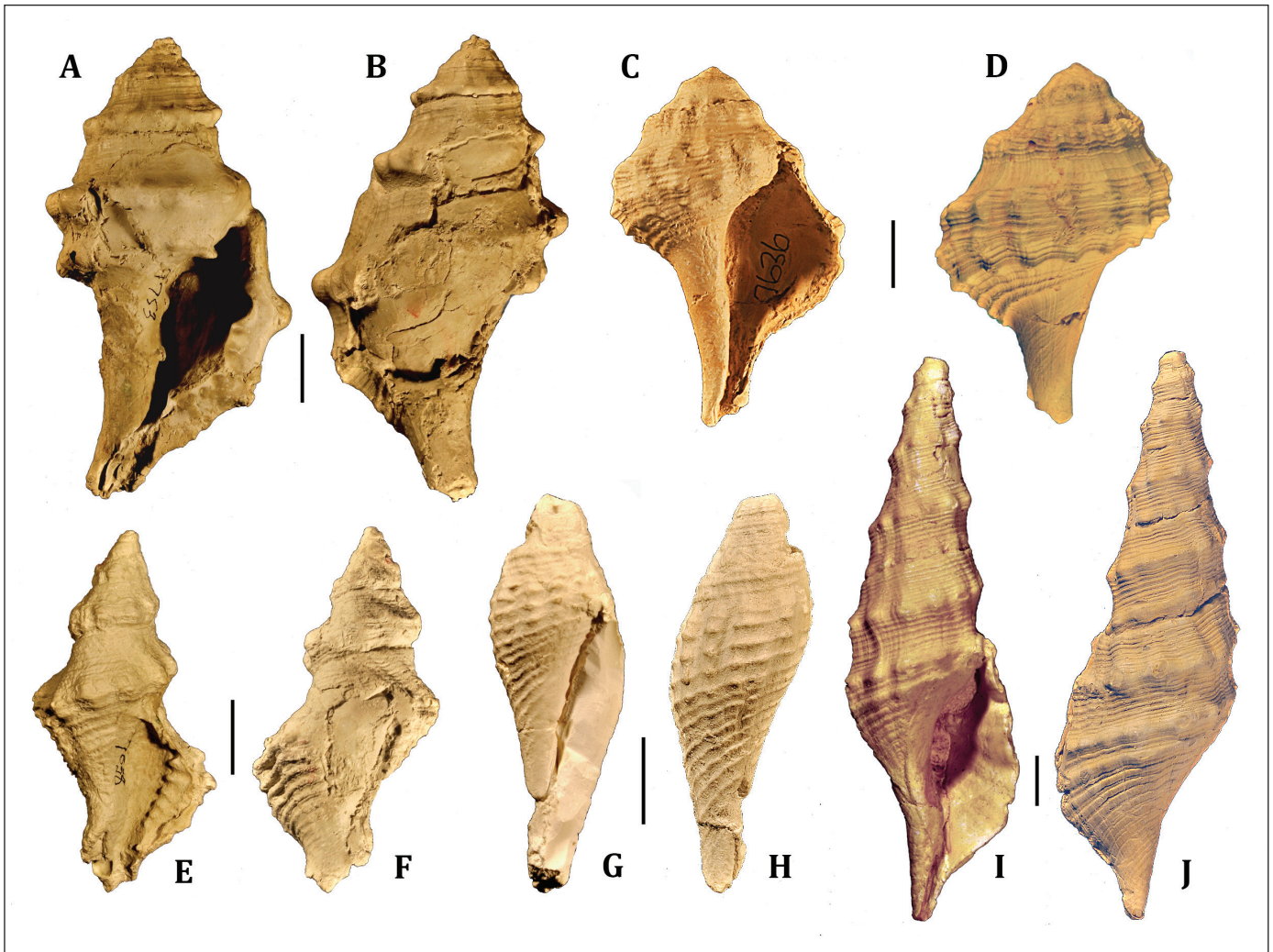


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Cover illustration: Representative Late Cretaceous endemic shallow-marine gastropod genera of the northeast Pacific.

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Late Cretaceous endemic shallow-marine gastropod genera of the northeast Pacific: biodiversity and faunal changes

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Endemic genera of shallow-marine gastropods in the Cretaceous Northeast Pacific Subprovince (NEP), extending from Alaska to northern Baja California Sur, Mexico, are tabulated and discussed in detail for the first time. None are known in Lower Cretaceous or Cenomanian strata, but 43 genera, nearly two-thirds of which are neogastropods, are recognized in Upper Cretaceous strata. Their first appearance was at the beginning of the Turonian, which coincided with the warmest time of the Cretaceous and one of its highest sea-level stands. Fourteen new subtropical endemic genera appeared then, and 10 (71%) were neogastropods. Tethyan-influenced thermophilic mollusks (nerineid, acteonellid, neritid, and cypraeoidean gastropods, as well as rudistid bivalves) were present. A turnover at the Turonian/Coniacian boundary occurred when cooler waters migrated southward, resulting in the subtropical endemics being abruptly and nearly completely replaced by 10 warm-temperate new endemic neogastropods, which commonly had long-living lineages persisting through the Campanian or early Maastrichtian. Eight (80%) of these new genera were neogastropods. During these cooler water times in the Coniacian and nearly all of the Santonian, there was an absence (“gap”) of Tethyan-influenced and other thermophile mollusks. New endemic genera, were added during an origination event in the early Campanian and also during another one in the late Campanian. Fewer and fewer new neogastropod genera appeared during each of these origination events, whereas new endemic genera of non-neogastropods increased. Rudistids and thermophilic mollusks also returned in the Campanian. Most of the post-Turonian endemic genera went extinct at a turnover at the end of the early Maastrichtian (=“Middle Maastrichtian Event”), rather than at the K/Pg boundary mass-extinction event. Two new endemic genera, both neogastropods, originated just before the end of the Maastrichtian. They and three other Cretaceous endemic gastropod genera occur also in the NEP Cenozoic record, thereby imparting a somewhat transitional aspect between these two faunas. The tectonically transported fauna of the middle Albian Alisitos Formation in northern Baja California, Mexico is confirmed to have lived in the tropical-water Caribbean Biotic Province of the Tethyan Realm.

Keywords: Endemism, gastropods, Late Cretaceous, Northeast Pacific Subprovince, Alisitos Formation

INTRODUCTION

Gastropods are common faunal components of Late Cretaceous shallow-marine assemblages found along the rim of the Northeast Pacific (NEP), a region extending from the Alaskan Peninsula southward to the northern part of Baja California Sur, Mexico (Fig. 1). In the last 20 years or so, there have been many publications focused on the systematic paleontology of the NEP gastropod faunas, and this new knowledge is the basis for this present investigation, which concerns the detailed analysis of the endemic genera of the fauna. The endemism aspect is more relevant than a study of the entire gastropod fauna because the endemics more precisely reflect the

environmental conditions of the NEP region through the Late Cretaceous.

Lower Cretaceous NEP gastropod faunas are, for the most part, very poorly known, and no endemic shallow-marine gastropod genera were detected in the literature. A discussion of the shallow-marine gastropod fauna in the Lower Cretaceous (Albian) Alisitos Formation, presently located in northern Baja California, Mexico (Fig. 1), is included herein, to help confirm the location of where this fauna originally lived.

