Evolution of a Peninsular Herpetofauna

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BIOGEOGRAPHY is a field of theoretical biology that functions to formulate theories best explaining the current facts of distribution in the light of knowledge on physiography, climate, ecologic relations, geologic history, and evolution. Biogeographic theory is tested by new information or new interpretations of previously known data from all germane fields as these amplify, verify, or modify the theory as originally presented. The development of sound biogeographic theories depends upon:

1. Comprehensive analysis of present distributional patterns for each species in the area under consideration.
2. Knowledge of the basic ecologic associations and limits for each species.
3. Evaluation of the degrees of similarity and difference between the biota under study and those of other regions.
4. Correlation of known facts of geodynamic and paleoecologic history for the investigated area with present distributional patterns and ecologic and biogeographic relations. Application of these steps incorporates most of the advantages of both ecological and historical biogeography. In addition this approach produces a solid foundation in biogeographic statics (see Darlington, 1957, for a book concerned primarily with static zoogeography). The method is most significant, however, in providing a basis for discussion of the dynamics of the origin and evolution of biotas in terms of past physiographic, ecologic and biologic history, even in the absence of adequate fossil records.

The present paper forms an attempt to construct a cogent theory satisfactorily explaining the current distribution of the amphibians and reptiles of Baja California and the probable historical processes responsible for evolution of the peninsular herpetofauna. The attempt depends upon proper utilization of the method outlined above and previously employed in a study of the herpetofauna of central and southern California by Peabody and Savage (1958).

Baja California offers particularly intriguing ground for biogeographic investigations. With the exception of the Malay Peninsula, which extends approximately 1,000 miles from north to south, the 800 mile long peninsula of Baja California forms the longest, well-isolated peninsular area in the world. The peninsula is further unique in its long geologic existence as a discrete unit, dating back to Eocene (Durham and Allison, 1960). The vegetation of the area is well-known and indicates a wide diversity in climate and habitat, ranging from pine woodland, oak woodland, and chaparral in the north, through desert scrub to subtropical thorn-scrub in the south. In addition isolated southern ranges are covered by oak-pine woodlands and chaparral separated from northern communities of a similar nature by 300 miles of desert (Wiggins, 1960). The herpetofauna is comprised of four species of salamanders, eight frogs and toads, two kinds of non-marine turtles, 39 lizards, and 35 species of snakes, a total of 88 forms. By comparison the climate and vegetation of the Malay Peninsula are relatively constant over its entire extent and the herpetofauna is composed of approximately two species of caecilians, 80 frogs and toads, 20 turtles, 95 species of lizards, 115 snakes, three crocodilians and no salamanders, a total of 315 species. In addition to the Baja California Peninsula, numerous continental islands along the Pacific Coast and particularly adjacent to the peninsular mainland in the Gulf of California, support large faunas of reptiles and a few amphibians. In most cases a considerable amount of endemism is typical of each island. Although the distribution and origin of these insular faunas offer a fascinating project in biogeographic analysis, the problem is but a minor theme related to the larger problem of the evolution of the herpetofauna of the peninsula. For this reason insular species have not been considered in the general discussion in this paper, except in cases where insular forms provide clues to a better understanding of the major peninsular patterns. For readers interested in the island herpetofauna reference may be made to Schmidt (1922), Van Denburgh (1922), and Cliff (1954).

Recent North American Herpetofaunas

The present distribution and biogeographic relations of the amphibians and reptiles of Baja California cannot be treated properly without an understanding of the general distributional patterns for the entire North American herpetofauna. For the last 10 years I have been accumulating data for a report on the origins and affinities of the amphibian and reptile fauna of America north of the Isthmus of Tehuantepec. The emphasis in the initial stages of the study was upon detailed analyses of the distribution of known recent species in the region. Evaluation of these basic data indicates that six major and two minor herpetofaunal units occur in North America. Of course each of these entities is of diverse origins historically, but at the present time each unit occupies a physiographic area of distinct ecology, so that the general distribution of herpetofaunas may be plotted on a map (Fig. 1). The boundaries marking the geographic limits of the several faunal areas are somewhat arbitrary and denote a zone of relatively rapid transition from one fauna to another. The boundaries as drawn were determined by outlining the geographic range of each species and selecting a zone where the majority of ranges ended as the point of faunal change. The complexity of interdigitation, altitudinal effects, climate, and physiology all insure a constant shifting of the boundary zone on a small scale. However, application of Ekman's Rule (1953): the faunal boundary may be drawn at the point of greatest faunal change, makes possible an adequate approximation of the extent of each faunal region.

The eight herpetofaunas of North America include:

1. *Neotropical Herpetofauna*—reaching the area under discussion in Mexico, along the Atlantic coastal plain and in the coastal and foothill regions of the Pacific slope; a rich fauna of tropical origins continuous with similar faunal groups of Middle and South America; Stuart (1950) points out that the Caribbean and Pacific assemblages of this fauna may be recognized as distinct.
2. *Boreal North America Herpetofauna*—a depauperate fauna of elements capable of withstanding extremely cold winters; a very few snakes and a few amphibians make up this fauna.
3. *Eastern Forest Herpetofauna*—a fauna characterized by many species of salamanders, frogs, and turtles, found in the conifer and hardwood forest belt of the northeast and central portions of the continent.
4. *Austroriparian Herpetofauna*—a warm temperate fauna rich in species composition, particularly frogs, turtles, and snakes, occurring along the Atlantic and Gulf Coastal Plains and up the Mississippi Valley.

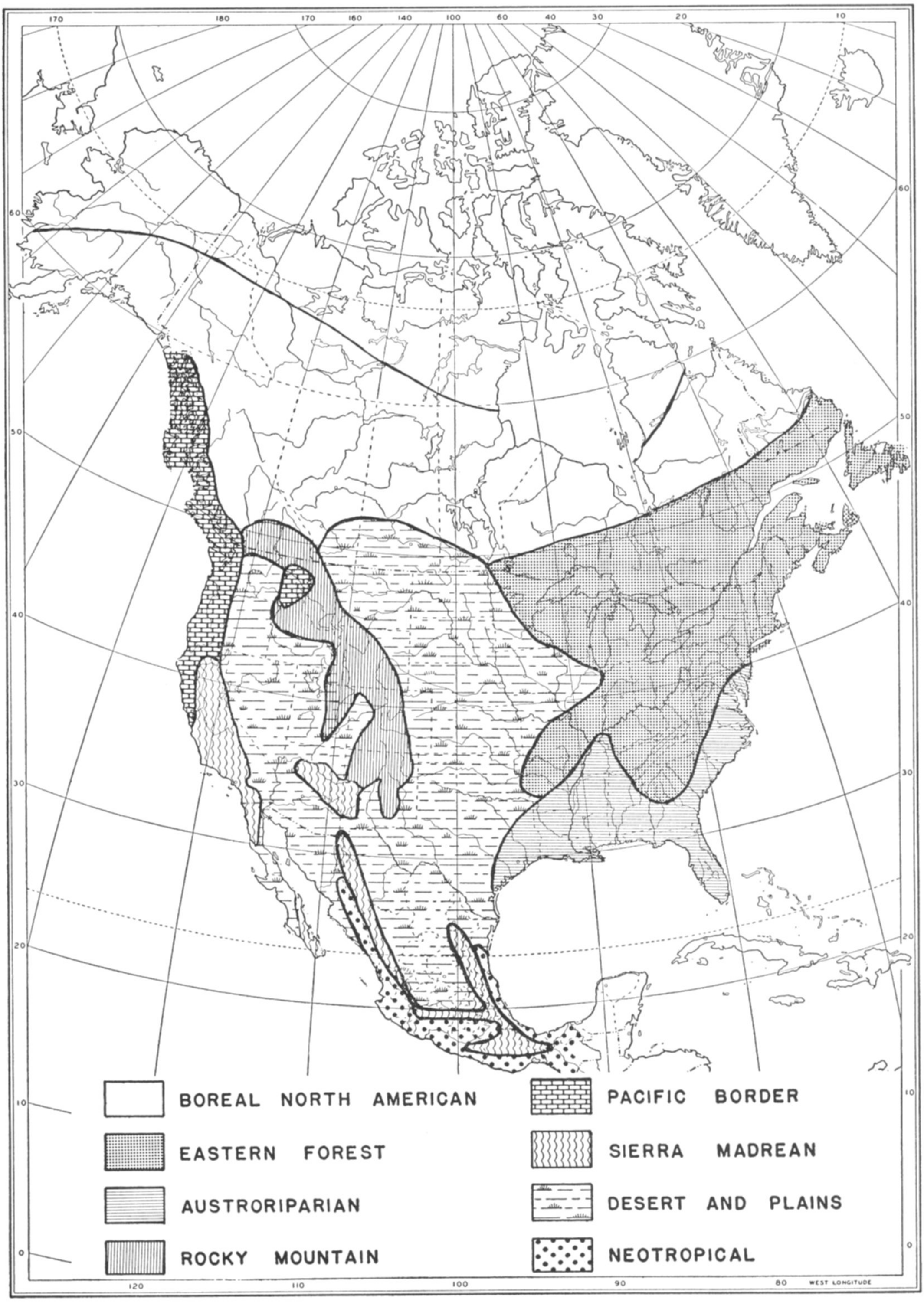

FIG. 1. Distribution of Recent North American herpetofaunas.

5. *Rocky Mountain Herpetofauna*—a depauperate fauna adapted for life in the rugged Rocky Mountain region; similar to Boreal North American Herpetofauna in group composition and species number.

6. *Pacific Border Herpetofauna*—restricted to the temperate coastal forest of the Pacific Northwest and its interior relicts; salamanders and frogs are the most striking elements of the herpetofauna.

7. *Sierra Madrean Herpetofauna*—found in warm climates associated with foothill physiography in California, Baja California, Arizona, New Mexico, and Mexico; dominated by lizard and snake species.

8. *Desert and Plains Herpetofauna*—a wide-ranging unit found in arid and semiarid regions of the American highlands; lizards and snakes are conspicuous elements.

TABLE 1—DISTRIBUTION OF NORTH AMERICAN HERPETOFAUNAS—RECENT

NEARCTIC REGION

I. BOREAL NORTH AMERICAN SUBREGION

II. EASTERN NORTH AMERICAN SUBREGION
  A. Eastern Forest Province
    1. Northeastern American Subprovince
    2. Appalachian-Ozarkian Subprovince
  B. Austroriparian Province

III. WESTERN MONTANE SUBREGION
  A. Rocky Mountain Province
    1. Northern Rocky Mountain Subprovince
    2. Southern Rocky Mountain Subprovince
  B. Pacific Border Province

IV. AMERICAN HIGHLAND SUBREGION
  A. Sierra Madrean Province
    1. Californian Subprovince
    2. San Lucan Subprovince
    3. Arizonian Subprovince
    4. Sierra Madre Occidental Subprovince
    5. Sierra Madre del Sur Subprovince
    6. Sierra Madre Oriental Subprovince
  B. Desert and Plains Province
    1. Great Plains Subprovince
    2. Chihuahua Desert Subprovince
    3. Sonoran Desert Subprovince

NEOTROPICAL REGION

These eight faunal entities exhibit different degrees of relationship to one another and it is convenient to group them into a comprehensive system (Table 1). Subdivisions of some importance are denoted in the table although not indicated on the map. The classification utilized follows the usual arrangement of biogeographic regions (Darlington, 1957). Each subregion is recognized on the basis of having a peculiar combination of families and genera and in being the center of adaptive radiation for many species groups. Biogeographic provinces in the sense employed here are not equal to the much smaller ecologic units called biotic provinces by Dice (1943). As used in this paper a Biogeographic Province is an area occupied by a distinctive major fauna, which differs from adjacent major faunal units in species composition. A useful device in determining the status of certain faunal regions is provided by a measure of faunal difference, the Coefficient of Difference (C.D.). The Coefficient of Difference for any two compared faunal units is calculated from the formula C.D. $=1-\frac{C}{N_2}\times 100\%$. C is equal to the number of species common to the two areas and N_2 is equal to the number of species in the larger of the two faunas. It has been found in the course of my analysis that major faunal differences are indicated when the C.D. is equal to 50% or more. As a convenience herpetofaunal provinces in this system are faunal units having a C.D. equal to or greater than 50% when compared to any other fauna.

