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On the Biogeography of the Herpetofauna at Saguaro National Monument

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ABSTRACT

The known monument herpetofauna of 57 species is briefly addressed. Explanatory biogeography is discussed for desertscrub taxa at lower elevations, and woodland and forest taxa at higher elevations on the monument and beyond. Specific aspects of desert ecosystem structure underlying the presence/absence of potential Sonoran Desert lizard and snake congeners are discussed. Within this biogeographic framework lies the explanation for the situation at Saguaro National Monument where the most xeric-adapted taxon in a given species pair is the one that is missing from the monument herpetofauna. Species in the rattlesnake genus *Crotalus* illustrate especially well biogeographic aspects of the south-north Madrean Archipelago and the east-west Madrean Line in southeastern Arizona and adjacent New Mexico. The Madrean Line divides in two the mountain island Madrean Archipelago between the Sierra Madre Occidental (south) and the Rocky Mountains (north). This Southwest biogeographic line is as sharp as the world's most famous one, Wallace's Line, which divides the Malay Island Archipelago in two.

INTRODUCTION

The space allotted is, of course, insufficient to discuss the entire herpetofauna at Saguaro National Monument (SNM). Hence, my focus will be on fascinating biogeographic stories in which parts of the herpetofauna of the monument participate. A brief summary of the amphibian and reptilian taxa that occur on the monument is followed by a look at two biogeographic patterns involving (1) the herpetofauna of the lower elevations, which lives wholly or predominantly in desertscrub and desert-grassland communities, and (2) the herpetofauna of the upper elevations, which lives wholly or predominantly in woodland and forest communities.

THE HERPETOFAUNA

Four worldwide groups of vertebrates are represented in the monument herpetofauna, the anurans (frogs and toads), the turtles, and the lizards and

snakes (Table 1). Ecological and distributional information for these species is provided in Lowe (1964a), Black (1982), Lowe and Holm (1986, 1991), Lowe et al. (1986), and Stebbins (1985). Only one reptilian species, the blacktailed rattlesnake (*Crotalus molossus*), is found throughout the 6,600 ft (1.25 vertical mi) elevational range of the monument.

In the discussion that follows for the lower monument, desertscrub species-pairs of iguanid lizards and colubrid snakes are examined as present-or-absent congeners in the herpetofauna. A biogeographic explanation is given for the distribution pattern that is observed.

Six rattlesnake species occur in the herpetofauna at SNM, most of which are not high mountain species (Table 2). As noted, only one of the six, the blacktailed rattlesnake, occurs throughout the elevational range of both districts of the monument. One

of them, the sidewinder (*Crotalus cerastes*), occurs only in the desert Tucson Mountain District (TMD), which is the western unit of the monument.

One of the six, the Arizona black rattlesnake (*Crotalus viridis cerberus*), is found only in the forested Rincon Mountain District (RMD), where it reaches its southernmost distribution on the continent. As discussed below, this rattlesnake is of particular importance in one of several interesting and scientifically important Southwest biogeographical patterns that involve the herpetofauna and other vertebrate groups at the monument.

Three other species of rattlesnakes ("Mexican mountain rattlesnakes") that occur in other nearby mountain ranges in southeastern Arizona do not occur in the Catalina-Rincon Mountains and thus are not included in the monument herpetofauna (see detail maps in Lowe et al. 1986). A discussion for the upper elevation forest and woodland taxa centers on the biogeography of the forest and woodland rattlesnakes in southeastern Arizona and adjacent Mexico. The Rincon Mountain fauna, which includes the Arizona black rattlesnake, participates in this Southwest biogeographic story that involves present-and-absent congeners.

THE LOWER ELEVATIONS: SONORAN DESERTSCRUB AND DESERT-GRASSLAND

Recent discussions of natural habitats may be found in Niering and Lowe (1984), Bowers and McLaughlin (1987), and Lowe and Holm (1991). The Sonoran Desert communities are primarily creosotebush (*Larrea*) desertscrub, paloverde-saguaro (*Cercidium-Carnegiea*) desertscrub, and their ecotones that predominate on site from 2,020 ft upward to ecotones with desert-grassland at 3,700 ft and above.

The desert-grassland (or semidesert grassland) communities are climax mixtures of native perennial grasses, native dry-tropic shrubs and stem-succulents,

mesquite (*Prosopis*) and other often disclimax weedy perennials that prevail on widely altered native dry-tropic grasslands between 3,700 and ca 5,000 ft. At and above ca 4,500 ft, savanna-like ecotones are formed with oaks of the evergreen woodland above.

Desert Ecosystem Structure

When one travels through the deserts of the world and looks at them comparatively, it becomes apparent that deserts are comprised of three underlying features: (1) rockpiles, (2) bajadas¹, and (3) valley bottom fill (Fig. 1). The three components are contiguous and more or less subtly continuous subsystems of a collective ecosystem unit.

Superimposed on these three primary landscape features is (4) a pattern of drainage lines produced primarily by water, and (5) sandpiles that are produced primarily by wind. These five principal features are, of course, not peculiar just to deserts. They are simply more naked, if not more obvious, and thus perhaps more quickly if not more accurately assessed in the world's deserts and grasslands.

The Substratum

Both inside and outside of desert ecosystems, the nature of the natural substratum or "substrate" (bark, rock, sod, et al.) is one of a half-dozen critical controls that determines the presence or absence of a given reptilian or amphibian species on a particular site. In deserts especially, the soil texture (rock, gravel, sand, silt, clay, et al.) is one of the most important characteristics of the substratum for a large and diverse array of amphibians and reptiles.

