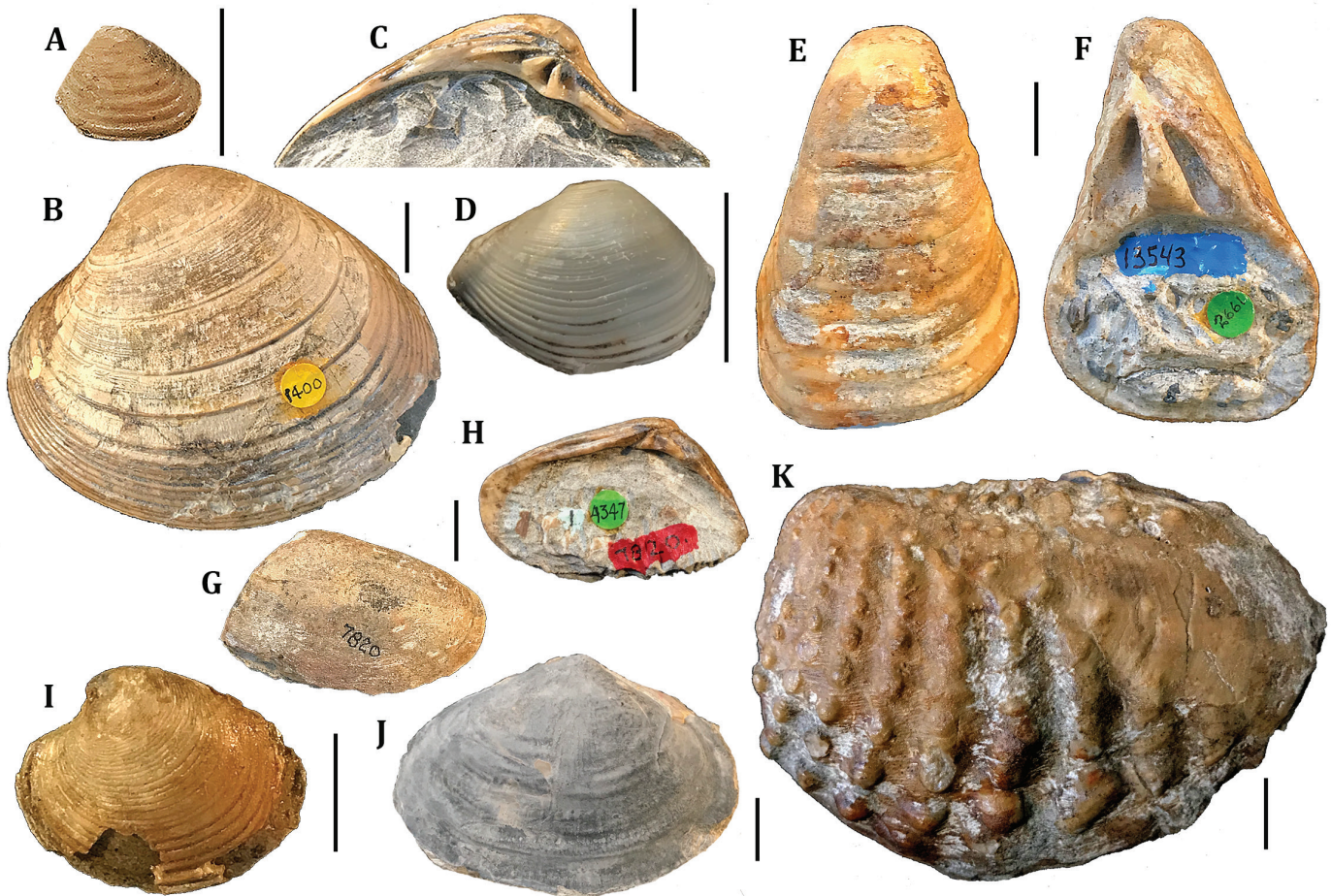


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Cover: Representative Cretaceous endemic shallow-marine bivalve genera/subgenera of the northeast Pacific. See Figure 4 for taxonomic details. Scale bars=10 mm.

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Faunal change in Cretaceous endemic shallow-marine bivalve genera/subgenera of the northeast Pacific

RICHARD L. SQUIRES^{1,2}

¹Professor Emeritus, Department of Geological Sciences, California State University, 18111 Nordhoff Street, Northridge, California, 91330-8266, USA

²Research Associate, Invertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California, 90007, USA; richard.squires@csun.edu

Endemic shallow-marine Cretaceous bivalves in the northeast Pacific region (NEP), extending from southwestern Alaska to the northern part of Baja California Sur, Mexico, are tabulated and discussed in detail for the first time. Twenty-three genera/subgenera are recognized. Their first appearance was in the Valanginian, and their biodiversity continued to be very low during the rest of the Early Cretaceous. The bivalves of the middle Albian Alisitos Formation in northern Baja California are excluded because they did not live in the NEP. The highest number (13) of NEP endemic bivalve genera/subgenera occurred during the Turonian, which was the warmest time of the Cretaceous. At the Turonian/Coniacian boundary, when cooler waters migrated southward, there was a moderate dropoff in endemics that persisted until an origination event near the beginning of the early Maastrichtian, when 11 were present. Five of the 11 were present also during the Turonian, but the others were newcomers. Only three survived the turnover associated with the “Middle Maastrichtian Event” (MME), and none survived the K/Pg boundary mass-extinction event.

