ABSTRACT Current theories regarding colonization of South America by mammals are divided between those supported by fossil evidence, which suggest the original mammal fauna of the isolated continent was augmented by early immigrants (primates, caviomorph rodents, and later, procyonids) with a final large influx of northern mammals occurring with the formation of the Panama land bridge, and an opposing view which states that the purported “recent invaders” are too taxonomically and ecologically differentiated to have colonized since the land bridge arose. The second theory suggests that most extant mammals entered before the Plio–Pleistocene land connection. An analysis of degree of physiological adaptation, natural history, distribution patterns, and a multivariate assessment of convergent evolution of Monte Desert rodents indicate that South American cricetine rodents are not highly specialized for desert life. Their degree of adaptation could be accounted for, in large part, by adaptations for arid or semiarid Andean habitats. No Monte Desert rodent has developed the specialized desert traits that have evolved in most desert rodent faunas of the world, although extinct marsupials similar to living bipedal desert rodents were present in the Monte as recently as late Pliocene. Evidence suggests that Monte caviomorphs have been associated with the desert for a longer period than cricetines, and that the latter represent a fairly recent invasion of the Monte Desert. The data thus support the first hypothesis of South American mammal colonization.

Mammal colonization patterns
There are at present two major conflicting views about the time of arrival of most mammals into South America. One hypothesis states that the arrival has been primarily since the middle of the Pliocene (1–3). The other argues for a much earlier migration into the continent (4–6). In the absence of recent new fossil evidence, progress in solving this problem has seemed to reach an impasse. While working on a project to determine the degree of convergence of the mammals of two disjunct desert scrub ecosystems, one in North America and one in South America, I have been able to devise an independent test of these two theories and find that this multifaceted approach supports the hypothesis of a late arrival into South America by murid (cricetine) rodents.

Since the Paleocene, the original mammal fauna of South America (which included marsupials, edentates, a number of ungulate groups, and condylarths) has been augmented by primates, caviomorph rodents, procyonids, and a large group of placental mammals with close taxonomic affinities to extant North American taxa. This last assemblage included seven orders and 16 families. G. G. Simpson and others (1–3) argue that this great influx of mammals occurred after the Central American land bridge formed, while Hershkovitz (4–6) feels that most, if not all, major groups had island-hopped, or crossed over water into the continent before the bridge was uplifted. Much of the debate centers about the degree of diversification of South American cricetine rodents, which represent 40 genera, and from 150 to 200 species. Hershkovitz suggests that such great differentiation of taxa, and adaptation for very specialized habitats, could not have occurred in the relatively short time since the mid-Pliocene. Nevertheless, fossil evidence indicates that caviomorph rodents and primates were in South America in early Oligocene, and that procyonids entered in earliest Pliocene (1–3). No cricetines appear as fossils before mid-Pliocene. Caviomorph rodents in continental South America today represent 11 families, 40 genera, and 120 species; primates are grouped into 2 families, 15 genera, and 62 species (7). Many of the various taxa are quite distinct, one from another, within each higher category, indicating an old fauna with intermediate extinction.

The arguments on both sides of this problem are logical, conflicting, and stimulating. They have led Savage (8), largely on a reinterpretation of the same data, to propose yet a third hypothesis, which seeks a middle ground between the previous theories. He felt that the Central American bridge formed in early Pliocene, that cricetine rodents entered over water in Miocene times, and that the bulk of mammal exchange between the continents took place after the land bridge was complete.

