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Society of Systematic Biologists

The Geologic History of Baja California and Its Marine Faunas

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Source: *Systematic Zoology*, Vol. 9, No. 2 (Jun., 1960), pp. 47-91

Published by: Taylor & Francis, Ltd. for the Society of Systematic Biologists

Stable URL: <http://www.jstor.org/stable/2411859>

Accessed: 04-01-2016 19:41 UTC

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Symposium: The Biogeography of Baja California and Adjacent Seas

THIS SYMPOSIUM of the Pacific Section of the Society of Systematic Zoology was held June 16 and 17, 1959, at San Diego State College, San Diego, California, in connection with the fortieth Annual Meeting of the Pacific Division of the American Association for the Advancement of Science. The symposium was organized by John S. Garth and Jay M. Savage of the University of Southern California. Dr. Enrique Beltran, Director, Instituto Mexicano de Recursos Natureles Renovables, Mexico, D. F., acted as general chairman and made introductory and concluding remarks.

THE SYMPOSIUM is divided into three parts: geologic history, marine biotas, and terrestrial and fresh-water biotas.

PART I. GEOLOGIC HISTORY

The Geologic History of Baja California and Its Marine Faunas

J. WYATT DURHAM AND EDWIN C. ALLISON

Introduction

BAJA CALIFORNIA, a 1300 kilometer-long peninsula which dominates the Peninsular Range province of western North America, occupies a geologically and biogeographically critical site at the northern boundary of the eastern Pacific tropics. Nowhere else between the United States and Nicaragua is a Cenozoic record of the eastern Pacific recognized. Latitudes between the southern tip of Baja California and the transverse Ranges of southern California, the limits of the Peninsular Range province, embrace the transition between two great faunal divisions of the eastern Pacific: the tropical west American and the north temperate west American. The Gulf of California, which separates Baja California from the mainland of Mexico, carries a narrow

salient of the tropical eastern Pacific far to the north.

High granitic peaks of the Sierra Juárez and the Sierra San Pedro Martir dominate northern parts of the peninsula of Baja California and continue a short distance beyond the latitude of San Diego as the northernmost extremity of the Peninsular Range province. A less lofty and more arid terrain characterizes central and southern parts of the peninsula. Granitic rocks and higher elevations appear again in the southern Cape region but with a climate marked by the summer rains and hurricanes of the tropics.

The physiography and climate of the Peninsular Range province have not been always as they are today. The peninsula of Baja California and the Gulf of California were probably recognizable after

the mid-Cretaceous orogeny, perhaps 100 million years ago, but later events have determined the modern configuration of the coast line. Throughout the Cenozoic period the boundaries of the Gulf expanded and contracted in harmony with submersion and emersion of the peninsula and adjacent areas on the eastern margin of the Pacific and with sedimentation at the mouth of the Colorado River. The peninsula of Baja California at times was restricted to a small northern area with its southern extent expressed in a series of islands. During times of emergence the peninsula expanded slightly to include areas beyond its present coasts.

Several modern summaries (Beal, 1949; Jahns, 1954; C. A. Anderson, 1950; Mina, 1957) of the geology and paleontology of Baja California are available but significant new discoveries made during the last decade and a half emphasize the incompleteness of our knowledge of the region. The new data underscore the need for a geologic history of the Peninsular Range province in order that the modern distributions of plants and animals on the peninsula and in the eastern Pacific may be considered in that perspective.

We have not attempted an exhaustive survey of the literature pertinent to the geology and paleontology of Baja California and to the biogeography of the marine invertebrates (foraminifers, corals, mollusks, echinoids, etc.) but, on the other hand, we have included considerable significant poorly known or unpublished information. Documentation is often accomplished by citation of a general work which, in turn, will provide references to more precise and detailed presentations of data.

Geological History

An excellent discussion of the geological history of western North America, including Baja California, and of the geological processes which have determined that history, is given by Philip B. King (1958) in the 1957 symposium sponsored by the American Association for the Ad-

vancement of Science: *The origins and affinities of the land and freshwater fauna of western North America*. The regional discussion provided by that paper is helpful in the interpretation of many aspects of Baja California geology.

The role that major strike-slip faulting has played in the tectonic history of California, prominently discussed in recent literature (Hill, 1954; Noble, 1954; Allen, 1957; P. King, 1959: 169-173), directly affects the interpretation of the geologic history of Baja California. Most discussion has centered upon the San Andreas fault zone and on the magnitude of right-lateral movement along that fault zone since the Jurassic period, whether hundreds of kilometers or merely a few kilometers. Fortunately for the purposes of this symposium the San Andreas fault, as interpreted by Hill (1954), lies to the northeast of the Peninsular Range province. It is only in evaluating the paleogeography of the Eocene and Pliocene epochs that major movement along that fault is of great concern. One of us (Durham) believes strongly that the evidence presented to date for major movement along the fault either is not critical or can be explained by other means and, accordingly, we have not visualized significant movement in making our paleogeographic interpretations.

Mesozoic

Cretaceous. The geological history of Baja California pertinent to the present discussion begins with the orogenic phase of mountain building: with the mid-Cretaceous folding of early Cretaceous (Aptian-Albian) volcanic and sedimentary rocks of the Alisitos formation (Santillán and Barrera, 1930: 9-10; Allison, 1955) and with their intrusion by granitic rocks of the Peninsular Range batholiths. Peninsular ranges and possibly an ancestral peninsula of Baja California emerged from that mid-Cretaceous orogeny, though they have been modified by subsequent events. The Alisitos forma-

tion and its equivalents, the San Fernando formation (Anon., 1924; Beal, 1949: 38-40) and the San Telmo formation (Woodford and Harriss, 1938: 1306-1310; Larsen, *et al.*, 1958: 46) cover major parts of the Pacific slope of the Peninsular Range. Probable equivalent formations in southern California (Table 1) are the Santiago Peak volcanics of the Santa Ana Mountains (Larsen, 1948: 22-30) and the Black Mountain volcanics of San Diego County (M. A. Hanna, 1926: 199-204; Larsen, 1948: 30-32). Pre-Miocene granitics of the Cape San Lucas area may have intruded similar rocks at the same time (Hammond, 1954: 66; Wisser, 1954: 50).

Rocks comparable to those of the Alisitos formation which occur near Arivechi, Sonora, and elsewhere on the east side of the Gulf of California (R. King, 1939), believed to have been deposited in a broad seaway across Mexico and the southwestern United States, were subjected to the same mid-Cretaceous orogeny. Similar radiometric age determinations of granitic rocks from the Sierra Nevada range in California, from Sonora, and from elsewhere along the western continental margin from Baja California to British Columbia indicate the great extent of that orogeny. Lead-alpha determinations give mean ages of 102-108 million years (Larsen, *et al.*, 1958) while potassium-argon determinations favor a younger age of 78-95 million years (Curtis, Evernden, and Lipson, 1958) on respective physical time scales for the emplacement of the batholiths.

The Alisitos formation is characterized by a great thickness of pyroclastic rocks with interbedded basic flows and biohermal limestones (Allison, 1955). That thickness is now known to be greater than 5000 meters. The site of deposition is inferred to have been a tropical sea isolated from major sources of continental sediments: perhaps a volcanic archipelago with broad submarine areas shallow enough to favor the development of great reefs of hermatypic corals and pachydont pelecypods.

Such reefs are perhaps the most striking feature of the Alisitos formation. Recurrent vulcanism often buried the area with great quantities of pyroclastic debris which, in turn, served as the foundation for the renewed development of reefs with their associated biotas. Locally, as exhibited in highest parts of the formation near Point San José, the pyroclastic debris accumulated in brackish and non-marine environments near the end of the Cretaceous vulcanism.

Rocks older than the Alisitos formation are not recognized on the peninsula of Baja California. Triassic marine deposits are known to the north, however, in the Santa Ana Mountains (Larsen, 1948: 18-22) and to the east in Sonora, Mexico (King, 1939: 1645-1659).

The duration of the mid-Cretaceous orogeny was short. It was followed, at least in northwestern Baja California and adjacent southern California, by rapid erosion and then by the submergence and deposition of normal clastic sediments before the end of the Cretaceous. A maximum submergence during late Campanian or earliest Maastrichtian time is represented by the Rosario formation (Beal, 1949: 40-44) in Baja California and in immediately adjacent San Diego County, California, by similar rocks to which the formational name "Chico" has been loosely applied (Bandy, 1951; Hertlein and Grant, 1954: 55-56; Popenoe, 1954: 20; F. M. Anderson, 1958: 64-67). *Baculites inornatus*, an uncoiled cephalopod, and *Neoflabellina numismalis*, a benthonic foraminifer, are characteristic fossils of the Rosario formation that lived only during the late Campanian and, perhaps, earliest Maastrichtian (Matsumoto, 1959b: 155-161; Hiltermann, 1952, Fig. 5). Mollusks of Turonian age in the Baker Canyon sandstone of the Ladd formation in the Santa Ana Mountains show that the submergence began earlier in the northern part of the province. The Coniacian, Santonian, and Campanian stages are probably represented in the Santa Ana Mountains

TABLE 1—CRETACEOUS FORMATIONS

EUROPEAN STAGES	GULF TROUGH	COASTAL SOUTHERN CALIFORNIA	NORTHERN BAJA CALIFORNIA	SOUTHERN BAJA CALIFORNIA
MAASTRICHTIAN			ROSARIO (Anon., 1924; Beal, 1948)	
CAMPAIGNIAN	“CHICO” (auct.) WILLIAMS: PLEASANTS SANDSTONE and SCHULZ SANDSTONE members (Popenoë, 1942)			VALLE SALITRAL, <i>partim</i> (Mina, 1956, 1957)
SANTONIAN	LADD: HOLZ SILTSTONE member (Popenoë, 1942)			
CONIACIAN	LADD: BAKER CANYON SANDSTONE member (Popenoë, 1942)			
TURONIAN	TRABUCO (Packard, 1916)			
CENOMANIAN		SANTIAGO PEAK VOLCANICS (Larsen, 1948) and BLACK MOUNTAIN VOLCANICS (Hanna, 1926)	ALISITOS (Santillán and Barrera, 1930), SAN FERNANDO Anon., 1924; Beal, 1948; and SAN TELMO, <i>partim</i> (Woodford and Harriss, 1938)	VALLE SALITRAL, <i>partim</i> (Mina, 1956, 1957)
ALBIAN				
APTIAN				
BARREMIAN				
HAUTERIVIAN				
VALANGINIAN				
BERRIASIAN				

by the Holz shale member of the Ladd formation and by the Shultz Ranch sandstone and Pleasants sandstone members of the Williams formation (Popenoe, 1942; Woodford, *et al.*, 1954: 67–69).

The possibility of an ancestral late Cretaceous Gulf of California cannot be explored as no pre-Eocene rocks have yet been found within the Gulf Trough. Formation of a depression along the east side of the Peninsular Ranges by the end of the mid-Cretaceous orogeny is not, however, an unreasonable possibility. Late Cenozoic faulting certainly modified the Gulf Trough (Wilson and Rocha, 1955: 42–43; Beal, 1949: 90, 93–94) but may not have been the ultimate mechanism responsible for its formation. Great areas on the west side of the Peninsular ranges scarcely have been disturbed since the mid-Cretaceous orogeny. There sediments of the Rosario formation were deposited over and against an essentially modern topography which has been preserved throughout the Cenozoic period by a long interval of relative structural quiescence.

Relationships of late Cretaceous deposits to the mid-Cretaceous orogeny have not been determined in the west central (Vizcaíno Peninsula–Cedros Island) and southern (Sierra Victoria–Cape San Lucas) parts of Baja California.

At times, Mesozoic and Cenozoic histories of the Vizcaíno Peninsula and of the major part of the Baja California peninsula appear to have been reversed: one area was emergent while the other served as a depositional site for marine sediments. Consequently, the hiatus between the Alisitos and Rosario formations along the west coast of northern Baja California is represented, at least in part, by marine deposits in the Vizcaíno Peninsula–Cedros Island area where definitive ammonites, *Mariella* (Allison, 1957) and *Submortoniceras* (Mina, 1957: 162), demonstrate that parts of the thick but intricately faulted Mesozoic section must be assigned to the late Albian or early Cenomanian as well as to the Campanian. The ammonites on which these age deter-

minations are based occur in beds mapped as the Valle Salitral formation by Mina (1956: 17–18; 1957: 159–162). Other pre-Cenozoic rocks of that area were mapped as the San Hipolito and the Eugenia formations (Mina, 1956: 15–17; 1957: 154–159).

Late Cretaceous rocks are not exposed on the surface of the peninsula of Baja California south of the Vizcaíno Peninsula area but the reported occurrence of foraminifers in two exploratory oil wells, San Angel No. 1 and Pozo Iray No. 2, in central Baja California (Mina, 1957: 243–261) suggest that late Cretaceous seas covered most of the southern half of the peninsula. No late Cretaceous rocks have been recognized in southernmost Baja California, however, an indication that the Cape San Lucas area was probably emergent then, as it appears to have been until late in the Cenozoic.

Cenozoic

Three discrepant chronologies ("mamalian," "megafaunal," and "microfaunal") are commonly used as standards of reference in studies of the California Cenozoic (see Durham, 1954: Fig. 3). Thus the age of the same deposit may be discussed in divergent terms by different authors. Inasmuch as most of the fossil data now available from Baja California is of the "megafaunal" type (that is, it is derived from mollusks, corals, and echinoids), that standard (Weaver, *et al.*, 1944; Durham, 1954) is arbitrarily taken as a basis for the correlations presented in this paper. A lack of recognized marine Oligocene deposits results, in part, from the use of the "megafaunal" standard in Baja California. The "Oligocene" of VanderHoof (1942), of Beal (1949: 51–53), and of Durham (1950a: 34–36) is earliest Miocene on the basis of this standard.

Paleocene–Eocene. Shorelines along the west coast of northern Baja California changed little from those of the late Cretaceous during the Paleocene and Eocene epochs (Figs. 1 and 2). Their positions are virtually unknown on the east side of

the Peninsular Ranges where the isolated occurrence of Eocene rocks in the Orocopia Mountains, north of the Salton Sea (Cole, 1958; Crowell and Susuki, 1959) furnishes the only known representation of early Cenozoic sedimentation in the Gulf Trough.