Keywords: biodiversity, Carditida, Myida, Mytilida, origination, Trigoniida, turnover, Venerida

INTRODUCTION

Bivalves are common faunal components of Cretaceous shallow-marine assemblages found along the rim of the northeast Pacific (NEP), a region extending from southwestern Alaska southward to the northern part of Baja California Sur, Mexico (Fig. 1). In the terminology of Kauffman (1973: fig 1), the NEP coincides with the Northeast Pacific Subprovince of the North Pacific Province, within the North Temperate Realm. The informal NEP designation was used also by Squires (2018) in his study of endemic shallow-marine Cretaceous gastropods. The present investigation is the first detailed study of the endemic Cretaceous bivalve fauna. The endemic aspect is more relevant than a study of the entire NEP bivalve fauna because the endemics more precisely reflect paleo-environmental conditions. Cretaceous hydrocarbon-seep bivalves from the NEP were not included in the present study because they predominantly occur in northern and central California, in isolated, hydrocarbon-seep “white limestones” within deep-water forearc deposits,

ranging in age from Late Jurassic to Eocene (Kiel et al. 2008, Kaim et al. 2014).

Squires (2018) provided overviews of the global Cretaceous conditions and of the NEP Cretaceous geologic setting. In their discussion of the evolution of yaadiine bivalves, Cooper and Leanza (2017) referred to the British Columbia, Oregon, and northern California area as the “Cordilleran Province.” However, yaadiine bivalves are found as far south as northern Baja California, Mexico (Saul 1978), thus the name NEP is retained here. The Cretaceous faunas of the southwestern part of Alaska and those of the Queen Charlotte Islands need more work in order to precisely determine the geographic locations of these faunas prior to their tectonic transport within suspect terranes. The molluscan fauna of the middle Albian Alisitos Formation in northern Baja California, Mexico was tectonically displaced from the tropical-water Caribbean Biotic Province of the Tethyan Realm and was not in the NEP region (Squires 2018).

Very few bivalves were reported previously as being

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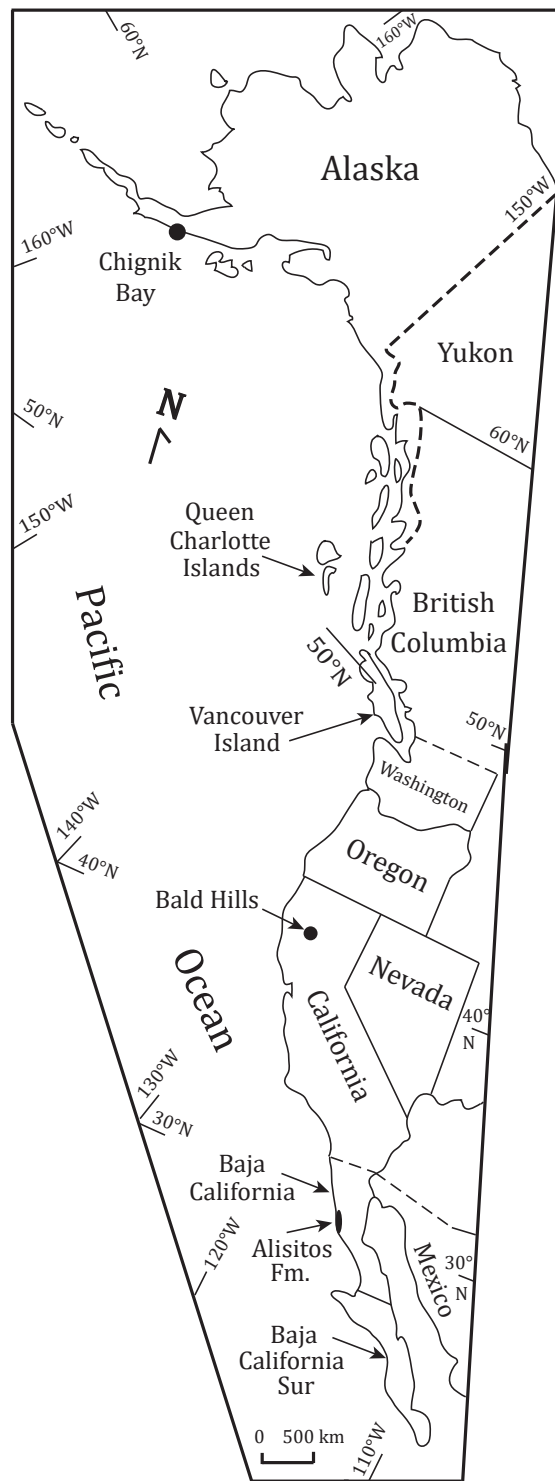


