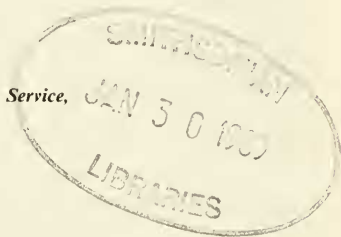# AN ECOGEOGRAPHIC ANALYSIS OF THE HERPETOFAUNA OF THE SIERRA SAN PEDRO MÁRTIR REGION, BAJA CALIFORNIA, WITH A CONTRIBUTION TO THE BIOGEOGRAPHY OF THE BAJA CALIFORNIA HERPETOFAUNA

By

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ABSTRACT: An ecogeographic analysis of the distributions of the herpetofauna of the Sierra San Pedro Mártir Region of Baja California was undertaken. The Mártir Region is part of northern Baja California from approximately latitude 30°N to 31°N. Over 3,000 locality records from the literature, museums, and field work were analyzed across a matrix of ecogeographic formations based on regional climates, physiography, and extant vegetation. Numerical and heuristic methods of biogeographic analysis indicated the 65 species present occur in seven distinct patterns. Examination of these contemporary patterns within and beyond the Mártir Region led to a hypothesis of five historical patterns of evolutionary development among the Baja California herpetofauna. This hypothesis indicates that vicariance, dispersal (diffusion), and in situ evolution are interacting phenomena contributing to contemporary herpetofaunal distributions in peninsular and insular Baja California and the Pacific Southwest.

INTRODUCTION

There is a growing consensus that ecological factors limit the geographic range of all organisms (e.g., Udvardy 1969; MacArthur 1972). Rotramel (1973:229) expressed it thusly: ". . . biogeographic areas originate from and are maintained by the interactions of organisms with physical and biotic factors in their environments." He noted a lack of placing proper emphasis on ecological factors in biogeographic analysis, which he attributed to historical influ-ences, and concluded that ". . . continued progress in solving the questions of the origins of biogeographic areas will require biogeographers to clearly distinguish the origins of species from the origins of areas and then develop new methods of eco-geographic analysis" (Rotramel 1973: 230).

The ecogeographic characteristics of a species' distribution can be viewed as the present summation of the continuous evolutionary process of interaction and compromise that occurs between that species and its environment. A new adaptation to the environment that promotes greater survivorship of offspring within an area, or population expansion into new areas, is a new characteristic of the ecological strategy of that

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species, and a new chapter in its evolutionary development. While congruent areas for different species are theoretically impossible if the areas are defined strictly in terms of the organisms' ecological niches, groups of species—both plant and animal—do coexist and coevolve in loose congruency in biotic communities. Given that the ecological parameters of a species are indicative of the historical process through which that species has evolved, it is logical to assume that a similarity of ecogeographic constraints among populations of different species in the same area may indicate a common history for those species. This common history may not have entailed direct ecological interactions but nonetheless constitutes a coevolution, where these species' distributions are similar even when examined on a scale approaching that of microhabitat. The elucidation of such similar ecogeographic patterns is the fundamental methodology of historical biogeography, and their elucidation and interpretation comprises the essence of the discipline.

The remote, mostly inhospitable, and sparsely populated peninsula of Baja California, preserved in a relatively pristine state, is an ideal natural laboratory for the study of phenomena that influence and regulate the distributions of terrestrial vertebrates. The biotic diversity and general community structure of the flora and fauna of the Baja California peninsula was reported by Nelson (1921). Schmidt (1922) made the first comprehensive study of the diverse herpetofauna of the Peninsular Region (peninsula and related islands), describing peninsular distributions on the basis of Nelson's Faunal Districts. Savage (1960) presented a classic historical analysis of the distributions of the peninsular herpetofauna, adding significantly to our understanding of the origins of these distributions and those of the entire North American herpetofauna. However, Savage's analysis had three shortcomings: (1) he assumed that the peninsula had existed as a more or less stable physiographic unit since the Eocene; (2) he chose not to incorporate vital evidence provided by the regional insular distributions; and (3) despite noting 13 different distribution patterns among the peninsular herpetofauna, he based his numerical comparison and subsequent distributional analysis on only four Herpetofaunal Areas, apparently modeled after Nelson's Faunal Districts. This resulted in an oversimplification of distri-

bution patterns and relationships, obscuring some and entirely concealing others. Nelson's (1921) Faunal Districts and Savage's slightly more refined Herpetofaunal Areas give a general picture of major herpetofaunal distribution trends on peninsular Baja California, but under close scrutiny, they fail to delineate ecological or geographic distribution barriers for much of the herpetofauna.

Greater ecological and geographical resolution is now possible with the extensive taxonomic and distributional data available from more recent studies of the regional herpetofauna. Loomis et al. (1974) compiled an updated checklist and reported the general distributions of the Baja California herpetofauna. Linsdale (1932), Tevis (1944), Murray (1955), Bostic (1971), Murphy (1975, 1976, 1983a), Welsh (1976a), Seib (1980), and Welsh and Bury (1984) have investigated community distributions in various parts of the peninsula. Numerous other authors have contributed to knowledge of distributions and ecology for single species of the regional herpetofauna (see species accounts below). However, a comprehensive ecogeographic study of the entire Baja California herpetofauna has yet to be conducted. Murphy's (1983a) study is the best attempt to date; using new distributional data from remote areas of southern Baja California and the Gulf islands, he defined more accurate southern peninsular biotic subdivisions for analysis.

Murphy lacked complete and accurate distributional data for some species in the northern areas; his analysis emphasized the southern peninsular patterns. He lumped several northern distribution patterns together in a "marginal track" and, I submit, underplayed their overall significance as evidence of important evolutionary trends complementing the tectonic events that shaped the distributions of much of the Baja California herpetofauna. The northern peninsular patterns are important because the north is the proposed "gate" for species migrating down from the continent (Savage 1960), and the majority of the lineages present in Baja California are represented there. Its diversity of habitat types, stemming from its marked elevational gradient, and from its situation between tropical and temperate latitudes, is the greatest on the peninsula.

This study focuses on the northern area of the peninsula, specifically on the Sierra San Pedro Mártir Region of north central Baja California
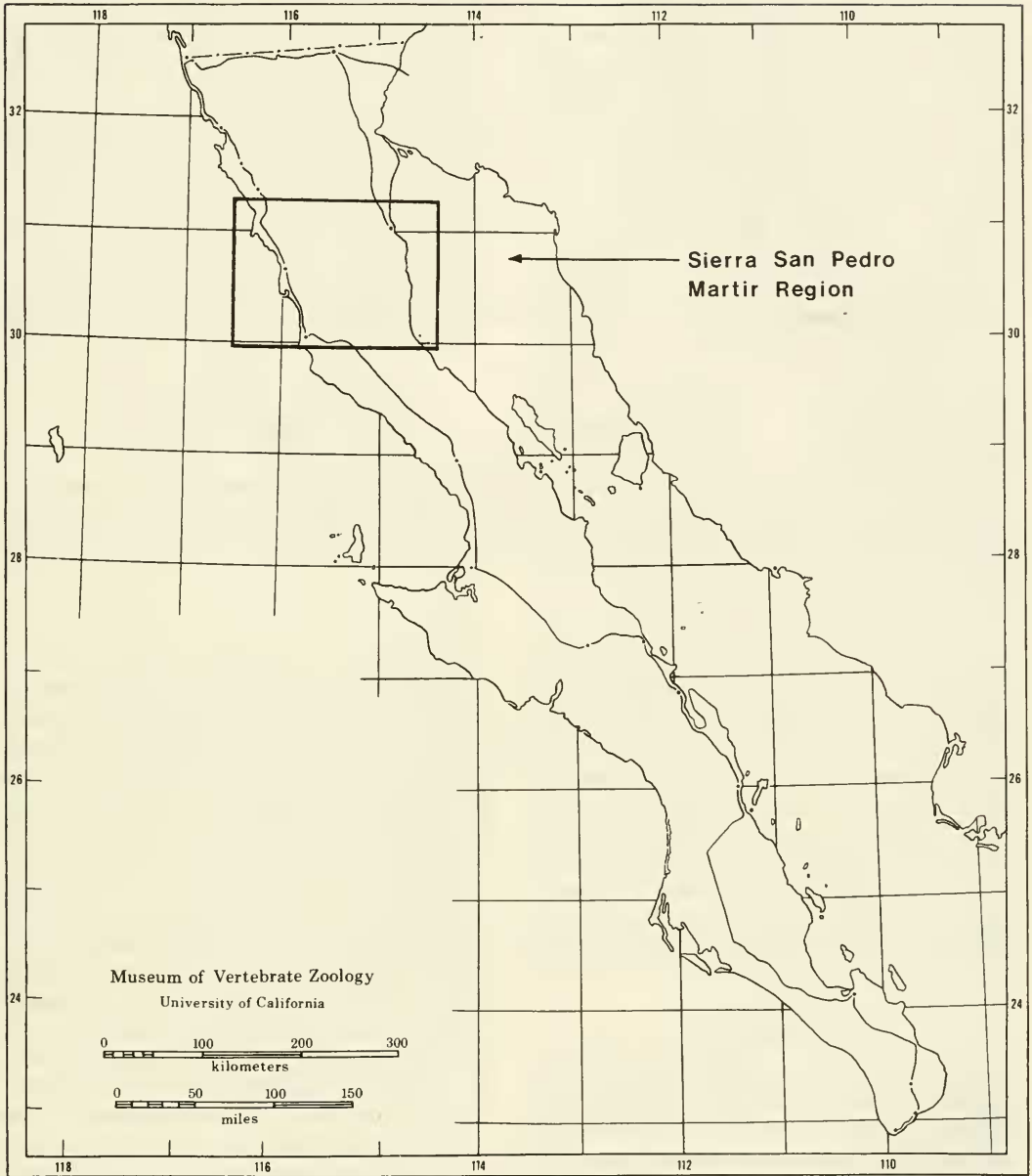
FIGURE 1.   The location of the Sierra San Pedro Mártir Region, Baja California Norte, México.

(hereafter referred to as the Mártir Region, or simply the Region). The Mártir Region consists of that area of northern Baja California from approximately 30°N to 31°N latitude (Fig. 1). It contains 65 species of reptiles and amphibians. Four of Nelson's five Faunal Districts and three of Savage's four Herpetofaunal Areas intersect within the Region (Fig. 2a). Hastings and Turner (1965) investigated the climates of Baja California. They correlated their data with the work of Shreve and Wiggins (1964) on plant distributions and described six phytogeographic divisions in Baja California. Three of these vegetation areas intersect in the Mártir Region (Fig. 2b).
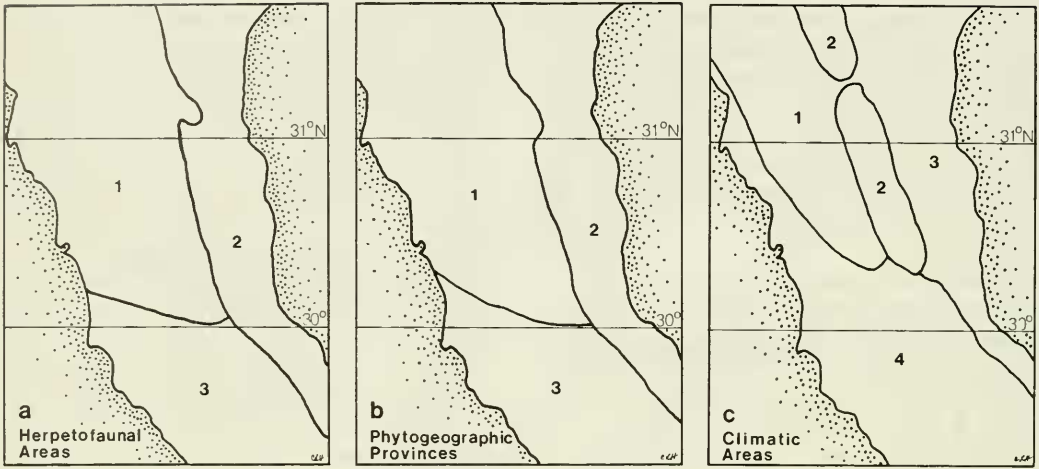
FIGURE 2.   Biotic and climatic subdivisions of the Sierra San Pedro Mártir Region, Baja California, México. a) Herpetofaunal Areas (Savage 1960): (1) Californian; (2) Colorado Desert; (3) Peninsular Desert. (b) Phytogeographic Provinces (after Shreve and Wiggins [1964] and Hastings and Turner [1965]): (1) San Pedro Mártir; (2) Lower Colorado Valley; (3) Vizcaíno. (c) Geographic relationships of the major climatic areas: (1) Pacific Climate; (2) Montane Climate; (3) Gulf Climate; (4) Central Desert Climate.

My approach was to formulate a base map of regional habitats with which to compare distributions and seek evidence of patterns across species. Such evidence was then used to define potential historical groupings. Independent evidence of congruency among overall distributions was then sought as corroboration for the groupings derived from the regional analysis. Such corroboration I considered as evidence that the regional groupings are each the result of a common evolutionary history among its members, and not the result of random processes.

ACKNOWLEDGMENTS

MATERIALS AND METHODS

The following procedures were followed in the investigations of the distributional patterns of the herpetofauna of Baja California: (1) derivation of a base map of the ecogeographic formations of the Sierra San Pedro Mártir Region on the basis of climatic data, physiographic features, and extant vegetation associations; (2)

compilation of locality and ecological data for the 65 herpetofaunal species occurring within the Mártir Region from field investigations, museum records, and available literature; (3) plotting of ecogeographic distributions of regional species, and grouping of species whose distributions are similar and thus indicative of a possible historical relationship; (4) assessment of the validity of such proposed historical groupings by comparison of intra-Regional patterns with broader distribution patterns (in the rest of Baja California and beyond), to seek corroborative evidence of a common evolutionary history.

Derivation of Regional Ecogeographic Formations

Heyer (1967:259) described a life zone as "an ecological altitudinal or latitudinal zone, characterized by specific climate parameters and secondarily by vegetation." Miller's (1951) "ecologic formations" reflected geomorphological components that sometimes play a greater role in the distribution of species than do altitudinal or vegetative parameters. I have incorporated both these concepts in my division of the Region into "ecogeographic formations." These formations were delineated on the basis of both field data and literature pertaining to physiographic features, climate, and dominant vegetational associations (using perennial plant species). Biogeographic assemblages generally represent gradients with regard to space, time, and biotic form, and boundaries between assemblages are therefore at best approximate and variable, changing continuously, and varying somewhat for each biotic form (Udvardy 1969). Therefore, I have used ecotones to establish approximate boundaries between ecogeographic formations.

Compilation of Species Accounts

The herpetofauna throughout the Mártir Region was surveyed from 22 June to 13 August 1973, from 9 April to 25 June 1974 (except 6 days in late May 1974), for 2 weeks in June 1976, and 2 weeks in May 1979. Much of the Region is accessible by road and many areas were reached by vehicle. In the more remote and inaccessible central and south central parts of the Region travel was by foot. A total of 2,187 km by road and 766 km by trail were logged during these investigations. Approximately 80–90% of the areal ex-

tent of the Mártir Region was observed. Elevation (with a barometric altimeter), physiography, climate, vegetation, and microenvironmental conditions were recorded wherever animals were observed or collected. Distributional, ecological, and behavioral data were recorded on the 65 species that comprise the herpetofauna of the Mártir Region. Two hundred thirty-one voucher specimens were collected; now deposited in the Museum of Vertebrate Zoology, University of California, Berkeley. Additional locality records of captured and released or observed animals totaled 523. Museum and literature records used in the study totaled 2,618. A total of 3,372 locality records were obtained from 65 collecting sites. The collecting sites are listed, north to south, in Appendix A, and are shown in Figure 3. Distributional data from the following museums were used: California Academy of Sciences (CAS and SU), San Diego Natural History Museum (SDNHM), Los Angeles County Museum of Natural History (LACM), and the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ). Sources for literature records are noted in the species accounts. All known localities of museum and literature records were visited to determine existing vegetational and physiographic features, and to note available habitat types. Phylogenetic organization of families in the species accounts follows Stebbins (1985). Subspecific nomenclature was used in all cases where subspecies have been described; otherwise the currently recognized species names were used. Common names used are from Collins et al. (1978) or Stebbins (1985).

Derivation of Regional Distribution Patterns

Two different methods were used to compare the distributions of regional species. Following Savage (1960) and Murphy (1983a), numerical techniques of analysis were used. Peters (1971) pointed out that although numerical methods in biogeography are capable of making quantitative distinction between areas, they cannot distinguish whether said areas have a real basis in nature. This problem was addressed by using regional ecogeographic formations as the primary areas for numerical comparison instead of preestablished faunal or vegetation provinces or the equal quadrants technique often used with numerical faunal analyses.

Secondly, a two-phased heuristic method was
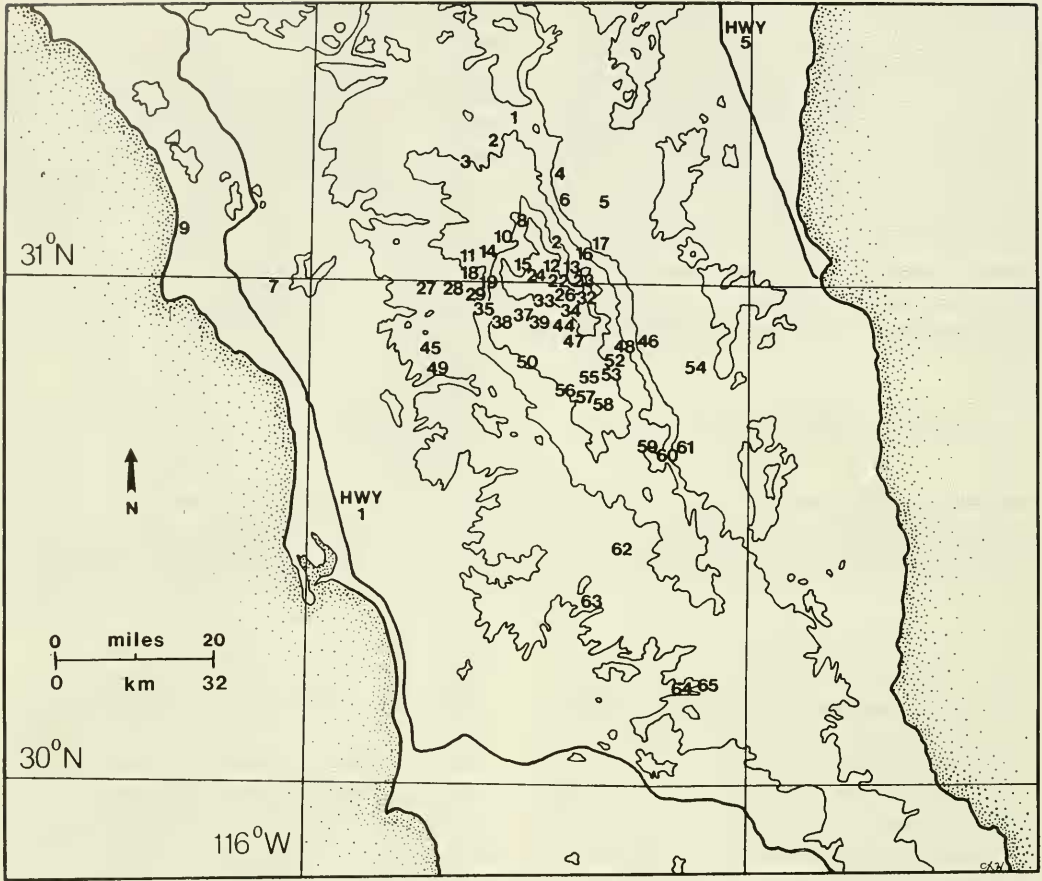
FIGURE 3.   Location of collecting stations in the Sierra San Pedro Mártir Region, Baja California Norte, México. Stations 20, 21, 25, 30, 31, 36, 40–43, 51, and 60 have been omitted; these stations are adjacent to the next highest number, e.g., station 20 and 21 are near station 22. Exact locations and elevations of stations are in Appendix A. Topographic intervals equal 610 m (2,000 ft).

used to analyze regional distributions. Phase one consisted of a comparison of distributions across a transect of regional ecogeographic formations, and phase two was a comparison of overall regional distributions as plotted on maps based on Figures 3, 4, and 5.

My numerical–heuristic strategy of analysis was similar to the approach of Morafka (1977) except that he used two numerical techniques, faunal resemblance coefficients (two formulas) and an equal quadrants analysis. I used three faunal resemblance coefficients and no equal quadrants analysis. Both the numerical and heuristic methods are discussed in more detail in the section on zoogeographic analysis.

Distributions Beyond the Mártir Region

Distributional congruency beyond the Mártir Region for those taxa linked ecogeographically within the Mártir Region was considered to be indicative of possible historical links and a shared evolutionary history. Evidence for such extraregional congruency was sought using independent means. The method of establishing and comparing the combined distributions of related forms, conspecific or congeneric, or both (individual tracks), in order to establish or deny broad geographical congruency between unrelated taxa—and thus demonstrate more general distribution patterns (generalized tracks)—follows

the principles and method indicated by Croizat (1964).

Results

The Environment

The Sierra San Pedro Mártir Region refers to that area of northern Baja California between the Pacific Ocean, the Gulf of California (Sea of Cortez), and latitudes 31°20'N and 30°00'N (Fig. 1), an area of approximately 150 km². The mountain range central to the Region, the Sierra San Pedro Mártir, hereafter referred to as the Sierra, is over 3,000 m in elevation, and transects the center of the Mártir Region from north to south. The Colorado Desert is east of the Sierra, and foothill ranges and the San Quintín Plain are to the west. The Mártir Region is at the southern extreme of the north temperate zone and is influenced by two diverse climates, the Pacific and Gulf regimes (Hastings and Turner 1965).

Physiographic Features

The topography and geography of the Sierra San Pedro Mártir were described by Nelson (1921) and Henderson (1960). Woodford and Harris (1938) described the geology and geomorphology of the Region, and Allison (1964) discussed the topographic relationships of the Mártir Region with the features of surrounding regions.

Information on the general physiography of the Mártir Region was obtained from topographic maps (Estados Unidos Méxicanos, Series 501), flight navigation charts (U.S. Dept. Commerce CH-22, 1979), and Robinson (1972). Based on these sources and my field investigations, I subdivided the Region into nine primary topographic elements, each with a unique and relatively homogeneous physiography (Fig. 4).

The Sierra consists of an elevated, granitic fault block dated from the mid-Cretaceous (Silver et al. 1956). The fault block is a segment of the Baja California Cordillera, and is considered part of the Peninsular Range Physiographic Province (Allison 1964), which extends from the Transverse Ranges of southern California (at the latitude of Los Angeles) south along the length of Baja California.

The northern extremity of the Sierra is at San Matías Pass (980 m), which is probably a transverse fault (Allen et al. 1956). The southern extremity of the Sierra is in the vicinity of Cerro Matomí (30°24'N, 115°10'W), south of which the Sierra gradually decreases in elevation and is covered by lava-capped mesas. Here, the mountains grade into the North Central Desert. The area from Cerro Matomí south to 30°N latitude was designated the North Central Desert Topographic Element (Fig. 4).

The eastern slope of the Sierra, designated the East Scarp Topographic Element (Fig. 4), is a steep and fairly straight fault scarp rising 1,220–2,120 m above the desert floor. A series of steep canyons transect this scarp, and terminate in piedmont alluvial fans, opening onto Valle de San Felipe and Valle Chico, two continuous desert valleys paralleling the scarp base at about 600 m elevation. These valleys are part of, and contiguous with, the southern Colorado Desert. The Colorado Desert extends from California and Arizona, south along the Gulf coast of Baja California to the vicinity of Bahía de Los Angeles (29°00'N, 113°15'W). This desert from 31°20'N latitude south to Bahía de Los Angeles was designated the South Colorado Desert Topographic Element (Fig. 4). All topographic elements from the ridge of the East Scarp, east to the Gulf of California, comprise the Gulf Slope.

The west slope of the Sierra consists of a series of lesser fault scarps with intervening steps between that drop more gradually than the East Scarp. They range from 915 m to 1,525 m. This area is designated the West Scarp Topographic Element. Below the West Scarp Topographic Element is a series of foothill ranges that drop gradually to a coastal plain. The foothill ranges and the coastal plain are designated the Western Foothills, and the San Quintín Plain Topographic Elements, respectively (Fig. 4).

The corrugated Main Scarp of the Sierra San Pedro Mártir is 13–16 km wide, 64 km long, and is bordered and transected by irregular, boulder-stacked ridges. The Main Scarp contains four major, and numerous minor, alluvial-filled, meadow expanses; several of these meadows contain year-round surface water. The Main Scarp was subdivided into the Upper Main Scarp Topographic Element, consisting of those areas north of Tasajera Ridge and above 2,300 m (7,550 ft), and the Lower Main Scarp Topographic Element, consisting of those areas south of Tasajera Ridge and below 2,300 m (Fig. 4). Tasajera Ridge
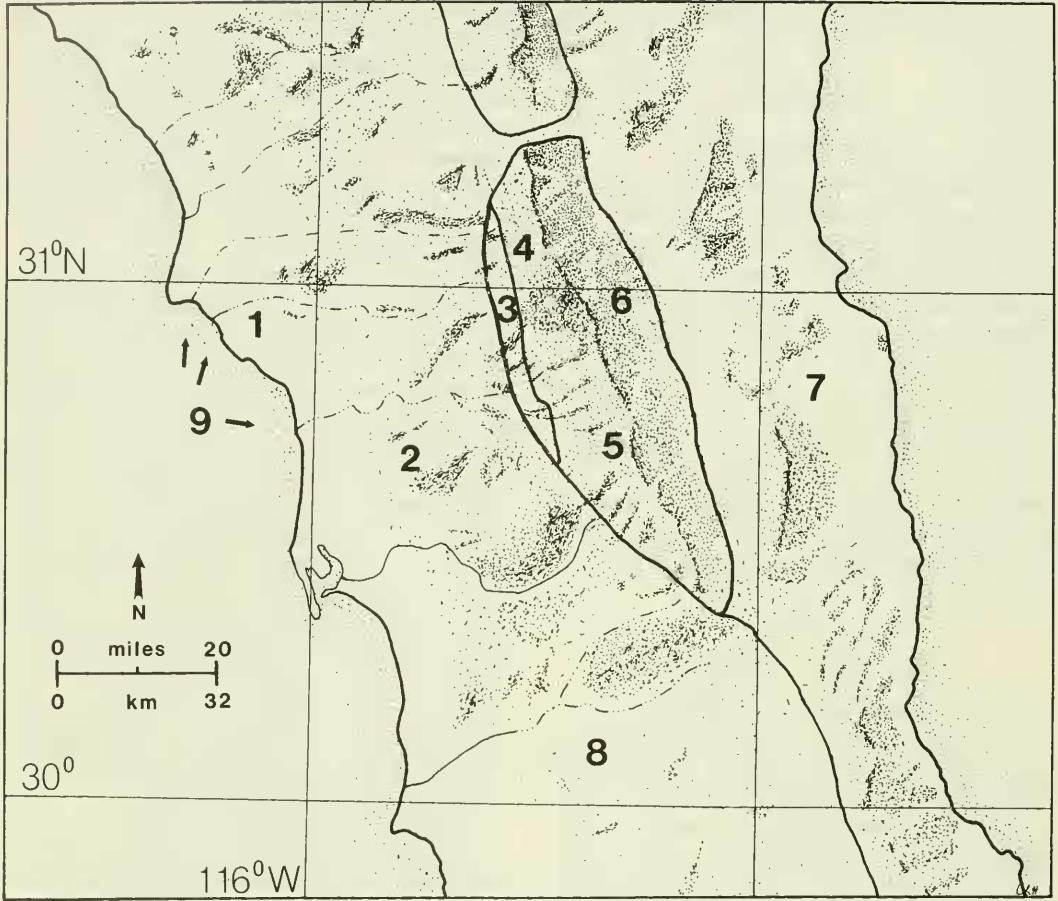
FIGURE 4.   Geographic relationships of the major topographic elements of the Sierra San Pedro Mártir Region, Baja California Norte, México. (1) San Quintín Plain; (2) Western Foothills; (3) West Scarp; (4) Upper Main Scarp; (5) Lower Main Scarp; (6) East Scarp; (7) South Colorado Desert; (8) North Central Desert; (9) Western Arroyos.

transects the Main Scarp at about midlength, and runs west to east at 30°57′N latitude.

The Pacific Slope is west of the crest of the Sierra San Pedro Mártir and north of the North Central Desert Topographic Element (Fig. 4). It is transected by a system of westerly directed canyons, carrying partly subterranean runoff from the Sierra, 72 km west to the Pacific. These arroyos were designated the Western Arroyos Topographic Element (Fig. 4). In subsequent sections, the suffix "Topographic Element" has been omitted, and the capitalized geographic entity is used to designate these topographic divisions (e.g., West Scarp Topographic Element = West Scarp).

Regional Climates

The climate of the Mártir Region results from the interaction of regional topography with two major climatic regimes that govern weather conditions over most of Baja California. The climatic regimes consist of the relatively cool, moist Pacific Coastal Regime, produced by the cold California Current with its prevailing westerly winds, and the considerably warmer drier Gulf Regime (Hastings and Turner 1965; Meigs 1966).

Hastings and Turner (1965) postulated that seasonal differences in variability and amount of precipitation produce the distinctive vegetation-

al associations of their phytogeographic provinces (Fig. 2b). Lacking quantitative data, they lumped the Sierra San Pedro Mártir with all of northwestern Baja California in the San Pedro Mártir Phytogeographic Province. My observations within this province indicated more complex vegetational relationships. I found this montane area to have a climate and vegetation sufficiently unique to warrant separate consideration.

The Sierra has predictable winter and spring precipitation, often falling as snow in the winter (J. Alonso, Mexican National Observatory, pers. comm.). A summer rainfall pattern results from a thermal low pressure cell to the east of the Sierra, causing moist air to flow east across the mountains. Afternoon thunder showers occur almost daily from late June through September as a result of orographic uplift. Data from San Juan de Dios (elevation 1,400 m) in the Sierra Juárez, 144 km north of the Sierra San Pedro Mártir, show the highest annual precipitation (33.4 cm) yet reported for northern Baja California (Hastings and Humphrey 1969). The Main Scarp of the Sierra San Pedro Mártir is considerably higher in elevation than the Sierra Juárez and thus probably receives the highest annual precipitation in Baja California.

The precipitation percolates down through the granitic sand and the soil surface dries rapidly in the warm summer air. Flash-flooding from unusually heavy rainfall occurs occasionally on all scarps. Lightning regularly accompanies these storms and is responsible for fires on the forested plateau. Underbrush is scarce throughout much of the forest, perhaps due to fires.

The Main Scarp, and the upper reaches of the West and East scarps, areas influenced by the high elevation weather system of the Sierra, have been designated the Montane Climatic Area (Fig. 2c).