Resulting primarily from weathering and the erosional forces of water and gravity, there is a downward gradient in soil particle size distribution that extends across the entire ecosystem unit. That is, from the rock parent material above, downward across the bajada slope to the finer textured soils of the flatter valley bottom fill below (Fig. 2). Accordingly, many of the severest desert conditions are

¹The bajada is the flanking detrital skirt that surrounds the rockpile (mountain, rocky butte, etc.) of its source; the familiar alluvial fan is a portion of a bajada. Earlier in the upland erosional cycle, bajadas are steeper and, partly as coalesced fans, are composed of relatively deep alluvial soil as in Figs. 2 and 3 representing the study area in basin and range topography. Later in the erosional cycle, bajadas are less steep and may exhibit relatively shallow soil across outward sloping bedrock from the base of the rockpile. The latter bedrock surface, with essentially no soil nor vegetation, is also called a pediment, which term (meaning sloping surface) is borrowed from classical Greek architecture, where the triangular space forming the gable of a roof is the pediment. Bajada evolution—from the fanform bajada to the pediform bajada—in the erosional cycle in aridlands is illustrated in *Putnam's Geology* (Birkeland and Larson 1978) and elsewhere.

reached for both plants and animals on the fine textured soils between desert ranges, where the least plant-available soil moisture is due to finer soil particle size. Thus it is not unexpected that some of the most highly specialized adaptations for desert living, such as extremes in sand swimming and drought resistance, are associated with fine textured soils located in the valley fill component of desert ecosystems.

It may be only somewhat less expected, when the observer comes upon desert specialists that are adapted for rock-dwelling. Indeed, in deserts some of the most extreme desert specialists live at one or the other of two most extreme substratum types on the gradient—rockpiles and sandpiles—at opposite ends of the substratum particle size distribution. Such extreme specialists are few in number and spectacular in adaptation. Among their representatives in the Sonoran Desert are the chuckwalla (*Sauromalus obesus*) specialized for life on and in desert rockpiles, and the fringe-toed lizard (*Uma notata*) specialized for life on and in shifting sandpiles.

Most reptilian and amphibian desert taxa, however, are centered adaptively at varying ecological positions away from these extreme substratum conditions of continually moving sand, and solidly positioned pilerock. Therefore, not surprisingly, we find that most of the amphibian and reptilian desert taxa of the world are adapted to relatively less extreme substrata that usually characterize the bajada-valley fill gradient.

Sonoran Desert Biogeography in Arizona

A simple diagrammatic profile of SNM as shown in Figure 3, illustrates that the monument area contains a truncated desert ecosystem lacking one of the three principal ecological subsystems. The missing subsystem is valley bottom fill, which supports desertscrub biotic communities dominated by creosotebush-white bursage (*Ambrosia dumosa*) and their few associates on primarily flatland fine-textured soils (Figs. 1 and 2). An examination of species-pairs that are present-or-absent congeners, shows that the Sonoran Desert reptilian taxa absent ("missing") from SNM are those species and genera requiring desert microenvironments peculiar to the missing subsystem.

All of these taxa absent from SNM are present, for example, in the herpetofauna at Organ Pipe Cactus

National Monument (ORPI), which area contains desert ecosystem units with all principal ecological subsystems represented (Figs. 1 and 2). Organ Pipe Cactus National Monument is at a lower base elevation in southwestern Arizona and SNM is at a higher base elevation in southeastern Arizona. In the cases where paired-species combinations are examined in herpetofaunal comparisons for the two monuments (Table 3), the result is as predicted: the most xeric-adapted species of the species pair is the one that is missing from the herpetofauna at SNM.

The taxa absent from SNM occur in flatland communities dominated by creosotebush-white bursage at ORPI, more or less throughout Shreve's (1951) Lower Colorado Valley subdivision of the Sonoran Desert that extends eastward into the Avra Valley and to within a short distance of SNM (Fig. 3). Thus, in fact, all the listed desert elements of the herpetofauna absent from SNM reach to the western doorstep of, but do not enter, the monument.

Saguaro National Monument could have included a representative portion of the historically and biologically significant Avra Valley within its boundaries with relative ease 50-60 years ago, perhaps even 30-40 years ago. The then essentially pristine and little known area of Avra Valley that lies directly below the western boundary fence of SNM has since become variously occupied, and is now largely destroyed. Saguaro National Monument was established by presidential proclamation in 1933 and the TMD portion was added in 1961.

One would think that since President Hoover in 1933 proclaimed all of the forested Rincon Mountains (to Rincon Peak at 8,482 ft) to be included in SNM, which he did amid little protest, surely he could have proclaimed a small part of the huge and nearly unoccupied Avra Valley to be included, if not some part of the Santa Cruz Valley. A President in the 1940s or 1950s could have still accomplished the task for the National Park Service (NPS), certainly for a part of the Avra Valley area. But such thinking today is with the clarity of hindsight in a much more knowledgeable world. The problem in the early 1930s was ecological. Ecology was then a young and little-known science, and a fully coherent concept of the *ecosystem* much less the *Sonoran Desert*, was not at hand. The problem later in the 1960s was political; it was too late.