Cretaceous hydrocarbon-seep gastropods from the NEP are not included in the present study. The majority of them occur in northern and central California, in

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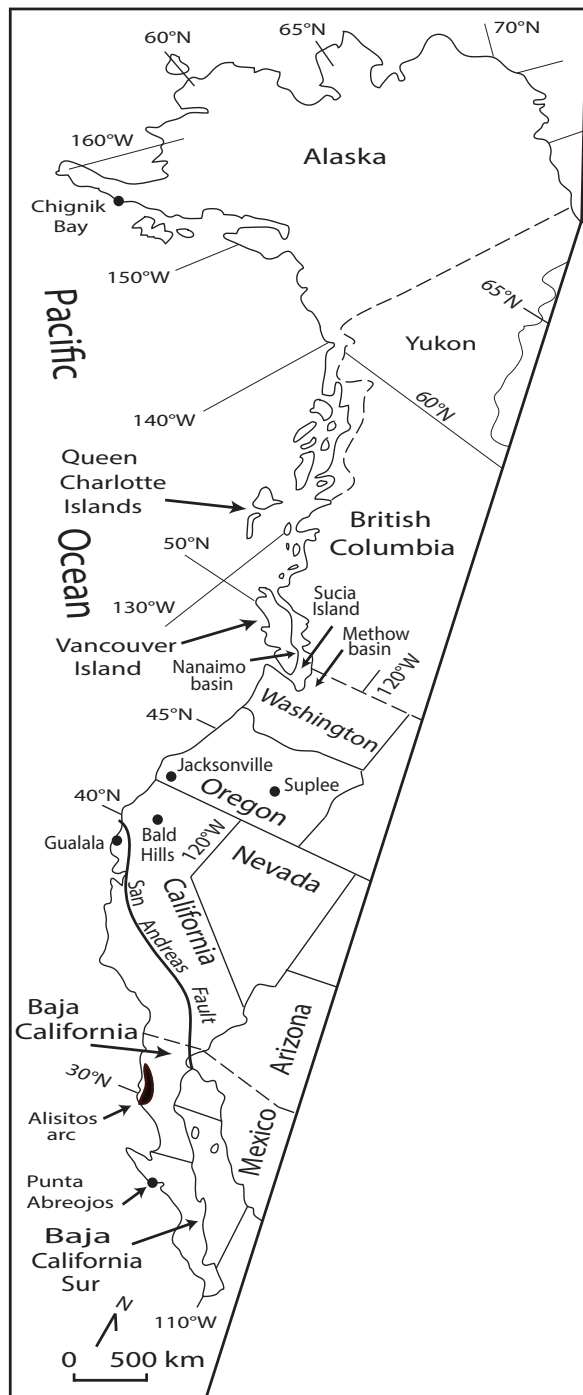


Figure 1. Index map of the NEP region.

isolated hydrocarbon-seep “white limestones” within forearc deposits, ranging in age from Late Jurassic to Eocene (Kiel et al. 2008, Kaim et al. 2014).

OVERVIEW OF CRETACEOUS GLOBAL CONDITIONS

Cretaceous tectonism was on-going and included the continued opening, from south to north, of the Atlantic

Ocean. Suspect terranes were actively accumulating along the east Pacific Ocean margin (Riddihough 1988). Ocean-crust production and extensive volcanism occurred during the “middle” Cretaceous (Skelton et al. 2003). There were several oceanic anoxic events (OAEs) during the Early Cretaceous but only two in the Late Cretaceous: OAE-2 (referred to as the “Bonarelli Event” in Europe) at the Cenomanian/Turonian boundary and OAE-3 at the Coniacian/Santonian boundary. Wagreich (2012) reported that OAE 3 was largely absent in the Pacific region. According to Jenkyns (2010), the major forcing function of OAEs was an abrupt rise in temperature brought on by global warming. The Cretaceous was characterized overall by a warm equable climate (“greenhouse”), and tropical and polar temperatures were warmer than today (Hay 2008). Sea-surface temperatures were warm, especially during the thermal maximum at the beginning of the Turonian. Afterward, and until the end of the Cretaceous, there was a cooling trend (Forster et al. 2007; Linnert et al. 2014). Eustatic sea levels were high, especially during the Late Cretaceous, but during the end of the Cretaceous there were rapid and significant sea-level changes and a fluctuating climate (Miller et al. 2011). There were probable ephemeral closures across the Caribbean Seaway in southern Mexico during the Coniacian and Santonian (Iturralde-Vinent 2003). Platform-system carbonates with rudist bivalves and colonial corals were common during the “middle” Cretaceous in equatorial areas (Skelton et al. 2003). Glaciation, if any, was very restrictive, and short-term polar ice might have occurred only in the early Maastrichtian and only in Antarctica (Thibault et al. 2016). There was a bolide impact approximately 300,000 years before the end of the Cretaceous (Keller 2008). Extensive continental-flood basalts (Deccan Traps) formed in India at the end of the Cretaceous, and these outpourings of lava most likely affected the global climate (Keller et al. 2011).

NEP CRETACEOUS GEOLOGIC SETTING

Cretaceous rocks, which are widespread in the NEP region, are commonly within amalgamated sequences of tectonic terranes (suspect terranes), and there might be as many as 50 suspect terranes in California alone (Williams and Howell 1982). The NEP region has been the site of subduction-zone tectonics and associated igneous and high-grade metamorphic activities that began in the Jurassic and continued into the Cretaceous and Cenozoic. Elongate forearc basins developed and received voluminous siliciclastic deep-marine, turbidite-related sediments (Nilsen 1986). Early Cretaceous

buchiid bivalves and scattered ammonites are present in these continental-margin marine sequences (Jones et al. 1969) [now recognized as turbidite sequences], whereas shallow-marine gastropods are scarce (Anderson 1938) and poorly known. Shallow-marine deposits, which were mainly limited to shoaled waters along the edges of the forearc basins, were subject to uplift and erosion (Nilsen 1986). Associated shallow-marine fossils would have been subject to being reworked and transported into deep-water turbidite sequences, and, in some cases, in conglomerate beds. Early Cretaceous Albian and Cenomanian shallow-marine gastropods are uncommon in the NEP region (Murphy and Rodda 1960, Squires and Saul 2002a), and the Albian fauna from the Bald Hills in northern California (Murphy and Rodda 1960) is particularly important for this present paper because it represents the earliest known *in situ* NEP Cretaceous faunas.

Late Cretaceous shallow-marine gastropod faunas of Alaska are very poorly known because paleontological collections nearly exclusively emphasized ammonites and/or inoceramid bivalves, both of which have been used extensively for biostratigraphic zonation. It is probable also that few gastropods were present to begin with (William Elder, personal communication 2018). The only known Late Cretaceous Alaskan locale having a NEP shallow-marine endemic gastropod genus present is at Chignik Bay (Fig. 1). This locale plots within the Peninsular terrane that makes up the western half of the Wrangellia-composite terrane complex in Alaska (Plafker et al. 1994).

Gastropod-bearing Cretaceous strata occur in the Queen Charlotte Islands of British Columbia, but early workers mixed fossils of Jurassic and Cretaceous age in their collections (Haggart 1987). Along the east coast of Vancouver Island (Fig. 1) and immediate vicinity to the south (Gulf Islands), strata of mostly late Santonian to late Campanian age have yielded a rich diversity of mollusks. These strata, along with the Queen Charlotte Islands strata, are part of the Insular Superterrane, whose accretionary history has been postulated by two mutually contradictory hypotheses based on paleomagnetic data (Cowan et al. 1997, Ward et al. 1997). One hypothesis indicates that the Insular Superterrane was already in place in its current position (more or less), relative to western North America, by the Cretaceous and perhaps earlier. This basically “in place” hypothesis is evidenced by the coexistence of Archaen-Early Proterozoic, Middle Proterozoic, and Mississippian detrital zircons in the Queen Charlotte, Nanaimo, and Methow basins (Fig. 1), thereby indicating derivation from the Canadian Shield

and deposition in northern latitudes (Mahoney et al. 1999). A second hypothesis, known as the “Baja British Columbia” or “Baja BC” hypothesis, indicates that the Nanaimo Basin deposits were transported approximately 3,500 km northward, from a depositional latitude of approximately $25^{\circ}\pm 3^{\circ}\text{N}$, equivalent to that of modern-day Baja Sur, California (Ward et al. 1997). A third hypothesis indicates a depositional site not farther south than 40°N (northern California) (Kodama and Ward 2001). This third hypothesis, which has an intermediate amount of transport versus the other two hypotheses, is supported by studies on shallow-marine mollusks (Haggart et al. 2005), acilid bivalves (Squires and Saul 2006a), volutid gastropods (Saul and Squires 2008a), opine bivalves (Squires and Saul 2009), a ficiid? gastropod (Squires and Graham 2014), and decapod crustaceans (Schweitzer et al. 2003).

