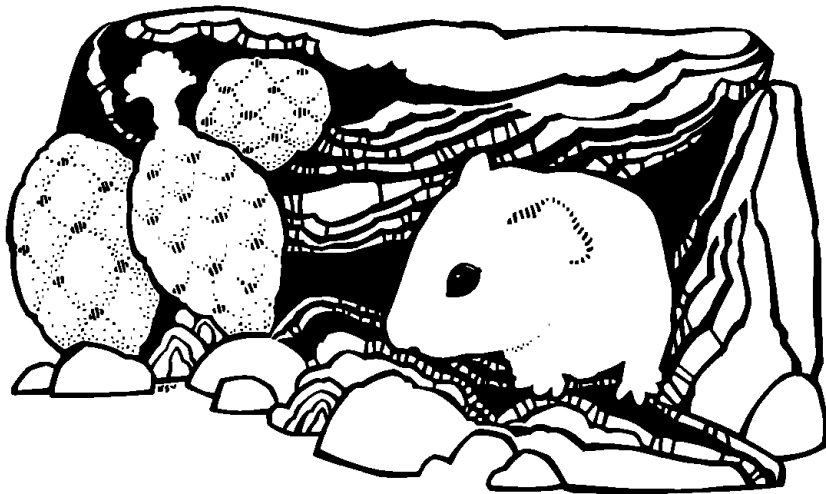


CHAPTER 3:

The Biota: The dependent variable

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Testing the primary hypothesis ideally calls for two regions that possess identical physical environments and a phylogenetically unrelated biota. In the previous chapter the similarities and differences of the physical environment were explored. In this chapter we discuss the extent to which the second premise in the research design is met. First we specify criteria by which the phylogenetic similarity of the biota can be assessed and establish the geographical units to be compared. Then we perform an assessment of phylogenetic similarity. Finally we consider how the history of the biota and the actual period of occupancy of the study sites might have influenced the amount of convergence that has occurred or could be expected to occur.

CRITERIA FOR DETERMINING PHYLOGENETIC SIMILARITY

The best available criterion for assessing the phylogenetic similarity of two biotas is their taxonomic affinity, i.e., number of species, genera, and families common to the two biotas. The taxonomic system is not strictly phylogenetic since it is based largely on the phenotypic resemblance of extant species (Davis and Heywood, 1963; Henning, 1966) but taxonomists weigh more heavily those phenotypic traits that their experience has led them to believe are conservative, that is, those characters that do not provide immediate adaptation. For example, greater taxonomic weight is given to plant reproductive characters which appear to be conservative, than to vegetative characters which are clearly rapidly modified by natural selection. Therefore, since taxonomists try to erect a classification that reflects communality of descent rather than adaptation to similar functions, their classifications are very well suited for our particular purpose.

There are problems in using number of common taxa of different categories as a criterion of phylogenetic similarity. One is that the degree of affinity of taxa of the same rank is not necessarily the same. Thus two genera might be common to both Argentina and the southwestern United States but be represented in one case by two very closely related species and in the other by two distantly related species. A comparison of only the number of common genera will not detect that difference. Another problem is that in certain groups taxa are narrowly defined while in other groups they are defined very broadly; hence what in one family is considered a single genus, in another might be subdivided into several genera. There is no way of resolving these problems, other than by an analysis of each case.

Because taxonomists cannot always detect convergences, use of taxonomic affinity as a criterion of phylogenetic similarity probably errs in the direction of indicating a larger phylogenetic similarity than that which actually exists. The same is true if too inclusive a criterion is used in defining taxa, although too narrow a criterion will give an underestimate. Since erring by overestimating the effect of phylogeny works against the hypothesis of

convergence, most of the biases in the taxonomic system are conservative and need not concern us.

GEOGRAPHICAL SCALE OF THE MOST MEANINGFUL COMPARISON

The relevant space scales for floral and faunal comparisons need to be considered carefully. Three main possibilities exist: (a) to compare the biota of the primary sites; (b) to compare the biota of the general vicinity of the primary and secondary sites; or (c) to make a comparison of the biota of the entire biogeographical regions of the study sites, i.e., the Monte in Argentina and the Sonoran Desert in the United States and Mexico. The best geographical scale depends both on the group of organisms being considered and on the particular type of studies that were undertaken with them. In the case of the flora a comparison restricted to the primary site offers too narrow a frame of reference. Since the detailed plant-ecological studies were done primarily in the area of the Bolsón de Pipanaco in Argentina, and at different places in the area of the Silver Bell and Tucson Mountains, the Avra Valley and the Saguaro National Monument (East and West) in Arizona, a comparison of the floras of these two areas will give the best indication of the extent to which the requirement of phylogenetically unrelated biota has been met.