It will be noted that the herpetofauna of Baja California is composed of elements from two of the major recent herpetofaunas, the Sierra Madrean and Desert and Plains units.

Historical Elements of North American Herpetofaunas

Emmett Reid Dunn (1931) was the first to attempt an explanation of the centers of origin and evolution for the American herpetofaunas. His interpretations were based on analysis of modern distributional data, conservative geological principles, and general acceptance of the ideas of Matthew (1915) as these are applicable in terms of amphibian and reptile ecology. Dunn recognized three principal faunal units: a) The South American Element, b) The Old Northern Element, and c) The Holarctic Element. He regarded these units as derived from three historical waves, each sweeping down from the north into southern areas. The oldest wave according to Dunn was the South American Element which moved into Latin America during late Cretaceous and early Tertiary times. Dunn suggested that his Old Northern Element reached Middle America in Miocene and swept on into South America after the closure of the Panamanian portal in the Pliocene. The Holarctic Element was conceived of as a very modern circumpolar unit which crossed into North America from Asia in Pliocene and Pleistocene times. Stuart (1950, 1951, 1954a, 1954b, 1957, 1958) more recently has suggested a fourth major element, the Autochthonous Middle American Element, which developed from northern groups of the South American Element following the submergence of the Panamanian bridge in early Tertiary. Stuart's Autochthonous Middle American Element includes certain groups placed by Dunn in his South American Element.

Dunn and Stuart were both hampered to a considerable extent in their analyses by the lack of fossil herpetofaunas for Cenozoic times, particularly of the crucial middle Tertiary. This handicap is still a reality in any attempt to evaluate the history of the North American herpetofaunas, although recent finds or reworking of old materials (Brattstrom, 1955a, 1955b, 1958a, 1958b; Hecht, 1959; Zweifel, 1956) now give herpetologists some hints in developing theories of faunal origin. Unfortunately, the fossil finds for western North America (reviewed by Peabody and Savage, 1958) are relatively rare and currently no amphibians or reptiles of pre-Pleistocene age are known from Baja California. As a result evaluation of the broad panorama of herpetofaunal differentiation in North America and particularly in the critical areas of the west must be based upon correlations with documented physiographic and ecologic changes during Cenozoic.

A particularly valuable asset provided the biogeographer of Cenozoic times and not considered in the work of Dunn and Stuart is the extensive paleobotanic record for the Era gradually uncovered during the last 30 years. Of greatest significance to the present thesis is the concept of three major geofloras undergoing evolution and dispersion in the Americas during Tertiary times as developed by Chaney (1938, 1940, 1944, 1947) and Axelrod (1950). Elsewhere (Peabody and Savage, 1958) I have pointed out that the Cenozoic herpetofaunas of the west may be correlated broadly with these Tertiary geofloras. In fact I am now convinced that correlation of geologic and geofloral history forms a firm basis for revaluation and further development of concepts of the historical origins, relationships, and dispersion of the fundamental herpetofaunal elements found today throughout North America. The fundamental historical units of modern herpetofaunas and the distribution of the herpetofaunas themselves as outlined in the previous section exhibit a striking association with one or the other of the three Tertiary geofloras, and distinctive plant associations derived from these geofloras today dominate each of the biogeographic areas described above (Fig. 1, Table 1). That the association of herpetofaunas and geofloras is a long-term condition is indicated by the scanty fossil record. Brattstrom (1955a) finds essentially tropical species in Eocene material from near San Diego associated with tropical vegetation now found far to the south. Hecht (1959) in considering a tropical or subtropical faunal unit from Wyoming Eocene deposits concludes that descendent forms are now found in Middle America and his material is from an area well represented by Eocene floral material of a tropical type, today found far to the south in Middle America. Peabody (1954, 1959) also presents evidence for the close association of herpetofaunas with geofloral aggregations through time. His material of a fossil ambystomatid from the Paleocene of Montana and of a salamander assemblage from the early Pliocene of the Sierra Nevada of California demonstrates clearly the continuous association of representatives of modern genera or their close allies with temperate forests similar to those still occupied by these forms.

The three Tertiary geofloras represented in North America and the modern herpetofaunas associated with their derivative elements are as follows:

Neotropical Tertiary Geoflora—Neotropical Herpetofauna.

Arcto-Tertiary Geoflora—Boreal North American, Eastern Forest, Austroriparian, Rocky Mountain, and Pacific Border Herpetofaunas.

Madro-Tertiary Geoflora—Sierra Madrean and Desert and Plains Herpetofaunas.

Naturally, a given herpetofauna is composed of a complement of species originating from several sources. A considerable proportion of the species in each unit, however, originated in or near the area now occupied by the faunal assemblage. For these reasons present day herpetofaunas are mixtures of species of diverse historical origins, although a particular fauna is dominated by derivatives of one of the historical units defined below. Since these historical elements of the modern herpetofaunas show a close correlation with the well-documented geofloras in both current and past distribution, the major features of herpetofaunal history may be perceived and followed through the obscuring mists of time by reference to the known facts of geofloral and ecologic history combined with an appreciation of geologic change. The fundamental historical assemblages, their geofloral associations, optimum climatic requirements, and their place and time of origin are summarized below and in tabular form (Table 2).

South American Element—descendents of the generalized Tropical American herpetofauna that dominated much of North and South America in early Tertiary; the South American Element originated from the Tropical American groups restricted during most of Cenozoic to the South American island, but subsequently invaded Middle America after closure of the Panamian portal in late Tertiary (Simpson, 1950); associated with the Neotropical Tertiary Geoflora; corresponds to South American Element of Stuart (1950).

Middle American Element—descendents of tropical groups trapped in Middle America by inundation of the Panamanian Isthmus in early Tertiary; derived *in situ* in Middle America from ancestors belonging to the generalized Tropical American herpetofauna; associated with the Neotropical Tertiary Geoflora; equal to the Autochthonous Middle American Element of Stuart (1950) who traces its history in Central America.

Old Northern Element—descendents of temperate circumpolar groups found in the far northern continental areas in early Tertiary, but forced southward as the limits of tropic and temperate zones were restricted during the long-term climatic shift throughout Tertiary time; origin in areas around the Arctic basin, but now found far to the south and eliminated from the extreme north; associated with the Arcto-Tertiary Geoflora; corresponds to older element of Old Northern Element of Dunn (1931).

TABLE 2—HISTORICAL ELEMENTS OF NORTH AMERICAN HERPETOFAUNAS

UNITS	GEOFLORAL ASSOCIATION	CLIMATE	ORIGIN	EXAMPLES
A. SOUTH AMERICAN ELEMENT	Neotropical Tertiary	Tropical	From generalized Tropical American unit; ultimately from Paleotropics	*Atelopus* *Atractus* *Caiman*
B. OLD NORTHERN ELEMENT	Arcto-Tertiary		Palearctic	
1. Eastern American Complex		Cool temperate		*Cryptobranchus* *Gyrinophilus*
2. Western American Complex		Cool temperate		*Dicamptodon* *Ascaphus*
3. Central American Complex		Warm temperate		*Pseudoeurycea* *Staurotypus*
4. Southeastern American Complex		Warm temperate		*Siren* *Graptemys*
C. MIDDLE AMERICAN ELEMENT	Neotropical Tertiary	Tropical, subtropical	From generalized Tropical American unit	*Basciliscus* *Xenosaurus*
D. YOUNG NORTHERN ELEMENT	Madro-Tertiary		From generalized Tropical American unit	
1. Madrean Complex		Subhumid		*Gerrhonotus*
2. Desert and Plains Complex		Semiarid, arid		*Crotaphytus* *Phyllorhynchus*
E. HOLARCTIC ELEMENT	Arcto-Tertiary	Cool temperate	Recent invaders from Eurasia	*Bufo boreas* *Rana sylvatica*

Arranged in approximate order from most ancient to most recent in America.

Young Northern Element—descendents of generalized Tropical American herpetofauna of early Tertiary isolated in North America by the Panamanian portal and subjugated to the stimulus of extreme physiographic revolution and the increasing climatic shift toward arid conditions characteristic of middle and late Cenozoic times in western North America, including Mexico; originating *in situ* from tropical ancestors beginning in mid-Eocene and becoming well-established if not dominant over vast areas of subhumid to arid climates and diverse topography by mid-Miocene; closely associated with the Madro-Tertiary Geoflora; equal to younger element of Old Northern Element of Dunn (1931).

Holarctic Element—modern circumpolar species groups closely allied to Eurasian types; probably recently derived from Eurasian forms in late Cenozoic and reaching America across the Bering land connection in Pliocene and Pleistocene (Simpson, 1947); associated with modern coniferous and deciduous forest components of the Arcto-Tertiary Geoflora; part of the Holarctic Element of Dunn (1931).

Contrary to the views of Dunn (1931) and Stuart (1950) the principal feature of herpetofaunal evolution in North America has been the *in situ* development of newer faunal elements from descendents of the faunas represented early in Tertiary time, rather than through waves of north-south dispersion. Basically, the Americas in early Cenozoic were occupied by two principal faunal groups: a) in the north by the ancestral Old Northern genera associated with the Arcto-Tertiary Geoflora in what is now the extreme northern United States north to the Arctic Sea; and b) over the rest of the American continents by the generalized Tropical American herpetofauna associated with the Neotropical Tertiary Geoflora. After separation of the two continents in late Paleocene the ancestral Tropical American herpetofauna underwent evolution in three primary centers: 1) in isolation in South America to become the basic herpetofauna of the region today; 2) in the area just north of the Panamanian portal from stranded groups rather closely allied to their South American cognates; and 3) in the western United States and Mexico. The first mentioned forms evolved into the South American Element associated with Neotropical Tertiary vegetation. The second group developed into the Middle American Element which is also associated with Neotropical Tertiary vegetation. The third element, the Young Northern Element, did not become fully differentiated until middle Cenozoic following the rapid physiographic and climatic changes affecting western North America from Eocene onward. Concurrent with the origin of the Young Northern Element in response to the changing environments of Middle Tertiary times, the Old Northern Element expanded southward as a general trend toward lower temperatures affected the region. The climatic shift ultimately restricted the Neotropical Tertiary geofloral derivatives to their present area of tropical occurrence. In the western and central portions of North America a long-term tendency toward increasing aridity produced a new vegetational association, the Madro-Tertiary Geoflora, from marginal Neotropical Tertiary types. Evolving in association with the Madro-Tertiary Geoflora from Oligocene onward has been the Young Northern Element of the herpetofauna, likewise derived from generalized Tropical American ancestors but gradually becoming adapted to arid conditions. Members of the Holarctic Element invaded the continent across the Bering land corridor at the time of Pliocene and early Pleistocene emergence and constitute a very small part of the total species composition of the modern American herpetofauna.

