only known specimen, and its preservation is moderately good. A poorly preserved specimen from LACMIP Locality 7047 [*ex* CIT Locality 868], Lower Lake area, Lake County, northern California (LACMIP 7047.74, Type LACMIP 14929). "Martinez Formation" may be this species. This fauna contains *Turritella infragranulata* Gabb, 1864, in the Herndon Creek area, Lower Lake, Lake County, northern California (Stanton 1896) and Saul (1983: p. 102) confirmed Stanton's (1896) report of this turritellid and assigned it to the Thanetian Stage.

Eocypraea sp. cf. *E. inflata* (Lamarck, 1802)
Figs. 8G–I

Eocypraea castacensis (Stewart, 1926 [1927]). Vokes, 1939, p. 154 [in part], pl. 20, fig. 14 [not fig. 9, = *Bernaya kaylinae* n. sp.].

Cypraea castacensis (Stewart). Ingram, 1942. p. 103 [in part], pl. 8, fig. 6 [not fig. 5, = *Bernaya kaylinae* n. sp.].

Eocypraea (*Eocypraea*) *moumieti* Dolin and Dolin, 1983. p. 36. Groves, 1997. p. 8. Not *Eocypraea moumieti* Dolin and Dolin, 1983. Not *Eocypraea inflata* var. *moumieti* Dolin and Dolin, 1983. p. 46.

Eocypraea (*Eocypraea*) sp. cf. *E.* (*E.*) *inflata* (Lamarck, 1802). Groves, 2011. p. 50, figs. 11, 12. Groves and Squires, 2021. p. 231.

Referred Specimen—Hypotype (of Vokes, 1939, of Ingram, 1942, of Groves, 2011) UCMP 15815 (Figs. 8G–I), length 27.3, width 18.7 mm, height 15.1, UCMP Locality A-1282.

Occurrence—Domengine Formation, middle Eocene, Reef Ridge, Fresno County, central California.

Etymology—Originally from Latin *inflata* for the highly inflated shell.

Remarks— The hypotype of Vokes (1939), Ingram (1942), and Groves (2011) most closely resembles *Eocypraea inflata* (Lamarck, 1802) from middle Eocene (Lutetion/Bartonian) strata of France, Belgium, and England. This is particularly evident from the illustrations of Cossmann (1903: pl. 9, figs. 18, 19), Cossmann and Pissaro (1911: pl. 32, fig. 162-7), and Wenz (1941: fig. 2882). It superficially resembles *Luponovula maniobraensis* (Squires and Advocate, 1986) from the lower Eocene ("Capay Stage") Maniobra Formation of Riverside County, southern California. *Luponovula maniobraensis* is more elongate, has coarser dentition, has a prominent basal callus, and is larger than *Eocypraea* sp. cf. *E. inflata*.

Dolin and Dolin (1983: p. 37, table on p. 46 [as *Eocypraea inflata* var. *moumieti*]) reported *Eocypraea moumieti* Dolin and Dolin, 1983, which is known from the Gan Basin, Pyrénées Atlantique Department, France, as also occurring in California. They reported that this California occurrence is questionably "*castacensis*" Vokes, 1939, but Vokes was not the author of *castacensis*. That particular specimen (hypotype UCMP 33808 of Vokes, 1939) is now *Bernaya kaylinae* n. sp. In summary, *E.* sp., cf. *E. inflata* (Lamarck, 1802) occurs very rarely in the NEP region, whereas *E. moumieti* Dolin and Dolin, 1983 does not occur in this region.

Perrilliat et al. (2003: p. 48, pl. 2, figs. 33, 34) reported a specimen of a middle Eocene cypraeoidean as *E.* (*E.*) *inflata* (Lamarck, 1802) [hypotype IHN 6736] from the San Juan Formation, Chiapas, southern México. Unfortunately, this specimen is too poorly preserved to afford a positive identification.

Eocypraea sp.
Figs. 8J–L

Cypraea n. sp. Smith, 1975. p. 469, 479, pl. 2, fig. 10 [as *Cypraea* sp.]. Groves and Squires, 2021. p. 227.

Referred Specimen—Hypotype (of Smith, 1975) CASG 61666.04 [*ex* LSJU 10236, *ex* LSJU 6582] (Figs 8J–L), CASG Locality 61666 [*ex* LSJU Locality 2073; = UCMP Locality A-9717].

Occurrence—Basal part of Lodo Formation, late Paleocene (Thanetian Stage). Tumey Hills, Fresno County, central California.

Remarks—Only a single specimen is known, and Smith (1975) provided only a lateral view. This view, as well as the basal and dorsum views, are also shown in this present paper. The aperture is filled with matrix, but otherwise the specimen has fairly good preservation. However, key features are obscured and a species name cannot be assigned at this time.

GROVESIA Dolin and Ledon, 2002

Type Species—*Prionovolva* (*Grovesia*) *ganensis* Dolin and Ledon, 2002, by original designation (of Dolin and Ledon, 2002: p. 334). Lower Eocene (Ypresian), Gan, Pyrénées-Atlantiques Department, France.

Diagnosis—Size small. Shell moderately inflated, can be somewhat narrow and tapered. Dorsum smooth. Fossula auriform. Terminal fold short. Columellar teeth carinated, extending partially across basal face, especially on posterior half of base. Outer lip coarsely denticulate, with short but stout denticles. Siphonal canal open. Posterior (exhalant) canal poorly delimited (Dolin and Ledon, 2002: p. 334).

Geologic Range—Early Eocene (Yepresian) to late Eocene (Priabonian) (Fehse, 2021, in part). In the NEP *Grovesia* ranges from the upper lower Eocene ("Domengine Stage") to middle Eocene ("Tejon Stage") (new information). Also questionably upper middle Eocene (Priabonian) in Washington (new information).

Remarks—Dolin and Ledon (2002: p. 334) placed their new subgenus, *Grovesia*, in the extant genus *Prionovolva* Iredale, 1930, but Dolin and Pacaud (2009: pp. 288, 289) recognized *Grovesia* as a distinct genus. *Grovesia mathewsonii* (see below) and *G. castacensis* form a lineage (Fig. 1), ranging from the early middle ("Domengine Stage") to late middle Eocene ("Tejon Stage") in the NEP region (new information). Fehse (2021) noted that *Grovesia* ranges from the Late Cretaceous (Cenomanian) to late Eocene (Priabonian). He included the Cretaceous species *Cyproglobina aegyptia* Schilder, 1932b and *C. strombecki* Schilder, 1922, which are both questionably *Grovesia*.

Specimens of *Grovesia castacensis* and *G. mathewsonii* (below) are many times poorly preserved and identifications were made as 'best judgements' by the authors. Throughout the duration of the pandemic it was impossible to verify nonfigured identifications cited by Dickerson (1915, 1916), Anderson and Hanna (1925), and Weaver (1953) in person.

Grovesia castacensis (Stewart, 1926 [1927]) n. comb.
Figs. 8M–P, 9A–B

Cypraea (*Luponia*) *bayerquei* Gabb, 1869. pp. 163, 164, 225 [as *C.* (*L.*) *Bayerquei*]; pl. 27, figs. 43a–c [in part]. Cooper, 1888. p. 280 [in part]. Arnold, 1906. p. 15. Not *Eocypraea bayerquei* (Gabb, 1869).

Cypraea bayerquei Gabb. Whiteaves, 1895, p. 128 [as *Cypraea Bayerquei*]. Dickerson, 1915. pp. 43, 60, pl. 6, figs. 4a, 4b. Dickerson, 1916. pp. 421, 432, 448 [in part]. Anderson and Hanna, 1925. pp. 43, 105–107 [in part]. Not *Eocypraea bayerquei* (Gabb, 1869).

Cypraea castacensis Stewart, 1926 [1927]. p. 370; pl. 28, fig. 10. (New name for *Cypraea bayerquei* Gabb, 1869, [not Gabb, 1864]). Ingram, 1942. p. 103; pl. 8, fig. 5 [= *Bernaya kaylinae*, n. sp.], fig. 6 [= *Eocypraea* sp., cf. *E. inflata* (Lamarck, 1802)]. Keen and Bentson, 1944. p. 151–152 [in part]. Ingram, 1947a. pp. 88, 89 [in part]. Ingram, 1947b. p. 144, 145. Squires, 1984. pp. 23, 24, fig. 7b [= *Bernaya kaylinae* n. sp. paratype].

Eocypraea (*Eocypraea*) *bayerquei castacensis* (Stewart). Schilder, 1932. p. 214 [as *E.* (*E.*) *bayerquei castacensis*]. Schilder and Schilder, 1971. pp. 67 [as *Eocypraea* (*Eocypraea*) *bay. castacensis*], 103.

Eocypraea castacensis (Stewart). Vokes, 1939. p. 154, pl. 20, fig. 9 [= *Bernaya kaylinae* n. sp.], fig. 14 [= *Eocypraea* sp., cf. *E. inflata* (Lamarck, 1802)]. Fehse, 2001. p. 20. Groves and Squires, 2021. pp. 226 (as *Cypraea*), 222, 232 (as *Eocypraea* (*E.*) sp., cf. *Eocypraea* (*E.*) *castacensis*).

Eocypraea (*Eocypraea*) *castacensis* (Stewart, 1926 [1927]). Schilder, 1941. p. 103. Groves, 1992. p. 106. Groves, 1993. p. 11. Groves, 2011. p. 46 (table 1).

Sulcocypraea mathewsonii (Gabb, 1869). Squires and Groves, 1993. pp. 83, 84, figs. 2–4. Groves, 1994a. p. 247. Nesbitt, 1998. p. 13, pl. 1, fig. 13 (fig. oriented upside down). Not *C. mathewsonii* [= *G. castacensis* (Stewart, 1926 [1927])].

Grovesia mathewsonii (Gabb). Dolin and Pacaud, 2009. p. 289. Not *G. mathewsonii* [= *G. castacensis* (Stewart, 1926 [1927]).

Eocypraea (*Eocypraea*) *castacensis* (Stewart, 1926 [1927]). Squires, 2000. p. 896 [not *G. castacensis* (Stewart, 1926 [1927])] [= *Subepona leahae* n. sp.].

Eocypraea bayerquei castacensis (Stewart). Fehse, 2021. p. 42.

Holotype and Type Locality—UCMP 11690 (= figured specimen of Dickerson, 1915, pl. 6, figs. 4a, 4b) (Figs. 8M–O), length 12.2 mm, width 7.4 mm, height 5.9 mm. UCMP Locality 452, Tejon Formation (Metralla Member), Grapevine Creek, Kern County, southern California.