Figure 1. Index map of the NEP region.

endemic to the region. Saul (1978) reported *Yaadia* Crickmay (1930) as being an endemic bivalve during the Cretaceous, but Cooper and Leanza (2017: p. 329) restricted the genus to being endemic mostly during the Early Cretaceous. The latter workers also named two new

genera of Late Cretaceous yaadiines, *Louella* Cooper and Leanza (2017) and *Popenoella* Cooper and Leanza (2017) and reported both as endemic to the NEP region. Saul and Popenoe (1992) reported *Calva* Popenoe (1937) as being endemic to the NEP region during the Cretaceous, and Squires and Saul (2006) reported *Xenomylus*, which they named, as being endemic to this region during the Late Cretaceous (Maastrichtian).

MATERIALS AND METHODS

The geologic ranges of the Cretaceous NEP shallow-marine bivalve genera/subgenera per stage were obtained from all the relevant published papers (Table 1), especially those dealing with systematic paleontology. Most of these taxa are of genera, but some of these genera include subgenera. Therefore, for clarity the combination “genera/subgenera” is used. All the genera and subgenera were based on named species. None were based on “sp.” reports. In the literature, geologic ranges are given normally as generalized entire stages, and ranges involving substages (early, middle, late) have only been used mainly for the Campanian and Maastrichtian. If the published time-range data involve discontinuous ranges, that is how they are reported here, rather than assuming they continuously extend from the earliest record to the latest record. Plots of the published ranges (Fig. 2) were used for counting the number of newly appearing genera/subgenera present per stage (or substage). The term “origination” pertains to increases of three or more of new genera/subgenera. The term “turnover” refers to a change in the composition of a biota, at any specified taxonomic level (Gilinsky 1998). The term “turnover” as used here refers to a time when four or more genera/subgenera disappeared and were replaced by newcomer taxa. The clade-classification scheme of Bieler et al. (2010) is used because it is a comprehensive one that also includes extinct taxa. LACMIP is the institutional abbreviation for the Natural History Museum of Los Angeles County, California.

RESULTS

On the basis of data derived from pre-existing publications, a total of 23 endemic genera/subgenera of Cretaceous shallow-marine bivalves are known in the NEP fauna, which does not include the displaced Caribbean Province Alisitos Formation tropical-water fauna in Baja California, Mexico. Ten families are represented, with venerids being the most common (Table 1). Temporal and numerical distributions (Figs. 2, 3) reveal that the first endemic genus, *Yaadia*, appeared during the Early

Table 1. Cretaceous shallow marine bivalve genera/subgenera endemic to the NEP, with authors, superfamilies, families, geographic distributions, and supplemental references. Abbreviations: **Q. Char. Is**=Queen Charlotte Islands, **Van Is**=Vancouver Island, **WA**=Washington, **OR**=Oregon, **CA**=California, **No**=North, **So**=South. *=Pre-Late Cretaceous species.

Genus/Subgenus	Order	Family	Location	Supplemental Reference
<i>Adelodonax</i> Saul (1989)	Venerida	Donacidae	No CA–Baja	
<i>Alleinacin</i> Squires and Ritterbush (1981)	Carditida	Astartidae	So CA	Squires (2018)
<i>Aphaea</i> Dailey and Popenoe (1966)	Venerida	Trapezidae	No–So CA	
<i>Califadesma</i> Saul (1989)	Venerida	Mesodesmatidae	No CA	
<i>Callistalox</i> Saul (1993)	Venerida	Veneridae	WA–So CA	
<i>Calva</i> (<i>Calva</i>) Popenoe (1937)	Venerida	Veneridae	No CA–Baja Sur	
<i>Calva</i> (<i>Egelicalva</i>) Saul and Popenoe (1992)	Venerida	Veneridae	Alaska–So CA	
* <i>Calva</i> (<i>E.</i>): one Early Cretaceous species	Venerida	Veneridae	No CA	
<i>Calva</i> (<i>Microcalva</i>) Saul and Popenoe (1992)	Venerida	Veneridae	Van Is–WA	
<i>Calva</i> (<i>Penecallista</i>) Saul and Popenoe (1992)	Venerida	Veneridae	So CA–Baj	
<i>Egrona</i> Saul (1993)	Venerida	Veneridae	So CA	
<i>Excorbula</i> Squires and Saul (2004)	Myida	Corbulidae	No–So CA	
<i>Louella</i> Cooper and Leanza (2017)	Trigoniida	Steinmanellidae	OR–No CA	Cooper and Leanza (2017)
<i>Notodonax</i> (<i>Aliodonax</i>) Saul (1989)	Venerida	Donacidae	No CA	
<i>Opis</i> (<i>Hesperopis</i>) Squires and Saul (2009)	Carditida	Astartidae	Van Is–Baja	
<i>Panzacorbula</i> Squires and Saul (2004)	Myida	Corbulidae	No–So CA	
<i>Popenoella</i> Cooper and Leanza (2017)	Trigoniida	Steinmanellidae	Van Is–So CA	Cooper and Leanza (2017)
<i>Pteroluter</i> Saul (1973)	Venerida	Mactridae	No CA	
<i>Rhaiphiale</i> Saul (1993)	Venerida	Veneridae	So CA	
<i>Rhectomyax</i> Stewart (1930)	Venerida	Kelliidae	No CA	Saul (1988)
<i>Willimactra</i> (<i>Petromactra</i>) Saul (1973)	Venerida	Mactridae	No–So CA	
<i>Willimactra</i> (<i>W.</i>) Saul (1973)	Venerida	Mactridae	No CA	
<i>Xenomytilus</i> Squires and Saul (2006)	Mytilida	Mytilidae	No–So CA	
<i>Yaadia</i> Crickmay (1930)	Trigoniida	Steinmanellidae	OR–No CA	Saul (1978)
* <i>Yaadia</i> : three Early Cretaceous spp.	Trigoniida	Steinmanellidae	Q. Char. Is–OR	