In summary, early Tertiary herpetofaunal elements were two in number, a generalized Tropical American unit and a temperate unit ancestral to the Old Northern Element. Physiographic and climatic changes provided the necessary circumstances and stimulus to the development of South American and Middle American Elements from the Tropical American unit in the tropics and of an arid derivative of the Tropical American unit in the warmer temperate regions, the Young Northern Element. The Old Northern Element of cooler and more humid areas has moved southward as the result of long-term cooling trends through Cenozoic, but has not successfully invaded the areas of Young Northern dominance because of the semiarid or arid environment. Representatives of the Holarctic Element of the cool temperate type have recently invaded the northern area of the continent. As shown by Axelrod (1958), Durham (1950), King (1958), MacGinitie (1958), and Simpson (1947, 1950) these views are fully compatible with current understanding of the physiographic, geologic, paleobotanic, and ecologic history of North America.

In detailed studies of herpetofaunistics it is usually necessary to evaluate historical origin more fully than is possible when only the five major elements are considered. Subdivision of each of the elements into units representative of the centers of differentiation within them increases the usefulness of the system. Species groups from primary centers of origin and dispersion of each element may be referred to as *complexes*. Minor units within a complex are called *components*. The herpetofaunal complexes of importance to an understanding of the development of the herpetofauna of Baja California are indicated in the accompanying table (Table 2). Inasmuch as the peninsula is dominated by species typical of the Desert and Plains and Madrean Complexes, the components of these two complexes are outlined in tabular form (Table 3). Current distribution of the majority of species within a given complex or component centers around appropriate biogeographic province or subprovince limits, respectively. However, no herpetofaunal province or subprovince is populated exclusively by a single historical complex. Utilization of the complex and component concepts are extremely useful in evaluating the historical relationships of any assemblage of amphibians and reptiles. They may be employed in evaluation of the faunal composition for recent faunas, as will be undertaken in the next section of this paper, or in determination of the relationships of fossil assemblages. Component analysis for fossil faunas is particularly important in ascertaining the previous distribution and possible history of the particular species assemblage under investigation.

TABLE 3—COMPONENTS OF AMERICAN HIGHLAND FAUNA

MADREAN COMPLEX

Californian Component—oak woodland, chaparral, pine woodland
Arizonian Component—oak woodland, chaparral, pine woodland
San Lucan Component—thorn-scrub, oak woodland, chaparral, pine woodland
Sierra Madre Occidental Component—oak-pine woodland, chaparral
Sierra Madre del Sur Component—oak-pine woodland
Sierra Madre Oriental Component—oak-pine woodland, chaparral

DESERT AND PLAINS COMPLEX

Great Plains Component—grasslands
Chihuahua Desert Component—desert woodland and scrub
Sonoran Desert Component—desert woodland and scrub

Actual application of this method to a particular fossil fauna may prove enlightening. Etheridge (1958) has recently discussed the herpetofauna of a Pleistocene locality from Cragin Quarry, Meade County, Kansas. This fauna is composed of remains of six species of lizards. Analysis of the small assemblage indicates that the members may be divided by complex or component as follows: 50% Chihuahua Desert Component, 40% Great Plains Component, and 10% Southeastern American Complex. These data indicate that forms now making up the Chihuahua Desert herpetofauna sometime in Pleistocene occurred farther north than at present and that the Cragin Quarry fauna may have lived in an area of mixed desert and grassland conditions.

In conclusion it must be emphasized that the basic unit of evaluation in utilizing the historical elements defined above is not the family or genus (contrary to Dunn, 1931). Species and species groups may be typical of a particular element, while other members of the same genus may have evolved as part of some other element. The genus *Rana* is an excellent case in point. Very clearly certain members of the group have entered America only recently and are part of the circumpolar Holarctic Element (*Rana aurora, Rana pretiosa,* and *Rana sylvatica,* for example). Other groups, as an example *Rana boylii* and its allies, have evolved as members of the Young Northern Element in conjunction with the development of Madro-Tertiary vegetation. Still other species groups, for example *Rana catesbeiana* and relatives, appear to be part of the very ancient Old Northern Element. In all likelihood the genus *Rana* has been in North America throughout most of Cenozoic and reference of the entire genus to one or the other historical element is misleading.

The Herpetofauna of Baja California

As pointed out in previous sections the recent herpetofauna of Baja California belongs to either the Sierra Madrean or Desert and Plains Provinces of the American Highland Subregion. The majority of species are representatives of the Young Northern Element, but some forms from the Old Northern Element are also present. The distribution of the recent species may be summarized as follows (see Fig. 2, Table 4):

1. A northwestern assemblage continuous with the herpetofauna of coastal and montane Alta California and associated with coastal sage scrub, oak woodland, chaparral, and pine woodland communities in a winter rain climatic area—The Californian Subprovince.
2. A northeastern desert assemblage continuous with the Colorado, Mojave, Arizona, and Sonora Desert areas and dominated by desert woodland and scrub vegetation in very arid winter rain belt—The Colorado Desert District.
3. A central peninsular assemblage occurring to the south of the California and Colorado Desert areas, also covered by desert woodland and scrub vegetation in an arid summer rain belt—The Peninsular Desert District.
4. An assemblage in the Cape region and montane areas to the north found east and south of the Peninsular Desert groups, associated with subtropical thornscrub, oak woodland, chaparral, and pine woodland communities in a summer rain climate—The San Lucan Subprovince.

The Californian and San Lucan Subprovinces are portions of the Sierra Madrean Province. The Colorado and Peninsular Desert Districts are subdivisions of the Sonoran Desert Subprovince of the Desert and Plains Province.

The general distribution of each species in the herpetofauna by basic areas is presented in the accompanying table (Table 4). Comparisons based upon the limits indicated for the biotic areas above and outlined on the accompanying map (Fig. 2) among these four units are presented in tabular form (Table 5). Interpretation of the faunal analysis is relatively simple. The Californian, San Lucan, and Colorado Desert centers differ markedly from one another, although a considerable degree of relationship is suggested for the first two. The Peninsular Desert area on the other hand is poorly differentiated from both the Colorado Desert and San Lucan faunas. As a matter of fact it seems to represent a transitional belt between the two, although different from both in total faunal aggregation. Another way in which to verify this concept is provided in an analysis of the degrees of endemism in each faunal unit (Table 6A). Again the Californian, San Lucan, and Colorado Desert areas are distinctive but not a single endemic occurs

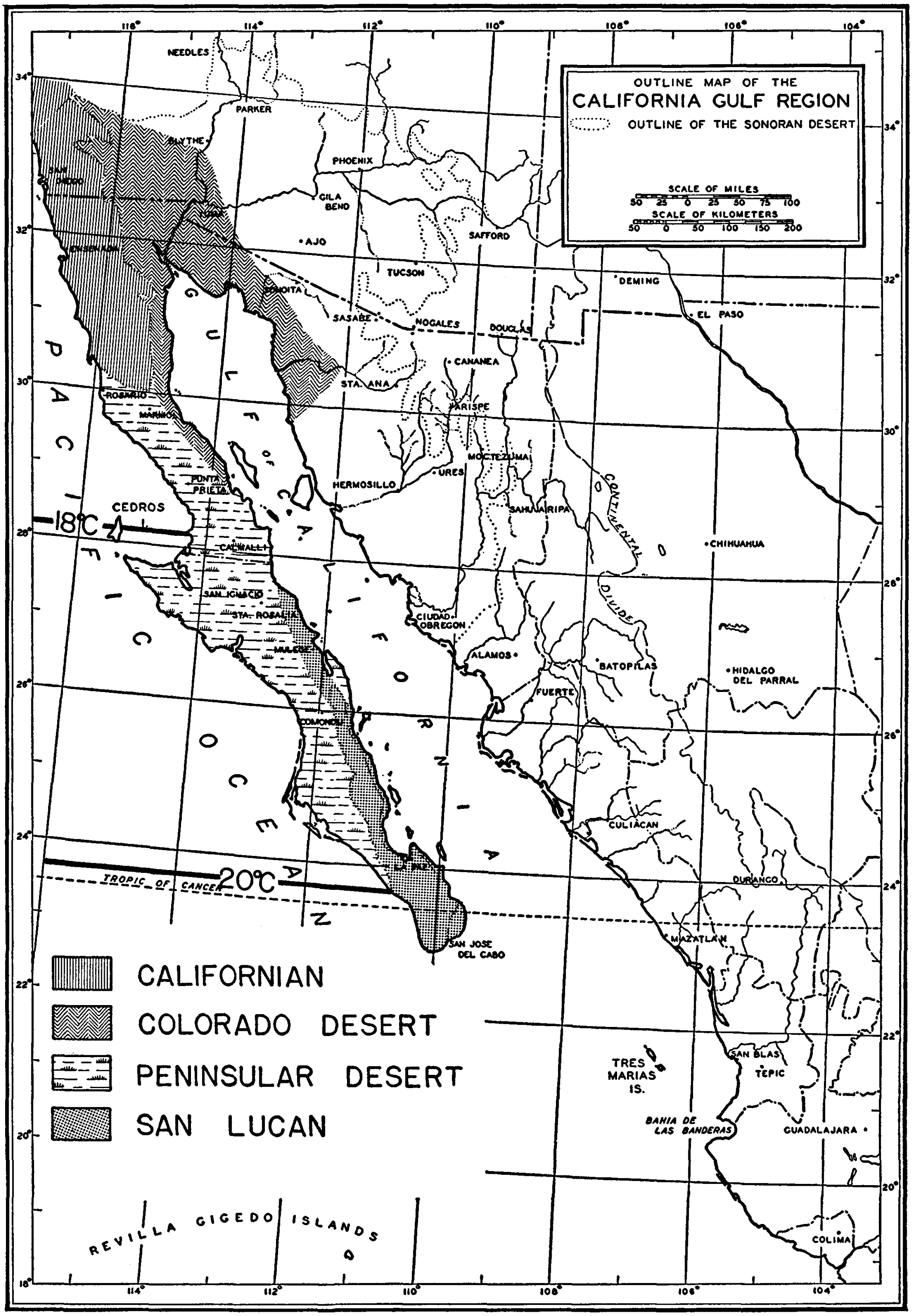

FIG. 2. Herpetofaunal areas of Baja California. Note the location of the minimum winter isotherms for marine surface temperatures.

