Origins and affinities of vertebrates of the North American Sonoran Desert and the Monte Desert of Northwestern Argentina

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Abstract

The Monte Desert of Argentina and the Sonoran Desert of North America are very similar in most aspects of their physical environments. The origins and the degree of affinity of the faunas of three classes of vertebrates in the two deserts are discussed. Heterotherms show high endemism, with 72.0% of the Monte species either endemic to the Monte or with Monte–Chaco distribution and with 61.4% of the Sonoran Desert heterotherms endemic to deserts of the southwest. Mammals show low endemism and their desert inhabitants generally belong to wide-ranging species. Mammals alone among these vertebrates show wide disparity between the two deserts in number of species, with more than twice as many in the Sonoran Desert as in the Monte.

Desert adaptation seems to have been occurring over much of western North America throughout much of the Cenozoic and in the present Monte– Chaco–Patagonia region since at least the Miocene.

The only species and most of the genera shared between the two deserts are wide ranging or volant mammals. Only one of seven families of anurans is common to both deserts. Reptiles have many families in common, while mammals of the two deserts have relatively few families in common.

Introduction

North and South America contain a number of arid and semi-arid regions, ranging from the Atacama Desert of northern Chile and southern Peru, which is one of the driest areas on earth, to dry habitats within the tropics, such as those found in northern Venezuela. Evolutionary studies of desert organisms on each continent are particularly interesting because the continents were isolated from one another from the Triassic to the late Pliocene, when the formation of the Central American land bridge united both continents and allowed extensive faunal interchange (Dietz & Holden, 1970; Patterson & Pascual, 1972). Thus one can use the geological record and palaeontological data to determine when particular groups of organisms may have had access to desert regions and compare their degree of adaptation and adaptational strategies to arid environments.

The Monte Desert of northwestern Argentina and the Sonoran Desert of North America are very similar to one another in climate and geomorphology (Morello, 1958; Simpson & Vervoorst, 1976). In addition, these deserts are of about the same age and support plant communities of very similar physiognomies (Solbrig, 1972, 1976, Figs 1, 2). It is largely because of these similarities, particularly the abiotic ones, that the Origin and Structure of Ecosystems Subprogram of the U.S. component of the International Biological Program chose the two deserts as study sites for an investigation into patterns and processes of convergent evolution of ecosystems. Since convergence requires that floras and faunas be phylogenetically distinct, it was necessary to compare the origins and affinities of the organisms occurring in both deserts. This report reviews the faunal makeup, origins, and taxonomic relationships of three classes of terrestrial vertebrates of the disjunct deserts.

Methods

The North American desert system is well studied as far as vertebrate distribution patterns are concerned. We have consulted a number of references in



Fig. 1. Hillside in Sonoran Desert near Tucson, Arizona. Columnar cactus is Cereus giganteus.



Fig. 2. Hillside in Monte Desert near Andalgalá, Catamarca Province, Argentina. Columnar cactus is Trichocereus terschecki.

compiling faunal lists for the various arid and semiarid areas of North America (principally Lowe, 1964; Stebbins, 1951, 1954 for reptiles and amphibians; Hall & Kelson, 1959 for mammals). The fauna of the Monte Desert and adjacent areas is much more poorly known, and we have relied heavily on our own field experience in the area to compile species lists. We have also used various published references to supplement our observations (Barrio, 1964a, b; 1965a, b; 1968; Cei, 1955a, b, 1959, 1962; Freiberg, 1942; Gallardo, 1966; Peters & Orejas-Miranda, 1970; Peters & Donoso-Barros, 1970; Reig & Cei, 1963 for reptiles and amphibians; Cabrera, 1957, 1960 for mammals).

Various divisions of the Sonoran and Monte deserts and adjacent areas were used in describing vertebrate distribution patterns. We realize that any such subdivisions of areas which may not in actuality be sharply delineated one from another is artificial to a certain extent. Nevertheless, since a species inhabiting a desert may possess a geographic distribution extending well beyond the desert's boundaries, it is necessary to examine its overall habitat requirements, and those of its genus (or family) in order to determine how that particular species managed to invade the desert in the first place. Naturally there is additional error in transferring records of occurrence from distribution maps to habitat maps. Since we are dealing with extensive areas, however (e.g. the Chihuahuan or Sonoran deserts), and since we have some knowledge of the ecological requirements of the great majority of vertebrates discussed, we feel that errors of this type are minimized.

We have not included Baja California as part of the Sonoran Desert, nor do we discuss the origins of its fauna. We have deleted this area in order to avoid the confounding effects of evolution on a peninsula and its offshore islands. No comparable area exists in or near the Monte Desert, and since we hope to determine whether the origins and overall distribution patterns of vertebrates in both deserts are similar, the inclusion of the northern peninsula would only seem to add noise to our analyses.

We have also excluded the vertebrates of the southern Monte (south of southern Mendoza) from the Monte endemic category. This is primarily because we are not personally familiar with the patterns of faunal occurrence in the southern portion of the desert, particularly as far as distributional limits are concerned. Available references indicate, however, that few endemics, and indeed few additional species, would be found in this general area. We therefore feel that the exclusion of this area will not greatly affect discernible patterns of colonization or taxonomic relationships of the faunas of the disjunct deserts. For both the Monte and the Sonoran Desert our discussions concern the lowland desert faunas and exclude those of the mountain ranges that are found in both of these regions.

Categories for vertebrate distribution patterns (see Figs 3 and 4)

(1) Sonoran-Endemic: Sonoran biotic province as delimited by Dice (1939), which includes the Mojave Desert.

(2) Sonoran-Chihuahuan: Category 1 plus arid and semi-arid regions of New Mexico, Texas, Chihuahua (Mexico) south of Zacatecas, San Luis Potosi.

(3) Sonoran-Chihuahuan-Grasslands: Category 2 plus the Great Plains Grasslands.

(4) Sonoran-Great Basin: Category 1 plus the Great Basin Desert.

(5) *Sonoran–Great Basin–Chihuahuan:* Categories 2 and 4 combined.

(6) Sonoran-Thorn Scrub: Category 1 plus adjacent thorn scrub habitat along the western Mexican Lowlands.

(7) All deserts-Grasslands: Category 5 plus Great Plains Grasslands.

(8) *Widespread:* Ranges well beyond deserts and grasslands.

(1) *Monte-Endemic:* Morello's (1958) northern, western, and eastern limits of the Monte, south to southern Mendoza and northeastern La Pampa.

