

Q
11
C18X
NH

SMITHSONIAN
JUL 29 1983
LIBRARIES

OCCASIONAL PAPERS

OF THE

CALIFORNIA ACADEMY OF SCIENCES

No. 137, 48 pages, 21 figures, 11 tables.

July 6, 1983

Paleobiogeography and Genetic Differentiation of the Baja California Herpetofauna

By

Robert W. Murphy

*Department of Biology, University of California, Los Angeles,
Los Angeles, California 90024*



SAN FRANCISCO

PUBLISHED BY THE ACADEMY

COMMITTEE ON PUBLICATIONS

Tomio Iwamoto, *Editor*
Frank Almeda
Daphne F. Dunn
William N. Eschmeyer
Frank H. Talbot

US ISSN 0068-5461

The California Academy of Sciences
Golden Gate Park
San Francisco, California 94118

PRINTED IN THE UNITED STATES OF AMERICA
BY ALLEN PRESS, INC., LAWRENCE, KANSAS

TABLE OF CONTENTS

ABSTRACT.....	iv
INTRODUCTION.....	1
ACKNOWLEDGMENTS.....	1
DEFINITIONS AND ABBREVIATIONS.....	2
THE HERPETOFAUNA.....	2
Composition.....	2
Herpetofaunal Areas.....	5
Generalized Tracks.....	9
Marginal Species.....	10
Southern Species.....	10
Ubiquitous Species.....	10
Transpeninsular Mesophilic Species.....	10
Transpeninsular Xerophilic Species.....	11
PREVIOUS SCENARIOS.....	11
DERIVATION OF FAUNAL ASSEMBLAGES AND THEIR AFFINITIES.....	14
Miocene and Earlier.....	15
Paleogeography.....	15
Paleoecology.....	16
Paleobiogeography.....	17
Pliocene.....	20
Paleogeography.....	20
Paleoecology.....	20
Paleobiogeography.....	20
Pleistocene.....	22
Paleogeography.....	23
Paleoecology.....	23
Paleobiogeography.....	24
Holocene.....	27
GENETIC DIVERGENCE OF INSULAR AND PENINSULAR POPULATIONS OF BAJA CALIFORNIA REPTILES: CORROBORATION OF THE SCENARIO.....	28
Peninsular Genetic Patterns and the Paleobiogeographic Scenario.....	28
Cape Area-Tropical Mainland Mexico.....	28
Transpeninsular Xerophilic Species.....	30
Transpeninsular Mesophilic Species.....	34
East-West Xerophilic Species.....	35
East-West Mesophilic Species.....	35
Insular Genetic Patterns and the Paleobiogeographic Scenario.....	36
Land-Bridge Islands.....	37
Old Islands.....	37
Summary.....	38
The "Clock" and the Paleobiogeographic Scenario.....	39
Santa Catalina, an Island of Questionable Age.....	40
SUMMARY.....	42
RÉSUMEN.....	44
LITERATURE CITED.....	45

ABSTRACT

MURPHY, ROBERT W. Paleobiogeography and genetic differentiation of the Baja California herpetofauna. *Occasional Papers of the California Academy of Sciences*, No. 137, 48 pages, 21 figures, 11 tables, 1983.—The evolutionary relationships of the amphibians and reptiles of southwestern North America are examined, using a synthesis of plate tectonics, paleogeography, and paleoecology. There is a very strong correlation between the nonbiological and the biological factors.

The following zoogeographic scenario is congruent with both factors. During the Miocene, about 13 million years before present (MYBP), the Cape area of Baja California broke away from mainland Mexico near the state of Colima, Mexico. Plate movements yielded isolated subpopulations, one on the Cape area (or associated islands) and the other remaining on the mainland. This subdivision is termed *transgulfian vicariance*. The islands that formed the Cape area of Baja California are postulated to be the center of origin for a number of western North America's reptilian groups such as the side-blotched lizards, the chuckwallas, and the desert iguanas. Near the close of the Miocene, the Cape area became attached to what is now the more northerly regions of the Baja California peninsula, allowing the northward dispersal of a number of reptile populations. By the beginning of the Pliocene, this terrestrial connection was broken yielding the formation of sister species on the Peninsular Ranges via allopatric speciation. The San Geronio Barrier was formed at the head of the Gulf of California around the early Pliocene approximately 4 MYBP, and is considered responsible for the formation of sister species on either side of the Gulf of California. It was eliminated by or during the Pleistocene, as the Gulf of California receded to its present location. Pleistocene glacial events had a minimal effect on the peninsular distributions of most reptiles; their major effect was in the forming and drowning of shallow-water islands in the Gulf. Pliocene–Pleistocene plate movements are responsible for the origin of the reptile populations on most deep-water islands.

This hypothesis for the origin and evolution of the herpetofauna of Baja California is supported by comparing patterns of genetic differentiation of the Baja California herpetofauna. Species of reptiles more or less restricted to the Cape area of Baja California have equivalent genetic differentiation from their presumed sister species on the mainland of Mexico. Similar genetic differentiation was found between sister species distributed north and south on the Peninsular Ranges, on the east and west sides of the Gulf of California, and on both deep- and shallow-water islands. Geological dating places the origin of the Cape area at about 13 MYBP. Transgulfian sister species are differentiated by a Genetic Distance (D) of about 0.8. Assuming that a D of 1 equals about 16 MY of divergence, the Biochemical Evolutionary Clock hypothesis predicts that the terrestrial connection between the Cape area and the more northerly Peninsular Ranges occurred more than 6 MYBP; these data are concordant with the geological predictions.

Similarly, the San Geronio Barrier is considered to have been formed about 3 MYBP and Isla Santa Catalina about 2 MYBP. No significant genetic differentiation was detected between species on the peninsula and those on shallow-water islands; these findings are also concordant with the clock hypothesis. Thus, the patterns of genetic differentiation appear to support my paleobiogeographic scenario, and the peninsula and islands of Baja California must be considered an evolutionary center rather than a refugium harboring a relict herpetofauna.

Paleobiogeography and Genetic Differentiation of the Baja California Herpetofauna

Robert W. Murphy*

INTRODUCTION

The Baja California peninsula and associated islands, extending 1300 km north to south, is an attractive area for the study of zoogeography, providing the opportunity to study aspects of both clinal and stepwise variation, possible attenuation of a linear gradient, and apparent "tracks" of distribution. Understandably, the peninsula has attracted much attention, and major papers by Nelson (1921), Schmidt (1922, 1943), and Savage (1960) have provided dispersal scenarios for the herpetogeography. The islands are of great interest as well, affording opportunities to examine the evolutionary consequences of isolation and to test biogeographic theories (MacArthur and Wilson 1963, 1967; Soulé and Sloan 1966; Case 1975; Wilcox 1978, 1980; Murphy 1982, 1983). Because recent geologic studies of the region indicate that the Baja California peninsula and associated islands have experienced significant plate activity, they provide a rare opportunity to examine the biological consequences of recent effects of continental drift. My study of the relationships of an insular population of the fossorial western blind snake, *Leptotyphlops humilis*, resulted in brief presentation of a generalized "transgulfian migration" theory (Murphy 1975), hereafter more properly termed *transgulfian vicariance*.

This paper contains a plate tectonic-based scenario to explain the evolution of the amphibians and reptiles of Baja California and, to a lesser extent, southern California. It must be emphasized that the paleobiogeographic scenario presented in this study is an attempt to form a set of testable working hypotheses on the biological consequences of continental drift. As hypotheses, they should be tested and, if found inadequate in explaining the evolutionary relationships of the Baja California amphibians and reptiles, should be modified or rejected. Refine-

ments will certainly be required as further investigations are made into the phylogenetic relationships and biogeography of extant amphibians and reptiles.

This study is organized into four major sections. In the first, the composition, faunal areas, and tracks of distribution of the herpetofauna are described. In the second section, previous theories explaining the tracks of distribution are reviewed in detail to facilitate comparison of the various proposals. In the third section I propose a new scenario for the evolution of the Baja California herpetofauna, based upon correlation of geologic events, paleoecological history, and tracks of distribution. Finally, the fourth section is a summary of the genetic data, which are used to corroborate various aspects of the scenario formed independent of them.

ACKNOWLEDGMENTS

All specimens used in the genetic analysis were imported on Mexico Scientific Collectors permits issued to me (65-78-866) and others. The cooperation of the Dirección General de la Fauna Silvestre is sincerely and greatly acknowledged.

For field assistance and/or donation of tissues from specimens, I am grateful to R. Ayrey, J. Cram, L. Hunt, C. Lieb, M. Mahlstedt, T. Papenfuss, F. Reynos M., R. Seib, A. Valdes R., T. Vaughn and family, M. Wong, and especially J. Ottley. Valuable critical evaluation, suggestions, and intellectual stimulation were provided by D. Buth, T. Case, M. Cody, G. Gorman, A. Leviton, C. Lieb, D. Morafka, E. Olson, A. Orme, J. Savage, L. Swan, H. Thompson, and numerous individuals at seminars presented at San Francisco State University, the University of Michigan Museum of Zoology, and the University of California at Los Angeles; any lingering errors or misinterpretations are mine. For laboratory and technical assistance I thank G. Adest, D. Buth, G. Gorman, Y. Kim, C. Lieb, and T. Vawter. Many of the figures were prepared by M. Kowalczyk. Rosalinda Aycinena-Derugin provided the Spanish Résumen. Field endeavors were sup-

* Research Associate, Department of Herpetology, The California Academy of Sciences, Golden Gate Park, San Francisco, California 94118.

ported by the Theodore Roosevelt Memorial Fund Grant in Support of Research (1978), the Regents of the University of California Research and Travel Grant 07427-5 (1978), and the University of California Patent Fund Research Grant 08613-5 (1978). The electrophoretic analysis was supported by the Department of Biology, UCLA, and NSF Grants DEB 77-03259 and GB-40070 to G. C. Gorman. Production of the manuscript was funded in part by the Fisheries Program, Department of Biology, UCLA, through the generosity of D. G. Buth. Wrennie Murphy and Mary Seraydarian typed drafts of the manuscript.

DEFINITIONS AND ABBREVIATIONS

The term "old" refers to those islands separated from another faunal source by an ocean depth of greater than 130 m (Fig. 1) and which are thought to have been formed more than 1 MYBP (million years before present); eustatically lowered sea level, the result of water bound in glaciers during the Pleistocene, would not have produced island-mainland terrestrial connections for these islands. The following islands are considered to be old: Ángel de la Guarda, Partida Norte, Salsipuedes, San Lorenzo Norte and Sur, San Pedro Mártir, San Esteban, San Pedro Nolasco, Monserrate, Santa Catalina (=Santa Catalán), San Diego, Santa Cruz, and Cerralvo.

The term "land-bridge" refers to those islands which would have had a land connection with the peninsula, or another larger island, during pleniglacial times up to 6000 YBP (years before present). These include El Muerto, Mejía, Smith, San Marcos, Santa Inés, San Ildefonso, Coronados, Carmen, Danzante, San José, San Francisco, Espíritu Santo, Partida Sur, Ballena, Tiburón, and Turners (=Lobos). Additional very small islands and satellite islands in the Gulf are listed in Murphy and Ottley (in press) along with their respective herpetofaunas. The herpetofaunas of the Pacific Coast islands are summarized by Wilcox (1980).

The term "oceanic" refers to islands of volcanic origin which presumably have never had a connection to the peninsula. The oceanic islands in the Gulf of California include Tortuga and Rasa (=Raza).

THE HERPETOFAUNA

Composition

The native herpetofauna of Baja California, exclusive of sea snakes, marine turtles, and strict-

ly insular species, is composed of 96 species of amphibians and reptiles, representing 50 genera distributed among 18 families (Table 1). The inclusion of insular populations would raise the number of species considerably. Excluding Isla Tiburón, which has its affinities with Sonora, Mexico, the total number of species would be about 130. Even with this increase, only a single genus would be added to the herpetofauna, the lizard genus *Sator* (Murphy and Ottley, in press). In defining the constituent peninsular herpetofauna of Baja California, it must be noted that many of the species on the peninsula (Table 2) are only marginally present. Woodhouse's toad (*Bufo woodhousei*), the Colorado River toad (*B. alvarius*), leopard frog (*Rana* "pipiens"), bullfrog (*R. catesbeiana*), spiny softshell turtle (*Trionyx spiniferus*), tree lizard (*Urosaurus ornatus*), and checkered garter snake (*Thamnophis marciatus*) occur in Baja California only in association with the Colorado River and/or its delta. Species found only at high elevations in the Sierra Juárez and/or the Sierra San Pedro Mártir may also be considered marginal. These include the yellow-legged frog (*Rana boylei*), sagebrush lizard (*Sceloporus graciosus*), Gilbert's skink (*Eumeces gilberti*), ringneck snake (*Diadophis punctatus*), California mountain kingsnake (*Lampropeltis zonata*), and western terrestrial garter snake (*Thamnophis elegans*). Although not restricted to mesic habitats, the western diamondback rattlesnake (*Crotalus atrox*) is found in Baja California only in the extreme northeastern corner of the peninsula. Accordingly, 14 of the 96 native species in Baja California may be considered marginal in distribution. Finally, two species of frogs—the clawed frog (*Xenopus laevis*) and bullfrog—and one snake, the Asian blind snake (*Ramphotyphlops braminus*), are known to be introduced (Funk and Croulet 1976; T. Fritts, U.S. Fish and Wildlife Service, personal communication, 1980; and Murphy and Ottley 1979, respectively). The slider turtle (*Chrysemys scripta*) and the spinytail iguana (*Ctenosaura hemilopha*) were probably introduced as a source of fresh meat by natives, as later discussed. Thus, 101 species occur on the Baja California peninsula (Table 2).

An understanding of the geographic distribution of taxa is paramount to sound biogeographical analysis and interpretation. This, in turn, is directly dependent upon accurate mapping. As detailed distribution maps are not available for most of the various species of amphibians and

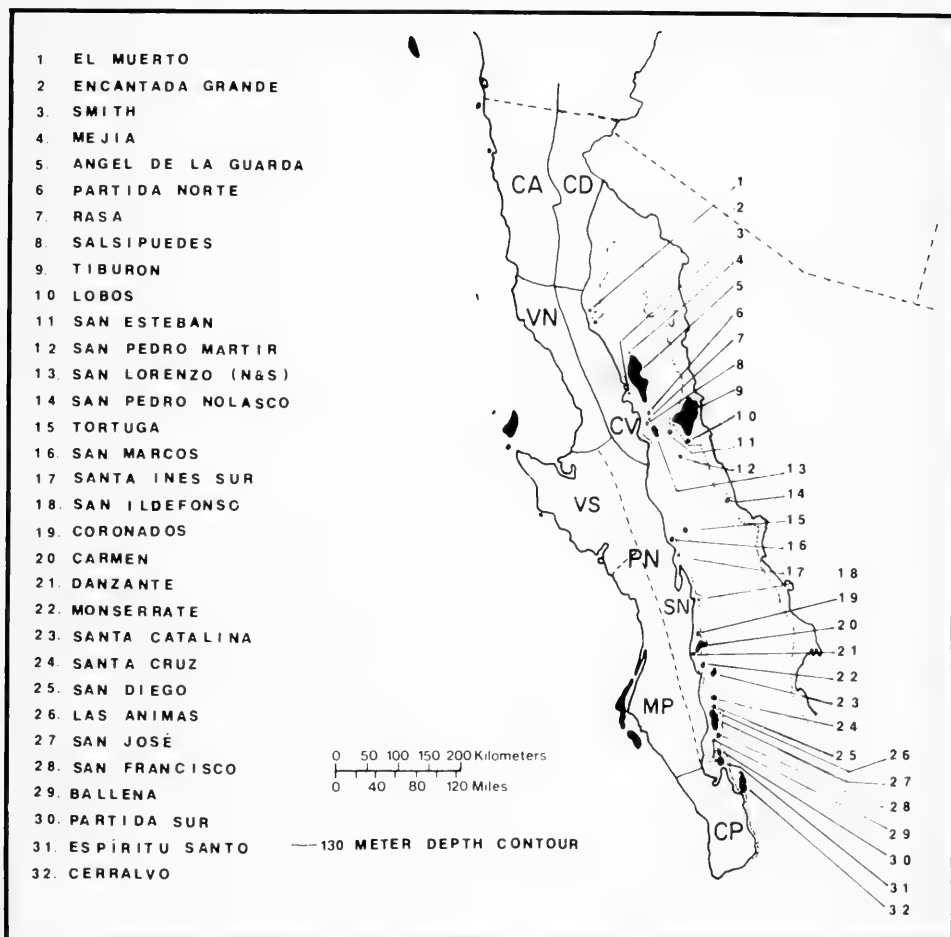


FIGURE 1. Islands in the Gulf of California and herpetofaunal areas and zones referred to in this report. Herpetofaunal areas are denoted as: CA, Californian; CD, Colorado Desert; VN, Vizcaíno Desert north; CV, Coastal Vizcaíno Desert; PN, Peninsular area; and CP, Cape. The three herpetofaunal zones of the Peninsular area are abbreviated as: VS, Vizcaíno Desert south; SN, San Lucan north; and MP, Magdalena Plains. The solid line on the map encloses major herpetofaunal areas, and the dotted lines separate the herpetofaunal zones of the PN.

reptiles on the Baja California peninsula and cannot as yet be constructed because of the absence of collections from various peninsular localities. I have used an alternative method here. The major "tracks" of distribution pattern are defined by dividing the peninsula into major regions and quantitatively comparing interrelationships among these herpetofaunal "zones." Phylogenetic relationships of the herpetofaunal elements are then superimposed on these tracks of distribution to suggest hypotheses explaining the evolutionary relationships of the herpetofauna of Baja California.

TABLE 1. TAXONOMIC COMPOSITION OF THE HERPETOFAUNA OF BAJA CALIFORNIA PENINSULA (exclusive of introduced or probably introduced species).

Group	Families	Genera	Species
Salamanders	1	3	3
Frogs and toads	4	4	13
Turtles	2	2	2
Amphisbaenians	1	1	1
Lizards	6	19	43
Snakes	4	21	34
Totals	18	50	96

TABLE 2. DISTRIBUTION BY FAUNAL ZONE OF THE PENINSULAR HERPETOFAUNA OF BAJA CALIFORNIA. Faunal zones: CA, Californian; CD, Colorado Desert; VN, Vizcaíno Desert north; CV, Coastal Vizcaíno Desert; VS, Vizcaíno Desert south; MP, Magdalena Plains; SN, San Lucan north; CP, Cape. Species occurrences: C, endemic to a single zone of Baja California but found elsewhere; E, endemic to a single zone of the peninsula; R, restricted to Baja California (including the Peninsular Ranges of southern California) but occurring in multiple zones; X, present in multiple Baja California zones and elsewhere.

Salamanders

<i>Aneides lugubris</i> (C)	CA
<i>Batrachoseps pacificus</i> (C)	CA
<i>Ensatina eschscholtzi</i> (C)	CA

Frogs and toads

<i>Xenopus laevis</i> ¹ (C)	CA
<i>Scaphiopus couchi</i> (X)	CV, VS, MP, SN, CP
<i>Scaphiopus hammondi</i> (C)	CA
<i>Bufo alvarius</i> (C)	CD
<i>B. boreas</i> (X)	CA, VN
<i>B. cognatus</i> (C)	CD
<i>B. microscaphus</i> (C)	CA
<i>B. punctatus</i> (X)	CA, CD, VN, CV, VS, MP, SN, CP
<i>B. woodhousei</i> (C)	CD
<i>Hyla cadaverina</i> (X)	CA, VN, CV
<i>H. regilla</i> (X)	CA, VN, VS, MP, SN, CP
<i>R. aurora</i> (C)	CA
<i>R. boylei</i> (C)	CA
<i>R. catesbeiana</i> ¹ (X)	CA, CD, VS, MP, CP
<i>R. "pipiens"</i> ^{2,3} (C)	CD

Turtles

<i>Chrysemys scripta</i> ¹ (X)	VS, MP, SN, CP
<i>Clemmys marmorata</i> (C)	CA
<i>Trionyx spiniferus</i> (C)	CD

Amphisbaenians

<i>Bipes biporus</i> (R)	VS, MP, CP
--------------------------	------------

Lizards

<i>Anarbylus switaki</i> (R)	CD, CV, VS, SN
<i>Coleonyx variegatus</i> (X)	CA, CD, VN, CV, VS, MP, SN, CP
<i>Phyllodactylus nocticolus</i> (R)	CD, VN, CV, VS, MP, SN
<i>P. unctus</i> (E)	CP
<i>P. xanti</i> (E)	CP
<i>Xantusia henschawi</i> (R)	CA, CD
<i>X. vigilis</i> (X)	CD, VN, CV, VS, MP, SN, CP
<i>Callisaurus draconoides</i> (X)	CD, VN, CV, VS, MP, SN, CP
<i>Crotaphytus insularis</i> (X)	CA, CD, VN, CV, VS, MP, SN
<i>Ctenosaura hemilopha</i> ¹ (X)	SN, CP
<i>Dipsosaurus dorsalis</i> (X)	CD, CV, VS, MP, SN, CP
<i>Gambelia wislizenii</i> (X)	CA, CD, VN, CV, VS, MP, SN, CP
<i>Petrosaurus mearnsi</i> (R)	CD, VN, CV

TABLE 2. CONTINUED.

<i>P. thalassinus</i> (R)	VN, CV, VS, MP, SN, CP
<i>Phrynosoma coronatum</i> (X)	CA, VN, CV, VS, MP, SN, CP
<i>P. mcalli</i> (C)	CD
<i>P. platyrhinus</i> (X)	CD, CV
<i>S. obesus</i> (X)	CD, VN, CV, VS, MP, SN, CP
<i>Sceloporus graciosus</i> (C)	CA
<i>S. hunsakeri</i> (E)	CP
<i>S. licki</i> (E)	CP
<i>S. magister</i> (C)	CD
<i>S. monserattensis</i> (R)	VS, MP, SN, CP
<i>S. occidentalis</i> (C)	CA
<i>S. orcutti</i> (R)	CD, VN, CV, VS, MP, SN
<i>S. rufidorsum</i> (R)	CA, VN, CV, VS
<i>S. zosteromus</i> (E)	CP
<i>Uma notata</i> (C)	CD
<i>Urosaurus graciosus</i> (C)	CD
<i>U. lahtelai</i> (E)	VN
<i>U. microscutatus</i> (R)	CA, CD, VN, CV, VS, MP, SN
<i>U. nigricaudus</i> (R)	SN, CP
<i>U. ornatus</i> (C)	CD
<i>Uta stansburiana</i> (X)	CA, CD, VN, CV, VS, MP, SN, CP
<i>Eumeces gilberti</i> (C)	CA
<i>E. lagunensis</i> (R)	MP, SN, CP
<i>E. skiltonianus</i> (C)	CA
<i>Cnemidophorus hyperythrus</i> (R)	CA, VN, CV, VS, MP, SN, CP
<i>C. labialis</i> (R)	CA, VN
<i>C. tigris</i> (X)	CA, CD, VN, CV, VS, MP, SN, CP
<i>Gerrhonotus multicarinatus</i> (X)	CA, VN, VS, SN
<i>G. paucicarinatus</i> (E)	CP
<i>Anniella geronimensis</i> (E)	CA
<i>A. pulchra</i> (X)	CA, CD
Snakes	
<i>Leptotyphlops humilis</i> (X)	CA, CD, VN, CV, VS, MP, SN, CP
<i>Ramphotyphlops braminus</i> ¹ (X)	VS
<i>Lichanura trivirgata</i> (X)	CA, CD, VN, CV, VS, MP, SN, CP
<i>Arizona elegans</i> (X)	CA, CD, VN, CV, VS, MP
<i>Chilomeniscus cinctus</i> (X)	CA, CD, VN, CV, VS, MP, SN, CP
<i>C. stramineus</i> (R)	MP, CP
<i>Chionactis occipitalis</i> (C)	CD
<i>Diadophis punctatus</i> (C)	CA
<i>Elaphe rosaliae</i> (R)	CD, VS, MP, SN, CP
<i>Eridiphas slevini</i> (R)	CV, VS, MP, SN, CP
<i>Hypsiglena torquata</i> (X)	CA, CD, VN, CV, VS, MP, SN, CP
<i>Lampropeltis getulus</i> (X)	CA, CD, VN, CV, VS, MP, SN, CP
<i>L. zonata</i> (C)	CA

TABLE 2. CONTINUED.

<i>Masticophis aurigulus</i> (E)	CP
<i>M. flagellum</i> (X)	CA, CD, VN, CV, VS, MP, SN, CP
<i>M. lateralis</i> (X)	CA, MP, SN
<i>Nerodia valida</i> (E)	CP
<i>Phyllorhynchus decurtatus</i> (X)	CD, CV, VS, MP, SN, CP
<i>Pituophis melanoleucus</i> (X)	CA, CD, VN, CV, VS, MP, SN, CP
<i>Rhinocheilus lecontei</i> (X)	CA, CD, VN
<i>Salvadora hexalepis</i> (X)	CA, CD, VN, CV, VS, MP, SN, CP
<i>Sonora bancroftae</i> (E)	CA
<i>S. mosaueri</i> (R)	MP, SN, CP
<i>S. semiannulata</i> (X)	CD, VN, CV, VS, SN
<i>Tantilla planiceps</i> (X)	CD, VN, MP, CP
<i>T. couchi</i> (X)	CA, VN, VS, MP, SN, CP
<i>T. elegans</i> (C)	CA
<i>T. marcianus</i> (X)	CD
<i>Trimorphodon biscutatus</i> (X)	CA, CD, VN, CV, VS, MP, SN, CP
<i>Crotalus atrox</i> (C)	CD
<i>C. cerastes</i> (C)	CD
<i>C. enyo</i> (R)	CA, VN, CV, VS, MP, SN, CP
<i>C. mitchellii</i> (X)	CA, CD, VN, CV, VS, MP, SN, CP
<i>C. ruber</i> (R)	CA, CD, VN, CV, VS, MP, SN, CP
<i>C. viridis</i> (X)	CA, VN, CV, VS

¹ Known to be, or probably, introduced into Baja California by man.

² Thought to be extinct because of the introduction of *Rana catesbeiana* (Vitt and Ohmart 1978). It is unknown if the original population of leopard frogs was *Rana pipiens* or *R. berlandieri*.

There are several nomenclatorial and phylogenetic problems associated with the herpetofauna of the Baja California peninsula. Most of these are detailed in the following sections, but one needs to be clarified here. Drewes and Leviton (1978), noting the recent discovery of the fourth known specimen of the Cape area endemic kingsnake (*Lampropeltis nitida*), pointed out that the validity of this taxon is questionable. I have thus chosen not to include it in Table 2.

As with the peninsular herpetofauna, numerous nomenclatorial problems exist with the insular herpetofauna, especially when the principles of holophyly (Hennig 1966; Farris 1979) are applied to the alpha taxonomy. These unresolved problems have been detailed elsewhere (Murphy 1982). However, it is assumed that they

will not alter the following discussions and interpretations.