THE UPPER ELEVATIONS: FOREST AND WOODLAND

The Southwest evergreen woodlands in the Rincon Mountains are oak (encinal) and pine-oak woodlands. At the lower woodland limits of 4,000-4,500 ft according to slope exposure, the encinal is an evergreen oak woodland of Emory oak (*Quercus emoryi*), Mexican blue oak (*Q. oblongifolia*), and Arizona oak (*Q. arizonica*) with the occasional presence of juniper and pinyon representation in the woodland. With gradual increase in elevation into the pine-oak woodland above, Chihuahua pine (*Pinus leiophylla*) joins with Mexican pinyon (*P. discolor*), alligator-bark juniper (*Juniperus deppeana*), and several evergreen oaks—principally silverleaf oak (*Q. hypoleucoides*), Arizona oak, Emory oak—and others. Mexican pine-oak woodland above 7,000 ft gradually merges with the montane conifer forest above.

The montane conifer forest is a mixed conifer forest with primarily pine and fir dominance varying according to slope exposure and elevation from approximately 7,000 ft to the top near 8,600 ft. Ponderosa pine (*P. ponderosa*) is the principal forest conifer, providing a pine forest with Gambel oak (*Q. gambeli*), madroño (*Arbutus arizonica*) and others. This forest usually becomes a mixed conifer community at increasing elevations, with presence of Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and white pine (*Pinus strobiformis*). These three coniferous trees reach their greatest stature and density on north-facing slopes above 7,800 ft.

Mountain Islands

In the four-corners area of Arizona-Sonora-Chihuahua-New Mexico, as elsewhere throughout much of the Southwest, the mountain island character of conifer-clad and other high wooded mountains is unmistakable (Fig. 4). Because of significant differences in base level to well over a thousand feet on different sides of a mountain in the Southwest, different biotic communities may contribute to the surroundings of the mountain at base level. Grassland is the single most prevalent formation at mountain base level in this four-corners area, as shown in Figure 4.

Dating from early in this century these mountain islands have been called "desert mountains," "desert mountain islands," "mountain islands in desert seas," etc. But for these conifer-clad "sky islands" (Heald

1951), such desert names "are inappropriate because they are not surrounded by desert" (Lowe 1964a), as Shreve (1915) first pointed out years ago. *The bases of these mountain islands are either primarily grassland, or these ranges are completely surrounded by grassland, not desert scrub* (Shreve 1915, 1919; Nichol 1937; Marshall 1957; Lowe 1964b; Martin and Mehringer 1965; Brown and Lowe 1977, 1980); see Gehlbach 1981 and Davis 1991 for the contrary view.

The grassland versus desert distinction again noted, is of basic importance to species dispersal and the explanatory biogeography of the mountain island archipelago. These lowlands have been involved, from full glaciation to the present time, in a series of community replacements from forests to woodlands to grasslands, and, locally, to desert scrub. The current grassland connectors (grassland seas) between the mountain islands in the archipelago have been *in situ* approximately 9,000 years (Van Devender 1990a,b and elsewhere).

Mexican Mountain Biogeography in the Borderlands

As in the case for certain desert species pairs that are present or absent in the herpetofauna at SNM, an interesting biogeographic story is associated with certain high mountain species that are present-or-absent congeners in the monument's forested Rincon Mountains. This is the story of the high Sierra Madrean fauna and flora that barely enters the United States, where it variously adjoins southernmost elements of the Rocky Mountain fauna and flora. The rattlesnake genus *Crotalus* is exemplary in this story of Madrean ("Mexican Mountain") biogeography in Arizona.

The Arizona black rattlesnake reaches its southernmost distributional limit on the continent in the Rincon Mountains of SNM, just short of the Arizona-Sonora boundary line. The current late Holocene distribution of rattlesnake species on high mountain islands in southeastern Arizona, and in adjacent southwestern New Mexico in the Sierra San Luis, Animas Mountains, et al. is illustrated in Figure 5. It is a biogeographic pattern that is repeated in many other taxa.

The rattlesnake genus *Crotalus* provides a glimpse into vicariance biogeography in an island archipelago. The pattern involves a distinctive south-north

mountain island deployment of principal groups of taxa (Fig. 5). One group is "southern" in origin with its ecological metropolis in the Sierra Madre Occidental of northwestern Mexico (Madrean); the other is "northern" in origin in the Rocky Mountains of the southwestern United States (Petran).

Two of the most interesting early findings for the herpetofauna and avifauna are indicated in Figures 4 and 5. One of these findings is the occurrence of a sharp biogeographic boundary line that divides in two the montane island archipelago—the Madrean Archipelago—lying between the Sierra Madre Occidental proper and the Colorado Plateau proper. The geographic position of this Madrean Line that divides the archipelago in two is approximated by the present location of Interstate Highway 10 (I-10) in southeastern Arizona and adjacent southwestern New Mexico (Fig. 4). This Southwest biogeographic boundary line—the Madrean Line—is as sharp as the world's most famous one, Wallace's Line, which divides the Malay Island Archipelago in two (Wallace 1859, 1863). Wallace's Line is unarguably the boundary line of greatest interest and prominence in biogeography.

The other especially interesting finding illustrated in Figures 4 and 5 is for the Sierra Pinaleño (Graham Mountains), the highest mountain range involved in the system. The Pinaleños provide an enigmatic situation that parallels that of the enigmatic Celebes (now Sulawesi) in the Malesian theater of Wallace's Line. The Pinaleño enigma, as illustrated here by rattlesnakes in the genus *Crotalus* (Fig. 5), results from the anomalous presence of Madrean (southern) taxa north of the boundary line ("I-10") on what is presumably a mountain island outlier of the Rocky Mountain (northern) massif.