TABLE 4—DISTRIBUTION OF THE BAJA CALIFORNIA HERPETOFAUNA BY FAUNAL AREA

SPECIES	CALIFORNIAN	COLORADO DESERT	PENINSULAR DESERT	SAN LUCAN
SALAMANDERS:				
Aneides lugubris	C			
Batrachoseps sp.	C			
Batrachoseps pacificus	C			
Ensatina eschscholtzii	C			
FROGS AND TOADS:				
Scaphiopus couchii			X	X
Scaphiopus hammondii	C			
Bufo boreas	C			
Bufo microscaphus	C			
Bufo punctatus	X	X	X	X
Hyla arenicolor	C			
Hyla regilla	X			X
Rana aurora	C			
TURTLES:				
Clemmys marmorata	C			
Pseudemys scripta				X
LIZARDS:				
Coleonyx variegatus	X	X	X	X
Phyllodactylus unctus				E
Phyllodactylus xanti		X	X	X
Xantusia henshawi	C			
Xantusia vigilis		X	X	X
Callisaurus draconoides		X	X	X
Crotaphytus collaris		X	X	
Ctenosaura hemilopha				C
Dipsosaurus dorsalis		X	X	X
Gambelia wislizenii		X	X	X
Phrynosoma coronatum	X		X	X
Phrynosoma m'callii		C		
Phrynosoma platyrhinos		C		
Sauromalus australis			X	X
Sauromalus obesus		C		
Sceloporus graciosus	C			
Sceloporus magister	X	X	X	X
Sceloporus occidentalis	C			
Sceloporus orcutti	X		X	X
Uma notata		C		
Urosaurus graciosus		C		
Urosaurus microscutatus		X	X	
Urosaurus nigricaudus				X
Urosaurus ornatus		C		
Uta mearnsi		C		
Uta stansburiana	X	X	X	X
Uta thalassina				E
Eumeces gilberti	C			
Eumeces lagunensis				E
Eumeces skiltonianus	C			
Cnemidophorus hyperythrus	X		X	X
Cnemidophorus labialis	E			
Cnemidophorus maximus				E
Cnemidophorus tigris	X	X	X	X
Bipes biporus			X	X
Gerrhonotus multicarinatus	C			
Gerrhonotus paucicarinatus				E
Anniella geronimensis	E			
Anniella pulchra	C			

TABLE 4—Continued

SPECIES	CALIFORNIAN	COLORADO DESERT	PENINSULAR DESERT	SAN LUCAN
SNAKES:				
Leptotyphlops humilis	X	X	X	X
Lichanura trivirgata	X			X
Arizona elegans	X	X	X	
Chilomeniscus cinctus	X		X	
Chilomeniscus stramineus				E
Coluber aurigulus				E
Coluber flagellum	X	X	X	X
Coluber lateralis	X		X	
Diadophis amabilis	C			
Elaphae rosaliae				E
Hypsiglena torquata	X	X	X	X
Eridiphas slevini				E
Lampropeltis getulus	X			X
Lampropletis zonata	C			
Natrix valida				C
Pituophis melanoleucus	X	X	X	X
Phyllorhynchus decurtatus		X	X	X
Rhinocheilus lecontei	X	X		
Salvadora hexalepis	X	X	X	X
Sonora bancroftae	E			
Sonora mosaueri			X	X
Sonora semianulata		C		
Tantilla eiseni	C			
Tantilla planiceps				E
Thamnophis couchii	C			
Thamnophis digueti				E
Thamnophis elegans	C			E
Trimorphodon lyrophanes				
Trimorphodon vandenburghi	C			
Crotalus atrox		C		
Crotalus cerastes		C		
Crotalus enyo	X		X	X
Crotalus mitchellii	X	X	X	X
Crotalus ruber	X	X	X	X
Crotalus viridis	X		X	
TOTALS:	50	32	32	45

X = present; E = endemic; C = endemic to area in Baja California but found elsewhere.
Because of the complexities of transitional areas, certain species that barely penetrate the margins of a particular faunal area have not been included.

in the Peninsular Desert. All species in this zone are found elsewhere on the peninsula, suggesting that the Peninsular Desert has been invaded by forms from the north and south. In another table (Table 6B) the actual composition of the Peninsular Desert herpetofauna and its probable sources are indicated.

Further analysis of distribution patterns provides a detailed picture of 13 different basic distributions with reference to the faunal areas. All 88 species of Baja California amphibians and reptiles fall into one of these patterns as indicated by percentages of the total faunal composition. Characteristic distributional patterns are illustrated in range maps (Figs. 3–7).

The relations of the total herpetofauna of the Peninsula to the rest of North America are surveyed in tabular form (Table 7) to complete the analysis. The table is designed to evaluate the general composition of the Baja California assemblage in terms of the historical complexes discussed in a previous section.

TABLE 5—COMPARISONS BETWEEN FAUNAL AREAS OF BAJA CALIFORNIA

	COEFFICIENT OF DIFFERENCE (C.D.)
Californian—Colorado Desert	72%
Californian—Peninsular Desert	60%
Californian—San Lucan	62%
Colorado Desert—Peninsular Desert	34%
Colorado Desert—San Lucan	60%
San Lucan—Peninsular Desert	41%

$$C.D. = 1 - \frac{C}{N_2} \times 100$$

$C =$ elements in common

$N_2 =$ total number of elements in larger fauna

The dominant forms in the region are members of the Young Northern Element. However, a significant but small representation of the species from the Pacific Border Component of the Western American Complex (Old Northern Element) is also present. All of the species from this latter assemblage are restricted to the Californian faunal area of relatively high winter rainfall and cool temperatures.

Origins and History of Baja California Herpetofauna

The composition and distribution of the amphibian and reptile fauna of Baja California are the products of complex interactions between a changing Cenozoic environment and the ancestral stocks of living species. The essential features of the history of the peninsular herpetofauna are variations on a theme of physiographic and climatic revolution throughout western North America from mid-Eocene to the present, with local emphasis provided by the barrier to dispersion formed by the Gulf of California. The detailed distribution of modern species within the region are the results of Pleistocene events but the dynamic evolution of the essential ingredients of the Baja California herpetofauna was initiated much earlier in Tertiary times.

The peninsula has existed as a more or less stable physiographic unit since the Eocene, with considerable fluctuation in southern extent between Eocene and Pliocene (Beal, 1948; Durham and Allison, 1960). The Gulf of California has acted as a strong barrier to biotic dispersion between the Mexican mainland and Baja California throughout peninsular history. The Gulf barrier was further intensified during most of Cenozoic since the marine waters reached northward into the Coachella Valley area of southern California to a much greater extent than at present. The stability of the peninsula and the long-term existence of a salt-water barrier to the east have required that all terrestrial immigrants, with the possible exception of a few trans-Gulf invaders,

TABLE 6—LEVELS OF DISTINCTIVENESS IN BAJA CALIFORNIA HERPETOFAUNAS

A. DEGREES OF ENDEMISM

FAUNAL AREA	N = TOTAL NO. SPECIES	E = ENDEMIC SPECIES	E/N × 100%
Californian	50	26	52%
Colorado Desert	32	10	31%
Peninsular Desert	32	0	0%
San Lucan	45	16	35%

B. COMPOSITION OF PENINSULAR DESERT FAUNA

FAUNAL UNIT	1.	2.
Californian	62%	25%
Colorado Desert	66%	28%
San Lucan	81%	44%

1. = % of total Peninsular Desert fauna found in other areas.

2. = % of total Peninsular Desert fauna found in other areas, exclusive of ubiquitous species.

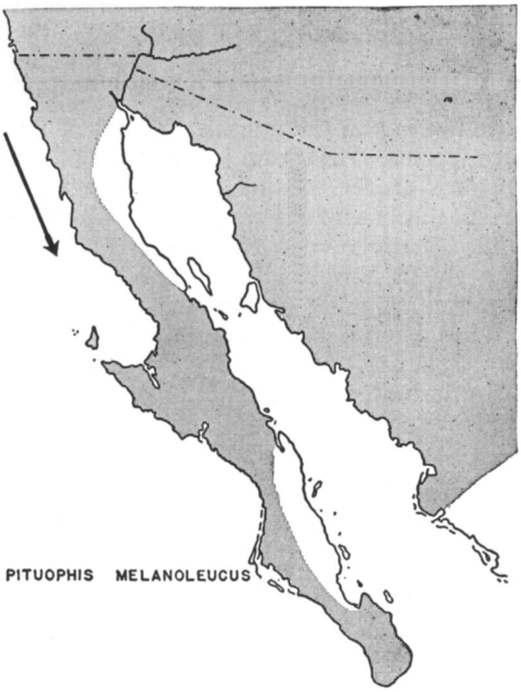

FIG. 3. Range of gopher snake, *Pituophis melanoleucus*, a ubiquitous Baja California species. Solid arrow indicates direction of dispersal since most recent glacial period.

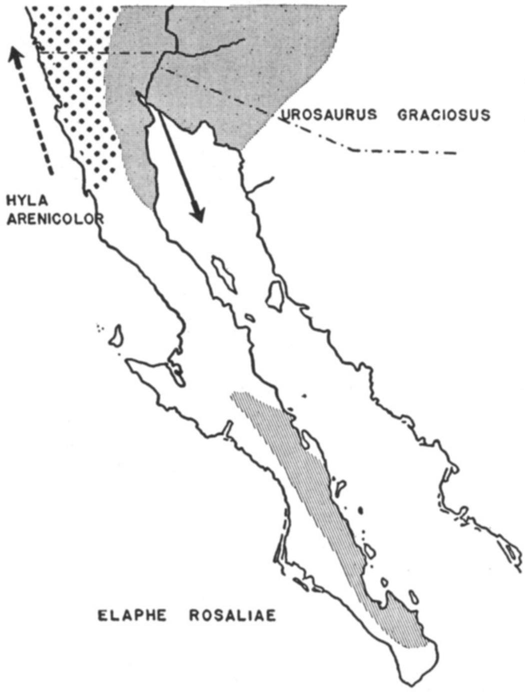

FIG. 4. Ranges of a Californian area endemic, cañon tree-toad, *Hyla arenicolor;* a Colorado Desert endemic, long-tailed bush lizard, *Urosaurus graciosus;* and a San Lucan endemic, Baja California ratsnake, *Elaphe rosaliae*. Solid arrow indicates direction of dispersion since most recent glacial recession; dashed arrow direction of contraction of range.

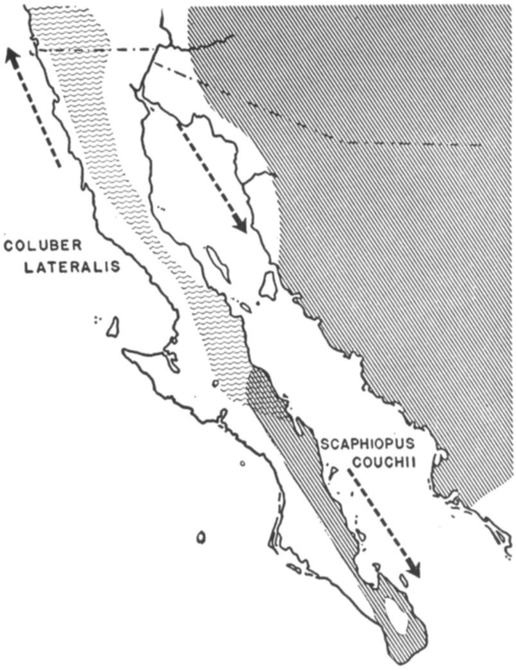

FIG. 5. Ranges of species occurring in two faunal areas in Baja California: a species with a Californian-Peninsular Desert distribution, California striped whipsnake, *Coluber lateralis;* a form with a Peninsular Desert-San Lucan distribution, Great Plains spadefoot, *Scaphiopus couchii*. Dashed arrows indicate direction of contraction of range with increasing aridity.

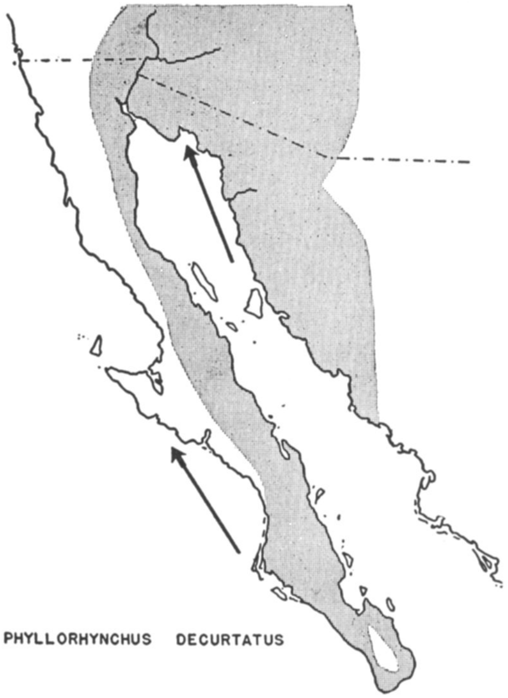

FIG. 6. Example of species occurring in three of the four major biotic areas of Baja California: the leaf-nosed snake, *Phyllorhynchus decurtatus*. Solid arrow indicates direction of dispersal into areas on increasing aridity since latest glacial recession.