Herpetofaunal Areas

Savage (1960) divided Baja California into four distinctive herpetofaunal areas. His Californian area included the western slopes of the Sierra Juárez and Sierra San Pedro Mártir north from El Rosario. The Colorado Desert area consisted of the eastern slopes of the Peninsular Ranges to the Gulf of California as far south as Bahía de los Ángeles. He defined the San Lucan area as including the southern Peninsular Ranges from Santa Rosalia south to the tip of the peninsula, excluding the Magdalena Plains which, with the Vizcaíno Peninsula and Vizcaíno Desert from El Rosario south, were termed the Peninsular Desert area. Savage's herpetofaunal areas are strongly correlated with phytogeographic regions (Fig. 2). Bostic (1971) considered Savage's northern Peninsular Desert area from roughly the 28th parallel north to El Rosario, including the western slopes of the northern Peninsular Ranges, a separate herpetofaunal area. Loomis et al. (1974) further subdivided the peninsula into seven areas based on political boundaries and floral and geological features; the major modifications included separating the Cape area (that area south of the Isthmus of La Paz) from Savage's San Lucan area, and the Vizcaíno Peninsula from the Magdalena Plains. For the present study I have used these subdivisions with one modification. I consider the Colorado Desert herpetofaunal area to consist of two separate zones: the northern zone extends from southern California and Sonora, Mexico, south to the region of San Felipe and includes the eastern slopes of the northern Peninsular Ranges; the southern area extends south from San Felipe to Bahía de los Ángeles. Near San Felipe there is an abrupt transition from the sand dunes of the Sonoran Desert to steep, rocky hills and mountains. The northern area is still called the Colorado Desert, but the southern portion is referred to here as the Coastal Vizcaíno Desert (Fig. 1).

The biological reality of these eight herpetofaunal zones is not easily tested at present; distributions of the various amphibians and reptiles have not been sufficiently studied in relatively inaccessible regions. Most notable is the paucity of herpetological collections from the Vizcaíno Peninsula, where only a handful of species

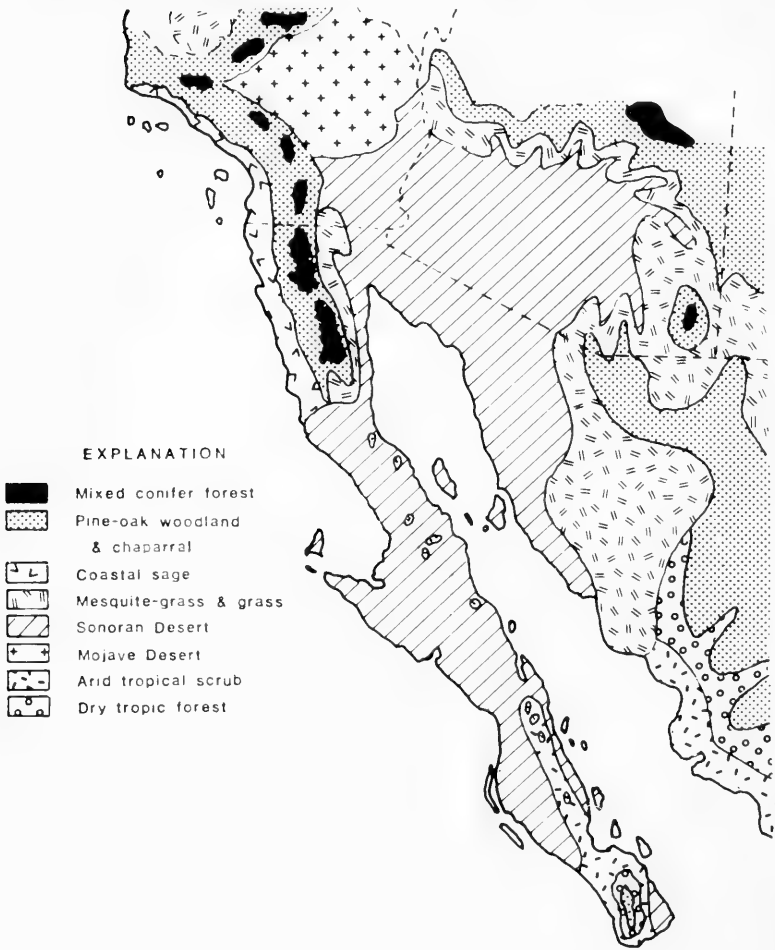


FIGURE 2. General distribution of the vegetation of Baja California and adjacent islands (adapted from Axelrod 1979).

have been recorded, and from the San Lucan zone, where collections are just now being made. Predictions about species occurrences in these regions can be made, however. In general, I have considered any species marginally occurring in a poorly known herpetofaunal area to be present in that area as long as suitable habitat is found.

Because detailed distributional data were not available, I analyzed the relationships of the eight herpetofaunal zones by using Faunal Resemblance Factor (FRF) coefficients (terminology following Duellman 1965). Numerical approaches to biogeographic problems clarify the main pattern of distribution. Simpson (1960) and Cheetham and Hazel (1969) reviewed the various FRF's, elucidating their assumptions, limitations, and use. Cheetham and Hazel (1969)

noted serious limitations to the use of most binary coefficients, which have been developed intuitively and tested empirically and are not, strictly speaking, statistical procedures.

The FRF's express the faunal relationship of two geographic units by expressing the relationship of the number of taxa in common to the total number. However, there are some 20 possible formulas for such comparisons, the results of which vary considerably, especially when the number of taxa occurring in one locality is more than twice that of the other (Cheetham and Hazel 1969). For the current study I have compared two diametrically opposed formulas: the Simpson FRF (SFRF) and the Braun-Blanquet FRF (BFRF) (referred to by Peters [1968] as the Jacquard Coefficient).

The SFRF selects the number of taxa in the smaller of the two faunas (N_1) for comparison with the number of taxa in common (C), and gives strong emphasis to the similarities:

$$\text{SFRF} = (C/N_1)100$$

In contrast, the BFRF selects the larger sample (N_2) for comparison and thus emphasizes differences:

$$\text{BFRF} = (C/N_2)100$$

With either FRF, a value of zero indicates that no taxa are shared; when all are shared, the FRF is 100. Other coefficients yield intermediate values of similarity.

Because the FRF's are binary (presence-absence) Q-mode bioassociational units, they may be affected by additions and/or deletions within the data set such as shifts in taxonomic level or new locality information. The taxonomic level used in this study is that of the species. Simpson (1960) noted that the proper taxonomic level would yield an array of coefficients ranging between 0 and 100 without notable clustering. FRF's calculated on operational taxonomic units (OTU's), or herpetofaunal zones, do not satisfy this criterion unless insular populations are included in the analysis. Excluding the islands, the data yield FRF's ranging from about 40% to over 90%; this range of values is adequate for the following interpretations. As previously noted, no assumption is made that the herpetofaunal records are complete. However, it is assumed that the faunas are well enough known to allow for sound interpretation of the relationships of the eight herpetofaunal zones.

The SFRF is used in this study as an indication of historical affinities, or evolutionary relationships. This bioassociational measurement compares the smaller of the two faunas, minimizing the effects of sampling error and faunas of unequal size, and thereby emphasizing similarities.

The BFRF is used in conjunction with the SFRF to test for ecological effects resulting in faunas of unequal size. Discrepancies between the bioassociational measurements indicate unequal faunal size. When a high discrepancy is encountered and provision made for sampling error, an examination into the possible reasons for the discrepancy is possible.

Using the larger of the two species pools as a base of comparison, the BFRF accounts for a number of variables not considered by the SFRF.

TABLE 3. MATRIX OF SIMPSON (above diagonal) AND BRAUN-BLANQUET (below diagonal) FAUNAL RESEMBLANCE FACTORS (FRF's). The number of species found in each herpetological zone is given in the diagonal as underscored values. Abbreviations for the herpetofaunal areas are as in Figure 1.

	CA	CD	VN	CV	VS	MP	SN	CP
CA	<u>53</u>	47	77	66	64	57	60	47
CD	45	<u>51</u>	70	78	69	64	67	51
VN	62	59	<u>43</u>	85	81	72	74	65
CV	51	63	81	<u>41</u>	88	78	80	71
VS	51	57	79	86	<u>42</u>	88	90	76
MP	47	55	70	73	84	<u>44</u>	90	86
SN	47	55	72	79	90	86	<u>42</u>	81
CP	43	49	57	59	65	78	69	<u>49</u>

For instance, if two herpetofaunal zones differ in number of inclusive species because one offers a greater variety of habitats, the BFRF yields a lower similarity value than the SFRF. The 96 species of amphibians and reptiles native to the Baja California peninsula (Table 2), including the marginally occurring populations, were used to calculate the two FRF's among the eight herpetofaunal zones; the resultant data matrices are given in Table 3.

To interpret the relationship of the herpetofaunal zones to each other, I clustered the FRF's, forming phenograms using the unweighted pair-group method with arithmetic averages (UPGMA) (Sneath and Sokal 1973). The UPGMA is an agglomerative hierarchical clustering technique which combines OTU's or groups of OTU's on the basis of some criterion of similarity. This method of clustering introduces the least amount of distortion (Rohlf 1970) as measured by the coefficient of cophenetic correlation (Sneath and Sokal 1973). Such coefficients generally range between 0.60 and 0.95; higher values indicate less distortion.

Because FRF's are not exact statistical procedures, the level of significance is difficult to ascertain. Some previous workers have considered an FRF of about 75% significant. The approach used here, however, is to look at the levels of hierarchical clustering.

The phenogram constructed from the clustering of the SFRF's (Fig. 3a) shows that the south-central peninsular herpetofaunal zones are more similar to each other in species composition than they are to either the northernmost or southernmost zones, suggesting that these zones had a

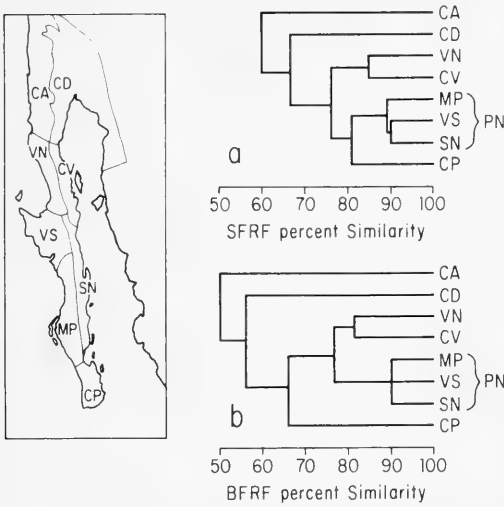


FIGURE 3. Phenograms produced from clustering Faunal Resemblance Factors of Simpson (SFRF) and Braun-Blanquet (BFRF) (see Table 3) calculated from distributional occurrences of amphibians and reptiles on the Baja Californian peninsula (Table 2). Abbreviations as in Figure 1.

similar developmental history. It can be further seen that these central zones are more similar to the Cape zone than to the two northern zones, indicating that there is a unique herpetofauna on the southern portion of the peninsula. If the 75% level is used as a cutoff to define significantly different herpetofaunal areas, the southern two-thirds of the peninsula would be considered separate from the Colorado Desert and Californian zones.

Figure 3b compares the eight herpetofaunal zones of the Baja California peninsula using the BFRF coefficient; the clustering sequence using the SFRF (Fig. 3a) is almost identical. The major difference is in the position of the Cape zone relative to the Vizcaíno Norte and Coastal Vizcaíno zones. In the SFRF phenogram the Cape is more similar to the south-central peninsular zones, whereas the BFRF phenogram depicts a closer relationship between the south-central and north-central zones. This discrepancy may in part reflect the distortion that results from the clustering technique; considerably greater distortion was found in the SFRF phenogram as measured by the cophenetic correlation coefficient (0.80 for the SFRF, 0.92 for the BFRF). Aside from the lower levels of distortion, it can be argued that the BFRF data matrix more realistically reflects

the biological relationships of the herpetofaunas of the eight zones. Assuming that the herpetofaunas are reasonably well known, differences in the number of species occupying an area reflect the diversity of available habitats and/or peninsular effects. Taylor and Regal (1978) demonstrated that the number of species of heteromyid rodents on the Baja California peninsula decreased from north to south, showing a peninsular effect. They suggested that the number of species of reptiles also decreased southward. However, Seib (1980) showed that the number of species of reptiles in key groups actually increased. In fact, the greatest numbers of species of amphibians and reptiles occur at the north and south extremes of the peninsula (Table 3). By yielding lower levels of similarity, the BFRF calculations more accurately show that these regions offer the greatest diversity of habitats. The SFRF does not reflect the same biological attributes of the composite herpetofauna and reflects similarity only in some aspect of evolutionary origin.

Because the BFRF phenogram better depicts biological reality and has a lower level of distortion, it is used to define the major herpetofaunal groups, or "areas," and thus to infer generalized tracks of distribution from which evolutionary hypotheses are formed. Six herpetofaunal areas may be defined for the purpose of analyzing the major tracks of distribution of the Baja California herpetofauna. The Californian, Colorado Desert, and Cape herpetofaunal zones are considered distinctive enough to be recognized as discrete areas; the Magdalena Plains, Vizcaíno Desert south, and San Lucan north zones may be considered a single area termed the Peninsular area. While the Vizcaíno Desert north and the Coastal Vizcaíno Desert zones are more similar to each other than to other zones, their similarity is not great, so for purposes of formation and evaluation of the generalized tracks I consider them as discrete areas. Both seem to be transitional areas sharing herpetofaunal elements among southern regions and the area directly to the north, and between themselves.

If these herpetofaunal areas reflect biological reality, comparable patterns of zonal relationships should be found for other ectothermic animals. I have calculated SFRF and BFRF coefficients from the distributional occurrences of the scorpions of Baja California (Williams 1980),

using the species level as the operational taxonomic unit (OTU). Phenograms resulting from clustering of these data by the UPGMA are shown in Figure 4. The cophenetic correlation coefficient for the SFRF is 0.90, and for the BFRF 0.91. Branching patterns are very similar to those for the herpetofaunal areas (Fig. 3), although the FRF's for the scorpions are much lower than for the herpetofauna, because of higher levels of endemism in the scorpions. The clustering sequence of the SFRF coefficients for the scorpions (Fig. 4a) is identical to that in the BFRF phenogram for the herpetofauna (Fig. 3b). The BFRF phenogram for the scorpions places the San Lucan Norte zone (Williams's Volcanic Province) outside of the cluster uniting the Cape and Magdalena Plains zones; this results from the San Lucan Norte zone's having a greater number of scorpions, with a greater proportion of these being endemic. The scorpion data support my concept that the northern Vizcaíno region should be considered as an area separate from the Cape and the south-central peninsula, as well as reinforcing my underlying assumption that the six herpetofaunal areas reflect biological reality.

Generalized Tracks

Among the 96 species naturally occurring on the Baja California peninsula, 27 unique patterns of distribution were found among the six herpetofaunal areas. Roughly 40% of the herpetofauna was found only in the four northernmost areas, and 20% in the southernmost areas. The remaining species were found throughout the peninsula, although not necessarily in every area. Another way to subdivide the herpetofauna is by each species' propensity to occur in a particular habitat, regardless of north-south distribution. Ubiquitous species, occurring in both relatively xeric and mesic habitats, compose about 24% of the total herpetofauna; xerophilic and thorn scrub-adapted species account for 27%; and the remaining species are relatively mesophilic. The high percentage of species associated with mesic habitats is not surprising, considering that a relatively large number of amphibians and reptiles are found only in the Californian area (Table 2) and near the Colorado River. All of these mesophilic species are found in association with chaparral, montane, and riparian habitats. We can subtract 6% if those in the Colorado Desert area along the Colorado River are considered

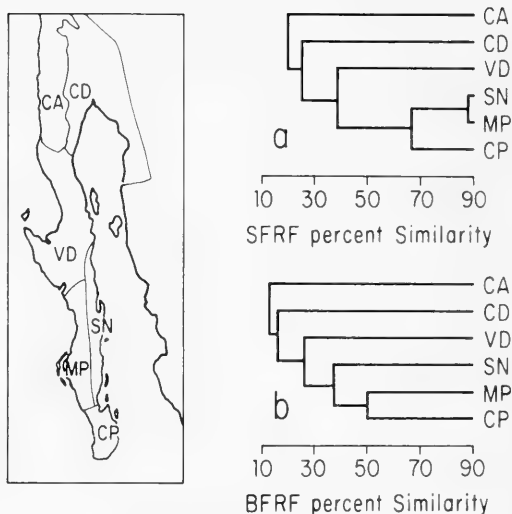


FIGURE 4. Cluster analysis of the FRF's calculated from distributional occurrences of scorpions (Williams 1980). The solid lines enclose major biogeographic areas of Williams, modified by combining the species occurrences in the Vancouverian area with the Californian for purposes of calculation, and considering the Volcanic Province of Williams synonymous with the San Lucan north (SN) area to facilitate comparison with Figure 3.

xerophilic. There are thus nine possible ways to subdivide the herpetofauna on the basis of propensity for a particular habitat and geographic distribution on the peninsula.

Analysis of the distributional patterns is more complicated than analysis of the nine possible generalized tracks. Some species endemic to the Cape area have sister species in the north. Similarly, some of the 16 species distributed throughout the peninsula (Table 2) are confined to the Peninsular Ranges south of the Transverse Ranges of southern California (e.g., the red diamond rattlesnake, *Crotalus ruber*). The nearest relatives of some species are in the Colorado Desert area of the southwestern United States, others are in tropical Mexico, and the relationships of others still await phylogenetic analysis. Seib (1980) treated this situation by subdividing the peninsular herpetofauna into three major groups: ecological isolates (non-transpeninsular species); mainland disjuncts and/or peninsular endemics whose hypothetical ancestors were from tropical Mexico southeast of the peninsula; and northern dispersers, or species with populations

(or near relatives) north and east of the peninsula. However, Seib's analysis does not include a number of distributional, systematic, and phylogenetic updates which have recently become apparent. By and large his groups do not reflect the distribution of the various herpetofaunal elements by habitat association; yet such associations are necessary for sound biogeographic interpretation.

The various species distributions can be divided into five major generalized tracks on the basis of geographic distribution and habitat association:

Marginal Species

Of the 96 species of amphibians and reptiles on the Baja California peninsula, 35 are considered marginal in distribution. These species are distributed among three minor tracks. Several species are found only in the relatively mesic habitats of the Californian area, or in both the Californian and Vizcaíno Norte areas. Several are found only in the Colorado Desert area or in both the Colorado Desert and Coastal Vizcaíno areas, mostly in association with the Colorado River and delta, as previously noted, or with the sand dunes of the Sonoran Desert, which extend as far south as San Felipe. The third minor track consists of species distributed among the four northern regions and, in general, those capable of surviving in both mesic and xeric habitats. All members of the Marginal Species track have more extensive distributions off the peninsula. (Three species having distributions that fall within this track do not belong to this group. The granite night lizard [*Xantusia henshawi*] is restricted to the Peninsular Ranges south of the Transverse Ranges and should be considered an endemic part of the peninsular herpetofauna. Unlike the marginal species, this species does not have populations that occur outside of the Peninsular Ranges geologic province. Two other species, the banded rock lizard [*Petrosaurus mearnsi*] and the Lahtel's tree lizard [*Urosaurus lahtelai*] appear to be restricted to the Peninsular Ranges and have phylogenetic affinities with more southerly species.)

In summary, marginal species account for about 36% of the peninsular herpetofauna of Baja California.

Southern Species

As delimited by the FRF's, the species of the southern peninsular herpetofaunal zones cluster together (Fig. 3). A total of 16 species are restricted to one or more of these southern areas, forming two minor tracks of distribution. The first is composed of eight species restricted to the Cape area, four in mesic mountain habitats, and four in xeric or transition habitats. The second consists of southern species shared between the Cape area and more northerly areas; these six species form five patterns of distribution (Table 2). Additionally, two species, the Baja California night snake (*Eridiphas slevini*) and Couch's spadefoot toad (*Scaphiopus couchi*) have a southerly distribution that extends north into the Coastal Vizcaíno area; the latter has an allopatric population in the Sonoran Desert outside of Baja California. Because *Sceloporus monserratensis* has been found in the Cape area (Murphy, unpublished data), there are no species of amphibians or reptiles endemic to the Peninsular area.

In summary, 17% of the herpetofauna of Baja California has a strictly southern track of distribution, half of these species being restricted to the Cape area.

Ubiquitous Species

There are 16 species on the Baja California peninsula that occur in every herpetofaunal area. These include 1 frog, 4 lizards and 10 snakes. Two additional species, the black-collared lizard (*Crotaphytus insularis*) and the glossy snake (*Arizona elegans*), may be added to this track. Both occur throughout most of the peninsula except in the southernmost areas. Thus, the 18 species in this track account for 19% of the total native herpetofauna of Baja California.

While snakes compose only 35% of the total peninsular herpetofauna, they account for 67% of the herpetofauna in this track. This disproportionate number of snake species may be a reflection of their dispersal ability and/or their ecological position as predatory carnivores.

Transpeninsular Mesophilic Species

A few species on the Baja California peninsula have distributions in, or almost in, every herpetofaunal area except the Colorado Desert area. Most of these species are restricted to the west coast of the peninsula at about latitudes 28°N to

29°N. The rainfall pattern in this region shifts from predominantly summer rains in the south to winter rains in the north. Most of these species may be unable to survive their season of activity without substantial amounts of available free water.

There are two minor tracks of distribution within this major track. Some species have essentially continuous distributions, such as the orangethroat whiptail lizard (*Cnemidophorus hyperythrus*). In total this minor track contains seven species (Table 2), among them the monophyletic peninsular radiation of the *Sceloporus magister* species complex, including (north to south) *S. rufidorsum*, *S. monserratensis*, and *S. zosteromus*. (*S. magister* occurs in the Colorado Desert area but is not considered a member of this peninsular radiation, as later discussed.) The second minor track of distribution consists of nine species that have disjunct populations in the north and south, or throughout the peninsula. Most of these are restricted to vicinities where surface water is present, e.g., the Pacific treefrog (*Hyla regilla*) and the western aquatic garter snake (*Thamnophis couchi*, including the subspecies *T. c. digueti*).

Thus about 17% of the herpetofauna of Baja California is associated with the Transpeninsular Mesophilic Species track.

Transpeninsular Xerophilic Species

The final major track is composed of species distributed throughout the peninsula except in the mesic regions of the northwest. The distribution of 10 species is continuous from the Cape area through the Colorado Desert area, and eight additional species are divided among three species groups which have one or more Cape area species and the nearest sister species just north. These are (north to south): the leaf-toed geckos (*Phyllodactylus nocticolus*—*P. unctus* and *P. xanti*), spiny lizards (*Sceloporus orcutti*—*S. hunsakeri* and *S. licki*), and small-scaled lizards (*Urosaurus microscutatus*—*U. nigricaudus*).

In all, 18 species composing almost 20% of the native herpetofauna belong to the generalized Transpeninsular Xerophilic Species track.

I reemphasize that among the various species constituting each of these five major generalized tracks of distribution, some have phylogenetic affinities with tropical Mexico and others with

territories north and east of the peninsula. This will be discussed later.

PREVIOUS SCENARIOS

A number of scenarios have been proposed to explain the patterns of distribution of single species, species groups, and the entire herpetofauna. Some studies have dealt exclusively with the peninsula, others just with islands; only a few have treated both. Previous evolutionary scenarios have with few exceptions assumed the permanency of the peninsula—i.e., its Eocene or earlier formation. Although current evidence does not support this idea, much value can be gained from a comparison of Matthewian (northern origin—southern dispersal) hypotheses with those based upon plate tectonics.

Although Nelson (1921) and Schmidt (1922, 1943) published the first significant zoogeographical treatments, Savage (1960) developed detailed hypotheses for the evolution of the peninsular herpetofauna. Savage's hypothesis, based on both geological history (King 1958; Durham and Allison 1960) and geofloral history (Chaney 1938, 1940, 1944, 1947; Axelrod 1948, 1950, 1956, 1957, 1958; MacGinitie 1958), assumes a strong correlation among geologic, geofloral and herpetofaunal histories (Savage 1960:189). The herpetofaunas were thought to evolve in a sequence dependent upon and parallel to their respective habitats.

With the onset of increasing aridity from the Miocene to the early Pliocene, according to Savage (1960), tropical types retreated to the south as early thorn-scrub communities invaded (Fig. 5a). Remnants of these groups associated with the thorn-scrub vegetation include the progenitors of sator lizards (*Sator*), the Cerralvo Island orangethroat whiptail (*Cnemidophorus ceralbensis*), the mole amphisbaenian (*Bipes biporus*), and the Baja California night snake (*Eridiphas slevini*). *Sator* and *C. ceralbensis* are today found only on islands in the Gulf of California; *E. slevini* occurs on Islas Cerralvo and San Marcos (Otterley and Tanner 1978) as well as on the peninsula.

Savage proposed that by the early Pliocene (Fig. 5b), additional representatives of xeric-adapted taxa had invaded the peninsula. These were the ancestors of dominant peninsular genera or species groups including banded geckos (*Coleonyx*), leaf-toed geckos (*Phyllodactylus*),

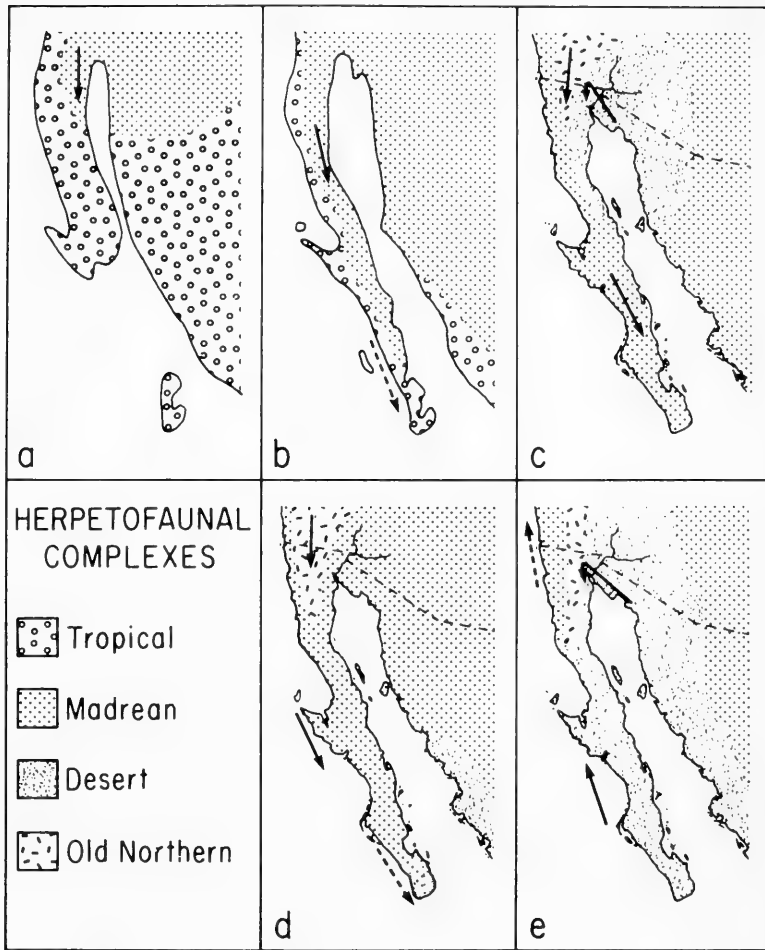


FIGURE 5. Summary of Savage's (1960) biogeographical scenario. Sequences are: (a) early Miocene; (b) early Pliocene; (c) late Pliocene; (d) Pleistocene at glacial maximum; (e) Pleistocene at interglacial. Solid arrows indicate expansions of herpetofaunal complexes; broken arrows indicate contractions. (Adapted from Savage 1960.)

night lizards (*Xantusia*), spinytail iguanas (*Ctenosaura*), horned lizards of the western species (*Phrynosoma coronatum*), granite spiny lizards (*Sceloporus orcutti*), small-scaled lizards (*Urosaurus microscutatus* and *U. nigricaudus*), rock lizards (*Petrosaurus*), skinks (*Eumeces*), whiptail lizards (*Cnemidophorus*), alligator lizards (*Gerrhonotus*), legless lizards (*Anniella*), blind snakes (*Leptotyphlops*), rosy boas (*Lichanura*), sand snakes (*Chilomeniscus*), night snakes (*Hypsiglena*), striped racer snakes (*Masticophis lateralis* and *M. aurigulus*), gopher snakes (*Pituophis*), ground snakes (*Sonora*), blackhead snakes (*Tantilla*), garter snakes (*Thamnophis*,

lyre snakes (*Trimorphodon*), and rattlesnakes (*Crotalus enyo* and *C. ruber*).