(2) *Monte-Chaco:* western limits of Monte east to San Luis, northern Córdoba, to Corrientes through Santa Fe, Chaco, Formoas and Paraguay northward.

(3) *Monte-Pampas-Patagonia:* Category 3 minus the Chaco.

(4) Monte-Chaco-Pampas-Patagonia: Category 2 then south and east through La Pampa; Buenos Aires through Neuquen, Rio Negro, Chubut and Santa Cruz.

(5) *Monte-Chaco-Cordillera*: Category 2 plus the slopes of the Andean or pre-Andean chain.

(6) Monte-Cordillera: Category 1 plus slopes of Andean or pre-Andean chain.

(7) *Widespread:* ranges well beyond the preceding areas.

Geographic origins of the desert vertebrates

The evolution of desert-adapted species will be conditioned by a variety of factors, in addition to the physical characteristics of the desert environment. Among terrestrial vertebrates, one set of factors is purely phyletic, with the various classes expectedly showing very different patterns of adaptation simply because of their different physiologies and morphologies. Another set of factors is biogeographical. What is the nature of source areas where selection may have produced attributes that are pre-adaptive for the evolution of desert species? Biogeographic factors of ecological and physical barriers and of long-range dispersal assume importance in comparing desert biotas that are isolated from one another.

When comparing desert adaptations of Monte and Sonoran Desert vertebrates, we note that both deserts represent an extreme in aridity within much broader regions of deficient but less severely deficient moisture. Transitions from these less arid areas to the deserts are typically gradual (e.g. from arid Chaco to Monte) and desert endemics may have distributions that deviate from map lines delineating actual desert boundaries (Kuchler, 1964; Cabrera, 1971).

Anurans

Endemic species of anurans are few in both deserts (Tables 1 and 2). The Monte has no endemic anuran among its fifteen species; the Sonoran Desert has three endemics (Table 3). Monte anurans are basically a depauperate Chacoan element (Blair, 1976). Thirty species have been listed for the Chaco (Gallardo, 1966). All fifteen Monte species occur in

Table 1. Geographic affinities of the vertebrates which are known from the Monte

| | Endemic | Monte– Chaco. | Monte– Pampas– Pat. | Monte- Cord. | Monte– Chaco– Pampas– Pat. | Monte– Chaco– Cord. | Wide |
|---------------------------|---------|------------------|---------------------------|-----------------|-------------------------------------|---------------------------|------|
| Amphibia | | | | | | | |
| Leptodactylus bufonius | | × | | | | | |
| mystaceus | | | | | | | × |
| ocellatus | | | | | | | × |
| prognathus | | × | | | | | |
| Physalaemus biligonigerus | | × | | | | | |
| Pleurodema cinerea | | | | × | | | |
| guayape | | × | | | | | |
| nebulosa | | | | × | | | |
| Ceratophrys ornata | | × | | | | | |
| pierotti | | × | | | | | |
| Lepidobatrachus asper | | × | | | | | |
| Ilanensis | | × | | | | | |
| Odontophrynus americanus | | × | | | | | |
| occidentalis | | × | | | | | |
| Bufo arenarum | | × | | | | | |
| Reptilia | | | | | | | |
| Geochelone chilensis | | × | | | | | |
| Amphisbaena angustifrons | | | | | × | | |
| Homonota horrida | | × | | | | | |
| underwoodi | × | | | | | | |
| Liolaemus darwini | × | | | | | | |
| goetschi | × | | | | | | |
| gracilis | × | | | | | | |
| marmoratus | × | | | | | | |
| robertmertensi | × | | | | | | |
| sp. A | × | | | | | | |
| sp. B | × | | | | | | |
| sp. C | × | | | | | | |
| Leiosaurus bardensis | × | | | | | | |
| catamarcensis | × | | | | | | |
| Cnemidophorus longicaudus | × | | | | | | |

| | Endemic | Monte– Chaco. | Monte– Pampas– Pat. | Monte- Cord. | Monte– Chaco– Pampas– Pat. | Monte- Chaco- Cord. | Wide |
|---|---------|------------------|---------------------------|-----------------|-------------------------------------|---------------------------|--------|
| Reptilia (continued) | | | | | | | |
| Teius cyanogaster | | × | | | | | |
| Tupinambis rufescens | | × | | | | | |
| Leptotyphlops borrichianus | × | | | | | | |
| melanotermus | | | | | | | × |
| Clelia occipitolutea | | × | | | | | |
| Elapomorphus bilineatus | | × | | | | | |
| tricolor | | | | | | | × |
| Leimadophis sagittifer | | × | | | | | |
| Lygophis lineatus | | | | | | | × |
| Lystrophis semicinctus | | × | | | | | |
| Oxyrhopus rhombifera | | | | | | | × |
| Philodryas burmeisteri | | | | | × | | |
| patagoniensis | | × | | | | | |
| pasmmopniaeus | | × | | | | | |
| Phimophis vittatus Baau datama dan tuinan atua | | × | | | | | |
| Pseudotomodon trigonatus Mionunus fuontalia | × | | | | | | |
| Micrurus frontalis | | | | | | | × |
| Boinrops ammodytotaes | | | | | × | | ~ |
| neuwieai Crotalus durissus | | | | | | | ~ |
| Crotatus aurissus | | | | | | | ^ |
| Mammalia | | | | | | | |
| Didelphis albiventris | | | | | | | × |
| Marmosa pusilla | | | | | | | × |
| Desmodus rotundus | | | | | | | × |
| Myotis levis | | | | | | | × |
| Eptesicus brasiliensis | | | | | | | × |
| Lasiurus borealis | | | | | | | × |
| cinereus | | | | | | | × |
| Histiotus montanus Tadarida hragilionaia | | | | | | | × |
| Fumona on | | | | | | | × |
| Zaadyug piahiy | | | ~ | | | | ^ ? |
| Chastophractus vellerosus | | | ^ | | | | • |
| Chlamyphorus truncatus | | | | | ~ | | ~ |
| Eligmodontia typus | | | | | ^ | | × |
| Phyllotis darwini | | | | | | | × |
| ariseoflavus | | | | | | | × |
| Undescribed phyllotine | × | | | | | | |
| Akodon varius | | | | | | | × |
| sp. | ? | | | ? | | | ? |
| Calomvs laucha | | | | | | | × |
| Orvzomvs longicaudatus | | | | | | | × |
| Octomys mimax | × | | | | | | |
| Tympanoctomys barrerae | × | | | | | | |
| Ctenomys fulvus | ? | | | ? | | | |
| Microcavia australis | | | | | | | × |
| Galea musteloides | | | | | | | × |
| Dolichotis patagonum | | | | | × | | |
| Dusicyon culpaeus | | | | × | | | |
| griseus | | | | | | | × |
| Conepatus chinga | | | | | | | × |
| Lyncodon patagonicus | | | | | × | | |
| Galictes cuja | | | | | | | × |
| Felis concolor | | | | | | | × |
| yagouaroundi | | | | | | | × |
| geoffroyi | | | | | | | × |