Those areas on the west side of the Sierra San Pedro Mártir, encompassing the lower elevations of the West Scarp, the Western Foothills, and the Western Arroyos were designated the Pacific Climatic Area (Fig. 2c). This area is characterized by frequent fog, cool oceanic temperatures, and relatively predictable winter and spring precipitation (Table 1, Western Foothills).

Those areas on the east slope of the Sierra San Pedro Mártir, and corresponding with the southern portion of the Lower Colorado Valley Phytogeographic Province (Table 1), were designated the Gulf Climatic Area; it encompasses the lower East Scarp and the South Colorado Desert Topographic Elements (Fig. 2c; Table 1). This area is one of the hottest places in the world (Meigs 1953) and is characterized by a lack of predictable rainfall. Shreve (1934) remarked that this area may be the most sparsely vegetated of any in North America.

The area designated the Central Desert Climatic Area corresponds with the northern portion of the Vizcaíno Phytogeographic Province (Table 1), and encompasses the North Central Desert Topographic Element (Fig. 2c; Table 1). This area has the driest summers of the four climatic areas. The lack of rainfall in the Central Desert is mitigated by cool Pacific air and frequent fogs, which provide considerable ground moisture. Bostic (1971) described the climate of the Central Desert in greater detail.

The narrow San Quintín Plain Topographic Element, extending northward to the vicinity of latitude 30°20′N, was included in the Central Desert Climatic Area (Fig. 2c). Hastings and Turner (1965) included this area with northwestern Baja California, placing it in their San Pedro Mártir Phytogeographic Province. Climatic data from this coastal plain were analyzed and compared with similar data from adjacent topographic elements to the northeast and south (Table 1). The climate of the San Quintín Plain falls between that of the two adjacent areas, but seasonal precipitation patterns are most similar to the Central Desert Climatic Area. Floral and faunal characteristics of the San Quintín Plain indicate that this area, and the proximate inland valleys, are within the influence of the Central Desert Climate (Short and Crossin 1967; Bostic 1968; this study).

References to the four climatic areas of the Mártir Region will use this format: Gulf Climatic Area = Gulf Climate.

Vegetative Elements

Following the approach of a similar regional study conducted by Schoenherr (1976) in the San Gabriel Mountains of southern California, the structure and distribution of Mártir Region vegetation communities were determined. Nelson (1921) reported on an extensive natural history survey of Baja California, and described vege-

Table 1. Summary of Climatic Data from the Sierra San Pedro Mártir Region, Baja California Norte, México; Reported by Phytogeographic Province and Topographic Element (Fig. 4).

Geographic area	Winter	Spring	Summer	Fall	Annual	Number of weather stations[1]
		Mean precipitation (cm)				
Phytogeographic province[2]						
Lower Colorado Valley	1.9	0.8	1.4	2.0	6.1	8
Vizcaíno	5.6	1.0	1.1	2.8	10.5	13+
San Pedro Mártir	9.2	4.1	1.8	2.7	17.8	27
Topographic element[3]						
South Colorado Desert	2.3	0.7	1.3	2.0	6.5	2
San Quintín Plain	8.1	2.8	1.6	2.1	13.5	4
North Central Desert	5.5	1.3	0.4	2.1	9.5	3
Western Foothills	9.7	3.5	4.0	4.3	18.9	7
Sierra Scarps[4]					(33.4)	0
		Mean temperature (°C)				
Topographic element						
South Colorado Desert	15.0	21.8	31.8	24.8	23.2	2
San Quintín Plain	13.2	15.2	19.3	18.0	16.4	4
North Central Desert	13.4	16.3	23.3	19.5	19.1	3
Western Foothills	11.9	16.6	22.7	18.7	17.2	7
Sierra Scarps			(no data)			0

[1] See Hastings and Humphrey (1969) for exact locations.

[2] Data from Hastings and Turner (1965).

[3] Mean precipitation and temperature data were summarized from weather stations within each topographic element; data are from Hastings and Humphrey (1969).

[4] Data from Sierra Juárez; see text.

tational characteristics and listed dominant species in accordance with Merriam's (1898) life zones. Wiggins (1944) surveyed the Sierra San Pedro Mártir and surrounding lowlands, Shreve (1936) described the complex vegetation west of the Sierra, and Chambers (1955) described the flora of a canyon on the East Scarp.

Seven vegetational associations are recognized within the Mártir Region (Fig. 5): Coniferous Forest, Chaparral, Pinyon–Juniper Woodland, Creosote Bush Scrub, Coastal Sage Scrub, Central Desert Scrub, and Riparian Woodland. These vegetational associations are modeled after the communities of Munz and Keck (1949, 1959) except where noted below. The dominant species of each association are listed in Table 2.

Coniferous Forest

Coniferous Forest vegetation occurs above 1,830 m on the Sierra Main Scarp, within areas influenced by the Montane Climate (Fig. 5, 6). The forest is open and parklike, with sparse undergrowth of low shrubs, forbs, and grasses.

At higher elevations (over 2,400 m), vegeta-

tional elements characteristic of Merriam's (1898) Canadian and Hudsonian zones (lodgepole pine [*Pinus murrayana*], white fir [*Abies concolor*], and quaking aspen [*Populus tremuloides*]) are intermixed with the dominant elements of Coniferous Forest. This impoverished boreal vegetation is best developed in deep canyons and on north-facing slopes of the Upper Main Scarp at the north end of the Sierra.

Chaparral

Chaparral covers extensive areas of the Pacific Slope of the Sierra, between 1,220 m and 2,120 m, and occurs in a narrow belt on the East Scarp between 1,670 m and 2,120 m (Fig. 5, 7). The dense and often impenetrable vegetation is commonly 2.5–3.0 m in height. Distribution of Chaparral on both versants corresponds with the steep scarp faces where the Montane Climate intergrades with the drier and warmer Pacific and Gulf climates.

Within the Chaparral, and particularly in shaded canyons and areas with surface and subsurface water, are patches of oak woodland. Oak
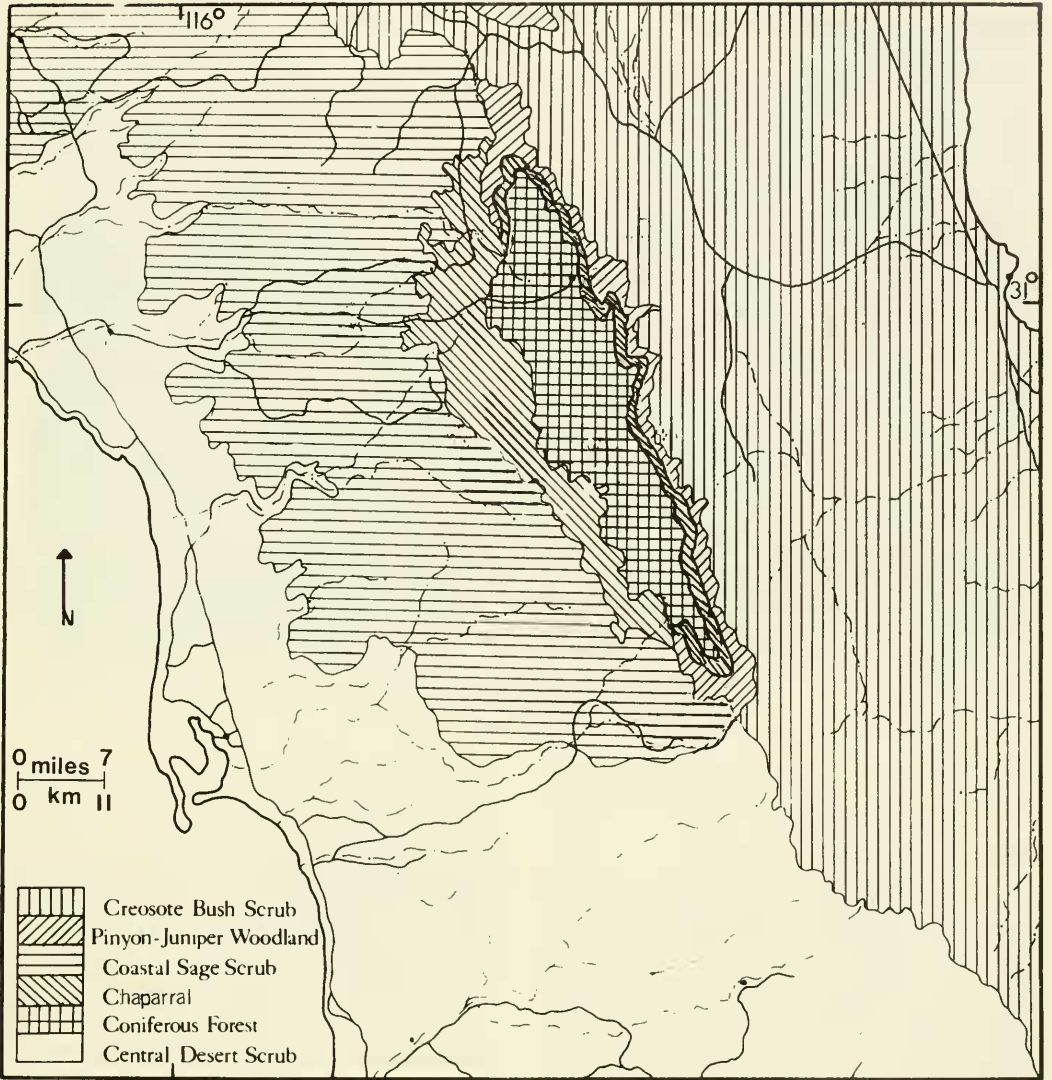
Figure 5. Vegetational associations of the Sierra San Pedro Mártir Region, Baja California Norte, México. Map is based on U.S. Dept. Commerce, CH-22 (1979). Distribution of vegetation is based on Shreve and Wiggins (1964), Short and Crossin (1967), and field investigations. Riparian Woodland Association occurs in all other vegetation types.

woodland in the Sierra San Pedro Mártir occurs primarily as riparian habitat, and is considered with the Riparian Woodland association.

Pinyon–Juniper Woodland

This vegetational type occurs between 920 m and 1,830 m on the East Scarp of the Sierra (Fig. 5, 8); this distribution coincides with areas of higher elevation dominated by the Gulf Climate.

Being high on the east versant of the Sierra, Pinyon–Juniper Woodland is probably also influenced to some degree by the Montane Climate. The trees in the Pinyon–Juniper Woodland vary from approximately 3.0 to 10.0 m in height, and are widely dispersed. Open shrub growth occurs throughout the Woodland. This association extends around the southern and northern ends of the range above 920 m and intergrades with Chaparral.

TABLE 2. DOMINANT SPECIES OF THE VEGETATIONAL ASSOCIATIONS OF THE SIERRA SAN PEDRO MÁRTIR REGION, BAJA CALIFORNIA NORTE, MÉXICO.

Vegetation association	Dominant species
Coniferous Forest	jeffery pine (*Pinus jeffreyi*), sugar pine (*P. lambertiana*), incense-cedar (*Libocedrus decurrens*), rose sage (*Salvia pachyphylla*), greenleaf manzanita (*Arctostaphylos patula*), pink-bracted manzanita (*A. pringlei*), snow bush (*Ceanothus cordulatus*), scrub oak (*Quercus* spp.)
Coastal Sage Scrub	flattop buckwheat (*Eriogonum fasciculatum*), California sagebrush (*Artemisia californica*), white sage (*Savia apiana*), century plant (*Agave shawii*), prickly pear (*Opuntia littoralis*), coastal cholla (*Opuntia prolifera*), *Ephedra californica*
Pinyon–Juniper Woodland	pinyon pine (*Pinus monophylla* and *P. quadrifolia*), California juniper (*Juniperus californica*), Mojave yucca (*Yucca schidigera*), barrel cactus (*Ferocactus acanthodes*), *Agave aurea,* scrub oak (*Quercus turbinella*), sugar bush (*Rhus ovata*)
Central Desert Scrub	datilillo (*Yucca valida*), elephant tree (*Pachycormus discolor*), century plant (*Agave shawii*), cardon (*Pachycereus pringlei*), cholla (*Opuntia* spp.), *Franseria chenopodiafolia,* Ocotillo (*Fourquiera splendens*), *Dudleya* spp.
Chaparral	bigberry manzanita (*Arctostaphylos glauca*), Mexican manzanita (*A. pungens*), chamise (*Adenostoma fasciculatum*), ceanothus (*Ceanothus leucodermis* and *C. greggi*), toyon (*Heteromeles arbutifolia*), red shank (*Adenostoma sparifolium*), scrub oak (*Quercus dumosa*), sugar bush (*Rhus ovata*)
Creosote Bush Scrub	creosote bush (*Larrea tridentata*), white bursage (*Franseria dumosa*), ocotillo (*Fourquieria splendens*), mesquite (*Prosopis juliflora*), agave (*Agave* spp.), palo verde (*Cericidium microphyllum*), yucca (*Yucca* spp.), ironwood (*Olneya tesota*), cholla (*Opuntia* spp.), catclaw (*Acacia greggi*), cardon (*Pachycereus pringlei*)
Riparian Woodland (Species composition varies greatly with elevation and slope; abbreviations refer to correspondence with above associations.)	willow (*Salix* spp.), wild rose (*Rosa californica*), jeffery pine (*Pinus jefferyi*), incense-cedar (*Libocedrus decurrens*) (CF); Oak (*Quercus* spp.), coffeeberry (*Rhamnus californica*) (Chp); Cottonwood (*Populus fremonti*) (P-J, CSS); Sycamore (*Platanus racemosa*), ceanothus (*C. leucodermis* and *C. greggi*) (CSS); mesquite (*Prosopis juliflora*), desert willow (*Chilopsis linearis*) (CBS and CDS); fan palm (*Washingtonia filifera*) (CDS)

Creosote Bush Scrub

Creosote Bush Scrub occurs below 1,070 m on the eastern side of the Sierra, in the influence of the Gulf Climate (Fig. 5, 9). The physiognomy of this vegetation is predominantly shrub, 0.7–4.8 m tall, and widely dispersed. Creosote Bush Scrub vegetation becomes more luxuriant along the base of the East Scarp, and to a lesser degree along the immediate Gulf coast of the South Colorado Desert. Qualitative observations suggest more plant species occur in these two marginal parts of the South Colorado Desert and the shrubs and cacti attain greater size here than in much of the central area of the desert. This phenomenon may be a result of increased surface or subsurface moisture, as Gulf Slope runoff (from the East Scarp and South Colorado Desert), which is primarily subterranean, is nearest the surface in these areas.

Fieldwork in the South Colorado Desert was restricted primarily to the basal slopes of the Sierra, and the two proximate desert valleys, Valle de San Felipe and Valle Chico. The Creosote Bush Scrub classification is expanded to include the entire South Colorado Desert, south to latitude 29°N, following Shreve and Wiggins (1964). At the north end of the Sierra, Creosote Bush Scrub extends over San Matías Pass (980 m) into Valle de Trinidad, where it intergrades with Coastal Sage Scrub. South of the Sierra San Pedro Mártir (beyond 30°25′N), Creosote Bush Scrub intergrades with Central Desert Scrub along the Baja California Cordillera.

Coastal Sage Scrub

The Pacific Slope below 1,220 m, from slightly beyond the north limit of the Mártir Region, south to the vicinity of latitude 30°15′N, is vegetationally complex. Shreve (1936) described this area from Arroyo Santo Tomás to Arroyo Socorro as being within a 10-mi transition zone (from north to south) between Chaparral and Sonoran Desert vegetation. However, the classification Coastal Sage Scrub was adopted as best reflecting the life-forms and species composition that dominate most of this area (Fig. 5, 10). The

FIGURE 6. The Lower Main Scarp Ecogeographic Formation at Rancho Viejo (station 37) in Coniferous Forest adjacent montane meadow.

plants are mostly "half-shrubs, one to five feet tall or somewhat woodier and larger, forming a more open community than chaparral" (Munz and Keck 1949:97). There are numerous locations along the lower Pacific Slope of the Region where elements of desert vegetation dominate. The most extensive of these areas is the San Quintín Plain (Fig. 11) and the valleys and low slopes immediately to the east. The Chaparral occurring on the lower Pacific Slope, with the exception of scattered stands at high elevations in the Western Foothills, is mostly dwarfed and depauperate. The desert scrub and Chaparral complexes are not the primary associations of the lower Pacific Slope.

Central Desert Scrub

The scrub vegetation changes noticeably in the vicinity of latitude 30°15'N on the Pacific Slope. The Creosote Bush Scrub of the lower East Scarp and Colorado Desert drainages, the Coastal Sage Scrub of the Western Foothills, and the Chaparral of the southern Sierran slopes interdigitate with a Sonoran vegetation characterized by sarcophyllous forms. Wiggins (1960) described this area as part of the Central Desert Phytogeographic Area of the Vizcaíno Province. Following the work of Aschman (1959), Wiggins (1960), and Bostic (1971), I also considered this area to have a unique biota. The plant association of this area is referred to as Central Desert Scrub in order to locate it geographically and to indicate its close structural relationship to the aforementioned scrub vegetational associations (Fig. 5, 12).

This classification is applicable to the vegetation of the San Quintín Plain, to the vicinity of latitude 31°20'N. Central Desert Scrub vegetation is denser and more lush on the San Quintín Plain than in the North Central Desert. Sarcophyllous forms dominate in many areas here, often occurring in impenetrable stands. Bostic (1971) noted that many of these plants are adapted structurally to collect moisture from the air (*Yucca valida, Agave* spp., *Dudleya* spp.). The regular fog and dew along this Plain probably provide a major source of water for these plants and explain the rich vegetation here.

Riparian Woodland

This plant association (Fig. 13) is based primarily on similarities of growth form and physical setting rather than simply on associations of

FIGURE 7.   The West Scarp Ecogeographic Formation in Arroyo San Rafael (station 10). The vegetation is primarily Chaparral, with elements of Pinyon–Juniper Woodland and Riparian Woodland evident on the lower slopes and in the canyon bottom, respectively. The Upper Main Scarp Ecogeographic Formation is in the background.

plant species. Each of the previously described vegetational associations contains a riparian element, with only a few species common to all riparian elements. The species vary considerably relative to elevation, however the presence of closed overstory, dense understory thickets, and lush, moist ground vegetation is common to the Riparian Woodland at all elevations of the Mártir Region. The protective cover and microclimatic conditions provided by riparian areas are important for many of the reptiles and amphibians in the Region.

The most prevalent plant species in riparian associations are willows (*Salix* spp.). They compose most of the vegetation in the dense understory thickets characteristic of the riparian corridors, and they are also a major component of the overstory. In proximity to Creosote Bush Scrub and Central Desert Scrub, willows are rare and are generally replaced by mesquite (*Prosopis juliflora*) and desert willow (*Chilopsis linearis*).

Grasses, sedges, and herbs form a dense mat of streamside meadow throughout riparian associations. This meadow is most highly developed within the Coniferous Forest, where extensive areas of wet meadow occur with little or no overstory. In scrub associations, meadow vegetation is reduced to narrow strips at streamside, rarely more than 1 m wide.

Ecogeographic Formations

On the basis of the physiographic, climatic, and vegetational data presented above, I have divided the Mártir Region into nine component ecosystems or ecogeographic formations (Fig. 14). Boundaries of the nine topographic elements closely approximate the ecotonal boundaries of the ecogeographic formations. For practical purposes, these boundaries will subsequently be treated as synonymous and each ecogeographic formation will be identified by its topographic component (Fig. 4). For the zoogeographic analysis, specimens were recorded first by vegetational association and secondarily by geographic locale. Thus, a specimen present in Chaparral on the Lower Main Scarp was scored in ecotonal vegetation on the Lower Main Scarp Ecogeographic Formation.

From west to east and from north to south, the nine ecogeographic formations of the Sierra San Pedro Mártir Region are: San Quintín Plain

FIGURE 8. The East Scarp Ecogeographic Formation in upper Cañón El Cajón (near station 51) in Pinyon–Juniper Woodland.

Ecogeographic Formation (northwest) (Fig. 11), North Central Desert Ecogeographic Formation (southwest) (Fig. 12), Western Foothills Ecogeographic Formation (Fig. 10), Western Arroyos Ecogeographic Formation (Fig. 13), West Scarp Ecogeographic Formation (Fig. 7), Upper Main Scarp Ecogeographic Formation (north) (see Fig. 7), Lower Main Scarp Ecogeographic Formation (south) (Fig. 6), East Scarp Ecogeographic Formation (Fig. 8), and South Colorado Desert Ecogeographic Formation (Fig. 9).

SPECIES ACCOUNTS
(see Appendix A for a list of collecting stations)

CAUDATA

Plethodontidae

Batrachoseps pacificus major (Camp, 1915), Garden Slender Salamander

Batrachoseps pacificus ssp.
San Pedro Mártir Slender Salamander

Batrachoseps pacificus major is known in northwestern Baja California south to Arroyo El Rosario (K. Yanev, pers. comm.). It is known from Colonett (LACM 34331–35) and from near Santo Tomás (MVZ 55102–12). Other localities are more common northward.

FIGURE 9. The South Colorado Desert Ecogeographic Formation near the Junction of Mexico Hwy 3 and 5 in Creosote Bush Scrub vegetation.

An undescribed subspecies of *B. pacificus* (see Yanev 1978) is known locally only from the upper scarps of the Sierra San Pedro Mártir down to 1,785 m elevation.

Brame and Murray (1968) speculated that *Batrachoseps pacificus major* and *Batrachoseps pacificus* ssp. are sympatric in the Sierra San Pedro Mártir. I found no records of *B. p. major* in the Mártir Region, east of Santo Tomás, 20 km from the Pacific coast. Apparently suitable habitat for *Batrachoseps* occurs inland along the arroyos of the Western Foothills, but surface moisture in these arroyos is seldom permanent, or dependable.

I collected a gravid female of *Batrachoseps pacificus* ssp. on 24 June 1973 at station 25 (MVZ 140701). Two individuals were observed beneath a log on moist sand in a clump of willow on 21 June 1974 at station 36. Other specimens are known from Arroyo Encantada (station 41; CAS 57219–32), Encantada Meadow (SDNHM 4132–36), and La Grulla (SU 12943). All of these localities correspond with riparian woodland habitat of the coniferous forest. *B. pacificus* ssp. also occurs in riparian habitat in the chaparral on the West Scarp. I collected two specimens

inside rotting logs in oak woodland on 11 April 1974 near station 29 at 1,785 m elevation (MVZ 140702–03); a series from La Zanja Creek (SU 12933–42) is from similar habitat.

SALIENTIA

Pelobatidae

Scaphiopus couchii Baird, 1854, Couch's Spadefoot

Wasserman (1970) indicates that *Scaphiopus couchii* is restricted to the Colorado Desert, and southward along the Gulf Slope to the Cape Region of southern Baja California. He lists no records on the Pacific slope of Baja California north of the Magdalena Plain. A specimen collected on Hwy 1, 5.3 km south junction of Hamilton Ranch Road, Valle de San Quintín (CAS 94808) and reported by Welsh (1976*a*) as possibly *S. couchii*, is actually a juvenile *S. hammondii*.

Scaphiopus hammondii Baird, 1854, Western Spadefoot

This toad is known from several localities on the Pacific Slope of Baja California north of the

FIGURE 10.   The Western Foothills Ecogeographic Formation 12 km west of Rancho San José (station 27) in Coastal Sage Scrub vegetation.

Mártir Region. Within the Mártir Region, Lins-dale (1932) reports it from Rancho San José (station 27) in the Western Foothills; it is known also from the northern San Quintín Plain at San Antonio del Mar (SDNHM 42095–96), 32 km south of San Vicente (LACM 90967–68), along Mexican Hwy 1, 5.3 km south junction of Hamilton Ranch Road, Valle de San Quintín (CAS 94808), and 10 km south of San Quintín (SDNHM 41404). These are areas of coastal sage and central desert scrub.

Bufonidae

Bufo boreas halophilus Baird and Girard, 1852*a*, California Toad

This toad is abundant in the riparian meadows and woodlands of the coniferous forest, occurring up to 2,800 m in or near riparian areas of the entire Pacific Slope; it is uncommon in the Western Foothills and in coastal areas. It frequents areas near standing or slow-flowing water.

FIGURE 11.   The San Quintín Plain Ecogeographic Formation between Mexican Hwy 1 and San Antonio Del Mar (station 9). The vegetation is Central Desert Scrub with elements of Coastal Sage Scrub.

Its southernmost locality is El Rosario (CAS 136714–15).

Adults are primarily nocturnal; diurnal surface activity in the summer was observed on the Main Scarp, but mostly during afternoon cloud cover or showers. Newly metamorphosed juveniles, common in late spring in the wet meadows of the Main Scarp, were continuously active, often in direct sun. Two incidences of cannibalism were observed among these juveniles.

Adult specimens were collected at stations 3 (MVZ 140712), 26 (MVZ 140704–05), 37 (MVZ 140706–07), and 43 (MVZ 140710); adults were observed at stations 27, 29, 44, 47, 57, 58, and 62. Juveniles were collected 29 June 1973 at station 43 (MVZ 140708–09) and 23 July 1973 at station 15 (MVZ 140711). They were observed between these dates at stations 12, 15, 27, 39, and 43. Larvae were observed or collected 25 June 1973 at station 22 (MVZ 140727) and 31 July 1973 at station 15.

Bufo microscaphus californicus (Camp, 1915), Arroyo Toad

This toad is uncommon on the Lower Main Scarp in riparian habitats of the coniferous forest; 2,300 m was the highest recorded elevation.

FIGURE 12.   The North Central Desert Ecogeographic Formation at San Juan de Dios (station 64) in Central Desert Scrub vegetation.

In riparian habitats in the chaparral of the West Scarp, they are common and also abundant in riparian habitats in coastal sage scrub at the West Scarp base. Tevis (1944) found this species at the Hamilton Ranch (Rio Santo Domingo) on the San Quintín Plain; this apparently is the southernmost record in Baja California.

In the San Bernardino Mountains of California where *B. microscaphus* is sympatric with *B. boreas,* the latter species occurs in cooler, moister habitats (Cunningham 1962). My observations of the microhabitat affinities of *B. boreas* and *B. microscaphus* in the Mártir Region concur with

those reported by Cunningham. Additionally, I found *B. microscaphus* only in or near fast-flowing water, whereas *B. boreas* occurred only in or near standing or slow-flowing water. It is apparently not known whether these two species of *Bufo* deposit their eggs in different habitats or their larvae show different habitat preferences. Larvae of both species were found together in several streams of moderate, steady flow (stations 15, 37, 43, and 57). A pair of *B. microscaphus* was observed in amplexus in fast-flowing water at 0905 on 3 May 1974 at station 10.

Adults were active at night; toads were twice

Figure 13.   Riparian Woodland vegetation in Arroyo San Rafael at station 14.

observed far from water, in coastal sage scrub and chaparral. On three occasions, they were observed returning to riparian habitat at dawn.

Adults were collected at stations 14 (MVZ 140719), 43 (MVZ 140713, 140738), 49 (MVZ 140715–18, 147512), and 56 (MVZ 140714). Juveniles were collected or observed 13 July 1973 at station 57 (MVZ 140739) and 3 August 1973 at station 49. Larvae were observed 13 July 1973 at station 43 and 31 July 1973 at station 15.

Bufo punctatus Baird and Girard, 1852a,
Red-spotted Toad

I observed this toad in riparian habitats with flowing water at three localities on the East Scarp surrounded by rocky creosote bush scrub habitat. Three specimens are known from the Main Scarp at La Grulla (SU 12945–47). The species also is known from the Sierra Juárez (CAS 121201–09). Bostic (1971) reported the species in the Central Desert.

Adults were observed or collected at stations 17, 46 (MVZ 140720, 140747), and 60; juveniles were collected on 24 April 1974 at station 17 (MVZ 140748). Larvae were observed or collected 14 April 1974 at station 46 (MVZ 140740) and 16 April 1974 at station 59. Larvae also were observed on 29 April 1974, 1 km above station 4.

Hylidae

Hyla cadaverina Cope, 1866,
California Treefrog

I found this frog in riparian woodland throughout the Sierra, but it was rare on the Main Scarp; the highest elevation recorded was 2,300 m. The species is common on the West and East scarps and in the arroyos of the Western Foothills. Adult males were heard chorusing at station 64, a spring in the North Central Desert. Duellman (1970) reported Hyla cadaverina from 32 km east of El Rosario. South of the Mártir Region, it is known from Bahía de Los Angeles (LACM 1305, 13163–69), 4.8 km N of Rancho Cataviñá (LACM 13173–95), and from Rancho Santa Ynez (LACM 107923–26, 113730–31); these localities are the southernmost records for the species in Baja California.

These treefrogs were usually found among steep
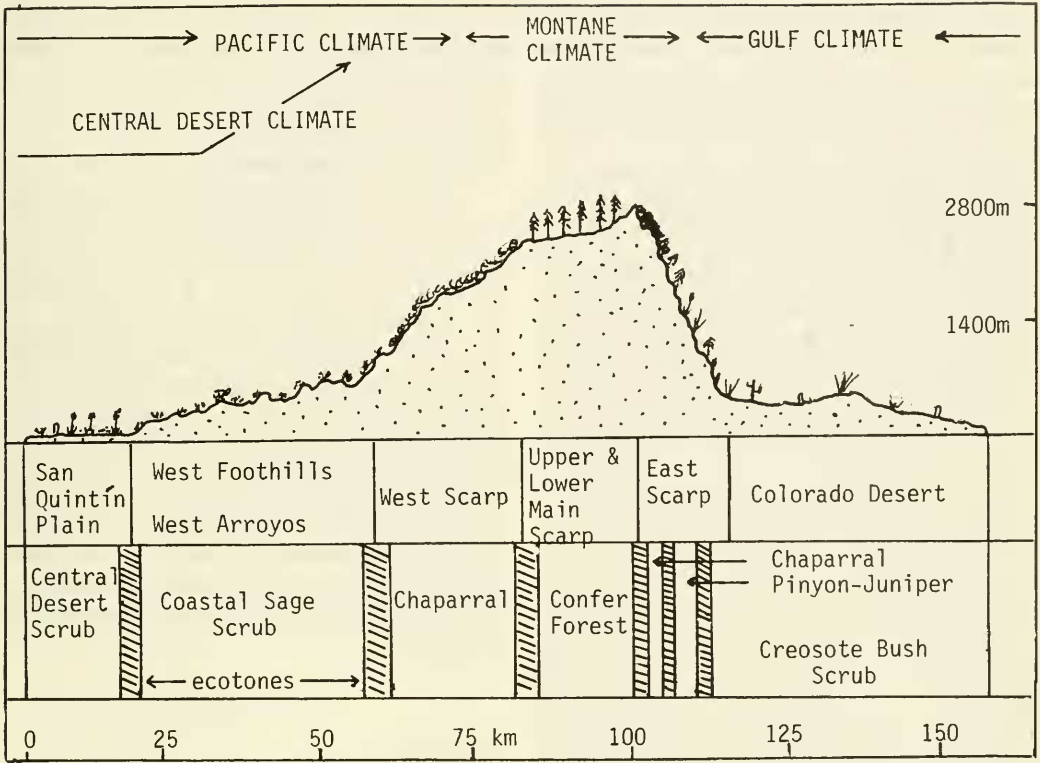
FIGURE 14.   The ecogeographic formations of the Sierra San Pedro Mártir Region, Baja California Norte, México at latitude 31°N. An ecogeographic formation is comprised of a topographic element (Fig. 4), a climatic element(s) (Fig. 2c, Table 1), and a vegetation association (Fig. 5, Table 2). Riparian Woodland Associations are present within all vegetations and form the primary vegetation in the Western Arroyos. A ninth ecogeographic formation, the North Central Desert, occurs south of latitude 31°N; it is continuous with the San Quintin Plain Ecogeographic Formation and contains similar vegetation.

granitic boulders and cliff facings above fast-flowing water. Cunningham (1964) observed the aquatic garter snake, *Thamnophis hammondii,* eating this frog. The substrate preference of this frog may be related to the predatory habits of *T. hammondii,* which was twice observed attempting to climb streamside rock faces in the near vicinity of perched treefrogs. On two occasions I observed these frogs on sand, gravel, and aquatic vegetation at streamside. These localities were isolated riparian sites created by springs on the lower East Scarp; *T. hammondii* was not observed at these localities (above stations 4 and 46). Boulders and rock facings were present in riparian habitat at these localities.