The same argument applies to the invertebrate fauna, but not to the vertebrate fauna. In the latter case some of our studies were directed at a comparison of species characteristics and community structures of animals ranging over larger areas of the Monte and the Sonoran Desert. Furthermore, because the number of species is fewer, and the mean ranges are larger, a comparison restricted to the Avra Valley area and the Bolsón de Pipanaco would tend to underestimate phylogenetic similarity, an error we wish to avoid. The vertebrate fauna of the entire northern Monte is therefore compared with that of the northern Sonoran Desert.

PHYLOGENETIC SIMILARITY OF THE BIOTAS

In documenting the extent to which the flora and fauna of the South American study sites are related at the family and infrafamily level to the flora and fauna of the North American sites, we shall restrict ourselves to those groups of organisms that were studied as part of the comparative investigation. They are: Tracheophytes among the plants; arachnids and selected groups of insects (Orthoptera, ants, and bees) among the invertebrates; and all groups of vertebrates except fishes.

Plants*

Engler (1876) and Bray (1898) were the first scientists to point out that the semidesert regions of Argentina shared species with the semidesert regions of northern Mexico and the United States, a disjunction of over 5,000 miles. The origin of these disjunctions has been debated repeatedly since that time (I. M. Johnston, 1940; Axelrod, 1941, 1948; Campbell, 1943; Raven, 1963; Solbrig, 1972, 1973). Since we need only to assess the affinities of these two floras we need not be concerned with the controversy over their origin.

From our own collections** the size of the floras of the Bolsón de Pipanaco and the Avra Valley region appears to be very similar. However, the areas over which we collected are not comparable, the Argentine area being considerably larger. At each site approximately 250 species belonging to 115 genera and 50 families were collected. Of this total there are 14 species (5.6 percent), 51 genera (44.3 percent) and 29 families (58 percent) in common between the two areas. On a purely numerical basis, therefore, the two floras show little similarity at the specific level, but a great deal of similarity at the supraspecific level (Appendix A).

Of the fourteen species in common (Appendix B) six are common widespread weeds: *Aristida adscensionis*, *Eragrostis cilianensis*, *Erodium cicutarium*, *Tribulus terrestris*, *Solanum eleagnifolium*, and *Nicotiana glauca*. The first four are of European origin; the last two come from South America. Of the remaining eight species, five are annual and three are perennial. *Chloris virgata* is common in the lower bajada and along washes at both sites. This species is common in temperate and tropical America, from the United States to Argentina. *Bouteloua aristoides* and *B. barbata* are both very common grasses in *Larrea* flats at both the North and South American sites. *Sporobolus pyramidatus* is a common perennial widespread in tropical America. *Boerhavia coccinea*, a short-lived perennial herb, is widespread in the New World. *Allionia incarnata*, an annual or short-lived herbaceous perennial, widespread at both sites, is found in the southwestern United States and Mexico, and from Venezuela to Chile and Argentina in South America. *Verbesina encelioides*, an annual herb, has a disjunct distribution between North and Central America (southern United States, Mexico, and West Indies) and South America (Bolivia, Paraguay, northern Chile, Argentina, and Uruguay). The final disjunction is a pair of very closely related species, *Larrea tridentata-Larrea divaricata*, the most common, abundant and characteristic species in the Sonoran Desert and over large areas of the Monte. *Larrea divaricata* in the Bolsón de Pipanaco is largely restricted to washes and more humid areas. *Larrea divaricata* is also found in four small pockets

*By O. T. Solbrig and B. B. Simpson.

**Made by C. H. Lowe and J. Cross in Silver Bell and P. Cantino and F. Vervoorst in the Bolsón de Pipanaco.

in Perú and Bolivia. *Larrea tridentata* is abundant throughout the Sonoran, Chihuahuan, and Mohave deserts. *Larrea tridentata* is almost identical to *L. divaricata* in its morphology, but hybrids are only partially fertile (Hunziker et al., in press). In the Bolsón de Pipanaco, *L. divaricata* is a common species and the related *L. cuneifolia* dominates the vegetation.

At the supraspecific level, all genera common to the two sites also extend into intervening areas of tropical America. Most are represented at both sites by distantly related species, but there are at least two cases of pairs of closely related tree species. One is the genus *Prosopis*, where the Arizona species, *P. velutina*, is closely related to three of the four species found in the Bolsón de Pipanaco, *P. nigra*, *P. chilensis*, and *P. flexuosa*, especially the last. The other is the genus *Cercidium*, represented in the Silver Bell area by *C. microphyllum* and *C. floridum*, and in Argentina by the similar *C. praecox*. Most of the genera shared between the two areas that have no common species are represented by either herbaceous perennials (11) or shrubs or tress (15). Three genera (*Jatropha*, *Cereus*, and *Opuntia*) are perennial succulents or semisucculents, while only four of the genera are annual taxa (Figures 3-1 and 3-2).

Although the number of species in both sample areas is similar, their distribution among life forms is not. The Silver Bell area has a much greater proportion of annual species (50 percent) than the Andalgalá region (34 percent). The latter has more herbaceous perennials, shrubs, trees, and succulents than the Arizona region. At both sites there are three species of root perennials, a species of hemiparasitic shrub, and a true root parasite (Figures 3-3 and 3-4). The washes and the mountain slopes of Catamarca and Arizona have more genera in common than the desert flats.