In the Miocene or early Pliocene, three genera, the slider turtle (*Chrysemys*), rat snake (*Elaphe*), and water snake (*Nerodia*), became established in the remaining thorn-scrub community.

By the late Pliocene (Fig. 5c), a number of species groups had entered from the north from mainland Mexican centers of desert vegetation, in response to increasingly arid conditions associated with mountain-building activity. Such species include Couch's spadefoot toad (*Scaphiopus couchi*), the red-spotted toad (*Bufo punctatus*), zebratail lizard (*Callisaurus draco-*

noides), desert iguana (*Dipsosaurus dorsalis*), longnose leopard lizard (*Gambelia wislizenii*), chuckwalla (*Sauromalus obesus*), spotted leaf-nose snake (*Phyllorhynchus decurtatus*), and speckled rattlesnake (*Crotalus mitchellii*). In association with mountain-building events, the ancestral stocks of the following recent groups entered the relatively humid regions of the peninsula: climbing salamanders (*Aneides*), slender salamanders (*Batrachoseps*), ensatina salamanders (*Ensatina*), and pond turtles (*Clemmys*).

In the Pleistocene, during maximum glacial periods (Fig. 5d), mesic Madrean forms with relatively high rainfall requirements, such as the western spadefoot toad (*Scaphiopus hammondi*), southwestern toad (*Bufo microscaphus*), and California treefrog (*Hyla cadaverina*), probably invaded the moister coastal regions of the peninsula. Two members of Savage's "Holarctic Element," the western toad (*Bufo boreas*) and the red-legged frog (*Rana aurora*), became established in the same region of the peninsula. At times of interglacial conditions (Fig. 5e), one or several waves of desert-adapted forms invaded the northeast region of the peninsula by traveling north from a Sonora refugium around the head of the Gulf of California. These "recent" invaders included the collared lizard (*Crotaphytus*), desert horned lizard (*Phrynosoma platyrhinos*), chuckwalla (*Sauromalus obesus*), desert spiny lizard (*Sceloporus magister*), tree lizard (*Urosaurus ornatus*), western whiptail (*Cnemidophorus tigris*), glossy snake (*Arizona elegans*), western ground snake (*Sonora semiannulata*), and western diamondback rattlesnake (*Crotalus atrox*).

Pleistocene events terminated in increased elevation of the mountains, increased aridity, and general temperature depression. With the development of less xeric conditions, "Madrean Complex" groups at times of glacial maxima dominated most of the peninsula, with "Desert and Plains Complex" groups restricted to Cape and Sonoran Desert regions (Fig. 5d). During interglacial times, environmental restriction of the Madrean Complex Faunas to a southern refuge both in mainland Mexico and on the peninsula allowed invasion of the peninsula by mainland desert elements, as the Madrean Elements were eliminated from central Baja California (Fig. 5e). Dispersal of Cape-refugium desert elements northward, to form a mixture of Cape species

and Mexican mainland types in the central Peninsula Desert, occurred simultaneously. This scheme would account for the Madrean Complex mesophilic species' being found in two disjunct regions: the northwest coastal and montane area, and the San Lucan (Cape) uplands (Savage 1960).

Soulé and Sloan (1966) commented on the biogeographic and evolutionary patterns of amphibians and reptiles inhabiting the islands in the Gulf of California, which they divided into probable recent, shallow-water islands and deep-water islands. Shallow-water islands are separated from mainland Mexico or the Baja California peninsula by a sea depth of less than 130 m, deep-water islands by a depth exceeding 130 m. Pleistocene glaciation resulted in sea-level changes of as much as 130 m, creating and drowning temporary land bridges between the mainland and the young or recent shallow-water islands, including Islas Tiburón, San Marcos, Carmen, Coronados, Danzante, San José, San Francisco, and Espíritu Santo, as well as many small coastal and satellite islands (Fig. 1). Thus, "biogeographic and evolutionary patterns found in the islands today are probably interpretable, in large part, as the result of Pleistocene events" (Soulé and Sloan 1966:149). Unfortunately, an analysis of the origin and relationship of the deep-water island herpetofaunas was not presented.

Taylor and Regal (1978) briefly treated the peninsular herpetofauna, suggesting that the number of species of reptiles decreased from north to south. Such peninsular effects would support Savage's (1960) scenario. However, Seib (1980) showed that the number of lizard and snake species belonging to various distributional groups actually increased in relative frequency from south to north. Consequently, he suggested, as I had earlier (Murphy 1975), a generalized southern, tropical Mexico transgulfian origin for many peninsular species.

Case (1975) and Wilcox (1978) applied the equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967) to the herpetofauna on the islands in the Gulf of California. Case in particular felt that the number of species of lizards on the Gulf islands resulted from ongoing interactions between colonization and extinction. Wilcox suggested that there were more species on the Gulf islands than predicted by equilibrium theory because of insufficient time

for relaxation to lower equilibrium levels of species diversity.

On the basis of species composition and species/area relationships, Savage (1967:226) hypothesized that the most distinctive elements in the insular herpetofauna colonized the Pacific coastal islands by "fortuitous over-water waif distribution" and are "depauperate chance samplings of the faunas of the adjacent mainland." Wilcox (1980) agreed with Savage, emphasizing that historical factors have resulted in these islands' having fewer species than predicted by the equilibrium theory of island biogeography; he did not consider the islands to be at equilibrium.

Aside from these general treatments of the herpetofauna, there have been numerous lesser contributions treating taxonomic groups. For instance, Conant (1969) examined the distribution of the water snake, *Nerodia valida*, in the Cape area of Baja California, and Yanev (1980) proposed over-water dispersal to explain the occurrence of populations of slender salamanders, *Batrachoseps pacificus*, on Pacific coastal islands. Most such reports are direct applications of Savage's (1960, 1967) or MacArthur and Wilson's (1963, 1967) biogeographic treatments.

Basic assumptions of both Savage's (1960) peninsular scenario and the insular scenarios of Case (1975) and Wilcox (1978) can be criticized. Elsewhere (Murphy 1983) I have reexamined the equilibrium scenarios as applied to the Gulf herpetofauna, suggesting that there is no ongoing interaction between colonization and extinction for most of the islands. Moreover, Case inappropriately lumps islands that fall into two distinctive climatic regimes: the Gulf islands north of latitude 28°N receive most of their rainfall in the winter, whereas the islands south of this latitude receive predominantly summer rains (Aschmann 1959).

Savage's (1960) scenario for evolution of the peninsular herpetofauna was based on two questionable critical assumptions: the permanency of the peninsula, and the development and distribution of the herpetofauna concomitant with the geoflora. It is now well established that the Baja California peninsula has *not* been a more or less permanent feature of western North America since the Eocene or earlier (see Atwater 1970). And the second assumption is doubtful. The Sonoran Desert region extends throughout most of the peninsula, except for the Californian herpe-

tofaunal area and most of the Cape area (Fig. 2). If the herpetofauna of Baja California developed concomitantly with the Madro-Tertiary vegetation, parallel patterns of distribution would be predicted. Thus, many of the mesophilic herpetofaunal species in the Cape area should be found further north in the San Lucan herpetofaunal zone (Fig. 1) in association with San Lucan vegetation (Fig. 2). Similarly, species found in the Colorado Desert herpetofaunal area should be found further south on the peninsula. But contrary to these predictions, the FRF's show that the Colorado Desert herpetofaunal area is unique (Fig. 3). Moreover, Cole and Van Devender (1976) and Van Devender and Mead (1978) showed that when juniper woodlands replaced the Sonoran Desert vegetation at times of maximum Wisconsin glaciation, the desert-adapted herpetofaunal elements maintained their distributions rather than retreating into xeric refuges.

Although there is an obvious correlation between habitats and herpetofaunal distributions—e.g., xerophilic species occur in desert habitats—it cannot be assumed that the herpetofaunal development depended upon vegetational development. Certainly other variables, such as physiography or interspecific competition for available habitats, cannot be dismissed. There is no a priori reason to expect that herpetofaunal distributions are directly dependent upon and co-evolve with vegetational distributions, as in certain insect groups (e.g., Ehrlich and Raven 1965). Because both of Savage's (1960) major assumptions can no longer be accepted, new hypotheses are needed to explain the major tracks of distribution of the herpetofauna of Baja California.

DERIVATION OF FAUNAL ASSEMBLAGES AND THEIR AFFINITIES

This paleobiogeographic scenario—a reconstruction of events, based on conceptual geologic and distributional models for evolution of the Baja California amphibians and reptiles—will be presented in chronological sequence, following the time-scale of Berggren and Van Couvering (1974) and Van Couvering (1978). The most significant departure of this time-scale from the more "classical" one is in placement of the Miocene–Pliocene boundary at 5.2 MYBP instead of an 11–13 MYBP transition. The Pliocene–Pleistocene boundary is placed at 1.6–2.0+ MYBP. Adoption of this time-scale is significant for the

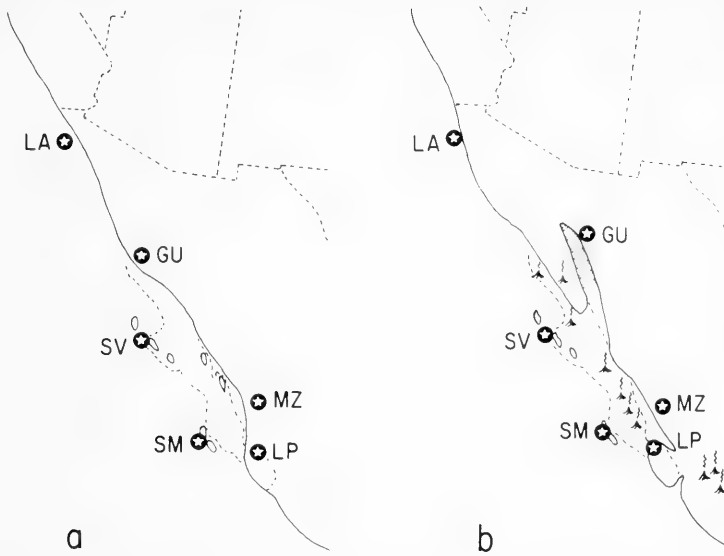


FIGURE 6. Reconstruction of the subaerial regions of southwestern North America during the Eocene (*a*), about 45 MYBP, and the middle Miocene (*b*), about 15 MYBP. Abbreviations indicate relative positions of: GU, Guaymas, Sonora, Mexico; LA, Los Angeles, California; LP, La Paz, Baja California Sur, Mexico; MZ, Mazatlan, Sinaloa, Mexico; SM, Islas Santa Margarita and Magdalena; and SV, Sierra Vizcaíno including Isla Cedros. Stippled area denotes temporary existence of the proto-Gulf of California.

correlation of paleoecologic and paleogeographic events.

The discussion will for the most part begin with the Neogene, although it will be necessary at times to refer to Paleogene events. The paleogeography and paleoecology will be briefly reviewed before the paleobiogeography discussion. Much of the detailed documentation and arguments will appear in forthcoming titles (Murphy, in preparation) and for the sake of brevity will not be presented here.

Miocene and Earlier

Paleogeography

The current distributions and evolutionary relationships of the amphibians and reptiles that eventually came to occupy the peninsula and islands of Baja California are most easily explained by the major geophysical, paleoecological, and paleogeographical events of the middle Miocene, about 15 MYBP, before formation of the Gulf of California (Figs. 6 and 7). During the early to middle Miocene, what now constitutes Baja California was adjacent to mainland Mexico where the Gulf of California is now (Atwater 1970; Atwater and Molner 1973). From Figure

6 it can be seen that much of "Baja California" was under the sea, with the notable exceptions of three granitic batholith regions: northeastern Baja California; the Vizcaíno peninsula, including Isla Cedros; and the Cape area (Mina 1957; King 1958, 1959; Durham and Allison 1960; Minch et al. 1975; Gastil et al. 1975). Significantly, the middle Miocene period in Baja California was characterized by a rejuvenation of orogenic events which continued the elevation of the northern Peninsular Ranges and emergence of the central Peninsular Ranges through volcanism (Fig. 8; Durham and Allison 1960; Karig and Jensky 1972). The low-elevation Peninsular Ranges existed as a westward extension of mainland Mexico, with a relief consisting of rolling hills (Gastil et al. 1975). To the east the Sierra Madre Occidental and Mexican Plateau were uplifted (King 1959).

By the close of the Miocene, the paleogeography had changed considerably. "Baja California" had migrated some 260 km northwest to the region of the Islas Las Tres Marias (Fig. 9), and the proto-Gulf of California began forming (Gastil and Jensky 1973). The initial (middle Miocene?) biogeographic effects of the proto-Gulf,

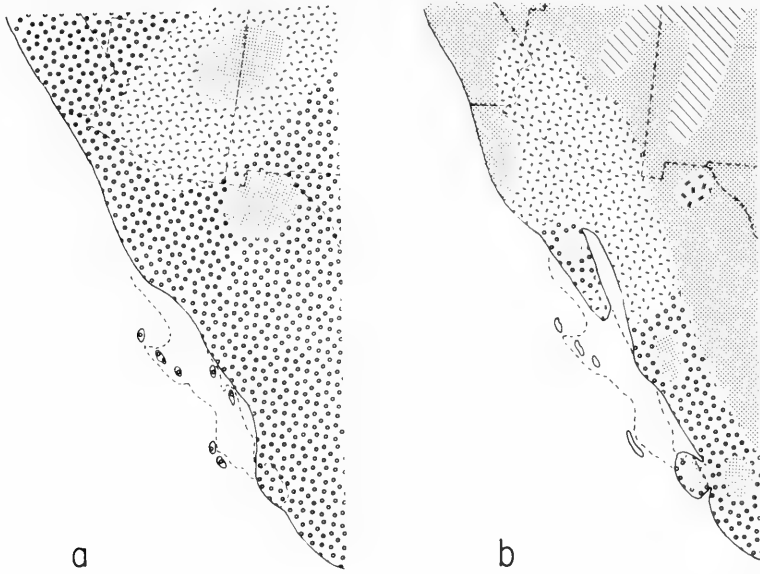


FIGURE 7. Generalized vegetation distributions during the Eocene (a) and middle Miocene (b) as hypothesized by Axelrod (1979:28). Vegetation distributions are superimposed on the subaerial regions of southwestern North America shown in Figure 6. Symbols as shown in Figure 2 with addition of diagonal lines representing deciduous and mixed conifer forests.

however, may be deemed trivial, for apparently the sea receded at least once, and possibly several times, and thus the Gulf was not a permanent geographic feature until around the Miocene-Pliocene boundary, about 6–5 MYBP. Significantly, because the proto-Gulf was not a permanent feature until the Miocene-Pliocene boundary, an isolated peninsula (Savage 1960) did not exist prior to that time. Thus, the only geographically isolated portions of the extant peninsula in the middle Miocene were the islands near (and including) the current Cape area (hereafter referred to as Cape Islands), the Sierra Vizcaino, and several southern peninsular-associated island localities (Fig. 6).

Paleoecology

The declining temperature and increasing aridity from the Eocene onward ultimately restricted neotropical-Tertiary geofloral elements to the south. According to Axelrod (1979), about 40 MYBP in the Eocene, subaerial regions of Baja California were dominated by dry tropic forest which extended virtually uninterrupted throughout most of northern Mexico (Fig. 7). Oak-piñon woodlands and arid tropic-scrub hab-

itats were restricted to higher elevations of the young, developing mountain regions. By the close of the Oligocene, the Madro-Tertiary geoflora predominated along the mountain chains and uplands of central Mexico (Axelrod 1975). The declining temperature and increasing aridity of the Paleogene continued into the Neogene and facilitated the spread of the Madro-Tertiary geoflora. Concomitantly, as the American plate moved northward, the neotropical-Tertiary geoflora retreated southward. In the middle Miocene, around 15 MYBP, the Madro-Tertiary geoflora was quite extensive (Fig. 7). Extreme western regions were apparently characterized by a neotropical or tropical flora (Peabody and Savage 1958; Savage 1960; Axelrod 1975, 1979). That emerged portions of the northern Peninsular Ranges must have been quite wet is corroborated by the abundance of deep Miocene streambeds (Gastil et al. 1975).

In the absence of fossil data, I assume that the Cape Islands supported a mixture of neotropical-Tertiary and Madro-Tertiary geofloras in the respective tropical and temperate climatic regimes; the temperate regime of the Cape resulted from altitudinal effects.

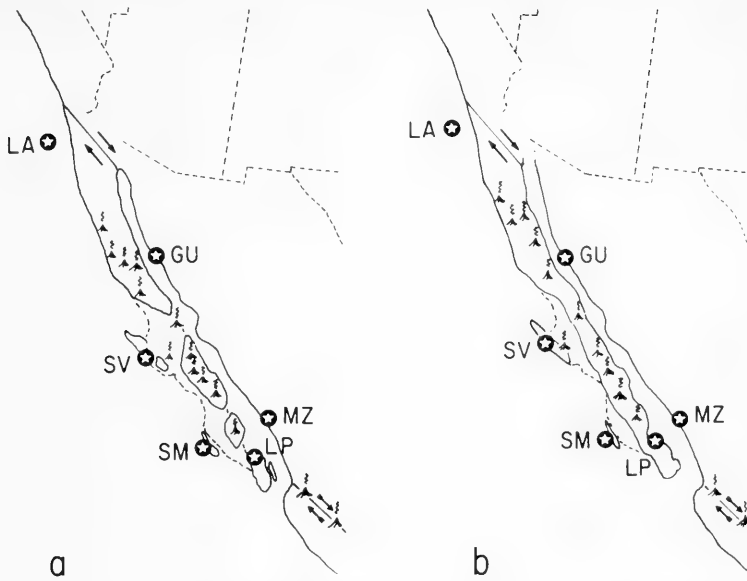


FIGURE 8. Reconstruction of the subaerial regions of Baja California and surrounding areas from the middle Miocene (a), about 10 MYBP, until the late Miocene (b), about 7 MYBP. Abbreviations as in Figure 6. Arrows indicate relative movement of the plates at their subaerial junctions. Note that the peninsula is completely formed by the late Miocene (b); the Cape is connected to the remainder of the peninsula.

Paleobiogeography

The presumed ancestral Miocene herpetofauna may be divided into two major assemblages; one composed of southern tropical and subtropical-associated organisms, the other associated largely with development of the Madro-Tertiary geoflora.

About 14 MYBP the Cape area of Baja California broke away from mainland Mexico near the western extreme of the Transverse Volcanic Range, becoming an island or a group of closely associated islands (Fig. 6). Herpetofaunal species belonging to several genera were probably distributed throughout the dry tropic forest (=neotropical-Tertiary geoflora), including the Cape area and adjacent Mexico. Constituent genera or their progenitors probably included a slender salamander (*Batrachoseps*), treefrogs (*Hyla*), leaf-toed geckos (*Phyllodactylus*), chuckwallas (*Sauromalus*), desert iguanas (*Dipsosaurus*), side-blotched lizards (*Uta*), tree lizards (*Urosaurus*), whiptails (*Cnemidophorus*), mole amphisbaenians (*Bipes*), blind snakes (*Leptotyphlops*), boa constrictors (*Boa*), Baja California night snakes (*Eridiphas*), blackhead snakes (*Tantilla*), and rat-

lesnakes related to the Middle American species (*Crotalus enyo*). Moreover, the barefoot geckos (*Anarbylus*), skinks (*Eumeces*), alligator lizards (*Gerrhonotus*), water snakes (*Nerodia*), and rat snakes (*Elaphe*), and possibly a basking turtle (*Chrysemys*) became isolated and entrapped on the newly formed Cape Islands. (*Chrysemys* is included only tentatively because of its possible human introduction into aquatic habitats of Baja California by Indians and/or Jesuit priests as a source of fresh meat; these turtles are still frequently eaten in remote places on the peninsula.) These genera represent four generalized tracks of distribution: Ubiquitous Species, Southern Species, and Transpeninsular Xerophilic and Mesophilic Species tracks. These taxa occur exclusively, or mainly, in western North America, with closest phylogenetic affinities to tropical-related species. Note from Figure 9 that the tropical scrub regions of western North America were in the Miocene distributed toward the Cape on pre-peninsular regions.

The Sierra Madre Occidental and Oriental and the Mexican Plateau were uplifted during the middle Miocene (King 1959), with concomitant effects on the distribution of the Madro-Tertiary

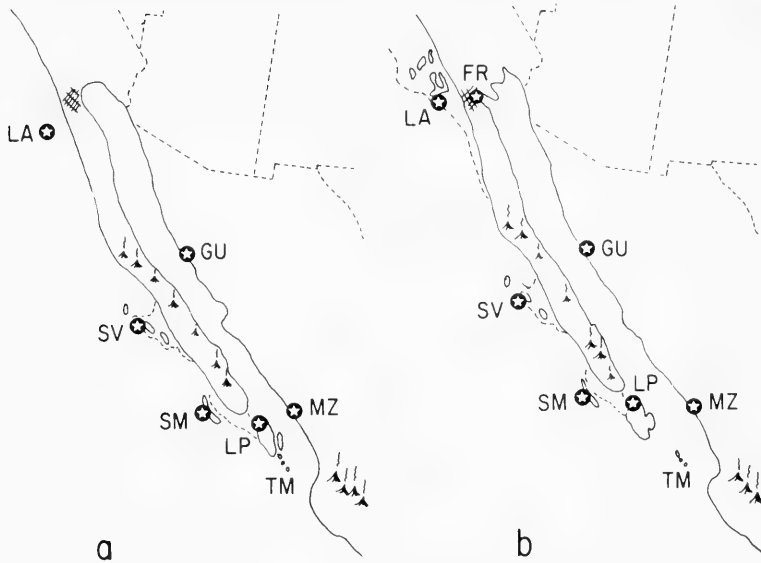


FIGURE 9. Reconstruction of subaerial regions of southwestern North America at the Miocene-Pliocene boundary, about 5 MYBP, and the middle Pliocene, about 3-4 MYBP. Abbreviations are the same as in Figure 6, plus: FR, faunal and floral regions of both the Mount Eden Beds and the Soboba Flora; TM, Islas Las Tres Marías. The cross-hatched region around FR denotes the hypothesized San Gorgonio Barrier. Note that the Cape area is once again isolated from the remainder of the peninsula (compare with Fig. 8).

geofloral-associated reptiles and amphibians. Most significantly, by the end of the Miocene, Cascadian orogenic events split the widespread populations into eastern and western halves, and as a direct result a number of sibling species pairs were formed, such as zebratail lizards (*Callisaurus draconoides* and *C. texanus*), horned lizards (*Phrynosoma coronatum* and *P. orbiculare*), and probably spiny lizards (*Sceloporus magister* and *S. orcutti* both sensu lato). Between the northern end of the Sierra Madre Occidental and the southern Rocky Mountains, the Cochise Filter Barrier allowed a continuity of gene flow for a few taxa until the Pliocene (Zweifel 1962; Lowe 1955; Pough 1966; Bogert and Degenhardt 1961; Fowlie 1965; and, particularly, Morafka 1977). These species are on the Ubiquitous and the two Transpeninsular tracks of distribution.

Evolution of the herpetofauna on Miocene islands resulting from geographic isolation was extremely important, but much of it may not have occurred on currently extant islands. It is not clear geologically if any of the extant Gulf islands are of Miocene origin; most evidence points to a Pliocene or Pleistocene origin for at least Isla Santa Catalina, a southern old island (Fig. 1).

Evidently the most significant island formations of the Miocene were the Cape islands. For example, it is possible that on these islands *Dipsosaurus*, the desert iguana, differentiated from a green iguana stock (*Iguana*); the chuckwalla from a spinytail iguana (*Ctenosaura*); and the banded rock lizard (*Petrosaurus*) from a sceloporine ancestor. Similarly, other "southern" forms such as the Baja California night snake (*Eridiphas*) presumably derived from night snake (*Hypsiglena*) and cat-eyed snake (*Leptodeira*) ancestral stock (Leviton and Tanner 1960), and the barefoot gecko (*Anarbylus*; Murphy 1974) from a banded gecko (*Coleonyx*-like) ancestor. These forms underwent morphological change considered sufficient to warrant generic recognition. Other lineages were more conservative. Transgulfian sister species belonging to the mole amphisbaenian genus *Bipes*, the leaf-toed gecko genus *Phyllodactylus*, and the tree lizard genus *Urosaurus*, for example, did not sufficiently diverge from one another morphologically to justify placement in separate genera.