Desert mammal convergence
I have been studying temperate South American mammal ecology for the last few years, and some of my findings are germane to the above hypotheses. My work has largely centered in the Monte Desert of northwestern Argentina (particularly near Andalgalá, Catamarca Province), where I have attempted to assess the degree of desert adaptation of mammals found there with that found in faunas from other desert regions, particularly the Sonoran Desert of the southwestern United States near Tucson, Ariz. Both deserts are remarkably similar in physiognomy, geomorphology, and climate (9–11). Deserts are harsh environments, and the number of ways in which small mammals may exploit resources and maintain thermal and osmotic balance are probably limited. I suggest that a number of characteristics that are obvious adaptations to desert life have a high probability of appearing among some representatives of any assemblage of small mammals exposed for sufficient time to selective pressures in a desert. For example, the propensity for bipedalism to develop among desert rodents throughout the world (7) implies that selective forces (for predator avoidance or more efficient seed gathering, perhaps) are particularly strong for the evolution of such traits. Since the Monte and Sonoran deserts are about the same age, and as old as some other deserts (9–11), I expect that a number of adaptations for
desert life will be common to some species of both faunas, assuming that the mammal groups involved had been associated with the desert for a similar (or at least sufficient) period of time. Thus a high degree of adaptation for xeric life, such as water conserving mechanisms and the entire array of physiological characteristics this implies, bipedalism, granivory, and so forth, would be expected to be represented in each fauna. This is not to suggest that each small mammal fauna of each desert of the world will possess exactly the same types of adaptations in exactly the same combinations, but that similar adaptations will commonly be found among some members of the various faunas.

**Physiological evidence**

Within the northern Monte Desert, a number of rodent species can be found in various arid and semiarid habitats (Table 1). Most, however, are limited to riparian situations where water flow occurs at least intermittently, and where dense woodlands (*Prosopis, Acacia, Cercidium, Bulnesia*) may be found. Rodents living in these areas climb readily into trees to forage on green plant material. Only a few species occur in more arid localities, and these are generally uncommon (but regular) inhabitants of creosote bush flats (*Larrea*) or saline areas with halophytic plants. The rodents living in the most arid microhabitats should be among the most desert-adapted of the southern species. Small rodents are not highly mobile, and most spend their entire life within a relatively small area. Thus they are highly subjected to selective forces favoring particular adaptations for existence in such habitats. Traits characteristic of evolution in a desert should therefore be particularly marked in such species, and I expect rodents to show much evidence of convergent evolution.

I thus examined physiological adaptations of South American Monte mammals in order to compare their degree of desert adaptation with that of North American desert species. I studied a number of aspects of the water balance of *Eligmodontia typus*, *Phyllotis griseoflava* and *P. darwini* (12, 13), inhabitants of Monte flats, or, for the latter two species, its arid hillsides, and found that none of them was independent of free water. The water loss curves of these species are compared with those of rodents from other desert and non-desert areas in North America in Fig. 1. Monte species appear to be intermediate to many northern desert species and those from more mesic areas in their rates of water loss. Monte species probably obtain water from succulent vegetation and/or insects. Although no other Monte mammal was examined physiologically, observations on natural history of a number of species suggest that all include moist vegetation as part of their diet. Although there may be genetic restraints on the ability of Monte rodents to evolve a high degree of physiological adaptation to aridity, the presence of *Phyllotis gerbillus* (14) of the Peruvian Sechura Desert (which is probably water-independent), and a water-independent non-desert species from bordering areas of the Monte suggest that Monte cricetines possess the necessary genetic plasticity.

**Table 1. The small rodent fauna of the Monte Desert and their habitats in the northern Monte**

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitats</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caviomorphs</td>
<td></td>
</tr>
<tr>
<td><em>Tymanoctomys</em></td>
<td>Lowland desert flats, low scrub areas, halophytic vegetation, sandy flats</td>
</tr>
<tr>
<td>barrerae</td>
<td></td>
</tr>
<tr>
<td><em>Octomyx mimax</em></td>
<td>Lowland desert areas with rocks, rocky desert foothills with large cacti, low scrub areas</td>
</tr>
<tr>
<td><em>Ctenomys fulus</em></td>
<td>Desert flats with <em>Larrea</em> or other low shrubs, riparian forests along dry gulies, upper bajadas</td>
</tr>
<tr>
<td><em>Microcavia australis</em></td>
<td>Desert washes with riparian forests, low scrub areas in high altitude northern-most Monte, permanent water forests</td>
</tr>
<tr>
<td>Cricetines</td>
<td></td>
</tr>
<tr>
<td><em>Eligmodontia typus</em></td>
<td><em>Larrea</em> flats, sandy lowland scrub areas, scrub areas interspersed with taller desert trees, sandy flats with halophytic plants</td>
</tr>
<tr>
<td><em>Phyllotis griseoflava</em></td>
<td>Desert washes with riparian forests, rocky desert hillsides and upper bajadas, permanent water forests</td>
</tr>
<tr>
<td><em>Phyllotis darwini</em></td>
<td>Rocky desert hillsides, permanent water forests</td>
</tr>
</tbody>
</table>

**Fig. 1. Rates of water loss during complete water deprivation (i.e., no free water available, air-dry seed diet) for three species of Monte rodents and selected North American rodents (27).**
is bipedal, although *E. typus* has elongate hind legs and may hop at times.