Erosion of several large islands along the course of the generally submerged southern half of Baja California probably supplied most of the sediments found in the Paleocene and Eocene formations of that region. The largest of the islands were located in the areas now occupied by the Vizcaíno Peninsula and by the Cape San Lucas area.

Relatively undisturbed Paleocene rocks (Malarrimo and Santo Domingo formations of Mina, 1956: 18–19; 1957: 162–165, 184–188) and Eocene rocks (Tepetate formation of Heim, 1922: 534–535; Bateque formation of Mina, 1956: 19–20; 1957: 165–170) are exposed on the surface or are known from well records along the west side of the central and southern parts of the peninsula (Table 2). These generally represent shallow water offshore, shallow water near shore, or even non-marine coastal deposits. Northward in Baja California the Paleocene epoch is represented by thin, near-shore marine deposits, known as the Sepultura formation (Santillán and Barrera, 1930: 14–20), with a discontinuous but wide distribution along the present Pacific Coast. In southern California the Silverado formation of the Santa Ana Mountains (Woodring and Popenoe, 1945; Woodford, *et al.*, 1954: 69; Mallory, 1959: 27–28) is of Paleocene age. The La Jolla formation of the San Diego area (M. A. Hanna, 1926, 1927; Mallory, 1959: 95, Table 10) and the Santiago formation of the Santa Ana Mountains (Woodring and Popenoe, 1945; Woodford, *et al.*, 1954: 69; Mallory, 1959: 45), and possibly the upper part of the Sepultura formation of Baja California, represent the marine Eocene. The Poway conglomerate, overlying the La Jolla formation in the San Diego area (Mallory, 1959: 97; Durham, *et al.*, 1954, Fig. 2),

contains marine and nonmarine fossils which locally record the shifting of middle and late Eocene strandlines.

The interpretation of the paleogeographic relationships of the Eocene Maniobra formation (Crowell and Susuki, 1959) of the Orocopia Mountains is difficult because of the position of outcrops on the northeast side of the San Andreas fault. A possible history of the Gulf Trough, preferred by the present authors, based mainly on an interpretation of the geology and paleontology of western and southern Baja California, suggests that an ancestral peninsula and trough appeared during the mid-Cretaceous orogeny. Subsequent depression and occupation of that trough by a southward opening sea may have taken place intermittently or continuously; certainly continuously since early in the Pliocene. On the basis of this hypothesis, the sea in which the Maniobra formation was deposited would have been joined to the Pacific through a seaway in the Gulf Trough.

Hypothetical right-lateral movement along the San Andreas fault zone of great enough magnitude to move rocks of the Orocopia Mountains away from rocks believed once to have been located immediately adjacent but which are now located 240 kilometers to the northwest (P. King, 1959: 169–173), would present the alternative or additional possibility of an Eocene seaway extending eastward from the Pacific into the area now occupied by the Maniobra formation.

The only other reported occurrence of marine Eocene rocks in the Gulf Trough is about 16 kilometers to the west of the outcrops of the Maniobra formation where fossiliferous cobbles are reported in a basal conglomerate of the Pliocene Imperial formation (Dibblee, 1954: 24; Crowell and Susuki, 1959: 582).

Oligocene. The Oligocene epoch, interpreted here in the "megafaunal" sense (Weaver, *et al.*, 1944; Durham, 1954), insofar as is now known was a time of emergence for the Peninsular Range province (Fig. 3). No marine deposits of this

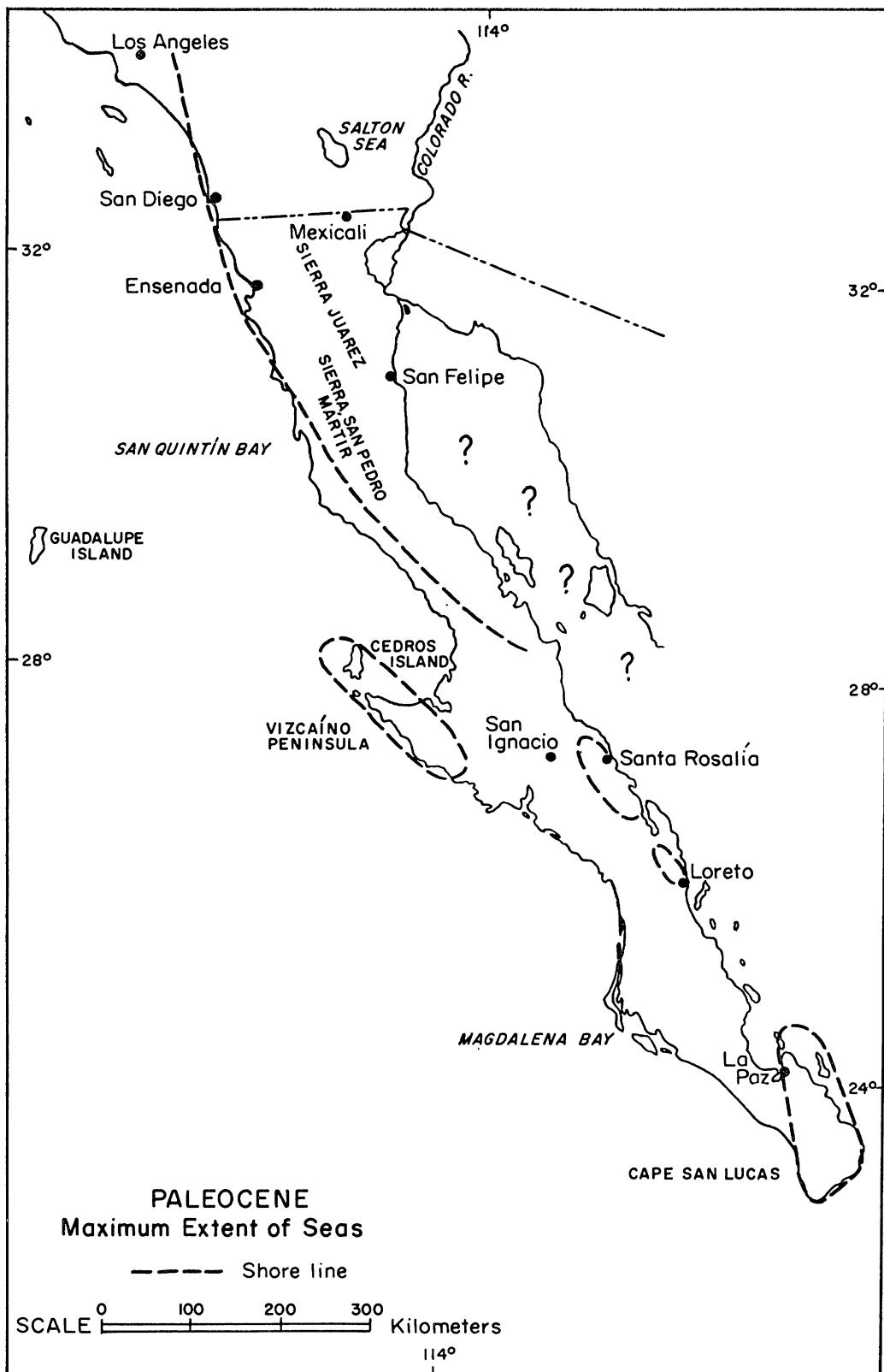


FIG. 1. Paleocene paleogeography.

TABLE 2—EARLY CENOZOIC FORMATIONS

SERIES	GULF TROUGH	COASTAL SOUTHERN CALIFORNIA	NORTHERN BAJA CALIFORNIA	SOUTHERN BAJA CALIFORNIA
OLIGOCENE				
		POWAY CONGLOMERATE (Ellis, 1919; Hanna, 1926)		
		SANTIAGO (Woodring and Popenoe, 1945)		
EOCENE	MANTOBRA (Crowell and Suki, 1959)	LA Jolla: ROSE CANYON SHALE, TORREY SAND, and DEL MAR SAND members (Hanna, 1926)	?SEPULTURA <i>partim</i> (Santillán and Barrera, 1930)	TEPETATE (Heim, 1922) and BATEQUE (Mina, 1956, 1957)
PALEOCENE		SILVERADO (Woodring and Popenoe, 1945)	SEPULTURA (Santillán and Barrera, 1930)	MALARROMO and Santo Domingo (Mina, 1956, 1957)

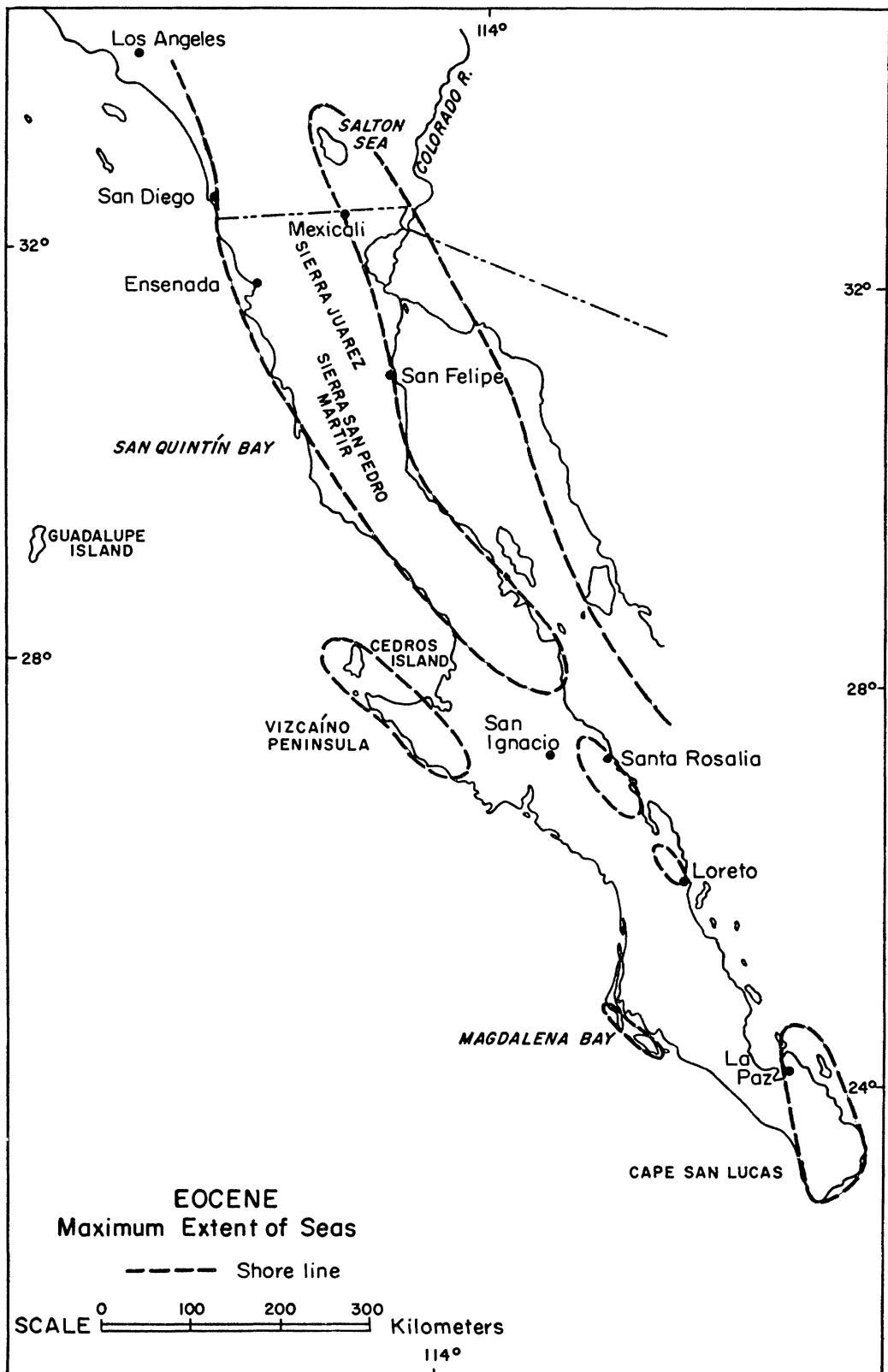


FIG. 2. Eocene paleogeography.

age have been recognized south of the Transverse Ranges of southern California. The sea apparently withdrew beyond present shore lines at the end of the Eocene epoch and did not return until the beginning of the Miocene epoch.

The non-marine Sespe formation of the Santa Ana Mountains and vicinity represents, in part, the Oligocene epoch (Jahns, 1954: 39). It rests on late Eocene rocks and is overlain by and grades laterally into early Miocene marine deposits of the Vaqueros formation. Late Eocene, Oligocene, and early Miocene terrestrial mammals are known from the Sespe formation (Durham, *et al.*, 1954, Fig. 2) in southern California north of the Peninsular Range province. So far as is known, however, equivalent non-marine sedimentary rocks do not occur in Baja California.

Miocene. Miocene seas spread widely, though not simultaneously, over the peripheral parts of southern California and Baja California. Elevated areas such as the Vizcaíno Peninsula and the Sierra de Victoria, at the southern cape, existed through at least part of the epoch as large islands. Those islands probably coincided in position, though not in extent, with similar islands of Eocene, Paleocene, and late Cretaceous times. Miocene sediments were derived from these and other islands along the submerged southern part of Baja California, and from volcanic centers located along the west side of the Gulf Trough.