The flora of the Monte is closely allied with that of the present-day Chaco. Sarmiento (1972) in a detailed study showed that forty-two out of fifty-eight characteristic genera of the Monte were shared with the dry Chaco and western Chaco woodlands. Vervoorst (1972) showed that species growing along washes and in the moister upper Bajadas were almost entirely Chaco species (Table 3-1) and that along the drier, lower bajadas and *Larrea* flats more characteristic Monte species are found. More than 60 percent of the Monte species and more than 80 percent of the genera are also found in the Chaco. There are, however, important Monte species that range well beyond the limits of the Chaco or the Monte.

The Sonoran Desert flora is derived from the Madro-Tertiary Geoflora which evolved in northern Mexico and the southwestern United States during the Tertiary (Axelrod, 1950, 1958). Thus the Sonoran Desert flora shares elements with other floras derived from the Madro-Tertiary such as the floras of the Mohave and Chihuahuan deserts, the Great Basin flora and the chaparral of California.

In summary then, the flora of the Bolsón de Pipanaco in Catamarca has only six native species, out of more than 250, in common with the area of Silver Bell in Arizona. On the other hand, over 40 percent of the genera and



FIGURE 3-1. *Dyckia velazcana* (Bromeliaceae), a succulent common on rocky slopes in the Bolsón de Pipanaco. The genus does occur in the Sonoran Desert in Arizona, but is found on rocky slopes at higher elevations. (Photo by O. T. Solbrig.)



FIGURE 3-2. *Jatropha macrocarpa* (Euphorbiaceae), an Argentine semisucculent. The leaves are not yet fully expanded. (Photo by O. T. Solbrig.)

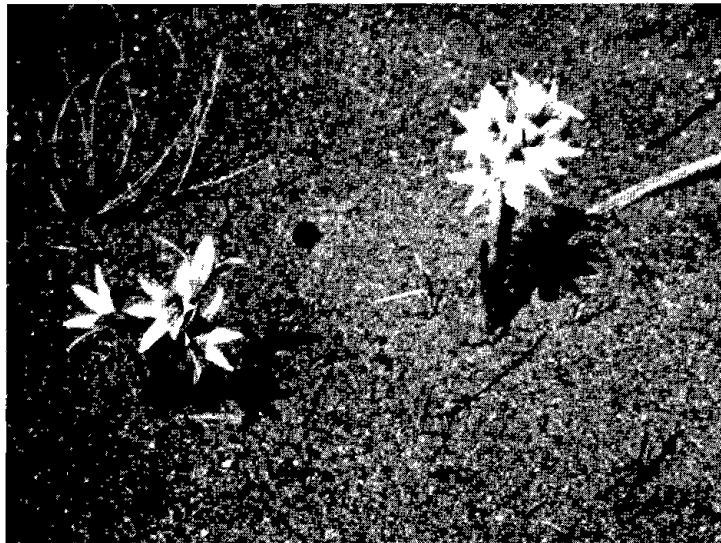


FIGURE 3-3. *Habranthus* sp. (Amaryllidaceae), a bulbous root perennial common in the Bolsón de Pipanaco. This photograph was taken two days after the first heavy rain of the summer. Prior to the rain, no parts of the plant were visible above the surface. (Photo by P. Cantino.)

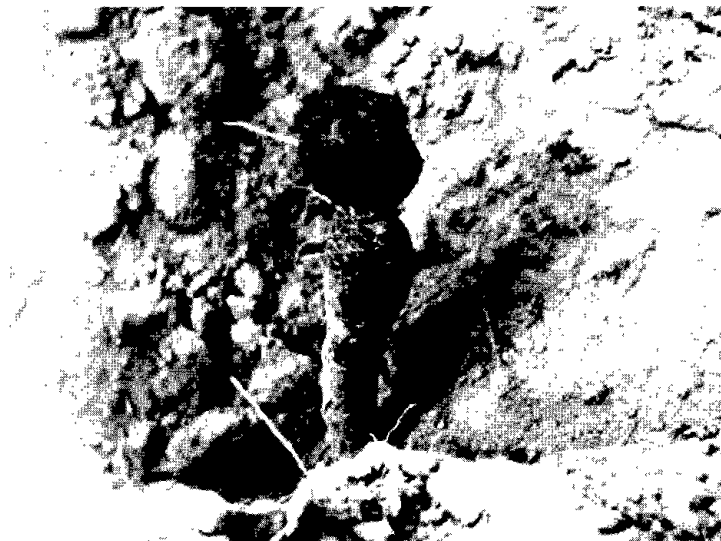


FIGURE 3-4. *Prosopanche americana* (Orobanchaceae), a parasite on the roots of *Prosopis* spp. The dark upper portion consisting of the leathery, three-petaled flower is the only part of the plant normally protruding above the ground. The remainder was excavated for this photo. (Photo by P. Cantino.)