Cretaceous (Valanginian). Endemism remained very low until the Turonian, when warmer waters arrived in the NEP region during the Cretaceous thermal maximum when the highest number (13) of genera/subgenera was present. During the influx of cooler waters southward during the Coniacian to Santonian (Saul 1986, Squires 2018), the number of endemic genera dropped by 50%. The number started to increase afterward, during the warmer times that existed (Squires 2018) during the Campanian and early Maastrichtian. The second-highest number of genera/subgenera (11) was recorded during the early Maastrichtian, but the numbers decreased at the end of the early Maastrichtian, which coincided with

the climate change of the global “Middle Maastrichtian Event” (MME). None survived into the Cenozoic (Figs. 2, 3). Representative species of NEP Cretaceous endemic bivalves are shown in Figure 4.

DISCUSSION

Early Cretaceous Record

Yaadia is the earliest known record of an endemic bivalve in the NEP region and appeared during Early Cretaceous (Valanginian) time. *Calva* (*Egelicalva*) Saul and Popenoe (1992) was the only addition added subsequently during the Albian, when the sea level rose

Genera/Subgenera (w/number of species)	Numerical age Ma														
	139	134	130	113	100	94	89	86	84	80	76	72	70	66	
	Val	Hau	Apt-Bar	Alb	Cen	Tur	Con	San	Camp			Maa		Cenoz	
									e	m	l	e	l		
<i>Yaardia</i> (2)	-	-		-											
<i>Calva (Egelicalva)</i> (7)				-											
<i>Calva (Calva)</i> (6)															
<i>Louella</i> (1)															
<i>Alleinacin</i> (1) →															
<i>Egrona</i> (1)															
<i>Pteroluter</i> (1)															
<i>Rhaiphiale</i> (1)															
<i>Excorbula</i> (3)															
<i>Williamactra (W.)</i> (2) →															
<i>Callistalox</i> (2)															
<i>Opis (Hesperopis)</i> (6)															
<i>Popenoella</i> (6)															
<i>Califadesma</i> (3)															
<i>Calva (Microcalva)</i> (2) →															
<i>Notodonax (Aliodonax)</i> (2)															
<i>Adelodonax</i> (2)															
<i>Rhectomyax</i> (1)															
<i>Willimactra (Petromactra)</i> (2)															
<i>Panzacorbula</i> (1) →															
<i>Calvia (Pennecallista)</i> (1)															
<i>Aphaea</i> (2)															
<i>Xenomytilus</i> (1)															
number of genera/subgenera	1	1	0	2	3	13	7	7	9	8	9	11	7	1	

Figure 2. Age ranges of NEP Cretaceous shallow-marine endemic bivalves, with originations, turnovers, and global mass extinction indicated. These age ranges are derived from existing publications for each genus/subgenus listed in Table 1. Abbreviations: **Val**=Valanginian, **Hau**=Hauterivian, **Apt-Bar**=Aptian-Barremian, **Alb**=Albian, **Cen**=Cenomanian, **Tur**=Turonian, **Con**=Coniacian, **San**=Santonian, **Camp**=Campanian, **Maa**=Maastrichtian, **Cenoz**=Cenozoic, **e**=early, **m**=middle, **l**=late. **MA**=mega-annum (in millions of years) numbers from Gradstein et al. (2012: fig. 27.6).