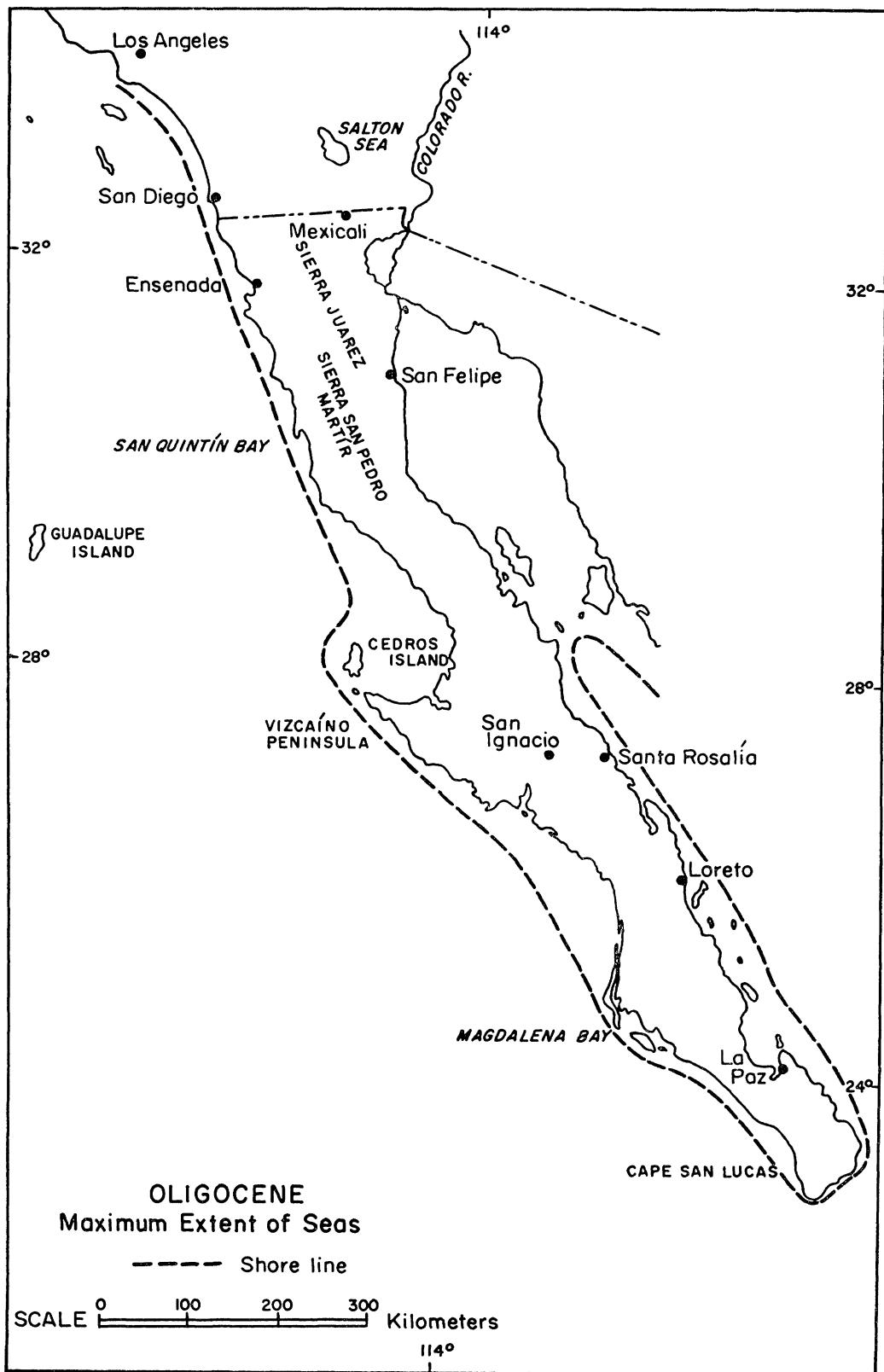
The earliest post-Eocene marine deposits known in the Peninsular Range province are those bearing the marine mammal *Cornwallius* (VanderHoof, 1942; Durham, 1950a: 34–36) otherwise known in the eastern Pacific only from the Sooke formation of Vancouver Island, and those with a *Turritella* of the *T. hamiltonensis*–*T. diversilineata* group. Both fossils suggest an age corresponding to that of the *Echinophoria apta* zone of the Weaver *et al.* (1944) correlation chart or lowest Miocene in terms of the “megafaunal” chronology. *Cornwallius* occurs in beds, referred by Durham to the San Gregorio

formation, which crop out along the west side of the Gulf of California about 125 kilometers north of La Paz. The *Turritella* occurs in arenaceous beds overlying argillaceous and diatomaceous rocks of the type San Gregorio formation near the village of La Purísima, southwest of Concepción Bay (Table 3). These *Turritella*-bearing rocks represent at least part of the Isidro formation (Heim, 1922: 539–541; Beal, 1949: 56–74) and probably the Purísima Nueva formation (Heim, 1921, 1922: 536–538) and San Raymundo formation (Mina, 1956: 24; 1957: 196–200). Parts of the “Monterey formation” (Dartton, 1921: 731–732; Heim, 1922: 538–539; Mina, 1956: 22–23; 1957: 192–196) and the Zacarias, Santa Clara, La Zorra, and San Joaquin formations (Mina, 1956: 21–23; 1957: 170–173) are equivalent to the Isidro and San Gregorio formations.

The earliest post-Eocene marine deposits of the northernmost part of the Peninsular Range province are the Vaqueros and Topanga formations of the Los Angeles basin and adjacent areas (Woodford, *et al.*, 1954: 69–71), considered to be slightly younger than any of the Baja California Miocene rocks discussed above. They are generally identified with early and middle parts of the Miocene epoch.

Middle Miocene deposits are not known to crop out in northern Baja California and immediately adjacent southern California but they have been identified in submarine exposures a short distance off shore at San Diego (Emery, *et al.*, 1952: 522–523) and at Ensenada (Walton, 1955: 999). Thus Miocene shore lines were not far removed from present shore lines in this area.

Marine deposits contemporary with the Vaqueros and Temblor formations of southern California appear to be distributed widely over the southern part of Baja California. The San Ignacio formation of Mina (1956: 23; 1957: 174–175, 200–202) and parts of the Isidro and “Monterey” formations of earlier authors (Dartton, 1921; Heim, 1922; Hertlein and



Jordan, 1927; Beal, 1949; Durham, 1950a) represent this Miocene interval.

Deposition of Miocene marine sediments began later and may have persisted later in the Vizcaíno Peninsula area than in the rest of Baja California. There the diatomaceous and tuffaceous rocks of the Tortugas formation (Mina, 1956: 23-24; 1957: 175-177), with the middle Miocene foraminifer *Valvulinaria miocenica* and the gastropod *Turritella ocoyana*, are separated by unconformities from the Pliocene Almejas formation above and from Cretaceous rocks below. The Vizcaíno Peninsula area persisted as an emergent feature into the early Miocene as it had during the earlier Cenozoic. It was again subject to erosion at the end of the Miocene and the beginning of the Pliocene.

Late Miocene marine faunas of the extreme northwestern part of the Peninsular Range province indicate deposition in a progressively deepening basin. Deposition was initiated with the middle Miocene nearshore sediments of the Topanga formation (Loel and Corey, 1932: 51-61) and culminated with early Pliocene deep water sediments of the Repetto and upper Capistrano formations (Natland and Rothwell, 1954; White, 1956). The intervening late Miocene rocks are referred to the Puente formation in the eastern Los Angeles Basin and to the Monterey formation and lower Capistrano formation along the coast to the south. Siltstones and sandstones are dominant in the Puente formation (Schoellhamer, *et al.*, 1953) while diatomaceous shale and siltstone characterize the Monterey and Capistrano formations (Woodford, *et al.*, 1954: 71-72; White, 1956: 239-243).

A widespread sequence of non-marine volcanic and clastic rocks overlies, at times with slight angular unconformity, early and middle Miocene rocks in the central and southern parts of Baja California. These rocks form the Comondú formation (Heim, 1922: 542-543; Beal, 1949: 74-77, 113-114; Wilson and Rocha, 1955: 54; Mina, 1956: 24-26; Mina, 1957: 177-178, 203-206). The formation is char-

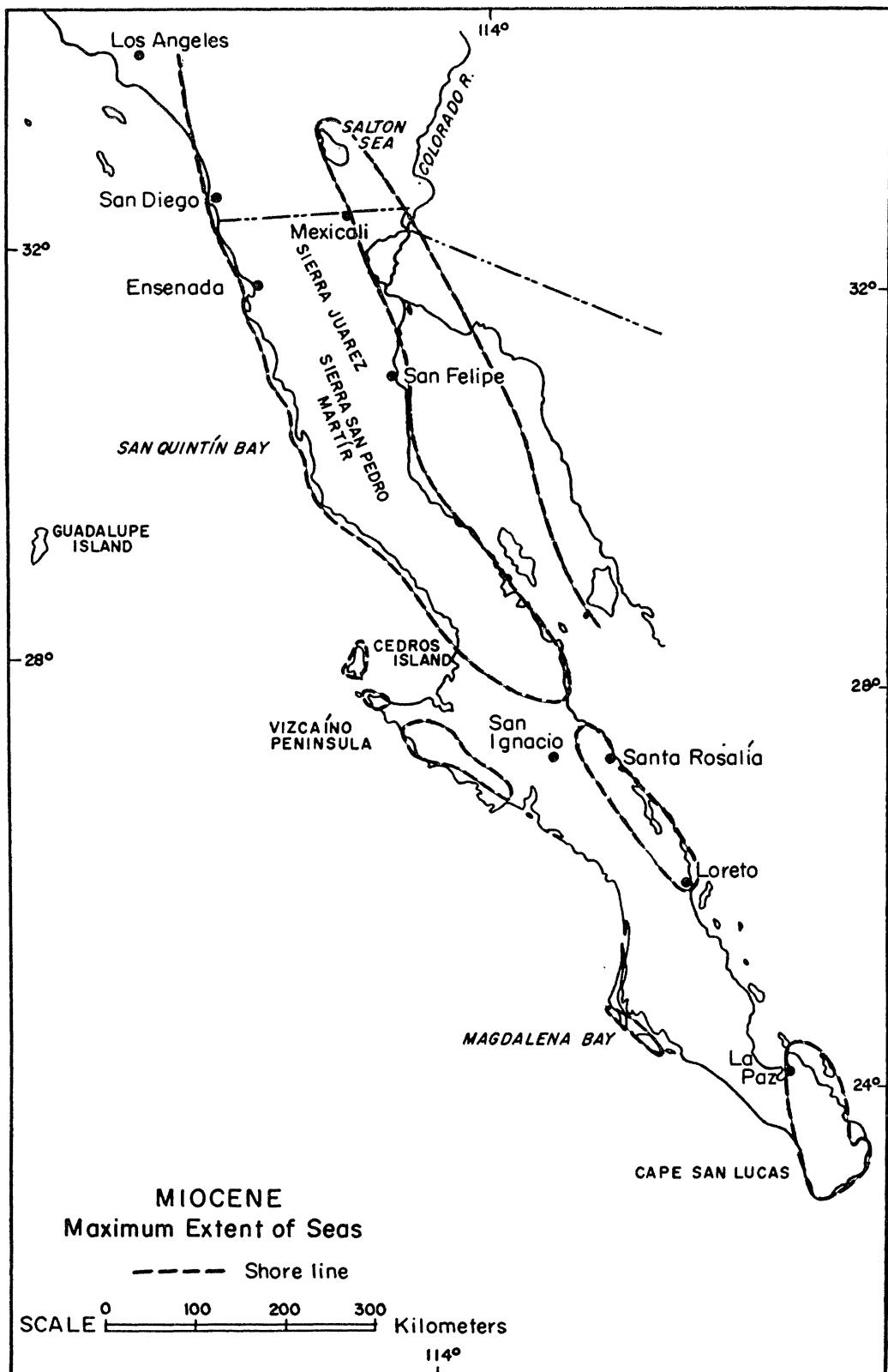
acterized by thick accumulations of volcanic flows and pyroclastics which grade westward into finer clastic and pyroclastic rocks. The volcanic centers that were the source of the Comondú volcanics were probably located close to the western margin of the present site of the Gulf of California (Beal, 1949: 74-77; C. A. Anderson, 1950: 47-48; Wilson and Rocha, 1955: 21).

Fossil evidence is not yet available to indicate the ages of the earliest and latest parts of the Comondú formation. Its widespread occurrence above rocks containing middle Miocene fossils and its sharp separation from Pliocene rocks along the western edge of the Gulf Trough have led most investigators to refer it to the late Miocene (e.g., Durham, 1950a: 33; Wilson and Rocha, 1955: 21-22; Beal, 1949: 53-54). The possibility cannot be excluded, however, that some of the volcanics and non-marine sediments assigned to the Comondú formation were deposited at either earlier or later times.

The Alverson Canyon formation (Tarbet and Holman, 1944; Durham, 1950a: 24; Tarbet, 1951) (or the Alverson andesite of Dibblee, 1954: 22) of the Imperial Valley area at the head of the Gulf Trough, like the Comondú formation farther south, is immediately overlain by richly fossiliferous marine Pliocene sediments. A correlation of the two volcanic formations has been suggested by Durham (1950a, Table 10) and on this basis the Split Mountain formation, which underlies the Alverson Canyon formation, would be Miocene in age. A precise determination of the age of the Alverson Canyon formation and confirmation of the existence of a possible Miocene penetration of the Gulf of California into that northern area awaits further information on fossils occurring in a 150 meter thick section of marine deposits within the generally non-marine Split Mountain formation (Tarbet, 1951). The Gulf of California outlined in Figure 4 reflects that possibility of a temporal correlation of the Alverson Canyon formation with the Comondú formation.