We conclude for the Pinaleños, as Wallace (1876) did for the Celebes, that the Pinaleños were not earlier united by extensive lands (highlands) to either the northern or the southern massif. Rather, as indicated best by the packrat midden data (Van Devender 1990a,b), faunal connections with dispersal under secular climatic change, came through woodland and forest communities across what are currently grasslands in the archipelago lowlands (Fig. 4). Thus, what is clear beyond reasonable doubt is that during the last dozen-odd glacial and interglacial faunal and floral dispersions, the Pinaleños have witnessed the

comings and goings—during the last dozen-odd glacial and interglacial faunal and floral dispersions—of Madrean taxa and Rocky Mountain taxa during the cyclical waxing and waning of their northern and southern distributional limits.

Thus, certainly the anomalous Pinaleños in the Southwest, like the anomalous Celebes for Wallace and those who followed in Malesia, speak clearly to the theory first proposed by Wallace (1876 and elsewhere) that present regional biogeography reflects events of the past—the geological floral and faunal history of the area.

These findings for the Madrean-Rocky Mountain montane archipelago system were made in the 1950s and 1960s by field zoologists at the University of Arizona engaged in detailing the ecological and geographical distributions of the Sierra Madrean and Rocky Mountain vertebrate faunas in southern Arizona and adjacent Mexico. We conducted a part of this field work in the Rincon Mountains of SNM. The first and most thorough field-based investigation of Madrean-Petran montane island distributional patterns is Marshall's (1957) *Birds of the Pine-Oak Woodland*. The most recent examination is by Davis (1991), who is studying the Madrean-Petran montane sedentary mammal fauna, inclusive of those in Saguaro National Monument (Davis et al., in press).

What about the plants? One of the striking similarities of the Southwest Madrean-Petran case to the classical one in Malesia is the nonconformity of many plant distributions to those of the animals. Many plant taxa including major dominants do not adhere nicely to the faunal boundary lines in either area, while some do fit the pattern. For the Malesian case, see contributors in Whitmore 1981, 1987; for the Southwest case see Shreve 1915; Marshall 1957; Lowe 1961; Whittaker and Niering 1964; Bowers and McLaughlin 1987.

For the Santa Catalina-Rincon Mountains and other ranges *north* of the Madrean-Petran boundary (Fig. 4), the *southern* representation of plant taxa is relatively weak in terms of the abundance (population densities) of major community dominants. This is true however strong may be the Madrean percentage of the total taxa in the flora (Shreve 1915 to Bowers and McLaughlin 1987). Major Madrean plant dominants and others dwindle in population densities northward of the Madrean Line reaching

extinction at or before the Mogollon Rim, which is a major boundary in the archipelago. The northward population diminution of Madrean plant taxa to extinction is controlled primarily by deficient winter heat—as in the case of their northward truncated physiognomy—in annual concert with progressively-northward deficient summer precipitation.

Between the Pacific and Atlantic coasts are five major south-north biotic corridors that extend in latitude across and beyond the Mexico-United States borderlands. The Madrean Archipelago lies within one of these corridors. The plant and animal populations in all of these south-north corridors obviously respond individually and differentially to the environmental constraints that determine taxon distributional limits. It is beyond reasonable doubt for the subtropical and tropical taxa, that winter-deficient heat northward, and summer deficient rainfall northward, provide major direct and indirect constraints on population distribution and population dispersal across the several degrees of latitude within each of the five corridors (Fig. 6). This conclusion was confirmed long ago by relevant data from many observers stationed in southern Arizona, beginning with Forrest Shreve (e.g., 1911) and John Thornber (e.g., 1911).

The Wilderness Act of 1964 defined wilderness as *an area of land untrammeled by man, with opportunity for solitude, containing ecological, geological, educational, scenic, and historical values*. In closing these brief remarks on investigations into what G. G. Simpson (1964) called “explanatory biogeography,” it should be underscored that our field investigations have included studies at SNM, which fortunately protects within its boundaries several presently untrammeled Sonoran Desert biotic communities. And, because of the mission of the NPS, the monument protects what will be the last untrammeled montane forest island—the Rincon Mountains—in all of the Madrean-Rocky Mountain island archipelago.

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Table 1. The amphibians and reptiles at Saguaro National Monument. From Lowe and Holm (1986, 1991).

Phylum Chordata

Subphylum Vertebrata

Class Amphibia (8 species in 4 genera)

Order Anura—Frogs and Toads (8)

Family Bufonidae—Toads (3)

Family Hylidae—Treefrogs (1)

Family Pelobatidae—Spadefoot Toads (2)

Family Ranidae—Frogs (2)

Class Reptilia (49 species in 35 genera)

Order Testudines—Turtles (3)

Family Emydidae—Pond and Box Turtles (1)

Family Kinosternidae—Mud and Musk Turtles (1)

Family Testudinidae—Tortoises (1)

Order Squamata (46)

Suborder Sauria—Lizards (19)

Family Helodermatidae—Beaded Lizards (1)

Family Gekkonidae—Geckos (1)

Family Iguanidae—Iguanids (12)

Family Scincidae—Skinks (1)

Family Teiidae—Whiptails and Allies (3)

Family Anguidae—Alligator Lizards and Allies (1)

Suborder Serpentes—Snakes (27)

Family Leptotyphlopidae—Blindsnakes (1)

Family Colubridae—Colubrids (19)

Family Elapidae—Coralsnakes and Allies (1)

Family Viperidae—Vipers and Pit-Vipers (6)

Table 2. The six rattlesnake species at Saguaro National Monument.