Referred Specimens—Hypotype (of Gabb, 1869) ANSP 4211 and of Stewart (1926 [1927]), p. 370, pl. 28, fig. 10) lost (Groves and Squires, 2018: p. 67). **Hypotype** (of Squires and Groves, 1993, figs. 2–4; as *Sulcocypraea mathewsonii*) UWBM 22052, Tukwilla Formation, Poverty Hill, King County, Washington. **Hypotype** (of Nesbitt, 1998, pl, 1, fig. 13; as *Sulcocypraea mathewsonii*) UWBM 78021, Tukwilla Formation, King County, Washington. **Hypotype (herein)** LACMIP 41206.2, LACMIP Type 14941 (Figs. 8P, 9A–B), LACMIP Locality 41206 [*ex* CSUN

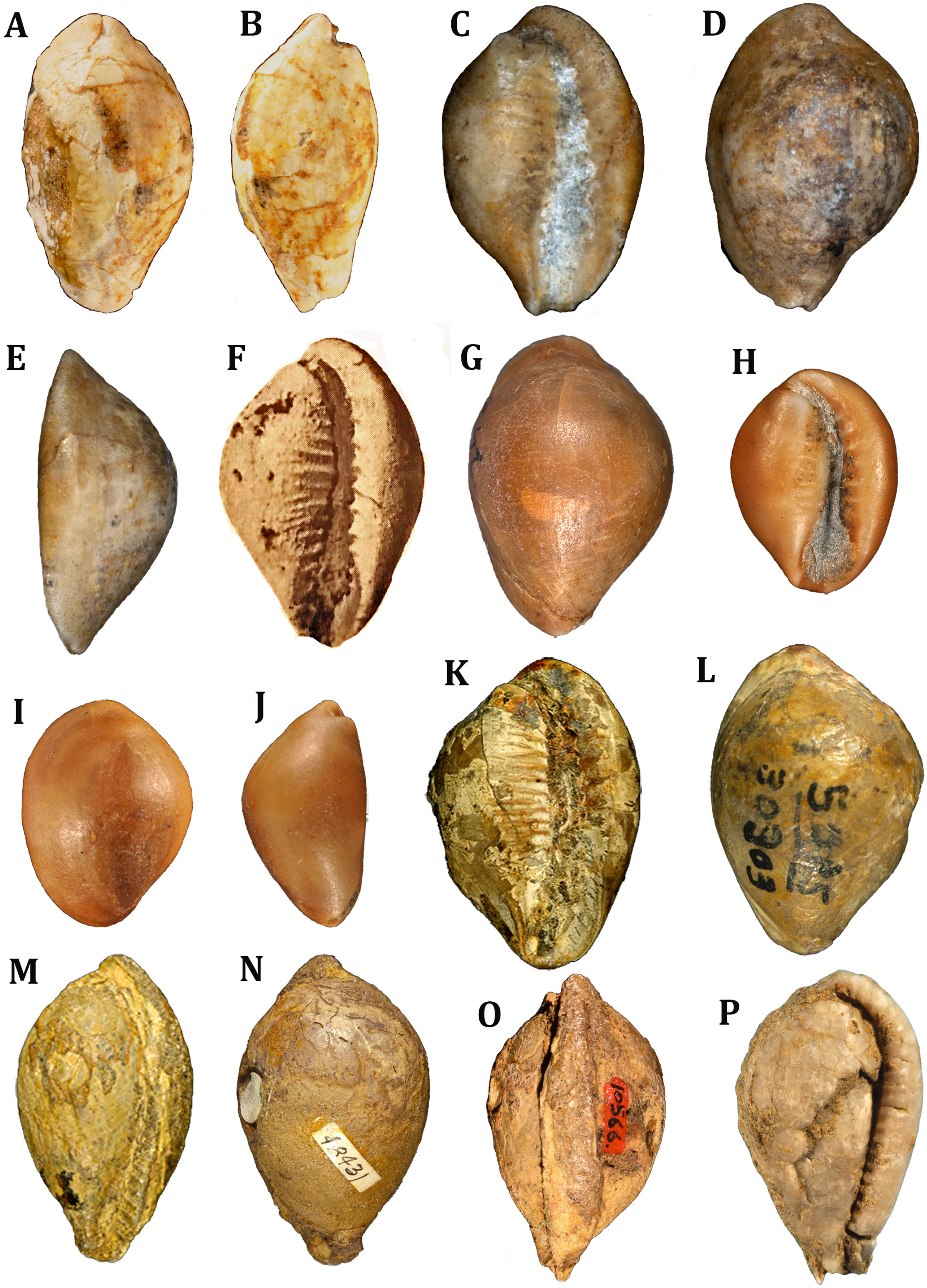
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Figure 9A–B. *Grovesia castacensis* (Stewart, 1926 [1927]), Tejon Formation (Eocene, "Tejon Stage"), Tehachapi Mountains, Kern County, southern California. Dorsal (A) and left (columellar) (**B**) views, 3.4x, length 15.5 mm, width 9.1 mm, height 6.9 mm, of hypotype LACMIP 41206.2, LACMIP Type 14941, base of Metralla Sandstone Member, Live Oak Canyon, LACMIP Locality 41206 [ex CSUN Locality 1206]. **C–L.** *Grovesia mathewsonii* (Gabb, 1869), Muir Sandstone (Eocene, "Domengine Stage" to "Tejon Stage"), near Martinez, Contra Costa County, northern California. Basal (**C**), dorsal (**D**), right (labral) views, 1x, length 10.7 mm, width 7.5 mm, height 4.7 mm, of holotype ANSP 4217. **F–G.** Basal (**F**) [as published] and dorsal (**G**) views, 2.9x, length 17.9 mm, width 11.6 mm, of holotype CASG 245.02 [*ex* CAS 816] of *Cypraea kerniana* Anderson and Hanna, 1925, Tejon Formation (Eocene, "Tejon Stage") Grapevine Canyon, Kern County, southern California. **H–J.** Basal (**H**), dorsal (**I**), left (columellar), (**J**) left (columellar) views, 2.7x, length 14.6 mm, width 10.8 mm, height 7.8 mm, of hypotype LACMIP 7155.9, LACMIP type 14930, Tejon Formation, Grapevine Canyon, LACMIP Locality 7155, Kern County, southern California. **K-L**. Basal (**K**), dorsal (**L**) views, 3.9x, length 14 mm, width 10.3 mm, of hypotype UCMP 30903, UCMP Locality 5085, Ardath Shale (Eocene, "Domengine Stage"), San Diego County, southern California. **M–P.** *Luponovula maniobraensis* (Squires and Advocate, 1986), (**M–O**)**.** Maniobra Formation (Eocene, "Capay Stage"), Orocopia Mountains, Riverside County, southern California. Basal (**M**), dorsal (**N**), and right (labral) (**O**) views, 1.3x, length 39.6 mm, width 22.8 mm, height 21.2 mm, of holotype LACMIP 10566.4, LACMIP Type 10566 [ex UCLA 48431], LACMIP Locality 23779. (**P**)**.** Basal view, Llajas Formation (Eocene, "Capay Stage"), north side Simi Valley, Ventura County, southern California, 2.1x, length 26.6 mm, width 15.8 mm, height 10.9 mm, of hypotype LACMIP 40491.1, LACMIP Type 14945 (LACMIP Locality 40491 [*ex* CSUN Locality 491]).

Locality 1206], Tejon Formation, base of Metralla Sandstone Member, Liveoak Canyon, Kern County, southern California. Additional specimens include one specimen (LACMIP 41202.27, LACMIP Type 14944) from LACMIP Locality 41202 [*ex* CSUN Locality 1202], basal Tejon Formation, Edmonston Pumping Plant, Kern County California, three specimens (LACMIP 16856.2, LACMIP Type 14942) LACMIP Locality 16856, Juncal Formation, Lockwood Valley, Ventura County, California, and an additional specimen from the Tejon Formation, Grapevine Canyon, Kern County, California (LACMIP Locality 12492). The aforementioned specimens from LACMIP Locality 16856 [= unpublished locality of Hartman (1957)] are indeed *G. castacensis* but the exact locality information cannot be verified with confidence and they noted here for the record. A single uncatalogued LACMIP specimen of *G. castacensis* with scant locality data of "San Diego area" from the Sternberg Collection (*ex* UCLA) was also examined.

Occurrence—Middle to middle upper Eocene, Washington and southern California. **"Tejon Stage"** (lower to middle part): "Tejon Group," (undifferentiated as to member), Martinez area, Contra Costa County, northern California (Stewart, 1926 [1927]). Tejon Formation, base of Metralla Sandstone Member of Tejon Formation, *Turritella uvasana sargeanti* Anderson and Hanna, 1925 "zone," Live Oak Canyon, Tehachapi Mountains, Kern County, southern California (new information). **"Tejon Stage" (upper part):** Tukwila Formation, near Seattle, western King County, Washington (Squires and Groves 1993; Nesbitt 1998). **Lower Galvinian Stage:** Discovery Bay, Jefferson County, Washington (Durham 1944).

Etymology—Originally named for Castac Lake/Castac Valley area, just east of Lebec, Kern County, southern California. [Note: Castac Lake is not the same geographic feature as Castaic Lake, Los Angeles County].

Description—Shell small to medium in size. Shell noticeably lenticular lengthwise, with same-shaped sides (not with lob-sided outer lip), somewhat flattened dorsally, smooth. Denticulation on outer lip much coarser and more closely spaced than that on inner lip.

Remarks—At least seven specimens of *G. castacensis* are known and undoubtedly many others exist in stratigraphic collections. Preservation is usually moderate to good. *Grovesia castacensis*, which is an uncommon species, was formerly reported by most previous workers as belonging to the eocypraeid genus *Eocypraea* Cossmann, 1903. Poorly preserved specimens of NEP Eocene cypraeoideans have been commonly misidentified as *Grovesia castacensis*, as reviewed in the following paragraphs.

Squires (1984: pp. 23, 24, fig. 7b) reported a specimen of *Cypraea castacensis* from LACMIP Locality 40374 [*ex* CSUN Locality 374], which is in the mappable unit referred to as "Stewart bed" of the Llajas Formation, Llajas Canyon, on north side of Simi Valley, Ventura County, southern California, but this occurrence is incorrect. The only cypraeoideans found at that particular locality are the new species *Subepona leahae* and *Bernaya kaylinae*, both of which described and named in this present report.