TABLE 3—LATE CENOZOIC FORMATIONS

SERIES	GULF TROUGH	COASTAL SOUTHERN CALIFORNIA	NORTHERN BAJA CALIFORNIA	SOUTHERN BAJA CALIFORNIA
TRES VÍRGENES VOLCANICS (Wilson, 1948, 1955)				
PLEISTOCENE	SANTA ROSALÍA (Wilson, 1948, 1955)	BAY POINT (Hertlein and Grant, 1939)	SWEITZER (Hertlein, 1929)	SALADA (Heim, 1922), ALMENAS (Mina, 1956, 1957), ?CUESTA (Heim, 1922), ?MESA SANDSTONE (Gabb, 1867)
MARQUER (Anderson, 1950; Durham, 1950a), INFIERNO (Wilson, 1948, 1955), BORGEO (Tarbet and Holman, 1944)	CARMEN (Anderson, 1950; Durham, 1950a), GLORIA (Wilson, 1948, 1955), PALM SPRING (Woodring, 1931)	PICO (Clark, 1921; Kew, 1923)	SAN MATEO (Woodford, 1925)	COMONDÚ (Heim, 1922)
PILOCENE	IMPERIAL (Hanna, 1926)	SAN DIEGO (Dall, 1898; Ellis, 1919)	CANTIL COSTERO (Santillán and Barrera, 1930)	TORTUGAS (Mina, 1956, 1957)
MARCOS (Anderson, 1950; Durham, 1950a), BOLEO (Wilson, 1948, 1955)	REPETTO (Reed, 1932)	REED (Reed, 1932)	VIDA SHALE members (Schoellhamer, <i>et al.</i> , 1953)	SAN IGNACIO (Mina, 1956, 1957), "ISIDRO," <i>partim</i> (Beal, 1948), "MONTEREY" (<i>auct.</i>)
?ALVERSON CANYON (Tarbet and Holman, 1944)	PUNTE (Eldridge and Arnold, 1907)	SYCAMORE CANYON, YORBA SHALE, SOQUEL SANDSTONE, and LA VIDA SHALE members (Schoellhamer, <i>et al.</i> , 1953)	SAN JOAQUIN, LA ZORRA, SANTA CLARA, and ZACARIAS (Mina, 1956, 1957)	SAN JOAQUIN, LA ZORRA, SANTA CLARA, and ZACARIAS (Mina, 1956, 1957)
?SPLIT MOUNTAIN (Tarbet and Holman, 1944)	?TOPANGA (Kew, 1923)	"MONTEREY" (<i>auct.</i>)	PURÍSIMA NUÉVA (Heim, 1921, 1922), "MONTEREY" (<i>auct.</i>)	PURÍSIMA NUÉVA (Heim, 1921, 1922), "MONTEREY" (<i>auct.</i>)
MIocene	SAN ONOFRE BRECCIA (Ellis, 1919; Woodford, 1925)	VÁQUEROS (Hamlin, 1904; Loel and Corey, 1932)	SAN GREGORIO (<i>anon.</i> , 1924, Beal, 1948), ISIDRO (HEIM, 1922), ?SAN RAYMUNDO (Mina, 1956, 1957)	SAN GREGORIO (<i>anon.</i> , 1924, Beal, 1948), ISIDRO (HEIM, 1922), ?SAN RAYMUNDO (Mina, 1956, 1957)
"SAN GREGORIO" (<i>auct.</i>)				



Pliocene. Pliocene seas transgressed farther over the margins of the Peninsular Range province than did those of the preceding epoch except in the central Baja California areas elevated at the end of the Miocene. In the Gulf Trough a shallow tropical sea spread northward briefly during the Pliocene epoch but was quickly displaced southward by rapid sedimentation at the mouth of the Colorado River, which now occupied a course apparently different from that of the earlier Cenozoic.

The depression of the floor of the Los Angeles Basin, initiated during the middle Miocene with intense vulcanism, culminated early in the Pliocene epoch with deposition of deep water sediments of the Repetto (Woodford, *et al.*, 1954: 73) and upper Capistrano (White, 1956: 239-243) formations. Stenobathic Foraminifera indicate that water depths of at least 1000 and perhaps 2000 meters were attained (White, 1956: 243-245; Natland and Rothwell, 1954: 40-41) during the early Pliocene. Later Pliocene sediments, referred to the Pico formation (Woodford, *et al.*, 1954: 73), were deposited in a shallowing basin in which the rate of sedimentation exceeded that of orogenic depression.

Southward along the Pacific coasts of southern California and Baja California the Pliocene is represented only by near shore deposits. Contemporary faunas within the Gulf Trough are represented by equally shallow water but tropical assemblages.

A few thin beds of pyroclastic sediments in the Los Angeles and San Diego basins indicate the occurrence of intermittent minor vulcanism through the late Miocene and the Pliocene (Eaton, 1958: 57; Wissler, 1943: 216-217; Hertlein and Grant, 1944: 59-60). In northwestern Baja California late Cenozoic vulcanism of greater intensity is manifested in thick beds of tuffaceous sediments and volcanic flows (Hertlein and Allison, 1959: 18-19).

Pliocene near shore deposits are represented in southern California by the San Mateo formation (Woodford, 1925: 217),

which crops out at San Onofre, and by the San Diego formation (Hertlein and Grant, 1944b: 46-63) which covers a wide area about San Diego. The Cantil Costero formation of northwestern Baja California (Hertlein and Allison, 1959) is approximately equivalent to the San Diego formation to the north. Further south, along the edge of Sebastián Vizcaíno Bay, on Cedros Island, and on the south side of the Vizcaíno peninsula, rocks of the Almejas formation (Mina, 1956: 26; 1957: 178-179) carry faunas which also can be compared with those of the San Diego formation (Beal, 1949: 79-81). Poorly known faunas of the Salada formation (Heim, 1922: 544-546; Mina, 1957: 208-209) in its southwestern Baja California type area exhibit closer affinities with contemporary faunas of the Gulf of California than with those of the Almejas formation. The Cuesta formation (Heim, 1922: 543-544) may be in part a continental equivalent of the Salada formation.

Marine fossils within the Gulf Trough indicate that a Pliocene gulf extended as far north as San Gorgonio Pass (Allen, 1957: 327-328), scarcely 80 kilometers east of the Pliocene Pacific coast. Terrestrial access to the peninsula of Baja California was probably more restricted during the Pliocene than at any other time during the Cenozoic period, except possibly during the Eocene.

Foraminifers recovered from drill cores taken in Cadiz and Danby dry lakes, eastern San Bernardino County (Bassett, Kupper, and Barstow, 1959: 106-109) indicate an even greater northward extent of the Gulf of California. That inundation may have taken place during the Pliocene epoch. The occurrence of the planktonic foraminifer *Globigerina* in sediments from Danby drill hole no. 1 (Todd. *in litt.*) is interpreted as evidence of an accessibility of that inland area to oceanic currents. Planktonic foraminifers do not occur in the living fauna of the land-locked Salton Sea (Arnold, 1958) with which the habitat of Cadiz and Danby fossil foraminifers might otherwise be compared.

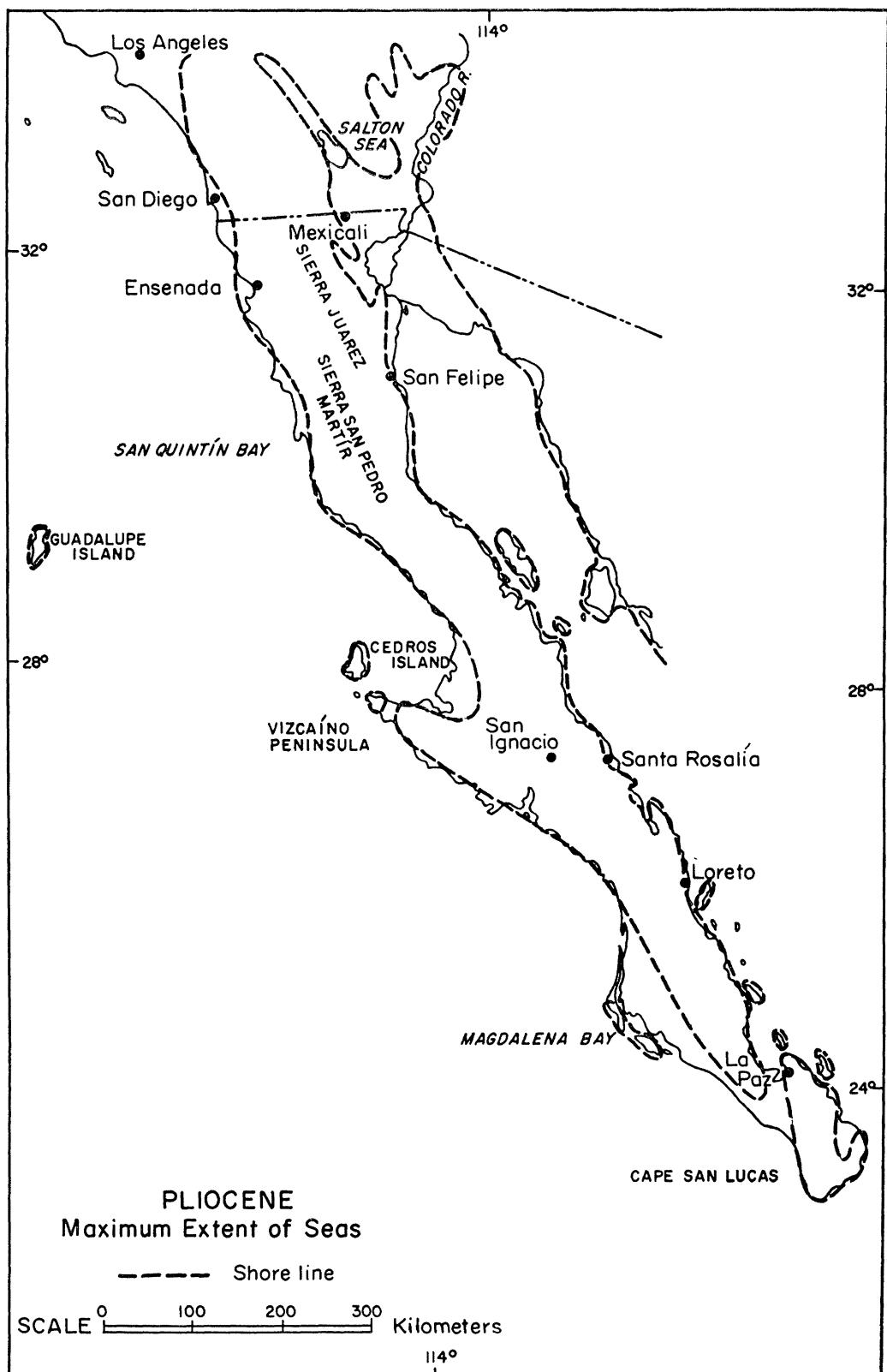


FIG. 5. Pliocene paleogeography.

Richly fossiliferous Pliocene marine deposits at the head of the Gulf Trough are known as the Imperial formation (G. D. Hanna, 1926; Woodring, 1931; Durham, 1950a: 30-34). It is separated from the underlying crystalline basement on the west side of the Imperial Valley by the two dominantly non-marine formations noted previously: the primarily non-marine Split Mountain formation below and the volcanic Alverson Canyon formation above. The two formations may be in part laterally equivalent (Tarbet, 1951: 260). Locally, a thick deposit of gypsum occurs at the base of the Imperial formation, the Fish Creek gypsum of Dibblee (1954: 22).

Several brackish, lacustrine, and continental formations overlie the Imperial formation. In the Imperial Valley area they are known as the Palm Springs formation, the Canebrake conglomerate, the Borrego formation, the Ocotillo conglomerate, and the Brawley formation. A volcanic unit (Truckhaven rhyolite) occurs in the northwestern part of the valley. Dibblee (1954) has outlined some of the stratigraphic and lateral relationships of these late Cenozoic rocks. Beds with oysters and other marine fossils within the Palm Springs formation (Durham, 1950a: 24) represent terminal phases of the marine invasion responsible for the deposition of the rich marine faunas of the underlying Imperial formation. The brackish-water pelecypod, *Mulinia pallida*, and a microfauna, similar to that now living in the Salton Sea, found high in the Borrego formation (Durham, 1954: 23) may reflect a later and less extensive northward spread of the Gulf sea.

Faunas similar to those of the Imperial formation occur along the western edge of the Gulf Trough farther south. The Boleo formation is recognized as an Imperial formation equivalent in the vicinity of Santa Rosalía where a threefold division of Pliocene marine deposits consists, in ascending order, of the Boleo, the Gloria, and the Infierro formations (Wilson, 1948: 1768; Wilson and Rocha,

1955: 33-39). A similar three fold division of Pliocene rocks on islands of the Gulf of California consists of the San Marcos, the Carmen, and the Marquer formations (C. A. Anderson, 1950: 12, *et seq.*; Durham, 1950a: 16, *et seq.*). The San Marcos formation, the Boleo formation, and the Imperial formation are recognized as approximate temporal equivalents.

Evaporite deposits, consisting chiefly of gypsum, occur at the base of the Boleo formation (Wilson and Rocha, 1955: 22-28, 125-126) near Santa Rosalía, and at the base of the San Marcos formation on San Marcos Island (C. A. Anderson, 1950: 30-32) and on South San Lorenzo Island (C. A. Anderson, 1950: 37). The origin of the Boleo and San Marcos gypsum, as of the Fish Creek gypsum, may have been in desiccated marginal gulf areas with restricted circulation or in saline lakes.

A retreat of the sea from the head of the Gulf Trough followed deposition of the Imperial formation as sedimentation at the mouth of the Colorado River exceeded the rate of subsidence of the trough. In the Imperial Valley Dibblee (1954: 25) reports that 3700 meters of non-marine sediments were penetrated by an exploratory well which did not reach identifiable marine deposits. Tarbet (1951: 263) reports that nearly 4300 meters of sediments may have been present in west central Imperial Valley at the end of the Pliocene. This great thickness gives some measure of the rate at which sediments were poured into the area and of the rate of subsidence of the northern end of the Gulf Trough.

Pleistocene. By the beginning of the Pleistocene the peninsula of Baja California had attained essentially its present outline. The Vizcaíno Peninsula and the Cape San Lucas area finally had become attached to the peninsula before the end of the Pliocene. During the Pleistocene, shore lines advanced and retreated over the margins of the Peninsular Range province in accordance with the eustatic sea level changes associated with the advances and retreats of the continental ice

sheets at higher latitudes. At the same time, there was recurrent faulting which elevated land along the western shore of the Gulf of California, but elsewhere within the province orogenic movements seem to have been minor except in restricted areas.

At higher latitudes the Pleistocene epoch was characterized by intensification of the climatic changes which accompanied expansions and retreats of the great ice sheets. The edges of these ice sheets did not reach the Peninsular Range province but evidence of valley glaciation has been recognized in the adjacent San Bernardino Mountains (Sharp, Allen, and Meier, 1959). Similar elevations, between 2700 and 3400 meters, are present southward in Baja California but the formation of glaciers does not seem to have been favored there.

The climate changes of the Pleistocene epoch are clearly manifested in the Peninsular Range province, however, by coastal terraces representing the changing eustatic sea levels. Changes in the distribution of stenothermal elements of near shore faunas reflect the changing oceanic temperatures that accompanied the oscillations of the continental ice sheets (Kanakoff and Emerson, 1959; Valentine, 1955). Pleistocene marine faunal changes brought about through organic evolution are scarcely detectable except in a few rapidly evolving lineages such as in the echinoid genus *Encope* (Durham, 1950a: 42-50).