TABLE 3-1 Percentage of Monte Plant Species Shared with the Chaco by Habitat

Community	Number of species	Common Chaco and Monte	Only Monte
Eroding Mountain Slope	12	58%	42%
Upper Bajada	57	63%	37%
Lower Bajada	18	39%	61%
Bottom Land	10	80%	20%
Canyon Forest	11	100%	—
Upper Wash	24	75%	25%
Lower Wash	12	83%	17%
Dunes	10	37%	62%
Halophytes	7	100%	—

nearly 60 percent of the families are present at both sites. In most cases the related species are herbaceous perennials or shrubs which are most commonly found in the more humid environments of the mountain slopes or in the washes. However, the most conspicuous common taxon, the genus *Larrea*, is the dominant element in the flats throughout most of the Monte and the Sonoran Desert.

Invertebrates

Our taxonomic knowledge of the invertebrate fauna of the Monte is still scanty and, although the invertebrate fauna of the Sonoran Desert is better known, it too is in need of more taxonomic research. The present discussion will be restricted to those groups with which we have had direct research experience: grasshoppers, ants, arachnids, and pollinating insects, especially bees. Data are based on our own collections supplemented from the literature (Appendixes D-F).

Grasshoppers*

The Argentine grasshopper fauna appears to be divisible into the same temporal strata recognized by G. G. Simpson (1950) for mammals, even though a fossil record is lacking. These are: (a) an ancient stock, endemic to South America, which has undergone extensive radiation and is now rich in species (Proscopiidae and Ommexechidae); (b) younger taxa which may have entered South America during late Oligocene to mid-Miocene and which have undergone moderate radiation (Romaleinae, Catantopinae); and (c)

*By D. Otte.

late immigrants, taxa that have recently penetrated South America, perhaps since the Pleistocene, and show little differentiation (Trimerotropis: Oedipodinae).

Ants*

The ant fauna of Arizona includes 209 recorded species (Hunt and Snelling, 1975). Only seventy-seven species are recorded as having been collected in Catamarca Province (Appendix O). The low species total for Catamarca reflects inadequate collecting activity in that region and makes comparison of the complete faunas problematical, but there is general similarity in sub-familial representation and generic composition. Twenty-seven species in seventeen genera were collected at an Avra Valley site (Appendix P); thirty-four species in seventeen genera were collected at a site in the Bolsón de Pipanaco (Appendix O). Though no species are shared between the sites there are ten genera in common (Appendix Q). The greater number of species collected at the Bolsón de Pipanaco site possibly reflects in part the generally favorable weather conditions during the study period there as compared to the generally unfavorable (hot, very dry) weather during the study period in Avra Valley. Despite an overall similarity of the ant faunas there are several conspicuous differences: the greater abundance of species associated with trees and *Prosopis/Acacia* washes in the Bolsón de Pipanaco than in the Avra Valley; the much greater richness of seed-gathering ants in the Avra Valley, and the much greater richness of fungus-growing ants (Myrmicinae, Attini) in the Bolsón de Pipanaco. Also, the Catamarca fauna includes eighteen species of Dolichoderinae, several of which (especially species of *Dorymyrmex* and *Forelius*) are much larger, more conspicuous, and more abundant than any of the eight Arizona species. The Arizona fauna, on the other hand, has a total of forty-two species of Formicinae in the genera *Lasius*, *Acanthomyops*, *Myremcocyclus*, and *Formica*, genera that do not occur in the Neotropical Realm. The contrasting diversities in these two groups may represent a pattern of parallel radiation under constraints of biogeographic separation. No other units of the ant fauna show such biogeographic difference in distribution of important genera, and in no other groups are such disparate species abundances seen.

Bees†

Both areas are rich in bee species with 116 at the Monte site and 188 from Silver Bell in the Sonoran Desert. With the exception of the recently

*By J. H. Hunt.

†By J. Neff.

introduced honeybee, *Apis mellifera*, no bee species are shared by the two sites and only twelve of the ninety-five total genera have representatives at each area. Total number of shared genera for the two deserts is probably in excess of twenty, but sparse knowledge of the Monte faunas hinders broad comparisons. At the family level, the faunas of the two deserts are quite similar with the minor exception of the absence of the relictually-distributed Melittidae from South America, although the distribution of species among the families at the two sites is rather distinctive (Appendix E). As noted by Michener (1940) the Sonoran bee fauna is a complex mixture of groups of northern and southern affinities. Cosmopolitan groups and groups of northern affinities such as *Andrena* and *Dufourea* are best represented in the spring while groups of southern or Neotropical affinities predominate during the summer bloom. The latter group includes many members of the Exomalopsini, Eucerini and Centridini of the Anthophoridae; most of the Panurginae (with the very important exception of *Perdita*) and the Oxaeidae. The Monte bee fauna has a number of obvious similarities to the Sonoran fauna, due both to the presence of virtually cosmopolitan genera such as *Anthidium* and *Colletes* as well as many of the widespread Neotropical elements which are at or near their northern extension in the Sonoran Desert. While many of the Neotropical elements are widespread throughout South and Central America (such as *Exomalopsis* and the Augochlorini) a number of groups such as *Protoxaea*, *Caupolicana*, and *Centris (Paracentris)* are essentially limited to temperate and/or semiarid regions and are absent in intervening wet tropical areas. Distinctive features of the Monte include the diversity and abundance of colletid bees, particularly among the Paracolletini and Xeromellisinae, as well as a number of distinctive groups of Eucerine and Exomalopsine genera and the unique *Canephorula*. An unusual disjunct distribution is found in the Eucerine genus *Martinapis*, which contains only two species, one in the Monte and the other in the Sonoran and Chihuahuan deserts of North America.