Groups of 5–30 individuals were commonly observed congregating in direct sunlight in the mist above cataracts and waterfalls in the after-noon. Individuals moved back and forth from shade to sunlight, perhaps for thermoregulation.

Adults were collected at station 35 (MVZ 140746), 41 (MVZ 140721), 49 (MVZ 140729–31), and 56 (MVZ 140722, 140724–25); they were observed at or near stations 4, 10, 16, 17, 20, 21, 23, 27, 46, 60, and 64. Juveniles were collected 13 July 1973 at station 56 (MVZ 140723); larvae were collected on 14 April 1974 at station 46 (MVZ 140741), and were observed through 29 April 1974 at stations 4, 16, 20, 21, 23, and 59.

Hyla regilla hypochondriaca Hallowell, 1854, Pacific Treefrog

Hyla regilla hypochondriaca ranges to 2,750 m in riparian habitat in the coniferous forest,

and was found in the riparian woodland in the Arroyos of the West Scarp and Western Foothills, west to the Pacific coast. Bostic (1971) reported *H. r. deserticola* (=*hypochondriaca*) from two localities in the Central Desert.

All *Hyla regilla* were observed near standing and slow-flowing water. Most animals were in aquatic vegetation at streamside or floating in the water. *H. regilla* was rarely observed more than 15 cm above the ground or more than 1 m from water. This contrasts with *H. cadaverina*, which was found in areas of fast water flowing over granite boulders where the frogs inhabited rock surfaces often 2–5 m above the water. These two treefrog species seldom occurred in sympatry within the Region as a result of the unique riparian microhabitats occupied by each; I found them together at a single locality (station 27). *H. r. hypochondriaca* was active diurnally only under conditions of deep shade or cloud cover; most activity was observed at twilight and at night.

Adults were collected at stations 44 (MVZ 11142–56) and 62 (MVZ 140746), and observed at stations 11, 12, 14, 19, 27, 29, 35, 37, 38, 39, 57, and 62. In excess of several hundred juveniles were observed 4 July 1973 at station 39. Larvae were observed 27 July 1973 at station 12 and 11 April 1974 at station 29.

Ranidae

Rana aurora draytoni Baird and Girard, 1852a,
California Red-legged Frog

This species was abundant on the Lower Main Scarp, in riparian woodland, and wet meadow habitats of the coniferous forest up to an elevation of 2,200 m. They also were found in Arroyos of the West Scarp and Western Foothills to the Pacific coast. Linsdale (1932) reported this species from San Ramón at the mouth of Rio Santo Domingo, which is apparently the southernmost record for the species in Baja California.

I observed *Rana aurora* basking and feeding during the day in streamside and aquatic vegetation associated with fast, slow, and standing water. It was not observed in rocky areas with cascading water. Most of the *R. aurora* were found near deep pools which were used for escape cover.

Adult specimens were collected at stations 38 (MVZ 140732) and 39 (MVZ 140733–35); animals were observed at stations 14, 27, 35, 37,

39, 42, 44, and 49. Larvae with well-developed legs were collected on 10 August 1973 at station 10 (MVZ 140736).

Rana boylii Baird, 1854,
Foothill Yellow-legged Frog

On several occasions I made extensive searches of the Lower Main Scarp near the western edge at La Grulla (station 39) where Loomis (1965) reported three specimens of *R. boylii*. I did not find this species here or along any other watersheds in the Sierra. The preferred habitat of *R. boylii*—fast-flowing water over gravel or cobble streambeds—is rare in the Mártir Region, and I suggest that *R. boylii* may be a marginal species in the Region as a result of habitat limitations. The abundance of *R. aurora* in montane riparian habitat may also contribute to the scarcity of *R. boylii*. Stream alterations due to mining activities and acid rain are other possible explanations for the scarcity or loss of this species from the Region.

TESTUDINATA

Emydidae

Clemmys marmorata (Baird and Girard, 1852a),
Pacific Pond Turtle

Linsdale (1932) reported *Clemmys marmorata* from Valle de Trinidad (probably in Rio San Antonio) and Arroyo San Telmo, on the Pacific Slope. A record from 3.2 km south of Valladares (CAS 56884–85) placed the species in a third arroyo to the south. P. Haneline (pers. comm.) collected a specimen of *C. marmorata* from 30 mi east of El Rosario (Rancho El Metate, station 65). In May 1974, I was informed by the ranch foreman at this locality that this animal was brought from a more northern population. I found *C. marmorata* in the deep pools of a perennial stream at Rancho San Antonio on Arroyo Santo Domingo, at the base of the West Scarp (station 49). This site is the southern distribution limit; incongruously, giant cardon (*Pachycreus pringlei*) and barrel cactus (*Ferocactus* sp.) occur a few meters from streamside. This turtle is uncommon in the Mártir Region, probably as a result of alteration of riparian habitat for agricultural purposes.

Seeliger (1945) reported that the six specimens she examined from Baja California are not sim-

ilar to either described subspecies in California. Bury (1970) suggested that an analysis of geographic variation in this species is needed.

Five specimens were collected at station 49 (MVZ 207759–63). An adult turtle was seen diving in a pool on the West Scarp, at 1,600 m in Arroyo de San Rafael (station 10).

SAURIA

Gekkonidae

Coleonyx switaki (Murphy, 1974), Barefoot Gecko

Fritts et al. (1982) reported *Coleonyx switaki* from eastern San Diego County, California and from Bahía de Los Angeles south of the Mártir Region. These and previous records (Murphy 1974) and the ecological preferences noted by Fritts et al. (1982) suggest a contiguous range for this gecko along the eastern flank of the Peninsular Range Mountains, although no specimens have been reported from the Mártir Region.

Coleonyx variegatus variegatus (Baird, 1859), Desert Banded Gecko

Coleonyx variegatus abbotti Klauber, 1945, San Diego Banded Gecko

The Desert Banded Gecko, *Coleonyx variegatus variegatus,* occurs in the Colorado Desert and south to San Felipe (Klauber 1945). A single specimen from the vicinity of Bahía de Los Angeles (CAS 121182) appears to be *C. v. peninsularis* Klauber (A. Leviton, pers. comm.). This specimen is apparently an unreported northern range extension for the subspecies on the Gulf Slope.

Coleonyx variegatus abbotti Klauber, the San Diego Banded Gecko, occurs on the Pacific Slope of the Mártir Region. This lizard was collected at Rancho San José (SDNHM 24390) and east of San Telmo (SDNHM 42542) in the Western Foothills; Bostic (1971) reported two specimens from the Central Desert.

I collected two specimens of *Coleonyx variegatus variegatus* in Valle de San Felipe near the east side of San Matías Pass (MVZ 140742–43). These specimens resembled *C. v. variegatus* (Klauber 1945) except that they had a clear and distinct nuchal light loop, characteristic of *C. v. abbotti.* Klauber (1945) postulated that these races intergrade across some low passes in the Peninsular Range, and the present specimens support this contention.

Phyllodactylus nocticolus (Dixon, 1964), Baja California Leaf-toed Gecko

Dixon (1969) indicated that *Phyllodactylus nocticolus* ranges along the east scarps of the Peninsular Range from California southward down the length of Baja California. He noted that *P. n. nocticolus* occurs through the Mártir Region. Bostic (1971) described a new subspecies, *P. n. sloani,* from the Central Desert, thus extending the species range to the Pacific Slope, south of the Mártir Region. The northernmost locality he reported was 39 km SE Rosario (29°48'N, 115°33'W).

I collected two specimens of *Phyllodactylus nocticolus* at station 65 (MVZ 140744–45) about 25 km NW of the above locality. This site is a volcanic slope with boulders, in Central Desert scrub vegetation. The geckos were both under exfoliating slabs of volcanic rock, 1.3 m above ground. These two specimens had 21 paravertebral tubercules, within the range of both *P. n. nocticolus* and *P. n. sloani,* but only 28 and 30 longitudinal rows, within the range of *P. n. nocticolus* and below that of *P. n. sloani* (Dixon 1964; Bostic 1971).

Iguanidae

Callisaurus draconoides Blainville, 1835, Zebra-tailed Lizard

Callisaurus draconoides occurs on both Gulf and Pacific slopes of the Mártir Region. It inhabits all scrub vegetations, and is most abundant in the creosote bush scrub of Valle de San Felipe and Valle Chico. It ranges through San Matías Pass into Valle de Trinidad (SDNHM 16869–81), and occurs at Rancho San José (Linsdale 1932), and 16 km west of station 10 in the Western Foothills. *C. draconoides* is uncommon, with a spotty distribution on the Pacific Slope of the Region; distribution and abundance increase southward into the Central Desert (stations 63, 64; Bostic 1971). North of the Region, it occurs at Punta Banda (LACM 94409) and east of Ensenada (LACM 107136).

This species was found in sandy areas of open benches and slopes, or on sandy soil around scattered outcrops. Specimens were collected at sta-

tions 2 (MVZ 140753), 4 (140750–51), and 63 (MVZ 140752); animals were observed at stations 1, 5, 46, 54, 61, 64, and 65.

Crotaphytus insularis vestigium
Smith and Tanner, 1972,
Baja California Black-collared Lizard

Smith and Tanner (1972) described *Crotaphytus insularis vestigium* and indicated a Gulf Slope range for the species through south central Baja California. It is known from the lower East Scarp of the Mártir Region (SU 17048; Linsdale 1932).

I collected two adult males at stations 49 (MVZ 140754) and 65 (MVZ 140755), on the Pacific Slope of the Region. These records confirm the validity of two unreported, and apparently ignored, specimens collected in 1935 from Rancho San José (station 27; SDNHM 24391–92). Van Denburgh (1922) reported this species at Trinidad, west of San Matías Pass, the northernmost record on the Pacific Slope. The lizard is now known from the Mártir Region, from the Pacific Slope of the Central Desert at Mesa de San Carlos (Bostic 1971), and near Rancho Cataviñá (LACM 16993, 63176). In Baja California Sur, it occurs at Arroyo La Purísima, 12.8 km southwest of Canipolé (SU 11545); 4.0 km northeast San José de Comondú; at Comondú; at La Purísima; and 9.6 km and 52.8 km north of Canipolé (Smith and Holland 1971). These records indicate a much greater distribution for this lizard in Baja California than the Gulf Slope range proposed by Smith and Tanner (1972, 1974).

Both specimens I collected were basking on boulders during the midafternoon. The site at station 65 is a rocky volcanic slope grown to Central Desert scrub; the site at station 49 is a granite outcrop in coastal sage scrub.

Dipsosaurus dorsalis dorsalis
Baird and Girard, 1852a,
Desert Iguana

This lizard is known from numerous localities in the Colorado Desert, south to Bahía de Los Angeles on the Gulf Slope (Murray 1955). Linsdale (1932) reported it from the Vizcaíno Desert near San Ignacio. A second race is recognized south of the Vizcaíno Desert through the Cape Region (Schmidt 1922). The species is absent from the Pacific Slope of Baja California north of latitude 29°N in the Central Desert Region.

I observed *Dipsosaurus dorsalis dorsalis* along the base of the East Scarp in Valle de San Felipe and Valle Chico (stations 5 and 54), and in a canyon bottom west of the scarp base (station 61). All observations of *D. d. dorsalis* occurred in creosote bush scrub on open benches and slopes with a sandy substrate.

Gambelia wizlizenii copei (Yarrow, 1882),
Cope's Leopard Lizard

Gambelia wizlizenii wizlizenii
(Baird and Girard, 1852b),
Longnose Leopard Lizard

Banta and Tanner (1968) indicated that *Gambelia wizlizenii copei* occupies most of the peninsula south of the Mártir Region, ranging north to the vicinity of San Felipe on the Gulf coast, and that *G. w. wizlizenii* occurs in the Colorado Desert of northeastern Baja, from the vicinity of San Felipe northward. On the Pacific Slope, *G. w. copei* ranges on the coast to just north of the Mártir Region and inland north just into the United States (Banta and Tanner 1968; Mahrdt 1973).

I collected four specimens of *Gambelia wizlizenii copei* on the Pacific Slope of the Mártir Region. I found two active males during midmorning at station 27 (MVZ 140756–57). They were on sandy soil under shrubs in an area of scattered granite outcrops, in coastal sage scrub. A third adult male was captured basking on a rock in creosote bush scrub at station 2 (MVZ 140759). A subadult female was captured emerging from a burrow at 0815 hr in coastal sage scrub/oak woodland ecotone at the head of Arroyo San Telmo (1,480 m elevation), station 19 (MVZ 140758). I observed one probable *G. w. copei* on the lower East Scarp in creosote bush scrub at station 46.

Petrosaurus mearnsi (Stejneger, 1894),
Banded Rock Lizard

This species has been reported from numerous East Scarp localities (Van Denburgh 1922; Linsdale 1932). It ranges south on the Gulf Slope to Bahía de Los Angeles (CAS 85338), and occurs north into California as far as Riverside County. *Petrosaurus* is absent from the Pacific Slope north of the Central Desert region.

I observed *Petrosaurus mearnsi* only in rocky

areas of both creosote bush scrub and pinyon–juniper woodland up to 1,220 m. Few individuals were seen on the ground as *P. mearnsi* seems to prefer steep rock faces from 1.5 to 5.0 m above ground. The angles of slope of perching sites measured for *P. mearnsi* were greater than those of all other species of lizards in the Region, commonly exceeding 90°. These lizards were active all day, with a midmorning peak. The greatest densities of lizards were at riparian edges in canyons of the East Scarp.

Specimens were collected at stations 17 (MVZ 140762) and 59 (MVZ 140760–61). I observed *P. mearnsi* at stations 4, 16, 20, 21, 23, 46, 48, 59, 60, and 61.

Phrynosoma coronatum (Blainville, 1835),
Coast Horned Lizard

Reeve (1952) indicated that the race *Phrynosoma coronatum schmidti* occurs on the Pacific Slope of the Mártir Region, south into the Central Desert, and northward to near the United States border. Bostic (1971) reported the species from the Central Desert, but he did not indicate subspecific affinities. *P. coronatum* appears to be absent on the Gulf Slope north of latitude 29°N.

I observed lizards in chaparral up to 1,400 m at station 18, and at many localities in coastal sage scrub. They frequented sand, soil, and rock rubble substrates. *P. coronatum* was active in direct sunlight and on substrates with unusually high surface temperatures (up to 49°C), when other lizard species were relatively inactive and seeking shelter in shade.

Specimens were collected at stations 10 (MVZ 140824), 18 (MVZ 140826), 27 (MVZ 140823, 140825), 28 (MVZ 140821), and 49 (140822).

Phrynosoma mcallii (Hallowell, 1852),
Flat-tailed Horned Lizard

Reeve (1952) reported three specimens of *Phrynosoma mcallii* from extreme northeastern Baja California (Colorado Desert). One record exists from further south, at the mouth of Guadalupe Canyon, at the foot of the Sierra Juárez (CAS 119077). This species has yet to be reported from the desert immediately east of the Sierra San Pedro Mártir. *P. mcallii* occurs in the vicinity of sand dunes and sandy flats (Stebbins 1985); such habitat is present in the Mártir Region, but is not continuous with similar habitat to the north.

Phrynosoma platyrhinos calidiarum (Cope, 1896),
Southern Desert Horned Lizard

Reeve (1952) reported seven records for *Phrynosoma platyrhinos calidiarum* in northeastern Baja California, four from the South Colorado Desert in the vicinity of San Felipe. Welsh and Bury (1984) reported it from three localities inland from the Gulf. Other records of note include: Valle de San Felipe (station 5; SU 18588), Montes de Media (SDNHM 25252), and 15 km north of Bahía de San Luis Gonzaga (CAS 91631). *P. platyrhinos* may occur south to the vicinity of Bahía de Los Angeles. Apparently it is absent on the Pacific Slope of the Mártir Region and in the Central Desert.

Sauromalus obesus obesus (Baird, 1859),
Western Chuckwalla

Gates (1968) first reported *Sauromalus obesus* in northern Baja California from specimens collected at six localities on the Gulf Slope. The northernmost locality was San Matías Pass (station 1); the southernmost record was 36 km southwest of Bahía de San Luis Gonzaga. I collected an adult female at station 16 (MVZ 140749) and observed individuals at stations 17 and 46 on the east scarp. Apparently this species is absent on the Pacific Slope of the Region.

Recent records from about 5 km north of Punta Prieta (MVZ 117420 and 117467–69) extend the known range of *S. obesus* south into the Central Desert. A single record from the Sierra Juárez at Cañón Cantillas (SDNHM 43974) fills some of the gap between Baja California populations and those known from southern California. This saxicolous species probably occurs throughout the east scarps of the Peninsular Range from California into the Central Desert of Baja California. Bostic (1971) reported *S. australis* from 50 km south of Punta Prieta in the Central Desert, thus indicating that a zone of sympatry between *S. australis* and *S. obesus* probably exists in the Central Desert in the vicinity of Punta Prieta. Seib (1980) implies that this zone of sympatry does not exist in the Central Desert, ignoring *S. australis* and treating all populations in the Central Desert as *S. obesus*. More work is needed to clarify relationships among the chuckwallas of Baja California.

Sauromalus obesus was unusually wary in the Mártir Region. Individuals sought cover in re-

sponse to movement at distances as great as 70 m. The lizards occurred on high cliff faces and ledges, and seldom ventured far from crevices where they sought cover. These large dark lizards contrast greatly with the pale granite surface of the Mártir Region. The wariness of *S. obesus* may allow use of these pale surfaces in an area with high densities of raptorial birds (Short and Crossin 1967). I submit that the dark color may be a thermoregulatory adaptation, which has a higher selective value than does cryptic coloration for predator avoidance. The extreme wariness of *S. obesus* may explain why this species remained unreported for so long in this area.

The specimen captured 12 June 1974 at station 16 contained six well-developed ova. Scutellation most closely matched the description for the race *Sauromalus obesus obesus* (Shaw 1945).

Sceloporus graciosus vandenburghianus
Cope, 1896,
Southern Sagebrush Lizard

This lizard was the most frequently observed reptile on the Main Scarp of the Sierra. Its distribution was limited to coniferous forest, conifer–chaparral ecotone, and related riparian edge habitats of the upper scarps, from 1,980 to 2,820 m. Lizards were active from 0500 to 1800 hr on boulders, logs, and occasionally on the forest floor; juveniles occurred mostly on the ground. In the Mártir Region, *Sceloporus graciosus vandenburghianus* exhibited frequent climbing behavior. Elsewhere, they are found mostly on the ground (Stebbins 1966).

The distribution of *S. graciosus* in the Mártir Region may be influenced by interspecific competition. I expected it to exist in the chaparral of the East and West scarps of the Region, a seemingly appropriate habitat. In fact, I found it in stands of open chaparral only above 2,100 m on the Main Scarp. The closely related *S. occidentalis* occurs in chaparral on the East, West, and Main scarps below 2,100 m. This suggests that *S. occidentalis* may be limited to lower areas with higher temperatures, whereas *S. graciosus* is found in cooler climes above 2,100 m. The mechanism of exclusion could be simple aggressive dominance of the larger species (*S. occidentalis*) over the smaller (*S. graciosus*), driving the latter away from critical resources at lower elevations (interference competition). Feeding

strategies may also play a role in segregating these two lizards. In the ecotonal vegetation between 1,970 and 2,100 m where these two lizards coexist, limited observations indicated a difference in their choice of perching and foraging sites. Adult *S. graciosus* were most often on elevated perches and descended to forage on the ground. *S. occidentalis* was always observed on the ground or on low boulders.

Specimens were collected at stations 8 (MVZ 140773–74), 25 (MVZ 140763), 38 (MVZ 140768–69, 147514), 39 (MVZ 140764–67, 147513), 47 (MVZ 140770–71), 55 (MVZ 140772), and 58 (MVZ 140785–86); observations were made at stations 12, 22, 24, 25, 30, 32, 36, 37, 42, 44, 47, and 55.

Sceloporus magister rufidorsum Yarrow, 1883,
Red-backed Spiny Lizard

Sceloporus magister uniformis
Phelan and Brattstrom, 1955,
Yellowback Spiny Lizard

Phelan and Brattstrom (1955) reported four subspecies of *Sceloporus magister* in Baja California. Hall (1973) indicated that these taxa can be divided into two distinct karyological groups indicating at least two, and possibly four, distinct species. Murphy (1983a), citing Hall and unpublished electrophoretic data, treated the forms as separate species. I reserve judgement until more information is available, treating the northern forms as subspecies. Two forms, one from each karyological group, occur in the Mártir Region: *S. m. uniformis* (2n = 26 chromosomes) in the Colorado Desert south to San Felipe on the Gulf Slope and *S. m. rufidorsum* (2n = 30 chromosomes) on the Pacific Slope, from just north of the Mártir Region south through the Central Desert. Subspecific morphological differences are primarily based on dorsal pattern and coloration of adult males, with the number of femoral pores as a secondary distinguishing character (Phelan and Brattstrom 1955).

I collected three adult males. A male from station 2 (MVZ 140799) had a uniform beige dorsum and a femoral pore count of 13-13, which closely matches the description of *S. m. uniformis*. An adult female from station 2 (MVZ 140798) also fits this description. The other males, collected at station 27 (MVZ 140793–94) were not similar to the described forms (Phelan and

Brattstrom 1955). These two males had a faint and diffuse rust color dorsally, and lacked any pattern or side bars. Femoral pore counts were 17-18 and 16-16, which corresponds to *S. m. rufidorsum* (15-20), not to *S. m. uniformis* (10-15). Other specimens of the *S. magister* complex collected were an adult female from station 62 (MVZ 140797), and three juveniles, two males, and one female from station 64 (MVZ 140795–96, 147517). All of these matched the description for *S. m. rufidorsum*.

This small sample suggests the possibility of integration between two forms occurring in the Mártir Region. Similarly, Bostic (1971) examined 13 males from the Central Desert and found only one specimen with a typical *Sceloporus magister rufidorsum* pattern. Further biochemical work is needed to describe variation in the *S. magister* complex in this part of Baja California.

Sceloporus magister was observed in all scrub vegetation on both the Gulf and Pacific slopes of the Mártir Region, up to 1,220 m, and south into the Central Desert. It was usually seen in association with plant forms that afforded protective cover. Lizard burrows were located at the base of plant species such as Mojave Yucca (*Yucca schidigera*), *Agave* sp., and Cholla (*Opuntia* sp.). Lizards often were observed up to 1.5 m above ground in a wide variety of woody plants. I saw *S. magister* in all regional edaphic types, including riparian edge, and on all substrates. *S. magister* was observed at stations 5, 9, 10, 16, 18, 63, and 65.

Sceloporus occidentalis biseriatus Hallowell, 1854, Great Basin Fence Lizard

This lizard reaches its southern limit in the Mártir Region, where it occurs primarily along the Pacific Slope. It was abundant in the chaparral of the West and Upper East scarps, and uncommon in conifer–chaparral ecotones on the Lower Main Scarp (stations 43 and 47). This species was absent above 2,120 m. On the lower Pacific Slope, in areas of coastal sage scrub, it was found only in riparian habitat.

In riparian woodland, *Sceloporus occidentalis* was highly arboreal, commonly found 1.5 m or more above ground on trees and fenceposts. Lizards foraged on the ground from these elevated perches; when startled, they returned to their perches. In the chaparral and conifer–chaparral ecotone, *S. occidentalis* was primarily ground-dwelling. In the conifer–chaparral ecotone, *S. occidentalis* is sympatric with *S. graciosus* (see above).

Specimens were collected at stations 10 (MVZ 140790), 19 (MVZ 140792, 147518), 27 (MVZ 140791), 29 (MVZ 140788), 35 (MVZ 140789), 43 (MVZ 140781), 47 (MVZ 140782–83), 53 (MVZ 140784), 55 (MVZ 140787, 147515), and 58 (MVZ 140785–86); observations were at stations 14, 19, 56, and 57.

Sceloporus orcutti Stejneger, 1893*a*, Granite Spiny Lizard

Sceloporus orcutti occurs on the rocky scarps of the Mártir Region in scrub vegetations, pinyon–juniper woodland, and chaparral. It reaches the conifer–chaparral ecotone on the Lower Main Scarp (station 39) at 2,080 m. It is most abundant on the lower East Scarp in rocky creosote bush scrub. This species is entirely saxicolous, and is associated with large boulders, outcrops, or rock faces.

Sceloporus orcutti was extremely wary and difficult to approach, reacting to my presence at a distance of about 30–40 m. I observed one lizard taken by a Harris' Hawk (*Parabuteo unicinctus*) and another by a Red-tailed Hawk (*Buteo jamaicensis*). The abundance of large raptorial birds in the Mártir Region, the dark body color of this spiny lizard, and the pale granite surfaces frequented by this species may together explain the extreme wariness displayed by *S. orcutti*. Mayhew (1963) mentioned this wariness and noted a southward increase in its intensity. *S. orcutti* is easily captured by noose at the north end of its range in the San Jacinto Mountains of California, but it becomes increasingly difficult to approach further southward, and is virtually impossible to noose in the Mártir Region. *Buteo* populations at the northern extreme of this lizard's range may be less dense, due to human interference, or there may be a greater choice of prey animals to select from. Both factors would result in less intense selective pressure for alertness in *S. orcutti*.

Sceloporus orcutti was collected at stations 17 (MVZ 140776–78), 27 (MVZ 140779, 147516), 46 (MVZ 140775), and 65 (MVZ 140780); observations were made at stations 2, 4, 10, 11, 14, 29, 35, 37, 39, 48, 49, 51, 56, 59, 60, and 62.

Uma notata notata Baird, 1859,
Desert Fringe-toed Lizard

Schmidt (1922) noted two records for *Uma notata notata* from the desert east of the Sierra Juárez, approximately 160 km north of the Mártir Region. Norris (1958) suggested this arenicolous lizard is restricted to contiguous sand dune habitat, which may explain its apparent exclusion from the Mártir Region, where dune habitat is not contiguous. On the other hand, the lack of records for *U. notata* may be an artifact of limited collecting.

Urosaurus graciosus graciosus Hallowell, 1854,
Western Brush Lizard

Urosaurus graciosus graciosus is known from the South Colorado Desert at San Felipe (Linsdale 1932); it ranges northward through the deserts of California and Arizona. Stebbins (1966) indicated that *U. g. graciosus* ranges through much of northeastern Baja California. I collected two adult males in creosote bush scrub at the base of the East Scarp, one in Valle Chico (station 61) (MVZ 140808), and the other in Valle de San Felipe near station 17 (MVZ 140809). Both specimens were 1–2 m above ground in ironwood trees (*Olneya tesota*). These localities extend the known range of this species slightly south and east.

Urosaurus graciosus graciosus is absent from the East Scarp and the Pacific Slope of the Mártir Region, and is also unknown from the Central Desert. *U. microscutatus* and *U. lahtelai* occur in these respective areas (see below and Rau and Loomis 1977); presence of these congeners may exclude *U. g. graciosus*.

Urosaurus microscutatus (Van Denburgh, 1894),
Small-scaled Lizard

Urosaurus microscutatus was common on the rocky scarps of the Mártir Region in all scrub vegetations, chaparral, and pinyon–juniper woodland; it occurs up to 2,120 m on the East Scarp, and 1,525 m on the West Scarp. The species is not present on open sandy desert and areas with few outcrops; it is absent in the South Colorado Desert and San Quintín Plain, and uncommon in the Western Foothills. Bostic (1971) reported it as uncommon in the Central Desert.

This species is arboreal, occurring up to 2.5 m above ground. It commonly descends from ele-

vated perches to forage on the ground. I found *Urosaurus microscutatus* on boulders and in vegetation, with females and young occasionally observed on the ground. Greatest densities were reached in the rocky creosote bush scrub areas of the East Scarp along the riparian edge.

Specimens were collected at stations 10 (MVZ 140814, 140819), 27 (MVZ 140820), 46 (MVZ 140815–16, 147519), 49 (MVZ 140812–13), 51 (MVZ 140811), 53 (MVZ 140810, 147520), and 59 (MVZ 140817–18); observations were made at stations 4, 11, 17, 19, 23, 48, 60, 61, 62, and 65.

Uta stansburiana elegans (Yarrow, 1883),
California Side-blotched Lizard

Ballinger and Tinkle (1972) indicated that a single race of the Side-blotched Lizard occurs throughout peninsular Baja California. This species is the most common and ubiquitous lizard in the Mártir Region at all elevations and in all vegetations except coniferous forest. On the Lower Main Scarp it ranges up to 2,120 m in chaparral.

Uta stansburiana elegans showed no special edaphic or substrate preference. It is mostly a ground lizard but occasionally occurs up to 1.5 m above ground on rock outcrops.

Specimens were collected at stations 10 (MVZ 140806), 27 (MVZ 140807), 35 (MVZ 140802), 45 (MVZ 140803), 46 (MVZ 140805), 49 (MVZ 140804, 147522), 54 (MVZ 140800, 147521), and 56 (MVZ 140801); observations were made at stations 1, 2, 4, 9, 14, 17, 19, 47, 48, 57, 59, 60, 61, 62, 63, 64, and 65.

Xantusiidae

Xantusia henshawi henshawi Stejneger, 1893*b*,
Granite Night Lizard

This saxicolous species occurs on all the rocky scarps of the Sierra San Pedro Mártir, up into the coniferous forest on the Lower Main Scarp at Arroyo Encantada (2,100 m; CAS 57294–96), and the conifer–chaparral ecotone at La Grulla (station 39; Murray 1955). I collected a specimen in chaparral at station 19 (MVZ 140828), and three specimens in coastal sage scrub at station 27 (MVZ 140827–28, 140830). I saw one on the East Scarp in pinyon–juniper woodland at station 51. The species undoubtedly occurs to the desert floor at the base of the East Scarp (Stebbins

1966; Lee 1975) but its secretive habits and the ideal protective habitat of the cliffs and canyons on the East Scarp make collecting difficult. All animals were found under exfoliating slabs on large granite boulders. The species is as yet unreported in the Central Desert, possibly because of the marked change in geomorphology that occurs at this latitude. The primarily granitic formations that dominate in the Mártir Region and provide cover for this species give way to volcanic formations in the Central Desert.