<i>Crotalus cerastes</i>	Sidewinder
<i>C. atrox</i>	Western Diamondback Rattlesnake
<i>C. tigris</i>	Rattlesnake
<i>C. scutulatus</i>	Mohave Rattlesnake
<i>C. molossus</i>	Blacktailed Rattlesnake
<i>C. viridis cerberus</i>	Arizona Black Rattlesnake

Table 3. Species-pairs in the Sonoran Desert that are present-or-absent congeners in the herpetofauna at Saguaro National Monument (SNM). The four congeners absent within the boundaries of SNM are present a short distance off site, on the nearly-adjointing Avra Valley bottom fill to the west of the monument boundary fence in the Tucson Mountain District (Fig. 3).

Organ Pipe Cactus National Monument		Saguaro National Monument
<i>Phrynosoma solare</i>	Regal Horned Lizard	<i>Phrynosoma solare</i>
<i>Phrynosoma platyrhinos</i>	Desert Horned Lizard	Absent
<i>Urosaurus ornatus</i>	Tree Lizard	<i>Urosaurus ornatus</i>
<i>Urosaurus graciosus</i>	Longtailed Brush Lizard	Absent
<i>Phyllorhynchus browni</i>	Saddled Leafnosed Snake	<i>Phyllorhynchus browni</i>
<i>Phyllorhynchus decurtatus</i>	Spotted Leafnosed Snake	Absent
<i>Chilomeniscus cinctus</i>	Banded Burrowing Snake	<i>Chilomeniscus cinctus</i>
<i>Chionactis occipitalis</i>	Western Shovel-nosed Snake	Absent

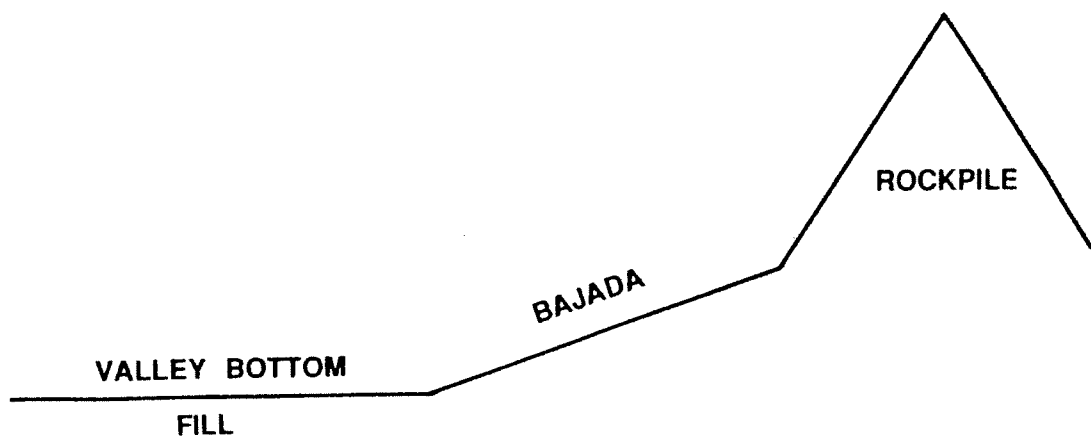


Fig. 1. Three major underlying features of desert landscape structure—the rockpile, its bajada, and the valley bottom fill, of a desert ecosystem.

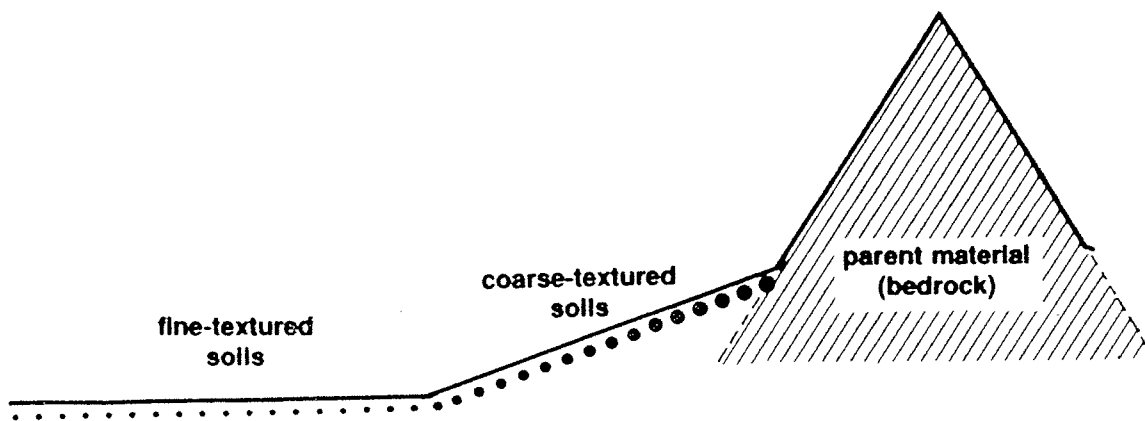


Fig. 2. Predominating soil textures are indicated in their relative positions (coarse to fine, not to scale) on the gradient of soil particle size distribution in the three subsystems of a desert ecosystem unit.