Arachnids*

Both deserts have approximately the same richness of genera of spiders, scorpions, and solpugids (Appendix F), but since the fauna of the Monte has not been studied as extensively, the slightly higher number of genera from the Sonoran Desert may be spurious. Approximately 30 percent of the genera and subgenera of spiders which live on the plants are shared between deserts, but these spiders represent roughly 70 percent of the number of individuals taken by quantitative sampling of the bushes. Similarly, predatory insects such as bugs (*Nabis* sp., *Geogoris* sp., in particular) and neuropterans (*Chrysops* sp.) share genera in the two continents. This taxonomic simi-

*By F. A. Enders.

larity between the faunas of predatory arthropods contrasts with the lack of relation found in comparisons of herbivorous arthropods (Appendix D). Also the arachnids which live on the ground are less closely related taxonomically, between continents, than are those which live on the bushes. The scorpions represent two distinct families, and solpugids are primarily Eremobatidae in North America, but Ammotrechidae in the Monte. On the other hand, some of the ground-dwelling spiders (genus *Lycosa*, for example) are more closely related probably because of the long distance dispersal by ballooning, not possible among solpugids and scorpions. This method of dispersal is reduced or lacking in spider species which show less taxonomic similarity between the two continents: e.g., Homalonychidae-Sicariidae.

*Vertebrates**

The Monte and the Sonoran Desert share very few species of vertebrates. Only ten out of ninety-eight bird and six out of eighty-four mammal species are common to both regions (Appendix G). All are widespread species, not restricted to the desert region. There are no common species of anurans or reptiles. The situation is not very different at the generic level. The only shared anuran genus, among eleven, is the nearly cosmopolitan *Bufo*. Only one of nineteen lizard genera (*Cnemidophorus*) is shared. Two of twenty-eight genera of snakes, the primitive pantropical *Leptotyphlops*, and the predominantly North American genus *Crotalus*, are represented in both deserts.

One family of anurans out of seven, three of five lizard families, and four of five snake families are represented in both deserts. Sixteen of thirty-five families of birds are present in both deserts. Finally, there are seven families of mammals shared by the Monte and the Sonoran Desert of a total of twenty-four present in either one or the other region. However, two of these are bats and three are wide-ranging carnivores. The overall phylogenetic similarity of the Monte and the Sonoran Desert vertebrate faunas, like the invertebrate faunas, is therefore much less than the similarity of the plants of these areas.

The amphibian and reptilian faunas of the Monte are largely shared with the Chaco (Table 3-2). Twenty-two (44 percent) of the fifty species of amphibians and reptiles that have been recorded for the Monte have Monte-Chaco distributions. Birds and mammals do not fit this pattern, for the largest element in both is one of widely distributed species, while only nine (15 percent) of the sixty-one bird species and none of the thirty-two mammal species have a Monte-Chaco distribution.

*By W. F. Blair, A. C. Hulse, M. A. Mares, and C. S. Tomoff.

TABLE 3-2 General Distributions of the Species of Terrestrial Vertebrates that Comprise the Monte and the Sonoran Desert Faunas

A. SONORAN DESERT						
Class	Endemic	Sonoran Chih.	Son. + adjacent	Sonoran Chih. grasslands	W. Mex. lowlands	Totals
Anurans	2		1	6	2	12
Lizards	8		7	4		19
Snakes	10	3	3	5	3	24
Turtles	1			1		2
Birds	6		14	3	34	57
Mammals	1	2	6	4	2	83
B. MONTE						
Class	Endemic	Monte-Chaco	Monte-Pat.	Monte-Chaco-Pat.	Monte-Chaco-Cord.	Totals
Anurans		10			2	14
Lizards	11	4				15
Snakes	2	6	1	1	4	14
Turtles		1				1
Birds	2	9	5		2	61
Mammals	3(4)			4	1	32

BRIEF HISTORY OF THE BIOTA OF THE SONORAN DESERT AND THE MONTE*

The most important historical difference between the Bolsón de Pipanaco and the Silver Bell area is the greater impact that Pleistocene glaciations had on the South American site. Also severe arid conditions may have existed for different periods of time in North America and South America (Chapter 2). It is important to assess the significance of this difference for the potential time available for convergence on the two sites. The papers of Axelrod (1950) and Solbrig (1976) dealing with the origin of flora of the Sonoran Desert and the Monte respectively and those of Patterson and Pascual (1968, 1972) on the evolution of mammals may be consulted for further details.