Xantusia vigilis vigilis Baird, 1858,
Desert Night Lizard

Xantusia vigilis wigginsi Savage, 1952,
Baja California Night Lizard

This lizard occurred most commonly in areas of open benches and slopes in creosote bush and Central Desert scrub on both the Gulf and Pacific slopes. Apparently it is absent in the coastal sage scrub of the Western Foothills. I collected one specimen on the rocky lower West Scarp at 1,400 m in pinyon–juniper woodland (station 10; MVZ 140833).

Savage (1952) indicated that the Mártir Region was the probable area of intergradation between the races *Xantusia vigilis wigginsi* of central Baja California, and *X. v. vigilis* of the southwestern United States. Two adult males from San Matías Pass (station 1) matched Savage's description of *X. v. wigginsi* on the basis of tail pattern, but showed a dorsal pattern found in both forms. A juvenile from station 1 had dorsal characteristics of *X. v. vigilis.* An adult from station 10 completely lacked a pattern, and did not fit any previous descriptions. A juvenile from the South Colorado Desert near station 54 had the dorsal pattern of *X. v. vigilis* and the tail pattern of *X. v. wigginsi.* One of each of two juveniles from station 62 in the north Central Desert fits closely the descriptions of *X. v. wigginsi* and *X. v. vigilis.* A series of specimens attributed to *X. v. wigginsi* (SDNHM 41340–52), was collected at San Telmo, a lowland locality of the Pacific Slope dominated by Central Desert scrub. The eight specimens I collected show characteristics of both subspecies, and failed to match either satisfactorily. These findings support Savage's speculation of intergradation in this Region.

All animals I collected were taken from rubble and dead fall of Mojave yucca (*Agave* sp.), barrel cactus, or *Echinocactus* sp. Specimens were collected at stations 1 (MVZ 140831, 147523), 2 (MVZ 140836–37), 10 (MVZ 140833), 54 (MVZ 140832), 64 (MVZ 140834–35); observations were recorded at stations 14 and 65.

Scincidae

Eumeces gilberti rubricaudatus Taylor, 1935,
Western Redtail Skink

Jones (1985) indicated that *Eumeces gilberti rubricaudatus* ranges south to the Sierra San Pedro Mártir in Baja California, but with an inland distribution. Rogers and Fitch (1947) reported *E. g. rubricaudatus* from the Pacific coast of the Mártir Region at San Antonio del Mar (station 9). A record from La Grulla (station 40; SDNHM 44291) indicates that they range into the coniferous forest–chaparral ecotone. I collected three specimens, from stations 14 (MVZ 140842), 27 (MVZ 140843), and 49 (MVZ 140841) and observed one at station 19. All were in deep riparian woodland; light intensity range 50–85 FC, relative humidity 33–41% (Welsh 1976*a*). Jones (1985) reported this species in the chaparral vegetation of the Mártir Region but failed to cite specimens, suggesting this may be an assumption based on habitat associations observed elsewhere. Evidence to date suggests that this species is restricted to the riparian corridors in the Region, and may occur along the moist coastal corridor of the San Quintín Plain. A record from Guadalupe Canyon in the Sierra Juárez (CAS 119087) suggests it may also occur in riparian vegetation on the East Scarp of the Mártir Region.

Eumeces skiltonianus skiltonianus
(Baird and Girard, 1852*b*),
Western Skink

This lizard is common in the coniferous forest of the Sierra, occurring up to 2,800 m (station 22). It also occurs on the West Scarp and at lower elevations on the Pacific Slope; records include Rancho San José (Linsdale 1932) and 6.6 km east of San Telmo (SDNHM 42741). Coastal records for *Eumeces skiltonianus* in the Mártir Region include: San Antonio del Mar (SDNHM 41990), 10 km southeast Punta Colnett (CAS 57556), San Quintín (CAS 55802), and Colonia Guerrero (LACM 107935).

On the lower Pacific Slope, in areas dominated by scrub vegetation, *Eumeces skiltonianus* appeared to be restricted to riparian habitat and the moist coastal corridor. Limited observations suggest this lizard reaches greatest densities in areas of riparian edge habitat.

Specimens were collected at stations 37 (MVZ 140838), 39 (MVZ 140839, 147524), and 50 (MVZ 140840). Sightings occurred at stations 10, 19, 22, and 38.

A site recorded from Cataviñá in the north Central Desert has recently come to my attention (D. Schmoldt, pers. comm. and 35-mm slide). This would constitute a new southern record for the subspecies if confirmed by a specimen.

Teiidae

Cnemidophorus hyperythrus schmidti
(Van Denburgh and Slevin, 1921),
Orangethroat Whiptail

Cnemidophorus hyperythrus schmidti occurs on the Pacific Slope from San Diego County, California, south through the Central Desert, where it ranges across to the Gulf coast, and through the Cape Region (Burt 1931). In the Mártir Region these whiptails were found in scrub vegetation of the western foothills and north Central Desert. Bostic (1968) found *C. hyperythrus* on the San Quintín Plain, but he considered habitat there to be suboptimal; *C. labialis* was far more abundant than *C. hyperythrus* in this area.

I found *Cnemidophorus hyperythrus* to be terrestrial and diurnal, showing preference for areas of fine-textured, soft soils with shrub cover. It was most abundant in riparian/scrub ecotone. I saw American Kestrels (*Falco sparverius*) capture individuals of *C. hyperythrus* on two occasions. Specimens were collected at stations 27 (MVZ 147525), 49 (MVZ 140844–46), 62 (MVZ 140849–50), and 64 (MVZ 140847–48).

Three subspecies of *Cnemidophorus hyperythrus* have been described from Baja California: *C. h. hyperythrus, C. h. schmidti,* and *C. h. beldingi* (Linsdale 1932). The northern race, *C. h. beldingi,* is generally distinguished by the presence of two middorsal stripes that are lacking in the central race, *C. h. schmidti* (Murray 1955). Murray noted a difference between races in the number of supraoculars that were separated by granules from the frontals, which he considered a more diagnostic character. Bostic (1971) de-

scribed 15 specimens from the Central Desert, the presumed range of *C. h. schmidti,* that match Murray's characters for *C. h. beldingi.*

The eight specimens I collected appear to be of the race *C. h. schmidti.* Available data (Table 3) indicate only slight differences between the subspecies. I suggest that there is insufficient differentiation to warrant three distinct races. With most morphological characters showing a north to south clinal variation, I consider the central peninsular region to be an area of intergradation for the ecotypes *C. h. beldingi* and *C. h. hyperythrus.* Burt (1931) recognized no subspecies.

Cnemidophorus labialis Stejneger, 1890,
Baja California Whiptail

Cnemidophorus labialis is endemic to north central Baja California, occurring primarily along the San Quintín Plain and the Pacific coast of the Central Desert Region. The northernmost record for *C. labialis* is Punta San José, about 40 km NW San Vicente (Bostic 1968). It ranges southward in the Central Desert to the vicinity of latitude 28°13′N. Bostic (1971) considered this to be near the southern limit of distribution. Vegetation in the range of *C. labialis* on the San Quintín Plain most closely approximates Central Desert scrub, with plant density increased and species composition altered slightly by the fog and cool, moist air. I did not collect any specimens of *C. labialis.*

Cnemidophorus tigris multiscutatus Cope, 1892a,
Coastal Whiptail

Cnemidophorus tigris tigris
Baird and Girard, 1852a,
Great Basin Whiptail

Cnemidophorus tigris multiscutatus occurs up to 1,980 m in the Mártir Region, on both sides of the peninsular divide in all types of scrub vegetation, pinyon–juniper woodland, and chaparral. It ranges to the coast on the Pacific Slope and south through the Central Desert (Bostic 1971). On the Gulf Slope, *C. t. multiscutatus* occurs in the south Colorado Desert in Valle de San Felipe and Valle Chico, along the base of the East Scarp. Murray (1955) collected the Great Basin Whiptail (*C. t. tigris*) from three Gulf coastal localities in the South Colorado Desert near San Felipe.

I found *Cnemidophorus tigris multiscutatus* only at ground level on sand, soil, rock, rubble,

TABLE 3. VARIATION IN MORPHOLOGICAL CHARACTERS AMONG SUBSPECIES OF *Cnemidophorus hyperythrus*. (See footnotes for sources of published data.)

Character	Subspecies				Mártir specimens
	beldingi	*schmidti*		*hyperythrus*	
Number of granules around midbody	72.8 ± 0.8 (66–79) 17[1]	75.2 ± 0.6 (66–83) 54[2]		77.6 ± 0.6 (69–90) 45[1]	75.0 (70–80) 8
Anterior supraoculars separated from the frontal by granules:					
only part of third	5[3]	10[4]	19[2]	28[5]	0
all of third	0	48[4]	14[2]	44[5]	8
only part of second	25[3]	3[4]	16[2]	4[5]	—
all of second	36[3]	15[2]		0	—
Number of middorsal lines:					
three	9[6]	0		48[4]	1
two	104[6]	2[4]	3[2]	15[4]	2
one (forked anteriorly)	46[6]	59[4]	56[2]	3[4]	5

[1] Data from Walker and Taylor (1968).
[2] Data from Bostic (1971).
[3] Data from Van Denburgh (1922).
[4] Data from Linsdale (1932).
[5] Combined data from Murray (1955) and Linsdale (1932).
[6] Data from Burt (1931).

or leaf litter. I observed it foraging throughout the day, mostly in the broken shade of the shrub understory. When startled or chased, these whiptails sought shelter in burrows.

Specimens were collected at stations 2 (MVZ 140857), 14 (MVZ 140854), 27 (MVZ 140855), 48 (MVZ 140853), 49 (MVZ 140852, 147526), 56 (MVZ 140851), and 62 (MVZ 140856, 147527). These animals resembled Bostic's (1971) collection of *Cnemidophorus tigris multiscutatus* from the Central Desert. *C. t. multiscutatus* was observed at stations 4, 5, 10, 17, 18, 19, 35, 46, 48, 49, 52, 57, 59, 60, 61, 62, 63, 64, and 65.

Anguidae

Elgaria multicarinata webbi (Baird, 1858), San Diego Alligator Lizard

Elgaria multicarinata webbi is known from coniferous forest areas on the Lower Main Scarp at La Grulla (Linsdale 1932), Arroyo Encantada (CAS 57038–42), El Alcatraz (CAS 57330), and at station 37. This lizard was found in chaparral on the West Scarp at stations 10 (MVZ 140860) and 35 (MVZ 140859) and on the East Scarp at station 53 (MVZ 140858). Western Foothills records include: Valladares (Linsdale 1932); Mesquite Spring, Valle de Trinidad (SDNHM 16864); and Rancho San José (Linsdale 1932). These Western Foothill records are all from sites containing riparian habitat. The chaparral habitat occupied by *E. m. webbi* at higher elevations is scarce below 1,220 m in the Western Foothills, and I suspect that its distribution below 1,220 m is localized primarily around the riparian corridors. Records from Cañón del Diablo (SU 17293–95) and Cañón El Cajón (Linsdale 1932) indicate a possible similar riparian distribution of *E. m. webbi* on the East Scarp below the chaparral association. Coastally, on the San Quintín Plain, I observed this lizard in Central Desert scrub at 1.7 km east of San Antonio del Mar (station 9), and it is also known from Colonia Guerrero (LACM 75501, 107933). Bostic (1971) indicated that this race occurs along the moist coastal belt of the Central Desert Region.

All specimens I collected were in areas of rocky outcrops, on granitic sand, soil, or rock rubble, except the individual near station 9, which was on open sandy ground near vegetation.

Anniellidae

Anniella geronimensis Shaw, 1940, Baja California Legless Lizard

Anniella geronimensis occurs coastally on the San Quintín Plain from Colonia Guerrero south to the vicinity of El Rosario (Shaw 1953; Bezy et al. 1977). This species is endemic to the Mártir Region and a single near-shore island. Shaw

(1953) reported *A. geronimensis* sympatric with *A. pulchra* in the vicinity of Colonia Guerrero.

Anniella pulchra Gray, 1852,
Silvery Legless Lizard

Anniella pulchra occurs on the Pacific Slope within the Mártir Region at San José (SDNHM 40394), Socorro (SDNHM 8842), east of San Telmo (SDNHM 42738), San Antonio del Mar (SDNHM 4900–10), and west of Colonia Guerrero (Bezy et al. 1977). A resident told me that *A. pulchra* occurred in sandy fields at the bottom of the arroyo at station 19. This site at 1,450 m may be the highest record for the species in Baja California. Stebbins (1954:303) reported *A. pulchra* from 1,950 m in the Giant Forest, Sequoia National Park in California. Its preference for moist, fine-textured soils, as reported by Miller (1944), probably limits *A. pulchra* to arroyo bottoms and coastal localities within the Mártir Region; its upward distribution in the Sierra is probably restricted by the steep, granitic west scarp.

Bury (1983) reported *Anniella pulchra* from an arroyo on the West Scarp of the Sierra Juárez, 60 km east southeast of Ensenada. Klauber (1932) recorded *A. pulchra* at Cañón San Salado, at the base of the East Scarp of the Sierra Juárez. Bury (1983) maintained that this locality is probably Arroyo Salado, 19 km south of San Vincente near the Pacific coast; he indicated that a second record from the Gulf Slope near San Felipe is also probably invalid.

SERPENTES

Leptotyphlopidae

Leptotyphlops humilis cahuilae Klauber, 1931*b*,
Desert Worm Snake

Leptotyphlops humilis humilis
(Baird and Girard, 1853),
Western Worm Snake

Klauber (1940) reported two subspecies of *Leptotyphlops humilis* in northern Baja California: *L. h. humilis* occurs on the Pacific Slope from San Diego County, California, south into the Central Desert Region, and *L. h. cahuilae* occurs along the Gulf Slope from California into central Baja California. Klauber also noted a record of *L. h. cahuilae* from the Vizcaíno Desert.

I collected two specimens of *Leptotyphlops humilis* on the lower Pacific Slope of the Mártir

Region: one was taken at 1950 hr, as it moved rapidly across a dirt road at 1,100 m in open, sandy, coastal sage, 6.2 km west of station 28 (MVZ 140861); the other was found at station 27 (MVZ 140862), crushed in a cow track. Both specimens agreed in dorsal pigmentation and in number of pigmented scale rows with the description of *L. h. humilis* (Klauber 1940). However, the specimen from station 27 had a dorsal scale count (285) exceeding that established for *L. h. humilis* (range 257–283), and in the range for *L. h. cahuilae* (280–305). This suggests a zone of intergradation on the Pacific Slope of the Mártir Region.

Previously unpublished records of *Leptotyphlops humilis humilis* on the Pacific Slope include 25 km east of San Telmo (CAS 123717) and 8.3 km south of Socorro Ranch (SDNHM 19231), San Telmo (SDNHM 42746).

Leptotyphlops humilis cahuilae was first reported from the south Colorado Desert at Punta San Felipe (Murray 1955); additional records are known from 58.5 km north of San Felipe (SDNHM 44262–63) and 8.3 km north of San Felipe (CAS 136368–69). There are three records for this subspecies from Bahía de Los Angeles, at the south end of the Colorado Desert (CAS 103465, LACM 2167, and SDNHM 19998). Klauber (1940) reported this subspecies as far south as the Vizcaíno Desert.

All records for the races of *Leptotyphlops humilis* from the Mártir Region are from areas of scrub vegetation.

Boidae

Lichanura trivirgata roseofusca Cope, 1868,
Coastal Rosy Boa

Three forms of the Rosy Boa are now recognized on peninsular Baja California. Klauber (1933), Lowe (1964), and Stebbins (1966) indicated that there are three subspecies (*Lichanura trivirgata trivirgata*, *L. t. gracia*, and *L. t. roseofusca*). Klauber (1931*a*) implied that *L. t. gracia* was intermediate between *L. t. trivirgata* and *L. t. roseofusca* on the basis of scale counts and color description. Gorman (1965) found no evidence of intergradation between *L. t. trivirgata* and *L. t. gracia*, and recognized two species: *L. trivirgata* and *L. roseofusca*.

Bostic (1971) reported two specimens from the Central Desert of Baja California that were sim-

ilar to Klauber's (1931*a*) description of *Lichanura trivirgata gracia*, but with dorsal and ventral scale counts matching *L. t. trivirgata*. One of these specimens was collected 167 km north of San Ignacio in the Vizcaíno Desert, previously the northernmost locality known for *L. t. trivirgata* in Baja California (Gorman 1965). This form is known from the Cape Region of Baja California and the west coast of México.

In the Mártir Region, the Rosy Boa is known from the lower Pacific Slope at numerous localities in the Western Foothills and on the San Quintín Plain, all corresponding to areas of coastal sage and Central Desert scrub. Specimens from this area match the description for *Lichanura trivirgata roseofusca,* which ranges north into California along the Pacific coast. Gorman (1965) ascribed a single specimen from the South Colorado Desert, 25 km south of San Felipe, to *L. roseofusca*. Welsh and Bury (1984) reported a specimen matching Klauber's (1931*a*) description for *L. t. gracia* from 56 km northwest of San Felipe in the Sierra San Felipe of the South Colorado Desert. *L. t. gracia* occurs in the high deserts of California and Arizona between the coastal California range of *L. t. roseofusca,* and the extreme southern Arizona and Sonora range of *L. t. trivirgata*. The northern Mojave Desert range of *L. t. gracia* is about 335 km away from the Central Desert and South Colorado Desert regions of Baja California where Bostic (1971) and Welsh and Bury (1984) collected *L. t. gracia*.

In view of this great distance, and the lack of low desert records for the species north of Baja California, it seems highly unlikely that a contiguous population of *Lichanura trivirgata gracia* exists across this area. The disjunct distribution of *L. t. gracia* between populations of *L. t. roseofusca* and *L. t. trivirgata* prompted my suggestion (Welsh 1976*a*) that *L. t. gracia* is a recurrent intermediate form, a thesis more recently entertained by Yingling (1982).

Colubridae

Arizona elegans eburnata Klauber, 1946*b*,
Desert Glossy Snake

Arizona elegans occidentalis Blanchard, 1924,
Western Glossy Snake

Arizona elegans pacata Klauber, 1946*b*,
Peninsula Glossy Snake

Klauber (1946*b*) reported *Arizona elegans occidentalis* at numerous localities along the Pacific Slope from the Mártir Region north into California. It has been reported as far south as El Rosario on the Pacific coast (SDNHM 44155). Seifert (1980) reported two specimens from the Central Desert south of Laguna Chapala.

A second subspecies, *Arizona elegans pacata,* is known from the Central Desert Region. Records are known from near Santo Domingo (Klauber 1946*b*), 43.4 km northwest of San Ignacio (Murray 1955), and 50 km west northwest of El Arco (Banta and Leviton 1963); more recently collected specimens are at CAS and MVZ (T. Papenfuss, pers. comm.).

Klauber (1946*b*) reported *Arizona elegans eburnata* in the Colorado Desert of California and Arizona, and implied its presence in northeastern Baja California. In June 1974, I collected a juvenile male at 2030 hr, 3.2 km southeast of Rancho Rosarito (station 62; MVZ 140868). The site was a sandy arroyo with creosote bush scrub vegetation. The pattern and scutellation matched those described for *A. e. eburnata* (Klauber 1946*b*). This specimen, the first for the subspecies in Baja California, extended the range to 80 km southwest of San Felipe, and is also the first record of the desert glossy snake from the Pacific Slope. Welsh and Bury (1984) reported six more specimens of this race from Mártir Region localities northwest of San Felipe. All records of *A. elegans* from the Mártir Region occurred in areas of scrub vegetation.

Chilomeniscus cinctus Cope, 1861,
Banded Sand Snake

Chilomeniscus cinctus is known from six localities on the Pacific Slope of the Mártir Region: Arroyo Seco (SDNHM 48150–52), San Antonio River, northeast of Arroyo Seco (SDNHM 43378), 14 km east of San Telmo (SDNHM 41325), 20 km east of San Telmo (SDNHM 42737), and Valle de Trinidad (SDNHM 30371). The first five sites are in low-lying canyons that are immediately east and contiguous with the San Quintín Plain. These areas are dominated by Central Desert and coastal sage scrubs. Valle de Trinidad is at the northwest end of the Sierra and is dominated by creosote bush scrub that is contiguous through San Matías Pass into the Colorado Desert. The Valle de Trinidad record in-

dicates that *C. cinctus* is probably present in the sandy habitats of the South Colorado Desert.

R. Seib (pers. comm.) reported this species from two localities in the north Central Desert: Mission San Fernando 3.3 km west of El Progresso (MVZ 117449) and 5.5 km north of Santa Inés parador, Mexican Hwy 1 (MVZ 117303). Two other unpublished records exist for *Chilomeniscus cinctus* in this area: 16.7 km south of Cataviña (SDNHM 42054), and 50 km south of El Mármol (SDNHM 38663). Bostic (1971) reported a specimen from 0.8 km north of San Javier. Numerous additional records exist for the Central Desert southward throughout the peninsula (R. Seib, pers. comm.), including three unpublished records from San Ignacio (SDNHM 3828–30) in the Vizcaíno Desert.

Chionactis occipitalis annulata (Baird, 1859), Colorado Desert Shovel-nosed Snake

The subspecies *Chionactis occipitalis annulata* is known from sandy alluvial soil in a limited coastal area north of San Felipe, within 3.2 km of the Gulf of California along Mexican Hwy 5 (Wake 1966a; Cross 1970). Welsh and Bury (1984) reported four more specimens from this area and two specimens from 11.2 km and 14.2 km west of the Gulf of California. This arenicolous snake is not known south of the Mártir Region; the discontinuity of suitable sandy habitat may account for its absence.

Coluber flagellum fuliginosus (Cope, 1895), Baja California Coachwhip

Coluber flagellum piceus (Cope, 1875), Red Coachwhip

Wilson (1973) indicated two subspecies of *Coluber flagellum* in the Mártir Region: *C. f. piceus*, ranging south through the Colorado Desert to the vicinity of Bahía de San Felipe, and *C. f. fuliginosus*, occurring at localities on the lower Pacific Slope, and south through the Central Desert. These areas contain scrub vegetation.

The dark phase of *C. f. fuliginosus* was observed twice during midmorning in open sandy coastal scrub at station 27 on the Pacific Slope. Both snakes were emerging from burrows. Another dark racer was observed above station 4 on the lower East Scarp but could not be identified to subspecies.

Wilson (1973) indicated a single record for

Coluber flagellum piceus in the South Colorado Desert, near San Felipe. Welsh and Bury (1984) reported seven records from inland localities north and west of San Felipe. These specimens were all red phase snakes.

Coluber lateralis lateralis (Hallowell, 1853), California Striped Racer

Two records exist for *Coluber lateralis lateralis* on the East Scarp: Cañón el Cajón (Linsdale 1932), and Cañón del Diablo (SU 17298). On the Pacific Slope, this race is known from five localities: San Antonio Mine (Murray 1955), Valladares Creek (CAS 56881), Socorro (SDNHM 10524), and San José (SDNHM 5130 and 8856). I collected two specimens on the Pacific Slope: one dead on the road in rocky chaparral at 1,320 m near station 29 (MVZ 140863), and another at station 19 (MVZ 140864). An individual was observed at 1140 hr in a hollow oak trunk in oak woodland; this snake was feeding on a *Peromyscus* sp. Available records indicate a preference for chaparral and riparian habitats on the east and west scarps and on the lower Pacific Slope.

Diadophis punctatus similis Blanchard, 1923, San Diego Ringneck Snake

Schmidt (1922) recorded *Diadophis punctatus similis* from San Matías Pass. This specimen was probably collected at a spring south of the Pass, and some 150 m higher, in pinyon–juniper woodland. This race is known from Rancho San José (SDNHM 36534), where it occurs in riparian habitat (Aida Meling, pers. comm.), and from an irrigated slope of Arroyo San Telmo, south of Colnett (R. Marlow, pers. comm.). These records, and habitat preferences of the species in other areas (Stebbins 1966), indicate it is probably restricted to the Pacific Slope of the Mártir Region, in riparian woodland corridors below 1,500 m elevation.

Elaphe rosaliae (Mocquard, 1899), Baja California Rat Snake

Elaphe rosaliae, long known from San Bartolo and Santa Rosaliá in Baja California Sur (Schmidt 1922; see Ottley and Jacobsen 1983 for additional localities), has been reported more recently from localities to the north. Hunsaker (1965) re-

ported two specimens at Cañón Guadalupe on the east scarp of the Sierra Juárez, and Stebbins (1985) reported a specimen from Mt. Spring, Imperial Co., California. These records indicate *E. rosaliae* ranges in the intervening area on the eastern slopes of the Peninsular Range through the Mártir Region (Stebbins 1985).

Hypsiglena torquata deserticola Tanner, 1946, Desert Night Snake

Hypsiglena torquata klauberi Tanner, 1946, San Diego Night Snake

Tanner (1966*a*) reviewed available material of *Hypsiglena torquata* and proposed that the Pacific Slope distribution for *H. t. klauberi* in Baja California was through the Mártir Region to the North Central Desert. Bostic (1971) reported a specimen of this race from near El Rosario. Tanner (1966*a*) suggested that *H. t. deserticola* occurs in northeastern Baja along the Gulf Slope. This was based on five specimens from the Central Desert Region that showed evidence of intergradation between *H. t. klauberi* and *H. t. deserticola*. Tanner also indicated that the species occurs near San Felipe. The above records and known habitat preferences of this species (Stebbins 1966) indicate that it probably inhabits all scrub and xeric woodland areas on both slopes of the Region.

Lampropeltis getulus californiae (Blainville, 1835), California Kingsnake

This snake is known from the East Scarp at Cañón El Cajón (Linsdale 1932). I observed a juvenile on the East Scarp at station 20. It was active in shade at 0840 hr on a rocky slope of pinyon–juniper woodland. This race is also known on the Gulf Slope at Bahía de San Luis Gonzaga (CAS 90227), an area of creosote bush scrub. Lower Pacific Slope records are relatively numerous, indicating that the snake occurs in coastal sage and Central Desert scrub south to El Rosario (SDNHM 1070, 41264). I observed two specimens on the lower Pacific Slope, at station 27; one was in coastal sage scrub, and the other under a cottonwood tree (*Populus* sp.) in a grassy field at the edge of riparian habitat. This snake has not been reported from the central South Colorado Desert or from the upper Sierran scarps.

Schmidt (1922) reported *Lampropeltis getulus yumensis* from Volcano Lake in the Colorado Desert of extreme northeastern Baja California. Two records from 11.6 km east of Cerro Prieto (32°25′N) are also in this area (MVZ 10761–62).

Lampropeltis zonata agalma Van Denburgh and Slevin, 1923, Baja California Mountain Kingsnake

I collected a single *Lampropeltis zonata agalma* active at 1635 hr in an area of rocky chaparral at 1,600 m, 1.7 km west of station 29 (MVZ 140871). This locality was about 10 km down slope from the nearest coniferous forest habitat. All other locality records for this snake in the Mártir Region (Zweifel 1952, 1974; SDNHM 46017; and R. Moran, pers. comm.) are from higher elevations, up to 2,800 m, in areas of coniferous forest.

Throughout its range, *Lampropeltis zonata* occurs sympatrically with the wide-ranging *L. getulus*, whose range circumscribes the areas occupied by *L. zonata* (Stebbins 1966). Storer and Usinger (1963) indicated that *L. getulus* is rare or absent in coniferous forests of the Sierra Nevada of California, habitat where *L. zonata* is found most commonly. *L. getulus* occurs up to 2,100 m (Stebbins 1966), but is uncommon in coniferous forest habitats, even where *L. zonata* is absent. Perhaps *L. getulus* is limited by an elevational factor such as temperature, and *L. zonata* replaces it in these higher, cooler areas. Out of coniferous forest habitats *L. zonata* is uncommon, but it does occur marginally in chaparral throughout its range (Zweifel 1952, 1974; this study).

Phyllorhynchus decurtatus perkinsi Klauber, 1935, Western Leafnose Snake

This snake is known in the Mártir Region only from the South Colorado Desert of the Gulf Slope; records exist from 21.8 km north of San Felipe (SDNHM 18917) and 1.6 km north of San Felipe (SDNHM 38108). Welsh and Bury (1984) reported four additional specimens from localities 50 km northwest of San Felipe. The subspecies *P. d. decurtatus* occurs from south of the Mártir Region through central Baja California and south into the Cape Region. Specimens are known from 16 km north of Rancho Cata-

viñá (LACM 20751), 16.2 km south of Punta Prieta (Bostic 1971), 16.7 km southeast of Mesquital (MVZ 50171) in the Central Desert, and from Bahía de Los Angeles (SU 21800) on the Gulf coast. R. Seib (pers. comm.) reported 14 additional records from the Central Desert southward.

Pituophis melanoleucus annectens
Baird and Girard, 1853,
San Diego Gopher Snake

Pituophis melanoleucus bimaris Klauber, 1946*a*,
Baja California Gopher Snake

Pituophis melanoleucus affinis Hallowell, 1852,
Sonoran Gopher Snake

Klauber (1946*a*) reported *Pituophis melanoleucus annectens* from numerous localities on the Pacific Slope of the Mártir Region up into coniferous forest, and north into California. Murray (1955) reported this form at 1,400 m in chaparral on the West Scarp. It is known along the coast at San Antonio del Mar (SDNHM 23800 and 32149), and Bostic (1971) reported this race in the Central Desert, 31.8 km southeast of El Rosario.

I collected three snakes that all correspond in pattern and color with *Pituophis melanoleucus annectens.* A snake was found crossing a road at 1730 hr, 15.2 km east of station 7 (MVZ 140869); a second individual was found on the road at 1400 hr, 4.8 km west of station 29 (destroyed in transit); and a third was found dead on the road in midafternoon at station 28 (MVZ 140870). The first locality was in an area of Central Desert/coastal sage scrub, and the other two sites were in areas of coastal sage scrub/chaparral ecotone.

The subspecies *Pituophis melanoleucus bimaris* occurs throughout the Central Desert (Klauber 1946*a*), whereas *P. m. affinis* is known from two localities in extreme northeastern Baja (Klauber 1946*a*). The latter form has not yet been reported in the desert east of the Sierra San Pedro Mártir, but Welsh and Bury (1984) reported a specimen from 9.1 km east of San Matías Pass that appears to be an intergrade between *P. m. affinis* and *P. m. annectens.*

Klauber (1946*a*) noted overlap in the ranges of *Pituophis melanoleucus annectens* and *P. m. bimaris* on the Pacific Slope through the Mártir Region, from El Rosario north to Alamo; he found no evidence of intergradation in the specimens he examined from this area.