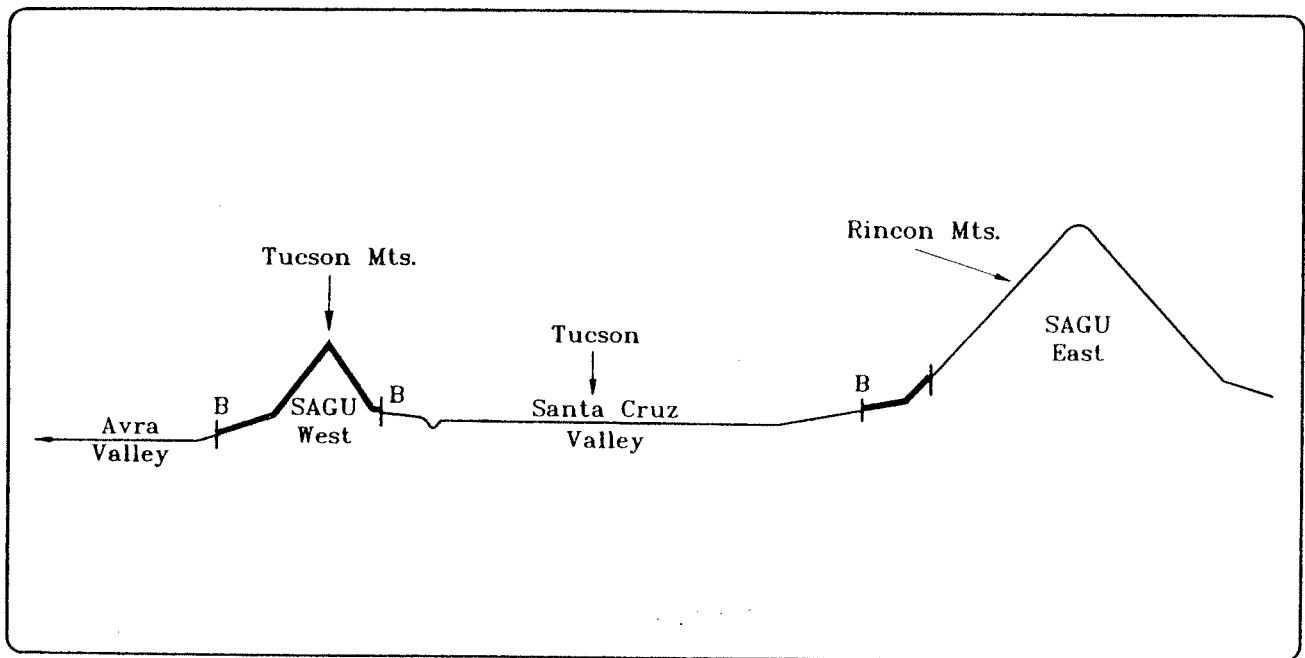


Fig. 3. Saguaro National Monument and environs in diagrammatic profile, not to scale. Sonoran Desert areas *within the monument* are indicated by bolder lines between hash marks. A complete three-part desert ecosystem unit does not occur within the boundaries of Saguaro National Monument. The monument includes bajada (B) and rockpile (RP) subsystems, while falling shy of the basin subsystem of fine-textured valley bottom fill (VF). Accordingly, members of several paired-taxa congeners in the Sonoran Desert herpetofauna do not occur on the monument (see Table 3).