It seems probable that only three extant islands are of Miocene origin: Islas Santa Cruz, San Diego, and Cerralvo (Fig. 1). I (Murphy 1975) earlier

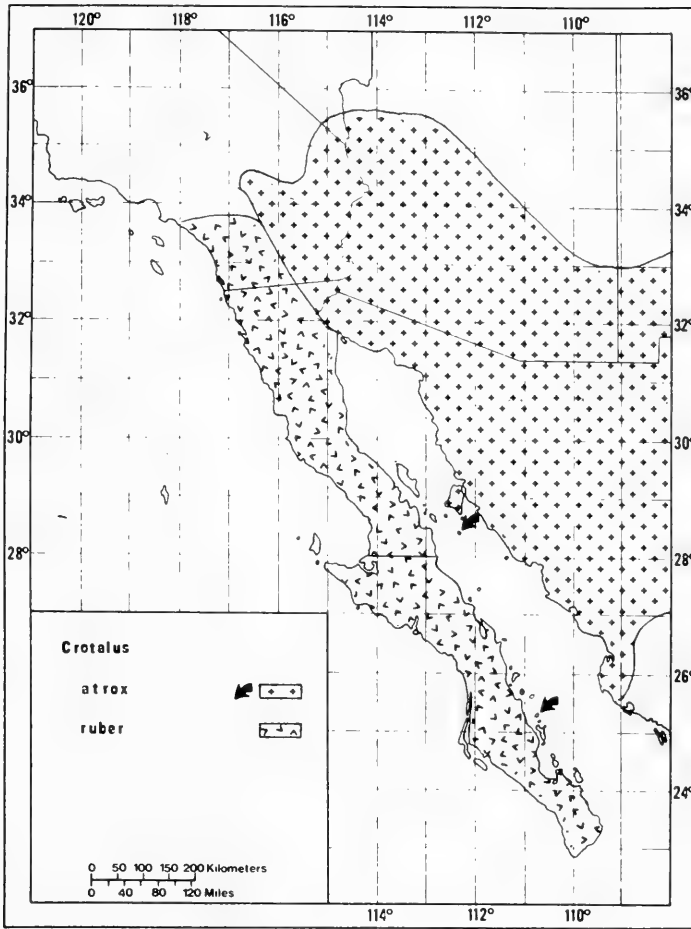


FIGURE 10. The western North American geographic distributions of the red diamond rattlesnake, *Crotalus ruber*, and the western diamondback rattlesnake, *C. atrox* (after Klauber 1972); island populations of *C. ruber* are not shown.

proposed that the genus *Sator*, which is recorded only from these three Gulf islands, was derived from a mainland Mexico stock as the islands broke away. Wyles and Gorman (1978), using immunological techniques to ascertain the closest relative of *Sator*, consider it a sister species of *Sceloporus utiformis*, recorded from the mainland Mexico states of Colima, Guerrero, Jalisco, Michoacán, Nayarit, and Sinaloa. This phylogenetic affinity was originally suggested by Dickerson (1919) and Schmidt (1922) on morphological grounds. Similarly, the western diamondback rattlesnake (*Crotalus atrox*) is recorded from Isla Santa Cruz but not from central and southern portions of the peninsula or other southern islands of Baja California (Fig. 10); it

occupies the arid regions of western and central mainland Mexico and northeastern Baja California. It seems probable that populations of the insular genus *Sator*, and possibly *C. atrox*, became established as the result of plate tectonic events rather than by rafting or swimming across the Gulf of California.

Thus, the most significant Miocene geohistory and paleoecological events were (1) the orogenic events giving rise to the Sierra Madres and the Mexican Plateau, forming a barrier to east-west dispersals of the fauna associated with the Madro-Tertiary geoflora; (2) rifting of the Baja California peninsula from mainland Mexico to the present-day location of Islas Santa Cruz, San Diego, and Cerralvo; (3) continued aridity trends,

resulting in spread of the Madro-Tertiary geoflora from the Sierra Madres of Mexico; and (4) initial formation of the proto-Gulf of California. Many of the herpetofaunal elements representative of the Miocene fauna of Baja California were present on the peninsula from the beginning through transgulfian vicariance, and not through dispersals along the Baja California peninsula as previous biogeographers (e.g., Schmidt 1922, 1943; Savage 1960) have proposed.

Pliocene

Near the Miocene–Pliocene boundary, 5 MYBP, a major resurgence of plate tectonic events occurred. The resultant plate movements had profound effects on the evolution of the peninsular and insular paleobiogeography, paleoclimatology, and paleoecology, and thus upon the herpetogeography. Indeed, the major Pliocene events, when combined with those of the Miocene, are ultimately responsible for the distributions and speciation of the populations of amphibians and reptiles which became the source for future island colonizations.

Paleogeography

Around 5 MYBP, Baja California began to move more rapidly northwestward (Larson 1972; Moore 1973; Atwater and Molner 1973), subsequently “drifting” from the present region of the Islas Las Tres Mariás to its present position. The resurgence of plate interactions and the union of Baja California with the Pacific plate (Atwater and Molner 1973) resulted in further uplift of the Peninsular Ranges; volcanic activity continued in the southern Peninsular Ranges, the Sierra de la Giganta (Mina 1957). The proto-Gulf of California had completely formed by 5 MYBP (Karrig and Jensky 1972; Gastil et al. 1975) and extended from the region of the San Geronio Pass near San Bernardino, California (Allen 1957), to its opening into the Pacific Ocean between the Islas Las Tres Mariás and mainland Mexico (Fig. 9; Moore 1973). In the central and southern peninsula, the Sierra Vizcaíno and possibly the Cape Islands remained isolated from the Peninsular Ranges. During the Pliocene, the Los Angeles (California) Basin was submerged beneath the Pacific Ocean. The combination of the flooding of the Los Angeles Basin and formation of the proto-Gulf of California greatly reduced terrestrial access to the top of the peninsula (Durham

and Allison 1960). It is possible that this narrow terrestrial connection was actually inundated by the Pacific Ocean (A. Orme, University of California, Los Angeles, personal communication, 1982), isolating the Baja California peninsula from the remainder of North America.

On the North American mainland, the middle Pliocene culmination of Miocene Cascadian orogenic events brought the Sierra Madre Occidental and Oriental and the Mexican Plateau to near their current high altitudes (King 1959; Eardley 1951). As a direct consequence of these orogenic events, the Cochise Filter Barrier became formidable to faunal exchange some 6–4 MYBP (Morafka 1977).

Paleoecology

These orogenic events seemingly had significant effects on the climate, and thus the flora as well. The newly formed, moderately high montane regions initiated the establishment of easterly rainshadows. As is supported by Axelrod (1975), the late Pliocene “climates in the middle latitudes (25–40 degrees north) were essentially equivalent to those of . . . the present” (Morafka 1977:179), although the deserts as we know them today did not develop until the last interglacial (Axelrod 1979).

Paleobotanical data are available from only a single fossil flora on Peninsular California, the Mount Eden Beds of southern California (Fig. 9). Axelrod (1937, 1950) showed that the terrestrial constriction at the head of the peninsula just 25 km west of the proto-Gulf of California was characterized by a mixture of Arcto-Tertiary and Madro-Tertiary assemblages. In total, eight habitats were represented: (1) desert; (2) arid subtropical scrub (similar to that in southern Baja California today); (3) coastal sage; (4) grassland; (5) chaparral; (6) live oak and walnut woodland; (7) digger pine woodland; and (8) big-cone conifer forest. Desert and arid subtropical (semi-desert) elements were presumably restricted to isolated exposed sites, such as steep schist and granitic hills in the basin of deposition; these were species that lived under conditions similar to those now found in the more mesic areas around the desert borders, rather than with real desert community. That the region was indeed mesic relative to true desert is supported by the occurrence of *Pinus sabiniana*, *P. coulteri*, *P.*

tuberculata, *Cupressus forbesii*, and *Pseudotsuga macrocarpa*.

Pliocene vertebrate fossils are available from the Mount Eden Beds of southern California and the Las Tunas local fauna of the Cape area of Baja California del Sur. The Mount Eden beds show both forest forms (sabre-toothed cats, wolves, and bears) and plains-grazing species (deer, antelope, horses, camels, boar and pigs, and four-toothed proboscideans) (Frick 1933). Judging from the modern flora as well as from both geologic and vertebrate evidence, this area was probably a low-lying basin occupied by shallow lakes and marshes, with adjacent highlands (Axelrod 1950). Terrestrial vertebrate fossils from the late Pliocene Las Tunas local fauna include one frog, a bird, and several reptiles and mammals (Miller 1979). The fossil herpetofauna consists of the unidentified frog, a tortoise (*Geocheilone*) related to species on the east coast of Mexico, a lizard (Iguanidae?), a boa (cf. *Boa*), a colubrid snake (*Pituophis?*), a rattlesnake (*Crotalus*) allied to the *C. atrox*-*C. ruber* group, and a crocodile (*Crocodylus* cf. *C. moreletii*). The presence of the crocodile, frog, and certain mammals indicates year-round fresh water.

Most of the shared taxa of the two localities consist of plains-grazing-type mammals (proboscideans, horses, camels, and antelope), although other mammals (woodrats and ground squirrels) and rattlesnakes are more characteristic of semiarid climates or subtropical savanna. Consequently, Miller (1980:801) felt that during the late Pliocene the area remained warm (no freezing) year-round, containing a relatively large, slow-moving stream in fairly close proximity to the Gulf, with the habitat one of subtropical savannas.

Paleobiogeography

Two scenarios can be deduced from the paleogeography and paleoecology of the late Miocene and early Pliocene. The constriction at the head of the peninsula may have been exceedingly important in forming a mesic filter barrier between xerophilic reptiles on either side of the proto-Gulf; i.e., the Baja California and Sonoran xerophilic species were isolated from one another in semidesert and dry tropic forest habitats. Alternatively, it is possible that a seaway isolated these same populations. In either event, the effects of this obstruction, termed the San Gor-

gonio Barrier, may have been as significant as those of the Cochise Filter Barrier, albeit not for so long a time.

The San Gorgonio Barrier (Fig. 9) should have prevented gene exchange between some or all populations. East-west reptile sister groups whose speciation may be attributable to this barrier include: tiger rattlesnakes (*Crotalus tigris*) and speckled rattlesnakes (*C. mitchellii*); red diamond rattlesnakes (*C. ruber*) and western diamondback rattlesnakes (*C. atrox*) (Fig. 10); and collared lizards (*Crotaphytus collaris*) and black-collared lizards (*C. insularis*). In addition, the barrier prevented the dispersal of such peninsula-evolved-and-restricted xerophilic taxa as the rat snakes (*Elaphe rosaliae*), banded rock lizards (*Petrosaurus mearnsi*), leaf-toed geckos (*Phyllodactylus nocticolus*), granite spiny lizards (*Sceloporus orcutti*), Baja California night snakes (*Eridiphas slevini*), and small-scaled lizards (*Urosaurus microscutatus*). These species belong to the Xerophilic Transpeninsular generalized track. Not only did the barrier prevent peninsular-evolved species from dispersing into other semidesert regions, it at least also prevented non-peninsular-evolved, desert-adapted reptiles from entering. Excluded taxa probably included xerophilic species belonging to the Marginal Species track such as the flat-tail horned lizards (*Phrynosoma mcalli*), brush lizards (*Urosaurus graciosus*), tree lizards (*U. ornatus*), and shovelnose snakes (*Chionactis occipitalis*).

Mesic-adapted (or mesic-tolerating) amphibians and reptiles were, of course, not restricted from or to the peninsula if a terrestrial continuum existed. Extant species such as the tiger whiptails (*Cnemidophorus tigris*), western blind snake (*Leptotyphlops humilis*), western aquatic garter snakes (*Thamnophis couchi*), striped racer (*Masticophis lateralis*), kingsnakes (*Lampropeltis getulus*), gopher snakes (*Pituophis melanoleucus*), and western rattlesnakes (*Crotalus viridis*) are among the taxa which currently occupy those habitats that Axelrod (1950) described as being characteristic of the Mount Eden Beds.

It could be argued that the seemingly strong constraints placed by the barrier on desert-adapted taxa may be due in part to the continued isolation of the Cape islands, which effectively prevented dispersal. We do not know when the Cape islands were joined via a terrestrial connection to the remainder of the Baja California

peninsula. Mina (1957) thought this occurred during the late Miocene or early Pliocene, whereas Durham and Allison (1960) placed it in the Pleistocene, and D. L. Anderson (1971) thought that the Cape area might have been isolated from about 25 to 3 MYBP. Inferences can be extrapolated from the herpetofaunal and fossil distributional patterns. If the Cape islands remained isolated from the remainder of the peninsula until the Pleistocene, then many of the Middle American elements and their Madro-Tertiary-associated derivatives (=Young Northern Elements of Savage 1960) would not be expected to have occurred on northern portions of the peninsula. Thus, we would not need to invoke the existence of the San Gorgonio Barrier to explain the peninsula-restricted distribution of many Baja California reptiles. However, if we assume that: (1) the southern, old islands were formed near the time when the Baja California peninsula was torn away from the North American plate, about 13 MYBP or later, as the geologic data suggest; (2) the Middle American Element-derived genera *Sauromalus* (chuckwallas) and *Dipsosaurus* (desert iguanas) evolved on the Cape islands; and (3) these two lizards' current distributions are primarily the result of vicariance events and not over-water dispersals, then a late Miocene or Pliocene Cape islands–Peninsular Ranges continuum is necessary in order to derive the Isla Santa Catalina (Fig. 1) herpetofauna, which contains both of these lizards. These assumptions are probable, considering the tectonic history of the region, the high degree of distinctiveness of the Santa Catalina Island herpetofauna (Murphy and Ottley, in press), and its close relationship to that of the Baja California peninsula rather than that of the mainland.

Miller (1980) encountered a similar biogeographical problem with his fossil data in finding close similarity of the Las Tunas local fauna to contemporaneous taxa in western North America. He concluded that the Cape islands were not isolated from 25 to 3 MYBP, as D. L. Anderson (1971) suggested, but rather that they had contact or near-contact with the mainland of Mexico near the northern edge of the state of Jalisco about 4 MYBP. Apparently Miller was unaware of the contributions of Atwater (1970), Atwater and Molner (1973), Christiansen and Lipman (1972), Gastil and Jensky (1973), Karig and Jensky (1972), and Smith (1976), which propose and

support the concept of middle Miocene Cape islands. The existence of a late Miocene–early Pliocene Cape–peninsula connection would explain contemporaneous taxa in the Cape and northward. Indeed, considering the geologic evidence for the origin of the Cape islands, Miller's data support the concept of a continuum uniting the Cape and the remainder of the peninsula by the Pliocene, permitting the interchange of subtropical thorn-scrub and chaparral herpetofaunas. This land bridge was only temporary, however; late Miocene and early Pliocene marine deposits occur across the Isthmus of La Paz (Beal 1948; G. A. Anderson 1950; Mina 1957; Durham and Allison 1960) (Figs. 8 and 9).

In summary, the paleoecological and paleogeographical events of the Pliocene reinforced the evolutionary trends which began in the Miocene. The persistence of the proto-Gulf of California and formation of the San Gorgonio Barrier isolated the developing xerophilic peninsular reptile populations from the remainder of western North America; in turn, nonpeninsular xerophilic populations were prevented from entering the peninsula. There was a continuous gene flow of mesic-adapted species across the narrow constriction at the head of the peninsula. The Cape islands' terrestrial connection with northern regions in the late Miocene or the early Pliocene was obliterated by the close of the Pliocene or early Pleistocene. In the Pliocene, Islas Santa Catalina and Monserrate (see below) were possibly formed by normal faulting from the peninsula and not from the mainland of Mexico. The Pliocene climatic trends of increasing aridity and declining temperature continued into the Pleistocene.

Pleistocene

The extent to which Pleistocene glacial events affected the distribution of amphibians and reptiles in Baja California has been a subject of controversy. Most previous biogeographers concerned with the evolutionary relationships of the Baja California herpetofauna (Schmidt 1922, 1943; Savage 1960) attributed the details of the modern distributions of many herpetofaunal elements to Pleistocene glacial events. Their studies were strongly influenced by, and to varying extents conform to, the "northern origin–southward dispersal" ideas of Matthew (1915). In contrast, Auffenberg and Milstead (1965) stated that

the most significant effect of the Pleistocene glaciations in the west was the drowning and formation of islands in the Gulf of California—and as will be shown, current paleoecological data support their ideas. Indeed, we have already seen that most of the peninsular distribution patterns can be explained by Miocene–Pliocene events. The same cannot be stated for most island populations, however, except for the southern old islands; i.e., the herpetofaunas of the northern old islands and the land-bridge islands were derived during the Pleistocene.

Paleogeography

The geography of Baja California and the islands in the Gulf of California changed considerably during the Pleistocene. Pasadenan orogenic events, as the result of Pacific and American plate interactions, continued the elevation of the Peninsular Ranges (Gastil et al. 1975), completed the Coast Range Corridor (Peabody and Savage 1958), and forced the Gulf of California to recede to its current position, although it widened as the peninsula continued its northwestern movement (Atwater and Molner 1973). Associated with these tectonic events was the formation, prior to 1 MYBP (Moore 1973), of the Ángel de la Guarda block, or island chain (except Isla Rosa), from peninsular material located north of the island block's current position (R. P. Phillips 1966) as shown in Figure 11. Both the Sierra Vizcaíno (Minch et al. 1976) and Cape islands (Mina 1957) were unified with the peninsula. Perhaps the single most significant event in relation to the Gulf of California island herpetofauna was the formation of land bridges between the peninsula and Gulf islands that were separated from it by an ocean depth of less than 130 m (Fig. 1), as a result of the lowered sea levels due to glaciation (Auffenberg and Milstead 1965).

Paleoecology

The Pleistocene was characterized by at least four southward expansions of the Laurentide Continental Glacier across North America, resulting in massive mammalian extinction (Evernden and Evernden 1970) and climate and habitat change. The extent to which Pleistocene glacial events changed the floral community structure may be significant for interpretation of the distribution patterns of Baja California amphibians and reptiles. Fortunately, the extent of

the change in western North America has been the subject of considerable attention and research during the past decade. Most of this research has been limited to the effects of the Wisconsin glaciation in the region around the head of the Gulf of California, from which extrapolations can be drawn on the extent of floral changes, especially as these affect the distribution of the Baja California herpetofauna.

Evidence elucidating the extent of habitat change with each consecutive glacial event has been reviewed by Axelrod (1966, 1975, 1979) and Van Devender and Spaulding (1979). Axelrod considered the Soboba-region (Fig. 9) habitats of the Aftonian, Yarmouthian, Sangamon, and Recent interglacials to be characterized by subhumid, semiarid, subdesert, and desert environments, respectively. Lower elevations of each interglacial were considered characteristically desert. The trend toward increasing aridity and spreading of desert habitats is strongly correlated with the formation of easterly rainshadows, which in turn are associated with increased elevation of the northern Peninsular Ranges and other mountain regions.

A single Pleistocene terrestrial vertebrate fauna has been reported from southern Baja California. Miller (1977) reported terrestrial mammals at several sites near San Miguel de Comondú associated with pluvial phases. Their presence implies "the presence of both wooded and grassland habitats, and hence a vegetation cover denser than that which now exists in these general areas in southern Baja California" (Axelrod 1979:33).

An abundance of data suggests a Mediterranean climate in the California region throughout the Wisconsin glaciation; apparently there was no drastic increase in winter rainfall (Fairbridge 1972; Saltzman and Vernecker 1975; Johnson 1977; Breckenridge 1978), as Arnold (1957) and Axelrod (1966) theorized. If the major change during the Wisconsin glaciation was lowering of the mean annual temperature by 7–8°C (Breckenridge 1978), what was the effect on the surrounding habitat? Packrat-midden studies (Cole and Van Devender 1976; Hendrickson and Prigge 1975; Phillips and Van Devender 1974; Van Devender 1974; Van Devender and King 1971; Van Devender and Spaulding 1979; Wells and Berger 1967; Wells and Jorgensen 1964) yield a predicted displacement of desert shrubs in the

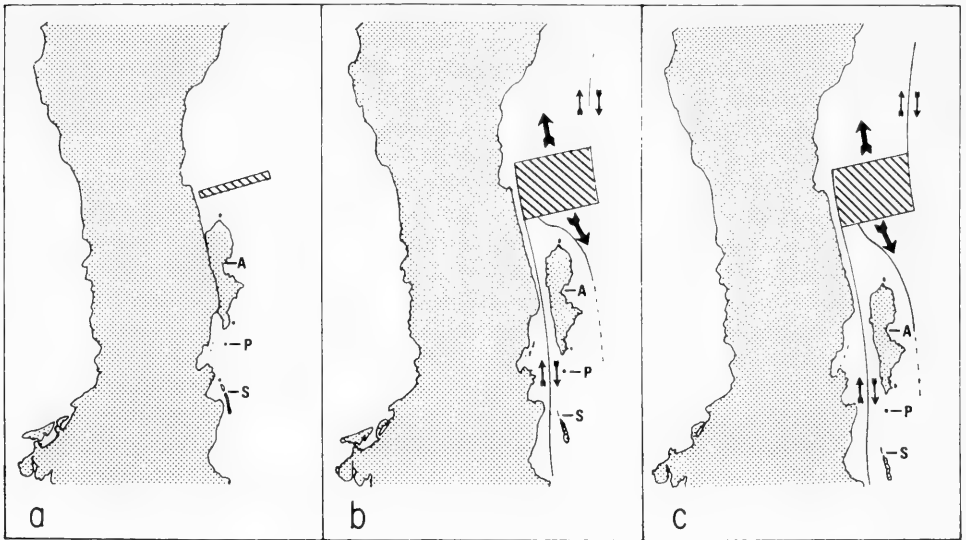


FIGURE 11. Sequential paleogeographic and tectonic reconstruction of the formation of the Ángel de la Guarda block, based on Moore (1973), Heney and Bischoff (1973) and R. P. Phillips (1966). (a) Reconstruction before plate movements, just prior to 1 MYBP; hatched region denotes the future location of the Delfin Basin spreading center. (b) Reconstruction of about 0.5 MYBP after the island block was formed; note the relatively northward direction of movement of the more westerly regions, as indicated by the arrows. (c) Reconstruction of the present. Islands are: A, Ángel de la Guarda; P, Partida Norte; S, San Lorenzo Norte and Sur.

southwest from about 1700 m elevation to near 700 m; i.e., the desert persisted at elevations below 700 m during the maximum extent of the Wisconsin glaciation 27,000–13,000 YBP. Moreover, the increased soil moisture afforded suitable conditions for coniferous woodlands 700 m lower into the deserts. The presumed displacement based solely on decreased annual temperature and not on increased rainfall is sufficient to account for the 750 m higher displacement of the habitats that Axelrod (1966) stated were modern equivalents of the Kansian Glacial Stage Soboba flora.

Paleobiogeography

At the beginning of the Pleistocene, the habitat communities of Baja California were more mesic than those of today. The San Gorgonio Barrier still existed. Later in the Pleistocene, when the Pacific Ocean and the Gulf of California receded as the peninsula presumably rose, and flora communities became essentially equivalent to those of today, a number of Sonoran Desert forms dispersed into the peninsula from around the head of the Gulf of California (Fig. 12). These immigrants, including the Colorado River toad (*Bufo*

alvarius), flat-tail horned lizard (*Phrynosoma mcalli*), and western shovelnose snake (*Chionactis occipitalis*), were able to occupy newly formed and vacant riparian (Colorado River) and sand-dune (Colorado River delta) habitats. Also invading this dune region were the Mojave Desert species, including the desert horned lizard (*Phrynosoma platyrhinos*), fringe-toed lizard (*Uma notata*), and sidewinder rattlesnake (*Crotalus cerastes*). The brush lizard (*Urosaurus graciosus*) may also be associated with Mojave Desert dispersal, although it is not dune-restricted. Similarly, a number of Chihuahuan–Mojave desert-adapted forms dispersed onto the peninsula, including the Great Plains toad (*Bufo cognatus*), longnose snake (*Rhinocheilus lecontei*), and checkered garter snake (*Thamnophis marcianus*). A number of arid-tolerant species dispersed onto the peninsula from the midwestern and eastern portions of North America; these include Woodhouse's toad (*Bufo woodhousei*), the leopard frog (*Rana* aff. *pipiens*), tree lizard (*Urosaurus ornatus*), and ringneck snake (*Diadophis punctatus*), all members of the generalized Marginal Species track of distribution (see Table 2).

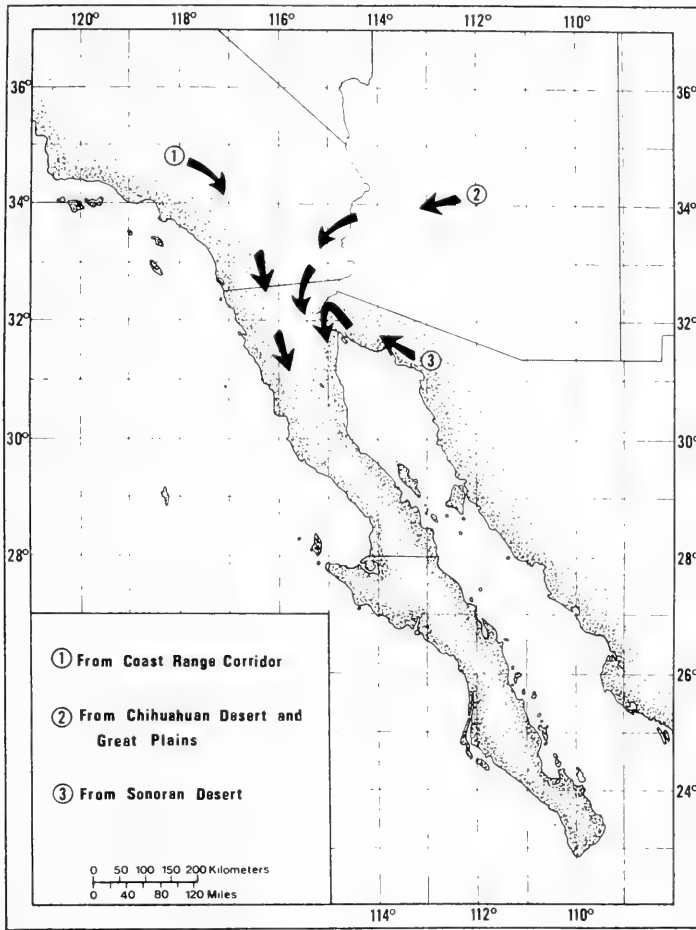


FIGURE 12. Dispersal routes of amphibians and reptiles that did not evolve on the Baja California peninsula. These dispersals occurred as result of the receding of the Gulf of California and elimination of the San Gorgonio Barrier.

Completion of the Coast Range Corridor (Peabody and Savage 1958) permitted the invasion of northern California forms (Fig. 12). Both oak-savanna- and chaparral-adapted elements, including two plethodontid salamanders (*Aneides lugubris* and *Ensatina eschscholtzi*) and the western fence lizard (*Sceloporus occidentalis*), utilized the corridor. The montane relicts of the Sierra San Pedro Mártir and Sierra Juárez, such as the sagebrush lizard (*Sceloporus graciosus*), California mountain kingsnake (*Lampropeltis zonata*), and western terrestrial garter snake (*Thamnophis elegans*), are only tentatively included, for they may represent Miocene–Pliocene invasions from further north.

With formation of the Coast Range Corridor,

members of the last major herpetofaunal assemblage, the Holarctic Element, entered (as noted by Savage 1960). These recent descendents of Asian forms, including the western toad (*Bufo boreas*), red-legged frog (*Rana aurora*), and the western pond turtle (*Clemmys marmorata*), crossed the Bering Land Bridge and subsequently dispersed southward along the west coast.