Squires (2008: fig. 20) reported a very partial specimen identified as *Eocypraea* (E.) sp., cf. *E*. (*E*.) *castacensis* from the upper lower Eocene Juncal Formation (LACM 13421.10, LACMIP Type 13421) (LACMIP Locality 17848) in Elsmere Canyon, Los Angeles County, southern California. Although this specimen is too incomplete for reliable identification as to any species, the small size of the columellar teeth are unlike those of *Grovesia castacensis* and is unlikely to be this species.

A questionable occurrence of *Eocypraea* (*Eocypraea*) cf. *E. castacensis* (Stewart, 1926 [1927]) was reported by (Perrilliat et al. 2003: pl. 2, figs. 39, 40) from the undifferentiated middle Eocene San Juan Formation, Chiapas, southern México. This specimen (hypotype IHN 5458) superficially resembles *G. castacensis*, but poor preservation prevents confirmation of its identification.

Grovesia castacensis is similar morphologically to *G. ganensis* (Dolin and Ledon, 2002: figs. 1A, 1B) from lower Eocene (Ypresian) strata in Gan, Pyrénées-Atlantiques Department, France and *G. nogrolensis* Dolin and Pacaud (2009: pl. 5, figs. 4–7) from middle Eocene (lower Lutetian) strata in Cava Albanello di Nogarole Vicentino, Vicenza Prov., northeastern Italy. *Grovesia castacensis* differs by having much fewer yet stronger outer lip teeth.

Grovesia mathewsonii (Gabb, 1869)
Figs. 9C–L

Cypraea (*Epona*) *mathewsonii* Gabb, 1869. pp. 164 [as *C.* (*E.*) *Mathewsonii*], 225 [as *C.* (*Epona*) *Mathewsonii*], pl. 27, figs. 44a, b; Cooper, 1888. p. 280; Arnold, 1906. p. 15; Keen and Bentson, 1944. p. 152 [in part].

Cypraea mathewsonii Gabb. Campbell, 1892. p. 51. Whiteaves, 1895 [as *C. Mathewsonii*]. p. 128 (as *mathewsoni*). Dickerson, 1915. pp. 43, 60, pl, 6, fig. 5a. Dickerson, 1916. pp. 421, 438, 448. Anderson and Hanna, 1925. pp. 43, 106, 107; Nelson, 1925. p. 425 (as *mathewsoni*). Stewart, 1926 [1927]. p. 371, pl. 28, fig. 5; Ingram, 1942. p. 105, pl. 9, fig. 12; Ingram, 1947a. p. 61, pl. 7, fig. 10. Ingram, 1947b. p. 147; Weaver, 1953. p. 43; Richards, 1968. p. 156.

Cypraea kerniana Anderson and Hanna, 1925. pp. 44, 104, 105, 107, pl. 13, figs. 9–11. Clark, 1926. p. 115 (as *Cyprea*). Stewart, 1926 [1927]. p. 371. Hanna, 1927. pp. 249, 259, 314, pl. 52, figs. 7, 9. Keen and Bentson, 1944. p. 152.

Sulcocypraea mathewsonii (Gabb). Schilder, 1927. p. 81; Schilder, 1941. p. 104. Groves, 1992. p. 106. Fehse, 2001. p. 22.

Sulcocypraea mathewsonii mathewsonii (Gabb). Schilder, 1932. p. 222 (in part) [as *S. mathewsonii mathewsonii*]. Schilder and Schilder, 1971. pp. 68 [as *Sulcocypraea mat. mathewsonii*], 131. Fehse, 2021. p. 44.

Sulcocypraea kerniana (Anderson and Hanna). Schilder, 1932. p. 222 [as *S. kerniana*]. Schilder, 1941. p. 104; Schilder and Schilder, 1971. p. 68, 125; Dolin and Dolin, 1983. p. 44.

Cypraea sp. B, Turner, 1938. pp. 19, 35.

Erato mackini Durham, 1944. pp. 117, 165, 166, pl. 18, figs. 7, 9.

Cypraea sp. B, n. sp. (sp. B of Turner?), Hoover, 1963. p. D-27.

Eratotrivia mackini (Durham). Schilder and Schilder, 1971. pp. 10, 129.

Luponovula mathewsonii (Gabb). Dolin and Dolin, 1983. pp. 42–44, 46 (table 1), figs. 28, 29a–c. Dolin and Ledon, 2002. p. 344. Not *Grovesia mathewsonii* [= *G. ganensis* Dolin and Ledon, 2002].

Sulcocypraea mathewsonii (Gabb). Squires and Groves, 1993. figs. 2–4. Not *Grovesia mathewsonii* (Gabb, 1869) = *G. castacensis* (Stewart, 1926 [1927]). Groves and Squires, 2018. p. 88. Groves and Squires, 2021. p. 227 (as *Cypraea*).

Prionovolva (*Grovesia*) *mathewsonii* (Gabb). Dolin and Ledon, 2002: pp. 335, 336.

Grovesia mathewsonii (Gabb). Dolin and Pacaud, 2009: p. 289.

Holotypes and Type Localities—Of *G. mathewsonii*, holotype ANSP 4217 (Figs, 9C–E), length 10.4 mm, width 7.0 mm, height 5.9 mm, Muir Sandstone near Martinez, Contra Costa County, northern California (Squires and Groves 1993). Of *G. kerniana*, holotype CASG 245.02 [ex CASG 816] (Figs. 9F–G), length 17.3 mm, width 11.8 mm, height 9.1 mm, CASG Locality 245, Tejon Formation, Grapevine Creek, Tehachapi Moutains, Kern County, southern California. Of *Erato mackini*, holotype UCMP 35337, length 9.6 mm, width 7.1 mm, UCMP Locality A1802, Lincoln Creek Formation, Discovery Bay, Jefferson County, Washington (Durham 1944).

Paratypes—Of *G. kerniana*: CASG 245.03 (ex CASG 817), length 14.9 mm, width 12.4 mm, height 9.9 mm and CAS 245.04 [ex. CASG 818] length 13.8 mm, width 10.2 mm, height 8.4 mm. Both from CASG Locality 245, Grapevine Creek, Kern County, southern California. Of *Erato mackini*, two paratypes UCMP 35338 and 35339, both from UCMP Locality A1802, Lincoln Creek Formation, Discovery Bay, Jefferson County, Washington (Durham 1944).

Referred Specimens—Hypotype (of Dickerson, 1915: pl. 6, fig. 5) CASG 66608.01 (*ex* CASG 298), length 16.7, width 12.1 mm, height 9.8 mm, CASG Locality 66608 (= CASG Locality 245), Tejon Formation, Grapevine Canyon, Kern County, California. **Hypotype** (of Hanna, 1927: pl. 52, figs. 7, 9 as *Cypraea kerniana*, as plesiotype) UCMP 30903 (Figs, 9K–L), length 14.3 mm, width 10.2 mm, height 8.4 mm, UCMP Locality 5085, Ardath Shale, San Diego County, southern California. **Hypotype (herein)** LACMIP 7155.9, LACMIP Type 14930 (Figs. 9H–J), LACMIP Locality 7155 [*ex* CIT Locality 707], Tejon Formation, Grapevine Canyon, Kern County, southern California (10 additional unfigured specimens (LACMIP 7155.10). Additional material examined: LACMIP Localities 7162 [ex CIT Locality 1840] (four specimens, LACMIP 7162.2, LACMIP Type 14931), LACMIP Locality 22340 [ex UCLA Locality 2340] (13 specimens, LACMIP 22340.52, LACMIP Type 14932) and LACMIP Locality 43272 (two specimens, LACMIP 43272.1, LACMIP Type 14933), all Tejon Formation, Grapevine Canyon, Kern County, California. One additional specimen (LACMIP 43273.1, LACMIP Type 14943) from LACMIP Locality 43273 (= UWBM Locality A7561), Tukwilla Formation, Poverty Hill area, King County, Washington collected by J.L. Goedert was examined is identified as *Grovesia* cf. *mathewsonii* but could represent an undescribed species.

Occurrence—Upper lower to middle upper Eocene, southwestern Washington, southwestern Oregon to southern California. **"Domengine Stage":** Tyee Formation, Drain/Comstock area north of Roseburg, southwestern Oregon (Turner 1938). Ardath Shale, San Diego region, San Diego County, southern California (Hanna 1927). **"Tejon Stage" (lower part):** Tejon Formation, Liveoak Member, Grapevine Canyon, Tehachapi Mountains, Kern County, southern California (Dickerson 1915, 1916; Anderson and Hanna 1925; present report). Galvinian Stage (*Molopophorus stephensoni* zone): Lincoln Creek Formation, northern part of southwestern Washington (Durham 1944). According to Armentrout (1974: p. 37, fig. 2, the *M. stephensoni* zone is correlative to the middle Galvinian Stage.

Etymology—Originally named for fossil collector Mr. Mathewson (Martinez, Contra Costa County, central California).

Description—Shell small, mostly smooth, moderately low convexity, and left-lateral side can be more inflated than right-lateral side (thereby producing "lop-sided" shape). Spire concealed by callus. Posterior end of shell protruding somewhat. Aperture fairly straight, widening anteriorly, and curved posteriorly. Outer lip teeth few (9 to 10), moderately strong, and widely separated. Inner lip teeth numerous, very small, and closely spaced. Basal surface with transverse ribs, variable in strength and number and not extending very far.

Remarks—At least 40 specimens of *G. mathewsonii* are documented here (see above) and undoubtedly many others exist in stratigraphic collections. The anterior end of the holotype is missing, and the preservation of the dorsum of the specimen is very poor. The basal view of the holotype of *G. mathewsonii*, with its distinctive lop-sided shell, is shown here for the first time (Fig. 8O). Additional specimens of *G. mathewsonii* (other than the type specimens of *kerniana*) from the Tejon Formation are also shown here also for the first time. Some worn specimens of *mathewsonii* appear to not have any spiral ribs on their base, but very low-angle lighting reveals their presence (e.g., see Fig. 9C).

As noted above, there has been considerable confusion in the literature concerning the identification of *Grovesia mathewsonii* versus *G. castacensis*. This confusion is most certainly related to their both being found in the Tejon Formation in Kern County, southern California. It is important to mention, however, that *Grovesia mathewsonii* occurs in the Liveoak Member of the Tejon Formation, whereas *G. castacensis* occurs in the stratigraphically overlying (i.e., younger; see Nilsen 1987) Metralla Member of the Tejon Formation. *Grovesia mathewsonii* differs from *G. castacensis* by having transverse ribs on the base and by having a lop-sided shell.