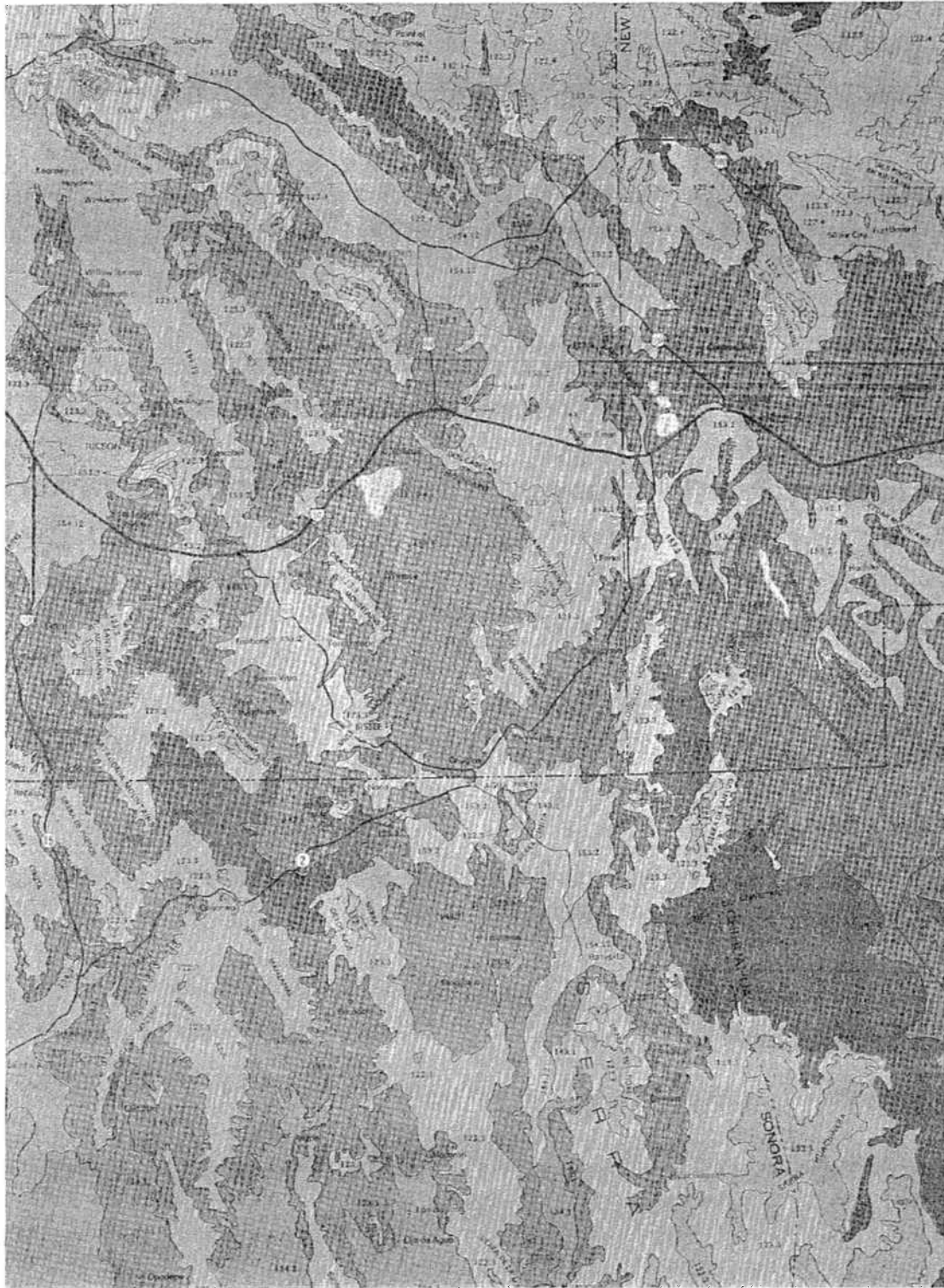


Fig. 4. Part of the vegetation map at scale 1:1,000,000 representing biotic communities in the North American Southwest (Brown and Lowe 1980). Mountain islands are shown in the Madrean-Rocky Mountain archipelago (or Madrean Archipelago) both north and south of the Madrean Line, a major Southwest biogeographic line with which today's Interstate Route 10 (I-10) coincides; this is the Southwest equivalent of Wallace's Line.