**Distribution patterns**

When distribution patterns of Monte rodents are examined (Table 2), it is evident that only a few species are wholly restricted to the geographic limits of the desert. Interestingly, all but one of these species are caviomorphs, elements of the old fauna. (The exception is a new species of phyllotine which I collected near Andalgalá. Only one specimen was taken, so it is presumptuous to speak of distribution pattern, although it may well be restricted to the Andalgalá area. This species possesses some degree of desert adaptation and somewhat resembles *E. typus* externally. It is not bipedal and does not possess greatly inflated auditory bullae or have other traits correlated with a very high degree of adaptation to a xeric existence.) *Eligmodontia typus*, *P. griseoflavus*, and *P. darwini* all extend well beyond the limits of the Monte. *Eligmodontia* is found from Tierra del Fuego to Peru, and from sea level to over 4500 m in the Andes. *Phyllotis griseoflavus* occurs in thorn scrub habitats to the east of the Monte and in high mountain scrub areas in Argentina, Paraguay, Bolivia, and possibly Brazil, from sea level to 3000 m, while *P. darwini* may be found in various forest habitats or high altitude scrub areas from the Straits of Magellan to Peru, over a great altitudinal range (15). The high puna, thorn scrub, and rocky Andean hillsides are dry habitats, and it would be expected that animals evolving in, and dispersing through, such environ-

![Fig. 2. Correlation phenogram of North and South American desert rodents, and the rodent fauna from a New Mexico coniferous community. Twenty-eight morphological characters used; cophenetic correlation coefficient = 0.852. With few exceptions, ecological equivalents are clustered together.](image)

**Table 2. Distributional patterns (latitude and longitude) of Monte Desert rodents**

<table>
<thead>
<tr>
<th>Latitude</th>
<th>50°-55°</th>
<th>55°-60°</th>
<th>60°-65°</th>
<th>65°-70°</th>
<th>70°-75°</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;20° S</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>5,7</td>
<td></td>
</tr>
<tr>
<td>20°-25° S</td>
<td>6</td>
<td>6</td>
<td>4,5,6,7</td>
<td>3,7</td>
<td></td>
</tr>
<tr>
<td>25°-30° S</td>
<td>6</td>
<td>4,6</td>
<td>3,4,5,6,7</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>30°-35° S</td>
<td>4</td>
<td>2,3,4,5,6,7</td>
<td>7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>35°-40° S</td>
<td>4,5,6</td>
<td>4,5,6,7</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>40°-45° S</td>
<td>4,5</td>
<td>6,7</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>45°-50° S</td>
<td>4,5</td>
<td>5,7</td>
<td>7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&gt;50° S</td>
<td>4,5</td>
<td></td>
<td>7,7</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1 = *T. barrerae*, 2 = *O. mimax*, 3 = *C. fulvus*, 4 = *M. australis*, 5 = *E. typus*, 6 = *P. griseoflavus*, 7 = *P. darwini*.

ments into southern South America would be somewhat preadapted to the aridity of the lowland desert. The cricetines do not appear to have evolved in the Monte Desert at either the generic or specific level, although the new phyllotine could be an exception. A number of caviomorph species are restricted to the Monte, including two genera (*Octomys* and *Tymanoctomys*); these are also inhabitants of the most xeric habitats. They have probably been associated with the desert for a long period. Distribution patterns can be interpreted as supporting the suggestion that caviomorph rodents have evolved for a longer period in the Monte, with some groups being autochthonous, while cricetines generally have more catholic habitat choices and seem to include the Monte as a small part of much broader distribution patterns.