 Table 1 (continued)

| | Endemic | Son Chih. | Son–Chih- Gr. | Son– GB | Son–GB– Chih. | Son– Thorn | Deserts & Grass | Wide |
|--|---------|--------------|------------------|------------|------------------|---------------|--------------------|------|
| Amphibia | | | | | | | | |
| Gastrophryne olivacea | | | × | | | | | |
| Scaphiopus couchi | | | × | | | | | |
| hammondi | | | × | | | | | |
| Bufo alvarius | × | | | | | | | |
| cognatus | | | × | | | | | |
| mazatlanensis | | | | | | × | | |
| microscaphus | | × | | | | | | |
| punctatus | | | × | | | | | |
| retiformis | × | | | | | | | |
| woodhousei | | | | | | | | × |
| Pternohyla fodiens | | | | | | × | | |
| Rana sp. (pipiens complex) | × | | | | | | | |
| Reptilia | | | | | | | | |
| Kinosternon flavescens | | | × | | | | | |
| Gopherus agassizi | | | | × | | | | |
| Coleonyx variegatus | × | | | | | | | |
| Callisaurus draconoides | | | | × | | | | |
| Cophosaurus texana | | | × | | | | | |
| Crotaphytus collaris | | | | | | | × | |
| wislizeni | | | | | × | | | |
| Dipsosaurus dorsalis | × | | | | | | | |
| Phrynosoma m'calli | × | | | | | | | |
| platyrhinos | | | | × | | | | |
| solare | × | | | | | | | |
| Sauromalus obesus | × | | | | | | | |
| Sceloporus magister | | | | | × | | | |
| Uma inornata | × | | | | | | | |
| notata | × | | | | | | | |
| scoparia | × | | | | | | | |
| Urosaurus graciosus | × | | | | | | | |
| ornalus Uta atamahuniana | | | X | | | | | |
| Chamidanhanus tiquis | | | | | v | | ~ | |
| Heloderma suspectum | ~ | | | | ~ | | | |
| I entotyphlops humilis | ^ | × | | | | | | |
| Lieptotyphiops numitis Liebanura trivirgata | ~ | ^ | | | | | | |
| Arizona elegans | ~ | | × | | | | | |
| Chilomaniscus cinctus | × | | ~ | | | | | |
| Chionactis occinitalis | × | | | | | | | |
| palarostris | × | | | | | | | |
| Hypsiglena torauata | | | | | | | × | |
| Lampropeltis getulus | | | | | | | | × |
| Masticophis flagellum | | | | | | | | × |
| Phyllorhynchus browni | × | | | | | | | |
| clecurtatus | × | | | | | | | |
| Pituophis melanolecus | | | | | | | | × |
| Rhinocheilus lecontei | | | | | | | × | |
| Salvadora hexalepis | | | | | × | | | |
| Sonora semiannulata | | | | | × | | | |
| Thamnophis marcianus | | | × | | | | | |
| cyrtopsis | | | × | | | | | |
| Trimorphodon lambda | × | | | | | | | |
| Micruroides euryxanthus | | × | | | | | | |
| Crotalus atrox | | | × | | | | | |
| cerastes | × | | | | | | | |
| mitchelli | × | | | | | | | |
| scutulatus | | × | | | | | | |
| tigris | × | | | | | | | |

Table 2. Geographic affinities of the vertebrates which are known from the Sonoran Desert

| | Endemic | Son– Chih | Son–Chih– Gr. | Son– GB | Son–GB– Chih. | Son– Thorn | Deserts & Grass | Wide |
|---------------------------------------|---------|--------------|------------------|------------|------------------|---------------|--------------------|--------------------|
| Mammalia | | | | | | | | |
| Didelphis virginiana | | | | | | | | × |
| Notiosorex crawfordi | | | | | | | | × |
| Desmodus rotundus | | | | | | | | × |
| Mormoops megalophylla | | | | | | | | × |
| Macrotus waterhousii | | | | | | | | × |
| Choeronycteris mexicana | | | | | | | | × |
| Leptonycteris nivalis | | | | | | | | × |
| Myotis yumanensis | | | | | | | | × |
| grisescens | | | | | | | | × |
| velifer | | | | | | | | × |
| occultus | | | | | | | | × |
| evotis | | | | | | | | × |
| thysanodes | | | | | | | | × |
| californicus | | | | | | | | × |
| volans | | | | | | | | × |
| subulatus | | | | | | | | × |
| Lasionycteris noctivagans | | | | | | | | × |
| Pipistrellus hesperus | | | | | | | | × |
| Eptesicus juscus | | | | | | | | × |
| Lasturus boreatis | | | | | | | | × |
| Cinereus Desuntenus | | | | | | | | ~ |
| Dasypierus ega Placotus townsandii | | | | | | | | \sim |
| Antrozous pallidus | | | | | | | | $\hat{\mathbf{v}}$ |
| Tadarida femorosacca | | | | | | | | × |
| hrasiliensis | | | | | | | | × |
| molossa | | | | | | | | × |
| Fumons peratis | | | | | | | | × |
| underwoodi | | | | | | | | × |
| Svlvilagus audubonii | | | | | | | | × |
| Lepus californicus | | | | | | | | × |
| alleni | | | | | | × | | |
| Ammospermophilus harrisii | | | | × | | | | |
| leucurus | | | | | | | | × |
| Spermophilus spilosoma | | | | | | | × | |
| mohavensis | × | | | | | | | |
| tereticaudus | | | | × | | | | |
| Thomomys bottae | | | | | | | | × |
| Perognathus flavus | | | | | | | | × |
| longimembris | | | | × | | | | |
| amplus | | | | × | | | | |
| formosus | | | | × | | | | |
| baileyi | × | | | | | | | |
| penicillatus | | × | | | | | | |
| pernix | | | | | | × | | |
| intermedius | | | | | × | | | |
| goldmani | | | | | | × | | |
| spinatus | × | | | | | | | |
| Dipodomys ordii | | | | | | | × | |
| panamintinus | | | | × | | | | |
| spectabilis | | | × | | | | | |
| merriami | | | | | × | | | |
| deserti | | | | × | | | | |
| Reithrodontomys fulvescens | | | | | | | | × |
| megalotis | | | | | | | | х |