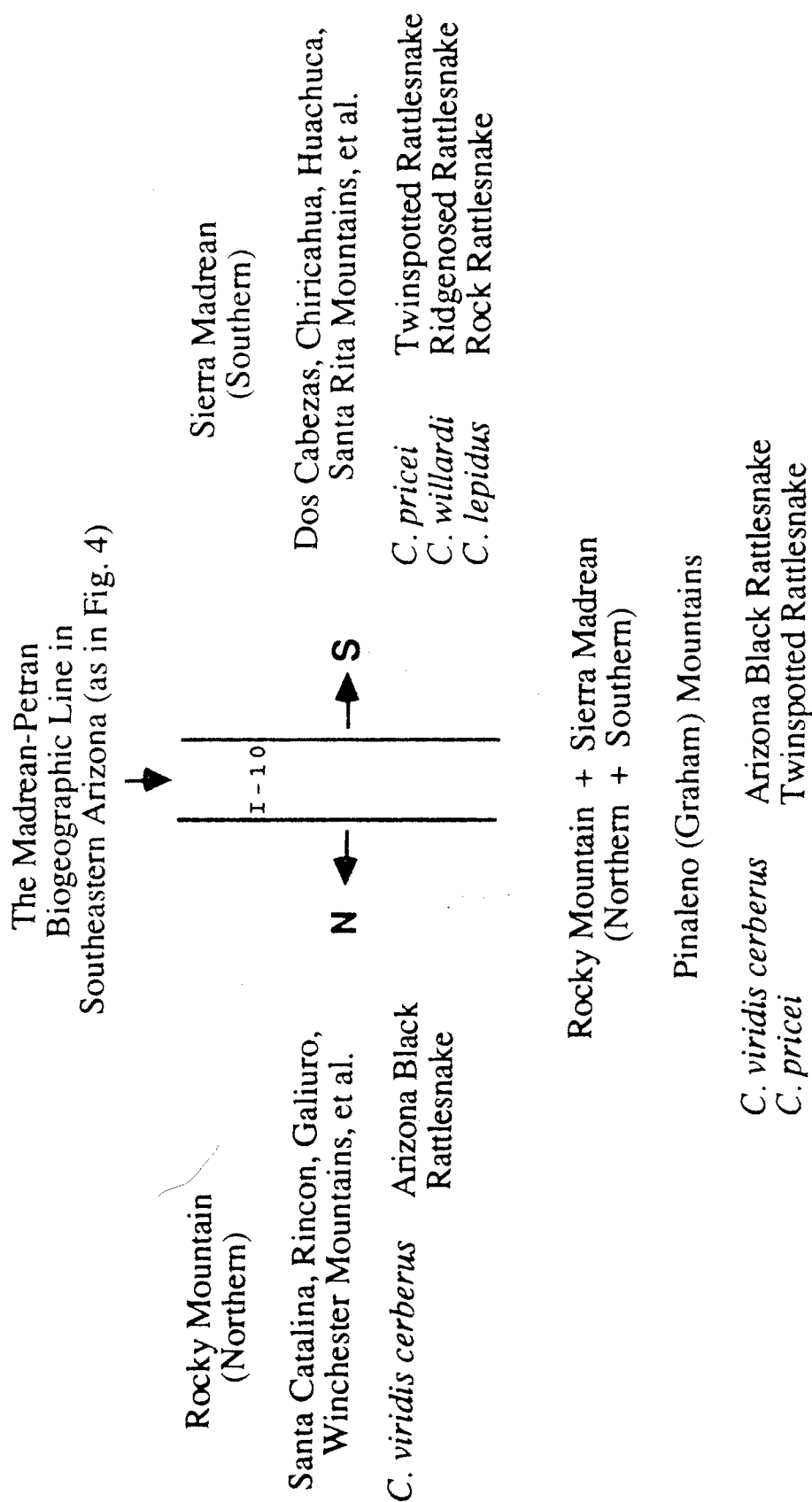


Fig. 5. The distribution of four species of mountain rattlesnakes (genus *Crotalus*) in southeastern Arizona. A fifth species, the blacktailed rattlesnake (*C. molossus*), occurs both north and south of the line. The enigmatic Pinalenos lie north of it (see Fig. 4).

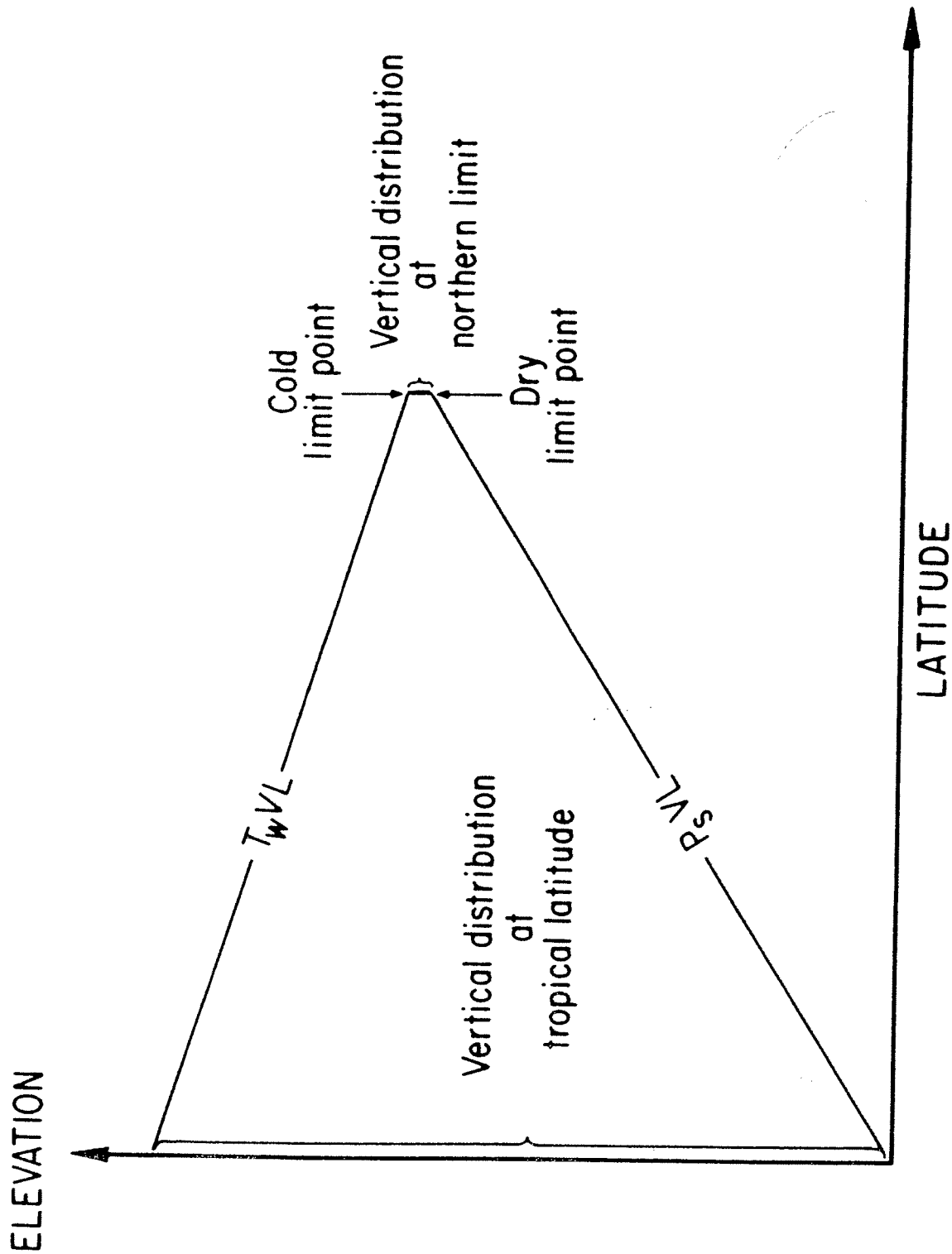


Fig. 6. Conceptual model of the pattern of northward limiting winter-deficient heat and summer-deficient rainfall—the climatic constraints that gradually restrict (to extinction) the northward distribution of tropical and subtropical taxa along the Madrean Archipelago, as within the other four S→N distributional corridors out of northern Mexico (see text).