Anderson and Hanna (1929) mentioned localities containing "cowries" in the lower part of the Tejon Formation in the Grapevine Canyon, Kern County, southern California. Most of these localities were demolished, however, by the subsequent building of and widening projects of Interstate 5 highway along the valley floor of this canyon. Fortunately, many well preserved specimens from this area were deposited at CIT, UCLA, and LACMIP by early collectors. Analysis of these specimens by the authors of this present report allowed for confirmation of *G. mathewonsii* as being present in the lower part of the Tejon Formation in Grapevine Canyon.

The holotype of *kerniana* (see Fig. 9B-C) is the same specimen figured by Anderson and Hanna (1925: pl. 13, fig. 9). When compared to the image available online (CASG website), however, the holotype of *G. kerniana* looks quite different as a large piece of the columellar base is missing.

Based upon careful examination of *Erato mackini* Durham, 1944 images, this species is herein relegated to the synonymy of *Grovesia mathewsonii* as the holotype and two paratypes are worn specimens of *G. mathewsonii*. They are significant specimens, however, as they represent the geologically youngest and farthest north known occurrence of *G. mathewsonii*.

Turner (1938: pp. 19, 35) in faunal lists included *Cypraea* sp. B, length 14.8 mm, width 9.0 mm, height 7.4 mm, from the middle Eocene ("Domengine Stage") Tyee Formation near Comstock near Drain, which is north of Roseburg, Oregon (Fig. 1, locality 8) (= UCMP Locality A-1134). Squires and Groves (1993: p. 83) identified *Cypraea* sp. B as *Sulcocypraea mathewsonii* (Gabb, 1869), but in the present report this taxon is identified as *Grovesia mathewsonii* (Gabb, 1869).

Dolin and Dolin (1983: table 1) erroneously reported *G. mathewsonii*, which they identified as *Luponovula mathewsonii* (Gabb) in France and Italy. Dolin and Ledon (2002: pp. 335, 336) noted that *G. mathewsonii* and *G. ganensis* Dolin and Leon (2002) are close morphologically, but they are not conspecific. Dolin and Pacaud (2009: p. 289), furthermore, reported that *Grovesia* is a distinct genus, and this assignment is used in this present report.

SULCOCYPRAEINAE Schilder, 1932
LUPONOVULA Sacco, 1894

Type Species—*Cypraea proserpinae* Bayan, 1870 [= *Cypraea rugosa* Broderip, 1827], by original designation (of Sacco, 1894: p. 44), middle Eocene (upper Lutetian), Roncà, Veneto Region, Italy.

Diagnosis—Shell dorsally swollen, right lateral side with prominent border, denticulation prominent on inner edge of outer lip, base can be smooth or sculptured with lateral ribs.

Geologic Range—Upper lower Eocene (terminal Ypresian Stage), France and Italy (Dolin and Pacaud 2009) and upper Paleocene (Thanetian Stage) and lower Eocene ("Capay Stage") of southern California (new information) to middle Eocene (lower Lutetian), Italy (Dolin and Pacaud 2009).

Remarks—*Luponovula* heretofore has been restricted to a few species from upper lower Eocene to middle Eocene strata in England, France, and Italy (Sacco 1894; Dolin and Ledon 2002; Dolin and Pacaud 2009). For the first time, this genus is reported as being present in North America (southern California) in lower Eocene ("Capay Stage") strata. As mentioned in more detail above (see *Grovesia mathewsoni*), Dolin and Dolin (1983) incorrectly assigned the southern California eocypraeid *Grovesia mathewsoni* to the genus *Luponovula*.

Luponovula maniobraensis (Squires and Advocate, 1986) n. comb.
Figs. 9M–P

Eocypraea? *maniobraensis* Squires and Advocate, 1986. pp. 856, 857, figs. 2.5, 2.6. Squires, 1991. p. 219, 220, 225; pl. 1, fig. 23.

Eocypraea (*Eocypraea*) *maniobraensis* Squires and Advocate. Groves, 1992. p. 106 [not 1987 as in table 1]. Groves, 1993. p. 11 [not 1983 as in text]. Groves, 1997. p. 8 [as *E.* (*E.*) *maniobraensis*]. Groves, 2011. p. 46 (table 1).

Eocypraea maniobraensis Squires and Advocate. Fehse, 2001. p. 20. Groves and Squires, 2021. p. 231 (as *Eocypraea*?). Fehse, 2021. p. 42.

Holotype and Type Locality—LACMIP 10566.4, LACMIP Type 10566 (*ex* UCLA 48431) (Figs. 9M–O), length 39.6 mm, width 22.8 mm, height 21.1. LACMIP Locality 23779 [*ex* UCLA Locality 3779; *ex* CSUN Locality 662], Maniobra Formation, Orocopia Mountains, Riverside County, southern California.

Referred Specimen—Hypotype (herein) LACMIP 40491.1, LACMIP Type 14945 (Fig. 9P), LACMIP Locality 40491 [*ex* CSUN Locality 491], Llajas Formation, is from a faulted area low in the stratigraphic section of this formation (see geologic map in Squires 1984: fig. 16) in Las Llajas Canyon, north side of Simi Valley, Ventura County, southern California [new information]. This Llajas Formation specimen has been crushed but retains enough morphological features to identify it as *L. maniobraensis*.

Occurrence—Lower Eocene ("Capay Stage"), Llajas Formation, southwestern Santa Susana Mountains, Los Angeles County, southern California, Ventura County (new information) to Maniobra Formation, Orocopia Mountains, Riverside County, southern California (Squires and Advocate 1986; Squires 1991).

Etymology—Originally named for the Eocene Maniobra Formation, Riverside County, southern California.

Description—Shell size medium; very inflated; ovate-pyriform. Shell widest medially. Base inflated. Spire involute. Aperture narrow and near right margin of shell; aperture elongate anteriorly and curved posteriorly. Aperture narrow and prominently curved. Outer lip narrow, with numerous teeth that become stronger toward anterior of aperture. Inner lip with numerous small teeth.

Remarks—This is an uncommon species. The anteriormost part of the holotype is missing. The dorsal view of this species is shown for the first time in Figure 4M. *Luponovula maniobraensis* most closely resembles *L. oligovata* (Sacco 1894: pl. 3, fig. 25; Cossmann 1903: pl. 7, fig. 2) of late early Oligocene age (Latorfian) from the Liguria and Piedmont regions of Italy and *L. normalis* (de Gregorio 1880: pl. 6, fig. 14) of middle Eocene age (Lutetian) from San Giovanni Illarione, Veneto, Italy. In comparison, *Luponovula maniobraensis* differs by having fewer teeth on its columellar lip, as well as having fewer and shorter teeth on the interior of its outer lip.

PEDICULARIIDAE Gray, 1853

Remarks—Lorenz and Fehse (2009) noted that the morphology of the marginal radular teeth of Pediculariidae differ distinctly from those of the Ovulidae, but that the zoological position of the Pediculariidae is not completely settled. They also noted that "the first results from DNA research seem to confirm its separation from the Cypraeidae and Ovulidae." The authors agree with this arrangement.

CYPAREDIINAE Schilder, 1927
CYPRAEDIA Swainson, 1840

Type Species—*Cypraedia cancellata* Swainson, 1840, by original designation [= *Cypraea elegans* G.B. Sowerby I, 1823] (of Swainson, 1840: p. 325), middle Eocene (Lutetian) Cotentin, Manche Department, France.

Diagnosis—Shell small to medium size. Pyriform, with moderate inflation. Spire involute. Sides with spiral ribs crossing similar longitudinal ribs (resulting in cancellate ornamentation), with or without nodes at intersections of ribs. Longitudinal ribs can be obsolete. Aperture narrow, curved posteriorly. Numerous fine teeth on both lips. Fossula very narrow, smooth. Anterior canal can be somewhat elongate (Wenz 1941).

Geologic Range—Late Cretaceous (Maastrichtian Age) to middle Oligocene, Europe, eastern Asia, southeastern United States, Caribbean, Ecuador, and México.

Remarks—The common name applied to species of *Cypraedia* is "reticulated" cowries.

Cypraedia sp.
Figs. 10A–C

Cypraedia sp. Squires and Demetrion, 1990. p. 102, figs. 2.8–2.10. Squires and Demetrion, 1992. p. 31, fig. 80.

Referred Specimens—Hypotype (of Squires and Demetrion, 1990 and Squires and Demetrion, 1992) IGM 5057 (Figs. 10A–C), length 19.5 mm, width 13.2, height 11.9 mm. LACMIP Locality 41220b [*ex* CSUN Locality 1220b].

Occurrence—Middle lower Eocene ("Capay Stage"), Bateque Formation, Baja California Sur, México.

Description—Shell ovate-inflated. Spire involute. Aperture narrow, cancellate ornamentation very fine and consisting of numerous equidistant spiral ribs (about 23) crossed by longitudinal ribs. Spiral ribs tend to alternate in strength on central part of base of shell and tend to become stronger than longitudinal ribs on anterior part of base of shell. Outer lip prominent, especially its posterior end. (Squires and Demetrion 1990, in part).

Remarks—This is a very rare gastropod. The preservation of the single known specimen is somewhat imperfect due to weathering, but the diagnostic characteristics of the genus are clearly present. In regard to its very fine cancellate structure, which is relatively uncommon on members of this genus, this specimen is most similar to the late Eocene (Bartonian Stage) specimen of *Cypraedia cancellata* Swainson, 1840 [= *C. elegans* G.B. Sowerby I, 1823] illustrated by Cossmann (1903: pl. 9, fig. 8) and by Cossmann and Pissarro (1910–1913: pl. 33, fig. 162-13 [two views]) of middle Eocene age (Lutetian Stage) in France. The Bateque Formation specimen differs by having a less inflated columellar side of its shell, a narrower inner lip, the presence of spiral ribs of alternate strength on the central part of basal side of the shell, and a more projected posterior end of its outer lip.

PEDICULARIINAE Gray, 1853
CYPRAEOGEMMULA Vredenburg, 1920

Type Species—*Trivia scabriscula* Koenen, 1890 [*non Trivia scabriscula* (Gray, 1827)], = *Cypraea liliputana* Schilder, 1922, by monotypy (of Vredenburg, 1920: p. 114), early Oligocene, Lattorf, northern Germany.

Diagnosis—Minute, ovoid, with visible spire (= protoconch) with patterns of rhombs. Dorsal surface of teleoconch ornamented with granulated spiral ribs not representing prolongations of apertural crenulations. Aperture nearly straight, terminated at each end by small canal. (Vredenburg 1920).

Geologic Range—Middle lower Eocene (middle Ypresian), southwestern Washington (Squires et al. 1996) and lowermost Oligocene, northern Germany (Schilder 1922).