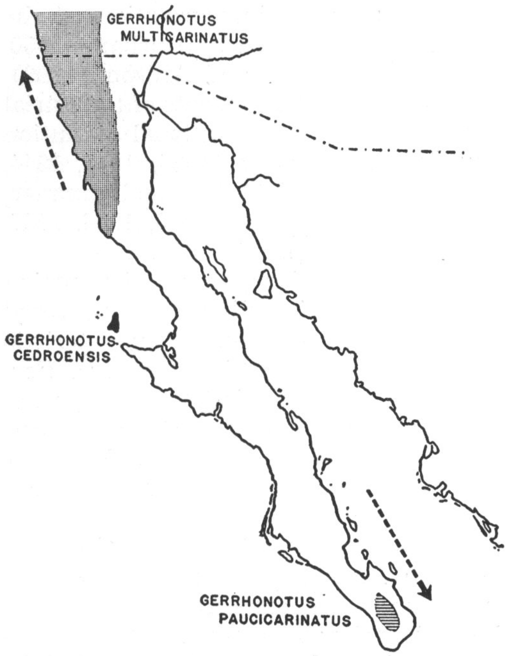

FIG. 7. Example of distribution pattern of paired allopatric species found in Californian and San Lucan biotic areas: the California alligator lizard, *Gerrhonotus multicarinatus*, and the San Lucan alligator lizard, *Gerrhonotus paucicarinatus*. Note the occurrence of a third allopatric form, *Gerrhonotus cedrosensis*, on Cedros Island off the Pacific coast of the peninsula. Broken arrows indicate contraction of ranges since glacial maximum.

1. Ubiquitous (found in all four areas)	13%
2. Endemic (total)	57%
Californian	28%
Colorado Desert	11%
San Lucan	18%
3. Restricted to Two Areas (total)	14%
Californian—Colorado Desert	1%
Californian—Peninsular Desert	3%
Californian—San Lucan	3%
Colorado Desert—Peninsular Desert	2%
Peninsular Desert—San Lucan	5%
4. Absent from One Area (total)	11%
Californian	5%
Colorado Desert	4%
San Lucan	1%
5. Paired Allopatric Species (Californian-San Lucan)	6%

TABLE 7—RELATIONSHIPS OF TOTAL BAJA CALIFORNIA FAUNA (88 SPECIES)

FAUNAS	% OF COMMON SPECIES
1. Eastern Forest Complex	2
2. Southeastern Coastal Plains Complex	3
3. Western American Complex	
a. Rocky Mountain Component	9
b. Pacific Border Component	18
4. Madrean Complex	
a. Californian Component	51
b. Arizonian Component	14
c. Sierra Madre Occidental Component	9
d. Sierra Madre del Sur Component	3
e. Sierra Madre Oriental Component	5
f. San Lucan Component	50
5. Desert and Plains Complex	
a. Sonoran Desert Component	50
b. Chihuahua Desert Component	24
c. Great Plains Component	21
6. Middle American Element	3

enter the region from the north. The present herpetofaunal assemblage of Baja California consists primarily of northern migrants or western Mexican forms that have invaded the peninsula from the north after passing around the head of the Gulf of California.

The geologic history of Baja California is closely associated with the development of the rest of western North America. As brilliantly outlined by King (1958) the entire western continental region has undergone vast physiographic convulsions and radical change from Eocene to the present. Of greatest significance to the evolution of current distribution patterns was extensive mountain building activity in late Cenozoic. Generally important to the development of the distinctive western herpetofauna was the uplift of the Rocky Mountain cordillera of the central United States and Mexico from Eocene onward as these ranges came to isolate the western regions from the influences of eastern groups. Of principal importance to evolution in Baja California was the uplift of the Sierra Nevada and Peninsular Ranges of the Pacific region to their present great heights during late Pliocene and Pleistocene. The effects of mountain building were most pronounced in northern Baja California where the Sierra Juarez and Sierra San Pedro Mártir attained maximum elevation to 10,000 feet and in the Cape region where the Sierra Laguna and Sierra Victoria attained elevations of 6,200 feet. Vulcanism contributed to the formation of mountains in the central peninsula in late Miocene, and some individual peaks of these ranges reach altitudes over 6,000 feet at the present. Mountain building contributed in two important ways to the development of the modern herpetofauna by 1) providing areas where altitudinal ecologic effects allowed the entrance into the peninsula of forms typical of cooler and moister areas to the north, and 2) making possible dispersion along ecologically suitable foothill environments southward into the Cape region during periods of lower temperature and higher rainfall in Pleistocene. Another minor effect, in the north, was the contribution to rain-shadow as relating to the development of arid conditions in the Colorado Desert. The central and cape mountain ranges may have also had a rain-shadow effect on the lowlands of adjacent western Mexico in the Pleistocene when the major storm-tracks must have moved across the peninsula toward Mexico. Today the principal storms moving into the area of the Mexican lowlands opposite the peninsula move up the Gulf of California from south to north and the peninsular ranges have little effect on rainfall characteristics of the adjacent mainland.

Climatic conditions and the general ecology of the peninsula have undergone marked changes since mid-Eocene correlated in a broad sense with the geologic and physiographic shifts summarized above. Although no well-documented fossil record of the terrestrial life of Baja California exists, the data from marine fossils and knowledge of the paleobotanic record elsewhere in western America allow reconstructions of the basic paleoecology of the peninsula throughout Cenozoic. The generalized survey that follows is based upon an interpretation of the marine data discussed by Durham (1950, 1954), and Durham and Allison (1960), integrated with the concepts of terrestrial paleoecology and vegetational evolution developed by Chaney (1938, 1940, 1944, 1947) and Axelrod (1950), and summarized by Axelrod (1948, 1950, 1956, 1957, 1958) and MacGinitie (1958).

In early Tertiary times the region which is now Baja California was covered by a humid tropical forest characteristic of the Neotropical Tertiary Geoflora. Forest associations of this general type apparently ranged as far north as present day southern Canada (Axelrod, 1958). Generally similar climatic and vegetational conditions apparently persisted in the region until at least Eocene time.

In the Eocene, MacGinitie (1958) reports three principal floras from western North America: a) a subtropic forest extending along the coast to about 55° N. Latitude (near the level of the minimum February isotherm of 18° C., according to Durham, 1950, and inland at least to Wyoming); b) a tropical flora along the Mississippi embayment coast in what is now western Texas and central New Mexico; and c) far to the north the warm temperate Arcto-Tertiary forests. Baja California appears to have been occupied by subtropical and possibly tropical forests at this period. Marine surface temperatures (winter minimum) were over 25° C. at the latitude of Cabo San Lucas.

During Oligocene there seems to have been a shift toward cooler temperatures along the western coasts (the 18° C., minimum isotherm for February was near 50° N. Latitude) and reduction in rainfall. However, no major changes in vegetation occurred until Miocene when elements of the Madro-Tertiary Geoflora appear to take on a greater dominance in response to a general increase in aridity (Axelrod, 1958). However, even in early Miocene the vegetation and climate of Baja California were probably similar to those of the adjacent Mexican mainland with subtropical vegetation predominating. By late Miocene subtropical environments were probably restricted southward or to the coastal areas by cooling temperatures and increasing aridity. The winter minimum isotherm of 18° C., was at the latitude of Los Angeles and the 25° isotherm was at the level of Cabo San Lucas by this time. Madro-Tertiary elements, particularly thorn-scrub, probably dominated over much of the northern two-thirds of the peninsula.

In the Pliocene the combined effects of temperature decrease, increased aridity, and mountain building activity appear to have resulted in restriction of the thorn-scrub to extreme southern Baja California. A continuous Madro-Tertiary floral unit of mixed oak woodland, chaparral, and more arid forms expanded down the length of the peninsula, and desert elements began to appear in the rain-shadow area of the northeast. In addition Arcto-Tertiary floral components probably entered Baja California for the first time on the higher ridges of the developing Sierra of northern Baja California. By the end of the Pliocene the modern floral units found in Baja California seem to have been established. The thorn-scrub complex persisted in the Cape region lowlands of relatively high temperatures and rainfall. The oak woodland and chaparral communities of the Madro-Tertiary Geoflora dominated as a continuous floral belt from the north throughout the waist of the peninsula and into the uplands of the Cape region. Desert vegetation probably was developing rapidly in areas of low rainfall in the northeast and gulf coastal areas under the influence of rain-shadow produced by the rising northern Sierra. The Arcto-Tertiary geofloral pine communities penetrated the peninsula from the north and continued to expand southward as a response to lowering temperatures and the availability of low mountain habitats. Marine temperature data indicate that the winter minimum isotherm for 18° C. now was off the coast of Baja California at about the level of Cabo Colnett (Durham, 1950).

Unfortunately, Pleistocene climate changes and geofloral shifts are not well-known for the far west. Consequently, the patterns during this period must be described less on the basis of paleoecology and paleobotany and more from interpretations of current distributions. It is obvious that temperatures and rainfall have fluctuated in a sequence generally correlated with the advance and retreat of glaciers during the Pleistocene on a continental basis. Deevy (1949) has summarized the evidence for this view for eastern North America. Martin (1958) reviewed the entire problem and provided a resumé of data which established the impact of these changes on western United States and Mexican species. Basically temperature shifts southward at glacial maxima forced temperate elements southward into regions occupied by warm-adapted types during periods of glacial recession. Temperature isotherms and correlated climatic conditions moved as much as 600 miles between glacial maxima and minima (Durham, 1950, 1954) along the west coast with profound local effects in altitudinal displacement. In addition, although rainfall fluctuated during glacial and interglacial stages, throughout the period each succeeding interglacial became more arid than those preceding it. Development of winter rain climate in coastal California and northern Baja California also appears to have taken place during the Pleistocene.

The effects of these three climatic features, temperature fluctuation, trend toward aridity, and the appearance of a winter rain belt, have all significantly modified the herpetofaunal composition of Baja California. Evidence from geofloral records in southern California (Axelrod, 1950) and marine surface temperature data, as well as faunal distribution suggest that two distinctive situations prevailed at glacial versus interglacial times. During interglacial peaks the peninsular ecology did not differ greatly from present conditions. The basic pattern of the late Pliocene was modified by increasing aridity in the rain-shadow area of the northeast and central regions of the peninsula. These shifts brought about further restriction of the thorn-scrub to the extreme Cape area, domination of most of the peninsula by desert vegetation, and fragmentation of the Madrean woodland-chaparral communities into a northern west coastal unit and a southern Cape upland unit. Increased elevation of the northern ranges allowed the Arcto-Tertiary communities to persist in these montane areas.

At periods of glacial maxima the picture changed markedly. The northern pine woodlands apparently moved somewhat southward and to lower elevations. The oak woodland and chaparral communities seem to have pushed southward and probably became co-extensive with comparable elements advancing northward and to lower elevations from the Cape mountains. Thorn-scrub seems to have maintained itself in the lowlands of the Cape region and possibly extended farther north along the Pacific coast. Desert vegetation was probably replaced by Madrean communities related to sage scrub and chaparral. Desert elements seemed to have survived in marginal thorn-scrub and chaparral areas of maximum temperature and minimal rainfall. At the heights of glacial recession desert conditions were re-established and desert vegetation re-constituted from these marginal communities and from desert immigrants from the Mexican mainland. The theory of desert replacement and re-constitution at glacial maxima and minima applies only to the peninsular region. The evidence a) that at maximum glaciation in the north, climatic conditions in central Baja California resembled those near Los Angeles today (Durham, 1950); b) that Arcto-Tertiary elements shifted far to the southward at this time (Chaney and Mason, 1934); and c) the current nature of the fauna of the central portion of the peninsula, all support this concept.