Orogenic elevation and depression of the coast line locally has obscured the effects of Pleistocene eustatic sea level changes but long stretches of the Baja California Pacific coast appear to have remained static. Radiocarbon age determinations and fossil occurrences identify certain undisturbed terraces along such coastal areas, both above and below the present sea level, with Pleistocene sea level changes. Some such evidence is summarized by Addicott and Emerson (1959: 24-30). The presence of earlier formed terraces is indicated by associations of

flat-lying pre-Pleistocene fossiliferous deposits with terrace surfaces (Hertlein and Allison, 1959).

Anomalously high Pleistocene coastal terraces occur at various elevations along the orogenically unstable western side of the Gulf Trough (C. A. Anderson, 1950: 23, 46-47). Locally, as near Santa Rosalía (Wilson and Rocha, 1955: 55), marine terraces have been elevated to at least 340 meters. Other reported occurrences of marine fossils at high elevations, particularly those on the relatively stable Pacific slope, need to be re-investigated. Wandering aborigines often left trails of shell debris far from the seashore in the Peninsular Range province and these remains have no doubt formed the basis of some of the reported occurrences of Pleistocene marine deposits at high elevations.

During part of the Pleistocene, presumably during one of the late pluvial episodes, a large lake, Lake Cahuilla (or Coahuilla) occupied a considerably larger part of Imperial Valley than is occupied by the extant Salton Sea. The high terraces around the Salton Sea are visible evidences of this former lake.

The occurrence of submarine terraces off southern California is treated in a recent work by Emery (1958). Several submerged terraces cut into consolidated Pliocene rocks give evidence of Pleistocene depressed sea levels. These terraces are associated with fossil calcareous algae which yield radiocarbon ages of from 17,000 to 24,500 years. The algae could not have grown at depths as great as 130 meters, where they are now found, and their redeposition from a shallower water habitat is believed unlikely. If the lowest terrace was cut at or near sea level, the water depth would have been less than 60 meters, thus permitting the algae to grow.

Eastern Pacific Marine Invertebrate Faunas

Features which distinguish marine invertebrates of Baja California and nearby

eastern Pacific areas from those of contemporary faunas of adjacent Pacific and Atlantic areas evolved through the late Mesozoic and Cenozoic periods. The isolation of eastern Pacific faunas, to which that differentiation is attributed, resulted from changing climates of the Cenozoic and the development of land and ocean barriers.

Faunal Provinces

Two of the major faunal divisions of the eastern Pacific are represented along the shores of Baja California. They are: 1) the tropical West American, and 2) the north temperate West American. Each can be variously subdivided according to the nature of the data emphasized and to the techniques used to manipulate those data (Bartsch, 1921; Ekman, 1953: 45-46, 151-152; Schenck and Keen, 1936, 1937, 1940; Newell, 1948; Keen, 1958: 1-8). The more generalized two-fold division, however, provides a faunal boundary whose position can be readily traced through the late Mesozoic and Cenozoic.

The present distribution of nearshore marine temperatures along the coasts of Baja California, particularly along the Pacific Coast, exhibits anomalies which are clearly reflected in the distribution of marine invertebrates. Alternating areas of warm and cold water cause a discontinuous distribution of warm and cold water faunas along the coast rather than a gradual transition from one to the other. Thus locating the boundary between the tropical and temperate zones along the Pacific Coast of Baja California is necessarily an arbitrary operation. The boundary might be picked at a point as far north as Sebastián Vizcaíno Bay, the northernmost stronghold of the tropical eastern Pacific fauna, or as far south as Cape San Lucas where such mollusks as the great California abalones are last seen.

The irregular distribution of near shore water temperatures along the Pacific Coast of Baja California and adjacent areas is brought about by the combined effects of coast line configuration, sub-

marine physiography, oceanic currents, and coastal meteorology. The current system consists of an outer California current carrying subarctic water southward and an inner counter current carrying equatorial water northward. Shoreward the counter current is seasonally disrupted above depths of about 200 meters by upwelling of deeper and cooler waters which replace surface waters blown away from the shore by north-northwest prevailing winds (Sverdrup, Johnson, and Fleming, 1942: 724-725). Spring surface temperatures in San Cristobal Bay, on the Pacific Coast of southern Baja California and south of the distinctly tropical Vizcaíno Bay fauna, are as low as 13° C. (Emery, *et al.*, 1957: Fig. 11) as a result of intense upwelling of cold water. Near shore surface temperatures on the north side of promontories (as inside Vizcaíno Bay), protected from upwelling by local coastal configuration and remoteness from deep water, and off shore colder temperatures of equivalent latitudes (see U. S. Navy Hydrographic Office Pub. 570), are often many degrees warmer.

Surface waters of the Gulf of California, which are more homogeneously tropical, support a rich fauna of benthonic invertebrates which reflects its benign surroundings by an almost complete dominance of tropical species. However, water temperature and faunal distributions within the Gulf are known even less adequately than those of the outer coast, so the possibility of isolated cooler water areas cannot be evaluated. Dilution of the waters of the head of the Gulf by the Colorado River must also influence the faunal composition locally but, again, the results of the detailed collecting necessary to detect such modifications have not been published.

Climates

Wide distribution of the fossil remains of characteristically tropical organisms at high latitudes indicates that a greatly expanded tropical belt persisted through the late Mesozoic and early Cenozoic.

Evidence presented elsewhere (Durham, 1950b) shows that, in the eastern Pacific, the northern limit of tropical seas was located at some position north of the southern end of Vancouver Island during the Cretaceous and early Cenozoic. Accordingly, palms and reef corals lived in Washington during the Eocene. During the same interval Baja California must have been subject to climates even more tropical than those of today.

A constriction of the tropical belt during the late Cenozoic, culminating with the continental glaciations of the Pleistocene, was expressed by a southward retreat of the isotherms in the eastern North Pacific. This shift of climatic boundaries led to the present position of the northern boundary of the tropics within the latitudinal limits of Baja California.

Winter surface temperatures of seas bordering the northern extremity of the Peninsular Range province were depressed by perhaps 10° C (Durham, 1954, Fig. 4) from their early Cenozoic levels. The total temperature change at the southern extremity of the province, in the vicinity of Cape San Lucas, is presumed to have been less because of its position nearer the equator.

This interpretation of Cenozoic marine climates is in accord with interpretations of North American continental climates presented by Dorf (1959), MacGinitie (1958), and others for the same time interval.

Dispersal Routes and Barriers

Two land barriers and an oceanic barrier have influenced the composition of eastern Pacific faunas, particularly the near shore benthonic faunas. The late Mesozoic and the Cenozoic faunas of Baja California have been critically affected by the narrowing and final closing of seaways across Central America and Mexico. The late Pliocene or early Pleistocene opening of the Bering Strait, on the other hand, is reflected principally by changes in the distributions of species of more northern

faunas, species which were able to exploit the new accessibility of Arctic and northern Atlantic waters. Trans-Pacific shallow water dispersals around the northern margin of the Pacific are likewise recognized in cooler water faunas of the late Cenozoic. Effects of wide oceanic expanses of deep water in isolating near shore benthonic invertebrates of the tropical eastern Pacific are less easily defined, though they appear to have served as significant barriers through most of the Cenozoic.

Central America Seaways. The biogeographical significance of seaways joining the tropical eastern Pacific and Caribbean-western Atlantic waters has been recognized and discussed widely. The distribution of marine middle Cretaceous deposits from Texas to Baja California and southward to Colombia shows that this broad Central American region was generally submergent (Fig. 6) at that time. Islands probably interrupted western parts of that tropical seaway, but apparently presented no serious obstacles to the distribution of shallow marine organisms. The broad seaway across Central America, the contemporary Tethyan Sea across southern Europe and Asia, and mid-Pacific "stepping stones" linking eastern and western Pacific shallow water areas (Hamilton, 1956) combined with the widely expanded tropics to provide a tropicopolitan, nearly cosmopolitan, distribution of many middle Cretaceous marine invertebrates. The tropicopolitan character of much of the fauna of that time is exemplified by the gastropods from the Aptian-Albian Alisitos formation of Baja California (Table 4).

The mid-Cretaceous orogeny, which ended with folding of the Alisitos formation and intrusion of granitic rocks along the western margin of the continent, restricted the previously widely submergent areas across Central America. Narrowed late Cretaceous seaways were further restricted to Pacific-Caribbean connections through Costa Rica, Panama, and Colombia (Olsson, 1932: 51-58, Fig. 3; Nygren, 1950) during the Cenozoic era (Fig. 7).

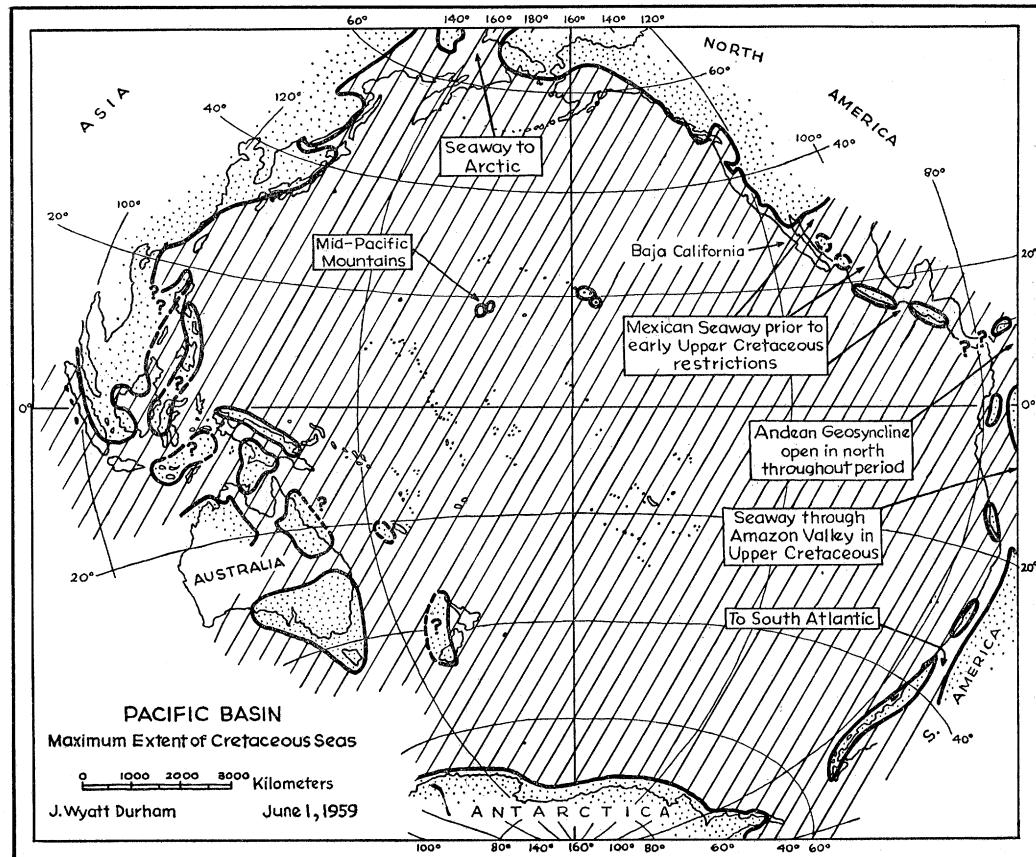


FIG. 6. Pacific basin, maximum extent of Cretaceous seas.

Those routes were finally closed during the late Miocene (Olsson, 1932: 39, 43¹).

The residual effect of these seaways is demonstrated by the composition of the fauna of the Pliocene Imperial formation and of the living molluscan fauna of the tropical eastern Pacific. R. A. Bramkamp, in an unpublished University of California doctoral thesis, reported 94 out of a total of 97 genera of fossil mollusks from the Imperial formation as also occurring in the Caribbean Miocene. Nearly 2500 living species are recognized by Keen (1958) in her recent study of living

shelled mollusks of the eastern Pacific from the Gulf of California to Colombia. She records 18 species as common to the

TABLE 4—WORLDWIDE RELATIONSHIPS OF 53 SPECIES OF CRETACEOUS (APTIAN-ALBIAN) GASTROPODA FROM PUNTA CHINA, LOWER CALIFORNIA (AFTER ALLISON, 1955).

	IDENTICAL SPECIES	MOST CLOSELY RELATED DESCRIBED SPECIES
India	2
Japan	4	2
Gulf of Mexico.....	9	12
Brazil	1	4
Europe	1	11
North Africa	3	3
Near East	4	3

¹ Olsson's assignment of the Pontian stage to the late Miocene rather than to the early Pliocene may modify the dating of that event in terms of the western United States "megafaunal" chronology.