The “Baja BC” hypothesis was used by Champion et al. (1981) to infer that the middle Campanian Pigeon Point Formation, located in San Mateo County, northern California has been tectonically displaced by as much as 2,500 km north of its original latitude in tropical waters (21°N) in southern Mexico. Elder and Saul (1993) reported, however, that the warm-temperate to subtropical molluscan fauna of this formation is supportive for a less tropical site of deposition.

The San Andreas Fault (Fig. 1) has displaced outcrops of NEP Cretaceous strata in southern and coastal northern California. The San Andreas Fault (Fig. 1) is a right-lateral strike-slip fault that extends for 1400 km. Estimates of cumulative right slip of basement terranes range from approximately 300 to 450 km along the southern and northern segments of the fault system, respectively (Beeson et al. 2017). Rudistid bivalves, which are indicative of warm oceans, are found in these displaced Cretaceous rocks west of the San Andreas Fault in northern to southern California and range from Turonian to Maastrichtian in age. The farthest north displacement of these rudistids is in the Gualala Formation of northern California (Elder et al. 1998). Rudistid-bivalve fragments also occur in NEP rocks not affected by the San Andreas Fault. For example, uncommon fragments are found in southern Oregon and northern California in Albian and Turonian strata (Anderson 1958).

NORTHEAST PACIFIC SUBPROVINCE (BIOTIC)

The region extending from south of the Alaska Peninsula to northern Baja California, Mexico was referred to by Kauffman (1973) as the “Northeast Pacific Subprovince” (Fig. 2), and this term is used here. This subprovince

had warm-temperate to subtropical coastal conditions during the Late Cretaceous (Sohl 1971, Saul 1986a, Kiel 2002, Saul and Squires 2008a, Squires and Saul 2009). The northernmost known locale of the Northeast Pacific Subprovince is of early Campanian age in Chignik Bay, Alaska Peninsula (Fig. 1). The endemic perissityid neogastropod *Zinsitys anassa* Saul, 1988a is found there, as well as in British Columbia, Washington, northern California, and southern California (Saul 1988a). Although the original geographic position of Chignik Bay is not known because it is geologically situated in a suspect terrane, this Northeast Pacific Subprovince gastropod fauna is present in rocks of the Alaska Peninsula. The southernmost known locale of this subprovince is near Punta Abreojos, Vizcaino Peninsula, northern Baja California Sur, Mexico (Fig. 1), where a middle Campanian fauna contains several gastropods and bivalves, some of which have been found commonly in similar age deposits in British Columbia, Washington, and California (Popenoe 1957, Elder and Saul 1993, Saul and Squires 2008b).

PREVIOUS REPORTS OF NEP ENDEMIC GASTROPOD GENERA

Biplica Popenoe, 1957 was reported by him as endemic to the Pacific coast gastropod assemblage. Sohl (1964) added five other genera: *Haydenia* Gabb, 1864, *Liocium* Gabb, 1869, *Sycodes* Gabb, 1869, *Lysis* Gabb, 1864, and *Tessarolax* Gabb, 1864. Sohl (1964) most likely added these genera because they were considered to be monotypic genera, hence, only found in California. Only *Haydenia*, *Liocium*, and *Sycodes*, however, are endemic. *Biplica* is now known from Japan (Kase 1990), the Russian Federation (Kaim and Beisel, 2005), and northern Australia (Stilwell and Henderson 2002). *Lysis* is known from elsewhere in the world (Saul and Squires 2008b), as is *Tessarolax* (see Saul and Squires 2015).

Saul (1986a) reported that the gastropod *Perissitys* Stewart, 1927 is “largely” endemic to the NEP. *Perissitys* is regarded in this present paper, however, to be endemic to the NEP. Popenoe and Saul (1987) stated that *Perissitys* might be present at a Coniacian or Santonian locale in Japan, based on a report by Hayami and Kase (1977), but better preserved specimens are needed for positive identification.

Saul (1986a) reported also that the gastropod *Pyktes* Popenoe, 1983 is “largely” endemic in California, and Kiel (2002) reported that it established an “endemic lineage” in California. This genus is not endemic to the Pacific coast. *Pyktes* has widespread distribution, and has been reported (Kiel and Bandel 1999), for example,

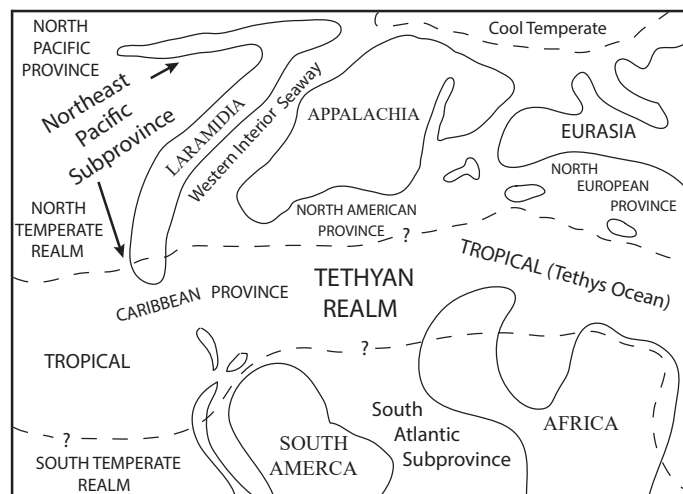


Figure 2. Location of the NEP region, from a portion of Kauffman's (1973:fig. 1) Cretaceous global paleobiogeographic provinces map.

from Santonian strata in South Africa.

Igonoia Squires (2011a) was reported by him to be endemic to the NEP region. Wild and Stilwell (2016) reported this gastropod, however, from Albian strata on a seamount in the eastern Indian Ocean. Saul and Squires (2008b) reported that the gastropod *Ariadnaria* Habe, 1961 helps to characterize the Northeast Pacific subprovince because the geologic age of this genus is late Albian to late Santonian age in California, but *Ariadnaria* is not endemic because its type species is an extant boreal Arctic circumpolar gastropod.

MATERIALS AND METHODS

Determination of which Cretaceous NEP shallow-marine gastropod genera are endemic was done by careful examination of all relevant published papers, especially those dealing with systematic paleontology. Genera used were based on those with named species. None were based on “sp.” reports. *Nerita* (*Bajanerita*) Squires, 1993 was reranked as genus *Bajanerita* Squires, 1993 by Sepkoski (2002). The clade classification scheme of Bouchet et al. (2017) is used because it is a comprehensive one that also includes extinct taxa. An exception to their scheme is used here: Trichotropidae Gray, 1850 is recognized as a distinct family (see Saul and Squires 2008b).

Cretaceous global-biologic realms are derived from Kauffman (1973). Geologic range data of the endemic NEP genera were plotted versus published information about global sea-level curves and ocean surface-water temperatures, as well as to shifts in water masses in the NEP region and co-occurrences of some Tethyan-influenced

and some thermophilic mollusks.