Monte

Very little factual evidence exists regarding the history of the flora and the fauna of the Monte during the Tertiary. Extrapolating from the fossil evidence that points to a subtropical forest in Patagonia at the end of the Cretaceous and early Tertiary, and the absence of any appreciable mountain barrier to the west of the region at that time, it can be assumed that the climate of the area must have been more mesic. However, the expected presence of subtropical high pressure zones and some geomorphological evidence of local aridity in the Cretaceous deposits of central Argentina (Gordillo and Lencinas, 1972) imply that there may have been a pronounced dry season at mid-latitudes (approximately 30° S). Also, the South Atlantic had a very limited surface at that time (Dietz and Holden, 1970). This has led Solbrig (1976) to postulate that the region that today is the Monte and dry Chaco had a savanna or deciduous forest type of vegetation, rather than a rain forest, at the beginning of the Tertiary. Phylogenetically this flora is supposed to be related to the present Chaco flora, and has been termed the "Tertiary-Chaco Paleoflora." This is the presumed parent stock for much of the flora of the present-day Monte and Chaco.

From the biogeographical standpoint the most important aspect of the Tertiary history of South America is its isolation from the biotas of other continents. The island nature of South America allowed the evolution of several distinctive groups of vertebrates, most notably notoungulates and marsupials. Prior to the Pliocene connection of North and South America only platyrrhine primates, caviomorph rodents, and procyonid carnivores had invaded the continent. It is still a matter of debate whether the first two came from the north (Wood and Patterson, 1971) or from Africa (Hoffstetter, 1972).

The fossil record of mammalian life in southern South America is very good. All but a few of the known fossil localities are in Argentina, but out-

side the present Monte area. The early Tertiary mammalian faunas from the Paleocene and Eocene of Patagonia consist of marsupials, edentates, and a variety of ungulates. In early Oligocene the first records of caviomorph rodents and platyrrhine primates are found. The forms from that early period appear to be adapted to a subtropical, forested region.

The Tertiary in South America is categorized by the slow lifting of the Cordillera de los Andes, particularly from the Miocene to the present (see Chapter 2). After a warm beginning, the climate began to cool and became drier starting in the Eocene. This climatic trend, and the increasing barrier to moisture laden winds from the west, led to a gradual replacement of the forests of the late Cretaceous and early Paleocene by grasslands and, eventually, more dry-adapted vegetation in Patagonia, the Pampa region, and probably the Monte region as well. Unfortunately the evidence is scanty and at times indirect. In Patagonia there is direct evidence of the deterioration of the climate (Menendez, 1972; Petriella, 1972), as well as indirect evidence from paleosoils (Volkheimer, 1971). One of the strongest bits of indirect evidence for the existence of extensive grasslands comes from the presence, from the Eocene on, of two well-developed and predominantly grazing lines of ungulates, the *Proterotheriidae* and the *Macraucheniiidae*.

The Pliocene provides the first unmistakable evidence for the existence of more or less extensive areas of semidesert (Vuilleumier, 1971; van der Hammen, 1972). With the rising of the Bolivar geosyncline in late Pliocene, South America ceased to be an island continent and became connected to North America. This had a very marked influence on the fauna of the continent (G. G. Simpson, 1950; Patterson and Pascual, 1968, 1972). Extensive faunistic interchanges took place during the Pliocene and Pleistocene between the two continents with eventual extinction of several of the South American mammalian lines such as marsupial carnivores, ground sloths, and notoungulates.

By the end of the Pliocene the landscape of South America was essentially identical to its present form (Chapter 2). However, the flora and fauna of the Pliocene was yet to be affected profoundly by the events of the Pleistocene. Vuilleumier (1971), and van der Hammen (1961, 1972) have reviewed the Pleistocene events in South America. In northern South America (Venezuela, Colombia, and Ecuador) one to three glaciations took place corresponding to the last three events in the northern hemisphere (Würm, Riss, and Mindel). In Perú, Bolivia, and northern Chile and Argentina, there were at least three, and in some areas possibly four glaciation events. All of these glaciations, with the exception of the Patagonian glaciation (Auer, 1960; Czajka, 1966) were montane rather than continental. Semidesert areas probably persisted in the Monte region during the Pleistocene, but the extent and the area must have fluctuated considerably (Chapter 2).

In late Pleistocene many areas of what is today the Monte became available for colonization by desert plants and animals. Given the broken nature of the topography in its northern part, there is the possibility that not all species were able to surmount the physical barriers of the large mountains

*By. O. T. Solbrig.

that surround some of the valleys such as the Bolsón de Pipanaco. This would be particularly true for small, flightless forms of animals.