Remarks—Koenen's (1890) *Trivia scrabriuscula* is a secondary homonym because Gray's *Cypraea scabriuscula* is a triviid. Vredenburg (1920) used Koenen's name when describing the genus *Cypraeogemmula*. The replacement name, *Cypraea liliputana* Schilder, 1922, for Koenen's name was allocated to the genus *Cypraeogemmula* by Schilder, 1927.

Cypraeogemmula is known from only two species: *C. warnerae* from the NEP region and *C. liliputana* from upper Eocene (Priabonian Stage) in Ukraine (Pacaud 2018c) and the lowermost Oligocene in Germany (Schilder 1922).

The following is a communiqué from P. Bouchet (MNHN, personal communication April 1996) to R.L. Squires: "Your recent paper in the last issue of the *Veliger* very appropriately places *Cypraeogemmula* in the family Ovulidae. You did not cite *Pedicularia*, but you will be astonished by the similarity of the juvenile/subadult *Pedicularia* and *Cypraeogemmula*. Both *Pedicularia* and *Cypraeopsis* feed on stylasterids and occur in bathyal environments (*Pedicularia* also in shallow water). This could shed light on the paleoecology of *Cypraeogemmula warnera* [*sic*]." Based on its similarity to modern species, Fehse (2018) stated that *Cypraeogemmula* is a synonym of *Pedicularia*. However, although similar, a total lack of any possible molecular evidence for the extinct *Cypraeogemmula* makes this purely an assumption. Lorenz and Fehse (2009) note that "taxonomy is based on geography, the shell sculpture, and morphometry" in Holocene species.

Cypraeogemmula warnerae Effinger, 1938
Figs. 10D–F

Cypraeogemmula warnerae Effinger, 1938. p. 365 (table 1), 381, pl. 47, figs. 29, 35. Weaver, 1942 [1943]. p. 394, 395, pl. 77, fig. 2. Durham, 1944. pp. 117, 165. Roberts, 1958. p. 25. Schilder, 1961. p. 147. Schilder and Schilder, 1971. p. 22, 168. Groves, 1993. p. 12. Squires and Goedert, 1995. p. 258 (table 1). Squires et al., 1996. p. 137–140, figs. 2–8. Groves, 1997. p. 7. Dolin and Ledon, 2002. p. 331. Lorenz and Fehse, 2009. p. 14, fig. 6c (figs. 2, 4 refigured from Squires et al., 1996). Dolin et al., 2013. p. 783. Fehse, 2018. p. 33, fig. 3.1(fig. 5 refigured from Squires et al., 1996). Lorenz, 2018. p. 698, pl. 345, fig. 3 (figs. 2, 4 refigured from Squires et al., 1996). Pacaud, 2018c. p. 7, 8.

Holotype and Type Locality—UCMP 33588, lost (D.R. Lindberg, personal communication, 1995, confirmed by A.A. Dineen (UCMP), March, 2022), altitude 4.1 mm, maximum diameter 3 mm (Effinger 1938), UCMP Locality 3607, "Gries Ranch beds," lower Lincoln Creek Formation, Lewis County, Washington.

Referred Specimens— Hypotype (of Squires et al., 1996, figs. 2–8) LACMIP 16655.37, LACMIP Type 11372 (Figs. 10D–F), LACMIP Locality 16655 [= LACMIP Locality 41563; *ex* CSUN Locality 1563], Crescent Formation, Larch Mountain area, Black Hills, Thurston County, southwestern Washington. Six specimens UCMP 35334-35336 (of Durham, 1944), Quimper Formation, Woodman's Station, Jefferson County, Washington, UCMP Locality A-1802. Three additional specimens (LACMIP 41567.1, LACMIP Type 14946), LACMIP Locality 16849 [= LACMIP Locality 41567; *ex* CSUN Locality 1567], upper Crescent Formation/lower McIntosh Formation transition zone, Garrard Creek area, Doty Hills, Lewis County, Washington and two specimens LACMIP Localites 16850 [*ex* CSUN Locality 1570] and 16850 [*ex* CSUN Locality 1567] were examined. Two specimens, LACMIP Locality 10037 [*ex* CIT 140] (LACMIP 10037.14, LACMIP Type 14934), Gries Ranch, Lewis County, Washington, collected 4 August, 1928 by N.M. Tegland.

Occurrence—"Capay Stage" (middle lower) Eocene to Galvinian Stage (upper Eocene part). **"CAPAY STAGE":** Upper part of the Crescent Formation, Black Hills, Thurston County, western Washington (Squires et al. 1996**)**. **MIDDLE EOCENE:** Transition beds between the upper part of the Crescent Formation and the overlying lower part of the McIntosh Formation, northern Doty Hills, Lewis County, western Washington (Squires and Goedert 1995). **GALVINIAN STAGE:** "Gries Ranch beds" in the lower part of the Lincoln Creek Formation, near Vader, Lewis County, western Washington (Effinger 1938); lower part of the Quimper Sandstone, Discovery Bay, Quimper Peninsula, Jefferson County, western Washinton (Effinger 1938; Durham 1944).

Etymology—Originally named for the late Mary Warner Effinger, wife of the author William L. Effinger [1905-1985] (UCMP).

Description—Shell minute, ovate. Protoconch (= spire in this species) visible, four whorls inclined to right side [initial whorl low, rounded, smooth, and naticiform; second whorl tabulate with oblique axial sculpture and with no sculpture anterior to the tabulation, third and fourth whorls with oblique decussate (rhomboidal) axial sculpture crossed by four or five spiral ribs, each spiral rib bisecting a rhomb and producing a triangular pattern, and protoconch set off from teleoconch by a smooth shelf. Aperture straight, widens anteriorly. Outer lip with about 28 transverse ridges, most of which extend completely across inflected surface. Inner lip with about 20 transverse ribs. Left edge of inner lip demarked by a prominent longitudinal ridge extending across the body whorl from tip of anterior to tip of posterior canal. Fossula obsolete. (Effinger 1938; Squires et al. 1996).

Remarks—The geologic occurrence of *Cypraeogemmula warneri* in the NEP region is unusual. Although it occurred during the "Capay Stage" in Washington, it

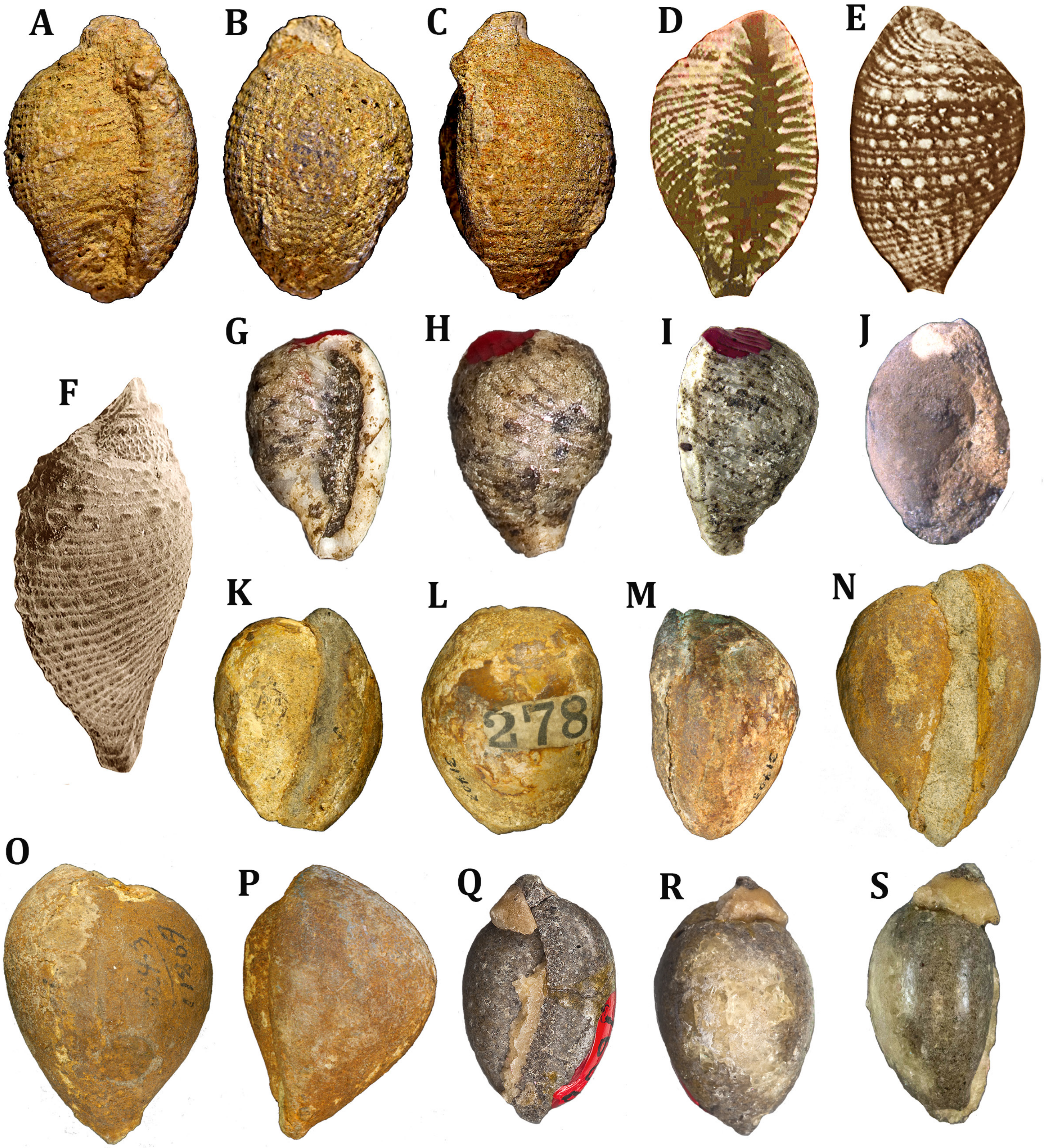

Figure 10. A–C. *Cypraedia* sp. Bateque Formation (Eocene, "Capay Stage"), Mesa La Salina, Baja California Sur, México. Basal (**A**), dorsal (**B**), and right (labral) side (**C**) views, 2.3x, length 19.5 mm, width 13.2 mm, height 11.9 mm, of hypotype IGM 5057, LACMIP Locality 41220b [*ex* CSUN Locality 1220b]. **D–F.** *Cypraeogemmula warnerae* Effinger, 1938. "Gries Ranch beds," Crescent Formation (upper part) (Eocene, "Capay Stage" to Galvinian Stage), Black Hills area, Washington. Basal (**D**) and dorsal (**E**) views, both 16x, and left (columellar) (**F**) view, 33x, of hypotype LACMIP 16655.37, LACMIP Type 11372, LACMIP Locality 16655 [= LACMIP Locality 41563; *ex* CSUN Locality 1563]. (continued on next page)