Knowledge of the biostratigraphy of NEP gastropods has vastly improved during the last several decades, but detailed biostratigraphic and paleomagnetic resolutions of most formations are still wanting. Published geologic ranges of the NEP Cretaceous gastropod genera are, therefore, based on broad time intervals (e.g., late Campanian). 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. Maastrichtian strata in the NEP region are scarce, relatively few shallow-marine mollusks have been collected from these beds, and the fossils that have been collected are, in general, not well preserved or studied (Saul and Squires 2008a). Based on usage in Squires (2017), the geologic age of the Rosario Formation in northern Baja California, Mexico is late Campanian to early Maastrichtian, and the geologic age of the “Garzas Sand,” “Tierra Loma Shale,” and “Quinto Silt” informal members of the Moreno Formation in central California are approximately late early Maastrichtian to early late Maastrichtian (Squires 2017). The exact ages of these members are not known. The genera whose ranges are affected by these uncertainties can be found in the Moreno Formation. They are the following: *Cidarina* Dall, 1909, *Garzasia* Saul and Squires, 2008b, *Gyrodes* (*Hyperita*) Woodring, 1957, *Bulbificopsis* Squires and Saul, 2003b, and *Bajanerita*? (Fig. 3).

The term “turnover” refers to a change in the composition of a biota, at a specified taxonomic level (Gilinsky 1998).

Institutional Abbreviations—ANSP, Academy of Natural Sciences at Drexel University, Philadelphia, Pennsylvania; LACMIP, Natural History Museum of Los Angeles County, Los Angeles, California, Invertebrate Paleontology Department; SDSNH, San Diego Natural History Museum, San Diego, California; UCMP, University of California Museum of Paleontology, Berkeley, California.

RESULTS

No endemic genera were detected from Lower Cretaceous or Cenomanian strata in the NEP region. The first appearance of endemic NEP region shallow-marine gastropods was in the Turonian, and new endemics were added as late at the latest Maastrichtian. Forty-three endemic genera of Late Cretaceous shallow-marine gastropods were recognized from the NEP region (Table 1), but three of these genera (*Alamirifica* Saul and Squires, 2003, *Bajanerita*, and *Pseudocymia* Popenoe and Saul, 1987) are also included as questionable genera. Future

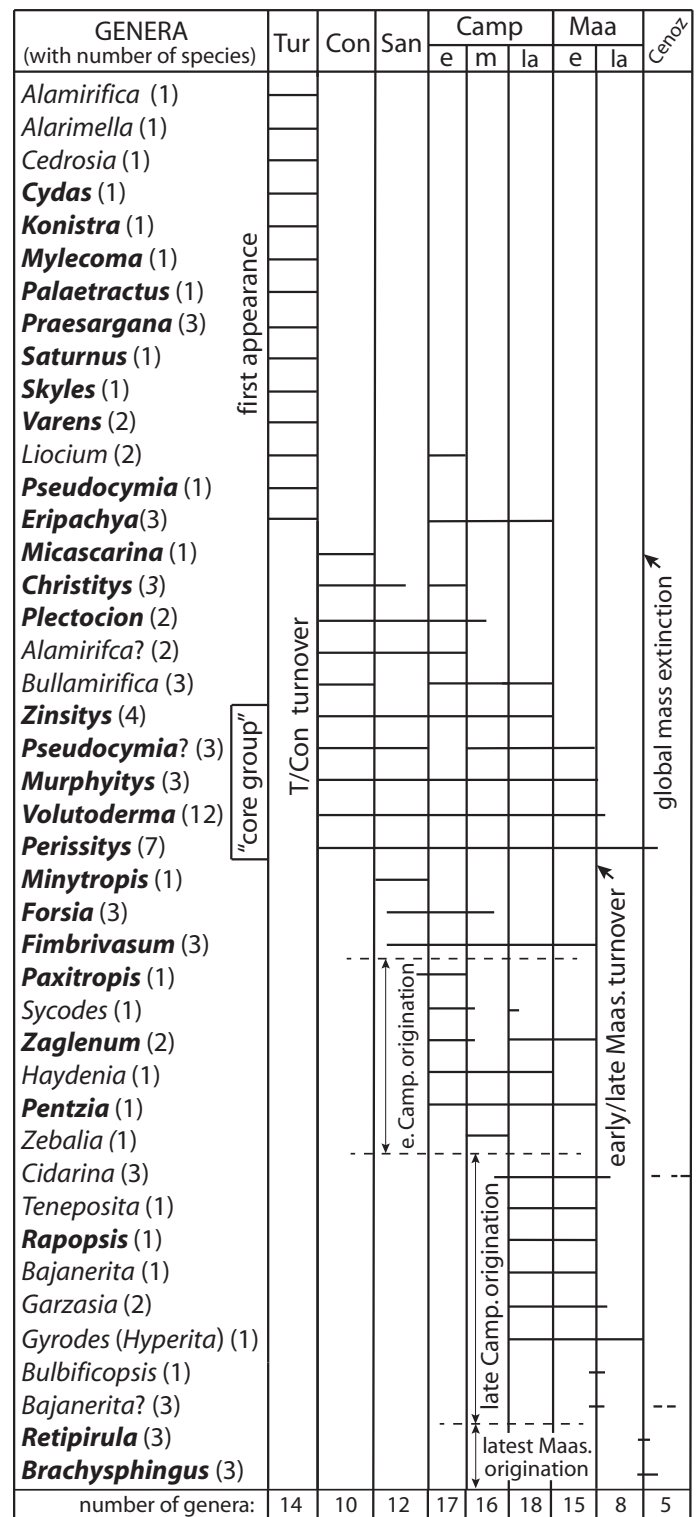


Figure 3. Geologic ranges of NEP Cretaceous shallow-marine endemic genera, with turnovers and originations indicated. Bold type indicates neogastropod genera. Dotted lines indicate approximate boundaries.

work is needed to definitely show them as unique genera.

Beyond the first appearance of many new subtropical

Table 1 Late Cretaceous shallow marine gastropod genera endemic to the NEP, with authors, subclasses or orders, families, geographic distributions, and supplemental references. **SC**=subclasses or orders, **Ca**=Caenogastropoda, **Ne**=Neritimorpha, **Ng**=Neogastropoda, **V**=Vetigastropoda; **Van Is**=Vancouver Island, **WA**=Washington, **CA**=California, **No**=North, **So**=South