Rhinocheilus lecontei lecontei
Baird and Girard, 1853,
Western Longnose Snake

Klauber (1941) reported two records from extreme northeastern Baja California. Other records from this area include: 51.2 km east of Mexicali (LACM 36576), east of Mexicali (SDNHM 19884–85; LACM 20821), and Tajo Canyon (SDNHM 18875). Few records exist for the eastern Mártir Region; Medica (1975) reported one specimen from San Felipe, and Welsh and Bury (1984) reported a specimen from 50 km north and 12 km west of San Felipe. There are several records from the Pacific Slope, both north into California, and within the Mártir Region as follows: 3.2 km and 11.2 km south of Santo Tomás (LACM 59125, 102711), 8.3 km east of Cabo Colnett (SDNHM 34003), 3.3 km south of San Simón (SDNHM 42094), 3.3 km north of San Simón (SDNHM 42632), and 12.7 km north of Arroyo Seco (SDNHM 42543). These Pacific Slope localities are in areas of coastal sage and Central Desert scrub, whereas the records from the Gulf Slope correspond with areas of creosote bush scrub. Records from 1.7 km west of El Mármol (SDNHM 42439), 24.2 km south of Rancho Santa Inés (CAS 143725), and San Borja (SDNHM 42439) confirm this species in the Central Desert. Lockington (1880) reported this snake from the vicinity of Magdelena Bay in Baja California Sur, but Klauber (1941) doubted the validity of this record. The two recent specimens from the Central Desert Region, and a record from Cerralvo Island off the Cape Region (Soule and Sloan 1966), give renewed credence to Lockington's record. Medica (1975) stated that this species will probably be found to inhabit all of Baja California.

Salvadora hexalepis hexalepis (Cope, 1867),
Desert Patchnose Snake

Salvadora hexalepis klauberi Bogert, 1945,
Baja California Patchnose Snake

Salvadora hexalepis virgultea Bogert, 1939,
Coast Patchnose Snake

A specimen of *Salvadora hexalepis* was collected at 0707 hr crossing a sandy road in chap-

arral–coastal sage ecotone at 915 m, 5.8 km east of station 27 (MVZ 140865). A second individual was found at 0906 hr in chaparral at station 11 (MVZ 140866). Both specimens fit the description of *S. h. virgultea* (Bogert 1945). This subspecies is known from the Pacific Slope of northern Baja California, from California to the vicinity of El Rosario. Records in the Mártir Region indicate an affinity to areas of chaparral, coastal sage, and Central Desert scrub vegetations.

Bogert (1945) described *Salvadora hexalepis klauberi* from the Central Desert, and indicated a zone of intergradation between *S. h. klauberi* and *S. h. virgultea* in the vicinity of latitude 30°N (El Rosario). His speculation that *S. h. hexalepis* might range into northeastern Baja in the Colorado Desert was confirmed by a specimen from the Gulf Slope of the Mártir Region reported by Welsh and Bury (1984).

Sonora semiannulata Baird and Girard, 1853, Western Ground Snake

Frost (1983) placed the two banded ground snakes of Baja California, *Sonora bancroftae* and *S. mosaueri*, in synonymy with the unbanded *S. semiannulata*; at that time he concluded that insufficient evidence existed to describe subspecies. Despite Frost's conclusion I think it important to bear in mind that the banded forms are superficially different from the unbanded *S. semiannulata*, and that their respective distributions are not inconsistent with other unique elements of the Baja California herpetofauna. Because of the possible zoogeographic implications of these populations I have chosen to treat the banded forms here as subspecies.

Stickel (1943) indicated that *S. semiannulata* occurred through the Colorado and Central Desert Regions of Baja California to Santa Rosaliá; however Frost (1983) indicated a lack of records to confirm the species in the Colorado Desert east of the Sierra San Pedro Mártir.

Klauber (1943) described the banded form *Sonora bancroftae* from a single specimen collected in Arroyo San Telmo, 3.3 km east of San Jorge, a site on the lower Pacific Slope of the Mártir Region, in an area of Central Desert/coastal sage scrub ecotone. A second individual is known from Rancho Buena Vista (SDNHM 36527), 27 km further east and slightly higher in the same arroyo in coastal sage scrub.

Stickel (1938) described another banded form, *Sonora mosaueri*, from three specimens collected at Comondú in Baja California Sur. It has since been reported from the Vizcaíno Desert in the vicinity of Santa Rosaliá (SDNHM 44468 and 46808), and in the Central Desert, 37 km south of El Rosario (SDNHM 46802). Stickel (1943) noted that *S. mosaueri* was closely related to, and might prove to be a subspecies of *S. semiannulata*. The distribution of the three forms of *Sonora* are in disparate, yet contiguous, areas of desert scrub vegetations.

Tantilla planiceps (Blainville, 1835), California Blackhead Snake

Cole and Hardy (1981) recognized no subspecies of *Tantilla planiceps*. Tanner (1966b) reported five specimens from the Pacific Slope of Baja California, three from north of the Mártir Region, one from 6.4 km south of San Vicente in the Western Foothills, and one from the Central Desert. Bostic (1971) reported a specimen from the Central Desert, 39 km southeast of El Rosario. These localities indicate that *T. planiceps* occurs in coastal sage and Central Desert scrub vegetations within the Mártir Region. A single record exists from the Gulf Slope at Arroyo El Tajo on the east scarp of the Sierra Juárez (SDNHM 45001), indicating *T. planiceps* is probably also present on the Gulf Slope of the Mártir Region.

Thamnophis elegans hueyi Van Denburgh and Slevin, 1923, San Pedro Mártir Garter Snake

This endemic subspecies of *Thamnophis elegans* is found only on the Main Scarp of the Sierra San Pedro Mártir (Van Denburgh and Slevin 1923) and occurs in riparian meadow and nearby moist woodland habitats of the coniferous forest.

Elsewhere, *Thamnophis elegans* occurs at all elevations up to 3,000 m, and is associated with a variety of terrestrial and riparian habitats (Stebbins 1966). In the Mártir Region, *T. elegans* is found only in and around marshy meadows and slow streams above 1,820 m. *T. hammondii* is also present, but uncommon in these areas; it occurs more frequently in and around the fast-flowing streams in the steep riparian areas below the Main Scarp where *T. elegans* is absent. My observations of foraging of *Thamnophis* spp. in

the Mártir Region suggest that both species may be localized to riparian habitats because of the moisture requirements of their amphibian prey species. The usually eurytopic *T. elegans* may be further limited to marshy habitats of the main scarp by the presence of *T. hammondii*. Foraging strategies may be an important factor in segregating these two species in areas of sympatry such as the Lower Main Scarp. *T. hammondii* is noticeably more aquatic, and was seldom observed out of water. It was observed in pursuit of anuran larvae and *Hyla cadaverina*. *T. elegans* seemed to prefer moist or damp habitats but was not observed in the water. It was observed feeding on toads on marshy ground.

An adult female collected 22 June 1974 (station 24) (MVZ 140876) contained eight small ova. An adult female found under a log at 1916 hr had recently ingested an adult *Bufo boreas*. Specimens were collected at stations 12 (MVZ 140875), 25 (MVZ 140872), 37 (MVZ 140873), and 40 (MVZ 140874); observations were made at stations 24 and 39.

Thamnophis hammondii (Kennicott, 1860), Two-striped Garter Snake

This snake occurs on the East Scarp and the Pacific Slope of the Region, frequenting only riparian habitat. It occurs to 2,120 m on the Lower Main Scarp in coniferous forest, on the East Scarp in creosote bush scrub and pinyon–juniper woodland, and on the Pacific Slope in arroyos dominated by chaparral and coastal sage scrub, ranging west to the San Quintín Plain. A juvenile was observed at station 65 in an irrigation ditch that flowed from an apparently permanent spring in Arroyo Edwardo, an area of Central Desert scrub. Records from El Rosario (SDNHM 41593; LACM 104069–71) are the southernmost for this species.

Thamnophis hammondii was observed underwater, along streamsides, on streamside rock faces, and up to 3.4 m above ground in riparian overstory (usually willow). I twice observed snakes in apparent pursuit of *Hyla cadaverina*. On three occasions, *T. hammondii* were observed underwater stalking and lunging at anuran larvae.

Specimens were collected at stations 17 (MVZ 140880), 37 (MVZ 140887, 147528), and 49 (MVZ 140878–79). Observations were made at stations 10, 16, 20, 21, 23, 27, 38, and 65.

Trimorphodon biscutatus vandenburghi Klauber, 1924, California Lyre Snake

An adult male, matching Gehlbach's (1971) description for *Trimorphodon biscutatus vandenburghi*, was found dead on a dirt road on the morning of 22 June 1973, at 1,520 m in rocky chaparral, 3.5 km west of station 29 (MVZ 140877). This subspecies is known in northwestern Baja California from six other specimens: 16 km north of Arroyo Seco on the San Quintín Plain (Murray 1955), 2.9 km north of El Rosario de Arriba (LACM 121552), 4.8 km east of La Rumerosa (SDNHM 121149), 2.2 km south of Cataviñá (CAS 146577), 27 km south of Santa Inés (MVZ 161561), and 32 km southeast of Punta Prieta (LACM 126261). Scott and McDiarmid (1984) showed a lack of records from the Gulf Slope of northeastern Baja California; Welsh and Bury (1984) reported the first specimen from 34 km east of San Matías Pass in the South Colorado Desert. Habitat preferences (Stebbins 1966) suggest the probable occurrence of this snake in pinyon–juniper, chaparral, and all scrub vegetations of the Mártir Region. The absence of contiguous rocky habitat may limit its distribution in parts of the Colorado Desert. Gehlbach (1971) indicated that *T. b. lyrophanes* of southern and central Baja California is known as far north as San Ignacio in the Vizcaíno Desert.

Vipiridae

Crotalus atrox atrox Baird and Girard, 1853, Western Diamondback Rattlesnake

This snake ranges into the Colorado Desert of extreme northeastern Baja California (Schmidt 1922; Linsdale 1932), and has been reported from Central Baja California (Alvarez and Huerta 1974). It has yet to be found in the Mártir Region. Suitable habitat for this species occurs in the South Colorado Desert; its apparent absence may be due to limited collecting in this remote region.

Crotalus cerastes laterorepens Klauber, 1944, Colorado Desert Sidewinder

Crotalus cerastes laterorepens is known from numerous localities in the South Colorado Desert from San Matías Pass to the vicinity of San Felipe (Linsdale 1932; Murray 1955; Welsh and

Bury 1984), south to San Francisquito on the Gulf coast (Klauber 1944). Residents of the Valle de Trinidad area informed me that it occurs at that Pacific Slope locality. All regional localities for this species are areas of creosote bush scrub. It has not been reported from the Pacific Slope south of the Mártir Region and the Gulf Slope south of San Francisquito. It may be excluded from these deserts by the presence of the closely related form *C. enyo.*

Crotalus enyo furvus Lowe and Norris, 1954, Dusky Baja California Rattlesnake

Crotalus enyo furvus was described by Lowe and Norris (1954) from four specimens collected along the San Quintín Plain, north of El Rosario. Their proposed range for *C. e. furvus,* based on vegetative and edaphic affinities, corresponds with Sonoran habitat of the Pacific coast of the Mártir Region (Short and Crossin 1967), herein considered as part of the Central Desert scrub vegetational association. Lowe and Norris's proposed range also corresponds closely to the San Quintín Plain. A record from 4.6 km north of Arroyo Seco (SDNHM 46196) is just north of this proposed range, in Central Desert scrub. Short and Crossin (1967) indicated that this habitat extends north to the vicinity of Rio San Antonio along the base of the foothills and as far as Punta Banda on the coast. Future work in the area may reveal that the northern limit of this snake corresponds closely with this habitat.

Crotalus enyo enyo is known in more arid habitats as far north as 17.2 km southeast of El Rosario (Bostic 1971), and from numerous southern localities of the Central Desert, Vizcaíno, and Cape Regions (Lowe and Norris 1954).

Crotalus mitchellii pyrrhus (Cope, 1867), Southwestern Speckled Rattlesnake

Crotalus mitchellii pyrrhus occurs on the Gulf and Pacific slopes of the Mártir Region. I observed two snakes on the rocky East Scarp at stations 17 and 21 (MVZ 140884), in creosote bush scrub and pinyon–juniper, respectively. A third individual was observed on the lower West Scarp at station 28 in coastal sage–chaparral ecotone. Klauber (1936) indicated the occurrence of other records from the Mártir scarps, Western Foothills, and northward on both slopes into the southern U.S. The three snakes I observed were

active during midmorning among boulders. Literature records and my observations indicate that *C. m. pyrrhus* is primarily saxicolous, although some records exist for other than rocky habitat (Klauber 1972).

South of the Mártir Region on the Gulf Slope, *Crotalus mitchellii pyrrhus* is known from Bahía de Los Angeles (SDNHM 19713–14). Specimens from 4.8 km north of (LACM 20005) and 28.8 km south of (LACM 20006) Rancho Cataviñá are apparently the first records of this species from the Pacific Slope of the Central Desert. The subspecies *C. m. mitchellii* occurs in the Vizcaíno Desert and south into the Cape Region of the Peninsula.

Crotalus ruber ruber Cope, 1892b, Red Diamondback Rattlesnake

This subspecies occurs from San Diego County, California, south through the Mártir Region and the Central Desert (Klauber 1972). It has been reported from numerous localities on the lower Pacific Slope in the Western Foothills and on the San Quintín Plain (Klauber 1972). I found it in the sandy desert at the base of the East Scarp. Welsh and Bury (1984) reported it from a Gulf coast locality north of San Felipe.

I observed two specimens at the base of the East Scarp in creosote bush scrub. One was found active in late afternoon shade on an open sandy slope at station 54, the other at station 17, coiled in the midafternoon shade of an overhanging rock among talus. I collected one specimen at night on the Pacific Slope, beside a dirt road, 5 km north of El Burro (station 3) (MVZ 140885), in an area of chaparral–pinyon–juniper ecotone.

Crotalus viridis helleri Meek, 1905, Southern Pacific Rattlesnake

I found nine records of *Crotalus viridis helleri* on the interior lower Pacific Slope of the Mártir Region, all corresponding with areas containing riparian woodland habitat: La Toya, Valladares Creek, and Rancho San José. Other records from the Mártir and Central Desert regions indicate that this species has an affinity for coastal habitats: San Antonio del Mar (CAS 57555); West of San Quintín Bay (SU 12141–42); Camalú Plains, 8.3 km north of Santo Domingo (SU 11574); Punta Camalú (CAS 40140); Playa Maria Bay (Klauber 1949); and 16.7 km south of

Jesús María (Bostic 1971). In the Sierra San Pe-
dro Mártir, I found *C. v. helleri* up to 2,120 m
on the Lower Main Scarp at stations 37 (MVZ
140822), 38 (MVZ 140883), and 39 (MVZ
147529), in coniferous forest and in conifer–
chaparral ecotone. This snake was most often
encountered in riparian edge habitat in these
areas. I also found a specimen in open chaparral
at 1,300 m. It was coiled in sand on a road at
2008 hr. *C. v. helleri* has not been reported from
the Gulf Slope of the Mártir Region.

This species frequents riparian, coastal, and
upland habitats but is apparently absent from
inland scrub areas of the Mártir and Central Des-
ert regions. However, two records are known from
arid situations in the Central Desert: 33.4 km
northwest of Bahía de Los Angeles (Klauber
1949), and 33.4 km southeast of Mezquital
(Murray 1955). Specimens from the Central Des-
ert are described by Murray (1955) and Bostic
(1971) as light in color. Specimens I found in the
Mártir Region were dark, almost black.

Jones (1981) and Ottley and Hunt (1981) re-
ported two records of *Crotalus viridis helleri* from
Baja California del Sur; these specimens repre-
sent the southernmost records for the species.

Zoogeographic Analyses

I used both a numerical analysis and a heuristic
comparison of distributions (based on locality
records listed in Species Accounts) across the
matrix of ecogeographic formations (Fig. 14) to
determine distributional patterns within the Re-
gion. Regional patterns were then extrapolated
beyond the Region to include the entire distri-
bution of each species in order to test for overall
geographic congruency between species linked by
a common ecogeographic pattern within the Re-
gion (analysis of tracks). Evidence of such overall
distributional congruency was considered indic-
ative of a common evolutionary history among
linked species.

Numerical Analysis

Cheetham and Hazel (1969) reviewed and dis-
cussed the use of numerical methods (Faunal Re-
semblance Factors or FRFs) in biogeography,
noting the inherent advantages, disadvantages,
and assumptions associated with binary coeffi-
cients. They listed some 22 possible formulas for
expressing the relationship of the number of taxa

in common between paired geographic units to
the total number of taxa present. In order to
ameliorate the disadvantages inherent with any
particular FRF, I employed three different FRFs
that tend to complement one another by em-
phasizing different aspects of faunal assemblages.
An FRF that emphasizes similarities can indicate
historical affinities and evolutionary relation-
ships between geographic areas, whereas an FRF
that emphasizes differences can test for sampling
error and the effects of faunas of unequal size,
situations minimized by similarity coefficients.
In addition to using a coefficient of similarity
and a coefficient of difference, I used a third coef-
ficient, one that emphasizes ecological relation-
ships between geographic units—a community
coefficient (Jaccard 1902). Subspecific differ-
ences were ignored for this analysis; distributions
were determined by species.

All available records (see Species Accounts)
were plotted on a schematic, southwest to north-
east, regional transect in the vicinity of latitude
31°N (all localities used are between 30°30′N and
31°30′N latitude). The ecotones between regional
ecogeographic formations (Fig. 14) were used to
delineate the units along the transect used for
numerical comparison. A species was considered
to occur within an ecogeographic formation only
if it ranged across the ecotone; marginal species,
those found only to occur in the ecotone and not
in a particular ecogeographic formation, were not
included. The fauna of each formation was com-
pared with those of all other formations using
the following three FRFs: Savage's (1960) Coef-
ficient of Difference ($CD = 1 - C/N_2 \times 100$);
Simpson's (1960) Similarity Coefficient ($SC = C/N_1 \times 100$), and Jaccard's (1902: *in* Morafka
1977) Community Coefficient ($CC = [(C/N_1 + N_2 - C) \times 100]$), where C = the number of
species in common, N_1 = the number of species
in the area with the fewest species, and N_2 = the
number of species in the area with the most
species.

Faunal resemblance factors are descriptive
rather than statistical indices (Cheetham and Ha-
zel 1969) and thus do not have levels of signif-
icance. I established a "level of significance" for
each coefficient on the basis of usage by previous
workers, and the relative correlation of the dif-
ferent coefficient values derived from the com-
parison of geographic units where N_1 approaches
or equals N_2. My primary emphasis, when eval-

uating FRF values, was to weigh all three values for each pair of geographic units, treating all units relative to one another, and to look for obvious clusters occurring in ranked coefficient values. Savage (1960) arbitrarily selected CD = 50% or greater as indicative of a unique faunal grouping and I follow his usage as a basis. Employing the 50% level of significance with Jaccard's CC and Simpson's SC indicated to me that they are more sensitive and less sensitive, respectively, than the CD for distinguishing unique faunal groupings. I have therefore partially weighted these coefficients. Those ecogeographic formation pairs with at least two of three coefficients meeting the following criteria: CD < 50%, CC ≥ 40%, and SC ≥ 60%, were considered to be related at a significant level.

Thirteen pairs met my criteria for significant relatedness (Table 4). The relationships between these 13 pairs are depicted phenographically (Fig. 15a–c). Subsequent pairwise analyses between ecogeographic formations using both average linkage (UPGMA) and single linkage (nearest neighbor) methods (SAS 1985) yielded results nearly identical to those depicted in Figure 15a–c.

Results of the numerical comparison indicate the presence of four distinct herpetofaunal areas within the Mártir Region, each showing some degree of overlap with one or more of the adjacent areas (Fig. 15a–c). These areas are:

(1) The Upper Main Scarp and the Lower Main Scarp—these two formations support the same montane herpetofauna (SC = 100%) with numerous species dropping out with increasing elevation (CD = 60%). The unequal fauna sizes between these two formations (7 vs. 20) account for the high SC and low CC values (CC = 40%).

(2) The Lower Main Scarp, West Scarp, and the Western Arroyos—these three formations support a fauna that apparently shares some ecological characteristics and possibly a convergent history with that of (1) above, but differ in their adaptation to the warmer and drier habitats of lower elevations, extending into some relatively extreme xeric areas where these species occur along the riparian corridors of the Western Arroyos, and similar habitats of the East Scarp.

(3) East Scarp and West Scarp—the high SC and CC and the low CD values between these formations indicate strong faunal affinities between these two rocky xeric woodland areas.

However, each of these two formations demonstrates only slightly less significant, differing affinities, with proximal formations; a situation that initially seems somewhat contrary and confusing. The East Scarp shows close faunal links with the Colorado Desert and the Western Foothills, while the West Scarp shows close affinities with the Western Arroyos and the Western Foothills (the FRF comparisons of the West Scarp and the Western Foothills are not depicted phenographically in Fig. 5a–c because they fell just below my levels of significance: CD = 49%, SC = 55%, and CC = 36%). I interpret these data to mean that two distinct overlapping faunas are present on the East and West scarps, each continuing with slightly differing distributions onto adjacent formations.

(4) The Colorado Desert, North Central Desert, San Quintín Plain, and the Western Foothills—all coefficient values between these four relatively open, scrub desert formations indicate strong faunal ties.

Further analysis of these numerical comparisons follows in conjunction with the results of the heuristic analysis below.

Heuristic Analysis

The heuristic analysis of distributions of regional species consisted of two parts: (1) a comparison of ecogeographic distributions along a schematic, southwest to northeast, regional transect between latitudes 30°30′N and 31°30′N (results depicted in Table 5); (2) a comparison of overall regional distributions established by plotting available literature and field records (Species Accounts) on maps based on Figures 3, 4, and 5 (results illustrated in Fig. 16). A species that occurred at two or more localities within a contiguous vegetation or physiographic area was assumed to occur throughout the contiguous habitat where suitable microhabitat existed, but not above or below the highest or lowest elevation records. I included locality records from the Sierra Juárez Region to the north and the Central Desert Region to the south to discern distributional trends over a wider area.
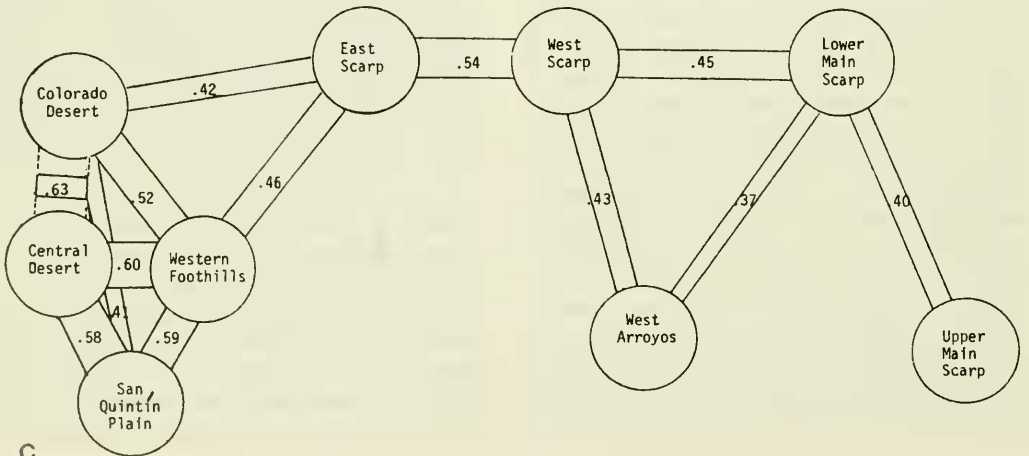
Three distinct patterns were apparent from the transect analysis (Table 5): (1) the High Sierran Fauna (I), with distributions corresponding closely to those of the Upper and Lower Main Scarp formations, areas linked by numerical
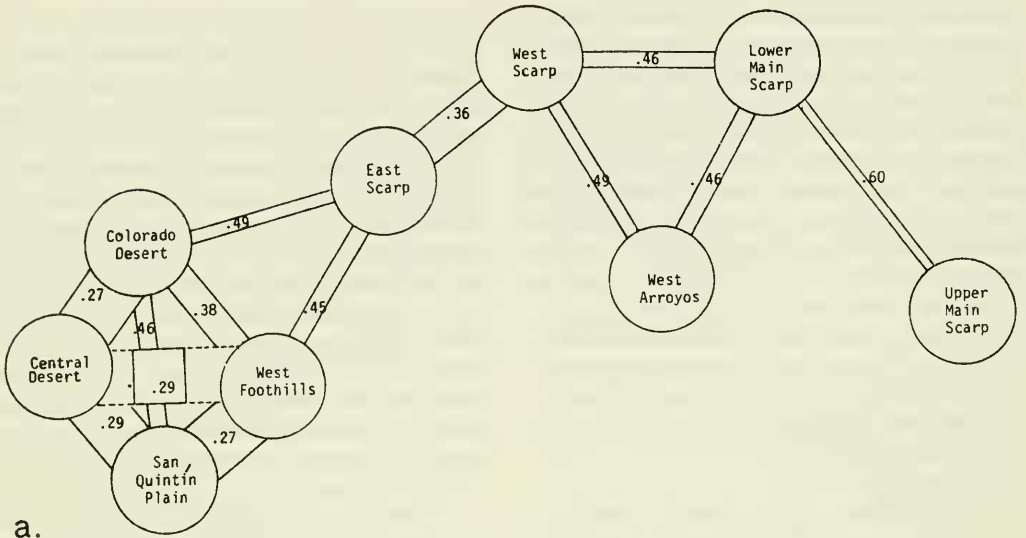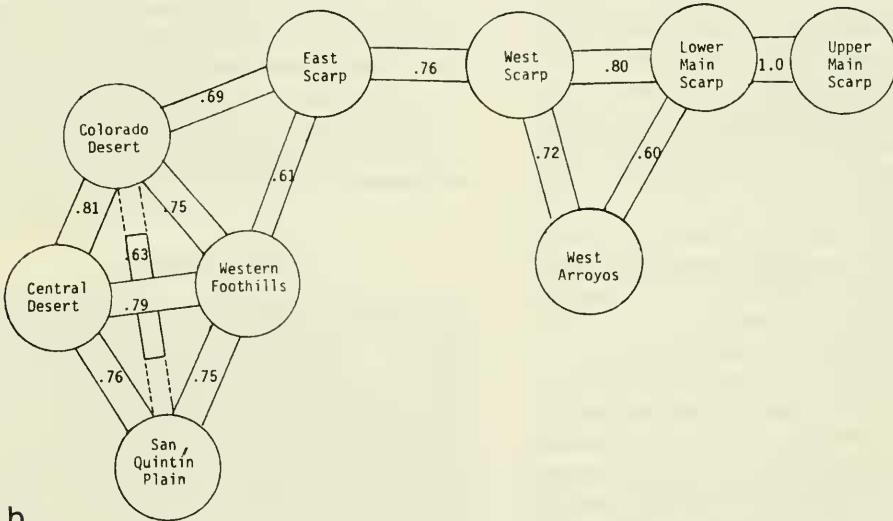
TABLE 4. COMPARISON OF REGIONAL HERPETOFAUNAS BY ECOGEOGRAPHIC FORMATION (FIG. 14) USING THREE FAUNAL COEFFICIENT FACTORS.[1] Number of species present in parentheses. C = number of species in common. Formation pairs with two of three coefficients as follows are considered to be related at a significant level: CD < 50%, SC ≥ 60%, CC ≥ 40%.

		Colo. Desert (35)	East Scarp (26)	Upper Main Scarp (8)	Lower Main Scarp (20)	West Scarp (31)	West Foothills (29)	West Arroyos (22)	San Quintín Plain (30)
East Scarp (26)	C	18							
	CD	49%							
	SC	69%							
	CC	41%							
Upper Main Scarp (8)	C	0	0						
	CD	100%	100%						
	SC	0%	0%						
	CC	0%	0%						
Lower Main Scarp (20)	C	3	9	8					
	CD	92%	66%	60%					
	SC	15%	45%	100%					
	CC	7%	24%	40%					
West Scarp (31)	C	12	20	6	16				
	CD	66%	36%	81%	49%				
	SC	38%	76%	75%	80%				
	CC	22%	54%	18%	45%				
West Foothills (29)	C	22	16	1	5	16			
	CD	38%	45%	97%	83%	49%			
	SC	75%	61%	12%	25%	55%			
	CC	52%	46%	3%	11%	36%			
West Arroyos (22)	C	2	9	4	12	16	5		
	CD	94%	66%	82%	46%	49%	83%		
	SC	9%	40%	50%	60%	72%	22%		
	CC	4%	23%	15%	37%	43%	10%		
San Quintín Plain (30)	C	19	13	2	5	15	22	8	
	CD	46%	57%	94%	84%	52%	27%	74%	
	SC	63%	50%	25%	25%	50%	75%	36%	
	CC	41%	30%	6%	11%	32%	59%	18%	
Central Desert (32)	C	26	15	2	6	14	23	6	23
	CD	27%	54%	94%	82%	57%	29%	82%	29%
	SC	81%	57%	25%	30%	45%	79%	27%	76%
	CC	63%	34%	5%	13%	28%	60%	12%	58%

[1] CD = Coefficient of Difference (CD = 1 − C/N_2 × 100) (Savage 1960); SC = Similarity Coefficient (SC = C/N_1 × 100) (Simpson 1960); CC = Community Coefficient [CC = (C/N_1 + N_2 − C) × 100] (Jaccard 1902, in Morafka 1977). N_1 = number of species in the area having the fewest species, N_2 = the number of species in the area with the most species.

comparison above, and indicating a montane fauna; (2) the Californian Fauna (II) with distributions corresponding closely to those of the second faunal area indicated numerically above, and encompassing primarily the Lower Main and West scarps and the Western Arroyos; and (3) the Colorado Desert Fauna (III). The endemic Colorado Desert Fauna is apparently too small, relative to the total number of xerophilic species present within the South Colorado Desert formation, to have been detected by the FRF analysis. The considerable overlap in ecogeographic

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FIGURE 15. Relationships between herpetofaunas of the ecogeographic formations (Fig. 14) based on (a) Coefficients of Difference (CD) (Savage 1960), (b) Coefficients of Similarity (SC) (Simpson 1960), and (c) Community Coefficients (CC) (Jaccard 1902, in Morafka 1977). Width of bars is directly proportional to degree of relationship, length of solid bars is inversely proportional to degree of relationship. Formation pairs with CD > 0.50 not included (except the Upper Main Scarp for which the smallest value is included). Formation pairs with SC < 0.60 not included. Formation pairs with CC < 0.37 not included. See Table 4 for all pairwise values.

TABLE 5. ECOGEOGRAPHIC DISTRIBUTION OF THE HERPETOFAUNA ON A SCHEMATIC TRANSECT OF THE SIERRA SAN PEDRO MÁRTIR REGION, BAJA CALIFORNIA NORTE, MÉXICO, IN THE VICINITY OF LATITUDE 31°N. Faunal groupings are based on coincident regional (Fig. 16) and overall areal (Fig. 11–21) distributions. Solid lines indicate occurrence throughout a formation; X without lines indicates occurrence restricted within a formation. (X) = occurrence only within Western Arroyos where they transect the Western Foothills (not considered a part of the foothills fauna). ?-----? = expected occurrence. * = resident of Pacific Northwest Track (see text and Fig. 17). ** = resident of Madrean Track (see text and Fig. 18).