Formation of the Peninsular Desert in the Pleistocene divided and isolated the mesic-adapted populations into northern (chaparral) and southern (thorn-scrub) units. As a consequence, north-south mesophilic sister groups were formed, as exemplified by the California striped racer (*Masticophis lateralis*) and Cape striped

racer (*M. aurigulus*); western skink (*Eumeces skiltonianus*) and Cape skink (*E. lagunensis*); and southern alligator lizard (*Gerrhonotus multicarinatus*) and Cape alligator lizard (*G. paucicarinatus*). Moreover, development of the Sonoran Desert was probably responsible for the separation of a once-continuous population that is now represented by the Vizcaíno striped whiptail (*Cnemidophorus labialis*) and the little striped whiptail (*C. inornatus*) from Arizona.

Savage (1960) proposed that during the Pleistocene glacial maxima, desert-adapted herpetofaunal elements were forced south into Cape-area and Sonora-Sinaloa refugia (Fig. 5*d*). California-district chaparral elements dispersed southward, essentially occupying the entire peninsula. During interglacial periods (Fig. 5*e*), Sonoran Desert elements migrated from a mainland refugium around the head of the Gulf of California and onto the peninsula and Cape-area desert refugia forms dispersed northward, reforming the Peninsular Desert; chaparral elements were again isolated from one another. Savage's scenario is based upon two assumptions: that (1) drastic floral changes (expansions and contractions) occurred, and (2) herpetofaunal displacements were concomitant with the floral change. This thesis was not adopted by Auffenberg and Milstead (1965) or Cole and Van Devender (1976). Although Van Devender and Mead (1978) concurred with Savage's first assumption, they and the other critics proposed that massive herpetofaunal dispersals did not occur.

Additional evidence supporting Auffenberg and Milstead's view that the effects of the Pleistocene glaciation did not drastically affect herpetofaunal distributions in the southwestern regions of North America is based on an analysis of the southern peninsular xerophilic herpetofaunal elements. Fewer than 12% of the xerophilic species are restricted to desert habitats; the rest can survive in thorn-scrub environments as well. Furthermore, Asplund (1967) has shown that both the desert iguana and zebra-tail lizards survive well in Cape-area thorn-scrub forests, despite their northerly restriction to desert environments. These data strongly support the view that if environmental changes to the extent that Savage proposed did occur, their effects on distribution of most of the herpetofaunal elements would have been minimal. Moreover, the 12% of the herpetofauna apparently restricted to desert envi-

ronments may be found to be even less, once the Sierra de la Giganta has been adequately collected.

I will now consider Pleistocene events which influenced distribution of the herpetofauna on the islands in the Gulf of California. The islands of the Ángel de la Guarda block, including (north to south) Mejía, Ángel de la Guarda, Partida Norte, Salsipuedes, and San Lorenzo Norte and Sur (Fig. 1), belong to the same block that migrated from the mid-northern peninsular region (Fig. 11). Because this island group originated from northern Baja California near its current location just prior to 1 MYBP, it should have carried with it Pleistocene desert-adapted representatives. Indeed, this conclusion is supported by the fauna of this island chain (Murphy and Ottley, in press). Endemic forms whose ancestors probably occurred at mid-peninsula during the Pleistocene are found on most of the islands; these forms include the banded gecko (*Coleonyx* sp.), Angel leaf-toed gecko (*Phyllodactylus angelensis*), zebra-tail lizard (*Calisaurus draconoides*), black-collared lizard (*Crotaphytus insularis*), desert iguana (*Dipsosaurus dorsalis*), giant chuckwalla (*Sauromalus hispidus*), side-blotched lizard (*Uta stansburiana*), western whiptail (*Cnemidophorus tigris*), leafnose snake (*Phyllorhynchus decurtatus*), and speckled rattlesnake (*Crotalus mitchellii*).

Absence of the desert spiny lizard (*Sceloporus magister*) and granite spiny lizard (*S. orcutti*), both of which are widespread throughout the peninsula as well as on many other peninsula-associated islands, is especially notable. One explanation is that *S. magister* invaded the peninsula too recently to have occupied the geographic region that formed the island chain, while *S. orcutti* at that time was restricted to more mesic peninsular habitats. Neither possibility seems likely, considering the ecological associations and current distributions of both species groups. One or both of these large spiny lizards might occur on the islands but not have been collected, although it seems unlikely that the considerable collecting on the islands has not produced a single museum specimen. However, the desert spiny lizard may indeed occur on Ángel de la Guarda in very low densities; the late Dennis L. Bostic reported collection of single specimen (J. R. Ottley, Dept. of Biology, Brigham Young University, personal communication,

1979), although it cannot be located. Another possibility is that one, or both, did occur on the island at one time, but have become extinct.

There are no geological data on the age of Islas San Pedro Mártir, San Pedro Nolasco, and San Esteban. It can only be assumed that these islands are of Pliocene or Pleistocene origin as well (Gastil et al., in press).

The second major Pleistocene effect was the creation of land bridges between Gulf islands separated from the mainland by an ocean depth of less than 130 m, among them Islas San Francisco, San Ildefonso, San Marcos, Mejía (from Ángel de la Guarda), Tiburón (from Sonora, Mexico), Ballena, El Muerto, Espíritu Santo, Partida Sur, Smith, Danzante, Encantada Grande, Carmen, Coronado, San José, Las Ánimas and additional small islands (Fig. 1; see Murphy and Ottley, in press). Wilcox (1978) showed a strong correlation between species diversity and "age" of the islands; age was estimated by determining the minimum channel depth and speculating when the land bridges were eliminated as eustatic events began (about 14,000 YBP). However, many of the island "ages" are not the same, as can be determined from independent calculations of age based upon minimum channel depth provided by Gastil et al. (in press). Wilcox's conclusion may be a result of autocorrelation of his independent variables as revealed by ridge-regression analysis (S. J. Wright and R. W. Murphy, unpublished data). As originally pointed out by Auffenberg and Milstead (1965) and Soule and Sloan (1966), these shallow-water Gulf islands derived their fauna from the mainland at this time of lowered sea level.

In summary, a number of significant evolutionary events can be attributed to the Pleistocene. Most noteworthy are: (1) receding of the Gulf of California and elimination of the San Gorgonio Barrier; (2) immigration of nonpeninsular-evolved species; (3) formation and persistence of the central Peninsular Desert, with resultant formation of north-south sister species; (4) unification of the Cape islands and Sierra Vizcaíno with the peninsula; (5) formation of the Ángel de la Guarda island chain and speciation of the insular herpetofauna; and (6) eustatic lowering of the sea level at times of maximum glaciation, thereby forming land bridges. Distributions of the Baja California herpetofauna which were present from Miocene and Pliocene times

were not significantly affected by Pleistocene glacial events.

Holocene

The major Holocene (historical) physiographic events were the formation of three volcanic islands in the Gulf of California: Rasa, Encantada Grande, and Tortuga (Fig. 1; Gastil et al., in press), and peninsular volcanic eruptions such as those in the Tres Virgines in 1764 (Ives 1962).

Isla Tortuga, a basaltic lava island on which active steam fumaroles have been reported (Dixon 1966), is oceanic, situated in the Gulf of California 63 km east of the mainland and 31 km northeast of San Marcos, the nearest island. The derivation of the two lizard and three snake species on this oceanic island, which never had a land connection with the peninsula, must have been fortuitous (by rafting or swimming). Case (1975) noted the outstanding colonizing ability of the side-blotched lizards (*Uta*); and the granite spiny lizard (*Sceloporus orcutti*) also appears to be a good colonizer, as indicated by its broad insular distribution (Murphy, in press). The swimming ability of rattlesnakes is well known (Cochran 1954; Klauber 1972). Although there are no published data, the common kingsnake (*Lampropeltis getulus*) and the night snake (*Hypsiglena torquata*) both appear to be good swimmers and successful colonizers (Murphy, in press), as supported by known insular occurrences (Murphy and Ottley, in press). The only "surprise" of the island is taxonomic recognition of the Tortuga rattlesnake (*Crotalus tortugensis*), a derivative of *C. atrox*. Genetic drift resulting from the founder effect (Mayr 1963), possibly coupled with strong selection pressures, may have formed this morphologically unique population.

The herpetofauna of Isla Rasa consists of two lizards, Tinkle's leaf-toed gecko (*Phyllodactylus tinklei*) and the side-blotched lizard (*Uta stansburiana*). As with the Tortuga rattlesnake, selection pressures and random genetic drift must have been very strong to have rapidly formed the distinctive morphology of the leaf-toed gecko. Indeed, Gorman et al. (1975) showed that even though the Adriatic lizards of the family Lacertidae were isolated on islands during the Pleistocene lowering of sea level, the individual island populations could be morphologically distinguished from one another, although they were scarcely divergent at electrophoretically de-

TABLE 4. GENETIC SIMILARITY (I) BETWEEN CAPE AREA REPTILES AND THEIR PRESUMED SISTER SPECIES ON THE MEXICAN MAINLAND.

Cape Area Species	Mainland Mexico Species	No. of Loci	I
<i>Bipes biporus</i>	<i>B. canaliculatus</i>	20	0.47
	<i>B. tridactylus</i>		
<i>Sator angustus</i>	<i>Sceloporus utiformis</i>	—	0.46 ¹
<i>Sator grandaevus</i>			
<i>Phyllodactylus unctus</i>	<i>P. paucituberculatus</i>	23	0.41
<i>Sauromalus australis</i>	<i>Ctenosaura hemilopha</i>	28	0.42
			$\bar{x} = 0.44$
			SE = 0.02

¹ Converted from Immunological Distance.

tectable loci. Thus it can be questioned whether Tinkle's leaf-toed gecko or the Tortuga rattlesnake have differentiated sufficiently to be recognized as distinct species; however, until more data on both are available, the nomenclature is best left unaltered.

The foregoing scenario for evolution of the Baja California peninsular and insular herpetofauna necessitates consideration of the region as an evolutionary center. The formation of two distinct genera, the desert iguana (*Dipsosaurus*) and chuckwalla (*Sauromalus*)—possibly from the green iguana and spinytail iguana, respectively—cannot be considered anything less than major evolutionary events. The concept of Baja California as an evolutionary center strongly contradicts most previous thinking, which considered the region a refugium harboring relict species.

GENETIC DIVERGENCE OF INSULAR AND PENINSULAR POPULATIONS OF BAJA CALIFORNIA REPTILES: CORROBORATION OF THE SCENARIO

My scenario for the paleobiogeography of the herpetofauna of Baja California reviewed in the previous section will now be examined using genetic (electrophoretic) data to discuss concordances and to bring into conformity possible discordances with the predictions. The data base is preliminary, reflecting some work in progress, although a few published works will be cited. Details of the unpublished electrophoretic studies, including materials and methods, allele frequencies, sample size, method of cladistic analysis, etc., will be presented in forthcoming works. Here it need only be stated that the degrees of

genetic similarity (I) and genetic distance (D) for the pairwise comparisons are based upon summarization of the electrophoretic data, following Nei (1972). The "Biochemical Evolutionary Clock" (Sarich 1977) will be applied to the generalized patterns of genetic differentiation.

Peninsular Genetic Patterns and the Paleobiogeographic Scenario

Cape Area—Tropical Mainland Mexico

My paleobiogeographic scenario predicted that a number of taxa became isolated on the Cape islands as they were formed about 12–14 MYBP (Gastil and Jensky 1973). Genetic divergence estimates are available for five pairs of presumed sister species that occupy the Cape area of the Baja California peninsula and mainland Mexico (Table 4).

1. *Bipes*.—The mole amphisbaenians, genus *Bipes*, provide a clear example of transgulfian vicariance (Murphy 1975). Three species are usually recognized in the genus: two are found in the states of Michoacán and Guerrero, and the third is abundant in the Cape area, Magdalena Plains, and southern Vizcaino Desert zones of Baja California. The mainland and peninsular taxa presumably continue to occupy the same geographical regions as in pre-vicariance time (Fig. 13). An electrophoretic study by Kim et al. (1976) provided an I of 0.47 between the peninsular species *B. biporus* and its mainland relatives.

2. *Sator*—*Sceloporus utiformis*.—The genus *Sator* is restricted to three islands in the southern Gulf of California: Islas Santa Cruz, San Diego, and Cerralvo. The genus is not easily distin-

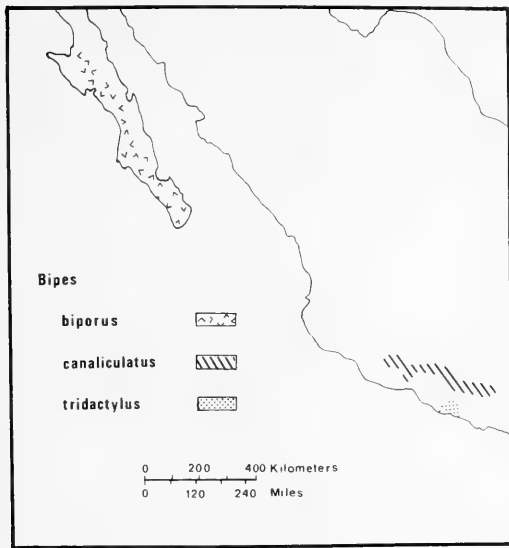


FIGURE 13. Distribution of the mole amphisbaenians, genus *Bipes* (after Kim et al. 1976).

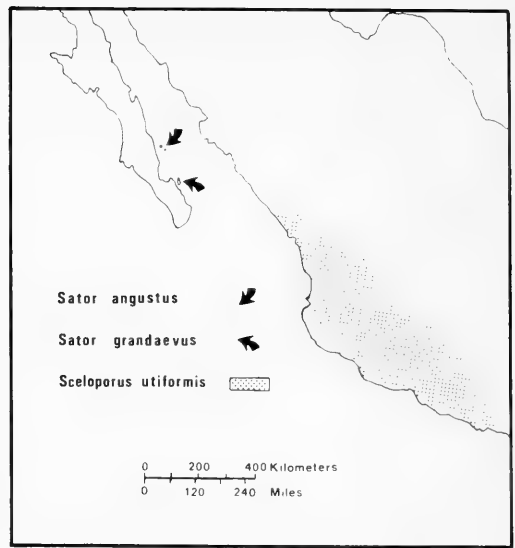


FIGURE 14. Distribution of the sator lizards, *Sator angustus* (Islas Santa Cruz and San Diego) and *S. grandaevus* (Isla Cerralvo), in the Gulf of California, and their closest relative, *Sceloporus utiformis*, on the mainland of Mexico (after Wyles and Gorman 1978).

guished from members of the genus *Sceloporus*, and early workers (Dickerson 1919; Schmidt 1922) suggested that *Sator* was most closely related to *Sceloporus utiformis*. An immunological study by Wyles and Gorman (1978) supports this idea. *Sceloporus utiformis* is widely distributed on the west coast of Mexico (Fig. 14). The immunological distance (I.D.) between the species pairs was determined to be a minimum of 23 units. Based upon the correlation of I.D. with *D* (Sarich 1977), it is possible to convert the I.D. value into *I*; the predicted *I* between *S. utiformis* and *Sator* is 0.46.

3. *Phyllodactylus unctus*—*P. paucituberculatus*.—There are approximately 20 species of leaf-toed geckos, genus *Phyllodactylus*, in North America, two of them currently recognized on the Baja California peninsula. The larger of these, *P. xanti*, occurs throughout the Peninsular Ranges; the smaller, *P. unctus*, is confined to the Cape area. *Phyllodactylus unctus* lacks enlarged scales called tubercles, which is unusual within this genus. Recently, a second population of non-tuberculate leaf-toed geckos was reported from Michoacán, Mexico (Dixon 1969); the overall morphological similarity between the two populations led Dixon to refer to the Michoacán population to *P. unctus*. Murphy and Papenfuss (1979) showed that the two "*P. unctus*" popu-

lations were not conspecific, and referred the Michoacán population to a previously described species, *P. paucituberculatus*. *Phyllodactylus unctus* and *P. paucituberculatus* are considered sister species, with an *I* of 0.41.

4. *Sauromalus*—*Ctenosaura*.—The chuckwallas, genus *Sauromalus*, are thought to be closely related to the spinytail iguanas, *Ctenosaura* (Mittleman 1942). My paleobiogeographic scenario infers that the chuckwallas evolved on the Cape islands. An *I* of 0.42 has been calculated for this pair.

5. *Eridiphas*—*Hypsiglena*—*Leptodeira*.—My paleobiogeographic scenario infers that the Baja California night snake, *Eridiphas*, became isolated from its ancestor as the Cape islands were formed. In this case, the ancestor also gave rise to both the night snakes, *Hypsiglena*, and the tropical-restricted cat-eyed snakes, *Leptodeira*. The *I*'s between each pair of these are much greater than those for the other presumed sister species. The most probable explanation for this discordance is that these genera did not diverge at the same time as the others. This seems likely because (1) the night snakes, *Hypsiglena*, are considered good over-water island colonizers (e.g., they occur on Isla Tortuga, an oceanic island);

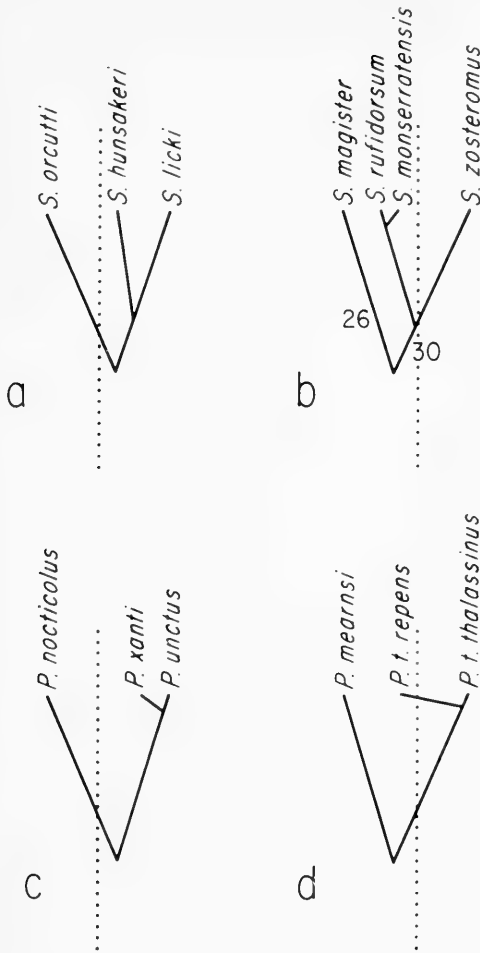


FIGURE 15. Cladograms depicting the phylogenetic relationships of four transpeninsular species groups of lizards: (a) granite rock lizards, *Sceloporus orcutti* complex; (b) desert spiny lizards, *Sceloporus magister* complex; (c) leaf-toed geckos, *Phyllodactylus*; (d) rock lizards, *Petrosaurus*. The dotted line divides the species north (left) and south (right) of the isthmus north of La Paz. Branches depict the relative amounts of genetic evolution as determined cladistically (except between the two subspecies of *Petrosaurus thalassinus*). Numbers on the tree branches in *b* are the $2n$ chromosome numbers within populations.

and (2) the Islas Las Tres Mariás, which have extant populations of night snakes (McDiarmid et al. 1976), were positioned near the Cape around 5 MYBP (Fig. 9; Gastil and Jensky 1973).

The I 's for the Cape islands-mainland species pairs (Table 4), exclusive of the snakes, are very similar to one another, with a mean value of 0.44;

TABLE 5. GENETIC SIMILARITY (I) BETWEEN TRANSPENINSULAR XEROPHILIC SISTER SPECIES.

Southern Species	Northern Species	No. of Loci	I
<i>Sceloporus hunsakeri</i>	<i>S. orcutti</i>	27	0.62
<i>Sceloporus licki</i>			
<i>Phyllodactylus unctus</i>	<i>P. nocticolus</i>	27	0.67
<i>Phyllodactylus xanti</i>			
<i>Petrosaurus thalassinus</i>	<i>P. mearnsi</i>	25	0.75
<i>Sceloporus zosteromus</i>	<i>S. "magister"</i>	28	0.76
<i>Urosaurus nigricaudus</i>	<i>U. lahtelai</i>	20	0.64
<i>Urosaurus microscutatus</i>			
			$\bar{x} = 0.69$
			SE = 0.03

indeed, the standard error of the mean is only 0.02 ($N - 1$ weighting). It is not possible to test the biogeographic hypothesis that these species formed on the Cape islands as the Cape broke away from mainland Mexico. The null hypothesis is that the peninsular taxa are more closely related to the tropical mainland Mexico sister species than to any other group. While a null hypothesis can never be proven to be true, I am unable to reject it with either *Bipes* or *Sator*. There are insufficient data with the leaf-toed geckos and chuckwallas to test the hypothesis.

Transpeninsular Xerophilic Species

Two patterns of transpeninsular non-transgulfian distribution have been identified: (1) in the intra-Cape area and (2) intra-peninsular. Because the Baja California peninsula is a north-south-tending, geographically isolated unit, the relationships within four of the five species groups are summarized by cladograms (Fig. 15) as well as I values (Table 5). Five group comparisons are available for analysis.

1. *Sceloporus orcutti* complex.—The granite spiny lizard complex consists of three species: *Sceloporus orcutti* on the Peninsular Ranges from southern California to the Isthmus of La Paz; *S. licki*, a rock-dwelling species in the Cape area; and *S. hunsakeri*, an arboreal Cape area endemic (Fig. 16; Hall and Smith 1979). The two Cape species are electrophoretically closer to each other, $I = 0.72$, than either is to *S. orcutti*, both I 's = 0.62. Moreover, the cladistic relationships (Fig. 15a) are concordant with these phenetic values, and all taxa appear to have equivalent rates of

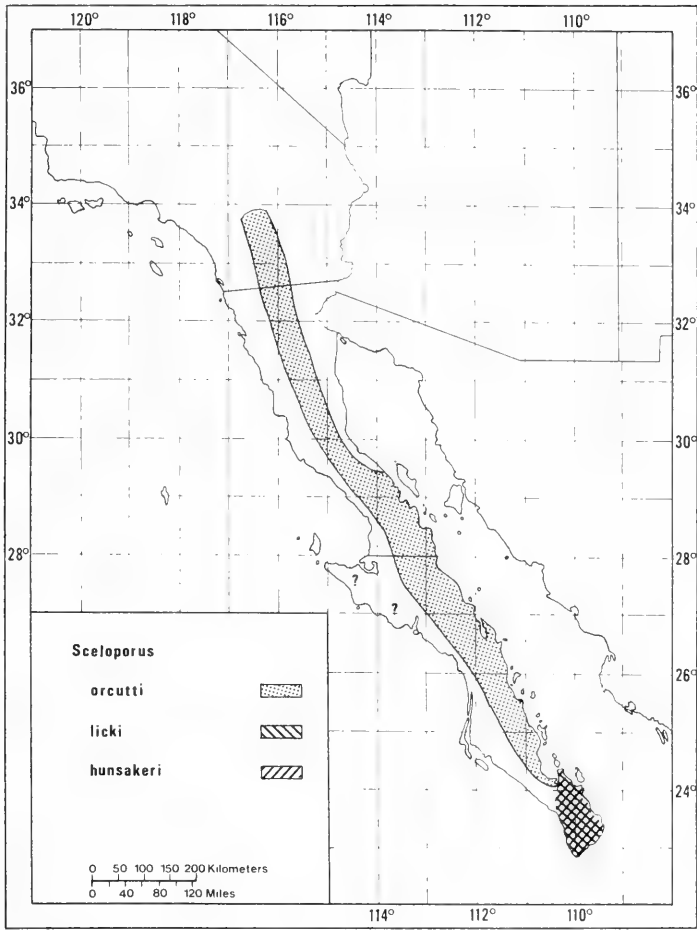


FIGURE 16. Peninsular distribution of the *Sceloporus orcutti* complex. Insular populations are not shown.

evolution; i.e., each has an essentially equivalent number of derived alleles in proportion to time, as determined cladistically (Kluge and Farris 1969).

2. *Phyllodactylus*.—A similar situation was found for the leaf-toed geckos. Three species, two of which are confined to the Cape area, can be biochemically and/or morphologically identified. The species on the Peninsular Ranges north of the Isthmus of La Paz is *Phyllodactylus nocicolus* (new combination), previously considered a subspecies of *P. xanti* (Dixon 1964, 1966). *Phyllodactylus xanti* is confined to the Cape area, where it is sympatric with the smaller, nontuberculate *P. unctus* (Fig. 17). Electrophoretic data indicate great complexity in this group, and per-

haps an uncoupling of morphological and biochemical evolution. As previously noted, the two sympatric, indeed syntopic, Cape area species are morphologically very different. However, there are no electrophoretic differences between the two in more than 25 presumptive gene loci sampled. Are they species, or could they be morphs, analogous to the association of cichlid fishes in the Cuatro Ciéneas region of Mexico (Sage and Selander 1975)? Both Cape area species have an I of 0.67 from the northerly sister species, *P. nocicolus*. The cladogram of the relationships of these leaf-toed geckos (Fig. 15c) is similar to that for the granite spiny lizards (Fig. 15a).

3. *Petrosaurus*.—The rock lizards, *Petrosaurus*, are also xerophilic, Peninsular Ranges species.

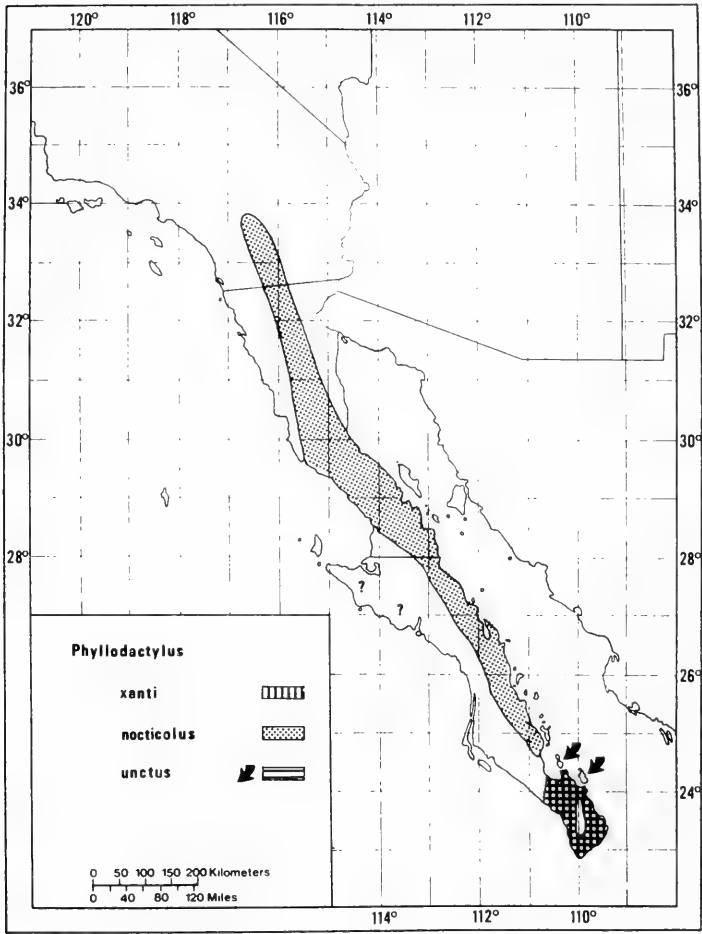


FIGURE 17. Peninsular distribution of the genus *Phyllodactylus* and insular populations of *P. unctus*. (*P. xanti* has not been recorded from any island.)