 Table 2 (continued)

| | Endemic | Son– Chih | Son–Chih– Gr. | Son– GB | Son–GB– Chih. | Son– Thorn | Deserts & Grass | Wide |
|------------------------------------|---------|--------------|------------------|------------|------------------|---------------|--------------------|--------|
| Mammalia continued | | | | | | | | |
| Peromyscus crinitus | | | | × | | | | |
| merriami | × | | | | | | | |
| eremicus | | | | | | | | × |
| maniculatus | | | | | | | | × |
| leucopus | | | | | | | | × |
| Onychomys torridus | | | | | | | | × |
| Sigmodon hispidus | | | | | | | | × |
| Neotoma lepida | | | | × | | | | |
| albigula | | | | | | | | × |
| Erethizon dorsatum | | | | | | | | × |
| Canis latrans | | | | | | | | × |
| lupus | | | | | | | | × |
| Vulpes macrotis | | | | | × | | | |
| Urocyon cinereoargenteus | | | | | | | | × |
| Bassariscus astutus | | | | | | | | × |
| Procyon lotor | | | | | | | | × |
| Nasua narica | | | | | | | | × |
| Taxidea taxus | | | | | | | | × |
| Spilogale putorius | | | | | | | | × |
| Mephitis mephitis | | | | | | | | × |
| macroura | | | | | | | | × |
| Felis onca | | | | | | | | × |
| concolor | | | | | | | | × |
| yagouaroundi | | | | | | | | × |
| Lynx rufus | | | | | | | | × |
| Dicotyles tajacu | | | | | | | | × |
| Odocoileus hemionus virginianus | | | | | | | | × × |

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 Table 2 (continued)

 Table 3. Approximate distributions of the species of terrestrial vertebrates that comprise the Monte and the Sonoran Desert faunas

| Class | Endemic | Son Chi. | Son.– Chi.– Grasslands | Son.– GB | Son.– GB– Chi. | Son.– Thorn Scrub | All Desert + Grasslands | Wide | Total |
|----------------|---------|-----------------|------------------------------|--|---------------------------|-------------------------|-------------------------------|-------|-------|
| Sonoran Desert | | | | | | | | | |
| Anura | 3 | 1 | 5 | _ | _ | 2 | _ | 1 | 12 |
| Lacertilia | 10 | | 2 | 2 | 3 | _ | 2 | _ | 19 |
| Serpentes | 10 | 3 | 4 | _ | 2 | | 2 | 3 | 24 |
| Chelonia | _ | | 1 | 1 | | | | _ | 2 |
| Mammalia | 4 | 1 | 1 | 9 | 3 | 3 | 2 | 60 | 83 |
| Class | Endemic | Monte– Chaco | Monte– Pampas– Pat. | Monte– Chaco– Pampas–Pat | Monte- Chaco- Cord. | Monte- Cord. | Wide | Total | |
| Monte | | | | `````````````````````````````````````` | | | | | |
| Anura | | 11 | _ | _ | 2 | | 2 | 15 | |
| Lacertilia | 12 | 3 | _ | 1 | | _ | _ | 16 | |
| Serpentes | 2 | 7 | | 2 | _ | — | 7 | 18 | |
| Chelonia | _ | 1 | | | | — | | 1 | |
| Mammalia | 3 | | 1 | 3 | — | 2 (3) | 25 | 35 | |

the Chaco and eleven are essentially limited to the Monte-Chaco. Two species are Monte-Cordilleran species that reach the western part of the Chaco, while two others are very widely distributed, with ranges extending into the humid tropics.

Of the three endemic anurans in the Sonoran Desert, *Bufo alvarius* appears to be an old relictual species without near relatives (Blair, 1972), while *B. retiformis* is a desert member of a species group (three species) of small, thick-skinned toads that ranges from the Pacific lowlands of Mexico across the Chihuahuan Desert and into the western part of the central grasslands. The third species is an undescribed member of the *Rana pipiens* complex (Platz & Platz, 1973; Pace, 1974).

Five species extend widely over the Chihuahuan Desert and eastward to the central grasslands (Table 2). One Sonoran toad (*B. microscaphus*) is a Pleistocene relict of the *B. americanus* group and occurs in isolated populations in the Sonoran and Chihuahuan deserts and in the southern California lowlands. Two species extend into the Sonoran Desert from the Pacific lowlands of Mexico. *Bufo mazatlanensis* belongs to the principally lowland tropical–subtropical *B. valliceps* group; *Pternohyla fodiens* apparently evolved from a stock that remains relict on the Mexican Plateau as *P. dentata* (Trueb, 1970). The one other anuran in the Sonoran Desert is a widely distributed species in North America.

Reptiles

Lizard patterns in both deserts differ markedly from those of anurans (Tables 1 and 2). Twelve of fifteen Monte species are endemic, three are Monte-Chaco in distribution (Sage, 1972), and the one amphisbaenid included here (*Amphisbaena angustifrons*) is Monte-Chaco-Pampas-Patagonia in distribution (Gans & Diefenbach, 1972). Eight of the endemic species belong to the single evolutionarily plastic genus *Liolaemus*, three of them undescribed (fide Sage, 1972).

Sonoran Desert lizards show a degree of desert endemism comparable to that evidenced by Monte lizards. In addition to the ten species that are endemic to the Sonoran Desert, seven others have ranges which extend for lesser or greater distances into the Great Basin and/or Chihuahuan deserts. Two of these have Sonoran–Great Basin distributions. Three others range in all three deserts. Two that occur in both the Sonoran and Chihuahuan deserts range eastward into the Great Plains grasslands. Two species that occur in all three deserts range eastward into the grasslands.

Five genera, *Callisaurus*, *Dipsosaurus*, *Heloderma*, *Sauromalus* and *Uma* are endemic to the desert systems of the southwest.

The snakes of the Monte are more diverse in their geographic affinities than either anurans or lizards. Of eighteen species, only two are endemic. Seven colubrids have Monte-Chaco distributions. Two species have a Monte-Chaco-Pampas-Patagonia distribution. Seven species range widely in South America.