**Multivariate analyses**

I utilized multivariate analyses to attempt to arrive at a more rigorous determination of convergence and degree of desert adaptation. Cluster analysis (16) groups organisms (or populations, species, etc.) together on the basis of number of shared characteristics over many measurements. I used morphological measurements that strongly implied ecological function rather than any random assortment of traits. Characteristics associated with desert life (e.g., degree of inflation of auditory bullae, degree of bipedality, color, countershading, and so forth), as well as more general ecological characters (e.g., body size, relative ear and tail lengths, vibrissae density, numerous dental traits which may reflect diet, and so on) were used in analyses. Thus, instead of clusters of animals with shared phenotypes, I expect organisms with similar niches (i.e., ecological equivalents) to be grouped together. Since desertic habitats have never been contiguous between the continents, possession of desert traits by species that have evolved from forest or montane ancestors suggests convergence. Those species that are closely equivalent would be tightly clustered, while species pairs only slightly similar, ecologically, should be more loosely grouped. For comparative purposes, the rodent fauna of a non-desert site (the Ponderosa pine community of the Sandia Mountains of central New Mexico) was included in analyses. The New Mexico fauna is phylogenetically closely related to that of the Arizona Desert (some genera and species are shared), while the two desert faunas are more distantly related (17–20). Thus, if a broad suite of characteristics were being used in analyses, a clustering of taxonomically closely related species might be.
expected, rather than a grouping of unrelated taxa. A correlation phenogram of species with similar ecologies (using 28 unweighted traits) is given in Fig. 2. A number of Sonoran Desert species have an ecological equivalent in the Monte. Thus field mice, peromyscines, are clustered with the two small desert phyllotines (*E. typhus* and *P. gerbillus*), while North American pack rats (*Neo*omys) are grouped with *P. griseoflavus*. Squirrels are clustered with cavies (*Microcavia australis*), and the closest cross-continental cluster occurs between fossorial rodents (tuco-tucos and gophers). All of these groupings are logical when the natural history of each species is considered (12). The caviomorph *Octomys mimax*, which is similar in overall ecology to pack rats, was loosely clustered with heteromyids (kangaroo rats and pocket mice), a group which is practically the apotheciosis of desert-adapted species. *Octomys* shares a number of desert traits with heteromyids. Distance measurements (rather than correlation) and a 44-trait analysis clustered *Octomys* with pack rats.

Principal Component Analysis (PCA) indicated that tuco-tucos (*Ctenomys*) possessed more desert characteristics than North American pocket gophers (*Thomomys*), and that *Octomys mimax* was one of the most desert-adapted Monte species. Basically, however, there were no ecomorphological equivalents of heteromyids in the Monte, although PCA ranked South American *E. typhus* and *P. gerbillus* as intermediate between northern pocket mice (heteromyids) at an upper level, and field mice at a lower level, in their degree of desert adaptation (Fig. 3).

Ecological equivalents of various degrees of similarity exist in both deserts, but if one wishes to examine all species of a community at one time, other methods such as canonical and discriminant function analyses must be used (21). I used the same morphological measurements and compared three communities: the Monte, Sonoran, and New Mexico Forest small rodent faunas. If community convergence has occurred, then when each fauna is plotted in n-dimensional space ($n = $ number of traits analyzed), the distance between the two desert faunas should be less than that found between the related northern faunas. Traits that maximize the variance between the various assigned groups are utilized in forming canonical variates. The first canonical axis (which accounts for 99% of the total group dispersion) is shown in Fig. 4. The desert faunas are closely converged when either is compared to the forest fauna. In the second analysis, I assigned two groups, the Sonoran Desert and Forest assemblages, and listed each South American species as being of unknown affinity. On the basis of shared characteristics, each southern species, except the cavy (*Microcavia australis*), was given 100% probability of pertaining to the Sonoran Desert fauna. *Microcavia*, which is most common in thorn scrub habitats to the east of the Monte and generally limited to forested areas within the northern lowland Monte Desert, was assigned to the Forest fauna.