The banded rock lizard, *P. mearnsi*, is recorded from southern California to south-central Baja California Norte, and the larger, more colorful San Lucan rock lizard, *P. thalassinus*, occurs south of this region to the tip of the peninsula. The two species occur sympatrically over an approximately 50 km region in south-central Baja California Norte (Ottley and Murphy 1981), although only one or the other species strongly dominates a given rockpile. The two subspecies of the San Lucan rock lizard, *P. t. thalassinus* in the Cape area and *P. t. repens* north of the Isthmus of La Paz, are genetically indistinguishable, but both are well differentiated from the banded rock lizard, *P. mearnsi* (Fig. 15d), with an *I* of about 0.75.

4. *Sceloporus magister* complex.—The desert spiny lizard complex on the Baja California peninsula was previously recognized as consisting of four subspecies, *Sceloporus magister uniformis*, *S. m. rufidorsum*, *S. m. monserratisensis*, and *S. m. zosteromus*. However, these taxa can be divided into two major karyological groups (Hall 1973): *S. m. uniformis* and *S. m. magister* have a diploid complement ($2n$) of 26 chromosomes, whereas *S. m. rufidorsum*, *S. m. monserratisensis*, and *S. m. zosteromus* have a $2n$ of 30. The derived $2n = 30$ character state can be further divided on the basis of chiasmata frequencies, by which the karyotypes of *rufidorsum* are distinguishable from those of both *monserratisensis* and *zosteromus*, which are identical. These data sug-

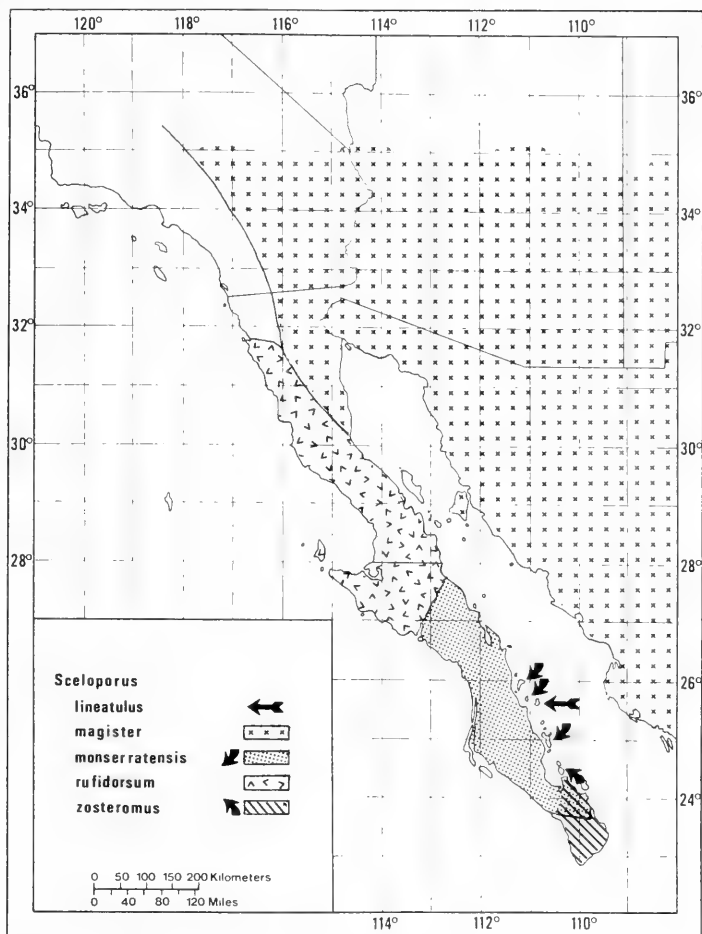


FIGURE 18. Distribution of the *Sceloporus magister* complex in southwestern North America following author's data and William P. Hall (1979, personal communication). The northern limit of *S. magister* is not shown.

gest that the races of *magister* (including *uniformis*), *zosteromus*, and *rufidorsum* should be recognized as distinct species; *monserratisis* would be considered a subspecies of *zosteromus* (Hall 1973, and personal communication, 1979). The biochemical data support some of Hall's findings (Fig. 15b). *Sceloporus monserratisis* and *S. rufidorsum* are very similar electrophoretically, with only a single locus separating them; there is no evidence that these two are hybridizing, even though the populations biochemically analyzed were only 20 km apart. These central peninsular populations have an I of about 0.70 to *uniformis* and $I = 0.77$ to *zosteromus*. Thus four peninsular species are now tentatively recognized: *S. magister*, including the subspecies *S.*

m. uniformis; *S. rufidorsum*; *S. monserratisis*; and *S. zosteromus* (Fig. 18).

5. *Urosaurus*.—The distributions of four Baja California species of tree lizards, *Urosaurus microscutatus*, *U. nigricaudus*, *U. lahtelai*, and *U. graciosus*, for which I 's have been calculated are shown in Figure 19. With the exception of *U. microscutatus* and *U. nigricaudus*, which I have not been able to distinguish electrophoretically, all species have I 's of 0.62–0.67 (Table 6).

As Figure 15 illustrates, there appears to be a clear trend. Measured by these methods, the southern taxa are genetically closer to one another than they are to the more northerly species. In my paleobiogeographic scenario, the Cape islands had a land connection with the remainder

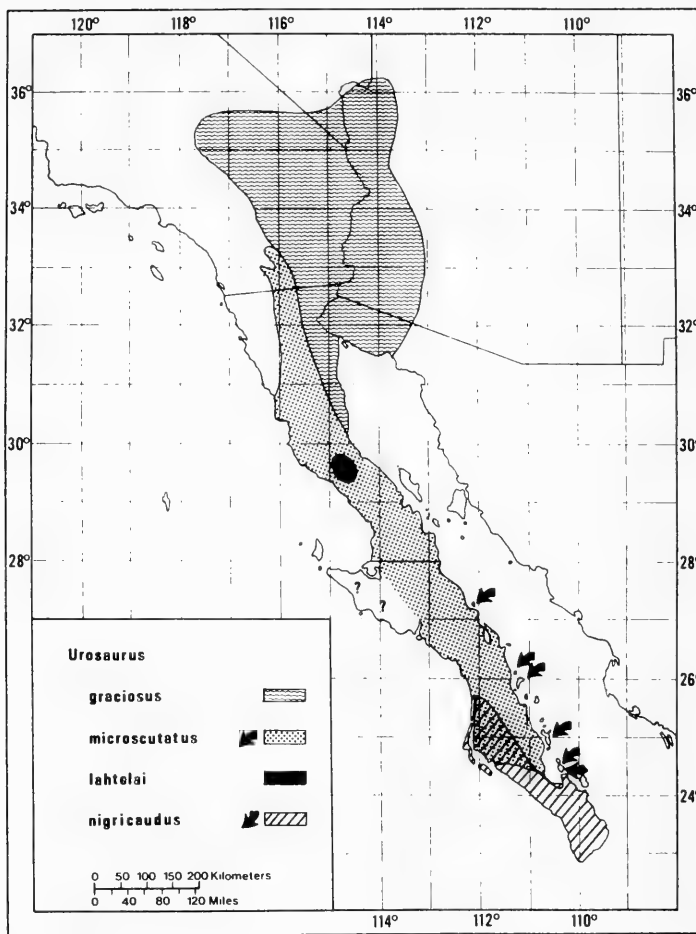


FIGURE 19. Distribution of four species of *Urosaurus* restricted to western North America.

of the Peninsular Ranges in the late Miocene or early Pliocene; more precise dating has not been determined by geologic methods. Biochemical data support the concept of an early Cape islands-peninsula connection that was subsequently obliterated, which would account for the Peninsular Ranges-restricted and/or -associated species.

Transpeninsular Mesophilic Species

My paleobiogeographic scenario inferred persistence of the mid-peninsula desert at low elevations during maximum glaciation. If the desert did persist, mesophilic reptiles and amphibians would have been restricted to the relatively mesic regions of the peninsula, particularly the Cape area and northern Peninsular Range. The gap in

the range would have occurred around the time of the Pliocene-Pleistocene boundary, about 2 MYBP. Data are available from a single pair of sibling species: the striped racer snake (*Masticophis lateralis*) found in the mesic regions of Baja California, and the San Lucan racer (*M. aurigulus*), which is confined to the Cape area (Table 2). The *I* of about 0.89 concurs with my scenario, considering that species of snakes distributed throughout the peninsula have *I*'s of about 0.97 between local populations from the Cape and southern California. It is important, however, to examine other mesic species pairs, such as *Gerrhonotus paucicarinatus*-*G. multicarinatus* and *Eumeces lagunensis*-*E. skiltonianus*, to further test this hypothesis.

East–West Xerophilic Species

The occurrence of multiple xeric-adapted species pairs on the east and west sides of the head of the Gulf of California was considered as evidence for formation of the San Gorgonio Barrier, which was presumed to have occurred around the Miocene–Pliocene boundary, about 5 MYBP. Three electrophoretic pair comparisons have been made.

1. *Crotaphytus insularis*—*C. collaris*.—The collared lizards, *Crotaphytus*, have previously been studied electrophoretically (Montanucci et al. 1975). Calculation of genetic similarity gives an average *I* of about 0.85 between the Baja California species, the black-collared lizard, *C. insularis*, and the western subspecies, *C. collaris*.

2. *Crotalus atrox*—*C. ruber*.—An *I* of 0.81 was derived from a study of the genetic differentiation between the red diamond rattlesnake of Baja California, *Crotalus ruber*, and its more easterly sibling, the western diamondback rattlesnake, *C. atrox*.

3. *Sceloporus magister*—*S. rufidorsum*.—The geographic distribution and genetic relationships of the desert spiny lizards were previously outlined. It is possible that the maintenance of genetic homogeneity between *Sceloporus rufidorsum* and *S. magister* resulted at least in part from the effects of the San Gorgonio Barrier. The *I* between these two lizards is about 0.75.

These three geminate species pairs have *I*'s that appear concordant with my paleobiogeographic scenario. The average value of *I* = 0.81 (standard error of *SE* = 0.04) indicates that a number of genetic changes have occurred in these populations and that there is no current genetic exchange between these species pairs.

East–West Mesophilic Species

The San Gorgonio Barrier would have prevented gene exchange between xerophilic taxa, but not mesophilic populations, if there was a terrestrial connection between the peninsula and what is now southern California. If gene flow was not interrupted for some taxa, mesic-adapted taxa isolated on either side of the Gulf of California should show very little genetic divergence. One snake and one lizard species have been investigated to date.

1. *Ctenosaura hemilopha*.—The spinytail iguana, *Ctenosaura hemilopha*, occurs on the Baja California peninsula from about Loreto south,

TABLE 6. GENETIC SIMILARITY (*I*) VALUES BETWEEN FOUR BAJA CALIFORNIA SPECIES OF TREE LIZARDS, GENUS *UROSAURUS*, BASED ON AN ANALYSIS OF 21 PRESUMPTIVE GENE LOCI.

	<i>U. nigricaudus</i>	<i>U. graciosus</i>	<i>U. lahtelai</i>
<i>U. microscutatus</i>	0.90	0.67	0.62
<i>U. nigricaudus</i>		0.65	0.67
<i>U. graciosus</i>			0.65

and on the Mexican mainland from central Sonora south to central Sinaloa. There is no significant difference between the two populations, although this may be the result of human activity. My paleobiogeographic scenario assumed that the chuckwalla, *Sauromalus*, were derived from the spinytail iguanas, yet the two occur sympatrically in Baja California. Another species of spinytail iguana, *C. similis*, is heavily exploited in some parts of its range, where it is a common source of meat (Fitch and Henderson 1978). It seems probable that a similar situation once existed with *C. hemilopha*. Mocquard (1899) reported that the lizard was commonly eaten by natives. The Indians who inhabited Baja California may have utilized *C. hemilopha* as a food item and brought it to the peninsula for this purpose. Thus caution should be exercised in interpreting these data.

2. *Lichanura trivirgata*.—The rosy boa, *Lichanura trivirgata*, is represented by three subspecies, *L. t. trivirgata*, *L. t. gracia*, and *L. t. roseofusca* (Ottley, Murphy and Smith 1980) (Fig. 20). *Lichanura t. trivirgata* is biochemically distinguishable from both *L. t. gracia* and *L. t. roseofusca* and is represented by two disjunct populations, one on either side of the Gulf of California, which cannot be distinguished from one another electrophoretically. As with the spinytail iguanas, the rosy boas do not provide clearcut evidence. The Sonora population may very well represent more recent colonization, perhaps in association with the milder winters at times of maximum glaciation.

Although these data suggest that some taxa were not affected by formation of the San Gorgonio Barrier, caution must be exercised in interpretation, because of the aforementioned variables and possibilities. Additional comparisons are necessary before any conclusions can be drawn.

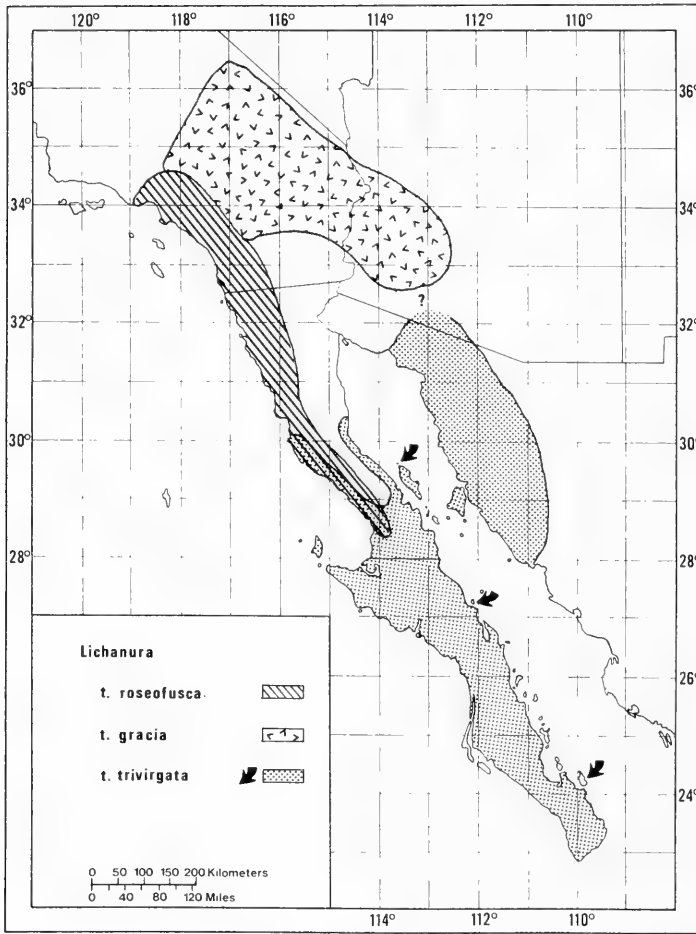


FIGURE 20. Distribution of the rosy boas, genus *Lichanura*.

Insular Genetic Patterns and the Paleobiogeographic Scenario

Genetic differentiation patterns of the peninsular populations establish a new data base for considering evolutionary and taxonomic relationships of the insular herpetofauna. For instance, the evolutionary relationships of the leaf-toed geckos, *Phyllodactylus*, and the spiny lizards, *Sceloporus*, are in need of review. Furthermore, the data necessitate reexamination of ecological scenarios such as the ones developed by Taylor and Regal (1978) and Seib (1980). Before meaningful conclusions can be drawn, however, we must examine in detail the patterns of genetic differentiation in the reptiles on the islands in the Gulf of California.

Electrophoretic data for over 30 Gulf island-peninsula species comparisons fall into four categories: (1) those for land-bridge islands, including Danzante, Espíritu Santo, and San Marcos; (2) old islands of continental origin, the Ángel de la Guarda block and associated islands; (3) an island of Pliocene–Pleistocene oceanic origin, Isla Monserrate; and (4) an old island of questionable origin and age, Isla Santa Catalina.

Concepts such as the levels of genetic variability of insular populations, the relict hypothesis (Brown 1957), the relationship of genetic differentiation to morphological evolution, and rates of evolution can be analyzed from the genetic data, and, significantly, phylogenetic relationships of the Gulf reptiles can be examined.

TABLE 7. GENETIC SIMILARITY (I) BETWEEN THREE LAND-BRIDGE ISLANDS AND THE ADJACENT PENINSULA.

Taxon	No. of Loci	Danzante	San Marcos	Espíritu Santo
<i>Sauromalus</i> sp.	26	0.99	0.99	0.92
<i>Cnemidophorus tigris</i>	24	0.95	0.95	—
<i>Dipsosaurus dorsalis</i>	32	—	0.96	0.98
<i>Phyllodactylus nocticolus</i>	28	0.99	0.99	—
<i>Phyllorhynchus decurtatus</i>	29	—	0.98	—
<i>Hypsiglena torquata</i>	30	0.98	0.97	—
<i>Trimorphodon biscutatus</i>	30	—	0.99	—
<i>Coleonyx variegatus</i>	37	—	1.00	—
<i>Sceloporus zosteromus</i>	28	—	—	0.94
	\bar{x} =	0.98	0.98	0.95
	SE =	0.01	0.01	0.02

These various facets of evolution will only be briefly touched upon here—and only in the context of the paleobiogeographic origin and relationships of the insular reptiles.

Land-Bridge Islands

As noted by Soulé and Sloan (1966) and Wilcox (1978), islands in the Gulf of California separated from a mainland source by a channel depth of less than 130 m (Fig. 1) probably had a terrestrial connection with the mainland at times of maximum glaciation; the land bridges were terminated about 14,000–6,000 YBP. Considering their relatively recent age, little, if any, genetic differentiation would be expected. Therefore, the I 's should be close to 1.00.

The island–peninsular species comparisons for Islas San Marcos, Danzante, and Espíritu Santo are given in Table 7. Out of 14 comparisons, unique alleles were detected for only 2 populations: the whiptail lizard (*Cnemidophorus tigris*) on Isla San Marcos and the chuckwalla (*Sauromalus ater*) on Isla Espíritu Santo. In the whiptail comparison, the discrepancy of a single unique allele in the island population is not surprising considering that this species has the highest level of genetic variability detected in any species of reptile examined to date (Gorman et al. 1977; Murphy, unpub. data). The chuckwalla comparison is not fully resolved. No genetic comparisons were made between the Cape area population of *Sauromalus* and that on Isla Espíritu Santo; the nearest available population sampled was from about 60 km north of the Isthmus of La Paz. It is possible that the Cape area population (Shaw 1945) is identical to that on Islas

Espíritu Santo and Partida Sur and represents a discrete taxon.

It should be pointed out that in most instances of comparison, the standard error (SE) of D , a log transformation of I , is larger than the D itself; and in all instances, two standard errors are larger than the genetic distance value. The SE of D is used for statistical purposes, because there is no established method for determining the SE of I ; thus neither the D 's nor I 's differ significantly from zero. These data concord with the assumptions of my paleobiogeographic scenario and with population genetics theory and what we know about mutation rates.

Old Islands

The herpetofauna representative of five old islands, four of which are thought to be of continental origin, were examined. Seven comparisons were made for Isla Monserrate, and six for Ángel de la Guarda and associated islands. My paleobiogeographic scenario presumes that the former is much older than the latter.

1. Isla Monserrate.—The precise geologic age of Isla Monserrate, a southern island in the Gulf of California (Fig. 1), is somewhat uncertain. It is composed of Miocene and younger volcanic and middle Pliocene marine rock overlaid in areas by early Pleistocene gravels. It was volcanically active during the Pleistocene, and perhaps as recently as several thousand years ago (G. A. Anderson 1950). An oceanic island formed from the uplifting of the ocean floor; it may never have had a terrestrial connection with the peninsula (contrary to Wilcox 1980), because the minimum

TABLE 8. GENETIC SIMILARITY (I) BETWEEN REPTILES ON ISLA MONSERRATE AND THE ADJACENT PENINSULA.

Isla Monserrate	Peninsula	No. of Loci	I
<i>Phyllodactylus nocticolus</i>	<i>P. nocticolus</i>	28	0.97
<i>Uta stansburiana</i>	<i>U. stansburiana</i>	27	0.75
<i>Sceloporus monserratenis</i>	<i>S. monserratenis</i>	28	0.93
<i>Sauromalus slevini</i>	<i>S. australis</i>	26	0.87
<i>Chilomeniscus cinctus</i>	<i>C. cinctus</i>	31	0.87
<i>Phyllorhynchus decurtatus</i>	<i>P. decurtatus</i>	29	0.98 ¹
<i>Crotalus ruber</i>	<i>C. ruber</i>	36	0.99
		$\bar{x} = 0.91$	
		SE = 0.03	

¹ From Murphy and Ottley (1980).

channel depth is about 160 m (Gastil et al., in press).

Island-peninsula comparisons have been made for four pairs of lizards and three pairs of snakes: *Uta* cf. *stansburiana*, *Sceloporus monserratenis*, *Sauromalus* sp., *Phyllodactylus nocticolus*, *Chilomeniscus cinctus*, *Phyllorhynchus decurtatus* (Murphy and Ottley 1980), and *Crotalus ruber* (Table 8). The average I of 0.91, with a standard error of 0.03, is considered conservative, because if Isla Monserrate was of oceanic origin the extant herpetofauna would have of necessity arrived by over-water colonization, and not all colonists would have arrived at the same time. Three of the taxa on Isla Monserrate, the red diamond rattlesnake (*Crotalus ruber*), leafnose snake (*Phyllorhynchus decurtatus*), and leaf-toed gecko (*Phyllodactylus nocticolus*), have much lower values of I than the remaining pairs (Table 8). Rattlesnakes are known to be good over-water colonizers (Klauber 1956, 1972), and so are leaf-toed geckos as evidenced by their presence on Islas Farallón and Rasa, volcanic oceanic islands in the Gulf of California (Murphy and Ottley, in press). I assume that the leafnose snake is also capable of over-water dispersal (Murphy, in press). Moreover, the I 's for the pairs of leaf-toed geckos, red diamond rattlesnakes, and leafnose snakes (Table 8) are typical for reptile populations on land-bridge islands (Table 7). The average I , then, based only upon the remaining four pairwise comparisons, is 0.86 ± 0.04 ; this probably more accurately reflects the expected level of genetic differentiation. The data support consideration of Isla Monserrate as an old or oceanic island and not a land-bridge island.

2. Ángel de la Guarda and associated islands.—The Ángel de la Guarda block is thought to have been formed sometime prior to 1 MYBP from the Baja California peninsula (Moore 1973). Reptiles inhabiting these islands would not be expected to have undergone a significant degree of genetic differentiation except through the random fixation of rare alleles. Data are available for the chuckwalla (*Sauromalus*) and the side-blotched lizards (*Uta*) (Table 9). I am indebted to Dr. Michael Soulé for permission to report portions of his unpublished data on northern populations of *Uta*.

Of the four available comparisons, only the *Uta* population from Isla Rasa and the chuckwalla, *Sauromalus hispidus*, population from Isla Smith have any notable degree of genetic differentiation, but these I 's are high. Because of the relatively high standard error of the respective D 's, the values are not considered significant, but it seems noteworthy that the genetic differentiation between *U. antiqua* of San Lorenzo Sur and peninsular populations of *U. stansburiana* is equivalent to that found for land-bridge islands (Table 7). This is another case of the apparent uncoupling of genetic and morphological evolution.

Summary

There are a number of concordances between the patterns of genetic differentiation and my paleobiogeographic scenario. An accurate test of the scenario would require the construction of cladograms for multiple species groups. Those that have been constructed (Fig. 15) seem to concord with that part of the vicariance scenario which hypothesized the connection of the Cape islands with the peninsula and the existence of two major islands composing the Cape islands (Fig. 9). My hypothesis that the Cape islands were responsible for the formation of a number of distinctive taxonomic forms, as they broke away from the mainland, has some corroboration. For instance, Wyles and Gorman (1978) suggested that *Sator angustus* and *S. grandaevus* formed a terminal node with *Sceloporus utiformis*; and there can be little doubt about the relationship of the transgulfian mole amphibaenians, genus *Bipes*. Finally, Mittleman (1942) stated that *Ctenosaura*, the genus of the spinytail iguana, was most closely related to the chuckwalla genus *Sauromalus*; the splitting of these

TABLE 9. GENETIC SIMILARITY (I) BETWEEN HERPETOFAUNA ON THE ÁNGEL DE LA GUARDA ISLAND BLOCK AND THE PENINSULA.

Island	Island Taxon	Peninsula Taxon	No. of Loci	I
Ángel de la Guarda	<i>Uta stansburiana</i>	<i>U. stansburiana</i>	16 ¹	0.98
Rasa	<i>Uta stansburiana</i>	<i>U. stansburiana</i>	16 ¹	0.91 ²
San Lorenzo Sur	<i>Uta antiqua</i>	<i>U. stansburiana</i>	16 ¹	0.98 ³
Smith ⁴	<i>Sauromalus hispidus</i>	<i>S. obesus</i>	26	0.92

¹ Data from Dr. Michael Soulé (personal communication).

² I is to Isla Ángel de la Guarda.

³ I = 1.00 to Isla San Esteban.

⁴ It is assumed that the Isla Smith population was derived from the Ángel de la Guarda block as the result of Indian activity.

genera forms a terminal node in the proposed phylogeny. This phylogeny, however, is not based upon cladistic principles, and other researchers, such as Avery and Tanner (1971), propose alternative trees also based upon phenetic analyses and also are not phylogenetic.

The relative degree of genetic differentiation between pairs of species on the various islands also seems concordant with my paleobiogeographic scenario and concepts of evolutionary population genetics. Populations on older islands seem to have less genetic similarity with their presumed sister species on the peninsula than do populations on younger islands.

The patterns of genetic divergence of the Baja California herpetofauna correlate with five major tracks of distribution. The Transpeninsular Xerophilic Species track seems to have either one species which extends throughout the peninsula and exhibits little or no genetic differentiation, or species groups with north-south species distribution whose pairs appear to have essentially equivalent genetic divergence. The Transpeninsular Mesophilic Species track has species with less genetic change than the xerophilic forms. Members of the Southern Species track are, for the most part, sister species to those on one of the above tracks. Little significant biogeographic information can be gained from intrapeninsular genetic data from Ubiquitous Species and Marginal Species track taxa.

One theme continues to appear in the comparisons. Species belonging to the same generalized track and with similar patterns of phylogenetic relationships have essentially equivalent amounts of genetic differentiation—i.e., similar values of I . Because of this pattern, it seems appropriate to examine these findings in light of the Biochemical Evolutionary Clock Hypothesis as applied to electrophoretically derived allozyme data (Sarich 1977).

The "Clock" and the Paleobiogeographic Scenario

There has been substantial support for the concept of a Biochemical Evolutionary Clock (e.g., Wilson et al. 1977; Wawter et al. 1980). This is a stochastic measurement, providing estimates of times of divergence among genetically isolated populations, rather than an accurate chronometer. The clock has been applied to multi-locus electrophoretic studies in which genetic distance (D ; Nei 1972) may be calculated, and to studies of albumin immunological distance (I.D.; Sarich 1969) in which divergence at a presumptive locus may be measured. Sarich (1977) demonstrated that these two units of measure are highly correlated. Because I.D. is presumed to be highly correlated with geologic time (Maxson et al. 1975), it is assumed that D is also highly correlated.