Genus	SC	Family	Location	Supplement. Ref.
<i>Alamirifica</i> Saul and Squires, 2003	?	?	So CA	
<i>Alamirifica?</i> Saul and Squires, 2003	?	?	Van Is, No CA	
<i>Alarimella</i> Saul, 1988a	Ca	Aporrhaidae	So CA	
<i>Bajanerita</i> Squires, 1993	Ne	Neritidae	So CA-Baja	Squires and Saul 2002b
<i>Bajanerita?</i> Squires, 1993	Ne	Neritidae	WA-CA	Squires and Saul 2002b
<i>Brachysphingus</i> Gabb, 1869	Ng	Buccinidae	No CA-Baja	Squires 1997
<i>Bulbificopsis</i> Squires and Saul, 2003b	Ca	Ficidae	No CA	
<i>Bullamirifica</i> Squires and Saul, 2005	Ca	cerithioid	So CA-Baja	
<i>Cedrosia</i> Saul and Squires, 2003	Ca	Potamididae	Baja	
<i>Christitys</i> Popenoe and Saul, 1987	Ng	Perissityidae	Alaska, No CA	
<i>Cidarina</i> Dall, 1909	V	Chilodontidae	Van Is, WA, No CA	Squires 2011b
<i>Cydas</i> Saul and Popenoe, 1993	Ng	Perissityidae	No CA	
<i>Eripachya</i> Gabb, 1869	Ng	Buccinidae	So CA	Squires and Saul 2003b
<i>Fimbrivassum</i> Squires and Saul 2001	Ng	Turbinellidae	Van Is-So CA	
<i>Forsia</i> Saul, 1998	Ng	Perissityidae	Van Is-So CA	
<i>Garzasia</i> Saul and Squires, 2008b	Ca	Trichotropidae	No CA-So CA	
<i>Gyrodes</i> (<i>Hypterita</i>) Woodring, 1957	Ca	Naticidae	No CA-Baja	Popenoe et al. 1987
<i>Haydenia</i> Gabb, 1864	Ca	Cassidae	Van Is-So CA	Stecheson 2004
<i>Konistra</i> Saul and Popenoe, 1993	Ng	Volutidae	No CA	
<i>Liocium</i> Gabb, 1869	Ca	Pseudomelaniidae	No CA	Squires and Saul 2003c
<i>Micascarina</i> Squires and Saul, 2003c	Ng	Fascioliariidae	So CA	
<i>Minytropis</i> Squires and Saul, 2005	Ca	Capulidae	No CA	
<i>Murphitys</i> Popenoe and Saul, 1987	Ng	Perissityidae	No CA-So CA	
<i>Mylecoma</i> Squires and Saul, 2003c	Ng	Fascioliariidae	No CA	
<i>Palaeatractus</i> Gabb, 1869	Ng	Melongenidae	No CA	Saul and Popenoe 1993
<i>Paxitropis</i> Squires and Saul, 2005	Ca	Capulidae	No CA-So CA	
<i>Pentzia</i> Squires and Saul, 2003b	Ng	Melongenidae	WA-Baja	
<i>Perissitys</i> Stewart, 1927	Ng	Perissityidae	Van Is-So CA	Popenoe and Saul 1987
<i>Plectocion</i> Squires and Saul, 2003c	Ng	Fascioliariidae	No CA	
<i>Praesargana</i> Saul and Popenoe, 1993	Ng	Sarganidae	No CA	Saul 1996
<i>Pseudocymia</i> Popenoe and Saul, 1987	Ng	Perissityidae	No CA	
<i>Pseudocymia?</i> Popenoe and Saul, 1987	Ng	Perissityidae	WA-Baja	
<i>Rapopsis</i> Saul 1988b	Ng	Tudicidae	So CA-Baja	
<i>Retipirula</i> Dall, 1907	Ng	Volutidae	No Ca-Baja	Saul and Squires 2008a
<i>Saturnus</i> Saul and Popenoe, 1993	Ng	Melongenidae	So CA	
<i>Skyles</i> Saul and Popenoe, 1993	Ng	Fascioliariidae	No CA	

Table 1 (continued). Late Cretaceous shallow marine gastropod genera endemic to the NEP, with authors, subclasses or orders, families, geographic distributions, and supplemental references. **SC**=subclasses or orders, **Ca**=Caenogastropoda, **Ne**=Neritimorpha, **Ng**=Neogastropoda, **V**=Vetigastropoda; **Van Is**=Vancouver Island, **WA**=Washington, **CA**=California, **No**=North, **So**=South

Genus	SC	Family	Location	Supplement. Ref.
<i>Sycodes</i> Gabb, 1869	Ca	Ficidae?	Van Is-No CA	Squires and Graham 2014
<i>Teneposita</i> Loch, 1989	Ca	Aporrhaidae	So CA	
<i>Varens</i> Saul and Popenoe, 1993	Ng	Volutidae	So CA	
<i>Volutoderma</i> Gabb, 1877	Ng	Volutidae	Van Is-Baja	Saul and Squires 2008a
<i>Zaglenum</i> Squires and Saul, 2001	Ng	Buccinidae	So CA	
<i>Zebalia</i> Squires and Saul, 2003a	Ca	Zygopleuridae	WA-So CA	
<i>Zinsitys</i> Saul, 1988a	Ng	Perissityidae	Alaska, No CA	

endemic genera at the Cenomanian/Turonian boundary, two turnover events of endemic genera were detected (Figs. 3, 4). The first one, which occurred at the Turonian/Coniacian boundary, involved the abrupt replacement of most of the subtropical endemic genera by new, cooler water endemic genera. Several of the latter genera are referred to herein as the “core group” because of their long residence times. Neogastropods dominated both of these turnover faunas, and there was near-total absence (“a gap”) of Tethyan-influenced and thermophilic mollusks during the Coniacian and nearly all of the Santonian. The second turnover event, which occurred at the end of the early Maastrichtian, involved the abrupt disappearance of many of the post-Turonian endemic genera, including most of the “core group.” This second turnover, which is recognized here for the first time, is temporally equivalent to the global “Middle Maastrichtian Event.” This event was a minor event at the end of climate warming in the early late Maastrichtian (Mateo et al. 2017).

There were two main origination events between the two above-mentioned turnovers. One origination event was in the early Campanian, and the other was at the beginning of the late Campanian. New endemic genera in the first radiation were mostly neogastropods, whereas new endemic genera in the second radiation were nearly all non-neogastropods. There was a third, but minor, origination event just before the K/Pg boundary. Only two new endemic genera were added, and both were neogastropods.

There is no evidence that the taxonomic composition of NEP shallow-marine endemic gastropod fauna underwent a cataclysmic event (e.g., bolide impact) at the K/Pg boundary. Most of the endemics went extinct

at the “Middle Maastrichtian Event,” and not at the K/Pg boundary (Figs. 3, 4). A few of the Late Cretaceous NEP endemic genera range into the Cenozoic.

The shallow-marine gastropods in the Albian Alisitos suspect terrane in northern Baja California are confirmed to represent a tropical (Tethyan) fauna, which did not live in the NEP Subprovince.

DISCUSSION

First Appearance in the Turonian

Endemic shallow-marine gastropod genera (14) abruptly made their first known appearance in the NEP region at the beginning of the Turonian (Fig. 3). Although no Cenomanian endemic shallow-marine gastropod genera were detected in the literature, their “absence” is possibly the result of the scarcity of Cenomanian shallow-marine outcrops in the NEP region. Sea-surface temperatures globally reached their highest for the entire Cretaceous during the late Cenomanian and Turonian interval (97–91 Ma) (Fig. 4). It was a time of a “hot-greenhouse” climate, when sea-surface waters at low latitudes reached approximately 35°C, thus, making this interval the warmest “greenhouse” climate in the last 115 million years (Friedrich et al. 2012). This interval also coincided with high sea levels of the Cretaceous (Fig. 4). During the Turonian, the latitudinal position of the subtropical/warm-temperate boundary was the farthest north (latitude 43°N) of the entire Late Cretaceous (Saul and Squires 2008a; Fig. 4). As a result, there was a significant influx of subtropical Tethyan-influenced genera, including actaeonellids, nerineids, neritids, and cypraeoidean gastropods, as well as rudistid bivalves (Fig. 4), into the NEP region. Rudistids are indicators of, at least,