somewhat (Haq et al. 1987, Miller et al. 2011), and the sea-surface temperature increased significantly (Forster et al. 2007, Linnert et al. 2014). Albian strata containing shallow-marine mollusks are scarce in the NEP region and are of middle Albian age. One location is in the Bald Hills of northern California, and the other is in the upper Alisitos Formation in Baja California, Mexico (Fig. 1). The Bald Hills fauna has similar warm-temperate-water mollusks (including two NEP endemic bivalves) found elsewhere in the NEP Subprovince. The Alisitos Formation fauna (no NEP endemic bivalves), is in a suspect-terrane

(Busby et al. 2006). The Alisitos fauna has a richly diverse tropical-water (Tethyan) fauna of mollusks (*in situ* rudistid bivalves, actaeonellid and nerineid gastropods) and other invertebrates (reef corals, large benthic foraminifera, club-shaped cidaroid echinoids), all very similar to those found in the tropical-water Caribbean biologic province in Texas and west-central Mexico (Allison 1974, Durham and Allison 1960, Saul 1986, Sohl 1971). *Calva (Calva)* appeared during the Cenomanian, when the sea level and the sea-surface temperature continued to increase (Figs. 2, 3).

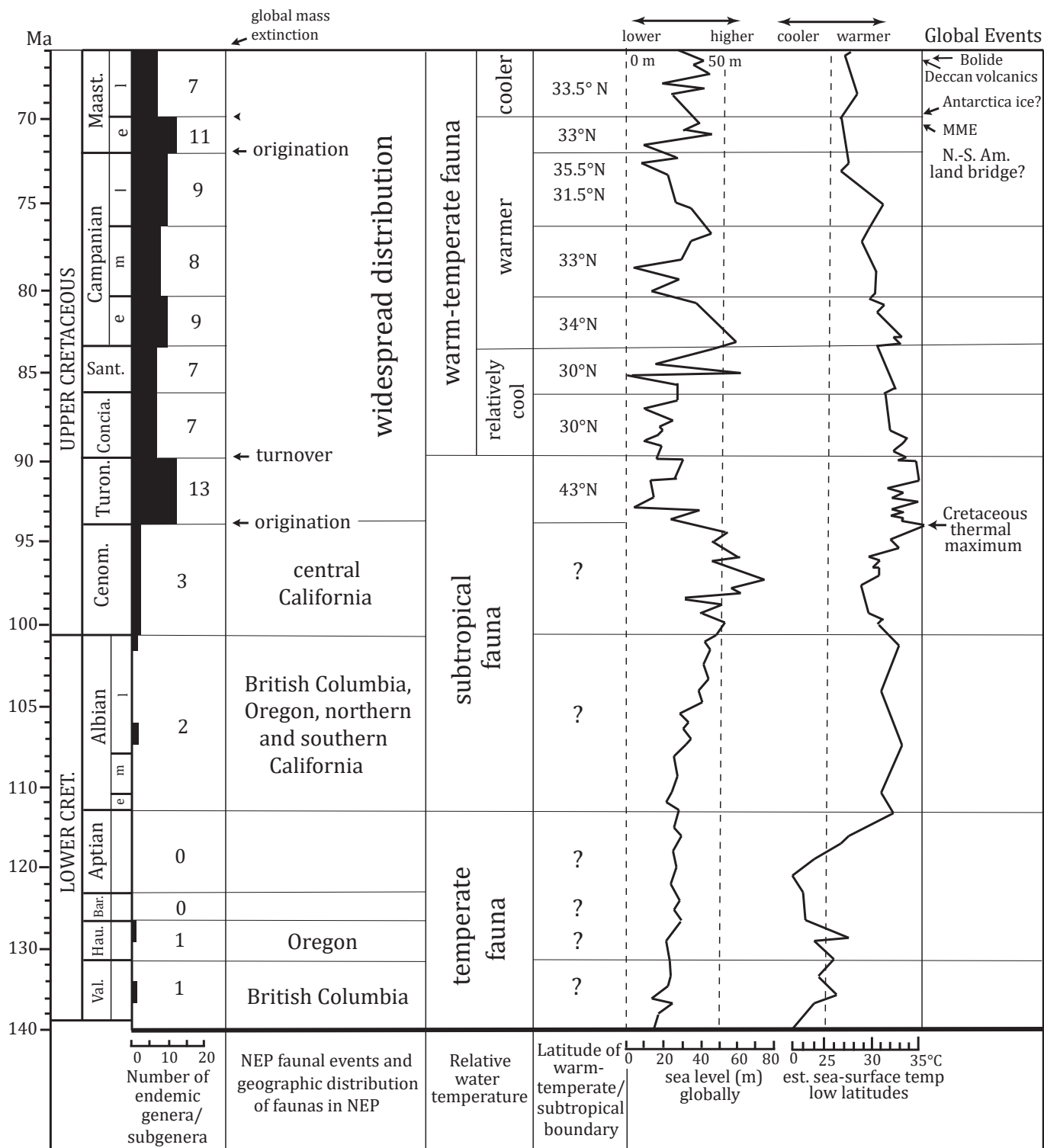


Figure 3. Temporal overview of NEP Cretaceous shallow-marine endemic bivalves. Geologic ages from Gradstein et al. (2012). Geographic distribution data based on Table 1. Latitude/boundary data from Saul and Squires (2008). Global-sea levels from Haq et al. (1987) and Miller et al. (2011: fig. 4). Valanginian ocean-temperature data from Pucéat et al. (2003). Hauterivian ocean-temperature data from Price et al. (2011). Aptian ocean-temperature data from Bonin et al. (2015). Albian to Maastrichtian sea surface-water temperatures (SSTs) data from Forster et al. (2007:fig. 2) and Linnert et al. (2014: fig. 2). Global events' data sources: Bolide impact (Keller 2008), Deccan volcanics (Keller et al. 2011), Antarctica ice (Thibault et al. 2016), mid-Maastrichtian event (MME) (MacLeod et al 1996), North to South American land bridge? (Iturralde-Vinent 2003). Abbreviations: Val.=Valanginian, Hau.=Hauterivian, Bar.=Barremian, Cenom.= Cenomanian, Turon.=Turonian, Concia.=Coniacian, Sant.=Santonian, Maast.=Maastrichtian, e=early, m=middle, l=late, Ma=milli-annum.