The snakes of the Sonoran Desert, like those of the Monte, show more diverse origins than do the anurans and lizards. In addition to the ten endemic species, three species have ranges that also include the Chihuahuan Desert. Two species range in all three deserts. Four of the Sonoran-Chihuahuan snakes range eastward into the Great Plains grasslands. Two species occur in the three deserts and range eastward into the grasslands. Three species range very widely in North America.

Five Sonoran Desert genera are endemic to the desert systems of the southwest and include *Lichanura*, *Chilomeniscus*, *Chionactis*, *Phyllorhynchus*, and *Micruroides*.

The Monte has a single terrestrial turtle, which is primarily Chacoan in distribution. The Sonoran Desert likewise has a single terrestrial species, which ranges northward into the southern edge of the Great Basin Desert. The Sonoran Desert also has an aquatic turtle, an inhabitant of both temporary and permanent ponds.

Geographical affinities of the heterotherms

Thirty-six (72.0%) of the heterothermal vertebrates of the Monte are either endemics or have a Monte-Chaco distribution (Table 1). This high affinity between Monte and Chaco is to be expected on geographic grounds. The Monte represents the xeric end of a moisture gradient that extends from the Brazilian Cerrado through the Chaco and Monte. In this vast area, selection toward xeric adaptation would be expected, with increased selective pressures in this direction as one proceeds westward. West of the Monte, the Andes are an effective barrier to the exchange of taxa with the Chilean lowlands. To the south, the cold Patagonian Desert is relatively limited in area, is climatically inhospitable for heterotherms, and was surely even more inhospitable during the glacial stages of the Pleistocene (Vuilleumier, 1971).

The Sonoran Desert, like the Monte, has a fauna of heterothermal vertebrates with a high proportion of desert endemics (Table 2). Thirty-five (61.4%) of the heterotherms in the Sonoran Desert are limited to desert systems of the southwest. The origins of this fauna are more complex than are those of the Monte vertebrates. This is principally attributable to the fact that, unlike the Monte, the Sonoran Desert is surrounded by source areas for taxa that are candidates for desert adaptation (Fig. 3). There is the Great Basin Desert to the north, a thorn scrub on the Mexican Pacific lowlands to the south, and the extensive Chihuahuan Desert to the southeast. This last grades into the mezquital of Tamaulipas and southern Texas, which is comparable to the Chaco of South America. To the east of the Sonoran Desert there is a moisture gradient through arid grasslands into the vast central grasslands that extend from the Texas coast into central Canada.

Mammals

Thirty-one species of mammals inhabit xeric parts of the northern Monte (A. Cabrera, 1957, 1960; Mares, 1973), while four others (two *Akodon*, one *Felis*, one *Oryzomys*) occur there in moist situations. The caviomorphs, *Octomys mimax* and *Tympanoctomys barrerae*, and an undescribed phyllotine species, are probably limited to the Monte desert. When taxonomic problems among fossorial *Ctenomys* are clarified, it seems certain that at least one, and perhaps more species will be found to be endemic to the Monte.

Twenty-five Monte species (71·4%) range far beyond the desert's boundaries (Table 1). Some of these, such as the carnivores *Felis concolor* and *F. yaquoaroundi*, or the chiropterans *Tadarida brasiliensis, Lasiurus cinereus, L. borealis,* and *Desmodus rotundus,* are found on both the North and South American continents throughout various types of habitats. Other mammals, such as the bats *Histiotus montanus* and *Eptesicus brasiliensis,* and the marsupial *Didelphis albiventer,* range throughout much of South America. The mustelids *Galictes cuia* and *Conepatus chinga,* the felid *Felis geoffreyi,* and the mouse opossum, *Marmosa pusilla,* are found throughout much of southernmost South America. One large group of species, including the canids

Dusicyon culpaeus and D. griseus, the mustelid Lyncodon patagonicus, and a number of rodents, is limited primarily to the main Andean chain and pre-Andean foothills, including the numerous arid valleys interspersed between the mountains. Among rodents, Phyllotis griseoflavus inhabits thorn forests to the east of the Monte, the main Andean chain and the pre-Andean chain. It ranges from southern Argentina to Bolivia, Paraguay, and possibly Brazil (Hershkovitz, 1962). A congener, P. darwini, is found from the Straits of Magellan to central Peru. One of the most desert-adapted Monte rodents. Eligmodontia typus, occurs from southern South America through Peru, with an altitudinal range of over 4500 m. The caviomorph rodents, Galea musteloides and Microcavia australis range primarily along the mountain chain of western South America, with the former extending out of Argentina to southern Peru. Both species extend eastward into either thorn scrub or grasslands.

Generally, species which are limited to the Monte Desert or adjoining semiarid habitats are representatives of pre-Pliocene-Pleistocene invaders of the South American continent; these include particularly armadillos, Zeadyus pichiy, Chaetophractus vellerosus, and Chlamyphorus truncatus, which range from the Monte into the thorn scrub, the Patagonian Desert, and/or the semiarid Cordillera. Among caviomorphs, the Mara or Patagonian 'hare' (Dolichotis patagonum), is primarily distributed through the Monte, dry Chaco and Patagonian areas, and also ranges into the Argentine pampas, or grasslands. The undescribed phyllotine is the only non-caviomorph or edentate that is possibly restricted to the Monte. All other Monte mammals seem to be fairly recent invaders of the desert and include the Monte as only a small part of much larger distributional patterns that range from desert through rain forest, including numerous habitats found between such precipitation extremes.

The Sonoran Desert mammal fauna, while being much more diverse than that of the Monte, is characterized by a smaller proportion of endemic species (4.8%), and a similar portion of wideranging species (72.3%). Some species, such as the lagomorph Lepus alleni, the sciurid Spermophilus tereticaudus, and the heteromyids Dipodomys deserti, Perognathus baileyi, P. amplus, and P. longimembris occur in the Sonoran Desert and contiguous desertic areas, such as the Baja California peninsula, the Chihuahuan desert, or the semiarid Mexican thorn forests. Any species evolving



Fig. 3. Distribution of North American arid and semiarid areas and the Great Plains grassland. Desert limits based on Jaeger (1957); grassland boundaries after Pitelka (1941).

in a more restricted Sonoran desert (Martin & Mehringer, 1965) would be expected to extend their ranges into similarly dry habitats as the deserts expanded during hypsithermal periods, such as are occurring at present. Unlike the northern Monte Desert, North American arid areas are not sharply delineated by high, rugged mountain ranges which would impede vertebrate movements to other habitats. The Sonoran Desert, and other North American arid areas, because of their broad current distributions and past restriction into smaller, more isolated pockets of desert habitat, would be expected to allow a more diversified desert fauna to form than was possible in the Monte Desert (Mares, 1973).