Sonoran Desert

The climatic changes that took place in the Sonoran Desert since Cretaceous time parallel largely what we know from the Monte area (Chapter 2). The evolution of the vegetation of the area is tied to the development of the Madro-Tertiary Geoflora at the beginning of the Cenozoic (Axelrod, 1950, 1958), its subsequent expansion during the Tertiary, and the evolution of a desert vegetation from some Madro-Tertiary elements since the early Pliocene.

The climate of the Sonoran Desert during the Cretaceous was warm and fairly humid, and the region was apparently covered by a subtropical forest which persisted into the Paleocene. The middle and late Cretaceous era of the western United States reflects a cooler climate than that indicated by succeeding Paleocene floras of the same areas. Geological evidence also indicates a seasonally-dry continental environment. Axelrod (1958) attributes this in part to the ridge of high pressure at mid-latitude that causes the western parts of continents at intermediate latitudes always to be the driest. However, these dry environments at this time were not severe and were restricted in area.

By the Eocene and Oligocene, conditions had apparently become drier since the first records of the Madro-Tertiary Geoflora are found at this time (R. W. Brown, 1934; Chaney, 1944; MacGinitie, 1953; Axelrod, 1958). The early examples of the Madro-Tertiary Geoflora from the Green River of Utah and the Florissant beds of Colorado, consist of genera that today are found in woodland, savanna, chaparral, and thorn shrub vegetation. Among them genera such as *Celtis*, *Platanus*, *Bursera*, *Prosopis*, and *Zizyphus* are found in the Sonoran Desert today. From the structure of the known fossil floras and from paleoclimatic considerations, Axelrod (1950, 1958) feels that the vegetation of the area at the time is best described as a subtropical savanna. Zweifel (1956) has suggested that *Scaphiopus couchi*, the most desert-adapted anuran in North America, may have evolved in the southwestern United States in mid-Oligocene. From the Oligocene there are also records of ancestors of two genera of Sonoran Desert lizard genera (Estes, 1970); *Paradipsosaurus* from the early Cenozoic of Mexico (probably Oligocene) which resembles *Dipsosaurus*, and *Heloderma*, a Sonoran Desert endemic genus, which is known from Oligocene beds of Colorado. The first records of Heteromyidae, which contains the most desert-adapted genera of rodents in North America, come also from the Middle Oligocene (Estes, 1970). Consequently, it appears that by the end of the Oligocene aridity was shaping the evolution of the biota in the southwestern United States.

From the Eocene on there was a worldwide drying trend, the underlying causes of which are not entirely understood (Chapter 2). This was paralleled by an expansion of the area occupied by the Madro-Tertiary Geoflora, and

the development of numerous adaptive types within it. According to Axelrod (1958) these types include plants with swollen bases for water storage (*Idria*, *Bursera*); winter deciduous habit (*Acacia*, *Populus*); drought deciduousness (*Bursera*, *Cercidium*); and different types of succulent Cactaceae. By early Miocene the Madro-Tertiary Geoflora was already the dominant vegetation in southeastern California (Axelrod, 1939), and by late Miocene it extended into the Central Great Basin. Although we do not have any record from southcentral Arizona, it is reasonable to assume that the Madro-Tertiary vegetation was present there at least by the end of the Miocene, if not earlier. This was not a desert vegetation as we know it today but a combination of woodland, chaparral, and subtropical shrub that occupied areas with different degrees of moisture and temperature, similar to the zonation that is found today in central California.

By the early Pliocene the region of the Mohave and Sonoran deserts was still characterized by oak woodland, chaparral, and thorn scrub vegetation. Some small areas of true desert on the lee of mountain ranges could have existed that did not enter the fossil record (Axelrod, 1958). The late Pliocene and Quaternary elevations of the Sierra Nevada-Cascade ranges and of the mountains of southern California created the semidesert conditions that exist today in the Sonoran Desert. The fossil evidence suggests that adaptations leading towards desert-adapted vertebrate taxa in North America were occurring over a wide part of the western half of the continent through much of the Cenozoic, particularly after the Miocene, corroborating the climate and plant data.

The Pleistocene did not have as drastic an effect on the Sonoran Desert as it had on the Monte because the absence of large neighboring mountain ranges precluded mountain glaciers. However, there were climatic changes in temperature and humidity (Chapter 2). As a result there were probably changes in the ranges of species, but the lack of closed valley systems surrounded by high mountains made reinvasion of the area a relatively easy matter.

In summary, the biogeographical events in the Cenozoic of the Sonoran Desert parallel largely those documented for the Monte. There is clearer and much firmer evidence for the gradual drying and the vegetational changes in the Sonoran Desert than there is in the Monte. The drying trend appears to have occurred somewhat earlier in the north, but this could possibly be due to incomplete evidence from South America. Pleistocene and post-Pleistocene events are, however, more dissimilar at the two localities. Since these late events determine the present-day distribution of the biota, this difference is significant in terms of the present research objectives.