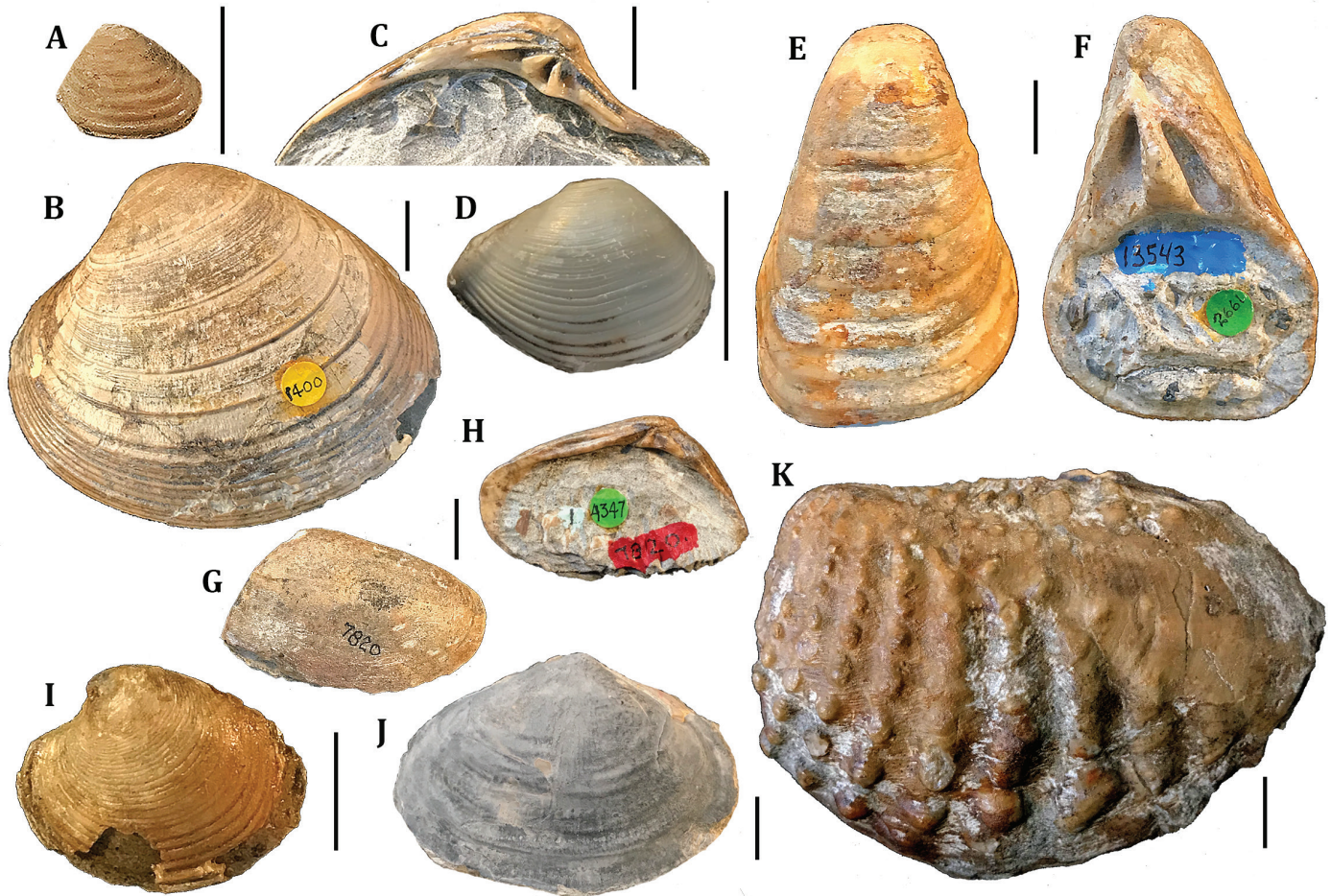


Figure 4. Representative species of NEP Cretaceous endemic shallow-marine bivalve genera/subgenera (shown in alphabetical order). **A.** *Alleinacin acerba* (Hanna, 1924), left valve in exterior view. Hypotype LACMIP 4276 from the Ladd Formation, Baker Canyon Member (Turonian), Santa Ana Mountains, Orange County, CA. **B, C.** *Calva* (*Egelicalva*) *bowersiana* (Cooper, 1894), left valve in exterior view (**B**) and hinge (**C**). Hypotype LACMIP 8192 from the Cedar District Formation (lower middle Campanian), Socia Island, San Juan County, WA. **D.** *Excorbula parkeyi* Squires and Saul (2004), right valve in exterior view. Holotype LACMIP 13117 from the Redding Formation, Member IV (Coniacian), Shasta County, CA. **E, F.** *Opis* (*Hesperopis*) *triangulata* (Cooper, 1894), right valve in exterior (**E**) and interior (**F**) views. Hypotype LACMIP 13543 from the Moreno Formation, informal Quinto B member, (upper lower to lower upper Maastrichtian), Merced County, CA. **G, H.** *Notodonax* (*Aliodonax*) *bolsae* Saul (1989), left valve in exterior (**G**) and interior (**H**) views. Holotype LACMIP 7820 from the Pigeon Point Formation (middle Campanian), San Mateo County, CA. **I.** *Rhaiphiale pharota* Saul (1993), left valve in exterior view. Paratype LACMIP 8241 [published by Saul (1993) as 8141] from the Ladd Formation, Baker Canyon Member, (Turonian), Orange County, CA. **J.** *Willimactra* (*Petromactra*) *truncata* (Gabb, 1864), right valve in exterior view. Hypotype LACMIP 10126 from the Chico Formation (lower Campanian), Butte County, CA. **K.** *Popenoella robusta* (Saul, 1978), left valve in exterior view. Holotype LACMIP 10189 from the Chatsworth Formation (middle Campanian), Los Angeles County, CA. Scale bars=10 mm.

Origination at the Beginning of the Turonian

Ten new endemic genera/subgenera of bivalves appeared during the Turonian, and they represent the first major origination of endemic bivalves in the NEP region (Figs. 2, 3). *Yaadia* became more widespread at this time and diverged into the endemic yaadiine genera *Louella* and *Popenoella* (Fig. 2, Table 1). This origination event of endemic bivalves is very similar to that recognized by Squires (2018) for the NEP endemic gastropod genera. The Turonian, as well as the late Cenomanian, coincided with the warmest interval of “greenhouse” climate in the last 115 million years (Friedrich et al. 2012) and also