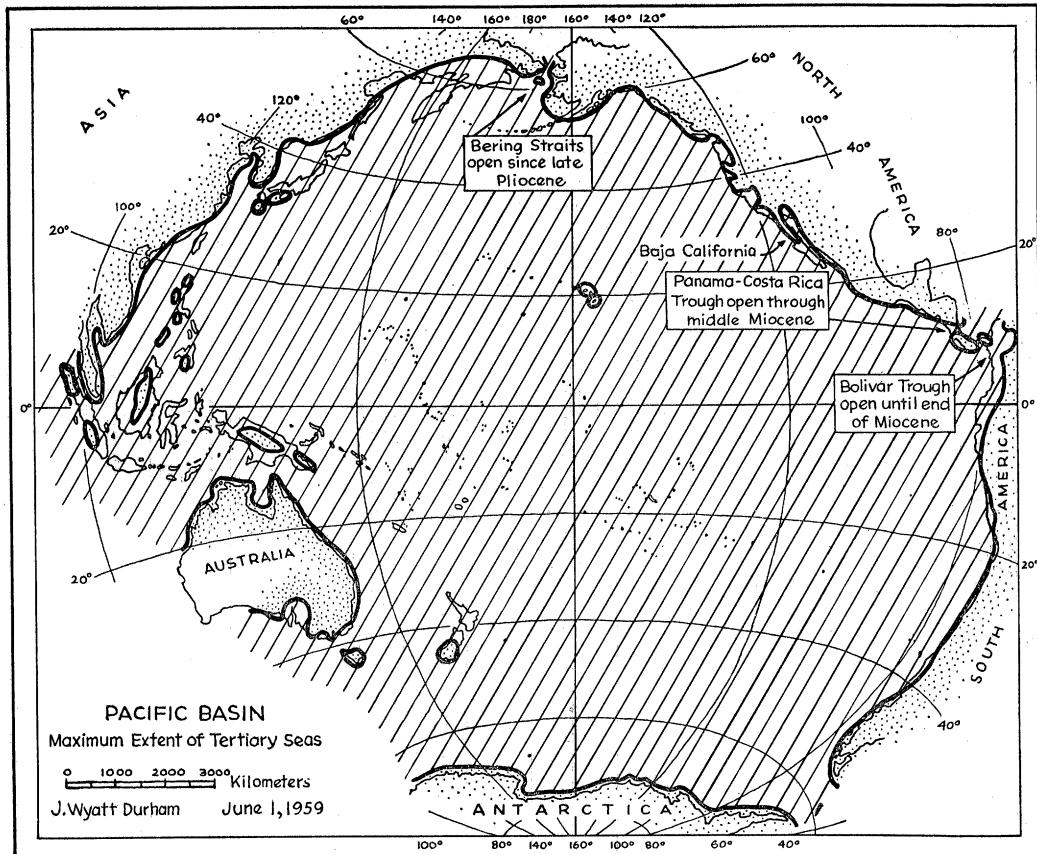


FIG. 7. Pacific basin, maximum extent of Tertiary seas.

Caribbean-western Atlantic and eastern Pacific, and 55 "analogous" species with the same distribution. Too little time has elapsed since those tropical faunas were joined across Central America for totally distinct faunas to have evolved on opposite sides of the post-Miocene land barrier.

Bering Strait. The Bering Strait, which serves as a dispersal route for North Pacific and North Atlantic marine invertebrates through the Arctic Ocean, was sealed by the Bering Land Bridge during most of the Cenozoic. In a recent synthesis of data pertinent to dispersals of land and sea animals across that area, Hopkins (1959) notes that the movement of terrestrial mammals between Asia and North America apparently was interrupted during the middle Eocene, but a

flooding of the Bering Land Bridge which might have limited mammalian dispersals is not recognized in the distribution of poorly known marine invertebrates of northern seas.

The late Cenozoic opening of this portal clearly resulted in the dispersal of marine faunal elements, previously endemic to the North Pacific, into the Arctic and North Atlantic. In addition to the mollusks noted by Hopkins (1959: 1520-1522), the echinoid genera *Echinarachnius* and *Strongylocentrotus* furnish notable examples of that migration. Both are known as early Pliocene fossils in the North Pacific and *Strongylocentrotus* is recognized in the Miocene as well, while *Echinarachnius* is derived from Miocene North Pacific ancestors. Yet the two

genera do not appear in the North Atlantic until the very late Pliocene and the Pleistocene. Similarly the following 12 species of pelecypods (Soot-Ryen, 1932; unpublished data) now living (or found as fossils) in the area from central California to Baja California, are among those which had origins in the pre-upper Pliocene of the Pacific Coast, and migrated into the Arctic Ocean and beyond with the opening of the Bering Straits: *Chlamys islandica* (Müller), *Mytilus edulis* Linnaeus, *Macoma calcarea* (Gmelin), *Modiolus modiolus* (Linnaeus), *Nucula tenuis* (Montagu), *Protothaca staminea* (Conrad), *Saxidomus giganteus* (Deshayes), *Siliqua patula* (Dixon), *Spisula polynyma voyi* (Gabb), *Thyasira gouldi* (Philippi), *Yoldia limatula* Say, *Zirfaea gabbi* Tryon.

East Pacific Barrier. The East Pacific Barrier (Ekman, 1953: 72-74), an expanse of deep ocean separating the shallow water areas of Hawaii and Polynesia from North America, is almost as effective in isolating the tropical faunas as is the Central American land barrier. Hertlein (1937) in discussing mollusks common to the eastern Pacific and Polynesia could list only 27 identical or analogous species out of the thousands known from the tropical Pacific. Five of these Pacific species occur only as far eastward as Clipperton Island, a small isolated atoll about 1000 kilometers southwest of the Mexican port of Acapulco. Clipperton Island has since been shown to support a thorough mixture of species from the two sides of the East Pacific Barrier (Hertlein and Emerson, 1953, 1957; Allison, 1959). That blending of Indo-Pacific and tropical American species occurs nowhere else. The distribution of other marine invertebrates is similarly affected by the barrier.

Clipperton Island, serving as a "stepping stone" for shallow water benthonic invertebrates, certainly modifies the effectiveness of the East Pacific Barrier but the possible effects of similar features on tropical Pacific faunas of earlier epochs are not apparent. Several former "step-

ping stones" of the Pacific that have been demonstrated are those of the mid-Pacific (Hamilton, 1956), and between Easter Island and South America (Fisher, 1958: 22-23), of mid-Cretaceous and late Cenozoic ages, respectively.

Composition

The evolution of the marine invertebrate fauna of Baja California is known most clearly through those groups that have significant fossil records: Foraminifera, Scleractinia, Echinoidea, Mollusca, Bryozoa, Brachiopoda, and Ostracoda. Unfortunately, few fossils have been described from Baja California and most of the relevant data comes from adjacent areas, especially from California.

Evaluation of the faunas is further hindered by the limited scope of published information on marine invertebrates. In recent years only two, the corals and echinoids, have been considered in comprehensive monographs (Mortensen, 1928-1948; Wells, 1956) with attention to worldwide details of both temporal and geographic distributions. Information on the Mollusca is often detailed and relatively thorough for small groups but no comprehensive synthesis is available to form the background for analyses such as those attempted for corals and echinoids (Tables 5, 6, 8 and 9). The distribution of eastern Pacific foraminifers is even less adequately documented and information on the ostracods, bryozoans, and brachiopods is extremely sparse and incomplete. Thus the discussion of these groups is limited largely to comments on individual taxa which the authors feel are representative and significant.

Foraminifera. Cretaceous and early Cenozoic foraminiferal faunas of the eastern Pacific reflect a history of expanded tropics and relatively unobstructed oceanic communications similar to that which is recognized in the distribution of other marine invertebrates. Large calcareous genera, such as *Orbitolina* of the northwestern Baja California middle Cretaceous

(Allison, 1955: 408) and *Pseudophragmina* of the southern California Eocene (Cole, 1958) were restricted to warm shallow water as were the reef corals with which they are often associated. Foraminiferal faunas from the middle Cretaceous (Allison, 1955: 408), late Cretaceous (Bandy, 1951), and early Cenozoic (Mallory, 1959) include many species known to occur in distant regions, demonstrating a much greater ease of faunal dispersal than is shown by the more provincial faunas of the later Cenozoic.

Several groups can be cited as representing the minor provincialism now recognized. The genus *Siphogenerinoides* underwent a rich and unique, though not exclusive, development in late Cretaceous seas bordering the American continents. Representatives of the genus are recognized first in late Albian or early Cenomanian rocks of Baja California and are richly developed in younger Cretaceous rocks of California, Colombia, and Peru (Stone, 1946b). *Stichocassidulina*, an equally distinctive genus, is known only from late Eocene deposits of the eastern Pacific (Stone, 1946a, 1949a, 1949b; Hofker, 1956: 932; Mallory, 1959: 226). *Ferayina*, an inhabitant of warm shallow seas of the middle and late Eocene, is known widely from America but not from Europe or Asia (Frizzell, 1949; Cizancourt and Frizzell, 1949; Hofker, 1956). The genus *Nummulites*, so characteristic of the early Cenozoic Tethyan sea, is meagerly represented in the New World by several species restricted almost entirely to the late Eocene (Cole, 1953; Beckmann, 1958).

The late Cenozoic faunas of Baja California and adjacent areas reflect an increasing provincialism. Distinctions, however, are generally at a specific level. Foraminiferal faunas of the Miocene (Kleinpell, 1938), Pliocene (White, 1956; Natland, 1950; Martin, 1952), Pleistocene (Cushman and Gray, 1946; Galloway and Wissler, 1927), and Recent (Bandy, 1953; Bandy and Arnal, 1957; Crouch, 1952; McGlasson, 1959; Natland, 1933; Walton,

1955; Zalesny, 1959) show prominent changes attributable to generally cooling climates. *Siphogenerina*, abundant in the northeastern Pacific during the early and middle Miocene, was confined to more nearly equatorial waters after the Middle Miocene except for an unrecorded occurrence of the genus in the relatively warm (Valentine, 1956) Pleistocene fauna of Potrero Canyon, southern California.

Scleractinia. Ninety genera of stony corals are now recognized in Cretaceous and younger faunas of the eastern Pacific (Vaughan and Wells, 1943; Wells, 1941, 1954, 1956; Durham, 1947; Durham and Barnard, 1952; Allison, 1955; unpublished data). Collections, particularly from the Cretaceous of Baja California and from the Eocene of southern Panama, are known to contain elements not considered here. Forty-seven of the 90 genera are classified as hermatypic (Table 5), that is, restricted to shallow tropical seas. The remaining ahermatypic genera (Table 6) are, or presumably were, generally eurytopic in their requirements.

The worldwide relationships of ahermatypic coral faunas of the eastern Pacific do not appear to have changed significantly throughout the late Cretaceous and the Cenozoic (Table 6). Their tolerance to deeper and cooler waters permitted dispersals across oceanic areas which served as barriers to the more stenopic hermatypic corals. As a result, eastern Pacific ahermatypic coral faunas are similar in aspect to those elsewhere in the world.

In contrast to the preceding, however, the affinities of the hermatypic corals (Table 5) of the eastern Pacific changed from time to time. Middle Cretaceous hermatypic coral faunas, best known from the Alisitos formation of Baja California (Allison, 1955: 408), shared many genera with western Pacific-Indian Ocean-eastern Tethys areas as well as with Atlantic-western Tethys areas. The strong trans-Pacific affinities disappeared during the late Cretaceous and remained unimportant through most of the Cenozoic. A

TABLE 5—EASTERN PACIFIC HERMATYPIC CORALS¹

XXXXX Western Pacific–Indian Ocean–eastern Tethys.
 OOOO Eastern Pacific.
 ++++ Atlantic–western Tethys.
 ? Questionable eastern Pacific occurrences.

	CRET. ²									
	E.	M.	L.	PALEOC.	EOC.	OLIG.	MIO.	PLIO.	PLEIST.	REC.
<i>Agaricia</i>					?			+++++	+++++	OOOO
<i>Antilloseris</i>						OOOO		+++++	+++++	
<i>Archohelia</i>				OOOOOOOOOOOOOOOOOOOOOOOOOOOO						
<i>Astreopora</i>				++++++	++++++	OOOO				XXXXXXXXXXXXXX
<i>Astrocoenia</i>				XXX	OOOO					
<i>Budaia</i>				OOOO						
<i>Cladocora</i>				+++++	+++++	+++++	+++++	+++++	+++++	OOOO
<i>Colpophyllia</i> ...						OOOO				
<i>Cyathophora</i> ...				OOOO						
<i>Cyclolites</i>				XXXX		?				
<i>Cyclomussa</i>						OOOO				
<i>Cycloseris</i>				++++++						XXXXXXXXXXXXXX
<i>Dermosmilia</i> ...				XXXX	OOOO					OOOO
<i>Dichocoenia</i>						OOOO				
<i>Diploria</i>						OOOO				

¹ Classification of genera lacking living representatives inferred from relationships, occurrences, and associations.

² Early Cretaceous = pre-Aptian
Middle Cretaceous = Aptian through Cenomanian
Late Cretaceous = post-Cenomanian

TABLE 5—Continued

	CRET. ²			E.	M.	L.	PALEOC.	EOC.	OLIG.	MIO.	PLIO.	PLEIST.	REC.
<i>Eusmilia</i>										○○○○○○○○○○○○○○			
										+++++ +++++			
<i>Favia</i>	XXXX								○○○○		XXXXXX	XXXXXX	
									+++++		+++++	+++++	
<i>Favites</i>		○○○○									XXXX	XXXX	
										+++++			
<i>Goniopora</i>									○○○○		XXXX	XXXX	
									+++++		+++++	+++++	
<i>Haimesiastrea</i> .		XXXX						○○○○○○○○					
									+++				
<i>Hydnophora</i> ...								○○○○			XXXXXX	XXXXXX	
								+++++			+++++	+++++	
<i>Isastrea</i>	XXXXXX				○○○○								
					+++++								
<i>Leptastrea</i>								○○○○			XXXXXX	XXXXXX	
								+++++			+++++	+++++	
<i>Leptophyllas- trea</i>								○○○○					
								+++					
<i>Leptoseris</i>								○○○○			XXXXXX	XXXXXX	
								+++++			+++++	+++++	
<i>Madracis</i>								XXXX			XXXX	XXXX	
								○○○○			○○○○	○○○○	
<i>Manicina</i>								○○○○			+++++	+++++	
								+++++			+++++	+++++	
<i>Montastrea</i>	XXXX				○○○○○○○○								
					+++++								
<i>Montipora</i>								XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	?
								○○○○					
<i>Montlivaltia</i>	XXXXXX				○○○○								
					+++++								
<i>Myriophyllia</i> ...					○○○○								
					+++++								
<i>Oulophyllia</i>								○○○○			XXXX	XXXX	
								+++++			+++++	+++++	
<i>Pachygyra</i>		○○○○											
		+++++											
<i>Pavona</i>										XXXXXX	XXXXXX	XXXXXX	
										○○○○○○○○	○○○○○○○○	○○○○○○○○	

TABLE 5—Concluded

³ Miocene or later occurrence on Nasca Ridge (Fisher, 1958, pp. 22-23).

TABLE 6—EASTERN PACIFIC AHERMATYPIC CORALS¹

XXXXX Western Pacific–Indian Ocean–eastern Tethys.
 OOOO Eastern Pacific.
 ++++ Atlantic–western Tethys.
 ? Questionable eastern Pacific occurrences.