Figure 10 (continued) G–I. *Eratotrivia crescentensis* (Weaver and Palmer, 1922), Crescent Formation (Eocene, "Capay Stage"), Port Crescent, Clallam County, Washington. Basal (**G**), dorsal (**H**), and right (labral) side (**I**) views, 5.5x, length 6 mm, width 4 mm, height 3.5 mm, holotype CASG 7587 [*ex* UWBM 201], UWBM Locality 358. **J–S.** *Nomina dubia*. **J.** "*Bernaya*" *fresnoensis* (Anderson, 1905), Avenal Sand (Eocene, "Domengine Stage"), Los Gatos Creek, northwest of Coalinga, Fresno County, central California. Basal (**J**) view, 0.9x, length 41.2 mm, width 27 mm, height 28 mm, of holotype CASG 61713.01. **K–M.** "*Eocypraea*" *bayerquei* (Gabb, 1864), Martinez Formation (Paleocene), Clayton, Contra Costa County, northern California. Basal (**K**), dorsal (**L**), and right (labral) side (**M**) views, 1.2x, length 30.4 mm, width 23.4 mm, height 17 mm, of holotype UCMP 31403. **N–P.** "*Sphaerocypraea*" *martini* (Dickerson, 1914). Martinez Formation (Paleocene, Thanetian Stage), south of Muir Station, Contra Costa County, northern California. Basal (**N**), dorsal (**O**), and right (labral) side (**P**) views, 1.1x, length 38.5 mm, width 22.7 mm, height 20.8 mm, of holotype UCMP 243. **Q–S.** "*Sulcocypraea*" *oakvillensis* (Van Winkle, 1918), Lincoln Creek Formation (lowermost) (Eocene, lower Galvinian Stage), eastern Grays Harbor County, Washington. Basal (**Q**), dorsal (**R**), and left (columellar) side (**S**) views, 1.8x, length 28 mm, width 15 mm, height mm, height 11.7 mm, of holotype CASG 7606.

apparently did not reappear until 15 million years laters in the lower Galvinian Stage in Washington. More collecting of this minute gastropod is needed. Fehse (2018) noted that presence of *Cypraeogemmula liliputana* Schilder, 1922 in Ukrainian strata, as reported by Pacaud (2018c), proves that *C. warnerae* is a synonym based on morphological similarities. Pacaud (2018c) noted that both *C. warnerae* and *C. liliputana* are close but noted protoconch and sculptural differences that separate the two species.

ERATOIDAE Gill, 1871

Remarks—Schilder (1933) noted that the Eratoidae differ anatomically and conchologically from all other cypraeoideans. His generic subdivisions were, however, based solely on shell features. Schilder's (1936) classification included radula and osphradia in addition to shell morphology. Cate (1977) produced the most complete monograph on living eratoids and adopted the classification scheme of Schilder and Schilder (1971), which is utilized herein.

ERATONIAE Gill, 1871
ERATOTRIVIA Sacco, 1894

Type Species—*Erato crenata* (Deshayes, 1835) [= *Eratotrivia crenularis* Schilder, 1927, non Oppenheim, 1901], by original designation (of Sacco, 1894: p. 62), Eocene (Lutetian), Chaumont, Haute-Marne Department, France

Diagnosis—Shell small, ob-ovate; spire concealed; columella region attenuated; slight canal; aperture narrow; outer lip thickened, crenulated internally; surface ornamented by spiral ribs which anastomose in the dorsal region; along the mid-dorsal line, the ribs are interrupted more or less by a shallow groove.

Geologic Range—Early Eocene (Ypresian Stage), Washington (Squires and Goedert 1994) to late Eocene (Bartonian Stage), Italy (Dolin and Pacaud 2009).

Remarks—In the NEP region, *Eratotrivia* occurs as *Eratotrivia crescentensis* (Weaver and Palmer 1922) of early Eocene age ("Capay Stage") in Washington.

Eratotrivia crescentensis
(Weaver and Palmer, 1922)
Figs. 10G–I

Eratopsis crescentensis Weaver and Palmer, 1922. p. 36, 37, pl. 11, figs. 10, 22. Weaver, 1942 [1943]. p. 393, 645 (table), pl. 76, fig. 21.

Eratotrivia crescentensis (Weaver and Palmer). Schilder, 1932. p. 81 [as *E. crescentensis*]. Schilder, 1933. p. 276. Schilder, 1961. p. 149. Schilder and Schilder, 1971. p. 12, 108. Squires and Goedert, 1994. p. 16, 18, figs. 37, 38.

Holotype and Type Locality—CASG 7587 [*ex* UWBM 201] (Figs. 10G–I), length 6 mm, width 4 mm, height 3.5 mm. UWBM Locality 358, Crescent Formation, at Crescent Bay, Clallam County, northern Olympic Peninsula, Washington (Weaver 1942 [1943]: p. 393).

Referred Specimens—Hypotype (of Squires and Goedert, 1994) LACMIP 16657.24, LACMIP Type 12162 [not 12228, as reported by Squires and Goedert (1994: pp. 16, 18)], length 4.86 mm, width 3.55 mm, and two additional specimens, LACMIP 16657 [= LACMIP Locality 41553; *ex* CSUN Locality 1553], Crescent Formation, Little River area, Grays Harbor County, Washington. Two specimens (LACMIP 41563.1, LACMIP Type 14947) from LACMIP Locality 41563 [ex CSUN Locality 1563], Crescent Formation, Larch Mountain area, Black Hills, Thurston County, southwestern Washington and one specimen (LACMIP 41553.1, LACMIP Type 14948) from LACMIP Locality 41553 [*ex* CSUN Locality 1553], also from the Larch Mountain area, Black Hills, Thurston County, Washington. **Hypotypes** UWBM IP 98539 (two specimens).

Occurrence—Lower Eocene, Washington. **"Capay Stage"**: Crescent Formation, Crescent Bay, Washington (Weaver and Palmer 1922); Crescent Formation, Little River, Grays Harbor County, southern Olympic Peninsula, Washington (Squires and Goedert 1994).

Etymology—Originally named for the Eocene Crescent Formation, Clallam County, northwestern Washington.

Description—Shell small and entirely covered with numerous oblique spiral ribs uniform in strength and extending into both lips; moderate convexity; posterior end flattish, anterior end protruding and tapered. Aperture moderately straight, widest just anterior to middle of shell. Outer lip inflated.

Remarks—*Eratotrivia crescentensis* is the only known trivid in the Paleogene deposits of the NEP region. Specimens are small and uncommon. They show reasonably good preservation.

NOMINA DUBIA

FAMILY AND GENUS INDETERMINATE

Family and Genus Indeterminate (genera assigned by Schilder and Schilder, 1971)

Remarks—The following four cypraeoidean taxa have been relegated to the rank of *nomen dubium* as holotypes of all four species are all poorly preserved internal molds. Unfortunately, they have all been cited often in the literature and have been the cause much confusion amongst NEP cypraeoidean taxonomy. This has been particularly true for ?*Cypraea bayerquei* Gabb, 1864 from the Martinez Formation of Contra Costa County, California. Better preserved topotypic material is required for these taxa to be reinstated as valid taxa.

"*Bernaya*" *fresnoensis* (Anderson, 1905)

Fig. 10

Cypraea fresnoënsis Anderson, 1905. p. 198, pl. 13, fig. 2. Schilder, 1924b. p. 236. Ingram, 1942. pp. 103, 104; pl., 8, fig. 9. Ingram, 1947a. p. 93, pl. 7, fig. 4 (as *Cypraea fresnoensis*).

Cypraea fresnoensis Anderson. Schilder, 1927. p. 164. Keen and Bentson, 1944. p. 152. Ingram, 1947b. p. 152.

Cypraeorbis (*Cypraeorbis*) *fresnoënsis* (Anderson). Schilder, 1932. p. 123 [as *C.* (*C.*) *fresnoënsis*].

"*Cypraea*" *fresnoensis* Anderson. Vokes, 1939. p. 26, 155.

Bernaya (*Bernaya*) *fresnoënsis* (Anderson). Schilder, 1941. p. 80.

Bernaya (*Bernaya*) *ellipsoides fresnoënsis* (Anderson). Schilder and Schilder, 1971. pp. 27 [as *Bernaya* (*Bernaya*) *ell. fresnoënsis*], 116.

Bernaya (*Bernaya*) *fresnoensis* (Anderson). Groves, 1992. p. 106. Groves, 1993. p. 11. Groves, 1997. p. 7.

Loxacypraea fresnoensis (Anderson). Petuch, 2004. p. 279.

Bernaya fresnoensis (Anderson). Groves and Squires, 2021. p. 226, 227 (as *Cypraea*).

Holotype and Type Locality—CASG 61713.01 [*ex* CASG 50] (a steinkern) (Fig. 10J), length 41.2 mm, width 28.1 mm, height 28.0 mm, CASG Locality 61713. The holotype was damaged in a fire resulting from the 1906 San Francisco earthquake, but the specimen was recovered and preserved in the CASG collection. The holotype is from a gulley outcrop, approximately 4 mi. north of Los Gatos Creek (sec. 25, T19N, R14E Mt. Diablo Baseline and Meridian), Fresno County, California, Eocene, Avenal Formation, Los Gatos Creek, Fresno County, California. Locality details given by F.M. Anderson, 14 January, 1941, "to the best of his recollection" (CASG holotype label).

Description—Shell subglobose, spire covered, canal produced a little in front, aperture narrow and curved, with no dentition visible. (Anderson 1905: p. 198).

Etymology—Originally named for Fresno County, central Califiornia.

Occurrence—Late early Eocene or early middle Eocene, central California. "Domengine Stage": Avenal Formation (Anderson 1905; Ingram 1942; Keen and Bentson 1944; Ingram 1947a, 1947b). Domengine Formation (Vokes 1939).

Remarks—Because this species is represented only by the poorly preserved holotype, Vokes (1939, p. 155) believed it should be classified as a "*Cypraea*," under the general heading of *incertae sedis*. Ingram (1947b: p. 152) considered it to be of doubtful specific rank. Schilder and Schilder (1971) placed *Bernaya* (*B.*) *fresnoensis* in synonymy with *B.* (*B.*) *ellipsoides* (d'Archiac and Haime, 1854), from the lower Eocene of northwest India, but they did not say why.