coincided with relatively high sea levels (Haq et al. 1987, Miller et al. 2011) (Fig. 3).

Based on the geographic distribution of rudist bivalves and volute gastropods reported from the NEP Cretaceous record (Saul and Squires 2008), during the Turonian, the latitudinal position of the subtropical/warm-temperate boundary was the farthest north (latitude 43°N) of the entire Late Cretaceous. As a result, there was a limited northward influx into the NEP region of subtropical Tethyan-influenced genera, including actaeonellids, nerineids, neritids, and cypraeoidean gastropods, as well as rudistid bivalves (Squires 2018). Rudistids are

indicators of, at least, marginal tropicality (Saul 1986), and during the Turonian they reached as far north as southern Oregon and northern California (Saul 1986). This Oregonian occurrence was based, however, on an incomplete specimen, named by Lupper and Packard (1930) as *Lithocalamus*. Skelton (2013) regarded this genus to be an *incertae sedis* and its status as a rudistid uncertain.

Turnover at Turonian/Coniacian Boundary and Subsequent Coniacian to Santonian Interval

The somewhat abrupt turnover at the end of the Turonian in the NEP region resulted in the extinction of 38% (five of 13) of Turonian endemic bivalve genera/subgenera (Fig. 2). This extinction was less severe than the end Turonian 86% extinction reported by Squires (2018) for the NEP endemic gastropods. The Coniacian sea-surface temperatures at low latitudes and sea levels decreased somewhat in comparison to that of the Turonian. During the Coniacian, the boundary between warm-temperate and subtropical waters migrated significantly southward approximately 13°, to approximately 30°N latitude (Fig. 3). As cooler water conditions expanded in the NEP, both the endemic gastropod genera (Squires 2018) and endemic bivalve genera/subgenera were affected. Saul (1986: p. 133) mentioned briefly that, beginning in the Coniacian in the NEP, there were faunal changes in gastropods, bivalves, and ammonites related to the arrival of a more temperate climate versus that of the Turonian. No Tethyan-influenced rudistid bivalves or gastropods are known from the Coniacian through nearly all the Santonian in the NEP region (Squires 2018).