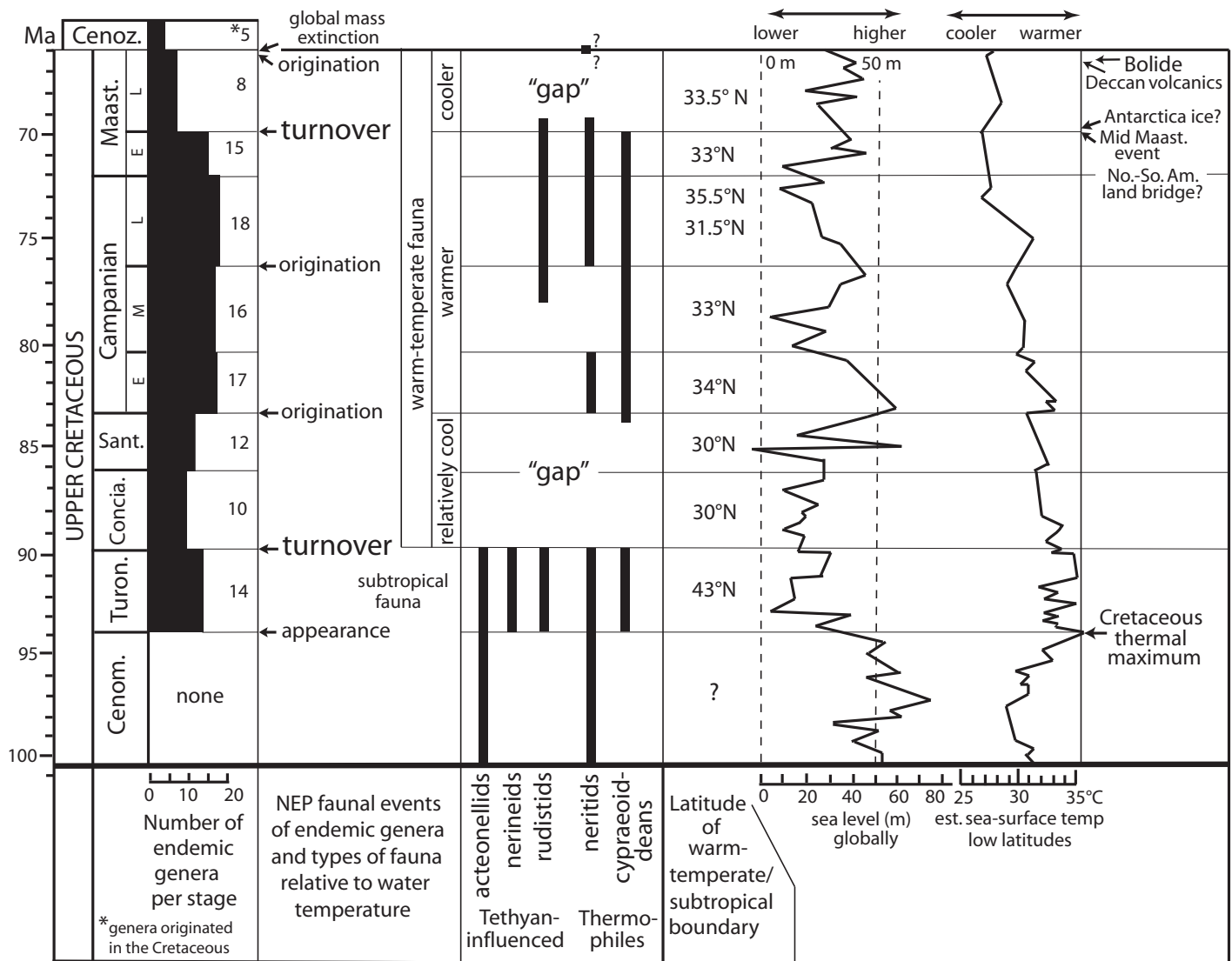


Figure 4. Geologic overview of NEP Cretaceous shallow-marine endemic genera. Geologic ages from [Gradstein et al. \(2012\)](#). Geologic ranges of non-endemic fossil groups in NEP region derived from the following sources: Actaeonellids ([Sohl and Kollmann 1985](#)), nerineids ([Saul and Squires 2002](#)), neritids ([Saul and Squires 1997](#)), cypraeoid-deans ([Groves 1990, 2004](#)), and rudistids ([Kodama and Ward 2001](#)). Latitude/boundary data from [Saul and Squires \(2008a\)](#). Global-sea levels from [Miller et al. \(2011:fig. 4\)](#). Sea surface-water temperatures (SSTs) data from [Forster et al. \(2007:fig. 2\)](#) and [Linnert et al. \(2014:fig. 2\)](#).

marginal tropicity, and they were present as far north as Oregon and northern California ([Saul 1986a](#)). The influx of all of these groups could have been facilitated during the Turonian by a northward-directed current, which was a component to the east-to-west movement of surface waters through a seaway that, according to [Johnson \(1999\)](#), existed at that time in southern Mexico.

Ten (71%) of the 14 new endemic genera that appeared during the Turonian in the NEP represent the first major diversification of neogastropods in this area. Neogastropods represent the geologically youngest of all the gastropod clades found in Cretaceous faunas

worldwide, and [Sohl \(1987\)](#) reported that their increased diversity was one of the major features of Cretaceous gastropod evolution. [Sohl \(1987\)](#) and [Taylor et al. \(1980\)](#) supported the concept that neogastropods originated in temperate European seas and had their main areas of diversification in relatively cool realms north and south of the tropical Tethys Sea. [Kiel \(2002\)](#), on the other hand, suggested that neogastropods originated in tropical waters. [Morris and Taylor \(2000\)](#) opined that although climatic and sea-level changes might have played a part in the early diversification of neogastropods, the rise of this group was more likely because of their evolutionary

breakthrough into carnivory.

Turonian/Coniacian Boundary Turnover

The abrupt turnover at the end of the Turonian in the NEP region resulted in the extinction of most (86%) of the subtropical NEP endemic neogastropods that had appeared earlier during the Turonian. Only two genera (*Liocium* and *Eripachya* Gabb, 1869) ranged into younger strata but did not reappear until the early Campanian. An abrupt turnover at the Turonian/Coniacian boundary has been recognized also in eastern North America and Europe, and ammonites and bivalves were especially affected (Kauffman and Hart 1996). Elder (1989) mentioned a molluscan-faunal turnover at the Turonian/Coniacian boundary in the Western Interior of the United States. He commented that the turnover there was associated with high sea level and unusual oceanographic conditions that disrupted molluscan-larval dispersal and adult distributions. Elder (1989) also reported that this turnover was less extreme relative to the one at the Cenomanian/Turonian boundary.

Popenoe et al. (1987) suggested that a change took place in marine conditions at the end of the Turonian in the NEP region. They noted that there was a significant decline in the diversity of gryodiform gastropods, as well as a decrease in the size of their specimens.

Coniacian Arrivals

During the Coniacian, 10 new endemic genera (Fig. 3) appeared in the NEP region, and the percentage of neogastropods (80%) was at its highest level for the Late Cretaceous. Five of the new endemic genera (*Murphyitys* Popenoe and Saul 1987, *Perissitys*, *Pseudocymia*?, *Volutoderma* Gabb, 1877, and *Zinsitys* Saul, 1988a), all of which originated together in the Coniacian, make up the “core group” (Fig. 5). This group established some long-lived and diverse lineages persisting mostly through the early Maastrichtian (Fig. 3). Except for *Volutoderma*, these “core group” genera belong to the extinct neogastropod family Perissityidae Popenoe and Saul, 1987, whose species commonly have a smooth, mammillate to globose protoconch of few whorls. Modern-day neogastropods with this kind of protoconch commonly have direct development (no free-swimming larvae) or a short planktonic stage, both of which could result in a restricted geographic distribution (Shuto 1974). Perissityids were most likely inherently endemic.

The persistence of the above-mentioned endemic “core group” indicates there were not drastic changes in environmental conditions in the NEP region during the

Coniacian through early Maastrichtian. Coniacian sea-surface temperatures (at low latitudes) declined relative to the Turonian, but global sea levels were similar to that of the Turonian. During the Coniacian, the boundary between warm-temperate and subtropical waters, however, migrated significantly southward approximately 13°, to approximately 30°N latitude (Fig. 4), as cooler water conditions expanded.

Saul (1986a:pp. 133–134) mentioned briefly that, beginning in the Coniacian in the NEP area, there were faunal changes in gastropods, bivalves, and ammonites related to the arrival of a more temperate climate versus that of the Turonian.

Coniacian to Latest Santonian “Gap” in Tethyan-influenced Gastropods and Rudistids

No Tethyan-influenced gastropods or rudistids are known from the Coniacian through nearly all the Santonian in the NEP region (Fig. 4). There is, however, one cypraeoidean known in uppermost Santonian strata on Vancouver Island (Groves 2004). The absence of these particular mollusk groups is referred to herein (Fig. 4), as the “gap,” which coincided with the first onset of warm-temperate (i.e., cooler) waters in the region during the Late Cretaceous. These waters arrived when the approximate latitude of subtropical/warm-temperate boundary retreated southward to about 30° (Saul and Squires 2008a). This “gap” has been observed also in the NEP region Late Cretaceous record of the endemic opine bivalve *Opis* (*Hesperornis*) (Squires and Saul 2009), as well as in the Late Cretaceous record of oysters, a thermophilic group (Squires 2017). In addition, in Coniacian strata of the NEP region, there is a questionable gap in the fossil record of the normally ubiquitous turritellid gastropods (Squires and Saul 2006b).