Age of desert occupancy

The large numbers of well-adapted endemic heterothermal vertebrates suggests relatively long existence of the two deserts. However, direct evidence as to just how long these deserts have existed is scarce. The fossil record provides a few clues that are indicative only if we assume that the fossil forms were ecologically similar to existing desert-adapted members of the same lineages. The most desert-adapted genus of anurans in North America is Scaphiopus (see Blair, 1976), which fortunately has a good fossil record. The three living species of one of the two subgenera (Spea) are restricted to deserts or grasslands. One of the two species of the other subgenus (Scaphiopus) occurs in the humid eastern United States but shows the xeric-adapted breeding pattern. The earliest known member of the family, Eopelobates from the late Cretaceous of Wyoming, apparently lived in a humid subtropical coastal plain environment (Estes, 1970a). Zweifel (1956) suggested that Scaphiopus couchi, the most desert-adapted anuran in North America, may have evolved in the southwestern United States in mid-Oligocene. Kluge (1966) described a fossil Scaphiopus from the Lower Miocene of South Dakota and concluded that the two subgenera had probably diverged by the Oligocene. Holman (1968) reported a fossil Scaphiopus (subgenus Scaphiopus) from the Lower Oligocene of Saskatchewan which is clearly related to S. holbrooki of the eastern United States, and he postulated that subgeneric divergence occurred in the Eocene or earlier.

The family Ceratophrynidae is the most xericadapted taxon of Monte anurans. *Wawelia* from the Upper Miocene of Patagonia is indistinguishable from the two living genera, *Ceratophrys* and *Lepi*- *dobatrachus*, on fragmentary available material (Lynch, 1971).

Among reptiles, only lizards provide clues to the age of the desert biota and only with respect to North America. Estes (1970b) has discussed the fossil evidence for the origins of the North American lower vertebrates. The oldest known North American iguanid lizard is Parasauromalus from the Eocene of Wyoming. Avery & Tanner (1971) have suggested that this may represent the ancestral stock of Sauromalus, which is a highly xeric-adapted desert endemic. Estes (1970b) presented Tertiary records for three other desert genera. Paradipsosaurus from the early Cenozoic of Mexico (possibly Oligocene) resembles Dipsosaurus, which is a Sonoran Desert endemic. Phrynosoma, a desert and grassland genus, was in existence in Nebraska by the Miocene. Heloderma, another desert endemic genus, is known from the Oligocene of Colorado. The family Teiidae is particularly interesting. Several teiids are known from the late Cretaceous of western North America, although only the single genus Cnemidophorus occurs there today (Estes, 1969, 1970b). One Cretaceous genus (Penetius from Montana) is said to resemble the extant Monte-Chaco endemic Teius. Another (Chamops from localities in Wyoming, Montana and Alberta) is said to resemble Callopistes of western South America and Tupinambis, which has a Monte-Chaco endemic species but is widely distributed as a genus in South America. The genus Cnemidophorus, living species of which are basically animals of open plant formations, including deserts, is known in North America from the early Miocene of Florida (Estes, 1963).

Fossil mammals provide additional clues. The family Heteromyidae contains the most desertadapted genera of rodents in North America, namely *Perognathus*, *Microdipodops* and *Dipodomys*. The family is known from the Middle Oligocene; the genus *Perognathus* appears in the upper Miocene. A kangaroo-rat type, *Eodipodomys*, is known from the Middle to Late Miocene of Nebraska (Voorhies, 1975).

Heteromyids have penetrated only the northern part of South America. There is no comparable group of rodents in the Monte (Mares, 1973); however, a group of small saltatorial marsupials (family Argyrolagidae) is known to have lived from mid-or late Pliocene to early or mid-Pleistocene in the area of the present Monte and Pampas (Simpson, 1970). These were morphologically quite striking parallels of *Dipodomys*, which leads to the strong



Figure 4. Distribution of arid and semiarid areas of Argentina and the Argentine pampas (grassland). Based on Morello (1958) and Cabrera (1971). The Chaco continues northward and eastward into Paragauy and is contiguous with the Brazilian Cerrado, which is also a thorn scrub type habitat.

presumption that they were adapted to similar ways of life as desert-adapted rodents.

The fossil evidence suggests that adaptations leading toward desert-adapted taxa in North America were occurring over a wide part of the western half of the continent throughout much of the Cenozoic. In South America, the more scanty fossil evidence indicates comparable trends in the area of the present Monte-Chaco-Pampas at least as far back as the Miocene (see Pascual, 1970).

| | Мо | onte | Sonora | n Desert | Shared | | |
|------------------|---------------|-------------|---------------|----------------|----------|---------|--|
| Family | Genera no. | Species no. | Genera no. | Species no. | Genera | Species | |
| Anura | | | | | | | |
| Pelobatidae | | _ | 1 | 2 | <u> </u> | | |
| Leptodactylidae | 4 | 10 | _ | _ | | | |
| Ceratophrynidae | 2 | 4 | _ | | | _ | |
| Bufonidae | 1 | 1 | 1 | 7 | 1 | | |
| Hylidae | | _ | 1 | 1 | | — | |
| Ranidae | | _ | 1 | 1 | | — | |
| Microhylidae | — | _ | 1 | 1 | | _ | |
| Lacertilia | | | | | | | |
| Amphisbaenidae | 1 | 1 | | _ | | _ | |
| Gekkonidae | 1 | 2 | 1 | 1 | | _ | |
| Iguanidae | 2 | 10 | 10 | 16 | _ | _ | |
| Teiidae | 3 | 3 | 1 | 1 | 1 | _ | |
| Helodermatidae | | _ | 1 | 1 | _ | _ | |
| Serpentes | | | | | | | |
| Leptotyphlopidae | 1 | 2 | 1 | 1 | 1 | _ | |
| Boidae | | | 1 | 1 | | | |
| Colubridae | 9 | 12 | 13 | 16 | | | |
| Viperidae | 2 | 3 | 1 | 5 | 1 | | |
| Elapidae | 1 | 1 | 1 | 1 | 1 | | |
| Chelonia | | | | | | | |
| Testudinidae | 1 | 1 | 2 | 2 | _ | _ | |
| Mammalia | | | | | | | |
| Didelphidae | 2 | 2 | 1 | 1 | 1 | | |
| Soricidae | _ | _ | 1 | 1 | | | |
| Desmodontidae | 1 | 1 | 1 | 1 | 1 | _ | |
| Phyllostomatidae | _ | _ | 4 | 4 | _ | _ | |
| Vespertilionidae | 4 | 5 | 8 | 17 | 3 | 2 | |
| Molossidae | 2 | 2 | 2 | 5 | 2 | 1 | |
| Dasypodidae | 3 | 3 | | | | _ | |
| Leporidae | | _ | 2 | 3 | | _ | |
| Sciuridae | _ | _ | 2 | 5 | | _ | |
| Geomvidae | | _ | 1 | 1 | | _ | |
| Heteromyidae | _ | _ | 2 | 15 | | _ | |
| Muridae | 5 | 8 | 5 | 11 | | _ | |
| Caviidae | 3 | 3 | | _ | | _ | |
| Octodontidae | 2 | 2 | | _ | _ | _ | |
| Ctenomvidae | 1 | 1 | | _ | _ | _ | |
| Erethizontidae | | | 1 | 1 | _ | _ | |
| Canidae | 1 | 2 | 3 | 4 | | _ | |
| Procyonidae | _ | _ | 3 | 3 | _ | _ | |
| Mustelidae | 3 | 3 | 3 | 4 | _ | _ | |
| Felidae | 1 | 3 | 2 | 4 | 1 | 2 | |
| Tavassuidae | _ | | 1 | 1 | _ | _ | |
| Cervidae | | _ | 1 | $\overline{2}$ | _ | _ | |
| | | | - | | | | |