The existence and/or general applicability of the clock have recently been challenged (e.g., Throckmorton 1978; Farris 1981). Most of the criticisms are centered on its stochastic nature, the nonmetric qualities of D , and assumptions of clustering techniques. As Farris (1981:22) notes: "The nonmetricity of Nei's distance shows that there never was an electrophoretic clock, at least one precise enough to show kinship directly." I concur with Farris that a matrix of D values cannot be clustered in infer divergence times and thus kinship within taxonomic groups, because of both the nonmetricity of D and the violation of geometric laws inherent in the clustering of distance matrices and/or similarity coefficients. There is, however, one valuable application of the clock which is not dependent upon clustering techniques.

Multiple pairwise comparisons will yield average values of genetic differentiation between sister species in separated, or once separated,

geographic regions, and thus this method has great potential as a biogeographic tool. Because the genetic distance data are not clustered, the non-metric attributes of D are of no consequence; in this application, D is only a relative measure of genetic divergence. Moreover, the use of multiple geminate species pairs will minimize the variation in observed D 's that results from the stochastic acquisition of new genetic information (alleles). Vawter et al. (1980) used this technique to examine genetic differentiation between populations of fishes from the eastern Pacific and western Atlantic (Caribbean) oceans. They found that sister species (including allopatric populations of the same species) from either side of the Isthmus of Panama had essentially equivalent levels of genetic differentiation. Calibration of their clock, however, was based on the correlation between I.D. and D (Sarich 1977), which equates a D of 1.0 with 18.9 MY of separation. Because I.D. is correlated with geologic dates and D is correlated with I.D., it follows that D is also strongly correlated with geologic divergence. However, Sarich's (1977) plot of the relationship between I.D. and D (his fig. 1, p. 25) shows a fair amount of variation around the regression line. It is impossible to determine from the correlation between I.D. and D just how much variation exists between D and geologic time. It is far preferable to calibrate such a D -based clock by directly correlating D 's with geologic dates.

For a biochemical clock to work two major assumptions must be made. (1) There must have been a vicariance event resulting in the formation of two or more populations with effectively equal numbers of individuals in terms of theoretical population genetics. New populations formed through dispersal of only a few individuals will show founder effects (Mayr 1963), which will distort the relative degree of genetic divergence between two geminate populations. (2) The habitats of the two new populations must be essentially equivalent, or at least diverge at parallel rates. If they diverge at unequal rates, natural selection could, and probably would, result in unequal rates of fixation of new or rare alleles, thereby distorting the amount of genetic differentiation between geminate species and making meaningful interpretation impossible. In other words, the two once-continuous populations must have undergone essentially equivalent amounts

of genetic change since the vicariance event, thus acquiring the same number of new alleles or character states. Unfortunately, most clock applications of electrophoretic data do not meet, consider, nor even acknowledge these assumptions, and there are probably very few geographic areas where this method of data analysis can be properly used.

These assumptions do seem to be probable for the species pairs that I have examined. Therefore the clock is applied in this study on a very limited basis. Multiple species pairs are used to corroborate hypothesized vicariance events and estimate the time of formation (or colonization) of an island of unknown age, Isla Santa Catalina. The clock first needs to be calibrated. For three transgulfian lizard pairs and one amphibaenian species pair, the mean value of I converts to an average D of 0.82. As it is thought that the Cape islands were formed in the middle Miocene, about 12–14 MYBP (Gastil and Jensky 1973), I consider a D of 0.82 equal to 13 MY of divergence. Each D of 1.00 equals roughly 16 MY of separation.

Table 10 summarizes the available electrophoretic data on estimated times of divergence (ETD) for five hypothesized vicariance events. The concordance between the ETD's and the geologic times of divergence (GTD) is exceptional; linear regression analysis yields a correlation coefficient of $r = 0.98$ between them, which is highly significant ($P < .001$). Genetic data for the Ángel de la Guarda block (Table 9) are excluded from the clock analysis, as only a single pair comparison is available for any given island and because of the relatively few presumptive gene loci scored for the side-blotched lizards (*Uta*).

This method of applying clock theory seems to provide a valuable, highly predictive, and corroborative tool for paleobiogeographical analysis.

Santa Catalina, an Island of Questionable Age

Both the precise locality of its continental origin and the age of Isla Santa Catalina (Fig. 1) are somewhat uncertain. My paleobiogeographic scenario infers from the geologic evidence that

TABLE 10. ESTIMATED TIMES OF DIVERGENCE (ETD) OF THE SISTER SPECIES PAIRS COMPARED TO THE GEOLOGIC TIMES OF DIVERGENCE (GTD). Divergence times are expressed in millions of years before present (MYBP).

Vicariance Comparison	No. of Sp. Pairs	Mean $I \pm 1$ SE	ETD ± 1 SE (MYBP)	GTD (MYBP)
Trans-Gulf of California	4	0.44 \pm 0.02	13.1 \pm 0.6	12-14'
Transpeninsular Xerophilic	5	0.69 \pm 0.03	5.9 \pm 0.7	Late Miocene
East-West Xerophilic	3	0.81 \pm 0.04	3.0 \pm 0.5	Early Pliocene
Land-Bridge Islands				
Danzante	4	0.98 \pm 0.01	0.4 \pm 0.2	0.01
San Marcos	8	0.98 \pm 0.01	0.3 \pm 0.1	0.01
Espiritu Santo	3	0.95 \pm 0.02	0.9 \pm 0.3	0.01
Old Island				
Monserrate	7	0.91 \pm 0.03	1.6 \pm 0.5	Pleistocene

¹ GTD used for calibration of the Biochemical Evolutionary Clock.

this granitic island became separated from the peninsula after formation of the proto-Gulf of California some 5-6 MYBP. The composition of the herpetofauna suggests that this occurred after initial formation of the continuum between the Cape islands and the peninsula, but long enough ago for the island species to substantially differentiate from the source populations.

Comparisons were made between Santa Catalina Island and adjacent peninsular populations of *Uta*, *Sceloporus* cf. *monserratis*, *Sauromalus*, *Cnemidophorus* cf. *tigris*, *Dipsosaurus*, *Phyllodactylus* cf. *nocticolus*, *Hypsiglena*, and *Crotalus* cf. *ruber*, and also with populations on nearby Isla Monserrate (Table 11), yielding an average ETD of 2.51 ± 0.53 MYBP. As with the

Isla Monserrate-peninsula comparison, this estimate is considered conservative because it includes the low I 's for two pairs of good over-water colonizers, rattlesnakes (*Crotalus catalinensis* and *C. ruber*) and the leaf-toed geckos (*Phyllodactylus bugastrolepis* and *P. nocticolus*). Indeed, the I for the geckos (Table 11) is typical for populations on land-bridge islands (Table 7), and a very low level of heterozygosity in the Santa Catalina population suggests over-water colonization. Elimination of these two taxa from the calculations results in an average I of 0.82, which converts to an ETD of 3.1 MY.

This estimate of time of divergence for the Santa Catalina herpetofauna is higher than that for Isla Monserrate (ETD = 2.4 MYBP). Empir-

TABLE 11. GENETIC SIMILARITY (I) AND ESTIMATED TIMES OF DIVERGENCE (ETD) IN MILLIONS OF YEARS BETWEEN REPTILE POPULATIONS ON SANTA CATALINA AND THE PENINSULA, AND ISLA MONSERRATE AND ISLA SANTA CATALINA.

Taxon	I			No. of Loci	
	Monserrate vs. Santa Catalina	Peninsula vs. Santa Catalina	Monserrate vs. Peninsula		
<i>Phyllodactylus bugastrolepis</i>	<i>P. nocticolus</i>	<i>P. nocticolus</i>	0.98	0.98	28
<i>Dipsosaurus dorsalis</i>		<i>D. dorsalis</i>		0.87	31
<i>Uta squamata</i>	<i>U. stansburiana</i>	<i>U. stansburiana</i>	0.76	0.75	27
<i>Sauromalus klauberi</i>	<i>S. slevini</i>	<i>S. australis</i>	0.90	0.81	26
<i>Sceloporus lineatulus</i>	<i>S. monserratis</i>	<i>S. monserratis</i>	0.85	0.88	28
<i>Cnemidophorus catalinensis</i>		<i>C. tigris</i>		0.80	24
<i>Hypsiglena catalinae</i>		<i>H. torquata</i>		0.83	29
<i>Crotalus catalinensis</i>	<i>C. ruber</i>	<i>C. ruber</i>	0.94	0.94	36
		ETD	\bar{x} = 2.0	1.60	
			SE = 0.8	0.64	

ical analysis of the data seems to support an estimate of equivalent ages for the two islands, and the T 's calculated for *Uta* from both islands to the mainland are identical (Tables 8 and 11). But surprisingly, the population of *Uta* on Monserrate was found to be morphologically identical to that of the peninsula (Ballinger and Tinkle 1972). Both island populations have an equivalent number of derived alleles, but they are not shared. These findings suggest separate colonizations; the Santa Catalina population was not derived from Isla Monserrate, nor vice versa. This also appears to be true for the lizards of the *Sceloporus magister* complex, but not for the chuckwallas. The chuckwallas share a unique, derived allele at a single locus, suggesting that the common ancestor differentiated in isolation on an island and not on the peninsula. However, it cannot be determined which of these two islands contained the parent population.

Although the leaf-toed gecko population on Santa Catalina has not differentiated biochemically from peninsular populations of *Phyllodactylus nocticolus*, it has a karyotype that can be considered derived (Murphy, in preparation) and may be unique for North American leaf-toed geckos. The karyotype of *P. nocticolus*, the closest relative of *P. bugastrolepis*, consists of a diploid complement of 38 acrocentric chromosomes in a graded series. The karyotype of *P. bugastrolepis* is identical in having a $2n$ of 38, but differs in the occurrence of two pairs of metacentrics (Fig. 21). Apparently, the Isla Santa Catalina population has undergone pericentric inversions at two pairs of chromosomes. Findings on the Islas Espíritu Santo and Cerralvo populations of *Cnemidophorus hyperthrus* and *C. ceralbensis*, respectively (Robinson 1973), are analogous.

Similarly, the rattleless rattlesnake (*Crotalus catalinensis*) is not electrophoretically well differentiated from the red diamond rattlesnake (*C. ruber*), with only one unique allele at a single locus. But besides the absence of a rattle matrix, *C. catalinensis* is much slimmer than most other species of *Crotalus* and behaviorally appears to be unique both in being very agile, with relatively rapid locomotion, and in its tendency to climb bushes, attaining heights of over 1 m. These attributes, when combined with the allozyme observations, provide yet another example of the

apparent uncoupling of relative rates of evolution.

If Monserrate and Santa Catalina are essentially equivalent in age, is Santa Catalina also an oceanic island? Three sources of information, two biological and one geological, suggest that it is of continental origin. First, the presence of the fossorial Santa Catalina island blind snake (*Leptotyphlops humilis levitoni*) suggests that the island was once connected to either the Baja California peninsula or mainland Mexico (Murphy 1975), although the herpetofaunal assemblage suggests that the connection was with the peninsula. Second, the higher level of endemism may indicate greater antiquity of the reptile population on Isla Santa Catalina. Indeed, this would be expected if Santa Catalina is of continental origin whereas Monserrate is oceanic. As previously noted, there seems to be an uncoupling of the rates of morphological evolution from time. Santa Catalina is primarily granitic in geologic composition, and is probably related (along with Islas San Diego, Santa Cruz, and Cerralvo) to the granitic rocks that compose the southern tip of the peninsula (G. A. Anderson 1950:43). No extensive marine beds have been reported. Santa Catalina may once have been submerged beneath the Gulf, but there does not seem to be any geologic evidence of this; it seems far more likely that this island is of continental origin.

SUMMARY

Biochemical data for various vicariance events and for land-bridge and old islands were analyzed in relation to my paleobiogeographic scenario. I found relatively older vicariance events associated with species pairs having relatively lower values of genetic similarity. My scenario, like the population genetics theory, assumes that no significant genetic differentiation should have occurred between land-bridge islands and the peninsula, as long as natural selection was not rapidly changing gene frequencies.

My scenario also presumes that little genetic differentiation should have occurred in reptiles on islands of the Ángel de la Guarda block, and that the genetically most distinctive populations should be found on southern old islands. These suppositions proved concordant with the biochemical findings. Two genera of lizards on the midriff islands were examined. The side-blotched

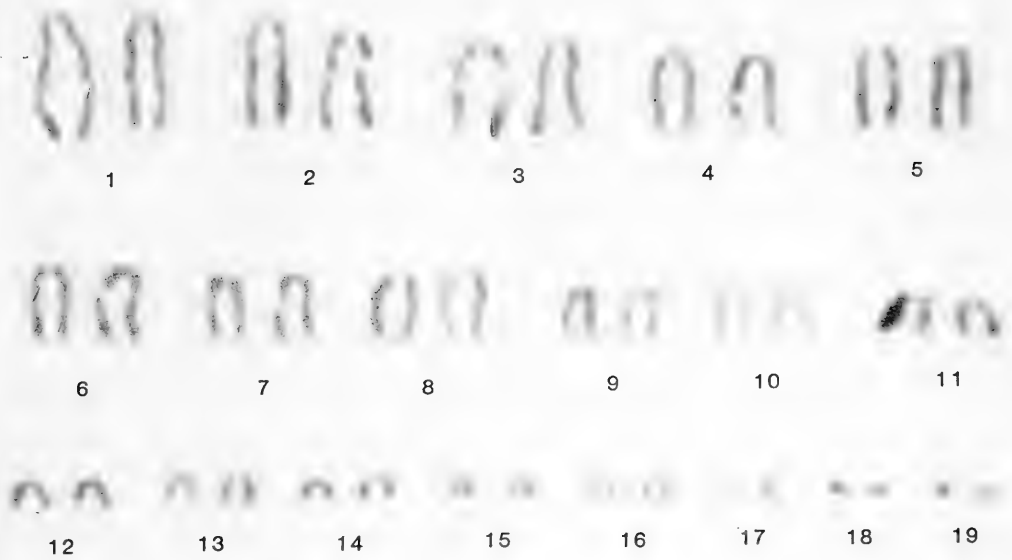


FIGURE 21. Karyotype of *Phyllodactylus bugastrolepis* from Isla Santa Catalina. Note the two pairs of metacentric chromosomes (pairs 15 and 19).

lizards (*Uta*) were found to be very similar to mainland populations (M. Soulé, unpublished data), and was the giant chuckwalla (*Sauromalus hispidus*). In contrast, the reptiles on Monserrate, a southern, old island of continental origin, were well differentiated biochemically, with an ETD of about 2 MYBP. Allozyme data provide strong evidence that Monserrate should be considered an old island, and not a land-bridge island as Wilcox (1978) reported.

Biochemical techniques were used to determine the geologic age of Isla Santa Catalina. Allozyme data suggest that Santa Catalina is about the same age as Monserrate, but only for the chuckwallas was a population on one island probably derived from the other, though direction could not be determined. In addition, the leaf-toed gecko population on Santa Catalina is karyotypically unique, even though it is electrophoretically identical with the peninsular population.

There was an apparent uncoupling of genetic and morphological rates of evolution in some cases—e.g., the two Cape area leaf-toed geckos

and some Gulf islands species are morphologically very different, yet biochemically identical.

Large species of widely distributed lizards occur on the northern midriff islands, while relatively smaller sister species occur further south. The larger body size and unique squamation of northern insular populations of *Uta* led Ballinger and Tinkle (1972) to propose that certain midriff islands harbor relict populations of “primitive” side-blotched lizards, but the electrophoretic data are not concordant with their morphological findings or hence with their conclusion. One of the populations most genetically differentiated is morphologically indistinguishable from the adjacent peninsular population at the subspecific level. Conversely, some of the morphologically “primitive” and distinctive insular species are biochemically indistinguishable from peninsular populations. The genetic data are concordant with my paleobiogeographic scenario and the history of the peninsula, but not, in this instance, with morphology.

An analogous situation occurs with the chuckwallas (*Sauromalus*). Morphologically, the most

derived and largest species, *S. hispidus* and *S. varius*, are found on the midriff islands (Murphy and Ottley, in press). These northern populations have been accorded specific status, but their southern sister species have not (e.g., see Soule and Sloan 1966). It is ironic that the genetically most distinctive populations are found on the southern islands of Santa Catalina and Monserrate, where the lizards exhibit the least amount of morphological divergence from the peninsular population, and the morphologically most distinctive populations are on the northern islands, where a lesser amount of genetic divergence is detected. Again, the genetic data are concordant with the geologic history of the Gulf of California, and not with the relative rates of evolution for the morphology of these lizards. Thus, the genetic data more accurately indicate the true phylogenetic relationships of these lizards, if my paleobiogeographic scenario is correct.

Where possible, electrophoretic data have been analyzed cladistically, i.e., in terms of primitive and derived character states (allelic distributions and composition), for each character (locus). Details of the analysis are too lengthy for inclusion in this paper, but one significant trend has come to light: island populations in general contain an equivalent or slightly greater number of derived character states than their peninsular sister populations. To put it another way, some island populations are evolving biochemically at a faster rate than the peninsular populations. These data, combined with the observed discordances between genetic and morphological rates of evolution and the concordance between genetics and paleogeography, cast doubt on the concept that the islands harbor "relict" populations (Brown 1957, as adapted, for instance, by Ballinger and Tinkle 1972). My data imply that island populations evolve genetically at least as rapidly as, and perhaps more rapidly than, mainland populations. Thus the islands in the Gulf of California cannot be considered refugia for relict reptilian species. Indeed, based on what we know about the genetics of relatively small, isolated populations, islands should generally not be expected to contain relict populations.

RÉSUMEN

Las relaciones evolucionarias entre los anfibios y los reptiles del suroeste de Norteamérica son examinados utilizando un síntesis de la tec-

tónica, la paleogeografía y la paleoecología. Existe una correlación muy fuerte entre los factores biológicos y no biológicos.

El guión zoogeográfico siguiente corresponde tanto a los factores biológicos como a los no biológicos. Hace aproximadamente 13 millones de años (MA) durante el Mioceno, el área de la capa de Baja California se separó del continente de México cerca del estado de Colima en México. Estos movimientos tectónicos resultaron en la creación de subpoblaciones aisladas—una localizada en el área de la capa (o en las islas asociadas), y la otra quedándose en el continente. Esta subdivisión se llama *vicariante transgolfiana*. Se postula que las islas que formaron el área de la capa de Baja California son el punto de origen de varios grupos reptiles de Norteamérica occidental tales como el lagartos *Uta* sp., *Sauromalus* sp., y *Dipsosaurus* sp. Al terminarse el Mioceno, el área de la capa se juntó con lo que ahora son las regiones más septentrionales de la península de Baja California, lo que facilitó la dispersión hacia el norte de varias poblaciones reptiles. Esta conexión terrestre se interrumpió en seguida al comenzar el Plioceno, lo que dio lugar a la formación de especies hermanas en las Cordilleras Peninsulares por medio de evolución alopatrica de las especies. La barrera de San Geronio se formó a la cabeza del Golfo de California acerca de finales del Mioceno y principios del Plioceno, hace aproximadamente 5 MA. Se ha propuesto que esta barrera causó la formación de las especies hermanas en cada lado del Golfo de California. Esta barrera fue eliminada durante el Pleistoceno, cuando el Golfo de California retrocedió hacia su posición actual. Además, se ha propuesto que los fenómenos glaciales del Pleistoceno tuvieron un efecto mínimo sobre la distribución peninsular de la mayoría de los reptiles. El efecto mayor fue la formación y el hundimiento de las islas de agua poco profunda en el Golfo. Los movimientos tectónicos durante el Plioceno y Pleistoceno fueron las responsables del origen de las poblaciones reptiles en la mayoría de las islas de agua profunda.

La hipótesis sobre el origen y la evolución de la herpetofauna de Baja California es apoyada al comparar las modalidades de diferenciación de la herpetofauna de Baja California. Se encontraron varias modalidades. Las especies de reptiles que fueron más o menos restringidas al área de la capa de Baja California tienen distancias equi-

valentes de diferenciación genética de las especies hermanas presuntas del continente de México. Se encontró una modalidad parecida de diferenciación genética equivalente entre las especies hermanas distribuidas al norte y al sur de las Cordilleras Peninsulares, al este y al oeste del Golfo de California y en las islas de agua profunda y de agua poco profunda. La datación geológica fija la fecha del origen del área de la capa acerca de hace 13 MA. Se encontró que las especies hermanas transgolfianas se diferencian de una distancia genética (D) de aproximadamente 0.8. Se utilizó esta fecha geológica para calibrar las estimaciones de distancia genética con las fechas de divergencia, utilizando la hipótesis del "reloj" bioquímico evolucionario. Suponiendo que un D de 1 es aproximadamente equivalente a 16 MA de divergencia, el "reloj" establece que la conexión terrestre entre el área de la Capa y las Cordilleras Peninsulares más septentrionales ocurrió inicialmente un poco anterior a hace 6 MA (coeficientes de similitud genética de aproximadamente 0.7 entre pares de especies hermanas a través de esta frontera). Estos datos corresponden a las estimaciones geológicas. De manera parecida, se calcula que la Barrera de San Gorgonio se formó hace 3 MA y la Isla de Santa Catalina hace 2 MA. No se encontró ninguna diferenciación genética significativa entre la península y las islas puente-terrestre (de agua poco profunda); estos resultados también corresponden al "reloj." De allí, las modalidades de diferenciación genética parecen apoyar al guión paleobiogeográfico. Al apoyar este guión, se concluye que la península y las islas de Baja California no se pueden considerar como un refugio para herpetofauna relictas. Al contrario, es evidente que el área de Baja California debe considerarse como un centro evolucionario.