SPECIES / Regional Herpetofaunas	NCD (CDS)[2]	SQP (CDS)	WA (RW)	WF (CSS)	WS (Chp)	LMS (Con)	UMS (Con)	ES (P-J, CBS)	CD (CBS)
I. High Sierran Scarps Fauna**									
Rana boylii						X------	?		
Batrachoseps pacificus ssp.					X	X	X		
Sceloporus graciosus						X		X	
Lampropeltis zonata						X	X		
Thamnophis elegans						X	X		
II. Californian Fauna**									
Bufo boreas*			X				X		
Bufo microscaphus			X			X			
Hyla cadaverina			X	(X)	X	X		X X	X
Hyla regilla	X	X	X	(X)	X	X	X	X	X
Rana aurora*			X	(X)	X	X			
Scaphiopus hammondii		X		X					
Batrachoseps p. major			X	X					
Clemmys marmorata*			X	(X)	X				
Anniella pulchra		X	X	(X)	X				?
Eumeces gilberti		X	X	(X)	X		X	?----?	?
Eumeces skiltonianus		X	X	(X)	X		X		
Elgaria multicarinata	X						X	X	X
Sceloporus occidentalis			X	(X)	X		X	X	X
Xantusia vigilis	X	X	X		X			X	X
Crotalus viridis	X						X	X----?	?
Diadophis punctatus			X	(X)	X------	?			
Coluber lateralis		X	X	(X)	X	X---?		?----	X
Thamnophis hammondii		?------	X	(X)	X	X		?--X	X
III. Colorado Desert Fauna									
Phrynosoma platyrhinos								X	X
Urosaurus graciosus								X	X
Chionactis occipitalis								X	X
Crotalus cerastes								X	X

<------------ecotones------->

[1] NCD = North central Desert; SQP = San Quintín Plain; WA = Western Arroyos; WF = Western Foothills; WS = West Scarp; LMS = Lower Main Scarp; UMS = Upper Main Scarp; ES = East Scarp; CD = Colorado Desert; see figure 4.

[2] ( ) = Dominant vegetation; see table 2.

distribution among the xerophilic species of the Region made it difficult to distinguish additional distinct faunal assemblages using the schematic ecogeographic transect format alone.

However, comparison of overall regional distributions indicated a total of seven patterns among the regional herpetofauna (Fig. 16). Patterns I, II, and III (Fig. 16) correspond with the

Table 5. Continued.

| SPECIES	ECOGEOGRAPHIC FORMATION[1]								
	N C D (CDS)[2]	S Q P (CDS)	W A (RW)	W F (CSS)	W S (Chp)	L M S (Con)	U M S (Con)	E S (P-J, CBS)	C D (CBS)
IV. Peninsular Range Fauna									
A. Pacific Slope Forms:									
Anniella geronimensis**		X_X							
Cnemidophorus hyperythrus	X				X				
Cnemidophorus labialis**	X	X							
Phrynosoma coronatum	X		X	X	X ?				
Crotalus enyo	X	X							
Sonora s. bancroftae		?	X	X ?					
B. Rocky Scarps Forms:									
Crotaphytus insularis	X			X				?--X--?	
Petrosaurus mearnsi								X	X
Phyllodactylus nocticolus	X							X	X
Sauromalus obesus								X	X
Sceloporus orcutti	X	X	X			X		X	X
Urosaurus microscutatus			X	X	X			X	X
Xantusia henshawi**				X X		X		X	X
Crotalus mitchellii	?			X X	X---?			?---X	X
C. Flatland Desert Forms:									
Callisaurus draconoides	X			X					X X
Dipsosaurus dorsalis									X X
Chilomeniscus cinctus	X	X	X	X X					X----?
Crotalus ruber	X		X	X	X				X X--?
Lichanura trivirgata	?---X		X	X X---?					?-X X
Phyllorhynchus decurtatus									X X
V. North American Ubiquitous Scrubland Fauna									
Bufo punctatus	X					X		X	X
Schaphiopus couchii								?-----X--?	
Cnemidophorus tigris	X	X------?	X	X		X	X		X
Coleonyx variegatus	X X------?			X X					X X
Gambelia wislizenii	X		X	X	X				X X
Sceloporus magister	X		X	X	X			?--X	X
Uta stansburiana	X		X	X		X		?-X	X
Arizona elegans	X		X	?---X--?				X	X
Hypsiglena torquata	X		X	X	X------?			?----------X	
Lampropeltis getulus	?-----X				X---?			?--X X----?	
Leptotyphlops humilis	?-----X----?----X--?							?----X	
Coluber flagellum	X		X	X	X			?--X	X
Pituophis melanoluecus	X						X	?------X-X--?	
Rhinocheilus lecontei	X		X	--?--				?--X-X	
Salvadora hexalepis	X		X	X	X---?			?------X	X
Sonora s. semiannulata	?-----?							?----?	
Tantilla planiceps	X----------?	?--X					?----------?	
Trimorphodon biscutatus	?----------X	?	X---?				?----------X-?	
	<------edotones------>								
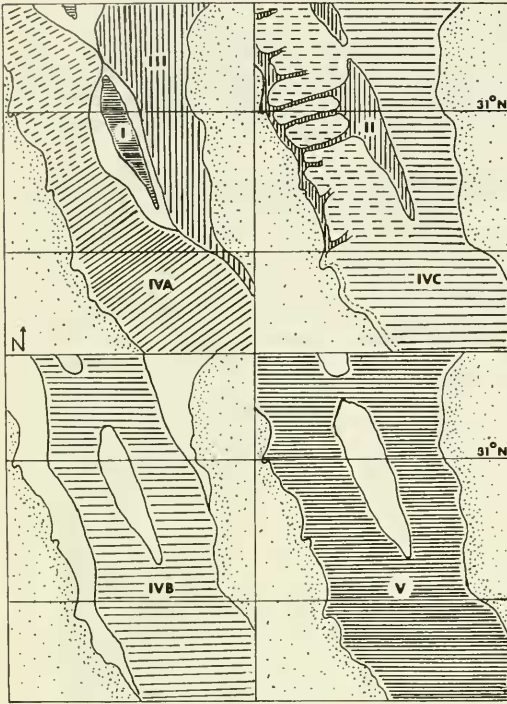
FIGURE 16. Distribution patterns of the herpetofauna of the Sierra San Pedro Mártir Region, Baja California Norte, México. Numerals refer to Table 5. In some cases member-species occur within, but not across the entire pattern range depicted; see Table 5 for exact regional distributions of individual species. Broken lines indicate fewer species of grouping indicated occur northward.

three derived above and numerically. The remaining species represent two relatively distinct groupings that occur throughout the xeric scrubland formations on both the Pacific and Gulf slopes (Fig. 16, pattern V), or only within some of the scrubland formations on one or the other, or both, slopes (Fig. 16, patterns IVa, IVb, IVc). Several species subsequently assigned to pattern IVc (Fig. 16) (*Callisaurus draconoides, Chilomeniscus cinctus, Crotalus ruber,* and *Lichanura trivirgata*) and pattern IVb (Fig. 16) (*Crotalus mitchellii*) had regional distributions that were indistinguishable from members of pattern V (Fig. 16) at this stage of analysis. Final assignment of these species, and those assigned to pattern V, was not possible until overall distribution patterns were compared (see Analysis of Tracks below).

The remaining three species assemblages (Fig. 16, patterns IVa, IVb, and IVc) are centered primarily along the East or West scarps or both, and

the Western Foothills, corresponding with the third faunal area derived numerically above (Fig. 15). This third FRF-derived faunal area is the least clearly defined probably due to the complex overlapping ecogeographic variations apparent among the several groups of species within this faunal area and their overlap with many of the species of pattern V. Pattern V (Table 5) corresponds closely with the fourth faunal area derived by the FRF analysis and covering the four scrubland desert formations (Fig. 15). Most species of pattern IVa (Fig. 16; Table 5) occur only on the Pacific Slope of northern or central Baja California. *Sonora semiannulata bancroftae* and *Anniella geronimensis* are endemic to the Mártir Region; *Crotalus enyo* and *Cnemidophorus labialis* have their northern limits slightly north of the Mártir Region. The remaining two members of pattern IVa (*Phrynosoma coronatum* and *Cnemidophorus hyperythrus*) range north across the U.S. border on the Pacific Slope. All of these species avoid rocky substrates, preferring sandy soils. Members of pattern IVc also show preference for sandy, fine-textured substrates, but demonstrate wider regional and overall distributions than members of pattern IVa, occurring throughout the xeric and subxeric scrub habitats on both the Pacific and Gulf slopes and ranging extensively beyond the Mártir Region (Fig. 16; Table 5). Pattern IVb species (Fig. 16; Table 5) are saxicolous species associated with the Peninsular Range scarps and bordering rocky scrubland habitats. Three of these species (*Petrosaurus mearnsi, Phyllodactylus nocticolus,* and *Sauromalus obesus*) occur only along the Gulf Slope north of 30°N latitude. The remaining pattern IVb members occur on both slopes of the Peninsular Range regionally and northward, except *Crotaphytus insularis,* which is absent from the Pacific Slope north of 32°N latitude. *Xantusia henshawi* is absent south of 30°N latitude.

Analysis of Tracks

Lastly, I conducted an analysis of the entire distribution of each taxon in Baja California using the Species Accounts and the following literature: Van Denburgh (1922), Schmidt (1922), Savage (1960, 1967), Soule and Sloan (1966), Stebbins (1966, 1985), Bostic (1971), Loomis et al. (1974), Conant (1975), Murphy (1983*a*), and Murphy and Ottley (1983, 1984). This last stage of the analysis sought to discern the generalized

tracks of the Baja California herpetofauna by comparing the geographic distributions of consanguineous forms (monophyletic lineages), seeking spatial congruency among unrelated taxa, the panbiogeographic method of Croizat (1964; see also Craw [1983] and Craw and Weston [1984]). Distributions were examined and compared for each lineage at the subspecific, specific, and generic levels. In each case of a proposed generalized track, the number of individual tracks indicative of the described generalized track exceeded the minimum three taxon/area statements (three individual tracks) considered as essential to support a hypothesis of a generalized track or pattern (Craw 1983).

I found evidence of at least five generalized tracks among the herpetofauna of the Sierra San Pedro Mártir Region: a Northwest Pacific Track, a Madrean Track, a Colorado Desert Track, a Peninsular Range Track, and a North American Desert and Plains Track.

The Pacific Northwest Track (Fig. 17)

The 20-plus species on this track are found along the western Pacific rim from Baja California north through California, Oregon, Washington, and into Canada, with a few forms occurring north to Alaska. Many species of this track have allopatric congeners in the northeastern United States. This track is characterized by endemic salamanders, most of which occur north of 35°N latitude in California; only the genera *Ensatina* and *Aneides* occur in Baja California. In southern California and Baja California, members of the Pacific Northwest Track (Table 6) occur as disjunct populations and are often isolated on mountain ranges. *Clemmys marmorata* is the only reptile of the Mártir Region that I believe is a member of this track. The anurans *Bufo boreas* and *Rana aurora* are included on this track, but their taxonomic and distributional patterns do not match the pattern as well as the other amphibians indicated. This may be due to their euryecious nature, and they may in fact have a common zoogeographic history with other track members. They may also represent another, more recent overlapping track, as they appear to be relatively young forms in North America that may have relatively recently diffused (Pielou 1979) south across cool temperate regions (Savage 1960). The M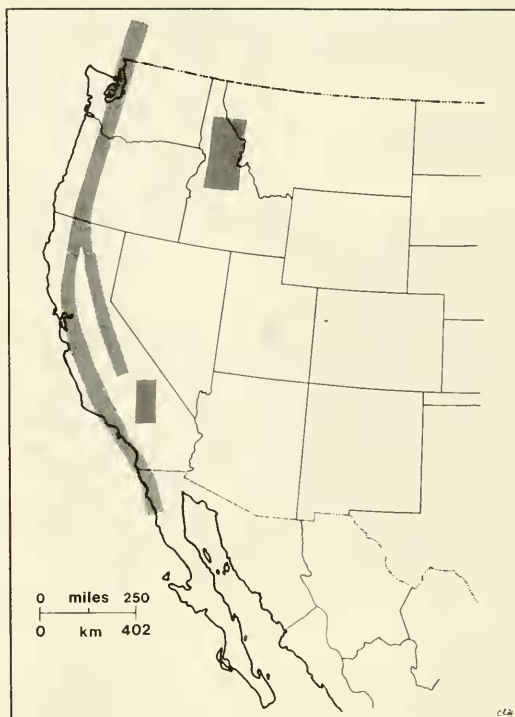ártir faunal elements of the Pacific Northwest Track are members of either the High Sierran or Californian faunas (Table 5; Fig. 16, I and II) and have their southern terminus in the Mártir Region.

FIGURE 17. Generalized tracks of the herpetofauna of the Baja California Region: Pacific Northwest Track.

The Madrean Track (Fig. 18)

The Madrean Track lineages exhibit a complex pattern of distribution across southwestern North America often involving two or more disjunct forms, for each lineage, within Baja California and additional disjunct, closely related forms, to the north and east in California and Arizona, with many lineages ranging into southwestern New Mexico and south into the Sierra Occidental of Mexico (not all member lineages presently occur across the full range of the track). These forms avoid lowland xeric habitats for the most part, or if they occur in such areas, they have adapted to microhabitats, and temporal activity patterns that ameliorate against the extremes of low moisture and high temperature (e.g., *Scaphiopus*, *Xantusia* spp.).

Within Baja California many of these forms occur in disjunct populations, with some occur-

TABLE 6.   RESIDENT TAXA OF THE GENERALIZED TRACKS OF THE HERPETOFAUNA OF THE BAJA CALIFORNIA REGION. Includes only those track members that occur within the Baja California Region. ( ) refer to Figures 17–21.

Pacific Northwest Track (17)

Aneides lugubris   *Rana aurora*
Ensatina eschscholtzii   *Clemmys marmorata*
Bufo boreas

Madrean Track (18)

Batrachoseps pacificus major   *Eumeces gilberti*   *Diadophis punctatus*
B. pacificus spp.   *E. skiltonianus* complex   *Coluber lateralis* complex
Scaphiopus hammondii   *E. skiltonianus*   *C. aurigulus*
Bufo microscaphus   *E. lagunensis*   *C. barbouri*
Hyla cadaverina   *Cnemidophorus labialis*   *C. lateralis*
H. regilla   *Elgaria* complex   *Lampropeltis zonata*
Rana boylii   *E. cedrosensis*   *Thamnophis hammondii* complex
Sceloporus graciosus   *E. multicarinata*   *T. hammondii*
S. occidentalis   *E. paucicarinata*   *T. digueti*
Xantusia vigilis (2 spp.)   *Anniella pulchra*   *T. elegans*
X. henshawi   *A. geronimensis*   *Crotalus viridis*

Colorado Desert Track (19)

Phrynosoma mcallii   *Urosaurus graciosus*
P. platyrhinos   *Chionactis occipitalis*
Uma notata   *Crotalus cerastes*

Peninsular Range Track (20)

Chrysemys scripta   *Sator* complex   *Cnemidophorus deppei* complex
Bipes biporus   *S. angustus*   *C. ceralbensis*
Coleonyx switaki   *S. grandaevus*   *C. hyperythrus* (3 ssp.)
Phyllodactylus angelensis   *Sauromalus* complex   *Lichanura trivirgata* (3 spp.)
P. apricus   *S. ater* (2 ssp.)   *Chilomeniscus* complex
P. bugastrolepis   *S. australis*   *C. cinctus*
P. homolepidurus nolascoensis   *S. hispidus*   *C. punctissimus*
P. nocticolus (9 ssp).   *S. klauberi*   *C. savagei*
P. partidus   *S. obesus*   *C. stramineus* (2 ssp.)
P. santacruzensis   *S. slevini*   *Elaphe rosaliae*
P. tinklei   *S. varius*   *Eridiphas slevini* (2 ssp.)
P. unctus (3 ssp.)   *Sceloporus magister* complex   *Nerodia valida*
P. xanti   *S. m. lineatulus*   *Phyllorhynchus decurtatus* (3 ssp.)
Callisaurus draconoides (6 ssp.) *S. m. monserratensis*   *Sonora semiannulata bancroftae*
Crotaphytus insularis (2 ssp.) *S. m. rufidorsum*   *S. s. mosaueri*
Ctenosaura hemilopha   *S. m. zosteromus*   *Tantilla planiceps*
Petrosaurus complex   *Sceloporus orcutti* complex   *Crotalus atrox* complex
P. mearnsi   *S. hunsakeri*   *C. catalinensis*
P. repens   *S. licki*   *C. exsul*
P. thalassinus   *S. orcutti*   *C. ruber* (2 ssp.)
Phrynosoma coronatum complex   *Urosaurus* complex   *C. tortugensis*
P. cerroense   *U. lahtelai*   *C. enyo* (3 ssp.)
P. coronatum (3 ssp.)   *U. microscutatus*   *C. mitchellii* (4 spp.)
                                  U. nigricaudus

North American Desert and Plains Track (21):
Group A: old vicariated lineages

Bufo punctatus   *Leptotyphlops humilis* (5 ssp.)
Scaphiopus couchii   *Hypsiglena torquata* (7 ssp.)
Coleonyx variegatus (6 ssp.)   *Lampropeltis getulus* complex
Uta complex   *L. catalinensis*
U. antigua   *L. getulus* (3 ssp.)
U. nolascensis   *L. nitida*
U. palmeri
U. squamata
U. stellata
U. stansburiana (2 ssp.)

TABLE 6. CONTINUED.

North American Desert and Plains Track (21):	
Group B: post-vicariant lineages	
Gambelia wizlizenii	*Rhinocheilus leconti*
Sceloporus magister uniformis	*Salvadora hexalepis* (3 ssp.)
Arizona elegans (3 ssp.)	*Sonora s. semiannulata*
Coluber flagellum (2 ssp.)	*Trimorphodon biscutatus* (2 ssp.)
Pituophis melanoleucus (3 ssp.)	*Crotalus atrox*

ring as allopatric species, occupying patches of relatively mesic habitats scattered sporadically down the length of the peninsula, with several lineages present on one or two Gulf or Pacific islands (e.g., *Hyla regilla, Eumeces skiltonianus– E. lagunensis, Elgaria multicarinata–E. pauci-carinata, E. cedrosensis, Coluber lateralis–C. barbouri* and *C. aurigulus, Thamnophis hammondii–T. digueti, Xantusia vigilis,* and *Crotalus viridis*). The remaining lineages of this track (Table 6) do not, for the most part, occur south of 30°N latitude in Baja California. North of 30°N latitude into California and northward, and east across the Mojave Desert through Arizona, New Mexico, and south into Mexico in the Sierra Madre Occidental, these taxa demonstrate a similar pattern of allopatric distributions with many of these lineages represented by two or three species across the scope of the track (e.g., *Bufo microscaphus; Hyla cadaverina, H. regilla–H. exima; H. arenicolor; Elgaria multicarinata–E. panamintina–E. kingi; Xantusia v. vigilis–X. v. arizonae, X. h. bolsonae,* etc.; *Lampropeltis zonata–L. pyromelana*).

The remaining lineages included on this track (Table 6) are somewhat less clearcut in their patterns of disjunction and taxonomic/geographic correlation with the above listed taxa, but sufficient aspects of the pattern are apparent in their distributions to support their inclusion as elements of the Madrean Track.

Within the Mártir Region, elements of the Madrean Track demonstrate ecogeographic affinities coincident with the mesic habitats of the Gulf and Pacific slopes (Table 5, I, II, and IV).

Colorado Desert Track (Fig. 19)

These species have distributions coincident with the hottest and driest portions of the southwestern deserts, the area where the Mojave, Colorado, and Sonoran deserts merge. Mártir faunal elements present on this track occur regionally only in the Colorado Desert formation (Table 5, III; Fig. 16, III). Species of the Colorado Desert Track demonstrate the most limited distributions and the lowest levels of geographic and taxonomic diversity within lineages of all the faunal assemblages described here for Baja California. Six species are included; the Colorado Desert fauna of the Mártir Region (Table 5, III), plus *Uma notata* and *Phrynosoma mcallii.*

Peninsular Range Track (Fig. 20)

Lineages of this track have their overall distributions coincident with all or much of peninsular Baja California and the Gulf of California islands, extending north along the Peninsular Range to San Gorgonio Pass in southern California. A few taxa of this track have radiated northeast into the Mojave Desert (e.g., *Crotalus mitchellii, Lichanura trivirgata,* and *Dipsosaurus dorsalis*) and southeast into the Sonoran Desert (e.g., *Lichanura trivirgata, Chilomeniscus cinctus, Phyllorhynchus decurtatus, Callisaurus draconoides, Dipsosaurus dorsalis*). Several interrelated characteristics of the lineages assigned to this track are: (1) pronounced endemism; (2) presence of most primitive extant forms; and (3) greatest levels of geographic and taxonomic diversity within lineages, all within insular and peninsular Baja California. Twenty-six species or species-complexes meet these criteria (Table 6). Twenty species-groups of the Peninsular Range Track occur in the Mártir Region (Table 5, IV), and exhibit three variations in regional distribution (Fig. 16, IVa, IVb, and IVc). Six taxa occur further south in peninsular and insular Baja California in the Central and Vizcaíno deserts and the Cape Region (*Chrysemys scripta, Bipes biporus, Ctenosaura hemilopha, Sator* spp., *Eridiphas slevini,* and *Nerodia valida*).
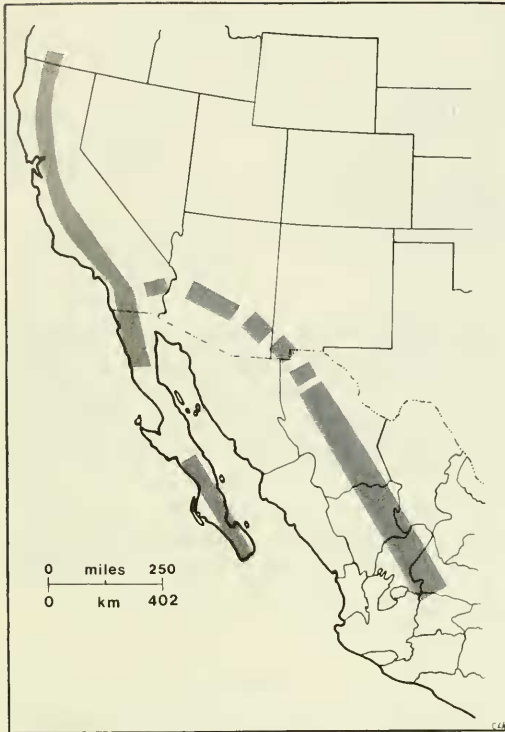
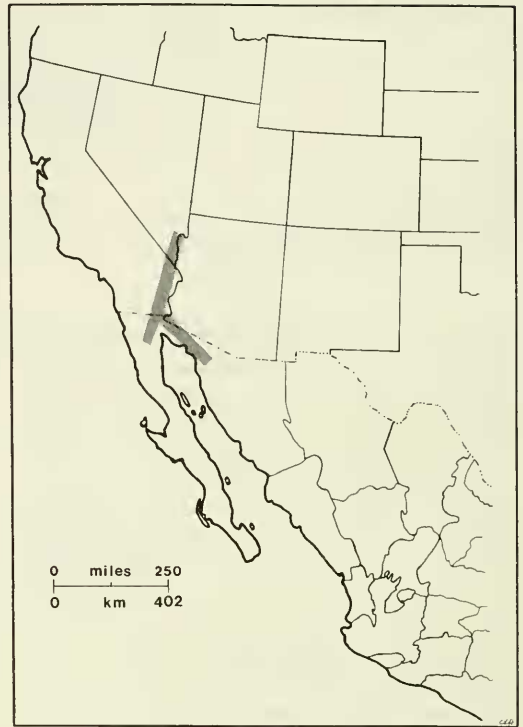FIGURE 18.   Generalized tracks of the herpetofauna of the Baja California Region: Madrean Track.

FIGURE 19.   Generalized tracks of the herpetofauna of the Baja California Region: Colorado Desert Track.

North American Desert and Plains Track (Fig. 21)

Species of this track possess broad distributions throughout the North American Desert Region, and into the Great Plains Region. These species are widespread in Baja California, occurring throughout most insular and peninsular xeric habitats. The 18 taxa of the North American Desert and Plains Track present in the Mártir Region demonstrate broad ecogeographic distributions throughout the scrub and woodland habitats of the Region (Table 5; Fig. 16, V).

The lineages of this track can be divided into two subsets on the bases of distributional variations on Gulf of California islands, and the level of divergence they show within the Baja California Region as a whole: (1) those lineages that show extensive divergence within the Baja California Region, including endemic taxa on some or all of the "old islands" (Soule and Sloan 1966; see also Murphy [1983*b*] and Murphy and Ottley [1984]) of the Gulf of California (Table 6,

Desert and Plains Track—group A); and (2) those lineages that show little divergence throughout peninsular Baja California and are absent from the "old islands" (Soule and Sloan 1966) (Table 6, Desert and Plains Track—group B). The taxa of group A appear to have a shared evolutionary history within the Baja California Region with the lineages of the Peninsular Range Track (Table 6). The taxa of group B appear to be relatively recent (post-Pliocene) emigrants in the Baja California Region despite sharing contemporary overall continental distributions with members of group A.

Geographic diversity and endemism within the lineages of this track, when considered within peninsular and insular Baja California, are not noticeably more extensive than in other parts of the North American Region (in contrast with member lineages of the Peninsular Range Track). On the contrary, with many lineages of this track, geographic diversity and endemism are greater beyond, than within, insular and peninsular Baja California.
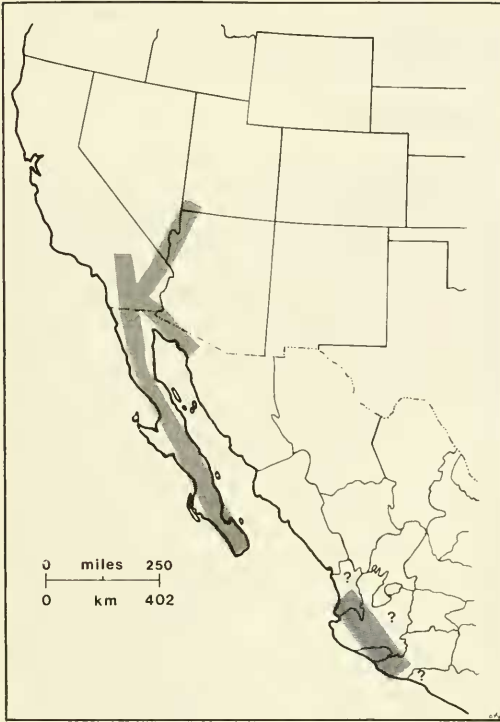
FIGURE 20. Generalized tracks of the herpetofauna of the Baja California Region: Peninsular Range Track. The extent of this track in southwest Mexico is greater than indicated, particularly southward.

FIGURE 21. Generalized tracks of the herpetofauna of the Baja California Region: North American Desert and Plains Track.

DISCUSSION

Theories on the historical biogeography of the herpetofauna of the Baja California Region have advanced on three parallel fronts: (1) with increased knowledge of contemporary herpetofaunal distributions and their ecogeographic affinities; (2) with new information about past climates and vegetation assemblages—the geofloral literature; and (3) with the advent of a new paradigm in geology—plate tectonics—depicting a dynamic rather than static landscape. Nelson (1921) and Schmidt (1922) compiled the first syntheses based on early distributional data of the peninsular biotas. Savage (1960) constructed paleoecological scenarios using data in the geofloral literature, and in conjunction with analyses of contemporary herpetofaunal distributions, presented a classic synthesis. Soule and Sloan (1966) and Savage (1967) discussed evolutionary relationships of the island herpetofaunas of the Gulf of California and proximate Pacific Ocean
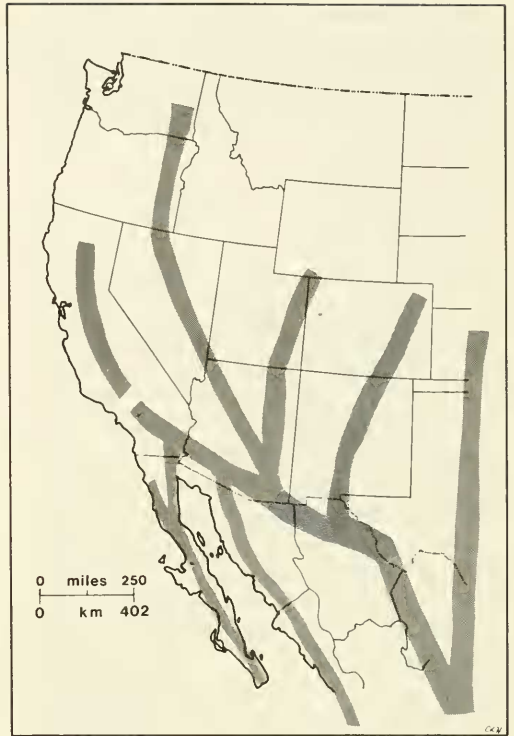
islands, respectively. However, Savage and earlier investigators based their analyses on the assumption of a static or fixed peninsula, requiring Recent distributions to have been derived primarily from north to south dispersals in the case of species present on the peninsula, or temporary land bridges or chance dispersal across water barriers in the case of species present on islands.

More recently, in conjunction with developing tectonic theory, Leviton and Tanner (1960), Robinson (1973), and Smith and Tanner (1974) examined biogeographic relationships within single taxa, and indicated that particular species of the southern Baja California herpetofauna exhibit distributions more consistent with a theory of vicariant origins resulting from past tectonic events than with a theory of north to south dispersals down a fixed peninsula. Murphy (1975), following this lead, proposed a "trans-gulfian" vicariance model, based on the dislodging of prepeninsular land masses from further south along

coastal Mexico during the Miocene, to explain contemporary distributions of many of the subtropical associated elements of the Cape Region and associated deep-water islands (*Bipes biporus, Nerodia valida, Ctenosaura hemilopha, Pseudemys scripta, Eridiphas sleveni, Sator angustus, Crotalus catalinensis*, and three subspecies of *Leptotyphlops humilis*). Welsh (1976*a, b,* 1981) indicated that distributional data for most of the Sonoran Desert herpetofauna of Baja California showed patterns of distribution and differentiation on peninsular and insular land masses indicative of long-term isolation and evolution consistent with a tectonic vicariant origin. Elements of the herpetofauna whose distributions are consistent with this scenario include some or all members of the following genera within the Baja California Region: *Callisaurus, Crotaphytus, Dipsosaurus, Petrosaurus, Phrynosoma, Sauromalus, Sceloporus, Uta, Urosaurus, Coleonyx, Phyllodactylus, Cnemidophorus, Lichanura, Leptotyphlops, Chilomeniscus, Hypsiglena, Lampropeltis, Phyllorhynchus, Sonora, Tantilla, Trimorphodon,* and *Crotalus.* Murphy (1983*a*) developed a comprehensive evolutionary scenario based on geomorphological and paleobotanical evidence and tectonic theory to further elucidate the possible vicariant events responsible for many contemporary herpetofaunal distribution patterns. Kim et al. (1976), Wyles and Gorman (1978), Murphy and Papenfuss (1979), and Murphy (1983*a*) presented electrophoretic data that, assuming the validity of the "biochemical evolutionary clock" (Sarich 1977), support the thesis of a vicariant origin from Miocene tectonic events to account for distributional patterns among major components of the contemporary herpetofauna of Baja California.