The apparent disappearance of the central peninsular flora and fauna during the Pleistocene as suggested by Nelson (1921), Johnston (1924), and Beal (1948) also support my concept. These authors invoke a marine flooding of the entire central peninsula to explain the apparent absence of desert communities in the region during glacial peaks. No extensive flooding of this region is satisfactorily demonstrated by geologic evidence (Durham and Allison, 1960) but the climatic changes outlined above indicate that the environment became highly modified and unsuitable for desert forms.

Re-invasion of the most arid segment of the peninsula by desert vegetation from further south along the Mexican mainland is an integral part of my theory. Whether desert conditions persisted in what is now southern Sonora and Sinaloa during the crucial glacial maxima or whether there was a re-constitution of desert vegetation from thorn-scrub and oak woodland and chaparral communities is not clear at present. In any event the most recent post-glacial changes included northward movements of desert vegetation from the Cape region and from the Sonoran desert area to the head of the Gulf of California and thence southward into the peninsula. The thorn-scrub community seems to be stabilized in the Cape lowlands, although an admixture of thorn-scrub and desert elements is typical of certain areas. Retreat of pine woodlands upward on the northern Sierra and restriction of oak woodland and chaparral communities to disjunct elements along the northwest coast and in the southern mountains complete the latest phase of Cenozoic history.

In summary, since the time of the origin of the early peninsula and gulf areas in the Eocene two long-term climatic and vegetational trends have molded the herpetofauna of the region. The first of these trends has been gradual modification of the Eocene tropical climate toward temperate and subtropic conditions. This climatic shift which involved gradual changes up to mid-Miocene has been intensified in the Pliocene and Pleistocene by the general restriction of the world-wide tropical belt southward (Axelrod, 1952). Vegetational changes associated with the climatic shift have been away from humid tropical vegetation of Neotropical Tertiary floral affinities toward dominance by mid-Miocene of the semi-arid antecedents of Madro-Tertiary components. In addition the temperate Arcto-Tertiary Geoflora invaded the northern region of the peninsula in late Pliocene.

The second major trend has been toward a more arid climate. Increasing aridity seems to have provided the stimulus for the development of characteristic Madro-Tertiary vegetation in western North America and the dominance of Madro-Tertiary derivatives in Baja California today. Rather late in origin have been the distinctive desert vegetational elements, which have lacked community stability in Baja California during the Pleistocene. A minor and probably recent trend has been the restriction of rainfall to the winter months in the northern sections of the peninsula. Summer rains are characteristic of the Cape region and the Peninsular Desert and this difference may explain the persistence of Neotropical Tertiary geofloral elements mixed with the Madro-Tertiary thorn-scrub in southern Baja California (Wiggins, 1960). The Colorado Desert portion of the peninsula has very low rainfall and the rains are concentrated in the winter.

The history of the herpetofauna is closely associated with the physiographic and climatic developments just discussed. As pointed out earlier in this article the several historical elements of the North American herpetofauna are broadly correlated with specific fragments derived from the three Tertiary Geofloras. The scanty available fossil evidence (Gilmore, 1928, 1938; Brattstrom 1955a, 1958a; and Peabody, 1954, 1959) suggests that the associations between herpetofaunal elements and specific geofloral derivatives have existed on a long-term basis and that the same complex of factors has operated in the evolution of modern vegetation and modern herpetofaunas. In any event, an interpretation of the history of the amphibians and reptiles of Baja California requires a reliance upon the well-documented geofloral record.

Baja California in Eocene time was apparently occupied by a herpetofauna associated with the Neotropical Tertiary floral elements of this essentially humid, tropical climatic area. Amphibians and reptiles in the tropical regions of North America at this time were remarkably distinct from recent assemblages in the region, but exhibit definite affinities to the faunas of both present day old and new world tropics. Since the American continents had only recently been separated by the Panamanian portal similar basic groups (families and some genera), probably inhabited both areas. Members of these tropical herpetofaunas belong to a generalized Tropical American unit, discussed in a previous section, which evolved into the basic herpetofauna of late Cenozoic South America. Lying far to the north of Baja California at this time, with its southern limits north of the present Canadian border, was a second major geofloral assemblage, the Arcto-Tertiary, typical of cooler more temperate climatic conditions. Amphibians and reptiles of the Old Northern Element are derived from ancestral forms which inhabited this northern region.

In the Oligocene the first marked changes in climate began to affect western North America. The general changes brought about southward dispersal of Arcto-Tertiary species and among amphibians and reptiles a correlative movement of Old Northern forms in the same direction. These forces had little direct influence on Baja California, except as they laid the basis of changes in the Miocene. Of considerably greater significance, however, was the *in situ* development of the Young Northern Element of the herpetofauna as Madro-Tertiary floral components began to sort out and become evident in this period. The ancestors of most living genera of characteristically

Madrean and Desert and Plains Complexes were originating at this time in savanna and scrub vegetational zones throughout tropical and subtropical portions of North America. The events of post-Oligocene history have given these Young Northern groups dominance in the west to the point where none of the forms in Baja California may be considered pre-Miocene relicts.

In early Miocene times (Fig. 8) Baja California still formed an area dominated by Neotropical Tertiary floral components. The climate appears to have been somewhat cooler and drier than earlier in the Tertiary and dry tropical and subtropical habitats probably predominated. The cognates of the South American Element of the herpetofauna during the period from mid-Eocene to Miocene seem to have been undergoing a gradual evolution into genera and species adapted to more arid and less equable climatic situations than had previously prevailed. This evolutionary challenge probably was correlated with the climatic and vegetational changes giving rise to the Madro-Tertiary Geoflora (Axelrod, 1958) and led to the development of the Young Northern Element of the American herpetofauna by mid-Miocene. Early invaders into Baja California were Young Northern Element forms associated with thorn-scrub communities. Today the remnants of these groups are associated with thorn-scrub vegetation in the Cape region or are isolated on southern islands in the Gulf of California. They include the insular lizards *Sator* and *Cnemidophorus ceralbensis,* the Cape amphisbaenid *Bipes,* and the snake *Eridiphas slevini* which is found on Cerralvo Island and in the Cape area.

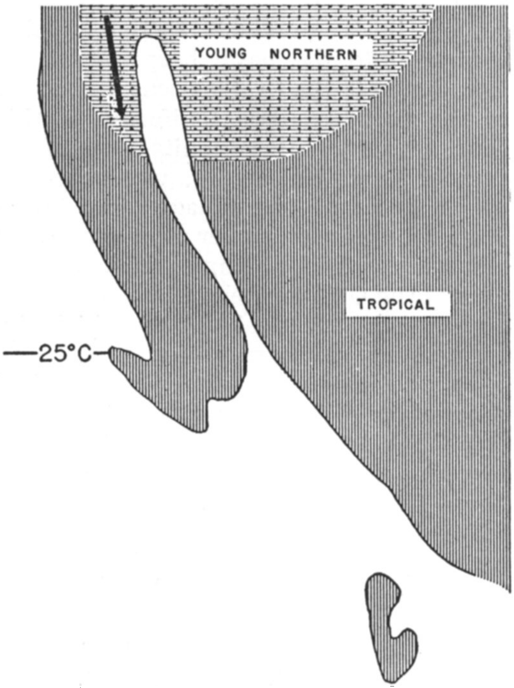

FIG. 8. Distribution of herpetofaunal elements in Baja California region in early Miocene. Location of marine surface minimum winter isotherm of 25° C. indicated. Solid arrow indicates direction of immigration of developing Madrean Complex species, following retreat of tropical types.

Old Northern Element forms ranged farther south at this time than previously, at least into what is now the northern portions of California, Nevada, Arizona, and New Mexico. The herpetofauna of the peninsula in mid-Miocene was essentially of evolving units of the Young Northern Element associated with marginal Neotropical Tertiary floral elements and the Madro-Tertiary Geoflora as it gradually replaced the Neotropical Tertiary over much of the region. The decrease in temperature and increased aridity responsible for floral evolution provided a stimulus to the invasion of the peninsula from the north by additional representatives of the Young Northern Element. By early Pliocene (Fig. 9) the ancestors of dominant peninsular genera were in Baja California. Apparently the herpetofauna was of a generalized composition of Madrean and Desert and Plains Complex types. Among present day inhabitants of the peninsula the following taxa appear to be derived from these Young Northern invaders: *Coleonyx, Phyllodactylus, Xantusia, Ctenosaura, Phrynosoma coronatum, Sceloporus orcutti, Urosaurus microscutatus-*

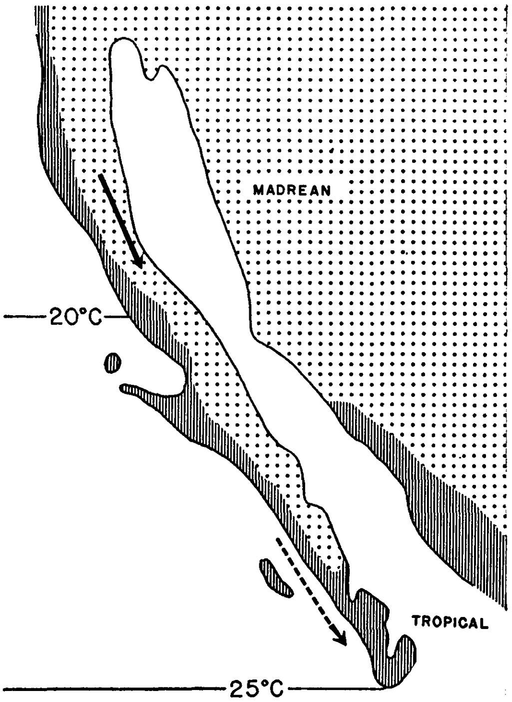

FIG. 9. Distribution of herpetofaunal elements in early Pliocene. Location of minimum winter isotherms for marine surface temperatures indicated. Solid arrow indicates direction of expansion of Madrean Complex species, broken arrow indicates contraction of ranges of more tropical types.

nigricaudus, *Uta mearnsi-thalassina*, *Eumeces*, *Cnemidophorus hyperythrus*, *Cnemidophorus maximus*, *Gerrhonotus*, *Anniella*, *Leptotyphlops*, *Lichanura*, *Chilomeniscus*, *Coluber lateralis-aurigulus*, *Hypsiglena*, *Pituophis*, *Sonora*, *Tantilla*, *Thamnophis*, *Trimorphodon*, *Crotalus enyo* and *Crotalus ruber*.

Elsewhere in North America the Arcto-Tertiary Geoflora and associated Old Northern Element continued to expand southward as cooling increased. Apparently at this time or earlier in the Miocene certain warm temperate forms of the Old Northern Element became associated with the remaining thorn-scrub community of Madro-Tertiary vegetation to become established in Baja California (*Pseudemys*, *Elaphe*, *Natrix*) and in the case of the first and last genera, in similar subhumid thorn-scrub areas of west Mexico (Fig. 9).