	CRET. ²			PALEOC.	EOC.	OLIG.	MIO.	PLIO.	PLEIST.	REC.
	E.	M.	L.							
<i>Aplocyathus</i> ...										XXXXXXXXXXXXXX
							OOOO			
							+++	+++++		
<i>Astrangia</i>										XXXX
							OOOO	OOOO		
							+++	+++++		
<i>Balanophyllia</i> ..							XXXX	XXXX		
							OOOO	OOOO		
							+++	+++++		
<i>Bathycyathus</i> ..				++++						OOOO
										+++
<i>Caryophyllia</i> ...				XXXX			OOOO	OOOO		
							+++	+++++		
<i>Ceratotrochus</i> ..				++++			XXXX	XXXX		OOOO
										+++
<i>Coenocyathus</i> ..						?				OOOO
							++++	+++++		
<i>Cyathoceras</i>										XXXX
										OOOO
										+++
<i>Dasmia</i>							OOOO	+++		
<i>Deltocyathus</i> ...				OOOO			XXXX	XXXX		
								+++		
<i>Dendrophyllia</i> ..							XXXX	XXXX		
								+++		
<i>Dendrosmilia</i> ...										OOOO
<i>Desmophyllum</i> .				XXXX						OOOO
<i>Discotrochus</i> ...		?					XXXX	OOOO		
<i>Endopachys</i>							+++	+++++		XXXX
										OOOO

¹ Classification of genera lacking living representatives inferred from relationships, occurrences, and associations.

² Early Cretaceous = pre-Aptian
Middle Cretaceous = Aptian through Cenomanian
Late Cretaceous = post-Cenomanian

TABLE 6—Continued

	CRET. ²			PALEOC.	EOC.	OLIG.	MIO.	PLIO.	PLEIST.	REC.
	E.	M.	L.							
<i>Flabellum</i>				XXXXXX	XXXXXXXXXXXXXX	XXXXXXXXXXXXXX	XXXXXXXXXXXXXX	XXXXXXXXXXXXXX	XXXXXXXXXXXXXX	XXXXXXXXXXXXXX
<i>Fungiacyathus</i> .				OOOO	OOOO	OOOO	OOOO	OOOO	OOOO	OOOO
<i>Heterocyathus</i> ..						XXXXXX	XXXXXXXXXXXXXX	XXXXXXXXXXXXXX	XXXXXXXXXXXXXX	XXXXXXXXXXXXXX
<i>Kionotrochus</i> ...				+++++						XXXXXX
<i>Lobopsammia</i> ..					+++++					OOOO
<i>Lophelia</i>							XXXXXX			OOOO
<i>Lophosmilia</i> ...				XXXX		OOOO				OOOO
<i>Madrepora</i>				+++						+++
<i>Micrabacia</i>				OOOO		XXXXXX	XXXXXXXXXXXXXX	XXXXXXXXXXXXXX	XXXXXXXXXXXXXX	XXXXXXXXXXXXXX
<i>Nomlandia</i>				++++						OOOO
<i>Oculina</i>					XXXXXX	OOOO	OOOO	OOOO	OOOO	OOOO
<i>Oulangia</i>					+++++	+++++	+++++	+++++	+++++	XXXXXX
<i>Paracyathus</i> ...						OOOO	OOOO	OOOO	OOOO	OOOO
<i>Phyllangia</i>						+++++	+++++	+++++	+++++	+++++
<i>Placosmilia</i>				OOOO	+++++					OOOO
<i>Platycyathus</i> ...					XXXX	OOOO		?		++++
<i>Platytrochus</i> ...					+++++	+++++				
<i>Rhizopsammia</i> .						OOOO	XXXXXX	XXXXXX	XXXXXX	XXXXXX
<i>Sclerhelia</i>							?			XXXX

TABLE 6—Concluded

	CRET. ²			PALEOC.	EOC.	OLIG.	MIO.	PLIO.	PLEIST.	REC.
	E.	M.	L.							
<i>Smilotrochus</i> ...				○○○○	?		XXXX			
	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Sphenotrochus</i> .		?					XXXXXXXXXXXXXX		?	○○○○
				+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Stephanocyathus</i>						○○○○○○○○	XXXXX XXXXXXXXXX			
							+++++	+++++	+++++	+++++
<i>Stephanophyllia</i> .						○○○○		XXXXX XXXXXXXXX		
						+++++	+++++	+++++	+++++	+++++
<i>Thecopssammia</i> .									○○○○	+++
<i>Trochocyathus</i> .	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
				○○○○○○○○	○○○○					
<i>Trochosmilia</i> ...		○○○○			○○○○		XXXXX XXXXXXXXXX			
		+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Tubastrea</i>							?		XXXX	○○○○
									+++	+++
<i>Turbinolia</i>						○○○○				
						+++++	+++++	+++++	+++++	+++++
Totals (Questionable occurrences included):										
E. Pacific	3	3	5	15	12	6	7	9	28	
Common to contemporary W. Pacific-Indian Ocean-E. Te-thys	0	0	0	9	7	5	5	7	18	
Common to contemporary At-lantic-W. Te-thys	3	2	3	13	8	6	6	6	19	
Endemic	0	0	0	0	0	0	1	1	1	

revival of trans-Pacific affinities is suggested by the occurrence in the eastern Pacific Pleistocene and Recent faunas of genera such as *Leptoseris*, *Pavona*, and *Pocillopora*. These genera are unknown in post-Miocene rocks of the Caribbean and tropical Atlantic but persisted through the late Cenozoic in the Indo-Pacific. The biogeographic relationships of eastern Pacific hermatypic coral species (Squires,

1959) supports that conclusion. The eastward attenuation of hermatypic coral faunas on islands across the tropical Pacific, with little or no replacement of eliminated western Pacific genera (Wells, 1954, Pl. 186), illustrates the continued effectiveness of wide oceanic expanses in limiting the distribution of such corals, despite the possibility of limited breakdown of the East Pacific Barrier.

Mollusca. No comprehensive review of the shelled mollusks living in the eastern Pacific is available, but from Keen's (1937) checklist of the fauna from San Diego to Alaska, and from her recent (1958) book on mollusks of the region from the Bay of Panama to the Gulf of California, it would appear that the total shelled molluscan fauna of the eastern North Pacific numbers well over 4000 species. Over half of that total are known only from the tropical eastern Pacific, the Panamic province of Keen and others. The marine waters of Baja California, embracing parts of both the north temperate and the tropical eastern Pacific, probably support a fauna of well over 2000 "shallow water" mollusks. As noted previously, the fossil record in Baja California is poorly known, but even in comparatively well studied California, the total number (1737) of recorded fossil, Cenozoic mollusks (Keen and Bentson, 1944) provides only a small sample of the late Mesozoic and Cenozoic molluscan faunas (Table 7) that lived in this region. Data from Oregon and Washington faunas (Weaver, 1943) do not appreciably change that tabulation. Nevertheless, the fossil record does furnish significant information on the history of the fauna.

The molluscan fauna of the Baja California middle Cretaceous as exemplified by gastropods (Table 4), of the Alisitos formation (Aptian-Albian), was essentially tropicopolitan. Dispersal of shallow

water benthonic mollusks was effected with relative ease through the wide tropical belt and uninterrupted seaways of that time. Reefs of the Alisitos formation, built by the aberrant sessile pelecypods *Caprinuloidae* and *Monopleura* and hermatypic corals, indicate that northern Baja California was well within the tropics. The northern limit of the middle Cretaceous tropics in the eastern Pacific must have been located far to the north, as Cretaceous reef corals are known from the Queen Charlotte Islands at about 53° North Latitude (Durham, 1950: 1252) and characteristically tropical mollusks are known from Oregon and California (F. M. Anderson, 1958).

Kossmaticeratid ammonites of the subfamily Marshallitinae exhibit a distribution which may have been characteristic of cooler water mollusks of the middle Cretaceous. These ammonites were common in Alaska and Japan, and occurred sparsely as far south as California in the eastern Pacific and India and New Zealand in the western Pacific (Matsumoto, 1959a: 82).

Comparable late Cretaceous kossmaticeratids, of the subfamily Kossmaticeratiniae, occurred principally in the southern hemisphere. They were characteristic of post-Turonian faunas of Antarctica, New Zealand, southwestern South America, South Africa, Madagascar, and southern India (Matsumoto, 1955, 1959a: 82).

The late Cretaceous faunas of Baja Cali-

TABLE 7—DISTRIBUTION OF CALIFORNIA CENOZOIC SHALLOW WATER MARINE MOLLUSCA

	APPROXIMATE NO. OF SPECIES ¹	SPECIES IN OTHER PROVINCES ²	"ANALOGOUS SPECIES" IN OTHER PROVINCES ²
Paleocene	170		3
Eocene	630	1	20
Oligocene	260	0	0
Miocene	370	0	5
Pliocene	300	11	
Pleistocene	523	13	
Recent	±1000	29	

¹ After Keen and Bentson, 1944.

² From Clark and Vokes, 1936; Clark and Durham, 1942; Keen, 1940; Merriam, 1941; Vokes, 1939; unpublished data.

fornia and adjacent areas still reflected a widespread tropical climate with isolated occurrences of reef corals and pachydont pelecypods such as *Coralliochama*, but the mollusks began to show a more distinctly provincial character. Popenoe (1957: 444), in discussing the restricted distribution of the gastropod *Biplica*, summarizes the nature of California gastropod-pelecypod faunas as follows: "The California Cretaceous gastropod-pelecypod faunas apparently did not continually move to pastures new, but lingered in the familiar pastures of the Pacific Coast seas for more than half of a very long period. This conclusion is based upon the generic composition of the later Cretaceous mega-faunas. In the fossiliferous beds throughout this range a characteristic generic assemblage recurs again and again. Genera such as *Nanonavis*, *Cucullaea*, *Meekia*, *Opis*, *Calva*, *Acila*, *Gyrodes*, *Perissitys*, *Volutoderma*, and many others are found throughout the Cretaceous of California from Albian beds up, or for a considerable part of this range. Each of these long-ranging genera comprises a succession of species generally closely related to one another, and as in the case of *Biplica* making up a genetic lineage and defining a series of specific biozones."

A summary of worldwide Cenozoic paleogeography, including discussions of the relationships of eastern Pacific molluscan faunas, is presented by A. M. Davies (1934) in the second volume of his *Tertiary Faunas*. Subsequent studies have not altered the broad pattern of relationships outlined in that work.

The provincialism of faunas of the northeastern Pacific, evident among late Cretaceous larger invertebrates, continued as a predominant factor in determining the composition of early Cenozoic molluscan faunas. Only one known species, *Vellates perversus* (Vokes, 1935), was distributed in all tropical seas. Other species which occurred in seas bordering Californian and adjacent latitudes had close relatives living in areas outside the eastern Pacific. The genera *Turritella*

(Merriam, 1941: 37-51), *Venericardia* (Verástegui, 1953: 8-11), *Barbatia* (Reinhart, 1943: 27-33), *Clavelithes*, *Gisortia*, *Harpa*, *Potamides*, and *Typhis* (Clark and Vokes, 1936: 861-862) include such species. Most such "analogous" species occur in western Europe and the Gulf of Mexico-Caribbean area. Certain mollusks, such as the genus *Acila* (Schenck, 1936: 35-41), were characteristic of, though not confined to, the Pacific Ocean even before the interruption of seaways across Central America was effected.

The strong provincialism which now marks the eastern Pacific temperate and tropical molluscan faunas developed at an accelerated rate during the late Cenozoic, chiefly as a consequence of the closing of Caribbean-Pacific connections. Such provincialism was similarly characteristic of late Cenozoic faunas in many parts of the world.

Many species now living in the tropical eastern Pacific have evolved so slightly from their Miocene ancestors with trans-American distributions that they are inseparable from sibling Caribbean forms. Post-Miocene changes produced marked distinctions, however, within other molluscan taxa. The genera *Strombina*, *Terebra*, *Cancellaria*, and *Chione* have diversified and flourished in the eastern Pacific (Keen, 1958: 2) while becoming impoverished in the Caribbean, relative to their status during Miocene and earlier epochs. Conversely, *Echinochama* (Nicol, 1952) and *Pecten* (*Euvola*) (Fleming, 1957: 16, Fig. 1) have undergone a greater and more persistent development in the Caribbean and tropical western Atlantic than in the eastern Pacific.

Distribution of tropical mollusks across the Pacific appears not to have significantly modified the content of late Cenozoic faunas of the eastern Pacific. American occurrences of pectens closely related to the living Japanese *Pecten albicans* (Fleming, 1957: 16) suggest a westward dispersal: Miocene in the western Atlantic-Caribbean (*P. humphreysi*), Pliocene in Baja California (*P. aletes*), Pleis-

tocene and Recent in the western Pacific (*P. albicans*).

Other mollusks which characterize eastern Pacific faunas, particularly tropical eastern Pacific faunas, are of the families Calyptraeidae, Turritellidae, and Turridae. Their great abundance and diversity in eastern Pacific waters is unique. The dominance of such mollusks, together with the relative paucity of species belonging to such characteristically tropical genera as *Cypraea* and *Tridacna* may be, in part, a reflection of the absence of widespread coral reef environments along the tropical American coasts.

Seasonal upwelling of cool water along the Pacific Coasts of the Americas caused by the shoreward movement of cool water from depths to replace surface waters blown offshore by prevailing northwesterly winds, limits the extent of eastern Pacific tropical faunas even beyond that brought about by the general eastward narrowing of the Pacific Ocean tropical belt. The effect of the upwelling phenomena on Pleistocene faunas of California and Baja California has been discussed by Valentine (1955). Although temperature data are lacking for most of the Pacific Coast of Central America, temperature records at Balboa, within the Gulf of Panama (Wooster, 1959, Fig. 21), suggest that upwelling may modify near shore faunas even within the central tropics. Cool temperatures recorded along the Pacific Coast of southern Baja California (Emery, *et al.*, 1957, Fig. 11) reveal the reason for discontinuous distribution of tropical and temperate molluscan faunas between Cape San Lucas and Scammon Lagoon. Tropical species find adequately persistent warm temperatures only within bays and on the north sides of coastal promontories where prevailing onshore winds prevent upwelling.