Petuch (2004: p. 279) erroneously placed *fresnoensis* in the cypraeid genus *Loxacypraea* Petuch, 2004 and inexplicably reported this Eocene species as present in the "Vaqueros and Coalinga Formations, Burdigalian Miocene of southern California."

The holotype, which is the only known specimen of this species, is a steinkern showing only a part of the shell present. The specimen resembles a cypraeoidean, and, if it is one, then its tiny spire resembles that of a *Bernaya*. Preservation is extremely poor, however, and the holotype might not even be a cypraeoidean.

"*Eocypraea*" *bayerquei* (Gabb, 1864)
Figs. 10K–M

?*Cypraea Bayerquei* Gabb, 1864. pp. 129, 130, 227, three unnumbered text figs. (= line drawings).

Cypraea bayerquei Gabb. Stoliczka, 1868. p. 52. Heilprin, 1882. p. 198. Campbell, 1892. p. 51. Stanton, 1896. p. 1025. Dickerson, 1914. p. 91, 96, 109 (in part), pl. 15, fig. 1. Schilder, 1924b. p. 213. Anderson and Hanna, 1925. p. 105 [in part]. Nelson, 1925. p. 425. Ingram, 1942. p. 103, Ingram, 1947a. pp. 87–88. Ingram, 1947b. p. 144. Keen and Bentson, 1944. p. 152 [in part].

Cypraea bayerquei Gabb. Gabb, 1869. pp. 163, 164; pl. 27, figs. 43–43c. Not *Cypraea bayerquei* (Gabb) [= *Grovesia castacensis* (Stewart, 1926 [1927)].

Eocypraea (Eocypraea) bayerquei (Gabb). Schilder, 1927. p. 74.

Eocypraea (*Eocypraea*) *bayerquei bayerquei* (Gabb). Schilder, 1932. p. 214 [as *E.* (*E.*) *bayerquei bayerquei*]. Schilder and Schilder, 1971. pp. 67 [as *Eocypraea* (*Eocypraea*) *bay. bayerquei*], 98.

Eocypraea castacensis (Gabb). Weaver, MS [1959]. p. 482, pl. 21, fig. 3. Not *Grovesia castacensis* (Stewart, 1926 [1927]).

Eocypraea (*Eocypraea*) *bayerquei* (Gabb). Groves, 1992. p. 106. Groves, 1993. p. 11. Groves, 2011. p. 46 (table 1).

Eocypraea bayerquei (Gabb) [not 1846 as in table]. Fehse, 2001. p. 20.

Eocypraea bayerquei bayerquei (Gabb) [not 1846 as in table]. Fehse, 2021. p. 42.

Holotype and Type Locality—UCMP 31403 [a steinkern] (Figs. 10K–M), length 30.4 mm, width 21.2 mm, height 17.0 mm. UCMP Locality IP12672, Martinez Formation, Clayton, Contra Costa County, central California.

Referred material—Hypotype (of Dickerson, 1914: pl. 15, fig. 1) UCMP Locality 11851, UCMP Locality 790, Lake County, California, "Martinez Formation."

Occurrence—Paleocene, Martinez Formation, Clayton, Contra Costa County, northern California, so-called "Cretaceous" = Paleocene (Keen and Bentson, 1944: p. 151).

Etymology—Originally named for fossil collector Mr. Bayerque (Clayton, Contra Costa County, central California).

Description—Shell medium size; smooth?; moderately inflated; spire covered; aperture wide and curving, both anteriorly and posteriorly; outer lip side of shell one-third width of inner lip side; posterior terminus of outer lip projecting.

Remarks—Groves and Squires (2018: p. 67) reported that the line drawings by Gabb (1864: pp. 129, 130) are definitely not the same specimen as the one figured by Gabb (1869: pp. 163, 164, pl. 17, figs. 43–43c) and identified as *C. bayerquei*. Groves and Squires (2018) also reported that Stewart (1926 [1927]: p. 370, pl. 28, fig. 10) noted the differences and renamed the Gabb (1869) specimen *Cypraea castacensis*. Unfortunately, prior to Stewart's renaming, the term *Cypraea bayerquei* was erroneously used in faunal lists by Dickerson (1914, 1915, 1916). Anderson and Hanna (1925) attempted to rectify the prior incorrect usage of *bayerquei* but did not solve the issue entirely. Schilder (1932) and Schilder and Schilder (1971) perpetuated Gabb's error by referring to *castacensis* as a subspecies of *bayerquei*. The authors have put forth a solution to these problems (see synonymy above) but limited collection access due to the pandemic made a complete solution impossible. The holotype of *bayerquei* is a steinkern and represents also a *nomen dubium*. Photographic images of the holotype are provided for the first time in this present report.

"*Sphaerocypraea*" *martini* (Dickerson, 1914)
Figs. 10N–P

Ovula martini Dickerson, 1914. pp. 110, 145, pl. 14, figs. 7a, 7b. Schilder, 1927. p. 164. Keen and Bentson, 1944. p. 183. Zinsmeister and Paredes-Mejia, 1988. p. 13.

Eocypraea (*Sphaerocypraea*) *martini* (Dickerson). Schilder, 1932. p. 218 [as *E.* (*S.*) *martini*]. Weaver MS [1959]. p. 481; pl. 21 [not pl. 20], figs. 13, 14.

Sphaerocypraea ? *martini* (Dickerson). Schilder, 1941. p. 104.

Sphaerocypraea martini (Dickerson). Schilder and Schilder, 1971. pp. 69, 131.

Sphaerocypraea levesquei (Deshayes, 1835). Dolin and Dolin, 1983. p. 46 (table).

Sphaerocypraea martini (Dickerson). Groves, 1992. p. 106. Groves, 1993. p. 11. Groves, 1997. p. 7. Groves and Squires, 2021. p. 241 (as *Gisortia* sp. cf. *G. clarki*).

Holotype and Type Locality—UCMP 11869 [a steinkern] (Figs. 10N–P), length 38.4 mm, width 27.7 mm, height 20.8 mm. UCMP Locality 243, Paleocene, Martinez Formation, near Martinez, north-central California.

Occurrence—Paleocene, Martinez Formation, northern California.

Etymology—Although there was not an official etymology noted by Roy Dickerson (1914), he and Bruce Martin were contemporaries at UCMP between 1912 and 1916 and it is therefore it is highly likely that this species was named for the late Bruce Martin [1885-1970] (UCMP).

Description—Shell large, ovate; smooth; very inflated (widest medially) and prominently narrowing anteriorly; spire covered or exposed; aperture moderately narrow; aperture fairly straight, dentition strong, especially on outer lip; outer and inner lips both smooth with broad, thin callus.

Remarks—The holotype of *S. martini* is an internal cast (steinkern) that cannot be assigned to any current genus and therefore is relegated to *nomen dubia* status. Schilder and Schilder (1971) questioned the validity of *Sphaerocypraea martini* as "the interpretation of the taxa is doubtful." This species is found with *Turritella infragranulata* Gabb, 1864 in the Herndon Creek area, Lower Lake, Lake County in northern California (Stanton 1896) and with *T. pacheoensis* Gabb, 1864 in the Vine Hill Sandstone near Muir Station, northern California (Weaver 1953). Saul (1983: pp. 33, 102) reported that both of these turritellids are of late Paleocene age (Thanetian Stage).

"SULCOCYPRAEA" OAKVILLENSIS (VAN WINKLE, 1918)
FIGS. 10Q–S

Cypraea oakvillensis Van Winkle, 1918. 76, 88, pl. 7, fig. 19. Ingram, 1942. p. 105, pl. 9, figs. 14, 15. Weaver, 1942 [1943]. p. 394, 645 (table), pl. 76, figs. 29, 30. Ingram, 1947a. pp. 98, 99, pl. 6, figs. 15, 16. Ingram, 1947b. p. 148.

Eocypraea (*Eocypraea*) *oakvillensis* (Van Winkle). Schilder, 1932. p. 214 [as *E.* (*E.*) *oakvillensis*].

Sulcocypraea ? *oakvillensis* (Van Winkle). Schilder, 1941. p. 104.

Sulcocypraea mathewsonii oakvillensis (Van Winkle). Schilder and Schilder, 1971. p. 68 [as *Sulcocypraea mat. oakvillensis*], 138. Fehse, 2021. p. 44.

Sulcocypraea oakvillensis (Van Winkle). Squires and Groves, 1993. p. 84. Groves, 1993. p. 11. Groves, 1997. p. 8. Fehse, 2001. p. 22.

Holotype and Type Locality—CASG 61715.01 [*ex* UWBM 140; ex CASG 7606] [a steinkern] (Figs. 10Q–S), length 21.9 mm, width 14.2 mm, height 11.7 mm. CASG Locality 61715 [= UWBM Locality 161] (Van Winkle, 1918) but same locality reported as UWBM Locality 169 by Weaver (1942 [1943]: p. 394). Approximately one mile west (1.6 km of Oakville, in Oakville Quarry, in sandstone overlying basalt, Grays Harbor County, sec. 19, T16N, R4W, Washington, on the Northern Pacific Railway (= BNSF Railway) [UWBM Locality 161] (see Armentrout 1975: fig. 3 for geologic map of the general area). Lincoln Creek Formation (Van Winkle 1918: p. 88; Weaver 1942 [1943]: p. 394; Ingram 1942, 1947a, 1947b; Squires and Groves 1993).

Description—Shell medium size, smooth. Sub-oval, widest about one-third the length of the shell from the posterior end. Aperture narrow. Outer lip incurved and bearing approximately 14 teeth on both lips.

Etymology—Originally named for Oakville, Grays Harbor County, western Washington.

Occurrence—Upper Eocene, Washington. **Galvinian Stage:** *Echinophoria dalli* Zone (Fig. 2), within the upper Eocene upper part of the Eocene to Oligocene Lincoln Creek Formation, Washington. The *E. dalli* Zone is correlative to Van Winkle's informally designated molluscan "*Barbartia merriami*" zone, which Armentrout (1975, p. 37, fig. 2) assigned to his formally designated upper Eocene Galvinian Stage. Both Van Winkle (1918) and Armentrout (1975) correlated the "*B. merriami*" Zone to the upper Eocene fauna of the Gries Ranch Formation. The *E. dalli* Zone part of the Galvinian Stage is correlative to the upper part of the Western European Priabonian Stage (Fig. 2).