It is possible that the cooling trend during the Coniacian and Santonian was the result of oceanic connections allowing the mixing of polar waters, or, it might have been related to the opening of a deepwater passage through the equatorial Atlantic gateway (Friedrich et al. 2012). At these times of buildup of cooler water endemics, especially neogastropods, there were also changes going on in the Caribbean seaway in southern Mexico. This seaway, which was a vital connection between the Pacific Ocean and the Tethys Ocean, experienced ephemeral constriction by the development of temporary volcanic arc islands during the Coniacian and Santonian (Imlay 1944, Alencáster 1984, Iturralde-Vinent and MacPhee 1999, and Iturralde-Vinent 2003). According to Johnson (1999), this constriction resulted in the lack of a

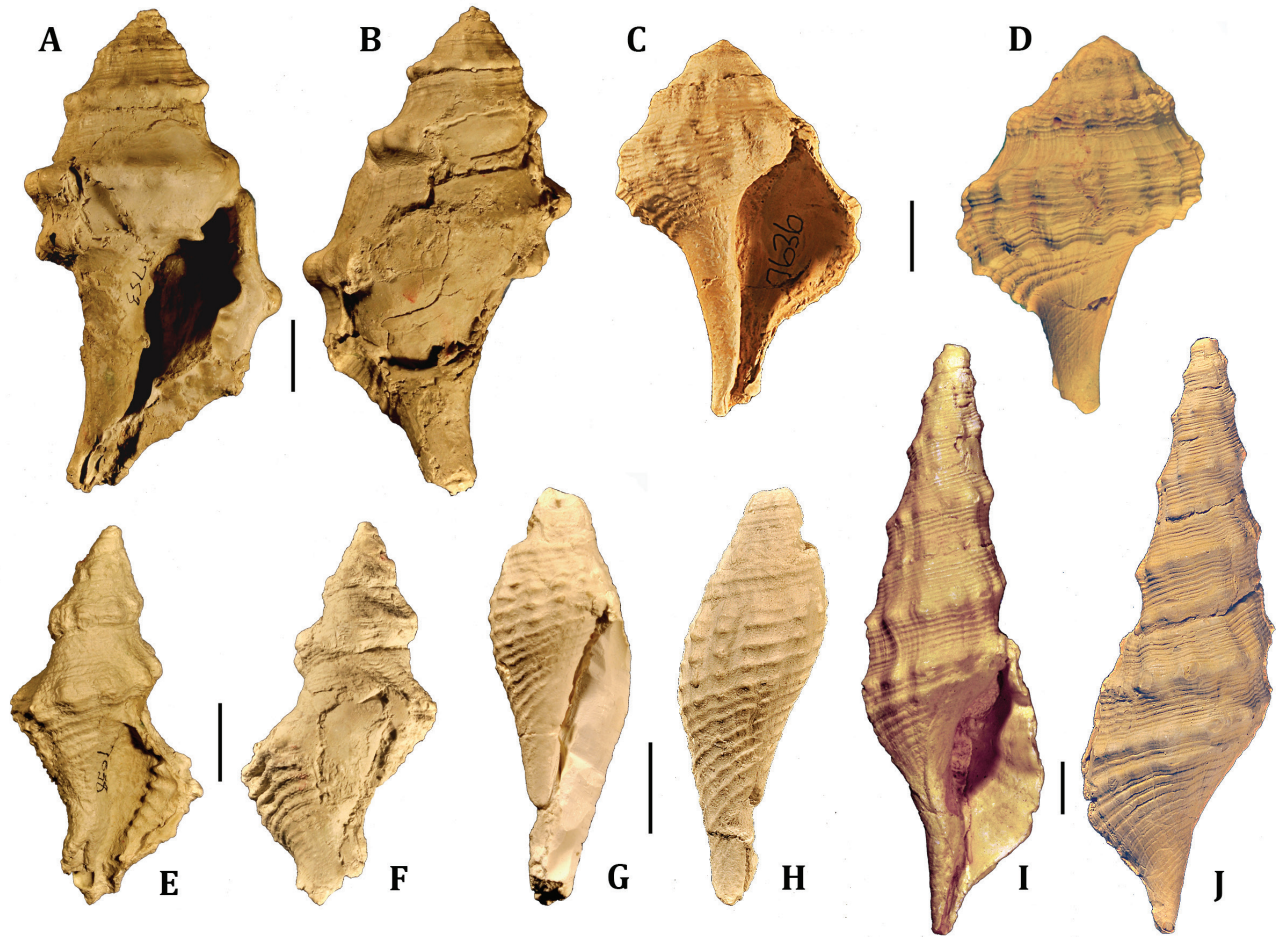


Figure 5A–I. Representative species of the “core group” of NEP Late Cretaceous endemic genera (shown in alphabetical order). Apertural and abapertural views shown for each genus. **A, B.** *Murphitys madonna* Popenoe and Saul, 1987, plasto-holotype, SDSNH 25958, Point Loma Formation (upper Campanian to lower Maastrichtian), Carlsbad Research Center, San Diego County, southern California. **C, D.** *Perssitys brevirostris* (Gabb, 1864), plasto-hypotype, UCMP 11069, Chico Formation (lower Campanian), near Pentz, Butte County, northern California. **E, F.** *Pseudocymia? kilmeri* Popenoe and Saul, 1987, plasto-hypotype, UCMP 37997, Rosario Formation (upper Campanian to lower Maastrichtian), Punta San Jose, northern Baja California, Mexico. **G, H.** *Volutoderma averillii* (Gabb, 1864), plasto-hypotype, ANSP 4298, Chico Formation (lower Campanian), Tuscan Springs, Tehama County, northern California. **I, J.** *Zinsitys anassa* Saul, 1988a, plasto-holotype, LACMIP 7246, Cedar District Formation (lower middle Campanian), Little Sucia Island, San Juan County, Washington. Scale bars = 10 mm.

northward-directed current that would have allowed for influx of warm-water gastropods through the seaway. Not having this current present could account for the near absence of Tethyan genera during these stages in the NEP region.

Early Campanian and late Campanian Origination Events

These two originations are shown indicated by dashed lines on Figure 3 because of the staggered nature of the appearances and disappearances of some of the new endemics. Four new endemic genera were added during the early Campanian, and the majority were neogastropods (Fig. 3). These new endemic genera, however, differed

from the Coniacian “core group” endemics by consisting of only 50% neogastropods, rather than being mostly neogastropods. Nearly all of these new endemic genera differed also by consisting of only a single species rather than having long-lived lineages made up of multiple species. *Pentzia* Squires and Saul, 2003b, one of these new endemic genera, is an exception, however, because although this neogastropod consists of a single species, it had an especially long geologic range of approximately 13 million years, from the early Campanian into the early Maastrichtian. Like the “core group,” the persistence of *Pentzia* indicates there were not drastic changes in environmental conditions in the NEP region during the Campanian through early Maastrichtian. Thermophiles

(neritids and cypraeoideans) reappeared during the early Campanian, as relatively warmer waters migrated somewhat northward (Fig. 4).