Eastern Pacific north temperate faunas, well represented by latest Cenozoic and Recent mollusks of the Baja California Pacific Coast, exhibit both tropical and more northern relationships. Genera such as *Acmaea* and *Crepidula* remain as char-

acteristic elements of north temperate faunas. Other genera, equally characteristic of the north temperate eastern Pacific faunas, exhibit relationships with Japanese and temperate western Pacific faunas. *Acila*, *Patinopecten*, *Mya*, *Haliotus*, *Searlesia*, *Neptunea*, and *Buccinum* are among such characteristically northern Pacific genera. Some appear to have Cenozoic origins in the western Pacific and others in the eastern Pacific. *Acila*, *Mya*, *Searlesia*, and *Neptunea* were provided access to the northern Atlantic by way of the Arctic Ocean with the late Pliocene opening of the Bering Strait.

South temperate faunas of the eastern Pacific, which meet the tropical eastern Pacific faunas on the coasts of northern Peru and Ecuador, share many characteristics with north temperate faunas. An absence of *Haliotus* and the abundance of the thaid, *Concholepas*, provide one of the most prominent distinctions.

Echinoidea. At least 99 genera of Echinoidea have occurred in the eastern Pacific since the early Cretaceous according to records now available (Mortensen, 1928-1948; Grant and Hertlein, 1938; Durham, 1955; unpublished data). Sixty-one genera (Table 8) are characteristic of the continental shelf environments most frequently represented in the fossil record, or are inferred to have occupied such environments by virtue of their fossil associations. A majority of the other genera (Table 9) of the eastern Pacific are unknown as fossils.

Eastern Pacific echinoid faunas of the Cretaceous and later periods had affinities with faunas of both the Atlantic-western Tethys and the western Pacific-Indian Ocean-eastern Tethys, with genera of the former area slightly dominant. The occurrence in the middle Cretaceous faunas of Baja California of species either characteristic of, or closely allied to, species of the Gulf of Mexico embayment is noteworthy. Late Cenozoic echinoid faunas of the eastern Pacific, however, are characterized by a number of endemic genera, particularly within the order

TABLE 8—EASTERN PACIFIC ECHINODIDS, 1. GENERA OCCURRING ONLY AT DEPTHS LESS THAN 600 M.
AND BETWEEN LATITUDES 50° N AND 50° S¹

XXXX Western Pacific–Indian Ocean–eastern Tethys.
 OOOO Eastern Pacific.
 ++++ Atlantic–western Tethys.
 ? Questionable eastern Pacific occurrences.

¹ Classification of genera lacking living representatives inferred from relationships, occurrences, and associations. Fossil species referred to *Cidaris* excluded because of inadequate data.

² Early Cretaceous = pre-Aptian
 Middle Cretaceous = Aptian through Cenomanian
 Late Cretaceous = post-Cenomanian

TABLE 8—Continued

	CRET. ²			PALEOC.	EOC.	OLIG.	MIO.	PLIO.	PLEIST.	REC.
	E.	M.	L.							
<i>Echinocorys</i> ...	X	X	X	O	O	O				
	+	+	+	+	+	+				
<i>Echinogalerus</i> ..			O	O	O	O				
			+	+	+	+				
<i>Echinometra</i> ...							O	O	O	X
							O	O	O	+
<i>Echinoneus</i>							O	O	O	X
							O	O	O	+
<i>Encope</i>							O	O	O	X
							O	O	O	+
<i>Eoscutella</i>				O	O	O	O			
				O	O	O				
<i>Epiaster</i>	X	X	X	O	O	O				
	+	+	+	+	+	+				
<i>Eucidaris</i>						?	O	O	O	X
						?	O	O	O	+
<i>Eupatagus</i>				X	X	X	X	X	X	X
				O	O	O				
				+	+	+				
<i>Heliocidaris</i>								?		X
<i>Hesperocidaris</i> .				O	O	O				O
<i>Heteraster</i>		?		+	+	+				
<i>Kewia</i>						X	O	O	O	O
<i>Lenita</i>					?		+	+	+	
<i>Linthia</i>				O	O	O	O	O	O	O
				+	+	+	+	+	+	+
<i>Loxechinus</i>							O	O	O	O
<i>Lytechinus</i>							X	X	X	X
							O	O	O	O
							O	O	O	O
<i>Megapetalus</i> ...				O	O	O				
<i>Mellita</i>					?		O	O	O	O
					?		O	O	O	O
<i>Mellitella</i>					?		O	O	O	O
<i>Meoma</i>							O	O	O	O
<i>Merriamaster</i> ..							O	O	O	O
<i>Metalia</i>							X	X	X	X

TABLE 8—Continued

	CRET. ²			E.	M.	L.	PALEOC.	EOC.	OLIG.	MIO.	PLIO.	PLEIST.	REC.	
<i>Moira</i>														Xxxxx
	+++	+++	+++											Oooooo oooooo oooooo
<i>Nacospatangus</i> .														oooo
<i>Nucleopygus</i> ...							oooo							Xxxx
	+++	+++	+++											+++
<i>Paleoechinoneus</i> .							oooo							
<i>Periaster</i>							+++	+++	+++	oooo				Xxxxxx xxxxxx xxxxxx
<i>Phyllacanthus</i> ..							?							
<i>Phyllobrissus</i> ..							oooo							
	+++	+++	+++				+++							+++
<i>Plagiobrissus</i> s.l.														oooo
	+++	+++	+++											+++
<i>Polydiadema</i> ...									?					
	+++	+++	+++											+++
<i>Psammechinus</i> .									?					+++
	+++	+++	+++											+++
<i>Pygopyrina</i>							Xxxx							
	+++	+++	+++				oooo							
	+++	+++	+++				+++							+++
<i>Remondella</i>														oooo ooooo
	+++	+++	+++											
<i>Salenia</i>							oooo		oooo					Xxxx oooo
	+++	+++	+++				+++	+++	+++					+++
<i>Scutaster</i>														oooooo
	+++	+++	+++											
<i>Schizaster</i>							oooo oooooo oooooo oooooo oooooo		Xxxx					Xxxx
	+++	+++	+++				+++	+++	+++	+++				+++
<i>Scutellaster</i>														Xxxx oooo
	+++	+++	+++											
<i>Tenuirachnius</i> ..														oooo
	+++	+++	+++											
<i>Tetrapygus</i>														oooo
	+++	+++	+++											
<i>Toxopneustes</i> ..														Xxxx oooo
	+++	+++	+++											
<i>Tripneustes</i>														Xxxxxx xxxxxx xxxxxx
	+++	+++	+++											oooo oooooo oooooo oooooo
	+++	+++	+++											+++
<i>Trochalosoma</i> s.l.							oooo							
	+++	+++	+++				+++							
<i>Vaquerosella</i> ..														oooo
	+++	+++	+++											

TABLE 8—Concluded

	CRET. ²			PALEOC.	EOC.	OLIG.	MIO.	PLIO.	PLEIST.	REC.
	E.	M.	L.							
Totals (Questionable occurrences included):										
E. Pacific	4	10	2	12	8	16	22	16	29	
Common to contemporary W. Pacific–Indian Ocean–E. Tethys	1	3	0	4	2	5	4	4	14	
Common to contemporary Atlantic–W. Tethys	3	9	1	7	6	7	12	10	19	
Endemic	0	1	0	2	1	6	8	2	7	

Clypeastroidea, or sand dollars (Durham, 1955). Oligocene and Miocene sand dollars were either endemic to the northeastern Pacific (*Astrodapsis*, *Remondella*, *Scutaster*, and *Vaquerosella*), or extended to both sides of the northern Pacific (*Kewia* and *Echinarachnius*). This development of distinctive sand dollars was foreshadowed by the Eocene genus *Eoscutella*, known only from California and Oregon. A rich and unique development of perforated sand dollars of the family Mellitidae (*Encope*, *Mellitella*, and by inference *Mellita*) in tropical seas bordering both sides of Central America began in the Miocene and has continued to the present. After the closing of the Central American portals at the end of the Miocene the members of this family evolved independently in the Caribbean and eastern Pacific, with *Mellitella* becoming extinct in the Caribbean during the Pliocene. Sand dollars of more temperate requirements (*Dendraster*, *Echinarachnius*, *Merriamaster*, and *Scutellaster*) characterized the areas from Baja California northward during the Pliocene. All of the non-mellitid genera except *Dendraster* and *Echinarachnius* became extinct by the end of the Pliocene. With the opening of the Bering Strait portal in the late Pliocene *Echinarachnius* extended its range into the Arctic and the northwestern Atlantic.

Among the regular echinoids, the genus *Strongylocentrotus* first appeared in the Miocene of the Pacific Coast and is now a common inhabitant of the littoral and sublittoral zones along rocky coasts from Baja California to Japan. With the opening of the Bering Strait portal, it, like *Echinarachnius*, dispersed through the Arctic Ocean into the North Atlantic where *Strongylocentrotus* is recognized in rocks as old as the late Pliocene Coralline Crag of England. The genus *Salenia*, long unrecorded in the eastern Pacific, is now known from the middle Cretaceous of Baja California and the early Oligocene of Oregon and from living specimens in the southeastern Pacific (all from unpublished data).

Other Invertebrates. Marine invertebrates, other than the four groups just discussed, either are represented by relatively few species and records in fossil and Recent eastern Pacific faunas or are so incompletely known that they contribute little biogeographic information.

Living bryozoans of the eastern Pacific adjacent to southern California and Baja California and their Pleistocene predecessors are fairly well known (Osborn, 1950–1952; Soule, 1959; Soule and Duff, 1957). Older Cenozoic and Cretaceous bryozoans, however, have been neglected.

The available information on post-Jurassic brachiopods of western North

TABLE 9—EASTERN PACIFIC ECHINOIDS, 2. GENERA OCCURRING AT DEPTHS GREATER THAN 600 M.,
OR WITH WIDE BATHYMETRIC DISTRIBUTION, OR AT LATITUDES HIGHER THAN 50° N AND 50° S¹

XXXXX Western Pacific-Indian Ocean-easter Tethys.
 OOOO Eastern Pacific.
 ++++ Atlantic-western Tethys.
 ? Questionable eastern Pacific occurrences.

	CRET. ²			PALEOC.	EOC.	OLIG.	MIO.	PLIO.	PLEIST.	REC.
	E.	M.	L.							
<i>Acasta</i>										XXXX OOOO
<i>Aeropsis</i>										XXXX OOOO
<i>Allocentrotus</i> ..										OOOO
<i>Araeosoma</i>										XXXX OOOO OOOO OOOO +++
<i>Brisaster</i>										XXXX OOOO OOOO OOOO OOOO OOOO +++
<i>Brissopsis</i>										XXXXXXXXXXXX XXXXXXXX OOOO ++++++
<i>Caenopedina</i> ...										XXXX OOOO +++
<i>Ceratophysa</i> ...										OOOO +++
<i>Coelopleurus</i> ...										XXXX OOOO +++
<i>Cystocrepis</i>										OOOO
<i>Dermechinus</i> ...										OOOO +++
<i>Echinocyamus</i> .	++									XXXX OOOO +++
<i>Echinolampas</i> ..										XXXXXX ? ++++++
<i>Echinarachnius</i> .										XXXXXX OOOO OOOO OOOO +++
<i>Echinus</i>										OOOO +++
<i>Goniocidaris</i> s.l. .										XXXXXXXXXXXX XXXXXXXX
<i>Helgocystis</i>										OOOO +++

¹ Classification of genera lacking living representatives inferred from relationships, occurrences, and associations.

² Early Cretaceous = pre-Aptian
 Middle Cretaceous = Aptian through Cenomanian
 Late Cretaceous = post-Cenomanian

TABLE 9—Continued

	CRET. ²			PALEOC.	EOC.	OLIG.	MIO.	PLIO.	PLEIST.	REC.
	E.	M.	L.							
<i>Hemiaster</i>		X X X X								X X X X
		O O O O O O O O								+++
		+++								
<i>Histocidaris</i>									X X X X	
									O O O O	
									+++	
<i>Homolampus</i> ...									O O O O	
<i>Idiobryssus</i>									O O O O	
<i>Kamptosoma</i> ...									X X X X	
									O O O O	
<i>Lovenia</i>					X X X X				X X X X	
					O O O O O O O O O O O O					
					+++++ ++++++ ++++++					
<i>Paleopneustes</i> ..							O O O O		+++	
<i>Paraster</i>								X X X X X X X X		
								O O O O		
								+++++ ++++++		
<i>Phrissocystis</i> ...									O O O O	
<i>Pilematechinus</i> .									O O O O	
<i>Plesiodiadema</i> ..									O O O O	
									+++	
<i>Plexechinus</i>									O O O O	
									+++	
<i>Pourtalesia</i>								X X X X		
								O O O O		
								+++		
<i>Pseudomaretia</i> .								X X X X		
								O O O O		
<i>Salenocidaris</i> ...								X X X X		
								O O O O		
<i>Spatangus</i>								X X X X		
								O O O O O O O O O O O O O O O O		
								+++++ ++++++ ++++++ ++++++ ++++++		
<i>Strongylocentro-</i> <i>tus</i>								O O O O O O O O O O O O O O O O	X X X X	
									+++	
<i>Tripylaster</i>									O O O O	
									+++	
<i>Tromikosoma</i> ..									O O O O	
									+++	
<i>Urechinus</i>									O O O O	
									+++	
Totals (Questionable occurrences included):										
E. Pacific	0	0	0	1	4	4	9	6	32	

TABLE 9—Concluded

	CRET. ²			E.	M.	L.	PALEOC.	EOC.	OLIG.	MIO.	PLIO.	PLEIST.	REC.
Common to contemporary W. Pacific-Indian Ocean-E. Tethys	0	0	0	0	0	0	0	0	0	0	2	1	17
Common to contemporary Atlantic-W. Tethys	0	0	0	1	1	1	3	2	2	20			
Endemic	0	0	0	0	2	3	4	0	0	6			

America has been summarized in a comprehensive work of recent origin (Hertlein and Grant, 1944a). They are relatively scarce and of limited diversity as compared to other groups of fossil invertebrates with good fossil records.

Ostracods of the warm temperate eastern Pacific are known principally from Todos Santos Bay (Benson, 1959) and from similar Pliocene and Pleistocene environments of southern California (Le Roy, 1943). Tropical eastern Pacific ostracods are relatively unknown. A single Eocene assemblage from northern California has been described (Marianos and Valentine, 1958).

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