Paleogeographic and Paleobotanic History of the Baja California Region

The following scenario is a shortened version that follows closely the synthesis developed by Murphy (1983*a*) but with some modifications as indicated below. Berggren and Van Couvering (1974) and Van Couvering (1978) present a geologic time scale that differs from the generally accepted time scale by placing the Miocene–Pliocene boundary at 5.2 MYBP (million years before present), rather than at 11–13 MYBP, and the Pliocene–Pleistocene boundary at 1.6–2.0 MYBP rather than at 1 MYBP. The Berggren

and Van Couvering time scale will be followed in subsequent discussion.

Miocene and Earlier

Paleogeography

The "two-fault" hypothesis of Atwater (1970), which indicates that two major migrating land masses have been active along Pacific coastal Mexico since at least the Miocene, is central to the hypothesis of a tectonic origin for many present-day herpetofaunal distributions of Baja California. Gastil et al. (1972) supported the "two-fault" theory and indicated further that "Peninsular California" was probably separated from coastal Mexico as several large fragments. These two land masses are: (1) "Alta California," defined here as consisting of present-day California from about Santa Barbara to San Francisco and west of the San Andreas fault (modified from Gastil et al. 1972), and (2) "Peninsular California," those areas south of the Transverse Ranges of southern California and west of the Gulf of California (Gastil et al. 1972). "Alta California" probably began its traverse 20–25 MYBP when it was torn from "Peninsular California" (then south of its present location, and part of coastal Mexico) from about Bahía San Sebastian Vizcaíno northward. The Pacific islands of Baja California north of Vizcaíno Bay and the Channel Islands of California are probably fragments that resulted from the traverse of "Alta California."

The dating for the separation of "Peninsular California" from coastal Mexico varies considerably from early Tertiary (60 MYBP; Gastil et al. 1972) to early Pliocene (5 MYBP; Moore 1973). Geological evidence (Atwater and Molnar 1973; Gastil and Jensky 1973) suggests that the southern end of Baja California from about La Paz south — the Cape fragment — originated from coastal Mexico near the Jalisco–Nayarit border in the mid-Miocene (12–14 MYBP). This and other separate island and island fault blocks have been simultaneously moving northwestward since mid-Miocene through Pliocene times. By the close of the Miocene, "Peninsular California" had migrated 260 km northwest to the region of the Islas Las Tres Marias (Gastil and Jensky 1973). Thus it appears that from the mid-Miocene, beginning about 14 MYBP, much of "Peninsular California" existed as an island archipelago. This archipelago included much of the present-day

Cape Region and associated deep-water islands (Santa Catalina, Santa Cruz, San Diego, and Isla Cerralvo—hereafter referred to collectively with the proto-Cape Region as the Cape Islands), as well as upland areas of the present-day Vizcaíno peninsula (possibly including Isla Cedros). Simultaneously, the northern Peninsular Ranges were beginning to uplift and separate as a result of subduction (Murphy 1983*a*). Murphy (1983*a*, fig. 6) indicated that the northern Peninsular Ranges were not totally separated from western Mexico at this time. A proto-Gulf of California was beginning to form about 14 MYBP but may not have become a permanent geographic feature until around the Miocene–Pliocene boundary, 6–5 MYBP (Gastil and Jensky 1973.)

Subduction along the fault system continued to elevate the northern Peninsular Ranges, and the central Peninsular Ranges began to emerge as a result of volcanism (Durham and Allison 1960; Karig and Jensky 1972). The Sierra Madre Occidental, the Sierra Madre Oriental, and the Mexican Plateau were also being elevated as a result of Miocene tectonic activities (King 1959). "Thus the only geographically isolated portions of the extant peninsula in the middle Miocene were the islands near (and including) the current Cape area, the Sierra Vizcaíno, and several southern peninsula-associated island localities" (Murphy 1983*a*). Murphy (1983*a*, fig. 8, and text) indicated that, by the late Miocene, the Cape Islands were connected temporarily to more northern portions of the peninsula, at least until about the Miocene–Pliocene boundary, when this connection was apparently inundated.

Paleobotany

Prior to the Eocene, neotropical floral elements dominated western Mexico; from the Eocene onward, however, declining temperatures and increasing aridity progressively restricted the neotropical-Tertiary geofloral elements southward (Axelrod 1979). Oak–pinyon woodlands and arid tropic-scrub habitats (Madro-Tertiary vegetation associations) were developing but were restricted to higher elevations of the young developing mountain regions in the interior. By the close of the Oligocene the Madro-Tertiary geoflora predominated along the mountain chains and uplands of central Mexico (Axelrod 1975). The declining temperatures and increasing arid-ity continued to facilitate the spread of Madro-Tertiary geoflora in upland areas. Lowland areas of Mexico west of the Sierra Madre Occidental were still dominated by a neotropical flora (Axelrod 1975, 1979).

Pliocene

Paleogeography

During the Pliocene, beginning about 5 MYBP, "Peninsular California" began a more rapid northwestward movement, from the present region of the Islas Las Tres Marias to its present location (Larsen 1972; Atwater and Molner 1973; Moore 1973). The resurgence of plate interactions and the union of "Peninsular California" with the Pacific Plate (Atwater and Molner 1973) resulted in further uplift of the Peninsular Ranges. Volcanism continued in the southern Peninsular Ranges, including the Sierra de la Giganta (Mina 1957). The proto-Gulf of California had completely formed by 5 MYBP (Karig and Jensky 1972; Gastil et al. 1975) and extended from the region of the San Gorgonio Pass in southern California (Allen 1957) to its opening into the Pacific Ocean between the Islas Las Tres Marias and mainland Mexico (Moore 1973). In the central and southern peninsula, the Sierra Vizcaíno and possibly the Cape Islands remained isolated from the northern Peninsular Ranges. During the Pliocene the Los Angeles Basin was submerged beneath the Pacific Ocean. The combination of the flooding of the Los Angeles Basin and the formation of the proto-Gulf of California greatly reduced terrestrial access to the northern Peninsula (Durham and Allison 1960); it may have in fact been totally isolated (Murphy 1983*a*). Murphy (1983*a*, fig. 9) refers to this probable restricted or eliminated terrestrial access to the northern Peninsular Ranges as the San Gorgonio Barrier.

Pliocene orogenic events brought the Sierra Madre Occidental, the Sierra Madre Oriental, and the Mexican Plateau to near their present elevations (Eardley 1951; King 1959). This resulted in at least a partial barrier to gene exchange between populations of xerophilic herpetofaunas in the proto-Chihuahuan and proto-Sonoran xeric habitats on either side at the northern end of the Sierra Madre Occidental; an area referred to as the Cochise Filter Barrier (Morafka 1977).

Paleobotany

The newly formed, moderately high montane regions initiated the establishment of easterly rainshadows. Axelrod (1975) indicated that by the late Pliocene, climates in the middle latitudes (25–40°N) were essentially equivalent to those of the present. The deserts as we know them today, however, did not develop until the last interglacial period (Axelrod 1979). The only paleobotanical data from "Peninsular California" are from the Mount Eden Beds at the north end of the Peninsular Range in southern California. These are characterized by a mixture of Arcto-Tertiary and Madro-Tertiary geofloral assemblages. Eight habitats were represented: (1) desert, (2) arid subtropical scrub, (3) coastal sage, (4) grassland, (5) chaparral, (6) live oak and walnut woodland, (7) digger pine woodland, and (8) big-cone pine conifer forest (Axelrod 1937, 1950). Murphy (1983a) assumes that the desert and arid subtropical scrub habitats were marginal and that the area was predominantly mesic in character. This interpretation is supported by vertebrate fossils from the same area (Frick 1933). Terrestrial and aquatic vertebrate fossil remains from the Pliocene in southern Baja California (Miller 1977, 1980) indicate a warmer climate than the present one with year-round fresh water, possibly a subtropical savanna habitat.

Pleistocene

Paleogeography

During this epoch, the most significant process of change—from the point of view of contemporary herpetofaunal distributions—appears to have been the rise and fall in sea level resulting from glacial fluctuations that alternately isolated and then connected many islands in the Gulf of California to larger peninsular land masses (those islands separated from the peninsula by an ocean depth of less than 130 m) (Auffenburg and Milstead 1965). Tectonic events continued as well, separating the Angel de la Guarda island block (Angel de la Guarda, Partida Norte, San Lorenzo Norte and Sur) from the peninsula, prior to 1 MYBP (Moore 1973). Tectonic activity also continued the elevation of the Peninsular Ranges (Gastil et al. 1975), completing the Coast Range Corridor in California (Peabody and Savage 1958), and forcing the waters of the Gulf of California to recede to their present position. The

Sierra Vizcaíno (Minch et al. 1976) and the Cape islands (Mina 1957) were unified with the peninsula.

Paleobotany

Geofloral data from Baja California and proximate areas of the southwest from the Pleistocene indicate a progressive drying and warming trend with each of the four interglacial periods (Axelrod 1966, 1975, 1979; VanDevender and Spaulding 1979). Axelrod (1966) characterized the region at the north end of the Peninsular Ranges during the interglacials as progressing from subhumid to semiarid, to subdesert, and finally to desert environments. Increased elevation of the northern Peninsular Ranges and other mountain regions of the southwest, created easterly rainshadows that promoted increased aridity and the subsequent expansion of desert habitats during the Pleistocene (Axelrod 1979). Evidence suggests that climates in southern Baja California continued to be relatively mesic during this epoch compared with those of northern peninsular areas. A fossil Pleistocene terrestrial vertebrate fauna from southern Baja California (Miller 1977) indicates both wooded and grassland habitats occurred in the area, indicative of denser vegetations than those presently in existence. In general, excepting the evolving desert plant communities, evidence indicates that mostly minor distributional perturbations in vegetation associations, rather than significant changes in vegetational components, occurred during the Pleistocene in southwestern North America (Axelrod 1966, 1975, 1979). Such perturbations were characterized by shifts in elevation of the vegetation communities of Baja California concomitant with glacial advances and retreats in more northern areas.

The Paleobiogeography of the Herpetofauna: Previous Scenarios

The broad paleobiogeographic scenarios of Savage (1960) and Murphy (1983a) provide the most current and comprehensive framework from which to discuss the evolutionary trends of the Baja California herpetofauna. Savage (1960) and Murphy (1983a) each developed a set of pertinent data essential to an overall understanding of the evolutionary mechanisms shaping herpetofaunal relationships in Baja California. Mur-

phy's paleobiogeographic scenario, based on current understanding of plate tectonics, clearly outdates Savage's hypothesis as to the primary mechanisms shaping the peninsular herpetofaunas. However, Savage developed, in broad outline, a powerful model to describe evolving North American herpetofaunal assemblages, the progenitors of the contemporary peninsular and insular herpetofaunas. He relied on the geological history (King 1958; Durham and Allison 1960), and more particularly the paleoecological history, in his reconstruction of Tertiary and Quaternary environments. This included the geofloral history as described in the work of Chaney, Axelrod, and MacGinitie (see Murphy [1983a] or Savage [1960] for complete citations) and the concept of interdigitating and evolving geofloras. Savage's inherent assumption was that herpetofaunas evolve in conjunction with broad changes in phytogeographic relationships. He defined four contemporary herpetofaunal areas in Baja California (Savage 1960) (Fig. 2a plus the Cape Region); these areas closely approximate the four contemporary phytogeographic provinces of the peninsula as defined by Shreve and Wiggins (1964; see also this paper Fig. 2b). Savage considered each of his herpetofaunal areas to be dominated by assemblages of species with a common evolutionary history. He noted that a given Recent herpetofauna is composed of ". . . a compliment of species originating from several sources. A considerable portion of the species in each unit, however, originated in or near the area now occupied by the faunal assemblages. 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 elements defined" (Savage 1960:189).

Murphy (1983a:14) challenged the assumption that particular herpetofaunas evolved in conjunction with and parallel to particular geofloras. His argument is supported by two examples that illustrate the absence of complete distributional correlation between groups of herpetofaunal species and particular contemporary vegetational associations of Madro-Tertiary vegetation in Baja California. These arguments are weak and based on a few rigid and very exacting applications of what was intended only to be a very general correlation. An exact correlation between a particular vegetational associa-

tion (e.g., the Sonoran Desert flora) and a particular herpetofauna (e.g., the Colorado Desert herpetofauna) was never assumed, intended, or implied in my understanding of Savage's model. Savage did not rule out the possible ameliorating effects of physiography or of interspecific competition, for example, in determining distribution. He used the evolving geofloras as evidence of existing paleoclimatic conditions and in so doing made the assumption only that contemporary and phylogenetic antecedent herpetofaunal assemblages occupy similar climatic regimes. This seems a valid assumption considering the taxa concerned are terrestrial ectotherms and have physiological limitations that translate directly into ecogeographic restrictions (Bartholomew 1958). This assumption also seems well supported by the fossil record. Murphy's arguments are further weakened by the fact that throughout his own paleobiogeographic scenario, he employs the same paleobotanical literature and makes the same general assumption that geofloras are evidence of paleoclimatic conditions that are indicative of certain historical herpetofaunal assemblages in a given region during a given time.

Generalized Tracks and Ecogeographic Patterns

The strength of Murphy's (1983a) presentation lies in the excellent paleobiogeographic synthesis he constructs to explain contemporary distribution patterns, and in the genetic evidence he presents to support many of his conclusions. However, I find his herpetofaunal assemblages ("tracks") to have serious shortcomings. Apparently this is a result of his misapplication of the concept of track (Croizat 1964), and the concomitant lack of distinction between contemporary distribution patterns and the diverse historical assemblages from which they derived.

It is important to clarify some terms and concepts critical to subsequent discussion. Murphy (1983a) describes six herpetofaunal areas in peninsular Baja California: Californian, Colorado Desert, Vizcaíno Desert North, Coastal Vizcaíno Desert, Peninsular Area (with three subdivisions), and the Cape Area. These herpetofaunal areas are basically broad phytogeographic units defined on the basis of major physiographic or geomorphological transformations and concomitant differences in the general botanical com-

position (based on Nelson 1921; Savage 1960; Shreve and Wiggins 1964; Bostic 1971; Loomis et al. 1974; and Murphy's own fieldwork). They are comparable in concept to ecogeographic formations (Fig. 14), but lack as fine a resolution because they each encompass a larger geographic area containing complex geomorphological formations with numerous vegetational communities. They are probably best characterized as ecogeographic provinces.

Murphy (1983a) compiles the herpetofaunal composition of these ecogeographic provinces and compares them quantitatively. From this analysis, he derives what he terms "tracks." He then states "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" (Murphy 1983a:3). The use of the term "track" in this sense is misleading and confusing. The original concept of "track" as developed and employed by Croizat (1964; see also Croizat et al. 1974; Craw 1983; Craw and Weston 1984) has two components. The first concept is that of the individual track; this concept depicts the spatial (geographical) expression of relatedness among disparate forms. The geographic distributions of all related forms of a given taxon (e.g., a species complex, members of a genus or family) from disparate geographic areas, when considered together and depicted spatially, comprise an individual track. The second concept, that of generalized or standard track (op. cit.) describes the phenomenon of congruency in space of more than one individual track. Both individual and generalized tracks are spatial expressions of evolutionary time. A generalized track, because of the spatiotemporal congruency it expresses, indicates historical homology among the individual tracks, and thus among the life forms represented. In other words, a generalized track is a spatial and temporal representation of a group of phylogenetically unrelated organisms that shared proximate space through time, or a common evolutionary history.

Murphy states (1983a:11): "I re-emphasize 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." In my understanding of

Croizat (1964), for unrelated life forms to be members of the same generalized track, they need to demonstrate distributional similarities throughout much or all of their respective ranges. In other words, one would find consistent spatial overlap among the phylogenetic lineages of each of the various member taxa of the generalized track. From the lack of this spatial overlap among represented lineages, one would have to conclude the presence of more than a single generalized track. Murphy's (1983a) use of the term "track" to describe herpetofaunal taxa that have present-day geographic overlap within Baja California, but lack such spatial congruency among their respective phylogenetic lineages elsewhere, is inconsistent with the concept of track.

The common denominator supporting Murphy's faunal groupings is consistent spatial overlap among species, geographic or ecologic, or both, only within parts of Baja California. Lacking the requisite geographic congruency among represented lineages beyond the Baja California Region, one would have to conclude that these groupings represent contemporary ecogeographic patterns, not historical patterns or tracks. They appear to be analogous with the heretofore described ecogeographic patterns of the herpetofauna of the Sierra San Pedro Mártir Region of northern Baja California (Fig. 16; Table 5; and text).

Subsequent use of the term track in this discussion should be understood in the sense used by Croizat (1964). When indicating Murphy's "tracks" quotation marks will be used to distinguish his from the generalized tracks that this investigation indicates exist among the herpetofauna of the Baja California Region. Savage's (1960) historical assemblages appear to be consistent with the temporal aspect of generalized tracks; these parallels will be indicated below. I consider his spatial designation of province consistent with the spatial aspects of generalized tracks, however, like Morafka (1977) I consider Savage's (1960) provinces to equal superprovinces. I follow Morafka (1977) in my use of province to indicate a geographical unit with uniform dominant physiography, vegetation, and fauna (see Dice 1943). My use of the term track, in the spatial sense, is synonymous with province or superprovince as indicated.

The terms track and generalized track, as used in the temporal sense and assemblage or histor-

ical assemblage, are used interchangeably and indicate historical biogeographic groupings; they represent events in evolutionary time. The term fauna is used to indicate a contemporary grouping of forms with similar ecogeographic restrictions; a province or track in the spatial sense may include one or more faunas but only a single fauna is considered the participant fauna (Morafka 1977). The terms fauna and track as used in the spatial sense represent the present, in ecological time; here considered to be subsets of the historical groupings.

Extant Faunas and Generalized Tracks

Savage (1960) did not list all of those species or species-groups he considered to have evolved together as part of a particular historical assemblage. But, using his examples of species with distributions representative of his historical assemblages, the list of extant vegetational associations occupied by Recent derivatives of his historical complexes and components, and the contemporary species composition of Savage's Herpetofaunal Areas, I assigned each contemporary species to a particular historical assemblage. The assignment of species and species-groups, though based on Savage's (1960) work, is my own interpretation and is thus subject to errors for which I alone am responsible. Murphy likewise did not list the member species for each of his nine possible "tracks," leaving the reader to decipher from his table 2 (Murphy 1983a) those species that fit the description for each of his "minor" and "major generalized tracks." He was unclear about proper assignment of some forms (e.g., on page 6, he assigns the *Sceloporus magister* complex, minus the nominal species, to his "Transpeninsular Mesophilic Track," but on page 32 he discusses this complex as part of his "Transpeninsular Xerophilic Track"). I have attempted to interpret Murphy's work and assign species in accordance with his descriptions; once again I alone am responsible for any errors.

The following hypothesis of interacting and overlapping generalized tracks comprising the contemporary herpetofauna of the Baja California Region is a working one that best integrates our current knowledge from pertinent fields. However, it is a hypothesis to be tested and changed wherever future investigations find it lacking.

The Generalized Tracks of the Baja California Herpetofauna

Savage's (1960) and Murphy's (1983a) Californian Herpetofaunal Area (Fig. 2a), consisting of the Pacific Slope of Baja California north of latitude 30°N, is the most biologically complex area of the Mártir Region, and probably of the entire peninsula. It is also one of the most poorly investigated by previous workers. Savage indicated that this area was dominated by an assemblage of species with more extensive ranges northward in coastal and montane California that shared an evolutionary history associated with derivatives of the Madro-Tertiary geoflora (the Californian Component of his Madrean Complex). In addition, he indicated that some elements of his Sonoran Desert Component of the Desert and Plains Complex occur within the Californian Area. This study indicates that elements of four contemporary faunas (High Sierran Scarps, Californian, Peninsular Range, and North American Ubiquitous Scrubland; Fig. 15, 16; Table 5), representing four different tracks (Pacific Northwest, Madrean, Peninsular Range, and North American Desert and Plains: Fig. 17, 18, 20, 21), overlap on the Pacific Slope of Baja California north of latitude 30°N.

The Californian Fauna together with the High Sierran Scarps Fauna (Table 5, I and II) match closely the species Savage indicated as endemic to and dominating the Californian Herpetofaunal Area. Several species within this area, as noted by Savage, are associated primarily with derivatives of the Arcto-Tertiary geoflora. These species, the High Sierran Scarps Fauna, are restricted to Arcto-Tertiary floral derivatives in northern Baja California and southern California. However, outside of Baja California, members of this fauna demonstrate broader ecological niches and occur in conjunction with more mesophilic derivatives of the Madro-Tertiary geoflora (see Species Accounts; Stebbins 1966, 1985). The variability in niche breadth in different parts of their range, and the presence of sympatric congeners within the Baja California Region, suggest that the geographic limits of the High Sierran Scarps Fauna result from competition. Overall distributions of these species closely match those of the Californian Fauna, suggesting that these two faunas have a very similar and perhaps parallel evolutionary history in western North

America. The relatively low Coefficient of Difference and high Similarity Coefficient and Community Coefficient values (Table 4; Fig. 15) between areas occupied by these two faunas are also indicative of a close relationship. With the exception of three species of the Californian Fauna (*Rana aurora, Bufo boreas,* and *Clemmys marmorata*) that are also associated primarily with Arcto-Tertiary geofloral derivatives, the species of the High Sierran Scarps Fauna and the Californian Fauna are considered to be contemporary members of the Madrean Track (Fig. 18; Table 5, 6; and below).

The Pacific Northwest Track

Rana aurora, Bufo boreas, and *Clemmys marmorata* are considered to be members of the Pacific Northwest Track (Fig. 17; Table 5, 6). This track is synonymous with Savage's Western American Complex of the Old Northern Element. Pacific Northwest Track members have the most tenuous toehold on the predominantly xeric Baja California peninsula. Several member species occur in scattered populations in a few canyons of extreme northwestern Baja (i.e., *Aneides lugubris* and *Ensatina eschscholtzii*). Members of this track probably dispersed into the Region following completion of the Coast Range Corridor (Peabody and Savage 1958) during the cooler and moister Pleistocene epoch. Two of these species, *Rana aurora* and *Bufo boreas,* appear to have derived from Asian forms, and as noted by Savage (1960), apparently dispersed across the Bering Land Bridge and down the west coast of North America during the Pleistocene (Savage's Holarctic Element). It is reasonable to propose that they constitute a second, more recent generalized track, one that overlaps the older Pacific Northwest Track.

The Madrean Track

The Madrean Track (Fig. 18; Table 6) is considered synonymous, in terms of process and pattern, with Savage's (1960) Madrean Complex of the Young Northern Element, but with a considerably different species composition. Savage distinguished a Californian Component and a San Lucan Component in his Madrean Complex. His San Lucan Component includes most of the species here assigned to the Peninsular Range Track (Table 6), as discussed below. Included as

contemporary elements of a San Lucan component of my Madrean Track (Table 6) are only those forms present as sibling species in the Californian and Cape regions (and on some Pacific coastal islands of Baja California) and absent from most or all of the Central and Vizcaíno deserts (e.g., *Eumeces, Hyla, Elgaria,* and *Coluber* "*lateralis* complex").

Savage (1960) considered his Madrean Complex the oldest assemblage in the Baja California Region. Such dating probably refers to those taxa that are here assigned to the Peninsular Range Track fauna (Table 6). Distribution of populations on "old" or "deep-water" islands of the Gulf of California (Soule and Sloan 1966; Murphy 1983b), and the concomitant relatively greater levels of divergence within lineages (see Species Accounts for taxonomic references), indicate that the members of the Peninsular Range Track are much older elements on the land masses of Baja California than are Madrean Track forms. Biochemical and electrophoretic analyses (Kim et al. 1976; Wyles and Gorman 1978; Murphy and Papenfuss 1979; Murphy 1983a) indicate a probable mid-Miocene divergence for several of the lineages of the Peninsular Range Track.

The Madrean Track fauna, both within and beyond the Baja California Region, appears to be a previously more widespread, vicariated (see Figure 18) assemblage of relatively mesophilic species-groups. The level of differentiation among disjunct populations of these forms within the Baja California Region appears to match Mayr's (1978) criteria for sibling species or semispecies. Divergence and endemism within lineages of Madrean Track elements beyond Baja California (in California, Arizona, New Mexico, and Mexico) are considerably greater than the level of sibling species, with most lineages having populations along the track that appear to meet the criteria of superspecies (Mayr 1978). The relatively greater differentiation within lineages of the Madrean Track beyond, compared to within Baja California, suggests a long-term historical relationship among these species-groups prior to their inhabiting Baja California, and an evolutionary history distinct from, yet probably paralleling, the lineages of the Peninsular Range Track.

Much of existing Baja California appears to have been inaccessible to southward emigration of terrestrial vertebrates (see Paleobiogeographic

History above), possibly from the mid-Miocene and probably from about the Miocene–Pliocene boundary until the Pleistocene. If so, after the mid-Miocene or the Miocene–Pliocene boundary and prior to the Pleistocene, Madrean Track elements could have reached Baja California only by being carried along on the migrating land masses, i.e., by "transgulfian vicariance" (Murphy 1975, 1983a). The complete absence of Madrean Track forms on the "old" or "deepwater" Gulf islands (Soule and Sloan 1966; Murphy 1983a, b; Murphy and Ottley 1983, 1984) discounts this possibility, although vicariance and subsequent extinction cannot be entirely ruled out. An alternative possibility is that some of these lineages were present on the proto-northern Peninsular Range land masses during the Miocene and vicariated at a later time (e.g., Miocene–Pliocene boundary) than did lineages on the Cape Islands. However, the relatively low levels of divergence between the Baja California populations of these lineages, their absence from the "old" or "deep-water" Gulf islands, and the increase in numbers of Madrean Track species present along a south to north transect in peninsular Baja California, strongly suggest a relatively recent (i.e., Pleistocene) diffusion—gradual movement across hospitable areas over long periods (Pielou 1979)—southward. The disjunct distributions (vicariance) of some Madrean Track elements along the peninsula suggests even more recent (mid-Pleistocene to Recent) fragmentation of ranges in conjunction with climatic shifts toward aridity (Axelrod 1967, 1975, 1979) or from possible periodic inundation of low-lying areas by changes in sea level, or both (Flint 1971).

At least two possible scenarios are suggested by the distributions of the Madrean Track lineages within Baja California. Firstly, the spatial relationships between the congeners of the Californian and the High Sierran Scarps Faunas (Table 5), which I propose to have resulted from competition, are consistent with a hypothesis of Pleistocene to Recent periodic diffusions by these lineages southward into Baja California. Late Pliocene or Pleistocene formation of a terrestrial connection between Baja California and southern California land masses and the concomitant orogenic uplift would have provided southward emigration routes as well as the upland retreats consistent with the contemporary distributions of these faunas. These contemporary distributions of mesophilic species, and those of more xerophilic species associated with other tracks discussed below, indicate that for at least part of this time, barriers to gene flow existed. Elements of the Madrean Track probably dispersed in successive diffusions across a partial or fluctuating barrier (San Gorgonio Barrier) during this time. Secondly, prior to this time, from mid-Miocene to Pleistocene, it is unclear what the nature of the terrestrial connection at the northern end of the extant peninsula was, or even if it existed. Some elements I have assigned to the Madrean Track have distributions that suggest they may have been present on the northern peninsular land masses at mid-Miocene, when increased tectonic activity vicariated their ranges, isolating them from ancestral stocks to the east (e.g., *Anniella geronimensis, Cnemidophorus labialis,* and *Xantusia henshawi*).

A hypothesis that incorporates both possible scenarios is preferred. Species like *Anniella geronimensis, Cnemidophorus labialis,* and *Xantusia henshawi* are not good candidates to support a Pleistocene diffusion hypothesis; their endemism, narrow niches, and low vagility are all indicative of species that are evolutionarily relatively conservative, with their present ranges probably contracting rather than expanding. They appear to be the remains of an ancestral fauna, a proto-Madrean Track fauna that may have vicariated in the Miocene. If this were indeed the case, these species could arguably be evidence of another, earlier, generalized track, possibly the result of the same geomorphological events that shaped the Peninsular Range track further south as discussed below. On the other hand, their sympatric congeners and the other species of the Madrean Track, probably made their appearance in the northern peninsula (and beyond), subsequent to Pleistocene climatic changes, sea level shifts, and related phenomena that promoted an ingress across the San Gorgonio Barrier. Under the cool moist conditions of Pleistocene glacial maxima, the more hydrophilic High Sierran Scarps Fauna could have undergone diffusion southward. The presence of *Lampropeltis zonata* and *Batrachoseps pacificus* on Todos Santos Island off the Pacific coast of Baja California supports the contention that cool, moist conditions were more widespread in northern Baja California in the past. With glacial retreat and the long-term drying and warming trend culminating in

the late Pleistocene to Recent (Axelrod 1967, 1975, 1979), conditions became increasingly favorable for the westward and southward dispersal of the warm-mesophilic Californian Fauna. Concomitant with these southward advances of the Californian Fauna, the High Sierran Scarps Fauna was increasingly restricted and relegated to habitats at higher, cooler elevations. With the advancing aridity, even the Californian Fauna became restricted; ranges became fragmented and populations in arid areas relegated to protect microhabitat, such as their present-day riparian corridor distributions at lower elevations in the Mártir Region (Table 5; Fig. 16). This scenario of diffusing and fragmenting faunas is consistent with the current evidence of geologic and climatic conditions during Pleistocene and Recent times. It is also consistent with and supportive of the thesis that sympatry within monophyletic lineages is evidence of dispersal (Croizat et al. 1974; Platnick and Nelson 1978).