Six of the endemic bivalve genera/subgenera present in the Turonian are also present in younger stages, but at least three of these have a “gap” in their post-Turonian record. *Calva* (*Calva*) is one of three taxa having significant gaps in their records. The other two are *Callistalox* Saul (1993) and *Calva* (*Microcalva*) Saul and Popenoe (1992) (Fig. 2). Saul and Popenoe (1992) reported that the *Calva* (*C.*) lineage was more thermophilic (i.e., not as tolerant of cool waters) than the *Calva* (*Egelicalva*) lineage. This observation explains why the *Calva* (*C.*) lineage is discontinuous during the cool times of the Coniacian, Santonian, and early part of the Campanian, whereas the *Calva* (*E.*) lineage is continuous during these times (Fig. 2). The same reasoning might apply to the discontinuous records of *Callistalox* (a Coniacian through Campanian “gap”) and that of *Calva* (*M.*) (a Santonian and early Campanian “gap”) (Fig. 2).

Jaitly and Mishra (2009: pp. 260–262, fig. 5I–J) reported

the NEP region early Campanian venerid *Calva* (*E.*) *butensis* Anderson (1958) as occurring also in Maastrichtian strata at a locale within the Ariyalur Group of South India. This Ariyalur venerid’s left-valve dentition is, however, unlike any NEP subgenus of *Calva*, including *Calva* (*E.*).

There was a slight increase in the number of NEP endemic genera/subgenera (two) during the early Campanian, but the increase is probably too small to be deemed significant. It coincided with a warming of the NEP waters, following a relatively cool time during the Coniacian and Santonian (Fig. 3). There was, however, an early Campanian origination event for the NEP shallow-marine gastropod genera (Squires 2018).

Origination Prior to the Early Maastrichtian

The number of NEP endemic genera/subgenera stayed generally about the same throughout the Campanian although a few disappeared and were replaced by newcomers (Fig. 2). There was a minor origination event, however, near the beginning of the early Maastrichtian. As a result, the second-highest number (11) of NEP Late Cretaceous endemic genera/subgenera occurred during the early Maastrichtian, and a few of them were holdovers from the Turonian (Fig. 2). A major change in ocean-water circulation might have occurred during the late Campanian to early Maastrichtian (Fig. 3) because of a temporary closure (1 to 3 million years) of the Caribbean by a possible land bridge between North and South America (Iturralde-Vinent 2003). How this event affected the origination event of endemic bivalves in the NEP is uncertain.

Turnover at the end of the Early Maastrichtian (“Mid-Maastrichtian Event”)

This turnover coincided generally with the globally recognized “Mid-Maastrichtian Event” (MME) cooling event at approximately 69 Ma (Fig. 3), when approximately one-third (four) of the NEP endemic bivalve genera went extinct. Squires (2018) also recognized the MME in the NEP endemic gastropod fossil record, when nearly half of the NEP endemic gastropod genera went extinct. Although there was a shift globally toward cooler sea-surface temperatures during the MME (Fig. 3), rudistids and other thermophiles were present in the NEP region, but they were nearing their disappearance from the Late Cretaceous because of the arrival of relatively cooler waters (Squires 2018). Also, as reviewed by Squires (2018), there were several major sea-level regressions (Adatte et al. 2002), a major change in ocean-water circulation (Iturralde-Vinent 2003) and cooling global climate

(MacLeod et al. 1996) during late Maastrichtian time.

Global Mass-Extinction Event at the Cretaceous/ Paleogene (K/Pg) Boundary

Calva (*Calva*), *Callistalox*, and *Xenomytilus* were the last remaining NEP endemic bivalves, and they went extinct at the K/Pg boundary (Fig. 2). Unlike the NEP endemic gastropods (Squires 2018), no Late Cretaceous NEP endemic bivalve genera/subgenera are known with certainty to extend into the Cenozoic. Saul and Popenoe (1992: p. 29) reported *Calva* (*Calva*) *baptista* Saul and Popenoe (1992), however, as being of latest Maastrichtian age to questionably earliest Cenozoic (earliest Danian) age in the basal San Francisquito Formation on Warm Springs Mountain, Los Angeles County, southern California.

The timing of many of the events near or at the K/Pg boundary, in the Figure 3 column “Global Events,” is under debate. Papers used by the present author for deriving these ages are the following: bolide impact (Keller 2008), Antarctica ice (Thibault et al. 2016), and Deccan volcanics (Keller et al. 2011).

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