Table 4. Composition of the vertebrate faunas of the two deserts

| | Monte | | | | Sonoran | | Shared | | | |
|---------|-------|------|------|------|---------|------|--------|------|------|--|
| Taxa | Fam. | Gen. | Spp. | Fam. | Gen. | Spp. | Fam. | Gen. | Spp. | |
| Anurans | 3 | 7 | 15 | 5 | 5 | 12 | 1 | 1 | | |
| Lizards | 4 | 7 | 16 | 4 | 13 | 19 | 3 | 1 | _ | |
| Snakes | 4 | 13 | 18 | 5 | 17 | 24 | 4 | 4 | _ | |
| Turtles | 1 | 1 | 1 | 2 | 2 | 2 | 1 | _ | _ | |
| Mammals | 12 | 28 | 35 | 18 | 43 | 83 | 5 | 8 | 6 | |

Table 5. Number of families, genera and species of vertebrates in each desert and number of taxa shared

Phylogenetic origins and similarities of the desert vertebrates

The different vertebrate classes differ greatly in the degree of similarity of the two desert biotas with respect to phylogenetic origins (Tables 4 and 5). The anurans are derived mostly from different families. Only one family (Bufonidae) and one genus (Bufo) are common to both deserts. Bufo contributes the majority (seven species) of the Sonoran Desert anurans. These are all desert- and grassland-adapted species, although B. woodhousei ranges widely in North America. Surprisingly, only one Bufo (B. arenarum) enters the Monte and does so by aquaticism as a means of avoiding the issues of desert existence. Bufo has existed in South America since the Paleocene at least (Estes & Reig, 1973) and available evidence points to its origin on that continent (Blair, 1972). Two relatively xeric-adapted types of toads (B. paracnemis and species of the B. granulosus group) occur in the dry Chaco but seemingly have been unable to invade the Monte.

The predominant anuran family in the Monte is the Leptodactylidae with four genera and ten of the fifteen species. The family, including one of its largest genera (*Leptodactylus*), occurs in the mezquital of North America; other genera (*Syrrhophus* and *Hylactophryne*) occur in the Chihuahuan Desert. Absence of the family from the Sonoran Desert may reflect a relatively recent northward movement of a principally South American group.

The most xeric-adapted anurans of the two deserts belong to different families (Ceratophrynidae, *Ceratophrys* and *Lepidobatrachus*, and Leptodactylidae, *Pleurodema*, in the Monte) and Pelobatidae (*Scaphiopus*) in the Sonoran Desert. The latter is a northern family that seems never to have entered South America. The Ceratophrynidae is an endemic South American family.

The only Sonoran ranid is a member of the widely distributed, ecologically tolerant *Rana pipiens*

complex, and exists in the desert region only near permanent water. The genus and family are represented in northern South America by one species that has invaded from North America.

The highly xeric-adapted (fossorial) hylid in the Sonoran Desert (*Pternohyla*) has no counterpart in the Monte. However, a differently xeric-adapted hylid (*Phyllomedusa sauvagei*) lives in the bordering dry Chaco and may yet be found in the Monte (see Shoemaker, Balding & Ruibal, 1972). Although we have not considered them components of the desert faunas, *Hyla* occurs in the canyons of the desert mountains of both continents: *H. pulchella* in the Monte, *H. arenicolor* in the Sonoran Desert.

Three families of lizards are shared by the two deserts, and all but one species in each desert belongs to one of these. The family Iguanidae is best represented, with ten species in the Monte and sixteen in the Sonoran Desert. The level of differentiation at the generic level is quite different in the two deserts. The ten iguanid species in the Monte belong to only two genera, while the sixteen species in the Sonoran Desert are distributed among ten markedly differentiated genera. This difference raises interesting questions about the past history of the lizards in the two deserts. The iguanids seem to have originated in the southern continent, with marked diversity as early as the Paleocene of Brazil, and later spread to North America (Estes, 1970b).

Three genera of Teiidae, a principally South American family, occur in the Monte. One, *Cnemidophorus*, with about thirty species in North America but only five in South America is the only genus common to both deserts. One genus and species of the pantropical, fossorial Amphisbaenidae occurs in the Monte. The family is in North America, with a relict species in Florida. The Sonoran Desert has one species (*Heloderma suspectum*) of the endemic North American Helodermatidae.

Four of the five families of snakes are found in both deserts. Two families (Leptotyphlopidae,

Elapidae) are represented by one genus in each desert, and only the Viperidae, with five species of *Crotalus* in the Sonoran Desert, shows significant speciation in either desert. The Colubridae, with nine genera and twelve species in the Monte and thirteen genera and sixteen species in the Sonoran Desert, provide the largest element. One boid, *Lichanura trivirgata*, is in the Sonoran Desert, while the boa constrictor, *Constrictor constrictor*, occurs in ecotonal areas adjacent to both deserts.