Four interrelated criteria were used to distinguish species of the Madrean Track from those of the Peninsular Range Track (discussed below). (1) Madrean Track species and species groups, for the most part, exhibit extensive ranges beyond the Baja California Region. Members of the Peninsular Range Track have their greatest, and in many cases their total, distribution within the Baja California Region. (2) In the Baja California Region, Madrean Track forms have comparatively less differentiation within monophyletic lineages compared to lineages of the Peninsular Range Track, on both peninsular and insular land masses. (3) Madrean Track forms are present only on some of the land-bridged islands (Soule and Sloan 1966; Murphy and Ottley 1983, 1984) of the Gulf of California and on some of the Pacific coastal islands of Baja California and California. They are absent from all of the "old" or "deep-water" islands (Soule and Sloan 1966; Murphy and Ottley 1983, 1984) of the Gulf, which are inhabited by numerous endemic forms of the Peninsular Range Track lineages and some elements of the North American Desert and Plains Track (discussed below). (4) As a general trend, Madrean Track forms appear to have their closest relationships within monophyletic lineages with forms occurring in California, Arizona, New Mexico, and the northwest central uplands of Mexico (e.g., *Rana boylii* [Zweifel 1955], *Lampropeltis zonata* [Tanner

1953], *Batrachoseps* [Wake 1966b], *Xantusia* [Bezy 1972; Bezy and Sites 1987]). Peninsular Range Track elements are most closely related to forms occurring in lowland areas from central Mexico southward (e.g., *Ctenosaura hemilopha* [Bailey 1928; Smith 1972], *Eridiphas* [Duellman 1958; Leviton and Tanner 1960; Cadle 1984; Dowling and Jenner 1987], *Phyllodactylus* [Dixon 1964, 1969; Murphy and Papenfuss 1979], *Cnemidophorus hyperythrus* and *C. ceralbensis* [Lowe et al. 1970; Robinson 1973], *Phrynosoma coronatum* [Presh 1969], *Sator* [Wyles and Gorman 1978], *Nerodia* [Conant 1969], and *Bipes* [Kim et al. 1976; Papenfuss 1982]).

Peninsular Range Track

The third contemporary fauna with elements in Savage's Californian Herpetofaunal Area of the Mártir Region is the Peninsular Range Fauna (Table 5, IV). Some of these taxa occur also in the Colorado Desert Herpetofaunal Area (Fig. 2a) and southward, throughout the length of the peninsula. The Peninsular Range Fauna is part of the larger Peninsular Range Track (Table 6; Fig. 20) comprised primarily of forms endemic to the Baja California Region and associated with warm–temperate and subtropical floral elements. Many forms of the Peninsular Range Track occur only south of the Mártir Region in the Central and Vizcaíno deserts, in the Cape Region, or on islands in the Gulf of California (see Murphy 1983a; Murphy and Ottley 1983, 1984).

These peninsular and insular endemics are the oldest lineages present in the Baja California Region, dating from mid-Miocene (Murphy 1983a). Savage (1960) indicated the members of this fauna were part of two of his southward dispersing waves: a Sonoran Component of his Desert and Plains Complex, and a Madrean Complex. However, the present distributions of these species and species-groups are more consistent with a theory of origin in Baja California based on vicariance, each distribution appearing—at least in part—to result from the migration and fragmentation of peninsular and insular land masses from coastal Mexico. Murphy (1975) proposed such a theory of vicariated origin to account for several of these lineages found in the Cape Region and on some associated islands; his "trans-gulfian migration" hypothesis. Welsh (1976a, b, 1981)

proposed a similar hypothesis to account for the distributions of most of the Sonoran Desert-associated lineages of Baja California (see list at beginning of Discussion), that are considered to have a shared evolutionary history with the more clearly vicariated subtropical Cape Island endemics of the Peninsular Range Track. Murphy (1983a) included these Sonoran Desert-associated lineages and added several more mesophilic lineages in his revised "trans-gulfian vicariance" model.

Murphy (1983a) included the mesophilic lineages *Batrachoseps, Hyla* (=*H. regilla* progenitor), *Eumeces,* and *Elgaria* in his "trans-gulfian vicariance" model. Exception is taken to the addition of these lineages, all of which are herein considered to be part of the Madrean Track. In adding these mesophilic genera, Murphy (1983a) assumed that the Cape Region or Cape Islands supported both Neotropical and Madro-Tertiary geofloral elements during the mid-Miocene when the area became separated from coastal Mexico: "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 resulting from altitudinal effects" (Murphy 1983a:16). Murphy was making the same kind of assumption (inferring presence of historically associated herpetofauna from presence of geoflora) that he criticized Savage for making. Despite his apparent contradiction, and "willingness" to join Savage and myself in making this kind of assumption, I think in this particular case, the assumption is invalid as I shall discuss below.

Axelrod (1979:28) indicated the presence of both Neotropical geofloral elements (dry tropic forest and arid tropic scrub) and Madro-Tertiary geofloral elements (oak–pinyon woodland) along coastal western Mexico during the Miocene. However, he stated that ". . . woodland presumably reached southward down a line of volcanos, linking the flora of the Cape Region with that of Sonora-Sinaloa-Nayarit-Jalisco, which probably lived above scattered dry-tropic forest and thorn forest" (1979:29). Whereas it seems possible that volcanism could have provided the requisite upland habitat in some parts of coastal western Mexico as Axelrod indicated, the Cape Islands land masses are areas of granitic batholith, not volcanic rock (Mina 1957; Gastil et al. 1975).

Furthermore, there is no evidence that this area had been uplifted to sufficient height by mid-Miocene to create the cooler climatic regime requisite for the Madro-Tertiary geoflora.

Even in the event that such vegetational elements existed at the right time and in the right place on the geomorphic progenitors of the Cape Islands, these vegetation communities would have been present on upland areas as islands of habitat surrounded by great expanses of Neotropical floral elements (Axelrod 1979:28). As such, (a) these "islands" would have been far removed from the northwest central highland and central plateau areas of Mexico considered to be the centers of differentiation and evolution of the Madro-Tertiary geoflora (Axelrod 1975, 1979), and (b) they would also most probably be highly depauperate. Therefore, it seems highly unlikely that these "islands" could contain and support the mesophilic elements of the ancestral herpetofauna that are thought to have evolved in association with the then-developing Madro-Tertiary vegetation.

The possibility that *Batrachoseps, Hyla, Eumeces,* and *Elgaria* vicariated on the Cape Islands in upland habitats during mid-Miocene cannot be entirely discounted. However, it seems highly improbable and less likely than the more parsimonious explanation that these genera are elements of the Madrean Track (Fig. 18), whose origins in the Cape Region are probably, as Savage (1960) suggested, the result of late Pliocene or Pleistocene diffusions down an existing peninsula.

The fossil herpetofaunal evidence that exists from the Cape Region (Miller 1977) dates from the late Pliocene and includes *Boa, Geochelone,* and *Crocodylus,* etc., indicating decidedly tropical conditions at least in the vicinity of this lowland site.

The noninsular forms of the Peninsular Range Track show three general patterns of distribution in the Baja California Region: (1) restricted endemic lineages — those lineages found only in one or more of the four southern ecogeographic provinces (Murphy 1983a) of the peninsula or on associated "deep-water" islands (Soule and Sloan 1966; Murphy 1983b), or both; generally south of latitude 28°N through the Cape Region (e.g., *Bipes biporus, Chrysemys scripta, Ctenosaura hemilopha, Sator* complex, *Nerodia vallida,* and *Eridiphas slevini*); (2) endemic lineages (note:

some of these lineages have member-species that when considered separately, fit the description in (1) above—those lineages that range throughout most or all of the Peninsular Ranges but not north of the San Gorgonio Barrier (e.g., *Cnemidophorus hyperythrus, Crotaphytus insularis, Petrosaurus* complex, *Phyllodactylus* complex, *Sceloporus magister* complex—those members with 2n = 30 chromosomes, *Sceloporus orcutti* complex, *Elaphe rosaliae, Crotalus enyo,* and *C. ruber*); (3) radiated lineages—those lineages that have expanded beyond the Peninsular Ranges into habitats of the Mojave and Sonoran deserts and north and east (*Callisaurus draconoides, Coleonyx switaki, Dipsosaurus dorsalis, Phrynosoma coronatum, Sauromalus* complex, *Chilomeniscus* complex, *Crotalus mitchellii, Lichanura trivirgata,* and *Phyllorhynchus decurtatus*).

Murphy (1983*a*) outlined a plausible paleobiogeographic scenario to account for the distributional permutations and divergence within lineages among the Peninsular Range Track fauna. Lineages with member elements distributed in accordance with each of the above described geographic patterns consist of sibling species along the peninsula, with one or two forms in the Cape Region and another form or forms to the north across the Isthmus of La Paz (e.g., *Petrosaurus, Urosaurus, Sceloporus orcutti* complex, *S. magister* complex, *Phyllodactylus* complex, and *Chilomeniscus* complex). Murphy attributed this species-pairs phenomenon to a temporary or fluctuating terrestrial corridor between the Cape Islands (Region) and areas to the north, probably during the late Miocene or early Pliocene (see his "Transpeninsular Xerophilic Track"). It would appear that more than a single vicariating event, or intermittent gene flow between more than two areas is involved here, based on the presence of more than two distinct forms among several of these lineages on the southern peninsula. Murphy (1983*a, b*) gives detailed accountings of the numerous unique patterns among insular distributions of the lineages of the Peninsular Range Track, and also for those insular-occurring forms I have assigned to the North American Desert and Plains Track (see Table 6 and below).

Assuming the validity of the hypothesis that species of the Peninsular Range Track predate— in Baja California—those species of the Madrean Track, then future electrophoretic or immuno-logical distance data should indicate a trend of greater genetic distance between Peninsular Range Track members and their southwest Mexican siblings, than that which would be found between the Madrean Track forms and their siblings beyond the Baja California Region (with the exception of some of the possible proto-Madrean Track forms like *Cnemidophorus labialis* and *Xantusia henshawi*). Good (1988) presented allozyme data for the genus *Elgaria* that indicate a closer relationship between *E. paucicarinata* of the Cape Region and *E. panamintina* of southeastern California, than between *E. paucicarinata* and *E. kingi* of western Mexico. Following Savage's (1960) scheme of historical herpetofaunas of North America, the lineages of the Peninsular Range Track would be called the Peninsular Range Complex of the Young Northern Herpetofauna.

The Colorado Desert Track

Peninsular members of the Colorado Desert Track (Fig. 19; Table 6) are found only in the Colorado Desert Herpetofaunal Area (Fig. 2a). The Colorado Desert was formed during the Pleistocene; it resulted from the continued elevation of the northern Peninsular Ranges, which forced the Gulf of California to recede (Atwater and Molner 1973), and the accumulation of alluvial deposits from the Colorado River filling in the head of the Gulf (Norris 1958). Species of the Colorado Desert Track have the most restricted distributions of the xerophilic herpetofauna of the Baja California Region; monophyletic lineages demonstrate the lowest levels of interpopulational morphological differentiation.

The limited distributions and minimal intralineal differentiation (see Adest 1977), together with their endemism, suggest a Pleistocene to Recent isolation and in situ evolution for these forms. The presence of congeners of several of these species among the Peninsular Range Track fauna (Table 6), suggests that competition may limit the spread of these species further south into other desert habitats of Baja California.

This is an incipient track and hence does not demonstrate the characteristics of spatial and temporal fragmentation among forms associated with older tracks (except see the distribution of the genus *Uma*; Stebbins 1985). The Colorado Desert Track becomes apparent when one ex-

amines the pattern of distributions of sibling forms in the Chihuahuan, Sonoran, and Peninsular deserts. In fact, these four desert areas, each considered here as a generalized track with its own participant fauna, can also be viewed as subsets of the more extensive and older North American Desert and Plains Track (see below).

Morafka (1977:187) hypothesized a faunal assemblage associated with the Colorado Desert he called the California Gulf Arch Assemblage. He considered this assemblage of 10 reptiles (*Dipsosaurus dorsalis, Sauromalus obesus, Callisaurus draconoides, Lichanura trivirgata, Chilomeniscus cinctus, Chionactis occipitalis, Phyllorhynchus decurtatus, Crotalus cerastes, Crotalus mitchellii,* and *Gopherus agassizii*) to be a secondary, more northerly centered ecological unit of the Sonoran Herpetofauna, a fauna centered to the south in Sonora and Sinaloa, Mexico. I agree that the fauna of the Colorado Desert show strong affinities with the Sonoran Herpetofauna, but I do not consider it a subset thereof. Despite the distributional similarities apparent among these forms, track analysis indicates his is a synthetic assemblage. It appears to me that his California Gulf Arch Assemblage is comprised of Peninsular Range and Sonoran herpetofaunal elements that have radiated into amenable habitats not otherwise occupied in each of the other areas, plus Colorado Desert Track forms that have evolved in situ; in both cases as a result of post-Pleistocene geomorphological and climatic changes favoring expansion of extreme desert habitats.

Adest (1987) analyzed allozyme data for *Callisaurus draconoides* from populations in the Cape Region of Baja California throughout much of the range including Nevada, and down the west coast of Mexico to the vicinity of Mazatlán. His results indicated low genetic diversity throughout the range, with some minor differences in populations near Mazatlán and on Isla Ceralvo in the Gulf of California. His data were inconclusive to resolve the question of a Pleistocene isolation in either a Sonoran or a Cape Region refugium (Savage 1960) or a California Gulf Arch refugium (Morafka 1977). However, he concluded that his data did not support a model of a Pleistocene Cape Region refuge for the species. Unfortunately he did not include samples from the population on Isla Angel de La Guarda, a deep-water island isolated from central peninsular Baja California 1 MYBP (Murphy 1983*b*).

Significant differences between this population and those tested by Adest (1987) would add credence to a hypothesis of a mid-latitude peninsular or insular refuge for *Callisaurus draconoides.*

Following Savage's historical groupings, the species of the Colorado Desert Track might be called the Colorado Desert Component of the Desert and Plains Complex.

The riparian herpetofauna of the Colorado River delta region (*Bufo alvarius, Bufo cognatus, Bufo woodhousei, Urosaurus ornatus, Thamnophis marcianus,* and *Trionyx spiniferus*) were not included in my ecogeographic analysis because none of them range south into the Mártir Region. With the exceptions of *Bufo alvarius* and *Urosaurus ornatus,* which have distributions characteristic of Sonoran Track forms, these species appear to be post-Pleistocene to Recent radiations from the east. *Trionyx spiniferus* and *Bufo woodhousei* appear to be elements of a western radiation of the Austriparian Herpetofauna (Savage 1960) centered in the southeastern U.S. *Thamnophis marcianus* appears to be a member of the Chihuahuan Track that has crossed the Cochise Filter Barrier (Morafka 1977), and *Bufo cognatus* appears to be a member of the North American Desert and Plains Track.

The North American Desert and Plains Track

The North American Desert and Plains Track (Fig. 21) overlaps four less extensive herpetofaunal tracks: the Peninsular Range Track, the Colorado Desert Track, the Sonoran Desert Track (encompassing parts of northern Sinaloa, Sonora, and southern Arizona), and the Chihuahuan Desert Track (including much of Mexico's central plateau—see Morafka 1977). Each of these tracks has an endemic herpetofauna, however these tracks also share many species and species-groups. As here employed, the term North American Desert and Plains Track encompasses the combined areas and fauna common to the Peninsular Range Deserts, Colorado Desert, Sonoran Desert, and Chihuahuan Desert generalized tracks, and extends into the high deserts and plains of the southwest, west, and central North America. This concept of an older (relative to the true desert tracks listed above), more comprehensive arid regions track is consistent with Morafka's (1977) concept of a Miocene–Pliocene "Moha-

via" Biota, and the Desert and Plains super-province of Savage (1960).

The fauna of the North American Desert and Plains Track occurs within all of both Savage's and Murphy's herpetofaunal areas of Baja California. Elements of this ubiquitous fauna appear to have populated the Baja California Region by two distinct means:

(1) The majority of these lineages (Table 6, North American Desert and Plains Track, group A) apparently accompanied the progenitors of the lineages of the Peninsular Range Track, having vicariated on prepeninsular and insular land masses as they were separated from coastal Mexico in the mid-Miocene. These species and species-groups are widely distributed on the "old" or "deep-water" islands of the Baja California Region and they all demonstrate relatively high degrees of morphological differentiation within monophyletic lineages on the peninsula and associated islands (Soule and Sloan 1966; Savage 1967; Ballinger and Tinkle 1972; Case 1975; Murphy 1983*a*, *b*; Murphy and Ottley 1983, 1984).

(2) Other elements (Table 6, North American Desert and Plains Track, group B) dispersed southward along the peninsula after Pleistocene to Recent climatic changes, which promoted corridors of xeric habitats at the northern end of the Peninsular Ranges, allowing for diffusion southward. Evidence for this diffusion hypothesis are the relatively low levels of morphological differentiation among all peninsular and insular populations of each lineage, and their exclusive occurrence on land-bridged islands of the Gulf of California and on some apparently recently isolated land-bridged islands of the Pacific side of the peninsula (Soule and Sloan 1966; Savage 1967; Ballinger and Tinkle 1972; Case 1975; Murphy 1983*b*; Murphy and Ottley 1983, 1984). These recently invading ubiquitous xeric forms could be considered as a distinct, overlapping generalized track analogous to the situation with the earlier Old Northern Element and the more recent, overlapping Holarctic Element on the Pacific Northwest Track. These more recent lineages might be considered a Holxeric Element of the Desert and Plains Track.

The hypothesis for the evolution of the North American Desert and Plains Fauna, proposed by Savage (1960), incorporates three distinct centers of evolution of xerophilic herpetofauna of North America. Dispersal and genetic introgression between these areas since the late Pleistocene and possibly during glacial minima has resulted in the present, relatively continuous distribution of much of this fauna. The endemic xerophilic herpetofaunas of the Peninsular Range Track, the Sonoran Desert Track, and the Chihuahuan Desert Track appear to be comprised of those forms with a competitive disadvantage in xeric habitats, such as restricted niches, or lower vagility, or both.

Summary

Theories of the historical biogeography of the the herpetofauna of the Baja California Region have developed in conjunction with the growing geofloral literature and the development of a new paradigm in geology, that of plate tectonics. Past syntheses by Schmidt (1922), Savage (1960), and Murphy (1983*a*) reflect this evolution of ideas. Five primary historical patterns or generalized tracks are proposed to describe the interaction of historical faunal assemblages that produced contemporary distributional patterns: the Pacific Northwest Track, the Madrean Track, the Peninsular Range Track, the Colorado Desert Track, and the North American Desert and Plains Track. Vicariance of peninsular land masses from western Mexico as a result of Miocene–Pliocene tectonic activity is the most significant process shaping extant patterns. In situ evolution during the Pliocene, Pleistocene, and Recent epochs, as well as radiations northward from these southern vicariated areas, and biotic dispersal—both diffusion and secular migration (Pielou 1979)—from proximate regions to the north and east played major secondary roles influencing present distributional patterns.

Resumen

Conduje un análisis ecogeográfico de la herpetofauna de la región de San Pedro Mártir en Baja California Norte, México. Se analizaron más de 3,000 archivos municipales conseguidos de la literatura, los museos, y investigaciones en el campo, por medio de una matriz de formaciones ecogeográficas basadas en los climas regionales, la fisiografía, y la vegetación existente. Métodos numericos y intuitivos de análisis biográfico indican que las 65 especies que se encuentran ocurren en siete distintos modelos de distribución.

Se analizan estos modelos contemporáneos en un contexto geográfico más ámplio para encontrar indicaciones de sus orígenes históricos.

Se han desarrollado las teorías de la biogeografía histórica de la herpetofauna de la región de Baja California en junto con la creciente literatura geofloral y el desarrollo de un nuevo paradigmo de la geología—el de "plate tectonics." Síntesis anteriores por Schmidt (1922), Savage (1960), y Murphy (1983a) reflejan esta evolución de ideas. Se propone cinco patrones históricos, o "generalized tracks" (Croizat 1964) para describir la interacción de "faunal assemblages" históricos que producen los modelos de distribución comtemporáneos: el "Pacific Northwest Track," el "Madrean Track," el "Peninsular Range Track," el "Colorado Desert Track," y el "North American Desert and Plains Track." La "vicariance" (Croizat et al. 1974) de tierras peninsulares del oeste de México como resultado de actividad tectónica es al proceso más significante en el porceso de la formación de los modelos que existen hoy dia. Evolución en situ durante las épocas Pliocena, Pleistocena, y Reciente, además de radiaciones hacia el norte de estas areas "vicariated" del sur, y "biotic dispersal" (diffusion and secular migration—Pielou 1979) de las regíones vecinas del norte y el este tomaron importantes papeles secundarios que influyeron los modelos de distribución que esisten ahora.

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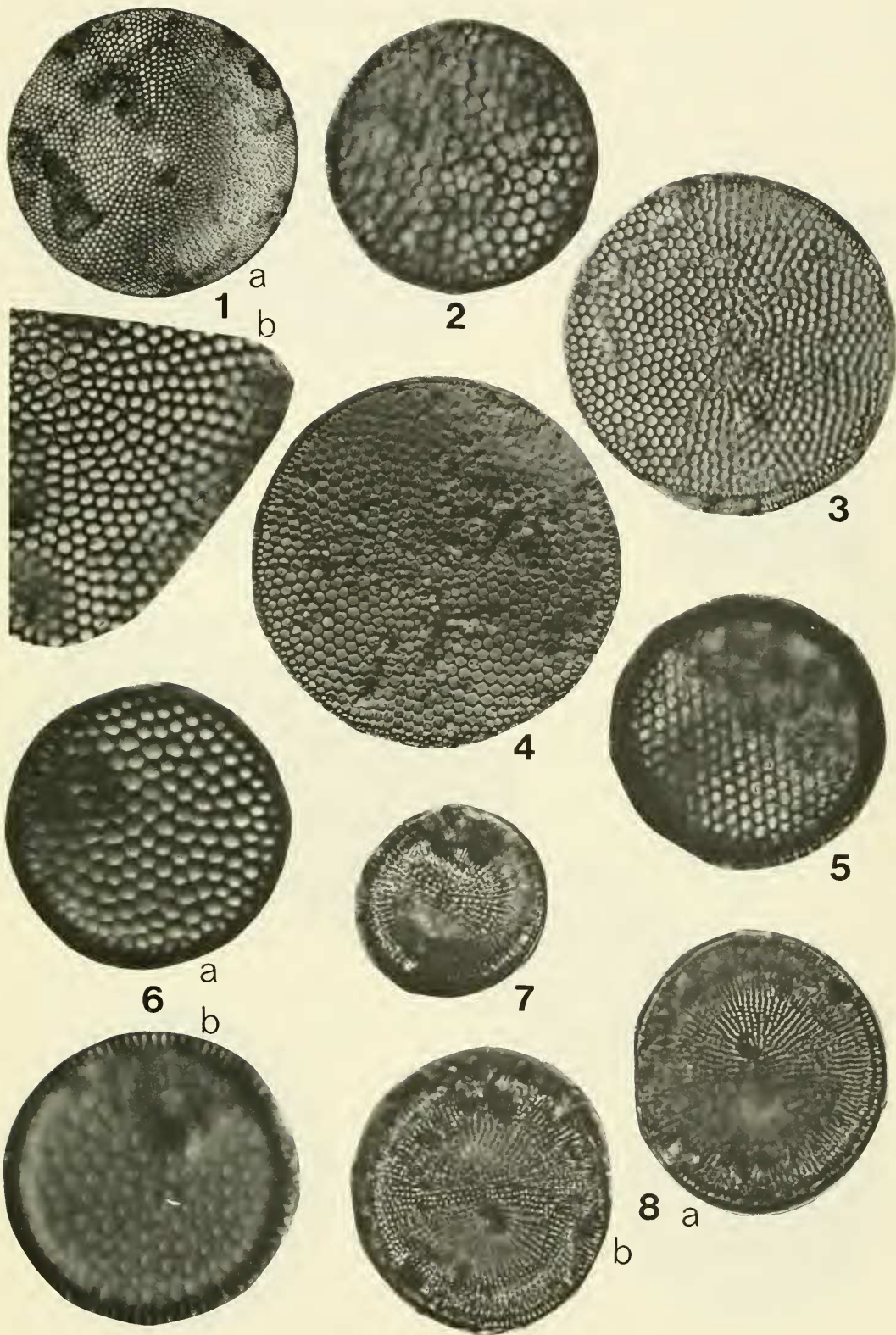
PEABODY, F. E. AND J. M. SAVAGE. 1958. Evolution of the

1 a
1 b
2
3
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6 a
6 b
7
8 a
8 b

Plate 7

FIGURE:
1. *Thalassiosira lacustris* (Grunow) Hasle; D = 60 μm; a: focus up, b: focus down, c–f: margin showing tubular processes.
2. *Thalassiosira lacustris* (Grunow) Hasle; D = 29 μm.
3. *Coscinodiscus nitidus* Gregow; D = 25 μm.
4. *Cyclotella pygmaea* Pantocsek; D = 13 μm.
5. *Cyclotella striata* (Kutzing) Grunow; D = 32 μm.
6. *Cyclotella striata* (Kutzing) Grunow; D = 20 μm.
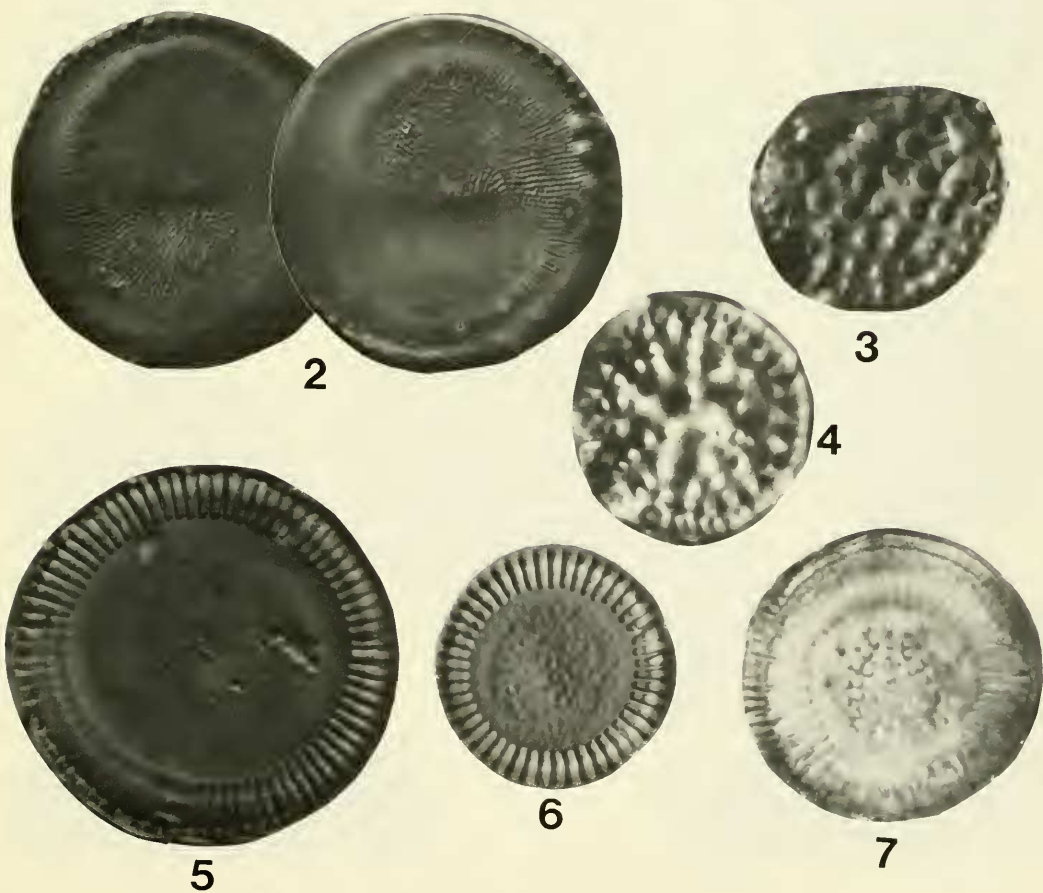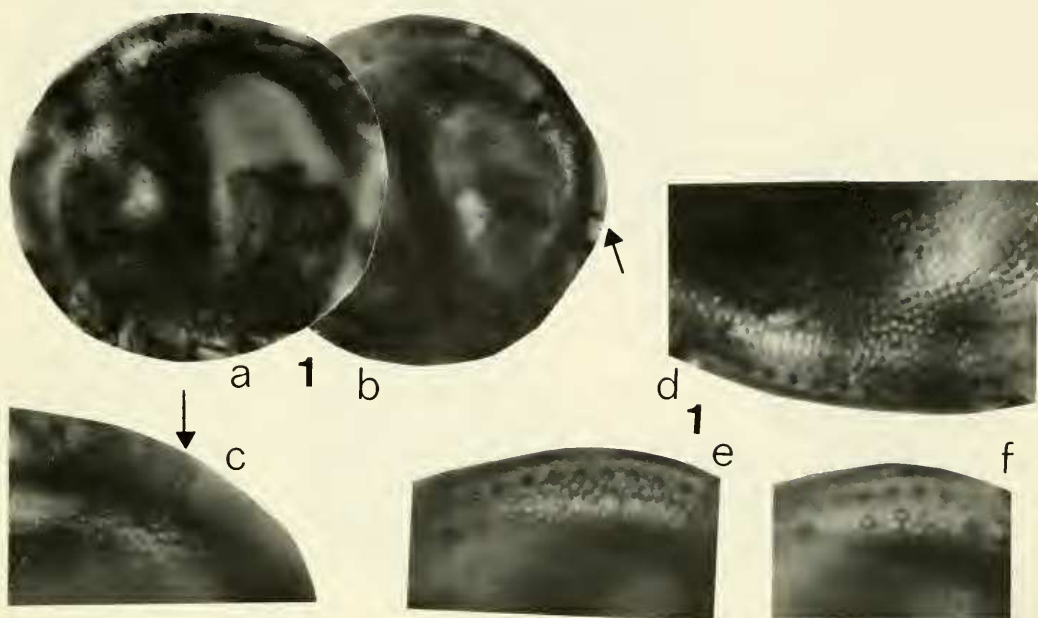7. *Cyclotella comta* (Ehrenberg) Kutzing; D = 30 μm.

Plate 8

Figure:
1. *Actinocyclus normanii* (Gregory) Hustedt; D = 46 μm.
2. *Actinocyclus normanii* (Gregory) Hustedt; D = 43 μm.
3. *Actinocyclus normanii* (Gregory) Hustedt; D = 49 μm.
4. *Actinocyclus normanii* f. *subsalsa* (Juhlin.-Dannt.) Hustedt; D = 23 μm.
5. *Actinocyclus normanii* f. *subsalsa* (Juhlin.-Dannt.) Hustedt; D = 27 μm.
6. *Actinocyclus normanii* f. *subsalsa* (Juhlin.-Dannt.) Hustedt; D = 18 μm.
7. *Actinocyclus normanii* (Gregory) Hustedt; D = 45 μm.
8. *Actinocyclus normanii* f. *subsalsa* (Juhlin.-Dannt.) Hustedt; D = 17 μm.
9. *Actinocyclus normanii* (Gregory) Hustedt; D = 32 μm.
10. *Actinocyclus normanii* f. *subsalsa* (Juhlin.-Dannt.) Hustedt; D = 22 μm; arrow shows pseudonodule.
11. *Actinocyclus normanii* (Gregory) Hustedt; D = 44 μm.
12. *Actinocyclus normanii* (Gregory) Hustedt; D = 48 μm; a, b: focus down, shows pseudonodule(s)?; b: marginal focus, enlargement; c: entire valve, focus down; d: focus up; e: focus down, marginal focus, shows striate margin.