In the Pliocene the effects of mountain building and the acceleration of increasingly arid trends brought about restriction of the relictual Neotropical Tertiary floral units southward. The Madro-Tertiary Geoflora developed into woodland-chaparral and desert components (Axelrod, 1958), as Madrean and Desert and Plains Complexes of the Young Northern Element of the herpetofauna underwent similar diversification. By late Pliocene (Fig. 10) the thorn-scrub persisted in southern Baja California but practically none of its original faunal components survived the competition of the aggressive Madrean invaders. A number of species groups appear to have invaded Baja California from the north at this time from mainland Mexican centers of desert

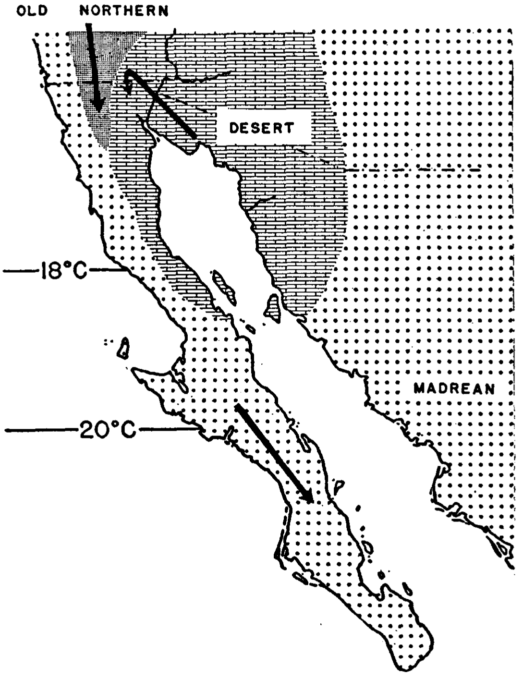

FIG. 10. Distribution of herpetofaunal units in late Pliocene. Solid arrows indicate direction of dispersion of Madrean and Western American Complex species, following southward retreat of thorn-scrub associates of Madrean group. Location of minimum marine surface isotherms indicated.

vegetation to occupy the arid regions of the peninsula. Ancestors of the following groups belonging to the Desert and Plains Complex probably became established in Baja California as a result of this invasion: *Scaphiopus couchii, Bufo punctatus, Callisaurus, Dipsosaurus, Gambelia, Sauromalus, Phyllorhynchus* and *Crotalus mitchellii.* Strictly Arcto-Tertiary associated members of the Old Northern Element (Western American Complex) became established in the montane and relatively humid areas of northwest Baja California at this time and included the ancestral stocks of the following recent groups: *Aneides, Batrachoseps, Ensatina,* and *Clemmys.*

The history of the herpetofauna of Baja California during the Pleistocene is complicated by an inadequate knowledge of the time, number, extent, and climatic influences of glacial correlated change throughout western America. Martin (1958) has surveyed current information and concludes that temperature depression and associated effects were of major significance in the west. Although it is not possible to more than sketch the Pleistocene history of the peninsula, it appears that from the end of the Pliocene onward three trends already begun in the Miocene and Pliocene have been intensified: a) decrease in rainfall with winter rain in the north; b) general decrease in temperatures, with temperate conditions established in the north; and c) increased mountain-building. These trends continued throughout the period but with temporal shifts due to the fluctuations of glacial and interglacial climates.

Apparently (Axelrod, 1957) three glacial cycles had major effects in the far west. In each succeeding interglacial period aridity increased. Although exact dating is not possible the general patterns at glacial maxima and minima have been outlined previously.

At times of glacial maxima (Fig. 11) temperatures became lowered and humidity increased. Under these circumstances thorn-scrub communities retreated and persisted only in the extreme southern Cape areas. Subhumid coniferous woodlands expanded in the northwest coastal and montane area. Oak woodland-chaparral communities dominated the entire central peninsula and scrub vegetation probably covered the northeast arid area as well. Madrean forms with relatively high rainfall requirements (*Scaphiopus hammondii, Bufo microscaphus,* and *Hyla arenicolor*) probably invaded the moister coastal regions from the north at this time. Two members of the Holarctic Element (*Bufo boreas* and *Rana aurora*) also became established in the nothern portions of the peninsula.

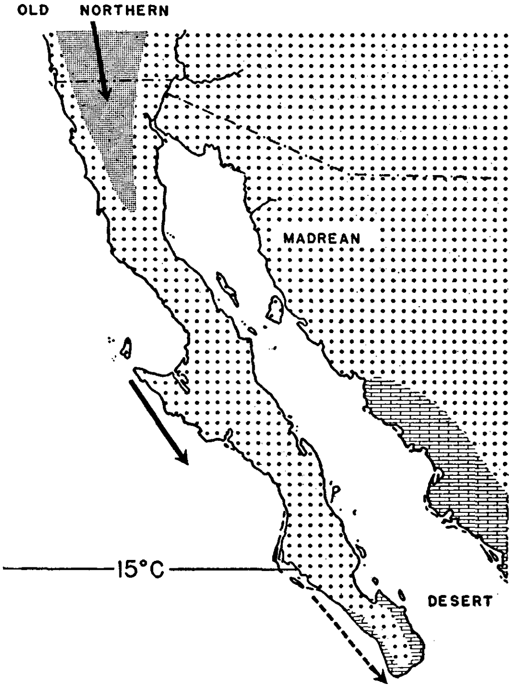

FIG. 11. Distribution of herpetofaunal complexes in Baja California at times of glacial maximum in Pleistocene. Solid arrows indicate direction of dispersion into peninsula from north, broken arrows the retreat of desert and thorn-scrub associates southward. Note the location of the minimum winter isotherm for marine surface temperature at level of Bahia Magdalena, which corresponds to situation near San Diego today.

Madrean Complex species of the Young Northern Element dominated in central

Baja California but desert forms were mostly restricted to the south in a thorn-scrub refugium in the Cape. Example species in the former category include forms which today make up the distinctive San Lucan and California Components: *Scaphiopus hammondii, Bufo microscaphus, Hyla arenicolor, Hyla regilla, Phrynosoma coronatum, Eumeces, Cnemidophorus labialis, Gerrhonotus, Anniella, Leptotyphlops, Coluber lateralis-aurigulus, Hypsiglena, Lampropeltis getulus, L. zonata, Diadophis, Pituophis, Tantilla,* and *Thamnophis.* Desert species of the Desert and Plains Complex restricted at glacial maxima into a thorn-scrub refugium in Southern Baja California included ancestors of the following: *Scaphiopus couchii, Bufo punctatus, Coleonyx, Callisaurus, Dipsosaurus, Sauromalus, Sceloporus orcutii, Cnemidophorus maximus, Chilomeniscus, Phyllorhynchus, Crotalus enyo,* and *Crotalus ruber.* At which interglacial period the fragmentation typical of each of these desert species groups occurred is problematical. In most of the cited examples a related geographical race or species seems to have developed from forms in a similar refugium region for Sonoran Desert representatives in western Mexico. Evidence from other sources indicates that Chihuahua desert species were also displaced southward at glacial peaks and probably survived in a scrub refugium during these periods (Fig. 13). In any event the evidence is strong that desert environments were all but eliminated in Baja California during certain times in the Pleistocene and that reconstitution of desert herpetofaunas occurred at glacial minima by invasion of the peninsular desert from the south (Cape refugium) and from the north by forms that had immigrated northward around the head of the Gulf of California from the Sonoran refugium. Recent northern invaders falling into this group include the following examples: *Crotaphytus, Phrynosoma platyrhinos, Sauromalus obesus, Sceloporus magister, Urosaurus ornatus, Cnemidophorus tigris, Arizona elegans, Sonora semiannulata,* and *Crotalus atrox.*

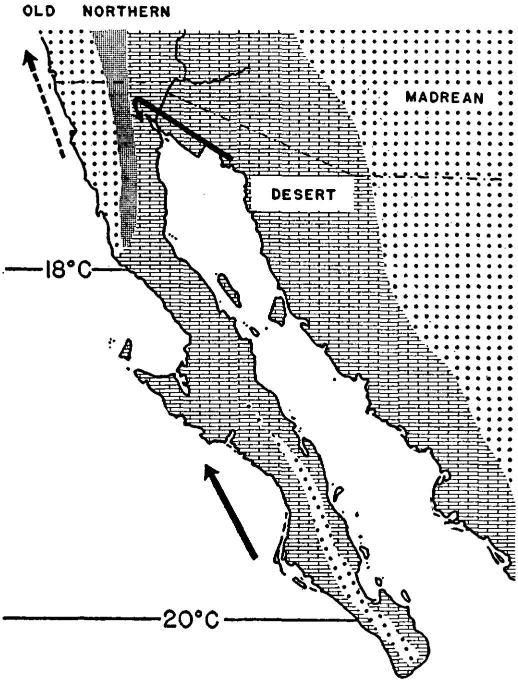

FIG. 12. Distribution of herpetofaunal complexes in Baja California at interglacial times. Solid arrows indicate direction of expansion by Desert and Plains Complex, broken arrow retreat of Madrean Complex. Location of marine surface isotherms for February indicated.

As temperatures and aridity increased (Fig. 12) during Interglacials desert vegetation and herpetofauna replaced the oak woodland-chaparral communities and Madrean herpetofauna except in the Californian and San Lucan areas. Fragmented ranges and origin of paired allopatric species (Fig. 14) in the California and San Lucan regions, separated by 300 miles of desert, have been the result. The desert zones in mid-peninsula were invaded by warm arid adapted forms from the Cape thorn-scrub refugium and by species moving around the Gulf of California from the mainland region as desert conditions expanded. A number of species beautifully illustrate the dual invasion of the central area (Fig. 15). Persistence of temperate faunal elements in the north even at glacial minima is apparently explained by

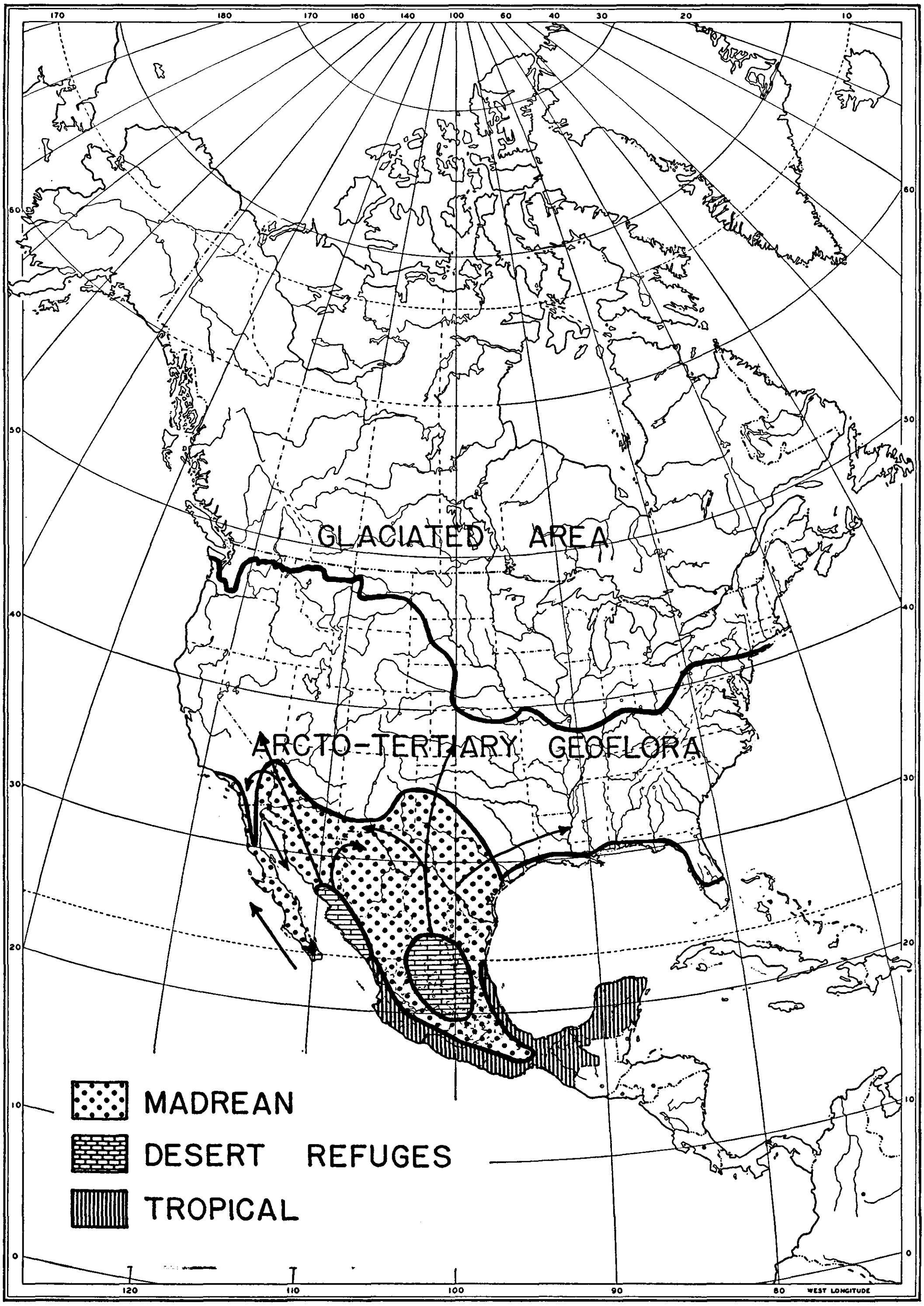

FIG. 13. Distributional pattern of herpetofaunal elements in North America at glacial maxima to indicate probable location of refugia for desert forms. Solid arrows indicate the general direction of dispersion for desert forms as glaciers retreated and arid conditions made more northern areas available for occupancy.