**Zoogeographic implications**

The multivariate analyses essentially support the physiological, distributional, and natural historical observations of Monte rodents. Overall faunal convergence of desert rodents is indicated when those communities are compared with a coniferous forest fauna. Also, a number of northern desert species find their analogue (albeit seldom an "exact" analogue) in the southern desert. Nevertheless, the most highly desert-adapted rodents in the United States, the heteromyids, have no close ecological equivalents in the Monte, although *Octomys mimax*, a caviomorph, approaches them in some desert traits. Fossorial tuco-tucos are extremely similar to pocket gophers, and are probably more desert-adapted than gophers.

At this point the situation is somewhat puzzling. The theory presented here would predict that a "classic" desert rodent should have evolved in the Monte, and yet no such species lives there today. *Eligmomdonia* appears to be evolving in that
direction, but it has not yet attained a very marked degree of desert adaptation. Why has this type of animal failed to evolve in the Monte? This problem was clarified for me when I encountered the paper by G. G. Simpson on fossil marsupials (family Argyrolagidae) which inhabited parts of the present-day Monte and bordering regions in the Pliocene (22). These marsupials were strikingly similar to living kangaroo rats or Old World desert jerboas. Apparently the entire morphological mosaic associated with a desert existence (and similarities presumably would extend to other areas of their biology) evolved in or near the Monte, and the group later became extinct. The existence of this group is important, for it demonstrates that suitable habitat existed at that time for such a strategy to have evolved and that such individuals lived in the Monte as recently as the Pliocene. This could explain why bipedal caviomorphs never evolved. Such a niche was filled by marsupials and the niche only became "empty" fairly recently in the evolutionary time scale. I speculate that it was probably not competition which caused the extinction of the argyrolagids, since no potential competitor is known. The Monte was greatly affected by Pleistocene periods of advancing and retreating ice. Some of the northern valleys where argyrolagids occurred were possibly occupied by glaciers. The southern Monte and adjacent habitats were also modified by Pleistocene glaciers and associated climatic effects (ref. 23, and B. Simpson, personal communication). Argyrolagids could have been restricted to a relictual area of desert where they faced new predators with varied hunting methods (the Pliocene-Pleistocene influx of northern carnivores), as well as some competition from invading cricetines and from caviomorphs. Such a relict desert area may have been located in what is currently the hottest and driest part of the Monte, and where autochthonous caviomorphs are found today. The Pleistocene Monte could have been greatly reduced in area and could have been an ideal setting for the subsequent desert marsupial extinction.

Cricetines are not known as fossils in South America before late Pliocene. My data suggest that they have not been associated with the Monte for an extended time period (i.e., pre-Pliocene). Desert adaptation evidenced by Monte cricetine fossils could well have evolved in response to selective pressures in Andean habitats which would have been preadaptations for life in the lowland Monte. Highly desert-adapted marsupials did exist in the Monte, however, and living caviomorphs also appear to have been present in the desert for a long time, as do armadillos (28). Interestingly, Australian murids have also diversified greatly since invading that continent and it was originally thought that a Miocene invasion was required in order to allow time for such marked speciation (24), but recent fossil evidence indicates that they did not enter before the Pliocene (25). The Australian continent is much less diverse in numbers of habitats and topographic relief than is South America, so it should not be too surprising to find an even greater diversification of cricetine rodents in the Neotropics. We are learning that population isolation and subsequent genetic diversification can occur much more rapidly than was previously supposed (26). Had cricetines been associated with the Monte for a long period, we would expect either fossils, or a high degree of desert adaptation, or both. We have neither. I suggest that diversity of living cricetine species is not so great, nor adaptations to very specialized habitats so pronounced, to warrant the supposition of an early invasion by this group into South America. If the cricetines do not support ideas of early colonization, then it may not be necessary to invoke a pre-Pliocene invasion by other mammal groups which are less diverse than the rodents, and which also have left no fossils. Occam's razor leads me to discount dispersal over a fairly extensive water barrier by diverse mammal taxa and their subsequent failure to leave fossil traces. While data of living species can be interpreted in various ways, only subsequent fossil discoveries will clarify the very interesting patterns of colonization of South America by mammals.

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