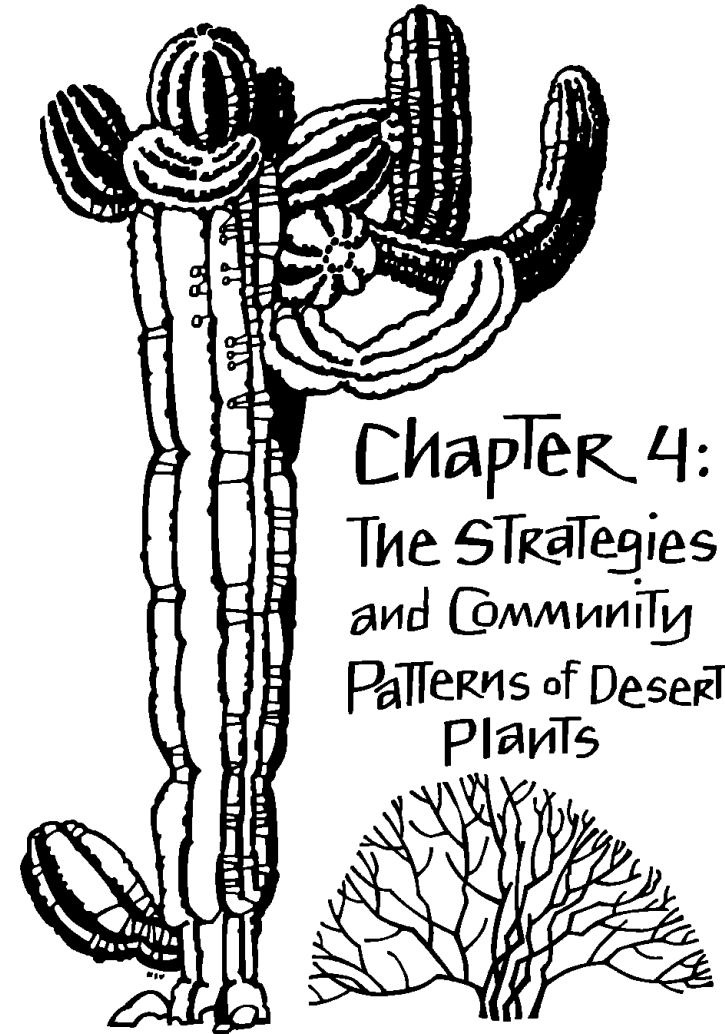
SUMMARY AND CONCLUSIONS

The flora of the Monte is derived from elements of a more tropical and mesic flora that at one time extended throughout South America from Vene-

zuela to central Patagonia. The flora of the Sonoran Desert is equally derived from a more tropical, southern flora, the ancestor of the Madro-Tertiary flora, which at one time extended through Central America from the Panamanian gap to the present southern United States. Whether the ancestral floras of the Monte in South America and of the Madro-Tertiary in Central America are the same cannot be stated with certainty. The present-day similarity of the flora of Brazil and Central America suggests that at the beginning of the Tertiary the South American and Central American floras were probably more similar than today. In each of these floras there were elements better adapted to drought conditions from which most of the present-day Monte and Sonoran Desert floras are derived. We feel that the great similarity of the flora at the family and generic levels between the Monte and the Sonoran Desert had its origin in this process of parallel or convergent evolution towards arid adaptation from common or closely related, more mesic ancestors. Some elements, particularly those few species of ephemerals that are common to the two areas, probably got there through long-range dispersal from one region to the other in recent times, and some, most notably the ancestral *Larrea divaricata*-*L. tridentata* probably had a more extensive range in tropical regions at one time (Pleistocene?) affording a kind of bridge for moving from one semidesert to the other (Raven and Axelrod, 1974). However, a very large number of genera and a fair number of the families are found only at one of the two areas, emphasizing the substantial independence of the evolution of the two floras.

The phylogenetic similarity of the flora of the Monte with that of the Sonoran Desert complicates, but does not invalidate, the research design for the following reasons. (1) All but fourteen of the species in the region where the intensive comparisons took place are different. (2) Although many genera are represented in both areas, the species at the two sites are usually not closely related and are often ecologically distinct. (3) A majority of the genera and many of the families are represented at only one of the two sites. Nevertheless, there is sufficient similarity that caution is required in distinguishing parallel evolution from convergence.

The fauna of the Monte and the Sonoran Desert are much less related phylogenetically than the flora. South America was an island continent during most of the Tertiary, which had a very profound influence on animals which as a rule are much less adept than plants at crossing water barriers. The species that are shared by both areas are invariably widespread species that occur in a variety of habitats such as the grasshopper *Trimero-tropis palidipennis*, the kestrel (*Falco sparverius*), or the cougar (*Felis concolor*). In spite of some phylogenetic similarities at the generic and familial level, the faunas are sufficiently unrelated to allow easy recognition of convergences.



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