Only two of the twenty-seven genera of snakes are common to the two deserts. These are the primitive fossorial, widely distributed *Leptotyphlops* and the primarily open-country-adapted *Crotalus*. The rattlesnake (*Crotalus durissus*) ranges from Mexico southward through open formations to the Monte and Chaco. This representative of a primarily North American genus may have reached the Monte during a dry phase of the Pleistocene when the Amazon forest was contracted into pockets (see Haffer, 1969). It is found in practically all open formation enclaves that have been explored in the present Amazon forest (Vanzolini & Williams, 1970).

Twenty-three families of mammals are represented in one or both of the deserts (Table 4). Seven of these are common to the two deserts. These include the Didelphidae, with two genera and species in the Monte and one of the genera (*Didelphis*) also in the Sonoran Desert. They include two families of bats, the Vespertilionidae, with four genera and five species, in the Monte and eight genera and seventeen species in the Sonoran Desert; and the Molossidae, with three genera and three species in the Monte and two genera and five species in the Sonoran Desert. Three wideranging species (*Tadarida brasiliensis*, *Lasiurus cinereus* and *L. borealis*) are common to both deserts.

Only one family of rodents, the Muridae (including Cricetines) is common to both deserts, with two genera and four species in the Monte and five different genera and eleven species in the Sonoran Desert. Three families of carnivores occur in both deserts. One canid (*Dusicyon*, with two species) occurs in the Monte; three canid genera (*Canis, Vulpes*, and *Urocyon*, with two species of *Canis*) occur in the Sonoran Desert. Three mustelids (*Lyncodon, Galictes* and *Conepatus*) are in the Monte. One species each of *Taxidea* and *Spilogale* and two species of *Mephitis* are in the Sonoran Desert. One genus (*Felis*) of cats occurs in the Monte, with three species. Two of these species (*F. concolor* and *F. yagouaroundi*) occur also in the

Sonoran Desert along with F. onca and Lynx rufus.

The mammal faunas of the two deserts are similar, then, to the extent that seven families, seven genera, and five species occur in both. The shared species, however, are either highly mobile bats or large wide-ranging carnivores.

Bats and carnivores aside, the differences in the desert faunas are rather larger than for the reptiles. Shrews (Soricidae) are absent from the Monte (the family only extending from North America into northern South America), while one genus and species (Notiosorex crawfordi) occurs in the Sonoran Desert. The family Leporidae is absent from the Monte, but has two genera and three species in the Sonoran Desert. One of these genera (Sylvilagus) ranges southward to Argentina but has not evolved a desert-adapted form. Three families that provide some of the most characteristic Sonoran Desert genera and species are missing from the Monte. The family Sciuridae (with two genera and five species of ground squirrels in the Sonoran Desert) has invaded South America, but the ground squirrels have not. The fossorial Geomyidae are a North American group, with one genus and species (Thomomys bottae) in the Sonoran Desert, but none in South America. The highly desert-adapted Heteromyidae. with two genera and fourteen species in the Sonoran Desert reach only into northern South America. The family Erethizontidae is on both continents but enters the desert only in North America, although Coendu spinosus enters northwestern Argentina in tropical areas (C. C. Olrog, personal communication). Two families of caviomorph rodents, the Caviidae with three genera (Microcavia, Galea and Dolichotis) in the Monte, and Ctenomyidae with one genus and species (Ctenomys fulvus) there, are important contributors to the Monte fauna that are absent in North America.

Three genera of Procyonidae (*Bassariscus*, *Nasua* and *Procyon*) occur in the Sonoran Desert. The family is absent from the Monte, although *Procyon* ranges south to northern Argentina. Two artiodactyl families, Tayassuidae and Cervidae, are represented in the Sonoran Desert by, respectively, one genus and species (*Dicotyles tajacu*) and one genus and two species (*Odocoileus hemionus* and *O. virginianus*). Both families are lacking in the Monte, although they occur in neighbouring regions to the north and east.

In general, the large differences in the two mammalian faunas at the familial level seemingly provide a favourable situation for evolutionary convergence.

Many families which occur in the Sonoran Desert are also found in northwestern Argentina. The large molossid bat, Eumops perotis, occurs in Tucuman, less than 60 miles from Monte habitats. Deer, peccaries, fruit bats, raccoons, 'porcupines,' and cottontails are all found only short distances from the boundaries of the Monte. Most of the species of these families that occur in Argentina are tropically or subtropically adapted. The southern half of the South American continent was reached by traversing the upthrusting Andean chain since the Pliocene-Pleistocene Central American land bridge formed (for the majority of mammals), or by crossing the extensive tropical forest. Probably most mammals moved southward along the western parts of the continent. Obviously few species were able to traverse the Cordillera and Precordillera, and even fewer were then able to adapt to the xeric regimen of the Monte.

Conclusions

(1) Although the two desert systems (Monte-Sonoran) are remarkably alike in many aspects, their vertebrates are generally only distantly related. Most shared genera and species are mammals that belong to taxa which are tolerant of numerous non-desert environments. Shared species and genera form only a small proportion of the total mammalian fauna (4.5%) of the species; 11.5% of the genera). They form an even lower proportion of the fauna of lower vertebrates, with no shared species and only 6.8% of the genera.

(2) The different classes of vertebrates show considerable differences with respect to the similarity of the two desert systems in terms of the numbers of species (Table 1). The numbers of anurans, lizards and turtles are similar in the two deserts. The greater species richness of snakes in the Sonoran Desert is unexplained. The greater species richness of mammals in the Sonoran Desert than in the Monte probably has an historical explanation. Many mammalian taxa which are represented in the Sonoran Desert occur relatively near the boundaries of the Monte Desert in non-desertic habitats, but have not invaded the desert. This can be accounted for by their relatively recent invasion of the South American continent, and their adaptations to invasion routes which included either montane habitats or tropical forests.

(3) Patterns of endemism are comparable between

the two deserts. Heterotherms show a high degree of endemism in both. Mammals show a high representation of species which are wide ranging and also occur beyond the respective desert–grassland systems.

(4) With respect to the age of the desert faunas, the living endemics and the available fossil record suggest that adaptations toward desert life were occurring in western North America during much of the Cenozoic and in South America at least as far back as the Miocene.

(5) The differential patterns of endemism and geological age of the various vertebrate groups form an almost ideal system for investigating the manner in which colonization of the deserts was effected, and of determining the process of convergent evolution in xeric environments.

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