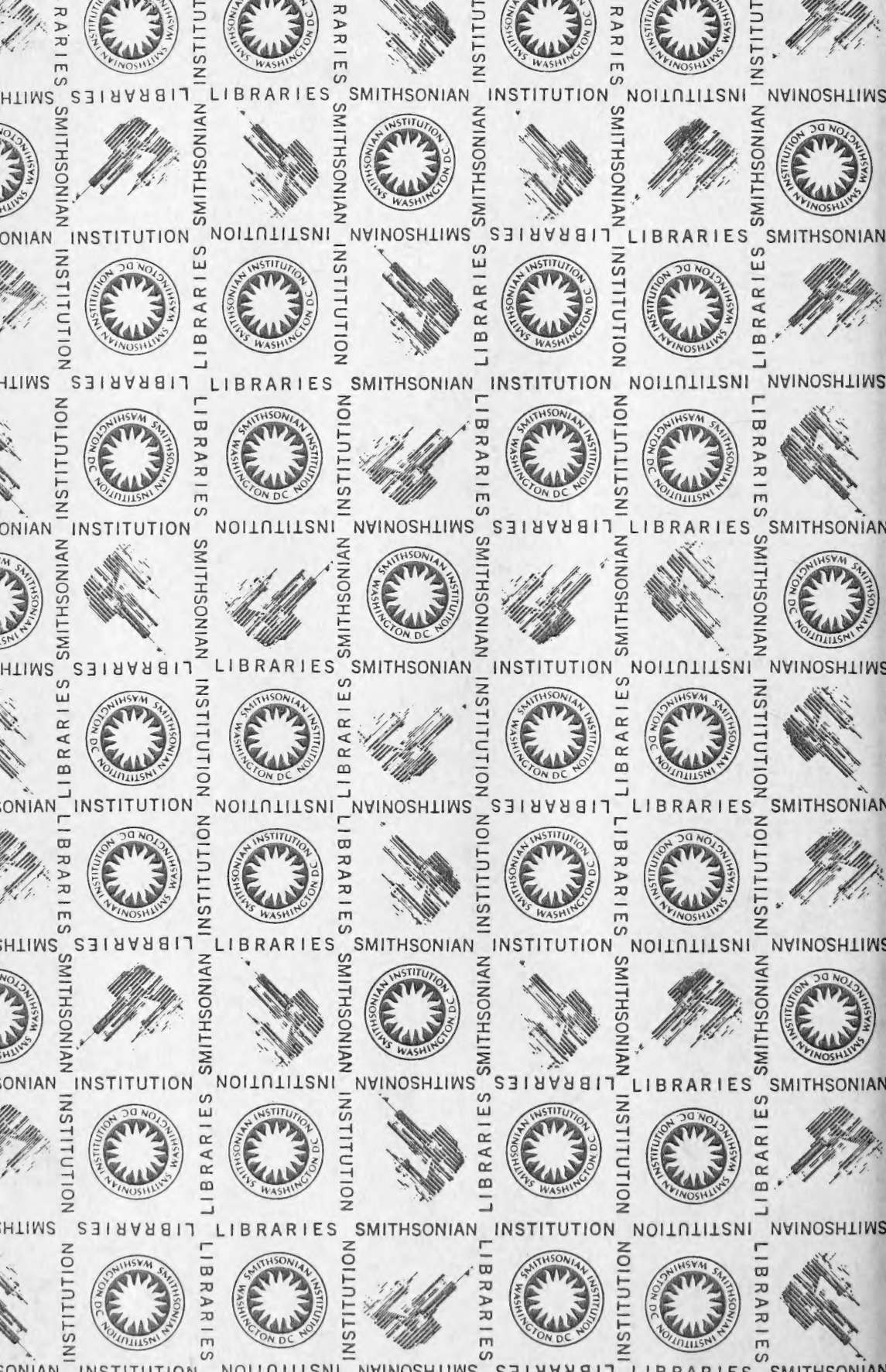
LITERATURE CITED

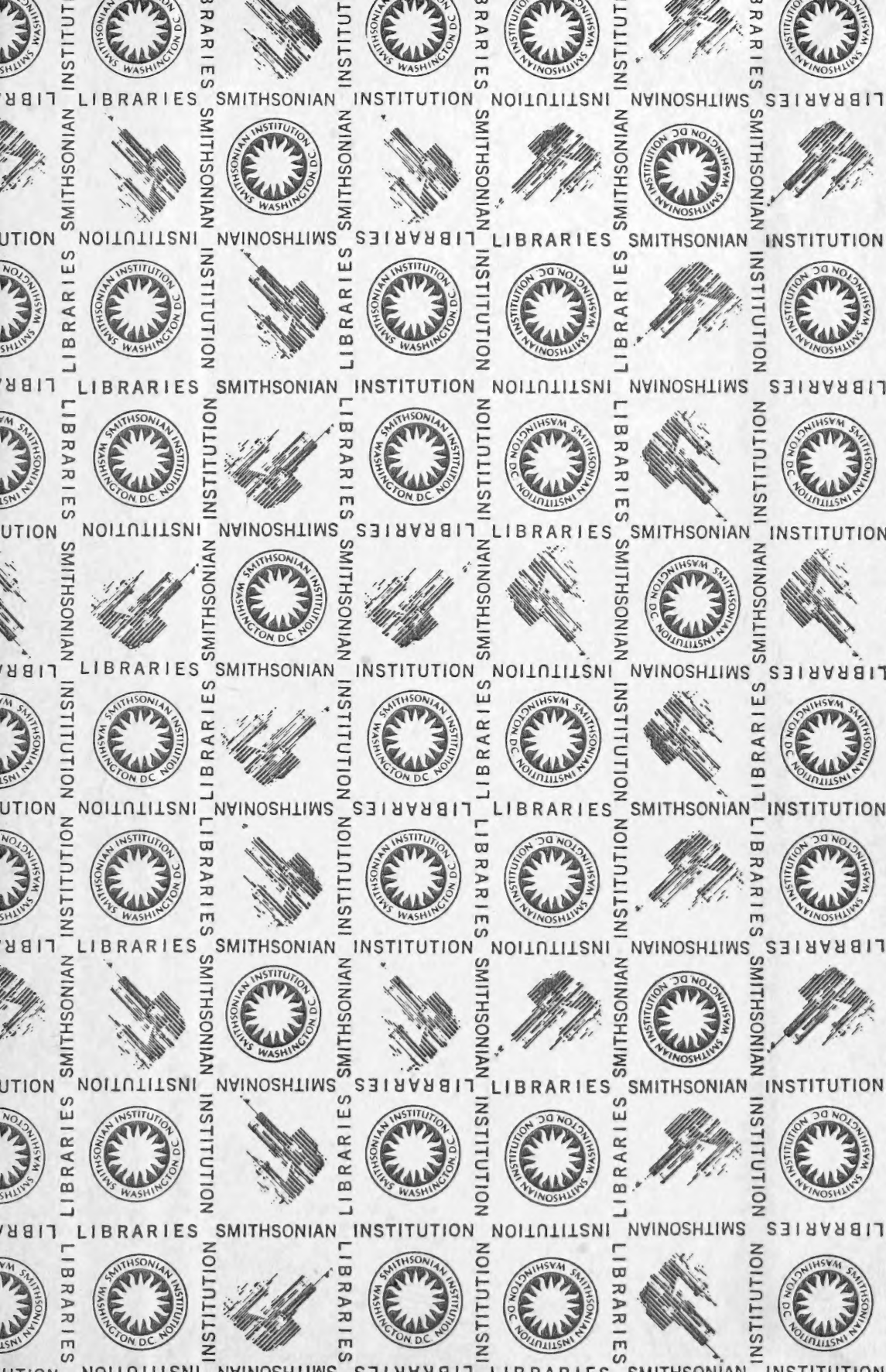
- ALLEN, C. R. 1957. San Andreas Fault zone in San Gorgonio Pass, southern California. *Geological Society of America Bulletin* 68:315-350.
- ANDERSON, D. L. 1971. The San Andreas Fault. *Scientific American* 225:52-68.
- ANDERSON, G. A. 1950. 1940 E. W. Scripps cruise to the Gulf of California, pt. 1. Geology of islands and neighboring land areas. *Geological Society of America Memoir* 43:1-53.
- ARNOLD, B. A. 1957. Late Pleistocene and Recent changes in land forms, climate, and archaeology in central Baja California. *University of California Publications in Geography* 10:201-318.
- ASCHMANN, H. 1959. The central desert of Baja California: demography and ecology. *Ibero-Americana* 42. University of California Press, Berkeley. 282 p.
- ASPLUND, K. K. 1967. Ecology of lizards in the relictual Cape flora, Baja California. *The American Midland Naturalist* 77: 462-475.
- ATWATER, T. 1970. Implications of plate tectonics for the Cenozoic tectonic evolution of western North America. *Geological Society of America Bulletin* 81:3513-3536.
- , AND P. MOLNER. 1973. Relative motion of the Pacific and North American plates deduced from sea-floor spreading in the Atlantic, Indian, and South Pacific Oceans. Pages 136-148 in R. L. Kovach and A. Nur, eds., *Proceedings of the Conference on Tectonic Problems of the San Andreas Fault system*. Stanford University Publications in the Geological Sciences 13.
- AUFFENBERG, W., AND M. W. MILSTEAD. 1965. Reptiles in the Quaternary of North America. Pages 557-568 in H. E. Wright, Jr. and D. G. Frey, eds., *The Quaternary of the United States*. Princeton University Press, Princeton, N.J.
- AVERY, D. F., AND W. W. TANNER. 1971. Evolution of the iguanine lizards (Sauria, Iguanidae) as determined by osteological and myological characters. *Brigham Young University Science Bulletin, Biological Series* 12:1-79.
- AXELROD, D. I. 1937. A Pliocene flora from the Mount Eden Beds, southern California. *Carnegie Institution of Washington Publication* 476:125-183.
- . 1948. Climate and evolution in western North America during middle Pliocene time. *Evolution* 2:127-144.
- . 1950. Further studies of the Mount Eden Flora, southern California. *Carnegie Institution of Washington Publication* 590:73-117.
- . 1956. Mio-Pliocene floras from west-central Nevada. *University of California Publications in the Geological Sciences* 33:1-322.
- . 1957. Late Tertiary floras and the Sierra Nevada Uplift. *Geological Society of America Bulletin* 68:19-46.
- . 1958. Evolution of the Madro-Tertiary Geoflora. *Botanical Review* 24:433-509.
- . 1966. The Pleistocene Soboba Flora of southern California. *University of California Publications in the Geological Sciences* 60:1-109.
- . 1975. Evolution and biogeography of the Madro-Tethyan sclerophyll vegetation. *Annals of the Missouri Botanical Garden* 62:280-334.
- . 1979. Age and origin of the Sonoran Desert vegetation. *Occasional Papers of the California Academy of Sciences* 132:1-74.
- BALLINGER, R. E., AND D. W. TINKLE. 1972. Systematics and evolution of the genus *Uta* (Sauria: Iguanidae). *Miscellaneous Publications of the Museum of Zoology, University of Michigan* 145:1-83.
- BEAL, C. H. 1948. Reconnaissance of the geology and oil possibilities of Baja California, Mexico. *Geological Society of America Memoir* 31:1-138.
- BERGGREN, W. A., AND J. A. VAN COUVERING. 1974. The late Neogene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 16:1-216.
- BOGERT, C. M., AND W. G. DEGENHARDT. 1961. An addition to the fauna of the United States; the Chihuahuan ridgenosed rattlesnake in New Mexico. *American Museum Novitates* 2064:1-15.
- BOSTIC, D. L. 1971. Herpetofauna of the Pacific Coast of north central Baja California, Mexico, with a description of

- a new subspecies of *Phyllodactylus xanti*. Transactions of the San Diego Society of Natural History 16:237-263.
- BRECKENRIDGE, G. R. 1978. Evidence for a cold, dry, full-glacial climate in the American Southwest. Quaternary Research 9:22-40.
- BROWN, W. L., JR. 1957. Centrifugal speciation. Quarterly Review of Biology 32:247-277.
- CASE, T. J. 1975. Species numbers, density compensation, and colonizing ability of the lizards on the islands in the Gulf of California. Ecology 56:3-18.
- . 1978. A general explanation for insular body size trends in terrestrial vertebrates. Ecology 59:1-18.
- CHANEY, R. W. 1938. Paleocological interpretations of Cenozoic plants in western North America. Botanical Review 4:371-396.
- . 1940. Tertiary forests and continental history. Geological Society of America Bulletin 51:469-488.
- . 1944. Introduction. Pliocene floras of California and Oregon. Carnegie Institution of Washington Publication 553: 1-19.
- . 1947. Tertiary centers and migration routes. Ecological Monographs 17:139-148.
- CHEETHAM, A. H., AND J. E. HAZEL. 1969. Binary (presence-absence) similarity coefficients. Journal of Paleontology 43: 1130-1136.
- CHRISTIANSEN, R. L., AND P. W. LIPMAN. 1972. Cenozoic volcanism and plate-tectonic evolution of the western United States. II. Late Cenozoic. Philosophical Transactions of the Royal Society of London, sec. A, Math and Physical Sciences 271:249-284.
- COCHRAN, D. M. 1954. Our snake friends and foes. National Geographic Magazine, Sept. 1954:334-364.
- COLE, C. J., AND T. R. VAN DEVENDER. 1976. Surface structure of fossil and Recent epidermal scales from North American lizards of the genus *Sceloporus* (Reptilia, Iguanidae). Bulletin of the American Museum of Natural History 156: 455-513.
- CONANT, R. 1969. A review of the water snakes of the genus *Natrix* in Mexico. Bulletin of the American Museum of Natural History 142:1-140; 22 pls.
- DICKERSON, M. C. 1919. Diagnoses of twenty-three new species and a new genus of lizards from Lower California. Bulletin of the American Museum of Natural History 41: 461-477.
- DIXON, J. R. 1964. The systematics and distribution of the lizards of the genus *Phyllodactylus* in North and Central America. New Mexico State University Research Center Scientific Bulletin 64-1:1-139.
- . 1966. Speciation and systematics of the gekkonid lizard genus *Phyllodactylus* of the islands in the Gulf of California. Proceedings of the California Academy of Sciences, 4th ser., 33:415-452.
- . 1969. The gekkonid lizard, *Phyllodactylus unctus* (Cope) in Michoacán, Mexico. Southwestern Naturalist 14: 255-256.
- DREWES, R. C., AND A. E. LEVITON. 1978. Rediscovery of *Lampropeltis nitida* Van Denburgh (Reptilia, Serpentes, Colubridae) in Baja California Sur, Mexico. Journal of Herpetology 12:102-103.
- DUELLMAN, W. E. 1965. A biogeographic account of the herpetofauna of Michoacán, Mexico. University of Kansas Publications, Museum of Natural History 15:627-709.
- DURHAM, J. W., AND E. C. ALLISON. 1960. The geologic history of Baja California and its marine fauna. Systematic Zoology 9:47-91.
- EARDLEY, A. J. 1951. Structural geology of North America. Harper, New York. xiv + 624 p.
- EHRlich, P. R., AND P. H. RAVEN. 1965. Butterflies and plants: a study of co-evolution. Evolution 18:586-608.
- EVERNDEN, J. E., AND R. K. S. EVERNDEN. 1970. The Cenozoic time scale. Geological Society of America Special Paper 124:71-90.
- FAIRBRIDGE, R. W. 1972. Climatology of the glacial cycle. Quaternary Research 2:283-302.
- FARRIS, J. S. 1979. The information content of the phylogenetic system. Systematic Zoology 28:483-519.
- . 1981. Distance data in phylogenetic analysis. Pages 3-23 in V. A. Funk and D. R. Brooks, eds., Advances in cladistics: proceedings of the first meeting of the Willi Hennig Society. The New York Botanical Garden, Bronx.
- FITCH, H. S., AND R. W. HENDERSON. 1978. Ecology and exploitation of *Ctenosaura similis*. The University of Kansas Science Bulletin 51:483-500.
- FOWLE, J. 1965. The snakes of Arizona. Azul Quinta Press, Fallbrook, California. 164 p.
- FRICK, C. 1933. New remains of trilophodont-tetrabelodont mastodons. Bulletin of the American Museum of Natural History 59:505-652.
- FUNK, R. S., AND C. H. CROULET. 1976. Geographic distribution: *Rana catesbeiana* (bullfrog). Herpetological Review 7:128.
- GASTIL, R. G., AND W. JENSKY. 1973. Evidence for strike-slip displacement beneath the trans-Mexican volcanic belt. Pages 171-180 in R. L. Kovach and A. Nur, eds., Proceedings of the conference on tectonic problems of the San Andreas Fault system. Stanford University Publications in the Geological Sciences 13.
- , J. C. MINCH, AND R. P. PHILLIPS. In Press. The geology and ages of the islands. Chapter 2 in T. J. Case and M. L. Cody, eds., Island biogeography in the Sea of Cortez. University of California Press, Berkeley.
- , R. P. PHILLIPS, AND E. C. ALLISON. 1975. Reconnaissance geology of the state of Baja California. The Geological Society of America Memoir 14, xiv + 170 p.; 6 maps.
- GORMAN, G. C., Y. J. KIM, AND C. E. TAYLOR. 1977. Genetic variation in irradiated and control populations of *Cnemidophorus tigris* (Sauria, Teiidae) from Mercury, Nevada with a discussion of genetic variability in lizards. Theoretical and Applied Genetics 49:9-14.
- , M. SOULÉ, S. Y. YANG, AND E. NEVO. 1975. Evolutionary genetics of insular Adriatic lizards. Evolution 29: 52-71.
- HALL, W. P. 1973. Comparative population cytogenetics, speciation, and evolution in the iguanid lizard genus *Sceloporus*. Ph.D. Diss., Harvard University.
- , AND H. M. SMITH. 1979. Lizards of the *Sceloporus orcutti* complex of the Cape Region of Baja California. Breviora 452:1-26.
- HENDRICKSON, J., AND B. PRIGGE. 1975. White fir in the mountains of eastern Mojave Desert of California. Madroño 23:164-168.
- HENNIG, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana. xvi + 263 p.
- HENYET, T. L., AND J. L. BISCHOFF. 1973. Tectonic elements of the northern part of the Gulf of California. Geological Society of America Bulletin 84:315-330.
- IVES, R. L. 1962. Dating of the 1746 eruption of Tres Virgines volcano, Baja California del Sur, Mexico. Geological Society of America Bulletin 73:647-648.
- JOHNSON, D. L. 1977. The California ice-age refugium and

- the RanchoLabrean extinction problem. *Quaternary Research* 8:149-153.
- KARIG, D. E., AND W. JENSKY. 1972. The proto-Gulf of California. *Earth and Planetary Science Newsletter* 17:169-174.
- KIM, Y. J., G. C. GORMAN, T. J. PAPANFUSS, AND A. K. ROYCHOUDHURY. 1976. Genetic relationships and genetic variation in the amphibia genus *Bipes*. *Copeia* 1976:120-124.
- KING, P. B. 1958. Evolution of modern surface features in western North America. *American Association for the Advancement of Science Publication* 51:3-60.
- . 1959. *The evolution of North America*. Princeton University Press, Princeton, N.J. 189 p.
- KLAUBER, L. M. 1956. Rattlesnakes: their habitats, life histories, and influence on mankind. University of California Press, Berkeley. 2 vol.; xxix + 1476 p.
- . 1972. Rattlesnakes: their habits, life histories, and influence on mankind, 2nd ed. University of California Press, Berkeley. 2 vol.; xxx + 1533 p.
- KLUGE, A. G., AND J. S. FARRIS. 1969. Quantitative phyletics and the evolution of anurans. *Systematic Zoology* 18:1-32.
- LARSON, R. L. 1972. Bathymetry, magnetic anomalies, and plate tectonic history of the mouth of the Gulf of California. *Geological Society of American Bulletin* 83:3345-3360.
- LEVITON, A. E., AND W. W. TANNER. 1960. The generic allocation of *Hypsiglena slevini* Tanner (Serpentes: Colubridae). *Occasional Papers of the California Academy of Sciences* 27:1-7.
- LOOMIS, R. B., S. G. BENNETT, S. R. SANBORN, C. H. BARBOUR, AND H. WEINER. 1974. A handlist of the herpetofauna of Baja California and adjacent islands. (Privately printed.) California State University, Long Beach. 10 p.; map.
- LOWE, C. H. 1955. The eastern limit of the Sonoran Desert in the United States with additions to the known herpetofauna of New Mexico. *Ecology* 36:343-345.
- MACARTHUR, R. H., AND E. O. WILSON. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17:373-387.
- , AND ———. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, N.J. xii + 203 p.
- MACGINITIE, H. D. 1958. Climate since the late Cretaceous. *American Association for the Advancement of Science Publication* 51:61-79.
- MATTHEW, W. D. 1915. Climate and evolution. *Annual Review of the New York Academy of Sciences* 24:171-318.
- MAXSON, L. R., V. M. SARICH, AND A. C. WILSON. 1975. Continental drift and the use of albumin as an evolutionary clock. *Nature* 225:397-400.
- MAYR, E. 1963. *Animal species and evolution*. Belknap Press of Harvard University, Cambridge, Massachusetts. xiv + 797 p.
- MCDIARMID, R. W., J. F. COPP, AND D. E. BREEDLOVE. 1976. Notes on the herpetofauna of western Mexico: new records from Sinaloa and the Tres Marias Islands. *Natural History Museum of Los Angeles County Contributions in Science* 275:1-17.
- MILLER, W. E. 1977. Pleistocene terrestrial vertebrates from southern Baja California. *Geological Society of America, Abstract with Programs* 9:468.
- . 1980. The late Pliocene Las Tunas Local Fauna from southernmost Baja California, Mexico. *Journal of Paleontology* 54:762-805.
- MINA, U. F. 1957. Bosquejo geológico del Territorio de la Baja California. *Boletín de la Asociación Mexicana de Geólogos Petroleros* 9:141-269.
- MINCH, J. C., R. G. GASTIL, W. FINK, J. ROBINSON, AND A. H. JAMES. 1976. Geology of the Vizcaíno Peninsula. Pages 136-195 in D. G. Howell, ed., *Aspects of the geologic history of the California Continental Borderland*. Pacific Section of the American Association of Petroleum Geologists, Miscellaneous Publication 24.
- MITTLEMAN, M. B. 1942. A summary of the iguanid genus *Urosaurus*. *Bulletin of the Museum of Comparative Zoology* 91:103-181.
- MOCQUARD, M. F. 1899. Contribution a la faune herpétologique de la Basse-Californie. *Nouvelles Archives du Muséum d'Histoire Naturelle, Paris*, ser. 4, 1:297-344; pls. 11-13.
- MONTANUCCI, R. R., R. W. AXTELL, AND H. C. DESSAUER. 1975. Evolutionary divergence among collared lizards (*Crotaphytus*), with comments on the status of *Gambelia*. *Herpetologica* 31:336-347.
- MOORE, D. G. 1973. Plate-edge deformation and crustal growth, Gulf of California structural province. *Geological Society of America Bulletin* 84:1883-1906.
- MORAFKA, D. J. 1977. A biogeographical analysis of the Chihuahuan Desert through its herpetofauna. Dr. W. Junk, The Hague, Netherlands. viii + 313 p.
- MURPHY, R. W. 1974. A new genus and species of eublepharine gecko (Sauria: Gekkonidae) from Baja California, Mexico. *Proceedings of the California Academy of Sciences*, 4th ser. 40:87-92.
- . 1975. Two new blind snakes (Serpentes: Leptotyphlopidae) from Baja California, Mexico with a contribution to the biogeography of peninsular and insular herpetofauna. *Proceedings of the California Academy of Sciences*, 4th ser. 40:93-107.
- . 1982. *The genetic relationships and biogeography of the Baja California herpetofauna*. Ph.D. Diss., University of California, Los Angeles.
- . In Press. The reptiles: origin and evolution. Chapter 6 in T. J. Case and M. L. Cody, eds., *Island biogeography in the Sea of Cortez*. University of California Press, Berkeley.
- , AND J. R. OTTLEY. 1979. Geographic distribution: *Ramphotyphlops braminus* (Asian blind snake). *Herpetological Review* 10:119.
- , AND ———. 1980. A genetic evaluation of the leaf-nose snake, *Phyllorhynchus decurtatus*. *Journal of Herpetology* 14:263-268.
- , AND ———. In Press. Checklist of the amphibians and reptiles on the islands in the Sea of Cortez. Appendix 6.1 in R. W. Murphy, *The reptiles: origin and evolution*. Chapter 6 in T. J. Case and M. L. Cody, eds., *Island biogeography in the Sea of Cortez*. University of California Press, Berkeley.
- , AND T. J. PAPANFUSS. 1979. Biochemical relationships, identification and variation of *Phyllodactylus unctus* and *P. paucituberculatus*. *Biochemical Systematics and Ecology* 8:97-100.
- NEI, M. 1972. Genetic distance between populations. *American Naturalist* 106:283-292.
- NELSON, E. W. 1921. Lower California and its natural resources. *Memoirs of the National Academy of Sciences*, Washington 16:1-194.
- OTTLEY, J. R., AND R. W. MURPHY. 1981. Geographic distribution: *Petrosaurus thalassinus repens* (central Baja rock lizard). *Herpetological Review* 12:65.
- , ———, AND G. V. SMITH. 1980. The taxonomic status of the rosy boa, *Lichanura roseofusca* (Serpentes: Boidae) *Great Basin Naturalist* 40:59-62.

- , AND W. W. TANNER. 1978. New range and a new subspecies for the snake *Eridiphas slevini*. Great Basin Naturalist 38:406–410.
- PEABODY, F. E., AND J. M. SAVAGE. 1958. Evolution of the Coast Range corridor in California and its effect on the origin and dispersal of living amphibians and reptiles. American Association for the Advancement of Science Publication 51: 159–186.
- PETERS, J. A. 1968. A computer program for calculating degree of biogeographical resemblance between areas. Systematic Zoology 17:64–69.
- PHILLIPS, A. M., AND T. R. VAN DEVENDER. 1974. Pleistocene packrat middens from the lower Grand Canyon of Arizona. Journal of the Arizona Academy of Science 9:117–119.
- PHILLIPS, R. P. 1966. Reconnaissance geology of some of the northwestern islands in the Gulf of California (abs.). Geological Society of America, Cordilleran Section Program, p. 59.
- POUGH, F. H. 1966. Ecological relationships of rattlesnakes of southeastern Arizona with notes on other species. Copeia 1966:676–683.
- ROBINSON, M. D. 1973. Chromosomes and systematics of the Baja California whiptail lizards, *Cnemidophorus hyperythrus* and *C. ceralbensis* (Reptilia: Teiidae). Systematic Zoology 22:30–35.
- ROHLF, F. J. 1970. Adaptive hierarchical clustering schemes. Systematic Zoology 19:58–82.
- SAGE, R. D., AND R. K. SELANDER. 1975. Trophic radiation through polymorphism in cichlid fishes. Proceedings of the National Academy of Sciences, Washington 72:4669–4673.
- SALTZMAN, B., AND A. D. VERNECKER. 1975. A solution for the Northern Hemisphere climatic zonation during a glacial maximum. Quaternary Research 5:307–320.
- SARICH, V. M. 1969. Pinniped origins and the rate of evolution of carnivore albumins. Systematic Zoology 18:286–295.
- . 1977. Rates, sample sizes and neutrality hypothesis for electrophoresis in evolutionary studies. Nature 265:24–28.
- SAVAGE, J. M. 1960. Evolution of a peninsular herpetofauna. Systematic Zoology 9:184–212.
- . 1967. Evolution of the insular herpetofaunas. Pages 219–227 in Proceedings of the Symposium on the Biology of the California Islands. Santa Barbara Botanic Garden.
- SCHMIDT, K. P. 1922. The amphibians and reptiles of Lower California and neighboring islands. Bulletin of the American Museum of Natural History 46:607–707.
- . 1943. Corollary and commentary for "Climate and Evolution." The American Midland Naturalist 30:241–253.
- SEIB, R. L. 1980. Baja California: a peninsula for rodents but not for reptiles. The American Naturalist 115:613–620.
- SHAW, C. E. 1945. The chuckwalla, genus *Sauromalus*. Transactions of the San Diego Society of Natural History 10:296–306.
- SIMPSON, G. G. 1960. Notes on the measurement of faunal resemblance. American Journal of Science 258:300–311.
- SMITH, A. G. 1976. Plate tectonics and orogeny: a review. Tectonophysics 33:215–285.
- SNEATH, P. H. A., AND R. R. SOKAL. 1973. Numerical taxonomy. W. H. Freeman and Company, San Francisco. xvi + 573 p.
- SOULÉ, M., AND A. J. SLOAN. 1966. Biogeography and distribution of the reptiles and amphibians on islands in the Gulf of California, Mexico. Transactions of the San Diego Society of Natural History 14:137–156.
- TAYLOR, R. J., AND P. J. REGAL. 1978. The peninsular effect on species diversity and the biogeography of Baja California. The American Naturalist 112:583–593.
- THROCKMORTON, L. H. 1978. Molecular phylogenetics. Pages 221–240 in R. A. Romberger, R. H. Foote, L. Knutsen, and P. L. Lentz, eds., Beltsville symposium II: biosystematics in agriculture. John Wiley and Sons, New York.
- VAN COUVERING, J. A. 1978. Status of late Cenozoic boundaries. Geology 6:169.
- VAN DEVENDER, T. R. 1974. Late Pleistocene plants and animals of the Sonoran Desert: a survey of ancient packrat middens in southwestern Arizona. Dissertation Abstracts International 34B:5590–5591.
- , AND J. E. KING. 1971. Late Pliocene vegetational records in western Arizona. Journal of the Arizona Academy of Science 6:240–244.
- , AND J. I. MEAD. 1978. Early Holocene and late Pleistocene amphibians and reptiles in Sonoran Desert packrat middens. Copeia 1978:464–475.
- , AND W. G. SPAULDING. 1979. Development of vegetation and climate in the southwestern United States. Science 204:701–710.
- VAWTER, A. T., R. ROSENBLATT, AND G. C. GORMAN. 1980. Genetic divergence among fishes of the eastern Pacific and the Caribbean: support for the molecular clock. Evolution 34:705–711.
- VITT, L. J., AND R. D. OHMART. 1978. Herpetofauna of the lower Colorado River: Davis Dam to the Mexican border. Proceedings of the Western Foundation of Vertebrate Zoology 2:35–72.
- WELLS, P. K., AND R. BERGER. 1967. Late Pleistocene history of coniferous woodland in the Mojave Desert. Science 155: 1640–1647.
- , AND C. D. JORGENSEN. 1964. Pleistocene wood rat middens and climatic change in the Mojave Desert: a record of juniper woodlands. Science 143:1171–1174.
- WILCOX, B. A. 1978. Supersaturated island faunas: a species-age relationship for lizards on post-Pleistocene land-bridge islands. Science 199:996–998.
- . 1980. Species number, stability, and equilibrium status of reptile faunas on the California islands. Pages 551–564 in D. M. Power, ed., The California islands: proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History, Santa Barbara, California.
- WILLIAMS, S. C. 1980. Scorpions of Baja California, Mexico, and adjacent islands. Occasional Papers of the California Academy of Sciences 135:1–113.
- WILSON, A. C., S. S. CARLSON, AND T. J. WHITE. 1977. Biochemical evolution. Annual Review of Biochemistry 46: 573–639.
- WYLES, J. S., AND G. C. GORMAN. 1978. Close relationship between the lizard genus *Sator* and *Sceloporus utiformis* (Reptilia, Lacertilia, Iguanidae): electrophoretic and immunological evidence. Journal of Herpetology 12:343–350.
- YANEV, K. P. 1980. Biogeography and distribution of three parapatric salamander species in coastal and borderland California. Pages 531–550 in D. M. Power, ed., The California islands: proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History, Santa Barbara, California.
- ZWEIFEL, R. G. 1962. Analysis of hybridization between two subspecies of the desert whiptail, *Cnemidophorus tigris*. Copeia 1962:749–774.





SMITHSONIAN INSTITUTION LIBRARIES



3 9088 01302 6372

BHL