The late Campanian corresponded to the highest number of endemic genera (18) in the NEP region (Figs. 3, 4). The origination coincided also with the rather abrupt presence of at least five new endemic genera. There was a significant dropoff, however, of neogastropods among these new genera, with the only new neogastropod being *Rapopsis* Saul and Popenoe, 1993. Global surface-sea level reached a relatively higher level than during the middle Campanian and there was some warming (Fig. 4). Tethyan-influenced gastropods (neritids and cypraeoideans) were present, as well as rudistids. The late Campanian to early Maastrichtian was the peak of the Mesozoic cypraeoideans in North America and also worldwide (Groves 2004). The rudist bivalve *Coralliochama* White, 1885, a warm-water indicator, was also an important faunal component in biostromal (non-reef) deposits in the upper Campanian to lower Maastrichtian Rosario Formation in northern Baja California, Mexico (Marincovich 1975). This bivalve is also found, but much less commonly, in scattered locales in the NEP region west of the San Andreas Fault. These locales have been offset northwardly several hundred kilometers by this fault. The farthestmost north of these locales is near Gualala, Mendocino County, northern California (Fig. 1). Elder et al. (1998) reported that the Gualala strata were originally deposited near the postulated northern boundary of the Tethys Realm of about 26°N. These strata were subsequently translated northward by the tectonic forces, including the San Andreas Fault, to their present location at 39°N.

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

This turnover coincided generally with the globally recognized "mid-Maastrichtian Event" (MME). During this event, in the NEP region, there was extinction of most of the remaining genera of the aforementioned "core group." *Volutoderma* and *Perissitys* were the only "core group" genera to survive, but *Volutoderma* did not survive very long during the late Maastrichtian (Fig. 3). This turnover also resulted in the extinction of the last members of endemic genera that appeared during the Santonian origination. Most of the members of the late Campanian origination also went extinct, and only *Cidarina* and *Bajanerita*? survived (Fig. 3).

Although there was a shift globally toward cooler sea-surface temperatures during the MME (Fig. 4), rudistids

and thermophiles were present in the NEP region, but they were nearing their disappearance from the Late Cretaceous. Their eventual absence in the early part of the late Maastrichtian supports the arrival of relatively cooler waters, which coincided with another cool-water "gap," similar to the one in the Coniacian and Santonian. Rare neritids were present questionably at the very end of the Cretaceous (Fig. 4).

MacLeod et al. (1996) reported that during the MME, there was a pulse of extinction, possibly caused by cooling, that affected inoceramid bivalves living in all of the world's oceans, and the extinction was diachronous. Mateo et al. (2017) reported that during the mid-Maastrichtian Event, there was a minor extinction, seemingly caused by the onset of cooling, that affected planktic foraminifera living in the Indian Ocean.

Bowman et al. (2013) suggested that ephemeral ice sheets existed on Antarctica during the early Maastrichtian. These might have been a precursor to two cooling trends in the late Maastrichtian that globally affected sea-surface waters, separated by a warming trend. Thibault et al. (2016) reported that both of these cooling trends were possibly caused by restrictive, short-term polar ice occurring only in Antarctica. Also during the Maastrichtian, there were several major sea-level regressions (Adate et al. 2002). Additionally, a major change in ocean-water circulation and global climate during the early Maastrichtian might have occurred because of a temporary (1 to 3 million years) closure of the Caribbean Sea by a land bridge between North and South America (Iturralde-Vinent 2003). All of these several relatively short-lasting fluctuations in both water temperature and sea level are factors that might account for the destabilization of the macrofaunal communities in the late Maastrichtian and the resultant decline of generic biodiversity in the NEP region.

A significant change in ocean-water circulation during the MME in the NEP region is reflected in the depositional environment of Marca Shale member of the Moreno Formation, in the western part of the San Joaquin Valley, central California. This member, which is gradational with underlying turbidites of the Tierra Loma Member containing some early to early late Maastrichtian turritellids and an ammonite species (Squires and Saul 2006a), consists of a 85 to 90 m-thick section of finely laminated diatomites (McGuire 1988). Diatomites are highly unusual in the Upper Cretaceous record of the NEP region. Davies and Kemp (2016) interpreted that these diatomites, as well as associated phosphorites, accumulated in an upper slope environment. They reported also that

the laminations represent varves and the diatomites and phosphorites indicate the presence of a strong coastal-upwelling regime, affected by seasonal-climate cycles in a strongly thermally stratified ocean. Modern-day oceans are thermally stratified (Kennett 1982), and it is likely that the depositional environment of the Marca Shale, as least locally, mimicked the modern-day ocean.

Latest Maastrichtian Origination

Two new endemic genera originated near the end of the Maastrichtian. They are the neogastropods *Retipirula* Dall, 1907 and *Brachysphingus* Gabb, 1869. Both are found at Warm Springs Mountains, northern Los Angeles County, southern California, where there is a rare conformable contact between uppermost Cretaceous and lower Paleocene strata (Kirby et al. 1991, Saul and Squires 2008a). *Brachysphingus* is found additionally in uppermost Cretaceous or possibly lowermost Paleocene strata at Dip Creek, central California, where there is another rare conformable contact between Cretaceous and Paleocene strata (Saul 1986b, Squires 1997).

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

This global event had a very minor impact on the shallow-marine endemic gastropods in the NEP region. In contrast, the extinction of endemic gastropod genera during the MME, approximately four million years before the K/Pg boundary, was much more severe (Fig. 3). *Peristys* survived the K/Pg event, as did the endemic genera *Cidarina* (an extant genus), *Bajanerita*?, *Retipirula*, and *Brachysphingus*. Their fossil record indicates a somewhat transitional aspect between the Late Cretaceous and Early Cenozoic NEP endemic gastropods. Saul (1983) reported similarly that there was no apparent trauma in the bioseries of shallow-marine turritellas at the end of the Cretaceous and the beginning of the Cenozoic in California.

Alisitos Fauna: A Displaced Tropical Fauna

The Alisitos Formation is in a suspect terrane referred to by Busby et al. (2006) as the “Alisitos arc,” which is now located within the geographic confines of the NEP region in northern Baja California, Mexico (Fig. 1). The geologic age of this fauna has been reported as either late Aptian (Allison 1955) or early Aptian (Allison 1974). The updated age used here is middle Albian, based on two Alisitos gastropod species, which are conspecific with two species from Texas. They are 1) *Trochactaeon* (*Neocylindrites*) *cumminsi* Stanton, 1947 [= *Actaeonella*

parvus (Stanton, 1947) of Allison (1955)] and 2) *Turritella seriatimgranulata* Roemer, 1849 [= *Turritella* (*Haustator*) aff. *T. (H.) seriatimgranulata* Roemer, 1849 of Allison (1955)]. Both species were reported by Akers and Akers (1997) to be characteristic of middle Albian strata in Texas.

In comparison to the other west-coast suspect terranes, the fauna of the richly fossiliferous biostromal limestones in the upper part of the Alisitos Formation differs significantly by containing abundant tropical-water *in situ* caprinid-rudistid bivalves, as well as algae, large benthic foraminifera, hermatypic reef corals, club-spined cidaroid echinoids, holoctypoid echinoids, and shallow-marine gastropods, including actaeonellids and a taxonomically diverse assemblage of nerineids (Allison 1955, 1974). Durham and Allison (1960) and Saul (1986a) recognized correctly that this fauna lived in tropical waters, which would have been south of the present-day latitude of the terrane. Sohl (1971) reported, furthermore, that the Alisitos fauna is a Tethyan fauna. Their conclusions are confirmed by this present study. The Alisitos fauna is unlike the other NEP faunas, including the Albian-age fauna in the Bald Hills area of northern California. The Alisitos fauna lived in a shallow-water, carbonate-platform limestone paleoenvironment, which, according to Voigt et al. (1999), was a common feature in the Tethys Ocean during the Albian. Kauffman (1973) expanded the western limits of the Tethys Realm into the Caribbean area (Fig. 3), rather than restrict this term to just the Mediterranean and West Pacific–Indian Ocean areas. Sohl (1971) reported that the Alisitos fauna is closely related to the Edwards Limestone in Texas and to Caribbean faunas. The Alisitos gastropod fauna is similar to an upper Aptian to lower Albian rudist-bearing fauna (Buitrón-Sánchez and López-Tinajero, 1995), in the western part of the Caribbean Province in Jalisco, west-central Mexico.

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