Remarks—"*Cypraea*" *oakvillensis* is important because its reported geologic age is apparently coincident with the geologically youngest Palaeogene cypraeoidean (namely *Cypraeogemmula warnerae* Effinger, 1938) found on the west coast of North America. Van Winkle (1922) and Weaver (1942 [1943]) both noted that the specimen was "smooth except for very faint lines of growth," which could mean that the specimen has sustained significant loss of shell since the original description was published. Unfortunately, this species is based only on its holotype, a specimen whose shell is mostly missing, thereby preventing positive identification as to a genus. "Until additional topotypes of *S. oakvillensis* are found, which seems unlikely due to poor exposures in the area, the name should be treated as a *nomen dubium*," as Squires and Groves (1993: p. 84) suggested. Plaster casts of the holotype are at the Burke Museum (University of Washington) in Seattle, Washington, as well as the original photographic negatives. Through the courtesy of J.L. Goedert, W. Wehr, and V.S. Mallory, a duplicate of the plaster cast of the holotype was sent to R.L. Squires.

NORTHEAST PACIFIC TAXA
MISIDENTIFIED AS CYPRAEOIDEANS

Turner (1938: p. 31, 34) listed *Cypraea* n. sp. and *Cypraea* n. sp. A as both being from the Spencer Formation in the Willamette Valley northern Oregon (UCMP Locality A-985). It is likely that these two designations represent the same specimen. Based on an examination of Turner's *Cypraea* n. sp. A by the senior author in the UCMP collection, the specimen is herein recognized as a cephalaspidean, not a cypraeoidean.

Perrilliat (2013: p. 134, figs. 4.5, 4.6, IGM 4398, PU Locality 1301) reported a specimen of cypraeid sp. from the Paleocene Sepultura Formation in Baja California, México. Paredes-Mejia (1989: p. 200, pl. 4, figs. 11–13) had reported this same specimen (as IGM 4391) as *Seraphs* (*Miniseraphs*) n. sp. In the opinion of the present authors, this specimen is most likely not a cypraeoid because its last whorl has non-cypraeoid looking apex and also because of the absence of apertural teeth, which are normally found in cypraeoids.

DISCUSSION

Prologue

The NEP Upper Cretaceous cypraeoidean record, summarized by Groves (2011), is represented by three genera (Groves 1990, 1992, 1993, 2004, 2011; Groves et al. 2011; Lorenz 2017). After the earliest Maastrichtian they are missing from the fossil record in the NEP. The only cypraeodian genera known from the Maastrichtian of the NEP region are *Protocypraea* Schilder, 1927, *Palaeocypraea* Schilder, 1928, and *Eocypraea* Cossmann, 1903, and their few species are of late Campanian/early Maastrichtian age (Groves 1990: fig. 2). Only one, *Protocypraea*, may questionably be found in the overlying NEP Paleogene fossil record and none are endemic to the NEP region. This trend of diminished biodiversity of NEP Maastrichtian cypraeoideans continued across the K/Pg boundary, and there are no known records of earliest Paleocene ("Danian" age) of this group in the NEP region.

It was not until the middle Paleocene (Selandian age) when cypraeoideans (in general), reappeared in the NEP region (Table 1, Fig. 3) as indicated by the genus *Propustularia* appeared for the first time. The NEP occurrences *Propustularia* and *Eocypraea* are based on extremely rare and overall poorly meager preserved remains in the Santa Susana Formation in the Simi Hills, Ventura County, southern California. This formation, which represents one of most complete Paleocene sections found in the NEP region (Zinsmeister 1983), is dominated by outer shelf-to-slope deposits containing turbidite sequences.

The late Paleocene (Thanetian age) record (Table 1, Fig. 3) of NEP cypraeoidean fauna is also poorly known because of few specimens and poor preservation. Based on this present study, three genera can be recognized: *Bernaya*, *Protocypraea*?, and *Eocypraea* and an indeterminate cypraeid. Their localities are more widespread than the NEP Selandian cypraeoideans. No cypraeoideans are known from the uppermost Paleocene to lowermost Eocene ("Meganos Stage") of the NEP region (Fig. 3). The reason is probably because shallow-marine outcrops of this age are rare in this region (Squires 1999).

The Early Eocene Warming Event

During the Paleocene and especially through early late Eocene time, global-warming ("greenhouse") conditions existed worldwide. The "Paleocene-Eocene Thermal Maximum" (PETM) (Fig. 3) occurred near the Paleocene-Eocene boundary, and there was 5° to 8°of warming (Sluijs et al. 2007). Also, at that time, sea level was a least 70 to 80 m higher 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; Das and Halder 2018). Conditions were ideal especially for the wide dispersal of Paleogene thermophilic macroinvertebrate groups, like cypraeoideans, that predominantly have larvae capable of having a planktotrophic (pelagic) existence in tropical-to-subtropical surface waters.

The "Capay Stage" warm conditions described above coincided with the highest biodiversity of NEP Paleogene cypraeoideans, with eight genera present. Most of these were new arrivals, but *Bernaya*, which was questionably present in the NEP late Paleocene, is present also in the "Capay Stage" as are two species of *Eocypraea* (Fig. 3).

The relatively widespread warm shallow-marine nearshore sandy depositional environments with rapid sedimentation (e.g., Llajas Formation in California and Bateque Formation in Baja California Sur, México) provided ideal living conditions and good preservation of the cypraeoideans. These warm conditions of both of these "stages" accounted also for richest diversity of hermatypic colonial corals in the NEP region. Eight colonial-coral genera (in masses up to 1 m across) were reported from coral-reef? deposits in "Capay Stage" strata in the Bateque Formation in Baja California Sur, México (Squires and Demetrion 1992). Five other colonial-coral genera (in small masses, up to 20 cm across) have been reported from "Capay Stage" Crescent Formation in Washington

(Durham 1942a, Bentson 1943). Similar thermophilic conditions existed also, at least locally, in the Domengine Formation in central California, where eight other, and mostly different, colonial-coral genera were reported from the "Domengine Stage" (Durham 1942b). Prior to the "Capay Stage" and "Domengine Stage," no hermatypic corals were reported from NEP Paleocene strata, and only a single hermatypic coral was reported from the "Meganos Stage." After the "Domengine Stage," only one hermatypic coral genus has been reported.

Some of the "Capay Stage" cypraeoidean species found in the NEP region differ only slightly in morphology from certain species found in western Europe and/or the Gulf Coast-México region. Hickman (2003) used the phrase "species pairs," to refer to these congenera so similar in their morphology as to indicate close phylogenetic relationship. Examples of cypraeoidean "species pairs" detected in the present study are the following: (1) *Bernaya kaylinae* and *B. marcominii* from France; (2) *Gisortia clarki* and *G. tuberculosa* from France and England, and (3) *Luponovula maniobraensis* and *L. oligovata* from Italy. All of these similar "species pairs" are indicative of a westward-directed amphiatlantic faunistic influx between western Europe and the NEP region. As reviewed and discussed by Squires (1984, 1987, 2019) and Harzhauser et al. (2002), this influx has been recognized, on the basis of gastropod and bivalve species, since the 1920's (Cooke 1924; Gardner and Bowles 1934; Vokes 1935; Clark and Vokes 1936; Gardner 1939; Palmer 1967; Squires and Demetrion 1992; Squires 1987, 2003, 2013, 2014, 2019). The consensus of all this research is that the Caribbean Sea was the portal, where periodic influxes of Paleocene thermophilic mollusks took place between the western Europe and the NEP region via a westward-directed current emanating from the Old World Tethys Sea in the southern western Europe region, passing near western Greenland, the Gulf Coast of the United States, northern and southern México in the Caribbean, and eventually reaching the west coast of North America (see Squires 2019: fig. 5).

The presence of *Eocypraea* in strata correlative to the Selandian Stage, Thanetian Stage, "Capay Stage," "Domengine Stage," and into the "Transition" and "Tejon" "Stages" helps in the cypraeoidean fauna helps to indicate warm oceanic conditions. The cypraeoidean fauna in the NEP region had its highest biodiversity of eight genera present during the "Capay Stage," with a 50 percent decrease to four genera during the "Domengine Stage" (Fig. 3).

Initiation of A Faunal Turnover and Eventual Arrival of Cool Waters

At the end of the "Domengine Stage," there was a faunal turnover (i.e., a noticeable and significant change in taxonomic composition of the NEP cypraeoidean genera). Although two genera, *Grovesia* and the minute shells of *Cypraeogemmula* persisted, gone were *Subepona* and *Bernaya* (Fig. 3). The two species of *Grovesia* were moderately widespread during that middle Eocene through early late Eocene interval ("Tejon Stage" and lower Galvinian Stage). The only newcomer was *Nucleolaria cowlitzian*a, a very rare cypraeoidean and the earliest occurrence of this genus.

As the faunal turnover progressed, three, and eventually only two genera remained: *Grovesia* and *Cypraeogemmula*. The last members of the NEP Paleogene cypraeoidean–fauna genera are small specimens of *Grovesia* and minute specimens of *Cypraeogemmula.* By the end of the Eocene, there was globally a transition from warm "greenhouse" conditions to a cooler "icehouse" climate mode (Squires 2003), and the cooling of the surface waters in the NEP region resulted in the complete disappearance of NEP cypraeoideans, until warm waters returned again during Miocene time (Groves 1994a).

Lineages

Six of the 13 NEP Paleogene cypraeoidean genera established lineages: *Subepona* (2 spp.), *Bernaya* (at least 4 spp.), *Protocypraea*? (2 spp.), *Gisortia* (2 spp.), *Grovesia* (2 spp.), and *Eocypraea* (at least 8 spp.). Six genera are represented by only a single species: *Nucleolaria*, *Propustularia*, *Luponovula*, *Cypraedia*, *Cypraeogemmula*, and *Eratotrivia*. None of the Paleogene cypraeoidean genera (a total of 12) are endemic to the NEP region.

Tectonic Factors

In regard to the Vancouver Island, British Columbia occurrence of *Protocypraea*? sp. 1, Squires and Saul (2006: p. 214) reported that the Upper Cretaceous shallow-marine rocks found on Vancouver Island were most likely tectonically derived from northern California, and it is likely that Paleocene rocks and associated fauna also underwent some degree of tectonic transport prior to their present-day geographic location.

Sea-floor spreading resulted in the opening of the Gulf of California (Fig. 1) during Miocene and Pliocene times. Since then, rocks of Paleocene and Eocene age west of the San Andreas Fault, in Baja California, México and western California (including San Diego), have undergone tectonic transport of about 300 km (185 mi) to the north-northwest (Matthews 1973, 1976; Abbott 1999: p. 168; Stanley et al. 2017). During this tectonic movement, which continues today, considerable clockwise rotation of certain parts of the upper crust, especially in southern California, have also taken place (Onderdonk 2005).

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