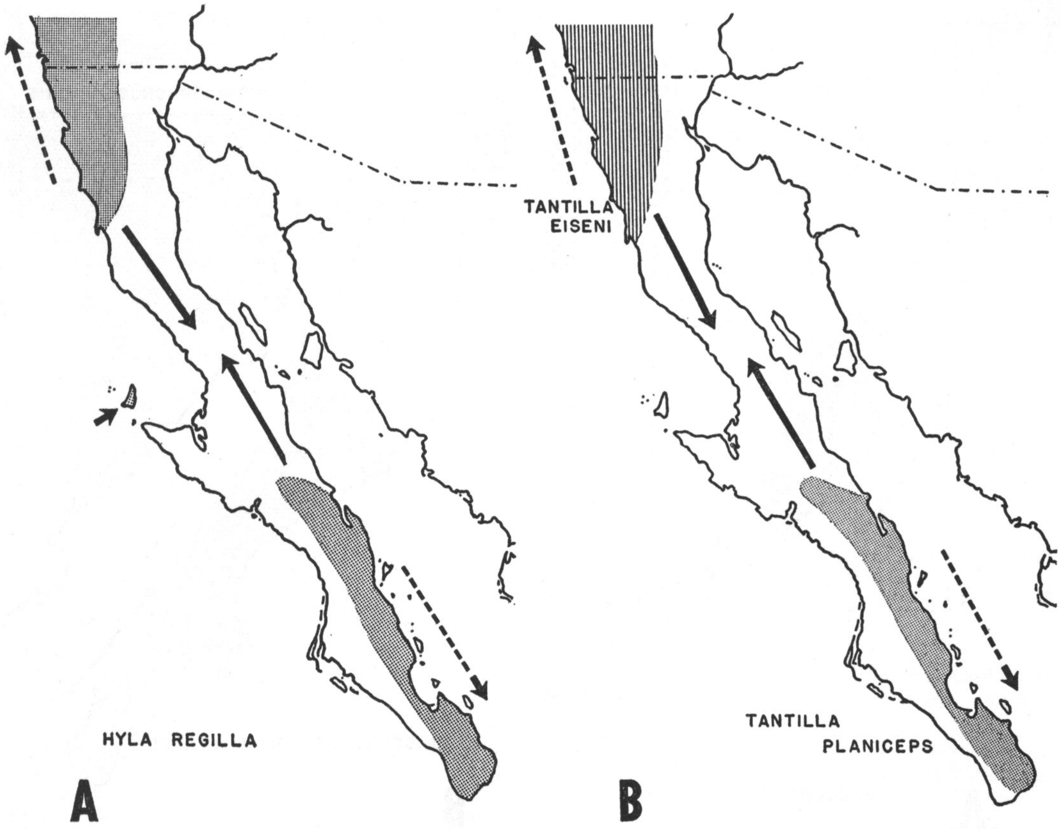

FIG. 14. Distribution patterns indicating interglacial fragmentation of continuous ranges of Madrean Complex fauna in Baja California. A. Range of the western treetoad, *Hyla regilla.* B. Range of California black-headed snake, *Tantilla eiseni* and San Lucan black-headed snake, *Tantilla planiceps.* Solid arrows indicate direction of dispersion by these forms at glacial maxima, broken arrows the contraction of ranges in interglacial periods.

the continued elevation of the northern Sierra.

Summary

Historically, the peninsular region has been invaded by four waves of immigrants from the north that have all but replaced the early Tertiary fauna of the area. The first wave consisted of groups of the Madrean Complex of the Young Northern Element which came to dominate the herpetofauna in the Pliocene. These groups invaded the peninsula from the north and ultimately formed the basic fauna of the Californian and San Lucan areas. Initial invasion correlated with lowering of temperatures and the development in the peninsula of Madro-Tertiary floral types. A second wave of desert adapted groups came into northern areas during the Pliocene as aridity increased. General temperature decreases in the northern Sierra montane area and increased elevation allowed a third wave of Arcto-Tertiary association to penetrate into Baja California concurrent with desert formation in the east and south. In the Pleistocene a second wave or even several waves of desert forms invaded the peninsula from the northeast at times of interglacial conditions.

Events in the Pleistocene culminated in increased elevation of the mountains, increased aridity, and general temperature

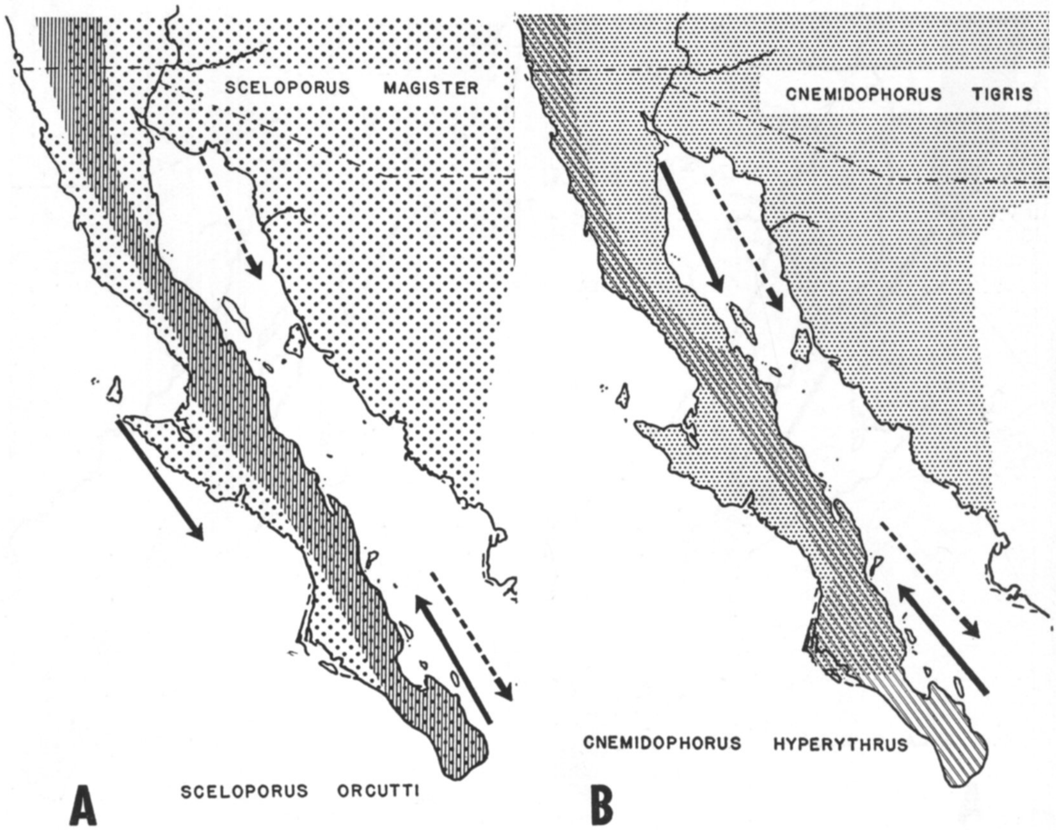

FIG. 15. Distribution patterns indicating dual invasion of Peninsular Desert area from north and south during postglacial periods. A. Ranges of desert scaly lizard, *Sceloporus magister,* and granite scaly lizard, *Sceloporus orcutti.* B. Ranges of orange-throated whiptail, *Cnemidophorus hyperythrus,* and western whiptail, *Cnemidophorus tigris.* Solid arrows indicate current, postglacial, direction of dispersion, broken arrows the contraction of ranges during glacial maxima.

depression. At glacial maxima Madrean Complex groups dominated most of the peninsula, with Desert and Plains Complex groups restricted to a Cape refugium. Similar restriction of arid adapted forms on the Mexican mainland to a southern refuge laid the basis for interglacial invasion of the peninsula by Mexican desert elements as Madrean groups were eliminated from central Baja California. Species from the Cape refugium also moved northward into developing desert areas so that the modern Peninsular Desert Fauna is a mixture of Cape forms and Mexican mainland types that moved around the head of the Gulf of California to invade Baja California. Madrean Complex species are now restricted to two disjunct areas: a) the northwest coastal and montane area and b) the San Lucan uplands. Northern mountain areas continue to support cooler adapted species because of continued uplift and higher rainfall conditions.

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The Fresh-water Fishes—Their Origins and Affinities

W. I. FOLLETT

Introduction

THE INDIGENOUS fishes that are known from fresh water in Baja California are referable to 17 families, 25 genera, and 29 species. All but *Xyrauchen, Gila, Ptychocheilus,* and perhaps *Cyprinodon,* are of marine affinities. The single endemic species is *Fundulus lima.*

With the exception of the one endemic species, there exists no such discrete assemblage of fishes as might strictly be designated the fresh-water fauna of Baja California. Four reasons for the absence of such a fauna are evident:

1. A discontinuity between certain coastal streams of southern California and the Tijuana River has prevented the fresh-water fishes of the Santa Ana system from extending farther south than the San Luis Rey River, San Diego County, California (see Culver and Hubbs, 1917:82). This restriction of the Santa Ana fauna suggests that the streams of that system were not connected with the Tijuana River or with streams farther south, during Pleistocene lowering of sea level.
2. Aridity, apparently of long standing, has prevented the coastwise dispersal of fishes by way of estuaries.
3. The abrupt escarpment along much of the eastern shore nearly precludes the formation of lagoons, which might have facilitated dispersal.
4. The Gulf of California is a barrier to the entry of fresh-water fishes from Middle America. (See p. 31, infra, for Middle American species erroneously recorded from Baja California.)

For these reasons, the fishes recorded from fresh water in Baja California are limited to various marine derivatives, except for the few strictly fresh-water species which (until extirpated by the white man) constituted the depauperate but highly specialized fauna of the lower Colorado River.

Origins

The fishes known from fresh water in Baja California represent dispersals from five distinct faunal areas:

1. From the northeastern Pacific coast, a southward dispersal of three euryhaline species: