

ANALYSIS OF CHANGING DIVERSITY PATTERNS IN CENOZOIC LAND MAMMAL AGE FAUNAS, SOUTH AMERICA

by

Larry G. MARSHALL * & Richard L. CIFELLI **

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* Institute of Human Origins, 2453 Ridge Road, Berkeley, California 94709, U.S.A.

** Oklahoma Museum of Natural History and Department of Zoology, University of Oklahoma, Norman, Oklahoma 73019, U.S.A.

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Mots-clés: Amérique du Sud, Faunes mammaliennes continentales, Cénozoïque, Chronofaunes, Extinction, Apparition, Théorie des équilibres, Diversité.

ABSTRACT

Comparison of various measurements of taxonomic evolution using stratigraphic range data for orders, families and genera of land mammals indicates several means by which deficiencies of the South American fossil record (e.g., presence of hiatuses, unequal temporal and geographic representation of ages, unequal systematic treatment) may be normalized, thus permitting a less distorted appreciation of diversity pattern and trend. Initial radiation of native taxa resulted in a relative equilibrium by early Eocene time. Subsequent increases in absolute diversity were apparently induced by immigration at the family level and by environmental factors at the generic level. Miocene through Pleistocene phases of faunal stability, herein characterized as chronofaunas, are punctuated by rapid turnover events resulting from a complex of factors, including adaptive radiation of immigrant taxa into unoccupied eco-space; environmental and concomitant habitat change induced by orogenic events of the Andes; and biotic interactions between native and immigrant taxa, including competition and prey naivete. The first two factors account for major faunal transitions in the South American middle and late Tertiary; immigration-induced turnover may have been of greater importance in shaping the character of the fauna upon the Great American Interchange and the arrival of man in the Neotropics.

RESUME

La comparaison de différentes mesures d'évolution taxonomique basées sur la répartition stratigraphique des ordres, familles et genres de mammifères terrestres indique différents moyens par lesquels des lacunes dans le registre fossile d'Amérique du Sud (par exemple, la présence de hiatus, l'hétérogénéité dans la répartition temporelle et géographique des étages mammaliens, le traitement systématique inégal) pourraient être normalisées, permettant ainsi une appréciation moins distordue de la diversité et de ses changements. La radiation initiale des taxons indigènes se traduit par un équilibre relatif à l'Eocène inférieur. Par la suite, l'accroissement de la diversité absolue provient apparemment d'une immigration au plan familial et de facteurs environnementaux au plan générique. Du Miocène au Pléistocène, les phases de stabilité faunique, caractérisées ici comme des chronofaunes, sont ponctuées par des événements de renouvellements rapides. Ceux-ci résultent, semble-t-il, d'un ensemble de facteurs, incluant les radiations adaptatives des taxons immigrants dans des espaces écologiques inoccupés, les changements de l'environnement, et ceux concomitants des habitats, induits par les phases orogéniques des Andes, et les interactions biotiques, dont la compétition et la naïveté des proies, entre taxons endémiques et les immigrants. Les deux premiers facteurs rendent compte des transitions fauniques majeures survenues dans le Tertiaire moyen et supérieur d'Amérique du Sud; les renouvellements provoqués par les immigrations pourraient avoir une grande importance pour déterminer les caractéristiques des faunes après le "Great American Interchange" et l'arrivée de l'homme dans les néotropiques.

INTRODUCTION

The land mammals of South America have been extensively used in the development of tempo and mode concepts in macroevolution (e.g., Simpson, 1953, 1965). Three features of the land mammal record of South America render it so extraordinarily useful for such studies.

First is its completeness. Fossil faunas are first well-represented in the Late Cretaceous and are known from every epoch of the Cenozoic. This record is so complete that the mammals have been used to subdivide Cenozoic time into discrete land mammal ages based on unique associations of taxa, stage of evolution of taxa, first and

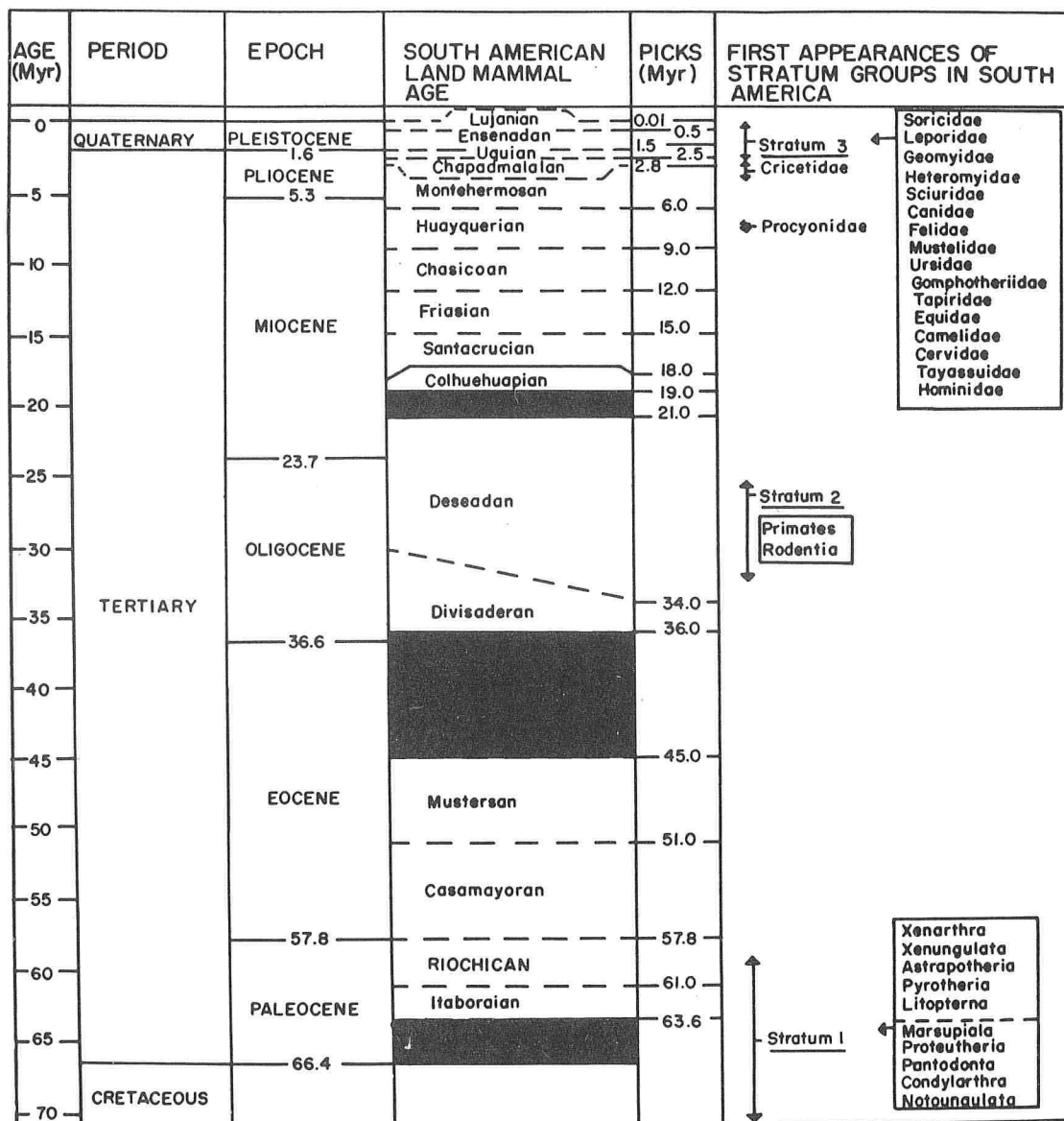


Figure 1. - Chronology of South American land mammal ages (adopted from Marshall, 1985, fig. 1). Solid areas denote hiatuses in knowledge of fossil land mammal faunas.

last appearances, and changing faunal associations through time (Evernden *et al.*, 1964; Savage & Russell, 1983). The relative time succession of these land mammal ages was first established by the Argentine paleontologist Florentino Ameghino (e.g., 1906) and by the early 1970's there was consensus regarding the approximate correlation of these ages with the geologic time scale (e.g., Patterson & Pascual, 1972). During the last 10 years many "key" rocks and faunas have been calibrated using radioisotopic dating and/or magnetostratigraphy, and an absolute time frame for the Age of Mammals in South America is now available (fig. 1). Most of the Tertiary part of this record is known primarily from Argentina in the southern part of the continent, and all but two of the land mammal ages recognized here (Itaboraian, Brazil; Friasian, Chile) are defined on Argentine rocks and faunas. The chronology of land mammal ages used in this study follows Marshall (1985) with the addition of age data for Deseadan and Santacrucian rocks and faunas published subsequently by Mac Fadden *et al.* (1985), Marshall, Cifelli, *et al.* (1986) and Marshall, Drake, *et al.* (1986). We regard the La Venta fauna of Colombia as Santacrucian in age rather than Friasian, based on data presented in Lundberg *et al.* (1986) and unpublished work by ourselves and colleagues.

The second feature relates to the fact that South America was an "island continent" during most of Cenozoic time and apparently had no direct land connection with any other continent from possibly 75 Ma until the appearance of the Panamanian land bridge about 3 Ma. Thus, the land mammals evolved largely in isolation, and the faunas are dominated by autochthonous and endemic taxa, some of which developed striking morphological similarities convergent with mammals elsewhere in the world (Cifelli, 1985).

Simpson (1940, 1950, 1980) recognized three "stratum groups" of South American land mammals based on their time of first appearance in the fossil record (see fig. 1). Stratum 1 includes groups present at or just prior to the beginning of the Age of Mammals, including the orders Marsupialia, Proteutheria, Pantodonta, Condylarthra and perhaps Notoungulata which are first recorded in the Late Cretaceous (Marshall & de Muizon, 1988); and Xenarthra, Xenungulata, Astrapotheria, Pyrotheria and Liptopterna which first appear in the early Tertiary. There is still no consensus as to whether these groups evolved in South America or dispersed there at or just prior to their first appearance in the fossil record. Stratum 2 includes platyrrhine primates and caviomorph rodents, which are first recorded in rocks of Deseadan age (fig. 1). It is now agreed that these groups arrived in South America as waif dispersants either from Africa or more probably from North America sometime in the late Eocene or earlier (e.g., Patterson & Wood, 1982). Stratum 3 includes taxa that participated in the Great American Faunal Interchange (Webb, 1976) during the Late Cenozoic. Procyonid carnivores are first recorded in rocks of Huayquerian age and cricetid rodents in rocks of late Montehermosan age in Argentina (fig. 1). These two groups probably arrived as waif dispersants from North or Central America prior to the emergence of the Panamanian land bridge. Other groups, including Insectivora (Soricidae), Lagomorpha (Leporidae), Rodentia (Geomyidae, Heteromyidae, Sciuridae, and additional Cricetidae), Carnivora (Canidae, Felidae, Mustelidae, Ursidae, and additional Procyonidae), Proboscidea (Gomphotheriidae), Perissodactyla (Equidae, Tapiridae), Artiodactyla (Camelidae, Cervidae, Tayassuidae), and eventually man "walked" to South America across the Panamanian land bridge following its appearance about 3 Ma (Webb, 1976; Marshall, 1985) (fig. 1).

The third feature is the influence of plate tectonics and associated orogenic movements on the evolutionary development of the fauna. The lateral, primarily westward, movement of the South American plate beginning about 100 Ma resulted in the initial isolation of some or all stratum 1 groups. Subsequent recurrent orogenic

activity linked to subduction among the western edge of the continental plate produced the Andes Cordillera, which became a barrier to moisture rich Pacific winds and eventually produced an intensified rain shadow along their eastern side in the southern part of the continent (Patterson & Pascual, 1972; Pascual, 1984). The uplift altered many local ecologies and created new ones (e.g., dry woodlands and forests, savannas, pampas grasslands, true deserts, high montane habitats) which provided mammals with new challenges and opportunities through time (Patterson & Pascual, 1972). During the last 3.5 Myr recurrent glacial advance and retreat in the Andes also affected the distribution of savanna and tropical habitats and the animals in them (Webb, 1978; Marshall & Patterson, 1981; Marshall, 1985). Lastly, both lateral and vertical movements of the South American plate, coupled with glacioeustatic drops in sea level, resulted in continental suturing with North America and formation of the Panamanian land bridge. This geological event permitted the Great American Faunal Interchange, which represents the best-documented example of an intermingling of two long-separated continental faunas in the fossil record (Webb, 1976, 1978; Simpson, 1980; Marshall, 1981; Marshall *et al.*, 1982).

SCOPE OF STUDY

The above three features of the South American record provide a unique opportunity to examine patterns and processes relating to changing diversity patterns of land mammal age faunas on that continent. In this study we analyze aspects of the land mammal record from Late Cretaceous to Recent, an approach which permits recognition of changes related directly to processes occurring in the Late Cenozoic from culminating trends in faunal composition begun much earlier. For this study we assess the patterns of land mammals as determined from knowledge of range data of orders, families and genera (a copy of our data set will be supplied to interested persons upon request). Our data set represents an upgrading of the ranges of fossil taxa presented in Marshall *et al.* (1983, 1984), and of living taxa presented in Webb & Marshall (1982). In compiling this new data set we consulted numerous colleagues with the specific purpose of obtaining a consensus of opinion regarding the validity and ranges of all taxa. Other interpretations regarding taxonomic usage we employ in our data set clearly exist, a feature which stems largely from the fact that we are "lumpers" as opposed to "splitters", and we omit taxa of dubious validity.

Earlier versions or aspects of this study have been presented by Webb (1976), Marshall (1981), Marshall *et al.* (1982), Webb & Marshall (1982), Raup & Marshall (1980) and Cifelli (1985). These and related studies demonstrate that upgrading of old data sets permits new insights into faunal diversity dynamics. We concur with Webb (1976) that the validity of such studies "is the product of the reliability of the taxonomy and the precision of the chronology upon which it is based."

We define some key terms as follows: diversity, all taxa in a clade or fauna during a given time period (in this case, land mammal age) including known and inferred occurrences (i.e., if a taxon is unknown in a given age, but is known from preceding and succeeding ages, it is recorded as present in the intermediate age[s]); originations, first known occurrences in the fossil record; and extinctions, last known occurrences in the fossil record. The following abbreviations are used: ka, thousands of years ago, a point in time; Ma, millions of years ago, a point in time; Myr, millions of years, a duration of time.

ANALYSIS OF DATA SET

The data set includes ranges of 18 orders, of which 9 (50%) are extinct and 9 (50%) extant; 86 families of which 50 (58%) are extinct and 36 (42%) extant; and 794 genera, of which 615 (77%) are extinct and 179 (23%) extant. We use several approaches for analyzing the data set in an attempt to identify recurrent patterns in each. This approach is employed because there are numerous techniques available to assess diversity changes through time, some of which have inherent biases and others which attempt to normalize for these biases.

SPINDLE DIAGRAMS

The diversity of families and genera are shown in the form of "spindle diagrams" in figures 2-7. The width of the spindles represents total diversity in each age, extended upward and downward to include the duration of that age. If a hiatus occurs between two ages, the diversities of sub- and superadjacent ages are extended to the middle of that hiatus to permit continuity of the spindles.

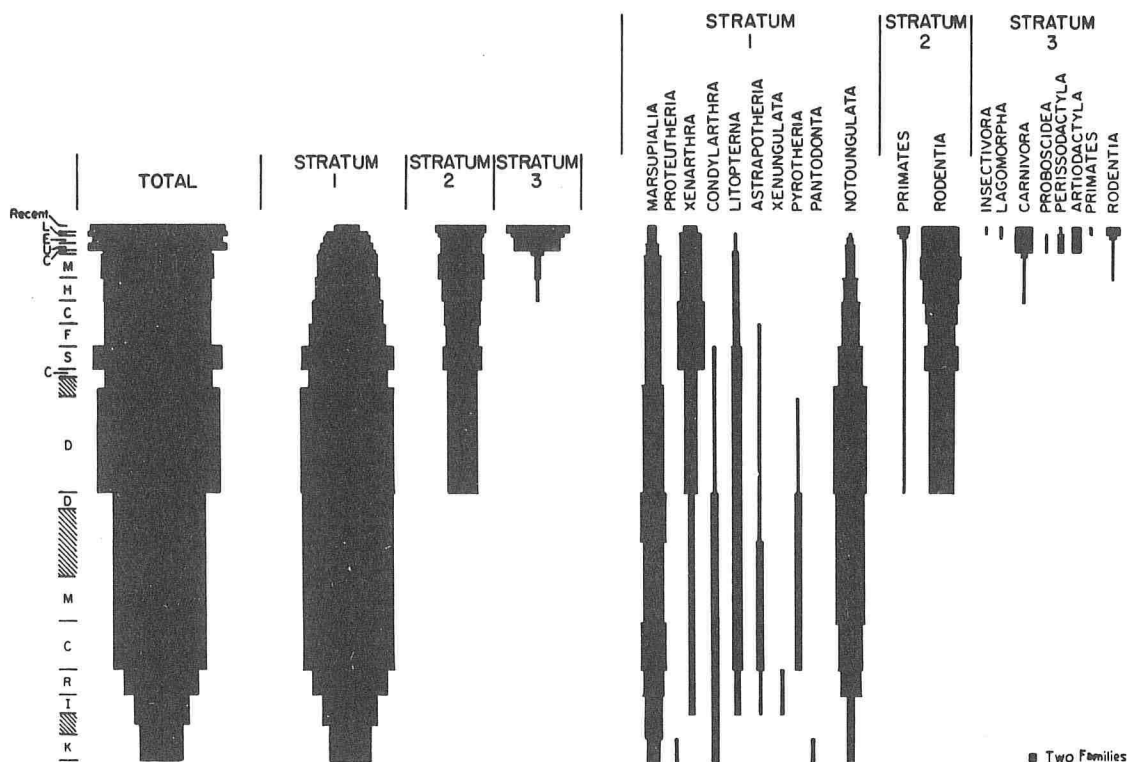


Figure 2. – Spindle diagrams showing total diversity of land mammal families (left), of families in each stratum group (center), and of families in each order within stratum groups (right). Time scale at left follows figure 1.

Family diversity

In figure 2, family diversity is shown for the total fauna, for each stratum group, and for orders within each stratum group. Total diversity increases markedly from Late Cretaceous to Casamayoran, remains constant until Deseadan, decreases slightly in Colhuehuapian, increases in Santacrucian, decreases slightly in Friasian and remains relatively constant until Uquian when it again increases (with some slight fluctuation) to a level retained in Recent faunas. Stratum 1 diversity shows a marked increase from Late Cretaceous to Casamayoran, which is retained (except for a slight decrease in Colhuehuapian) until Santacrucian when it begins a steady decrease until Chapadmalalan, and a sharp decrease thereafter; the largest decrease is from Lujanian to Recent.

The pattern of family diversity within each stratum group permits the following interpretation of trends in the total diversity pattern. The first half of the Cenozoic record shows diversification of stratum 1 with attainment of what appears to be an equilibrium level (see below) by Casamayoran time; a level retained until Deseadan. The sharp increase in Deseadan is due to the addition of stratum 2 families; the relatively constant diversity pattern between Friasian and Chapadmalalan is due to a decrease in stratum 1 and an inverse increase in stratum 2, with a balance between extinctions of one group and originations of the other; and the sharp increase from Uquian to Recent is due primarily to appearance of stratum 3 families (i.e., decrease of stratum 1 is offset by increase of stratum 3 and, to a lesser extent, stratum 2).

Family diversity within stratum 1 orders shows the following features: a) some orders (Proteutheria, Pantodonta, Xenungulata) are present early in the record, are represented by one family each, and persist for short periods of time; b) other orders (Condylarthra, Litopterna, Astrapotheria, Pyrotheria) appear early in the record, attain little family diversity at any point in time, and persist for long periods of time; c) Marsupialia show diversity increase in the early Cenozoic, a leveling-off and attainment of maximum diversity in the middle Cenozoic (with some minor fluctuations), and a decrease in the late Cenozoic; d) Xenarthra appear early in the record but attain little diversity in the first half of the Cenozoic, increase in diversity in the second half of the Cenozoic, with maximum diversity in Santacrucian to Chasicooan, and decrease in latest Cenozoic (Huayquerian to Recent); and e) Notoungulata appear early in the record and increase in diversity steadily until Deseadan, then decrease sharply thereafter and go extinct in Lujanian. In stratum 2 orders, Primates are represented only by one family from Deseadan to Ensenadan, then increase to three from Lujanian to Recent; Rodentia are very diverse at their time of first appearance in Deseadan and show a steady increase from Chasicooan to Chapadmalalan. Among stratum 3 orders, the Carnivora, Artiodactyla, and to a lesser degree the Perissodactyla, show notable diversity in Uquian, and Rodentia in Lujanian to Recent; the other orders (Insectivora, Lagomorpha, Proboscidea, Primates) are of minor importance in terms of family diversity.

The overall patterns of family diversity among potentially vicar (see below) orders suggests the following trends: a) diversity decline in Notoungulata and to a lesser degree Litopterna between Santacrucian and Chapadmalalan correlates with an inversely comparable increase of stratum 2 Rodentia (and with stratum 1 Xenarthra between Santacrucian and Chasicooan); b) Uquian to Recent decrease in Notoungulata and less so in Litopterna correlates with appearance of stratum 3 Proboscidea, Perissodactyla, and Artiodactyla; and c) decline in Marsupialia between Uquian and Recent correlates with appearance of stratum 3 Carnivora.

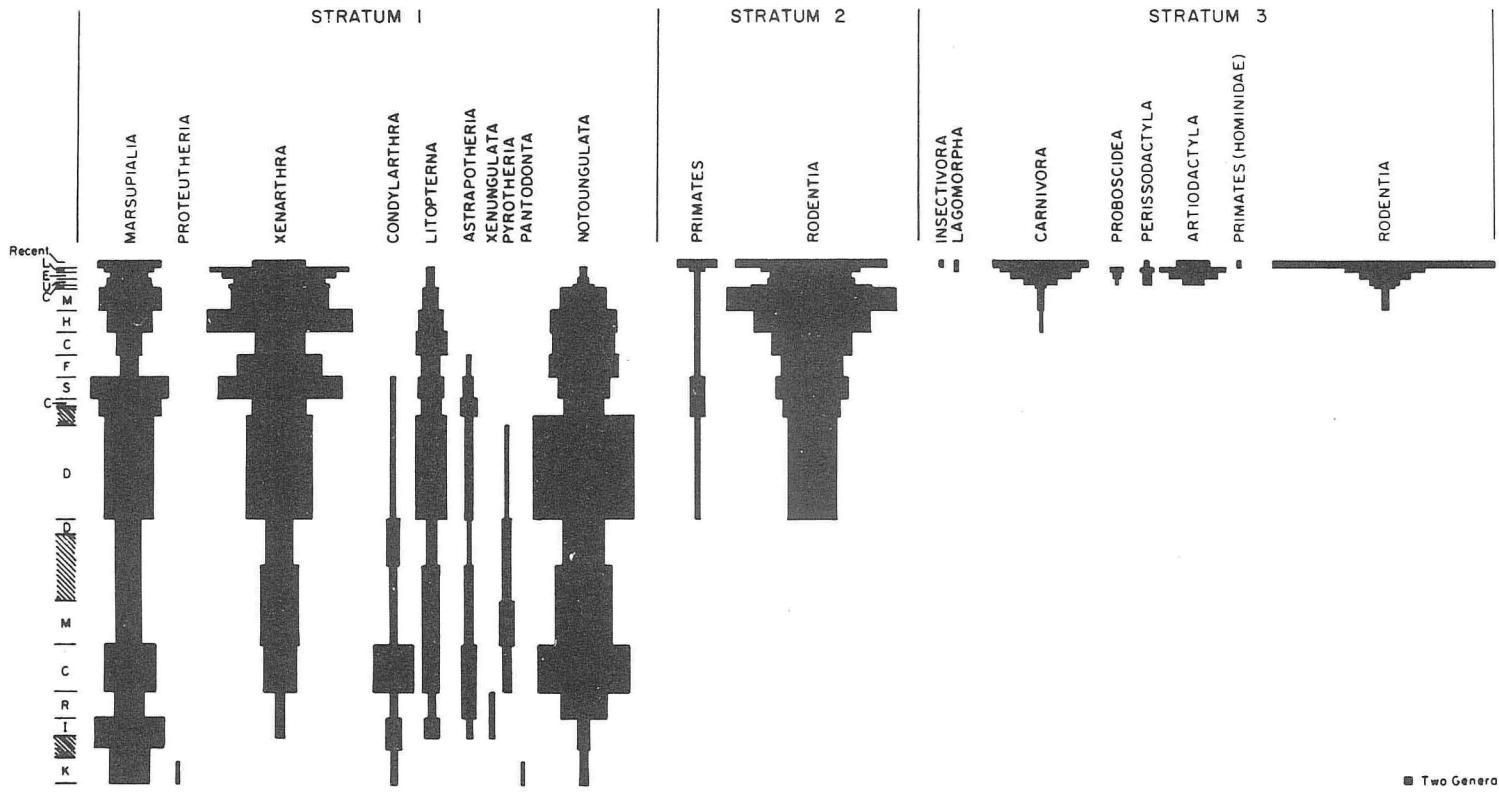


Figure 4.— Spindle diagrams showing diversity of land mammal genera in each order within each stratum group. Time scale at left follows figure 1.

Generic diversity

In figure 3, generic diversity is shown for the total fauna and for each stratum group. Total diversity shows a very sharp increase from Late Cretaceous to Itaboraian, a slight decrease in Riochican, then a sharp rise in Casamayoran, a sharp drop in Mustersan and Divisaderan, a significant rise in Deseadan, Colhuehuapian and more so in Santacrucian, then a sharp drop in Friasian and Chasicoan, a sharp rise in Huayquerian and Montehermosan, a drop in Chapadmalalan, then a sharp rise from Lujanian to Recent.

Stratum 1 post-Divisaderan diversity was very high in Deseadan, decreased in Colhuehuapian, increased in Santacrucian, decreased in Friasian and more so in Chasicoan, rose sharply in Huayquerian, declined steadily from Montehermosan to Uquian, rose steadily from Ensenadan to Lujanian, then declined sharply from Lujanian to Recent. Stratum 2 groups are very diverse at their time of first appearance, increasing in Colhuehuapian, decrease from Santacrucian to Friasian, increase steadily from Chasicoan to Montehermosan, decrease steadily from Chapadmalalan to Ensenadan, then increase sharply from Lujanian to Recent. Stratum 3 groups show a significantly steady increase from Huayquerian to Recent. Comparison of stratum diversity patterns shows the following: a) enrichment of total diversity in Deseadan by addition of stratum 2 groups; b) notable decrease of stratum 1 groups and inverse increase of stratum 2 groups in Colhuehuapian and Chasicoan to Montehermosan; c) inverse of (b) in Santacrucian and Friasian; d) decline of stratum 1 and 2 groups and inverse increase of stratum 3 groups between Chapadmalalan and Ensenadan; and e) enrichment of total faunal diversity by addition of stratum 3 groups.

The generic diversity of orders within each stratum group is shown in figure 4. Patterns within stratum 1 orders show the following features: a) three groups (Proteutheria, Xenungulata, Pantodonta) appear early in the record, are represented by only one or two genera, and persist for short periods of time; b) Astrapotheria and Pyrotheria appear early in the record, attain little generic diversity during any single age, and persist for long periods of time; c) Marsupialia are very diverse at their time of first appearance in Late Cretaceous and increase sharply in diversity in Itaboraian, decrease in Riochican, increase in Casamayoran, decrease during Mustersan and Divisaderan, increase steadily from Deseadan to Santacrucian, decrease sharply from Santacrucian to Friasian, increase steadily from Friasian to Montehermosan, decrease from Chapadmalalan to Ensenadan, then increase from Lujanian to Recent; d) Xenarthra show, with minor fluctuations, a steady increase from Itaboraian to Santacrucian, a sharp steady decrease from Santacrucian to Chasicoan, a very sharp rise in Huayquerian, a decrease in Montehermosan to Uquian, an increase in Ensenadan to Lujanian, then a very sharp decrease from Lujanian to Recent; e) Condylarthra attain maximum diversity in Casamayoran, but are low in diversity during the major part of their record; f) Litopterna show, with minor fluctuations, a slight increase from Itaboraian to Deseadan, a slight but consistent decrease from Colhuehuapian to Chasicoan, then a steady decrease from Chasicoan to Lujanian; and g) Notoungulata show a sharp increase between Late Cretaceous and Casamayoran, a decrease in Mustersan and Divisaderan, a sharp increase in Deseadan, a sharp decrease in Colhuehuapian, a steady increase from Colhuehuapian to Friasian, a high level between Friasian and Huayquerian, then a continuing decrease from Montehermosan to Lujanian with a very sharp drop between Montehermosan and Chapadmalalan. In stratum 2 orders, Primates reach minor diversity only in Colhuehuapian and Santacrucian, and show a steady increase from Ensenadan to Recent. Rodentia show a remarkably steady increase from Deseadan to Montehermosan, a decrease from Chapadmalalan to

Ensenadan, then an increase from Lujanian to Recent. Stratum 3 orders (particularly Carnivora, Proboscidea, Artiodactyla, Rodentia) show consistently sharp and steady increases between Uquian and Recent; the only notable decreases are extinction of Proboscidea and diversity drops of Perissodactyla and Artiodactyla between Lujanian and Recent.

The following between order trends in pattern of diversity change among potential vicar (see below) groups appear noteworthy; a) steady diversity increase of stratum 2 Rodentia between Friasian and Montehermosan correlates with concurrent decreases in stratum 1 Litopterna and Notoungulata; b) Chapadmalalan to Ensenadan decreases in Litopterna, Notoungulata, and stratum 2 Rodentia correlate with appearance and steady diversity increase of stratum 3 Carnivora.

The generic diversity of families within stratum groups is shown in figures 5 (stratum 1), 6 (stratum 2), and 7 (stratum 3). These figures illustrate the complex changing importance of each family through time with regard to their contribution to faunal diversity. Some notable features of stratum 1 families (fig. 5) include high diversity of: a) Caroloameghiniidae and Didelphidae in Late Cretaceous and Itaboraian; b) Borhyaenidae, Polydolopidae, Didolodontidae, Sparnotheriodontidae, Isotemnidae, and Oldfieldthomasiidae in Casamayoran; c) Borhyaenidae, Caenolestidae, Dasypodidae, Interatheriidae, and Notohippidae in Deseadan; d) Borhyaenidae and Caenolestidae in Colhuehuapian; e) Borhyaenidae, Caenolestidae, Dasypodidae, Megalonychidae, and Interatheriidae in Santacrucian; f) Dasypodidae, Megalonychidae, and Toxodontidae in Friasian; g) Dasypodidae and Toxodontidae in Chasicuan; h)

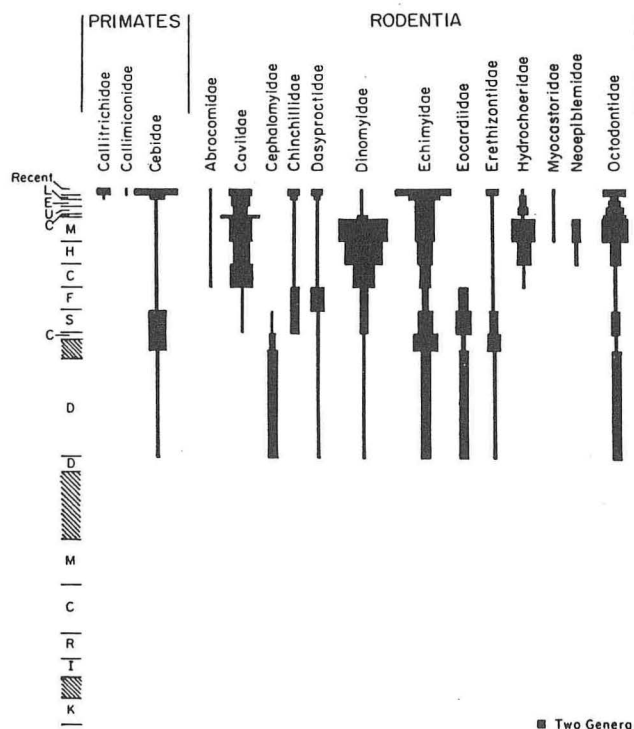


Figure 6. – Spindle diagrams showing diversity of land mammal genera in each family within each order in stratum 2. Time scale at left follows figure 1.

Dasypodidae, Glyptodontidae, Megalonychidae, and Toxodontidae in Huayquerian; i) Didelphidae, Dasypodidae, Glyptodontidae, and Toxodontidae in Montehermosan; and j) Didelphidae, Dasypodidae, Glyptodontidae, and Mylodontidae in Uquian to Lujanian. The persisting dominance of Dasypodidae between Casamayoran and Recent, large diversity of Borhyaenidae and Caenolestidae between Deseadan and Santacrucian, large diversity of Interatheriidae and Notohippidae in Deseadan, diversity increase of Didelphidae and Glyptodontidae between Huayquerian and Lujanian, diversity increase of Toxodontidae between Friasian and Montehermosan, and sharp decrease of Toxodontidae between Montehermosan and Chapadmalalan are particularly apparent.

Notable diversity features of stratum 2 families (fig. 6) include: a) sharp increase of Caviidae and Echimyidae between Chasicosan and Recent; b) sharp increase of Dinomyidae between Chasicosan and Montehermosan; and c) sharp increase of Hydrochoeridae and Octodontidae between Huayquerian and Montehermosan. The sharp decrease of Dinomyidae and Hydrochoeridae between Montehermosan and Chapadmalalan warrants special notice.

Notable diversity features of stratum 3 families (fig. 7) include: a) strikingly sharp increase of Cricetidae between Montehermosan and Recent; and b) less dramatic but nonetheless prominent increases in Canidae, Felidae, Mustelidae, Gomphotheriidae, Camelidae, Cervidae, and Tayassuidae from Uquian to Lujanian (or Recent). Extinction of Gomphotheriidae and Equidae, and decreases in Felidae, Camelidae, Cervidae, and Tayassuidae at the end of Lujanian time are prominent features of this stratum group.

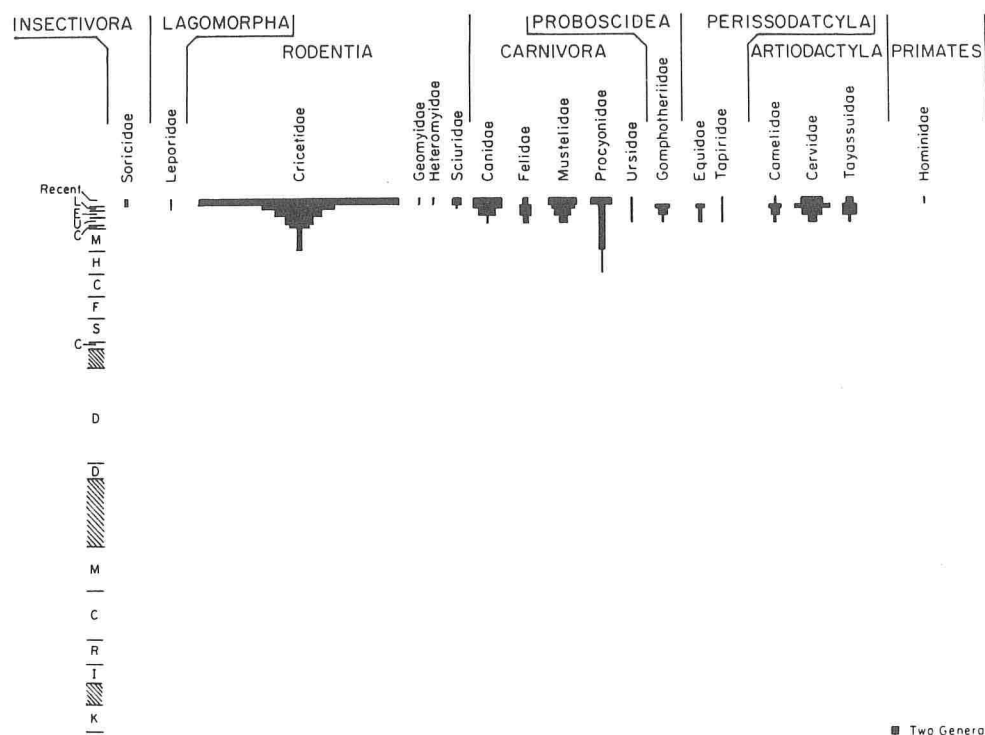


Figure 7. — Spindle diagrams showing diversity of land mammal genera within each order in stratum 1. Time scale at left follows figure 1.

COMPARISON OF DIVERSITY PATTERNS: FAMILIES AND GENERA

The total diversity of families and genera during Cenozoic time are plotted and compared in figure 8. The number of families increased from 15 in Itaboraian to 20 in Riochican, then to 25 in Casamayoran, remaining at that level until Deseadan when it increased sharply to 33, dropped to 29 in Colhuehuapian, rose to 35 in Santacrucian, decreased to between 29 and 30 between Friasian and Chapadmalalan, increased sharply to 37 in Uquian and remained at about that level thereafter; today there are 36 families.

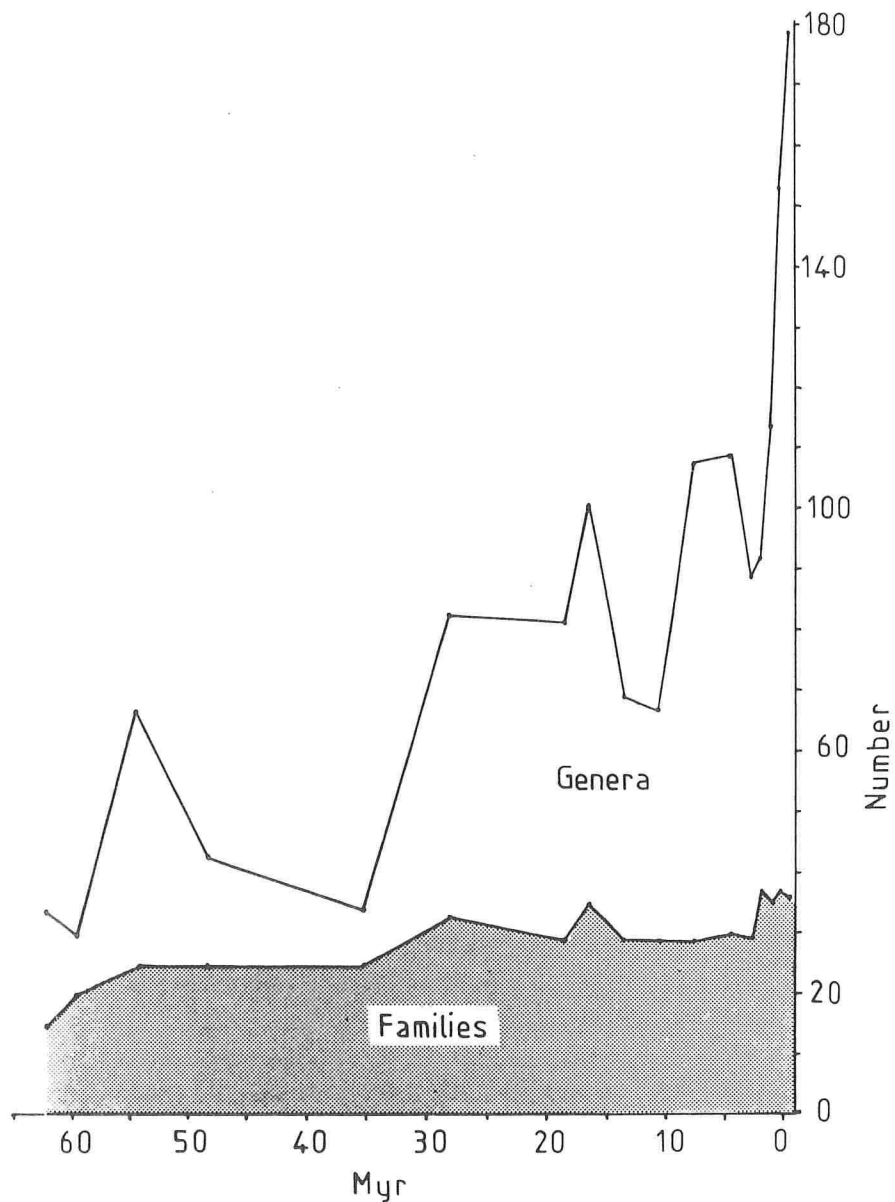


Figure 8. – Diversity of land mammal families and genera during Cenozoic. Time scale at bottom follows figure 1.

The taxonomically more robust generic data set shows a drop from 34 genera in Itaboraian to 30 in Riochican, a significant rise to 67 in Casamayoran, a drop to 43 in Mustersan, a further drop to 34 in Divisaderan, a rise to 83 in Deseadan, 81 in Colhuehuapian, and 101 in Santacrucian, a subsequent decrease to 69 in Friasian and 67 in Chasicosan, a rise to 108 in Huayquerian and 109 in Montehermosan, a sharp drop to 89 in Chapadmalalan, then a continued rise to 92 (Uquian), 114 (Ensenadan), 153 (Lujanian), and 179 (today).

The family data set suggests abrupt faunal enrichment by addition of stratum 2 and, later, stratum 3 groups, while the generic data set suggests more gradual but continued enrichment, albeit accelerated by the appearance of strata 2 and 3.

PERCENTAGE CONTRIBUTION OF STRATUM GROUPS TO FAUNAL DIVERSITY: FAMILIES AND GENERA

The percentage contribution of families and genera in each stratum group to total faunal diversity is shown in figure 9. These diagrams impress the sharp declining importance of stratum 1 groups following the appearance of stratum 2, and a later and sharper decline following the appearance of stratum 3. The abrupt increase in importance of stratum 3 groups is evident. Interestingly, stratum 2 contribution is relatively consistent through time in families (30 to 35%), while genera show a much larger fluctuation in relative importance (20 to 40%). Just prior to addition of stratum 3 groups, strata 1 and 2 contributed 60 and 40%, respectively, to family diversity; and 70 and 30%, respectively, to generic diversity. Today, the respective contributions of strata 1, 2 and 3 are 19, 37, and 44% for families; and 17, 29, and 54% for genera.

GENERAL PATTERNS OF EXTINCTION: FAMILIES

The known duration of extinct and extant families in figures 5-7 are plotted in increasing order of length in figure 10. The extinct and extant families are plotted separately to see what effect, if any, the "artificial truncation" of the Recent may have on duration patterns. The plot of extinct families (fig. 10, left) shows a relatively even distribution, going from families known from single localities and/or ages at left to those with ranges that span most of the Cenozoic at right. We interpret this general pattern to indicate that the probability of a family becoming extinct is unrelated to how long it has been in existence (although low generic diversity may increase a family's probability of going extinct; see below). The plot of extant family durations (fig. 10, right) shows definite "steps" in the pattern that are related to high origination events. From left to right, the first "step" of short durations represent families known only in Recent faunas; the second "step" at about 3.0 Ma represents the appearance of stratum 3 families; and the third "step" at about 35 Ma represents the appearance of stratum 2 families.

A second feature of family extinctions is that, except for those in the Lujanian (see below), families with low generic diversity were affected more than those with high generic diversity. Of the 45 families which go extinct in the Cenozoic, 29 (65%) are represented by one genus in the age it goes extinct; 5 (12%) by 2 genera, and 6 (13%) by 3 genera. (Likewise, all 9 orders which go extinct are represented by only one family at the time of last appearance.) Thus, a family's probability of going extinct increases as generic diversity decreases. The extinction event in the Lujanian involves 18% of all family extinctions in the Cenozoic, all of which had more than one genus at the time, and includes 50% of all multi-genus families that went extinct.

A third feature is that, at the time the 45 families went extinct, they included a

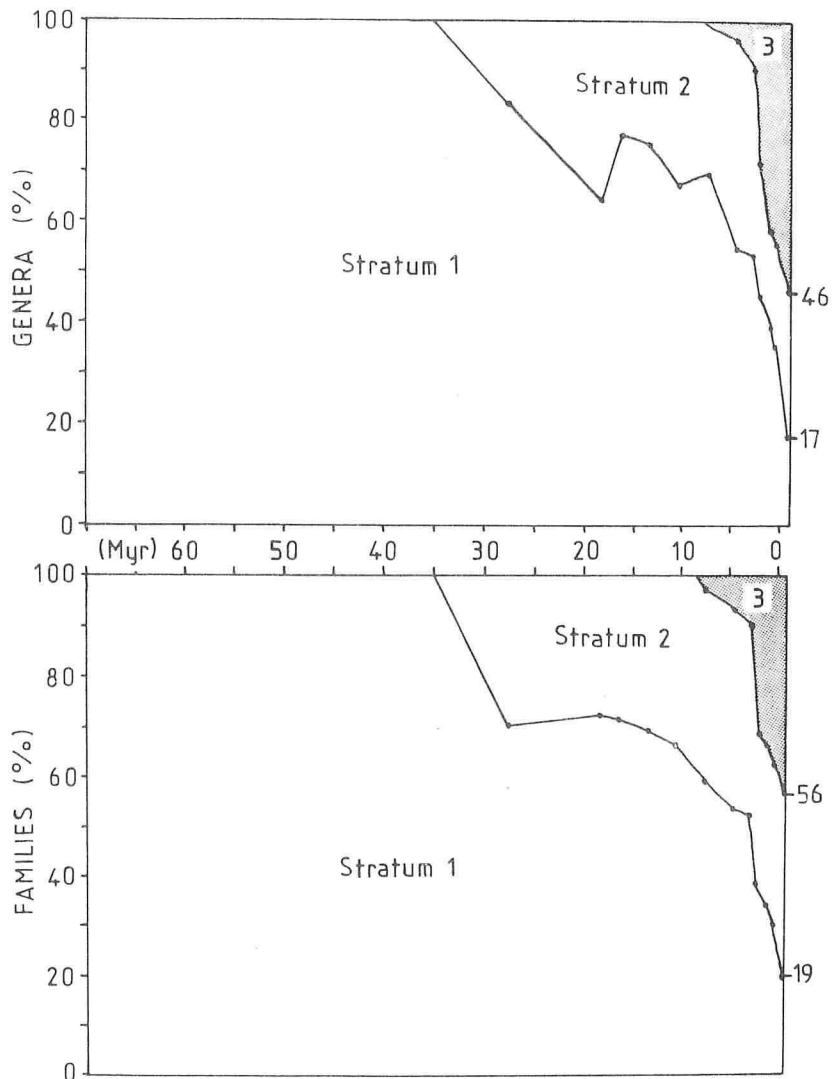


Figure 9. – Diagrams showing percentages of genera (top) and families (bottom) in stratum groups through time (stratum 3 is stipple). Time scale at bottom follows figure 1.

total of only 86 (14%) of the 600 generic extinctions recorded in the Cenozoic. Likewise, the 9 orders which go extinct are represented at the time of extinction by only 9 (20%) of the 45 families which go extinct, and these 9 families include only 14 (2%) of the 600 generic extinctions. Thus, the step from generic to family extinctions involves loss of 86% of the generic data set, and an additional 86% loss occurs in the step from families to orders.

A fourth feature is the number of genera present in families through Cenozoic time. The average number of genera/family in each age is computed in table 1. There is an overall trend for increase in number of genera/family through time; the average in the Paleocene and Eocene is 2.0, while all later faunas average 3.0 genera/family. Thus, present-day families average about 30% more genera than families in the early Cenozoic.

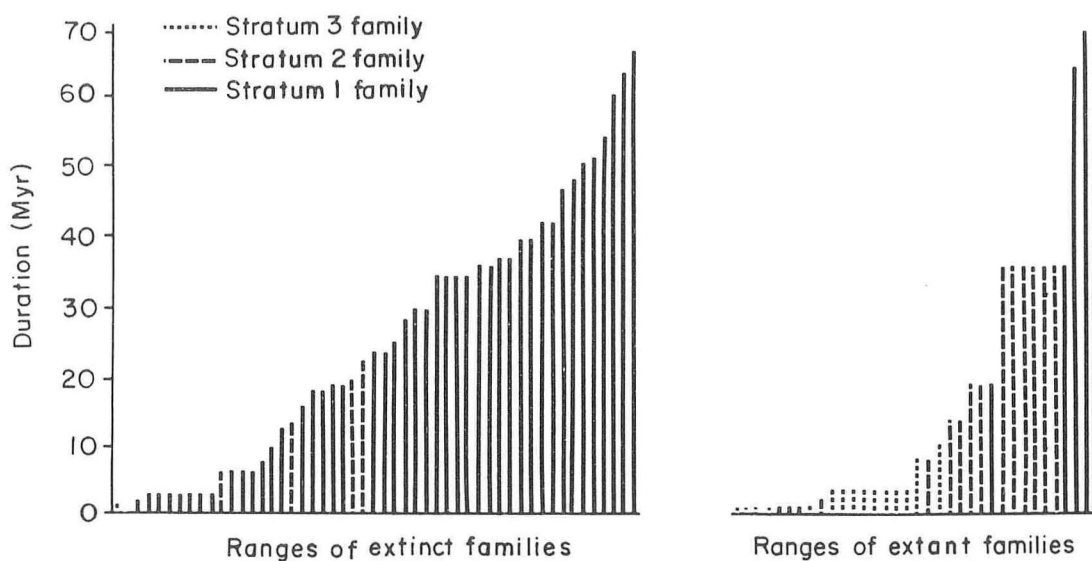


Figure 10. – Durations of extinct (left) and extant (right) mammal families in South America.

Age	d	Families					Genera					G/F	
		Si	Ei	Er	Oi	Or	Si	Ei	Er	Oi	Or		
R	–	36	–	–	7	–	179	–	–	85	–	5.0	
L	0.5	37	8	<u>16.0</u>	3	6.0	153	56	<u>112.0</u>	48	96.0	4.2	
E	1.0	35	1	1.0	0	0.0	114	9	9.0	40	40.0	3.3	
U	1.0	37	3	3.0	9	9.0	92	25	25.0	39	39.0	1.7	
C	0.3	29	2	<u>6.7</u>	1	3.3	89	37	<u>123.0</u>	19	63.0	3.1	
M	3.2	30	2	0.6	2	0.6	109	47	14.7	43	13.4	3.6	
H	3.0	29	1	0.3	4	1.3	108	46	15.3	63	21.0	3.7	
C	3.0	29	2	0.7	2	0.7	67	22	7.3	52	17.3	2.3	
F	3.0	29	2	0.7	0	0.0	69	55	18.3	31	10.3	2.4	
S	3.0	35	6	2.0	6	2.0	101	65	21.7	67	22.3	2.9	
C	1.0	29	0	0.0	0	0.0	81	35	35.0	65	65.0	2.8	
D	13.0	33	4	0.3	14	1.1	83	69	5.3	72	5.5	2.5	
D	2.0	25	6	3.0	2	1.0	34	10	5.0	10	5.0	1.4	
M	6.0	25	2	0.3	4	0.7	43	28	4.7	29	4.8	1.7	
C	6.8	25	4	0.6	7	1.0	67	58	8.5	51	7.5	2.7	
R	3.2	20	2	0.6	5	1.6	30	11	3.4	19	5.9	1.5	
I	2.6	15	0	0.0	9	3.5	34	27	10.4	34	13.1	2.3	
Total (average)		63.6	–	45	(0.7)	75	(1.0)	–	600	(9.4)	767	(10.7)	(2.9)

Table 1. – Extinction and origination rates of families and genera in each land mammal age. Abbreviations in column Age follow land mammal ages of figure 1; d, duration in millions of years (Myr) of land mammal ages (following figure 1); Si, number of taxa; Ei, number of extinctions; Er, extinction rate (= Ei/d); Oi, number of originations; Or, origination rate (= Oi/d). Far right column gives average number of genera per family in each land mammal age based on the proportion Si genera/Si families. Highest extinction rates are underlined.

SPECIFIC PATTERNS OF ORIGINATION AND EXTINCTION

The total number of originations and extinctions of families and genera are compared in figure 11, based on statistics presented in table 1. These diagrams are useful for visualizing gross origination and extinction patterns through time. For families, originations exceeded extinctions between Late Cretaceous and Mustersan, a feature which accounts for the general pattern of diversity increase in the early Cenozoic (fig. 8). Extinctions were slightly higher than originations in Divisaderan. In Deseadan, originations greatly exceeded extinctions as a result of addition of stratum 2, and this event resulted in faunal enrichment. Santacrucian shows a high peak of both origination and extinction, while the average diversity was the same as in preceding and succeeding ages, a feature which accounts for the abnormally high diversity peak in figure 8 between Chasicuan and Chapadmalalan, originations were only slightly higher than extinctions, and overall diversity remained relatively constant. Originations greatly exceeded extinctions in Uquian, and extinctions were notably higher than originations in Lujanian. These data document three major periods of faunal enrichment (Itaboraian-

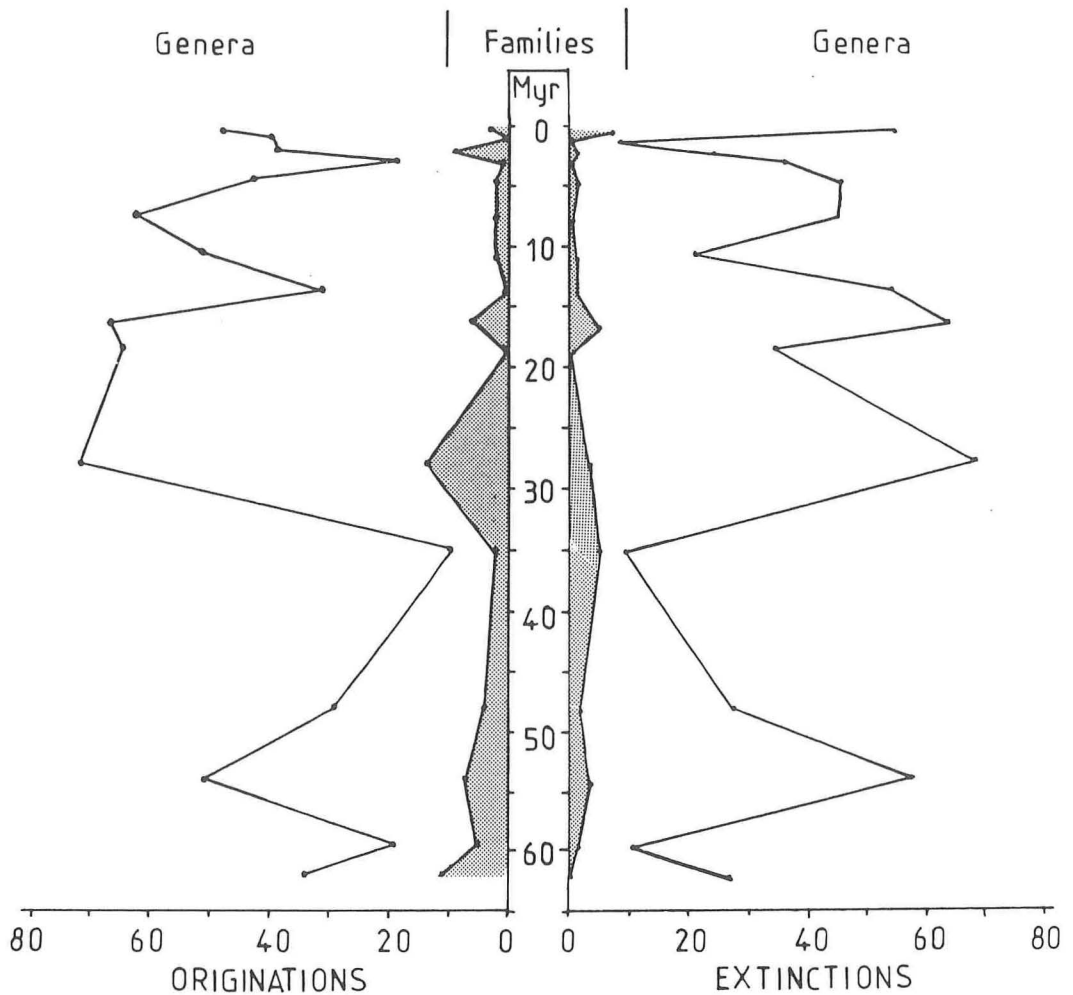


Figure 11. – Total number of originations and extinctions of families and genera. Vertical time scale follows figure 1.

Riochican, Deseadan, Uquian) and one predominant extinction event (Lujanian); the rest of the record shows relative stability in diversity due to a balance between originations and extinctions.

The generic pattern also shows a general overall balance between originations and extinctions. The permanent diversity increase in post-Deseadan faunas results from high originations and low extinctions in Colhuehuapian time (fig. 8). In Santacrucian, originations and extinctions are balanced. The sharp diversity drop in Friasian results from extinctions being about 45% higher than originations. In Chasicooan, originations are about 58% higher than extinctions, and in Huayquerian originations are 27% higher. Originations and extinctions are nearly balanced in Montehermosan, although extinctions are 8% higher. In Chapadmalalan, extinctions are 50% higher than originations; in Uquian, originations are 35% higher than extinctions; in Ensenadan, 78% higher; and in Lujanian, extinctions outstrip originations by 14%. The sharp diversity decrease in Chapadmalalan (fig. 8) is due to very low originations, while the sharp diversity increase from Uquian to Ensenadan is due to very high originations and very low extinctions. The Lujanian extinctions are basically balanced by originations. The overall trend for diversity increase between Friasian and Lujanian is attributed to originations averaging 27% higher than extinctions.

The above patterns demonstrate that diversity decrease can result from high extinction, low origination, or a combination of the two; the obverse is true for diversity increase. During the Cenozoic the total number of family originations (75, table 1) was about 40% higher than extinctions (45; table 1); the total number of generic originations (767, table 1) was about 22% higher than extinctions (600).

RATES OF TAXONOMIC EVOLUTION

Extinction and origination rates of total family and generic diversity are given in Table 1. Since extinctions (and originations) in a given time interval are cumulative indices (Lasker, 1978), they can be normalized for intervals of unequal duration by dividing total number of extinctions that occur in that interval by its duration, with the resultant rate thus expressed in terms of extinctions per Myr. Origination rates are calculated in the same manner (Webb, 1969).

The total average rate of family origination (1.10/Myr) was about 30% higher than that of extinction (0.7/Myr). The majority of family extinction rates were between 0.3 and 0.7/Myr, while higher rates occurred in Ensenadan (1.10/Myr), Santacrucian (2.0/Myr), Divisaderan (3.0/Myr), and Uquian (3.0/Myr); the highest rates are in Chapadmalalan (6.7/Myr) and particularly in Lujanian (16.0/Myr). The majority of origination rates were between 0.6 and 2.0/Myr, while higher rates occurred in Chapadmalalan (3.3/Myr), Itaboraian (3.5/Myr), and Lujanian (6.0/Myr); the highest rate was in Uquian (9.0/Myr). Origination rates exceeded extinction rates in Itaboraian-Mustersan, Deseadan, and Uquian; extinction rates exceeded origination rates in Divisaderan, Friasian, Chapadmalalan, Ensenadan, and Lujanian; while the rates were balanced, or nearly so, in Colhuehuapian, Santacrucian, Chasicooan, and Montehermosan.

The total average of generic origination (10.7/Myr) was about 12% higher than that of extinction (9.4). The majority of extinction rates were between 3.4 and 23/Myr, while high rates occurred in Uquian (25) and Colhuehuapian (35), and significantly high rates in Lujanian (112) and Chapadmalalan (123). The majority of origination rates were between 4.8 and 25, with high rates in Uquian (39) and Ensenadan (40), and very high rates in Chapadmalalan (63), Colhuehuapian (65), and especially Lujanian (96). Origination rates exceeded extinction rates in Itaboraian, Riochican, Colhuehuapian,

Chasicuan, Huayquerian, Uquian, and Ensenadan; extinction rates exceeded origination rates in Casamayoran, Friasian, Montehermosan, Chapadmalalan, and Lujanian; rates were balanced in Mustersan, Divisaderan, Deseadan, and Santacrucian.

If only exceptionally high rates for both families and genera are considered, the following patterns emerge: a) high family origination rates (3.5/Myr) in Itaboraian correlate with initial radiation of stratum 1 groups; b) high family (6.7) and generic (123) extinction rates in Chapadmalalan correlate with appearance of stratum 3 groups; c) high family (9.0) and generic (39) origination rates in Uquian, and high generic (40) origination rates in Ensenadan correlate with the major phase of arrival of stratum 3 groups; and d) very high family (16) and generic (112) extinction rates in Lujanian correlate with arrival of man (see below). The high generic extinction and origination rates in Colhuehapan are related to hiatus effects, as discussed below.

EXTINCTION AND ORIGINATION RATES AMONG STRATUM GROUPS: GENERA

Extinction and origination rates of genera in each stratum group from Deseadan to Lujanian are given in table 2. We first consider rates within each stratum group through time, then compare strata 1 and 2 from Deseadan to Chapadmalalan, and lastly, all three strata from Uquian (when diversification of stratum 3 begins) to Lujanian. For

Age	Stratum 1		Stratum 2		Stratum 1 & 2	Stratum 3	
	Ei	Er	Ei	Er	Er	Ei	Er
L	32	<u>64.0</u>	3	6.0	70.0	21	42
E	5	5.0	3	3.0	8.0	1	1
U	11	11.0	8	8.0	19.0	6	6
C	20	<u>66.7</u>	17	<u>56.7</u>	<u>123.0</u>	0	0
M	27	8.4	20	6.3	14.7	0	0
H	38	12.7	8	2.6	15.3	0	0
C	14	4.7	8	2.6	7.3	—	—
F	40	13.3	15	5.0	18.3	—	—
S	48	16.0	17	5.7	21.7	—	—
C	25	25.0	10	10.0	35.0	—	—
D	55	4.2	14	1.1	5.3	—	—
	Oi	Or	Oi	Or	Or	Oi	Or
L	14	28.0	12	24.0	52.0	22	44.0
E	8	8.0	6	6.0	14.0	26	26.0
U	14	14.0	7	7.0	21.0	18	18.0
C	7	23.3	7	23.3	46.6	5	16.7
M	19	6.0	21	6.5	12.5	3	0.9
H	43	14.4	19	6.3	20.7	1	0.3
C	34	11.3	18	6.0	17.3	—	—
F	21	7.0	10	3.3	10.3	—	—
S	52	17.3	15	5.0	22.3	—	—
C	37	37.0	28	28.0	65.0	—	—
D	58	4.4	14	1.1	5.5	—	—

Table 2. – Extinction and origination rates of genera in each stratum group. Abbreviations as in table 1.

stratum 1, origination exceeded extinction rates in Deseadan, Colhuehuapian, Santacrucian, Chasicoan, Huayquerian, Uquian, and Ensenadan; the reverse is true for Friasian, Montehermosan, Chapadmalalan, and Lujanian. Notable are the extremely high extinction rates in Chapadmalalan and Lujanian (66.7 and 64/Myr, respectively).

In stratum 2, origination exceeded extinction rates in Colhuehuapian, Chasicoan, Huayquerian, Ensenadan, and Lujanian; extinction exceeded origination rates in Santacrucian, Friasian, Chapadmalalan, and Uquian; they were balanced in Deseadan and Montehermosan. The outstanding feature is the very high extinction rate in Chapadmalalan (56.7/Myr).

Origination rates are consistently higher than extinction rates for all ages in which stratum 3 is present, with especially high rates in Uquian (18/Myr), Ensenadan (26), and Lujanian (44). Between the Deseadan and Chapadmalalan, stratum 1 had 2% more originations (271) than extinctions (267), while stratum 2 had 17% more originations (132) than extinctions (109). In terms of rates, stratum 1 had 21% higher extinctions (19/Myr) than origination (15/Myr), while stratum 2 had only 9% higher extinction (11/Myr) than origination (10/Myr) rates. The decrease in stratum 1 and increase in stratum 2 is attributed primarily to higher percentage of overall number of originations relative to extinctions of stratum 2, and the higher extinction rate in stratum 1.

For the three strata from Uquian to Lujanian, stratum 1 had 25% higher number of extinctions (48) than originations (36); stratum 2 had 44% higher number of originations (25) than extinctions (14); while stratum 3 had 58% higher number of originations (66) than extinctions (28). The combined total number of extinctions and originations of strata 1 and 2 was nearly the same (62 and 61, respectively). In terms of rates, stratum 1 had 27% higher extinctions (27/Myr) than originations (17/Myr); stratum 2 had 50% higher originations (12/Myr) than extinctions (6/Myr); while stratum 3 had 38% higher originations (29/Myr) than extinctions (18/Myr). Strata 1 and 2 combined had 12% higher rates of extinction (33/Myr) than origination (29/Myr). Although all of these differences are interrelated and of importance, the sharp decline of stratum 1 is largely attributed to the high number of originations and overall higher origination rates of stratum 3, and the high absolute number and rate of extinctions in stratum 1.

RUNNING MEANS

Running mean calculations for genera and families in the total fauna and in stratum groups are given in table 3. These are expressions of diversity and are calculated by the equation $S_i - O_i + E_i / 2$, where S_i is diversity, O_i number of originations, and E_i number of extinctions (Harper, 1975).

For families, there is a sharp increase in diversity from Itaboraian (9) to Casamayoran (19), a slight increase in Mustersan and Divisaderan (22 and 21, respectively) another slight increase in Deseadan (24), then relatively constant level (27 to 29) from Colhuehuapian to Chapadmalalan, an increase in Uquian (31) and Ensenadan (34), then a decrease in Lujanian (31). In stratum 1 there is a remarkably uniform level of 20 to 22 families from Mustersan to Friasian, then a continuing decrease to Chasicoan (18), Huayquerian-Montehermosan (16), Chapadmalalan (15), Uquian (13), Ensenadan (11), and Lujanian (8). Stratum 2 shows a sharp increase from Deseadan (4) to a uniform level of 8 to 9 from Colhuehuapian to Chasicoan, 10 in Huayquerian, then a constant level of 11 from Montehermosan to Lujanian. Stratum 3 shows a very sharp increase from 1 in Huayquerian to 2 in Chapadmalalan, 7 in Uquian, and 12 in Ensenadan and Lujanian.

The major patterns are: a) three plateaus in total diversity increase (Casamayoran-

	AGES	I	R	C	M	D	D	C	S	F	C	H	M	C	U	E	L
Families																	
Stratum 1		9	16	19	22	21	20	21	20	20	18	16	16	15	13	11	8
Stratum 2							4	8	9	8	9	10	11	11	11	11	11
Stratum 2												1	1	2	7	12	12
Total		9	16	19	22	21	24	29	29	28	27	27	28	28	31	34	31
Genera																	
Stratum 1		4	15	13	15	24	13	21	28	22	21	34	36	33	28	37	31
Stratum 2							0	10	7	4	9	18	25	21	17	18	22
Stratum 3												1	3	7	15	34	48
Total		4	15	13	15	24	13	31	35	26	30	53	64	61	60	89	101

Table 3. – Running mean calculations for genera and families in the Cenozoic. Abbreviations for ages follow figure 1.

Divisaderan, Colhuehuapian-Chapadmalalan, Uquian-Lujanian); b) the relatively constant level in stratum 1 from Casamayoran to Friasian, the gradual decrease from Chasicoan to Chapadmalalan, and sharp decline from Uquian to Recent; c) the slight decrease of stratum 1 from Friasian to Chapadmalalan is balanced by a comparable increase in stratum 2; and d) the sharp decline in stratum 1 from Chapadmalalan to Lujanian correlates with a sharp increase in stratum 3 (stratum 2 remained unchanged during this time interval).

For genera, there is a sharp increase in total diversity from Itaboraian (4) to Riochican (15), a relatively constant level (13 to 15) between Riochican and Deseadan (the Divisaderan high of 24 is clearly an artifact of data presentation and is ignored), a rise to between 26 and 35 from Colhuehuapian to Chasicoan, an additional increase to 53 in Huayquerian, another to between 60 and 64 from Montehermosan to Uquian, then a sharp increase to 89 in Ensenadan and 101 in Lujanian. The only notable pattern among stratum groups is the sharp increase of stratum 3 from Huayquerian to Lujanian.

EXTINCTION PERCENTAGE AND EXTINCTION PERCENTAGE RATE

Differences in total diversity among ages can be normalized by dividing the number of extinctions by diversity, giving an extinction percentage (table 4). To further normalize for ages of unequal duration, the percentage value is divided by the duration to give an extinction percentage rate (table 4). This percentage rate measures relative intensities of extinction, per-taxon rates, or number of taxa at risk (Raup, 1986, and references therein), and can be translated into what Van Valen (1985a, b) calls "probability of extinction per unit time," which expresses extinction as a proportion of the total number of extinctions per unit time. This is useful for evaluating extinction patterns because it normalizes for differences in both diversity and time.

For families, the vast majority of extinction percentage rates of stratum groups are between 0 and 0.05. Only four values are higher; stratum 1 has a value of 0.1 in Chapadmalalan and 0.12 in Divisaderan, and in Lujanian stratum 3 is 0.12 while stratum 1 is 0.32. The highest value for total diversity in any age is 0.44 in Lujanian.

For genera, most extinction percentage rates of stratum groups are between 0 and 0.30. Only four values are higher; stratum 1 is 0.31 in Colhuehuapian, 0.77 in Chapadmalalan, and 0.42 in Lujanian; and stratum 2 is 0.63 in Chapadmalalan. The highest total extinction rates per age are in the Chapadmalalan (1.4) and Lujanian (0.74).

For both families and genera, two significant extinction events are identified: a) in Chapadmalalan (high rates in stratum 1 families and genera, and stratum 2 genera); and b) in Lujanian (both high generic and family rates in stratum 1 and 3). High rates also occur in stratum 1 families in Divisaderan, and genera in Colhuehuapian.

		Extinction percentage (Ep)															
AGES		I	R	C	M	D	D	C	S	F	C	H	M	C	U	E	L
Families																	
Stratum 1		-0-	.10	.16	.08	.24	.12	-0-	.14	.03	.07	.03	.03	.03	.05	.03	.16
Stratum 2							-0-	-0-	.03	.03	-0-	-0-	.03	-0-	-0-	-0-	-0-
Stratum 2												-0-	-0-	-0-	-0-	-0-	.06
Total		-0-	.10	.16	.08	.24	.12	-0-	.17	.07	.07	.03	.07	.03	.05	.03	.22
Genera																	
Stratum 1		.79	.37	.87	.65	.29	.66	.31	.48	.58	.21	.35	.25	.23	.12	.04	.21
Stratum 2							.17	.12	.17	.22	.12	.07	.18	.19	.09	.03	.02
Stratum 3												-0-	-0-	-0-	.06	.01	.14
Total		.79	.37	.87	.65	.29	.83	.43	.64	.80	.33	.43	.43	.42	.27	.08	.37
		Extinction percentage rate (Epr)															
AGES		I	R	C	M	D	D	C	S	F	C	H	M	C	U	E	L
Families																	
Stratum 1		-0-	.04	.02	.01	<u>.12</u>	.01	-0-	.05	.01	.02	.01	.01	<u>.10</u>	.05	.03	<u>.32</u>
Stratum 2							-0-	-0-	.01	.01	-0-	-0-	.01	-0-	-0-	-0-	-0-
Stratum 2												-0-	-0-	-0-	-0-	-0-	<u>.12</u>
Total		-0-	.04	.02	.01	.12	.01	-0-	.06	.02	.02	.01	.02	.10	.05	.03	.44
Genera																	
Stratum 1		.30	.12	.13	.11	.15	.05	<u>.31</u>	.16	.19	.07	.12	.08	<u>.77</u>	.12	.04	<u>.42</u>
Stratum 2							.01	.12	.06	.07	.04	.02	.06	<u>.63</u>	.09	.03	.04
Stratum 3												-0-	-0-	-0-	.06	.01	.28
Total		.30	.12	.13	.11	.15	.06	.43	.21	.27	.11	.14	.13	1.4	.27	.08	.74

Table 4. – Calculations of extinction percentage and extinction percentage rate for families and genera in the Cenozoic. Abbreviations follow figure 1.

INTERPRETATION OF DATA SET

In this section we discuss features which may influence diversity patterns in the fossil record and relate these features to repetitive patterns and trends identified in the preceding section.

BIASES OF THE FOSSIL RECORD AND SAMPLING

Hiatuses

Gaps or missing time intervals in the fossil record may produce artificial truncations of stratigraphic ranges of taxa and give the impression of major origination and/or extinction events. In reality, the ranges of some or all taxa in a land mammal age bounded by one or two hiatuses may have extended into older and/or younger rocks but are not recorded due to erosion and/or non-deposition (Raup, 1979, 1986). In the South American land mammal record there are marked hiatuses in knowledge of faunas in the early Paleocene (about 3.0 Myr), late Eocene (about 9.0 Myr), and early Miocene (about 2.0 Myr; fig. 1). These hiatuses signal potential problems in the data set, as they may influence diversity patterns of adjacent land mammal age faunas.

This prediction is supported by the family data set, which clearly shows the effect hiatuses have on biasing origination and extinction patterns by producing artificial truncation of ranges. If we consider only those time intervals preceded by hiatuses (Maastrichtian, Itaboraian) and those known to have been sampled from many localities over large geographic areas (see area sampled biases, below) that follow hiatuses (Deseadan and Santacrucian; not Divisaderan and Colhuehuapian), then the number of originations are 11, 9, 14, and 6, respectively, with an average of 10 fam./age. The average number of originations in the other 12 ages not preceded by hiatuses is 3.7 fam./age. Thus, there is a 3:1 ratio favoring higher origination in ages preceded by hiatuses from those which are not. Extinctions show a similar pattern. The Maastrichtian, Mustersan, and Deseadan which are succeeded by hiatuses average 3.7 fam./age, while the other ages collectively average 2.8 fam./age. Thus, extinctions are about 25% higher in ages truncated by hiatuses.

Duration of time units sampled

The South American land mammal ages (fig. 1) are not all of equal duration, but range from 0.3 Myr (Chapadmalalan) to 13.0 Myr (Deseadan). This may bias comparison of diversity patterns between ages because those with longer durations will predictably have more "only occurrence" taxa (those restricted to that age) than will ages of shorter duration. Of the faunas represented by many localities over large geographic areas (Casamayoran, Deseadan, Santacrucian, Huayquerian, Montehermosan, Lujanian; see area sampled, below) the Deseadan (which has the longest chron, ca. 13 Myr) has 63 genera known only from that age; Casamayoran (ca. 6.8 Myr) has 45; Santacrucian (3.0 Myr), Huayquerian (3.0 Myr), and Montehermosan (3.2 Myr) have 43, 27, and 27, respectively; and Lujanian (0.5 Myr) has 14 (see table 5). Thus, the above prediction is supported by the data set.

Another aspect of this bias is that geochronologic age data is not available for all ages, and the correlation of some faunas with the geologic time scale is based primarily on knowledge of "stage of evolution" of those faunas. Thus, faunas of Itaboraian, Riochican, Deseadan, Santacrucian, Friasian (in part), Huayquerian, Montehermosan, Uquian, Ensenadan (in part), and Lujanian age have been calibrated using

geochronologic techniques (Marshall, 1985); the others have not. As a consequence, the boundaries assigned to the latter ages are only tentative. Incorrect age assignments and durations will produce spurious diversity patterns. Some potential examples include the "undated" Divisaderan, Colhuehuapian, and Chapadmalalan ages, which are all of short duration and of questionable validity (see below). The high family extinction rates in the Divisaderan and Chapadmalalan (table 1) and high generic origination and extinction rates in the Colhuehuapian and Chapadmalalan (table 1) may simply indicate the age durations to be too small. Another potential problem is that the Divisaderan, Colhuehuapian, and Chapadmalalan may simply be parts of succeeding or preceding ages, and that they may not warrant recognition as distinct ages. Divisaderan may represent an early Deseadan fauna (Simpson *et al.*, 1962; Marshall, Cifelli, *et al.*, 1986). Colhuehuapian may represent an early Santacrucian fauna (Pascual *et al.*, 1965). Friasian may represent a late Santacrucian fauna (Simpson, 1940; Pascual *in* Patterson & Pascual, 1972); Chapadmalalan may represent a late Montehermosan (Pascual & Odreman Rivas, 1971, 1973) or early Uquian (Marshall, 1985) fauna. Should such changes officially occur, they would alter the patterns of diversity as discussed in this study. It is also possible that Deseadan, which has the longest chron, may prove to warrant subdivision into two or more distinct ages. Thus, diversity studies of faunas as presented here may potentially identify problems in our knowledge of land mammal age duration and validity.

Area sampled

The land mammal age faunas are not equally sampled in terms of number of localities and geographic area. Those faunas represented by many localities over a large geographic area (Casamayoran, Deseadan, Santacrucian, Huayquerian, Montehermosan, Lujanian) will predictably have greater diversity than those sampled from only a few localities over smaller geographic areas (Riochican, Mustersan, Colhuehuapian, Friasian, Chapadmalalan, Uquian, Ensenadan). Other faunas (Late Cretaceous, Itaboraian, Divisaderan, Chasicosan) are known only from one, or principally one, locality.

The diversity pattern of genera (figs. 3, 8) supports this prediction. Greater diversity occurs in those faunas known from many localities over large geographic areas, while lower diversity appears in faunas known only from one or a few localities. Interpretation of the generic diversity pattern through time must thus focus on the better sampled faunas: Casamayoran, Deseadan, Santacrucian, Huayquerian, Montehermosan, Lujanian. Using only these data points (fig. 8) and looking only at running means (table 3), we see a continued increase in generic diversity during Cenozoic time. This general trend is supported by rate data (table 1), which shows that origination rates averaged 12% higher than extinction rates during Cenozoic time, and 27% higher between Friasian and Lujanian time.

Preservability and recovery

Small-sized taxa generally have less chance of being preserved as fossils because they are often more fragile and more easily destroyed by depositional processes. Also, small-sized taxa are typically recovered only by systematic and intense collecting of surface exposures and/or by screen washing of fossiliferous sediment. For the South American Cenozoic record, small taxa are abundantly known only in Itaboraian, Deseadan, Colhuehuapian, Santacrucian, and Huayquerian-Lujanian. In the other faunas, the records of small taxa are clearly under-represented.

Discussion

The data set suggests that familial patterns are less affected by biases of the fossil record and sampling than are generic patterns. This feature is due to the fact that families, as more comprehensive taxonomic units than genera, are more likely to be sampled, and that they have longer ranges than genera, thus enabling them to "outlive" vagaries of the fossil record. This generalization also appears to apply to biases of taxonomic treatment, discussed below.

TAXONOMIC TREATMENT

The clades and faunas of land mammals in South America have not received uniform taxonomic treatment and these differences may bias diversity patterns.

The taxonomy of some clades (e.g., Marsupialia, Condylarthra) have received recent monographic treatment, and the use of familial, generic, and species names is momentarily stable. Other clades (e.g., Dasypodidae, Glyptodontidae, Megatheriidae, Megalonychidae, Mylodontidae) have not received serious taxonomic revision since many of the taxa were described in cursory fashion at the turn of the century; consequently, the status and affinities of many genera and species are uncertain. For example, it is generally agreed that the Glyptodontidae is taxonomically oversplit and that serious revision will result in some (many?) generic and specific names falling in synonymy and hence a decrease in diversity within this clade. This prediction stems from the widely recognized fact that early students of South American mammals (e.g., F. Ameghino, L. Kraglievich, A. Castellanos, C. Rovereto) were "splitters" and recognized a plethora of names which are repeatedly shown to have been based on either fragmentary, indeterminate specimens or on multiple specimens from the same taxon.

With regard to faunas, some (such as the Riochican to Mustersan) have received overall taxonomic treatment (Simpson, 1948, 1967), while others (Deseadan, Colhuehuapian, Huayquerian, Montehermosan, Chapadmalalan, Uquian, Ensenadan, Lujanian) are in dire need of such an overview and synthesis. The remaining faunas have received considerable attention in recent years and the taxonomy of most genera and species is quite stable.

A final taxonomic bias is introduced by pseudoextinctions. When a taxon evolves into another of equal or higher rank it "appears" that the ancestral taxon became extinct and the descendent taxon originates. Yet, there is no real extinction or origination, only change within a lineage. These pseudoextinctions increase the number of apparent extinctions in any given time interval and originations in subsequent time intervals. Recognition of these pseudoextinctions and pseudoriginations is dependent upon detailed systematic studies of clades through time. We know of no study which attempts to factor out pseudoextinctions and pseudoriginations from the data set, although we recognize the need for such a study.

EQUILIBRIUM THEORY

A prediction of the MacArthur & Wilson (1967) equilibrium hypothesis is that, with time, a region (island, continental land mass, etc.) will become saturated with taxa and attain a diversity level where origination and extinction rates are stochastically constant. If origination rates increase diversity to a point above the equilibrium or saturation level, then a readjustment period of extinction and diversity decrease will predictably follow. Equilibrium will predictably persist until it is disrupted by: a) the

appearance of new taxa, which may result in competitive interactions of taxa or extinction of predator-naive prey and result in an immigration-induced biotic turnover episode (Webb, 1984); b) a change in physical environment that can alter habitats and result in an environmentally-induced biotic turnover episode (Webb, 1984); or c) a combination of the above. Turnover and replacement will predictably occur among ecological vicars, or "groups which have a similar role in nature and occupy the same trophic level within an adaptive zone" (Van Valen & Sloan, 1966); an adaptive zone being a niche of a higher taxon (Van Valen, 1971).

Three equilibrium plateaus in total diversity, indicated by the family data set (figs. 2, 8), are best reflected in running mean values (table 3): a) Casamayoran to Divisaderan (19 to 22 fam./age), b) Colhuehuapian to Chapadmalalan (27 to 29 fam./age), and c) Uquian to Recent (31 to 34 fam./age). The beginning of each plateau correlates with a distinct event of faunal enrichment (i.e., permanent diversity increase): a) adaptive radiation of stratum 1 and sharp diversity increase between Maastrichtian and Casamayoran resulted in attainment of first equilibrium plateau in family diversity (figs. 2, 8, 11) with very high family origination rates (3.5/Myr) in Itaboraian and originations exceeding extinctions from Itaboraian to Mustersan (fig. 11, table 1); b) addition of stratum 2 in Deseadan marks the beginning of second equilibrium plateau as shown by families (figs. 2, 8, 11) and genera (fig. 3); and c) addition of stratum 3 in Uquian marks beginning of a third equilibrium plateau: families (figs. 2, 8, 11) had an origination rate of 9.0/Myr, and genera (figs. 3, 8) had an origination rate of 18/Myr (table 2). The last enrichment event was continued in subsequent ages by high generic origination rates of stratum 3 taxa in Ensenadan (26/Myr) and Lujanian (44/Myr) (table 2).

Immigration-induced biotic turnover

Competition

Competitive replacement among vicars occur if the immigrant taxa are more efficient in consuming or preempting limited resources, such as food, living space, and nesting sites. In the fossil record, such replacement may be suggested, but not necessarily implicated, by immigrant success concomitant with decline of native taxa. The limited evidence now available suggests that competitive replacement of native ungulates by immigrant taxa may have occurred during the interchange (Webb, 1976) but, apparently, not during the Deseadan radiation of immigrant caviomorph rodents (Cifelli, 1985; see below).

Prey naivete

The concept of prey naivete, discussed by Diamond (1984, 1985), has broad implications for mixing of faunas. The concept is based on the observation that prey species may initially be naive about predators in general or about a "new kind" of predator in particular. As noted by Darwin (1871), "... we may infer... what havoc the introduction of any new beast of prey must cause in a country before the instincts of the indigenous inhabitants have become adapted to the stranger's craft or power." If an immigrant predator does not quickly over-exploit a new prey species and cause its extinction, then the prey species may adapt to the predator and the two may coexist. Two potential examples exist in the South American land mammal record: the arrival of stratum 3 Carnivora in the Uquian, and later of man at the end of the Lujanian.

Immigration-induced turnover caused by North American Carnivora, "the likes of which southern ungulates had never before experienced" (Webb, 1976), has long been entertained as a mechanism which selected against stratum 1 and/or 2 herbivores

and favored replacement by immigrant stratum 3 herbivores that were not predator naive. A scenario for this process is eloquently presented by Patterson & Pascual (1972): "Predation by the newly arriving carnivores may have contributed to some extinctions that occurred around the Pliocene-Pleistocene boundary. It is axiomatic that no predator can afford to exterminate its prey, but these predators were not in danger of doing that—they enjoyed an advantage: they were accompanying their usual prey and encountering new prey as they went. These they could have pursued to the point of great reduction or even extinction without seriously jeopardizing themselves. Furthermore, the new prey could have been at some disadvantage. Defensive behavior adapted to coping with the old set of predators, phororhacoid birds as well as marsupials, might have been less effective against the new.

"Humans arrived in South America about 12 ka (Marshall *et al.*, 1984), a time which coincides with the largest extinction event in the history of the South American land mammal fauna. Man has been credited as the sole or primary agent in these extinctions by a process called overkill, whereby the extinctions (exterminations) resulted from human hunting at a rate beyond the prey species' reproductive (replacement) capacity (Martin, 1984). These extinctions have been attributed to a special type of overkill called *Blitzkrieg*—"sudden extinction following initial colonization of a land mass inhabited by animals especially vulnerable to the new human predator" (Martin, 1984). Humans had hunting and killing techniques unknown to the native, human-naive South American mammals. Human involvement in these extinctions has long been entertained, and Darwin (*The Voyage of the Beagle*, 1839) pondered, "Did man, after his first inroad into South America, destroy the unwieldy *Megatherium* and other Edentata?"

Of the 37 families recorded in Lujanian faunas, 8 (21%) are extinct. These families include 6 from stratum 1 (Glyptodontidae, Megalonychidae, Megatheriidae, Mylodontidae, Macraucheniidae, Toxodontidae) and 2 from stratum 3 (Equidae, Gomphotheriidae). This is the only significant extinction event seen in the analysis of family diversity patterns through time (fig. 11) and involves only families that had multiple genera in them at the time of extinction. This event accounts for 18% of all family extinctions and 50% of all families with multiple genera at the time of extinction in the Cenozoic. Family extinction rates for the total fauna were 16/Myr (table 1), and extinction percentage rates (table 4) were 0.32 for stratum 1, 0.12 for stratum 3, and 0.44 for the total fauna (stratum 2 was unaffected). Of the 153 genera recorded in Lujanian faunas, 56 (37%) are extinct, and 35 (63%) of these belong to the above 8 families. Of these extinct genera, 54 (96%) were of large body size and classify as megafauna (Martin, 1984); 32 (57%) belong to stratum 1, 3 (5%) to stratum 2, and 21 (38%) to stratum 3. Extinction rates for genera in the total fauna (table 1) are 112 genera/Myr, and for stratum 1 (table 2) are 64/Myr; extinction percentage rates (table 4) are 0.42 for stratum 1, 0.28 for stratum 3, and 0.74 for the total fauna (stratum 2 was little affected). These extinctions were differential and involved primarily animals of large body size; thus, this extinction events represents a specific filtering process as the extinct taxa are not a random sample of the pre-extinction fauna. Climatic change at the end of the Pleistocene is also implicated as a cause for extinction of megafauna (e.g., Graham & Lundelius, 1984). Imprecision in the chronology of extinctions and of the arrival of humans in South America leaves us unable to weight the relative merits of overkill vs. climatic explanations.

Environmentally-induced biotic turnover

Passive replacement among vicars may occur when environmental changes result

in extinction of a taxon and its role (i.e., niche, adaptive zone) is subsequently filled by another native taxon or a timely immigrant. The successor taxon need not be competitively superior to the taxon it replaces (Marshall, 1981). In such instance, "it is not physical or behavioral limitations which guide a ... [taxon's]... evolutionary potential or success, but merely the opportunity to exploit an available zone which, because of the nature of the fauna, was open" (Hecht, 1975).

Many environmental changes in South America during Cenozoic time relate directly or indirectly to time and intensity of Andean orogeny (e.g., Pascual & Odreman Rivas, 1971, 1973; Patterson & Pascual, 1972; Webb, 1978; Marshall & Patterson, 1981; Pascual, 1984). The Andes Cordillera as we know it today is a geologically recent addition to the South American landscape (Simpson, 1940). The first unequivocal phase of Andean uplift began in Divisaderan-Deseadan time, and precipitated a change from warm woodland habitats that predominated the early Cenozoic (Paleocene-Eocene) to a regime of colder, drier climates with seasonal aridity, at least in southern Argentina. A second phase of uplift occurred between Deseadan and Colhuehuapian time (Simpson, 1940) and resulted in the establishment of savanna-woodland habitats over much of southern South America. "This tectonic phase appears to mark the beginning of the definitive uplift and structural formation of the southern Andes, which has continued rhythmically and periodically ever since with occasional climaxes in the later Tertiary" (Simpson, 1940). These new habitats provided opportunities for groups able to adapt to grassland environments, while decreasing or eliminating opportunities for groups previously specialized for closed woodland environments. As shown by the land mammal record, many groups with browsing adaptations (low crowned cheek teeth) went extinct during Divisaderan-Deseadan time (Sparnotheriodontidae, Pyrotheriidae, Colombitheriidae, Notopithecinae, Isotemnidae, Oldfieldthomasiidae), while many new forms with grazing adaptations (high crowned cheek teeth) make their first appearance (Hegetotheriidae, Interatheriinae, Mesotheriidae, Toxodontidae). These "grazing opportunities" were seized by many groups, and hypsodonty evolved independently at least six times in herbivore taxa of all sizes (Cifelli, 1985).

Mammal faunas of Colhuehuapian, Santacrucian, and Friasian time represent a relatively continuous evolutionary sequence predominated by groups which suggest a savanna and open woodland habitat. "The mammals of southern Patagonia... [during Colhuehuapian-Friasian time]... suggest a climate sufficiently genial to permit such now mainly tropical animals as porcupines, echimyids, dasyproctids, anteaters and primates to flourish there." These savannas and open woodlands "graded northward into the rainforest, woodland, and savanna of the tropical zone, then no doubt more extensive than at present" (Patterson & Pascual, 1972).

Another major phase of Andean uplift occurred at the end of Friasian time and marked the beginning of a significant increase in elevation of the main Cordillera (Herredo-Ducloux, 1963; Farrar & Noble, 1976). In Argentina, the sedimentation center shifted from Patagonia to the Pampas and northwest regions. The sediments shifted from predominantly pyroclastic to clastic (Patterson & Pascual, 1972; Pascual & Odreman Rivas, 1971, 1973). Coincident with these geologic changes, there began the desertification of Patagonia, with the appearance of drier forest habitats and precocious pampa habitats, and the northward retreat of savanna-woodland groups (Patterson & Pascual, 1972). Montehermosan and Chapadmalalan faunas in the Pampean region of Argentina suggest a warm-temperate, humid climate, contrasting to the cool-temperate climate of today (Pascual & Odreman Rivas, 1971).

The last major phase of Andean orogeny began in Montehermosan time and is still operative today. There was an increase of 2000 to 4000 m in elevation between 4.5

and 2.5 Ma (Simpson, 1975; Van der Hammen *et al.*, 1973). Rocks containing mammal faunas of Montehermosan and Uquian age in the respective provinces of Catamarca and Jujuy, NW Argentina, are tilted and structurally deformed, indicating that extensive orogenic movements occurred subsequent to their deposition (Marshall & Patterson, 1981). In faunas of Montehermosan age in NW Argentina we find the first unmistakable evidence of true desert environments and of temperate high montane biotas (Simpson, 1971, 1975; Van der Hammen, 1966, 1972). Cold dry temperate habitats developed in high latitudes (Pascual, 1984). The first evidence of glacial formation in the Andes occurred about 3.5 Ma (Clapperton, 1979), with numerous subsequent advances and retreats; the last glacial advance was 11-12 ka (Bradbury, 1982; Haffer, 1974; Cronin, 1981; Markgraf & Bradbury, 1982; Raven & Axelrod, 1975; Webb, 1978; Van der Hammen, 1974; Marshall, 1985). During glacial retreat, as occurred after the last glaciation ended about 10 ka the tropical lowlands became warm and wet, resulting in shrinkage of savanna-grassland habitats (Webb, 1978; Marshall, 1979, 1985). The repetitive advance and retreat of glaciers, and concurrent expansion and retraction of savanna and tropical biotas, permitted alternating opportunities for diversification of animals living in these habitats, while at the same time favored high extinction rates due to species area effects. In this latter case, extinctions would result from: a) decrease in living space (area and number of habitats) due to intensification of competition and/or predation; b) decrease in size of populations (low species abundance); and c) decrease in environmental heterogeneity and resources due to habitat fragmentation.

In summary, orogenic phases of Andean uplift correlate with environmental changes which have resulted in: a) initial disruption of equilibrium; b) creation of new environments and adaptive zones through time; and c) overall increase in environment heterogeneity, which provided new opportunities for the land mammals, favoring diversity increase from Divisaderan to Recent. Concurrent with these environmental changes were the immigration of stratum 2 groups in the middle Tertiary, and stratum 3 groups in the Late Cenozoic. Stratum 2 and 3 groups may thus have simply been timely immigrants able to exploit available (open) and/or new (opening) adaptive zones created by orogenically-induced processes.

Evolutionary relays

Both immigration- and environmentally-induced biotic turnover episodes will predictably result in evolutionary relays (Simpson, 1953), eco-replacement (Van Valen, 1971), or iterative evolution (Cifelli, 1969) —the successive abrupt or gradual replacement by adaptive radiations of sequential clades of taxa occupying the same adaptive zone. Since extinction and origination may be interactive counter-components of the same evolutionary process, it may be difficult or impossible to determine cause effect relationships for evolutionary relays. In other words, are sequential originations permitted by prior or concurrent extinctions, or are they the cause of those extinctions? For example, following the appearance of the Panamanian land bridge in the Late Cenozoic, did extinctions of stratum 1 and 2 taxa result from interactions with stratum 3 taxa or did their extinction permit the radiation of stratum 3 taxa in South America? In the latter case, extinctions may leave room for successful originations (Van Valen, 1985a, b). Theoretically, recycling of adaptive zones made available by extinctions may result from a combination of immigration and speciation. In addition, since immigration- and environmentally-induced biotic turnover influences may occur concurrently, as clearly happened in South America, it may be difficult to isolate the effects of each. Radiations may be triggered by: a) creation of new adaptive zones; b)

innovation of new structural adaptations within a clade; c) immigration of taxa in new areas; and d) a combination of the foregoing (Van Valen, 1985a, b). All of these features may produce accelerated rates of origination within clades.

Assessments of evolutionary relays typically employ taxocene analysis (Whittaker, 1972; Levandowsky & White, 1977) —the assumption that a clade can and will in the course of its adaptive radiation fill most of all available niches within a particular adaptive zone (Hecht, 1975). As demonstrated elsewhere (e.g., Patterson & Pascual, 1972; Marshall & Hecht, 1978; Marshall, 1977, 1981) and below, such assumptions are not necessarily valid and their application may obscure events in life history.

A number of evolutionary relays have been suggested and/or studied in the South American land mammal record (e.g., Marshall, 1981 and references therein). We focus attention on the two which have a large data base and which have received the majority of previous attention: a) carnivorous adaptive zone; and b) large herbivore adaptive zone between Deseadan and Recent.

Carnivorous adaptive zone

Stratum 1 occupants of the carnivorous adaptive zone were members of the dog-like marsupial family Borhyaenidae, which ranges from Late Cretaceous to Montehermosan, and the Huayquerian to Chapadmalalan sabertooth marsupial family Thylacosmilidae. Borhyaenids came in all sizes; some were smaller than the living Virginia opossum, while the Deseadan age *Proborhyaena gigantea* was larger than a Grizzly Bear (Marshall, 1977). The postcranial remains of borhyaenids suggest that they had poor cursorial abilities, and the small- to medium-size forms had semi-arboreal capabilities (Marshall, 1977). Borhyaenids reached their evolutionary climax in Santacrucian, and in subsequent ages they show a decrease in diversity and body size (Patterson & Pascual, 1972). Other occupants of the carnivorous adaptive zone in early and middle Tertiary faunas included gigantic snakes, semi-terrestrial crocodiles, and large predaceous ground birds, the phororhacoids (Marshall, 1977). Phororhacoids first appear in the Deseadan; during the tenure of their existence through the Montehermosan, they came to be represented by three families, which by mammalian standards included medium, large, and gigantic size groups (Patterson & Pascual, 1972; Patterson & Kraglievich, 1960). Phororhacoids had marked cursorial abilities, carnivorous specializations of the beak and skull, and in some cases reached a height of over 3 m. These cursorial specializations permitted phororhacoids to dominate the expanding grassland and pampa habitats, and by Montehermosan time they had completely replaced the large borhyaenids, at least on the savanna grasslands of Argentina (Marshall, 1977). Thus, when stratum 3 Carnivora arrived to South America in Uquian time, the borhyaenids were already extinct; if any competition resulted, it would have been with the native phororhacoids. The record shows that the arrival of stratum 3 Carnivora in Uquian time does indeed correlate with the extinction in South America of phororhacoids, and also with a diversity decline of medium-sized carnivorous marsupials of the family Didelphidae (figs. 2, 4).

Megaherbivore adaptive zone

Stratum 1 occupants of the megaherbivore adaptive zone include members of six ungulate (Condylarthra, Litopterna, Astrapotheria, Pyrotheria, Xenungulata, and Notoungulata) and one non-ungulate (Xenarthra) order. Early Tertiary radiations resulted in the appearance of a number of medium- to large-sized taxa within various lineages of the ungulate groups by Casamayoran time. Dental structure suggests browsing adaptations for these forms. Two aspects of South American history appear to

have affected a dramatic restructuring of the mammalian herbivore community by Deseadan time: climatic change and the appearance of stratum 2 rodents. Because the Deseadan is preceded by a very poorly known fauna (Divisaderan), we remain largely in ignorance of the initial changes in native groups (which are marked by structural "gaps" between Mustersan and Deseadan time) and the early radiation of caviomorphs. It is clear, however, that the major trends in ungulate evolution —cursoriality and hypsodonty— were made in response to the expanding grasslands resulting from increased aridity (see above, and Patterson & Pascual, 1972; Cifelli, 1985). Because the caviomorph rodents include larger forms adaptively similar to the smaller ungulates, it has been suggested that competition between them resulted in an immigration-induced biotic turnover episode, with the native ungulates losing ground to the rodents (Simpson, 1980). The record of the Deseadan, however, shows that precisely those groups likely to be affected (the rodent-like interatheriids and hegetotheriids) actually flourished during this time, suggesting that both ungulates and rodents were responding alike to environmental opportunities presented at that time (Cifelli, 1985).

Several groups, mostly comprised of browsers (e.g., Rhynchippinae, Pyrotheriidae, Isotemnidae), became extinct by the end of the Deseadan; presumably a culmination of the Oligocene-Miocene environmentally-induced episode of turnover. Colhuehuapian and Santacrucian faunas otherwise much resemble that of the Deseadan in terms of composition and, although there is evidence of sequential replacement by ecologically equivalent taxa in successive ages, the fauna as a whole remained remarkably stable. By the Friasian, however, marked compositional changes had occurred. Among the ungulates, Adiantidae, Astrapotheriidae, Leontinidae, Notohippidae, and primitive Toxodontidae (Nesodontinae) became extinct. Advanced Toxodontidae, on the other hand, experienced a great radiation, and several other ungulate families (Mesotheriidae, Hegetotheriidae; fig. 5) were successful as well. Among the Xenarthra, the initial radiations of the megalonychid, mylodontid, and megatheriid sloths was beginning. Significant radiations among stratum 2 rodents occurred also, although these began somewhat later, in the Chasicuan. The cause and significance of these changes in the megaherbivore groups remains to be established; the success of some forms, such as toxodontids, seems to be related to renewed climatic change and increased aridity, as discussed above.

Despite the several Late Tertiary radiations just noted, the stratum 1 ungulate families suffered from continual attrition during the Neogene. By the time of the interchange, there remained about a dozen genera placed in four families. Most of these became extinct in the early Pleistocene. The correspondence of these extinctions to the appearance of stratum 3 ungulates in South America, the relatively stable number of megaherbivore genera through this time interval, and the close ecological comparability of the immigrants to the natives, suggest strongly that active replacement of stratum 1 by stratum 3 taxa occurred (Webb, 1976). The xenarthran megaherbivores did not experience significant turnover at this time, although one group (Glyptodontidae) apparently underwent a modest radiation.

Discussion

Two potential relays are indicated by the familial and generic data sets: a) passive replacement of stratum 1 ungulates by stratum 1 xenarthrans and stratum 2 rodents during Friasian-Chapadmalalan (fig. 2, table 3); and b) active replacement of stratum 1 ungulates (Notoungulata, Litopterna) by stratum 3 ungulates (Proboscidea, Perissodactyla, and Artiodactyla) during the early Pleistocene. These patterns clearly illustrate that the sharp decrease of stratum 1 families (particularly notoungulates and

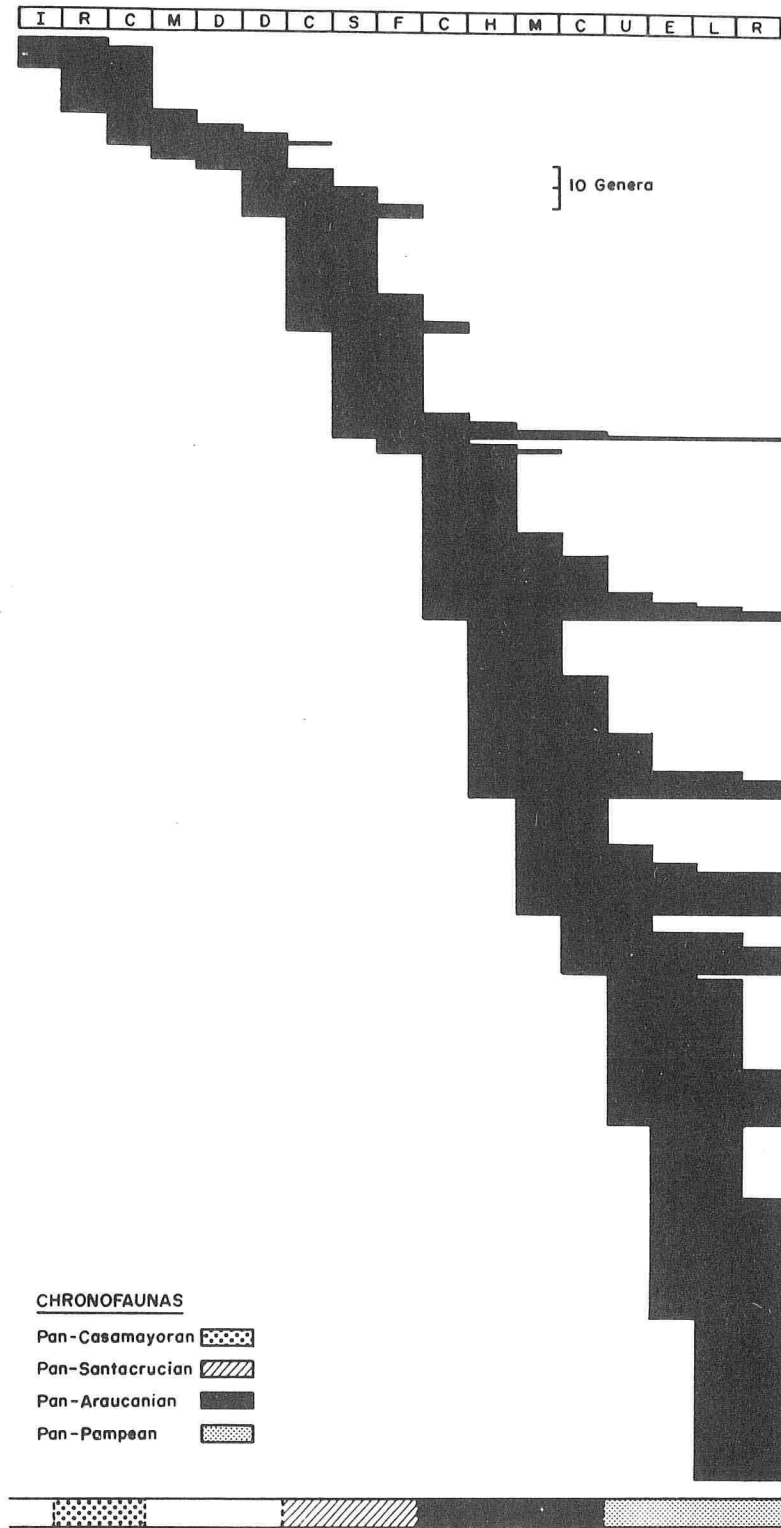


Figure 12. – Distribution of land mammal genera that occur in multiple ages (after table 5) and chronofaunas.

litopterns) between Uquian and Recent represents a trend of declining diversity begun in Friasian (or earlier) time, and that the extinction of these groups involved several phases and, probably, causes.

The data also show only two major extinction events in the Cenozoic. The first, which occurred in the Chapadmalalan, is marked by high family extinction rates (6.7/Myr) among strata 1 and 2 (table 1); high family extinction percentage rates (0.1) in stratum 1 (table 4); high generic extinction rates in stratum 1 (66.7/Myr), stratum 2 (56.7/Myr), and total fauna (123/Myr; table 2); and high generic extinction percentage rates in stratum 1 (0.77), stratum 2 (0.63), and total fauna (1.4; table 4). This extinction event was followed in Uquian time by high origination rates in stratum 3 families (9.0/Myr) and total genera (39/Myr; table 1). This event resulted in a decline of stratum 1 and 2 taxa, and correlates with the arrival of stratum 3 "walkers" (see above). The second extinction event occurred at the end of the Lujanian time, affected primarily strata 1 and 3 megafauna, and correlates with the arrival of man.

CHRONOFAUNAS

Olson (1952) defined a chronofauna as "a geographically restricted, natural assemblage of interacting animal populations that has maintained its basic structure over a geologically significant period of time." Tedford (1970) revised subsequent usage of this term (e.g., Webb, 1969) and concluded that a chronofauna refers to "an ecologically adjusted group of animals with specific geographic limits and chronologic range as revealed by the fossil record." Chronofaunas are thus conceptually useful biostratigraphic units for the study of community restructuring. Abrupt changes as would occur between successive chronofaunas are useful in subdividing geologic time. As with land mammal ages, first appearances of taxa will predictably be more useful in defining chronofauna boundaries than will last appearances (Woodburne, 1977).

In South America, the terms "formations" (Ameghino, 1906), "ciclos faunísticos" (Kraglievich, 1930, 1934; Pascual *et al.*, 1965; Pascual & Odreman Rivas, 1971, 1973; Reig, 1981), "grupos" (Frenguelli, 1930), and "faunal types" (Simpson, 1940) have been applied (with one exception) to multiple land mammal age faunas, and these terms are conceptually and operationally equivalent to chronofaunas (Marshall *et al.*, 1983). Simpson's (1940) use of "faunal types", for example, include: Pan-Casamayoran (Riochican-Mustersan), Deseadan (Deseadan), Pan-Santacrucian (Colhuehuapian-Chasicosan), Araucanian (Huayquerian-Montehermosan), and Pan-Pampean (Chapadmalalan-Lujanian).

In an attempt to quantify taxonomic affinity of each land mammal age and to identify and investigate chronofaunas, we summarize in Table 5 the cumulative ranges of genera through time. The first line at the top of Table 5 gives the number of "only occurrence" genera, and in subsequent lines are given the ranges and number of genera that occur in two or more ages. The following differences and similarities (fig. 12) are apparent: a) Riochican and Casamayoran have 15 co-occurring genera (these ages show closest overall similarity of all Paleocene and Eocene faunas); b) Itaboraian shares 7 genera with Riochican and 5 with Casamayoran; c) Mustersan is transitional between Casamayoran and Divisaderan, sharing 8 genera with each; d) Divisaderan also shares 8 genera with Deseadan, and is thus transitional between Mustersan and Deseadan; e) Deseadan shares 12 genera with Colhuehuapian and thus shows more affinity with that age than with Divisaderan; f) Colhuehuapian, Santacrucian, and Friasian are very similar in faunal composition, and Santacrucian is transitional in sharing 32 genera with both Colhuehuapian and Friasian (11 occur in all three ages); g) a very sharp break occurs between Friasian and Chasicosan, and only 11 genera are shared; h) Chasicosan is

very similar to Huayquerian, with 43 genera occurring in both ages; i) Huayquerian is also very similar to Montehermosan and 61 genera occur in both; j) Chasicoan and Montehermosan share 22 genera; k) Chapadmalalan shares 64 genera with Montehermosan or earlier faunas and 45 with Uquian or later faunas, indicating a 30% greater similarity to the former age; l) Chasicoan and Chapadmalalan share 16 genera; m) Uquian shows more similarity with later (Ensenadan) than earlier (Chapadmalalan) faunas, sharing 63 genera with Ensenadan as opposed to 45 with Chapadmalalan; n) Ensenadan shares 103 genera with Lujanian; o) Lujanian shares 96 genera with Recent; and p) Uquian and Lujanian share 60 genera.

The data presented in table 5 and figure 12 indicate the existence of four distinct age groupings; a) Riochican-Casamayoran; b) Colhuehuapian-Friasian; c) Chasicoan-Chapadmalalan; and d) Uquian-Lujanian. We believe that these groupings qualify as chronofaunas, and for these we employ, with slight modification, Simpson's (1940) names as follows: Pan-Casamayoran (Riochican-Casamayoran), Pan-Santacrucian (Colhuehuapian-Friasian), Pan-Araucanian (Chasicoan-Chapadmalalan), and Pan-Pampean (Uquian-Lujanian) (see fig. 12). The temporal boundaries of the latter three chronofaunas correlate with major phases of Andean uplift, concurrent environmental change, and community reorganization.

Our data set further indicates that the remaining faunas (Itaboraian, Mustersan, Divisaderan, Deseadan) do not warrant inclusion in a chronofauna arrangement. Itaboraian shows closest affinity with the Pan-Casamayoran chronofauna; Mustersan is intermediate between Casamayoran and Divisaderan; Divisaderan is intermediate between Mustersan and Deseadan; and Deseadan shows more affinity with Colhuehuapian and the Pan-Santacrucian chronofauna. Nonetheless, it is clear that the Pan-Santacrucian chronofauna has its "roots" in the Deseadan, particularly regarding composition of families. This suggests that the adaptive zones which characterize the Pan-Santacrucian chronofauna were developed incipiently in Deseadan time. Many of the families which appear for the first time in the Deseadan continue through the Pan-Santacrucian chronofauna, and some beyond.

CONCLUSIONS

Analysis of pattern in South American land mammal taxonomic evolution is complicated by several biases inherent in the fossil record of that continent. First, ages preceded by hiatuses or well sampled ages following poorly sampled ones (Maastrichtian, Itaboraian, Deseadan, Santacrucian), are characterized by apparently high origination rates; those succeeded by hiatuses or poor sampling intervals (Maastrichtian, Mustersan, Deseadan) are characterized by similarly inflated extinction rates. Second, longer time intervals, such as the Deseadan, have a relatively higher diversity than shorter ones, such as Lujanian, due to the presence of a greater number of "only occurrence" taxa. Third, some land mammal ages, such as the Casamayoran, Mustersan, Divisaderan, and Colhuehuapian, have not been dated geochronologically; estimates of evolutionary rate are crude in these cases, especially where (as in the case of the Colhuehuapian) the duration is short. Fourth, the land mammal ages have not been equally sampled in terms of geographic area and number of localities; interpretation of generic diversity patterns must thus focus on the better-sampled ages: Casamayoran, Deseadan, Santacrucian, Huayquerian, Montehermosan, Lujanian. Finally, biases of taxonomic treatment may affect analysis of diversity trends; this is particularly true for many of the xenarthran groups, which have not received recent comprehensive treatment. Consideration of these sampling and/or taxonomic biases of the data set

permits a better appreciation of diversity trends and patterns through Cenozoic time. Thus normalized, the record suggests periodic times of faunal enrichment and attainment of diversity equilibrium, and disruption of equilibrium as a result of environmentally-induced and/or immigration events.

Initial radiations of stratum 1 taxa into available niches and adaptive zones resulted, by Casamayoran time, in establishment of an equilibrium, at least at the family level. Major disruption of the fauna occurred just prior the Deseadan, with two factors involved. First, Andean uplift increased aridity and environmental heterogeneity, with resultant radiations of stratum 1 taxa, particularly those adapted to more open grassland environments. Significant extinctions also occurred, with the most-affected groups being archaic browsing forms characteristic of Paleocene and Eocene faunas. Secondly, stratum 2 groups appeared and radiated, with the result being overall enrichment (rather than replacement) of the fauna. Colhuehuapian to Friasian faunas are compositionally similar, suggesting a relative stability or equilibrium; by the Friasian, however, the xenarthrans and caviomorphs assumed increased importance as mammalian herbivores in South America (an adaptive zone previously dominated by stratum 1 ungulates). This trend of passive replacement continued through the Miocene and Pliocene. Increased turnover rates and compositional changes—presumably related to orogenic processes in the Andes Cordillera, which further increased aridity—occurred by the Chasicuan, with significant radiations among the caviomorphs, toxodontid notoungulates, and cingulate xenarthrans; another period of stability was maintained through the Chapadmalalan. Further phases of orogenic activity, and onset of glacial climatic regimes, characterize the period spanning Uquian to Recent. Most of the remaining native ungulates disappeared in the early Pleistocene, perhaps as a result of active replacement by stratum 3 herbivore groups, or prey naivete with respect to stratum 3 carnivore groups, which appeared in South America at that time. Terminal Pleistocene extinction of South American megafauna is compatible with an hypothesis of human overkill.

Periods of faunal stability interspersed with episodes of faunal disruption corresponding to orogenic activity and enrichment as a result of immigration are the outstanding features of the Cenozoic land mammal record of South America. The characteristic feature of each age, and in a number of cases the similarity in faunas of adjacent ages, permit the recognition of chronofaunas which mark periods of relative stability in South American land mammal history: Pan-Casamayoran, Pan-Santacrucian, Pan-Araucanian, and Pan-Pampean (fig. 12).

It is difficult to isolate the effects of environmentally-induced and immigration-induced factors since both may occur concurrently (as in Deseadan and Chapadmalalan-Recent). It appears, however, that environmentally-induced episodes of turnover resulted in gradual and protracted faunal changes, while immigration-induced episodes had more of a catastrophic or instantaneous effect on the fauna. This latter point is underscored by the extremely high extinction rates seen in native taxa coincident with the arrival of stratum 3 taxa in Chapadmalalan time and of man at the end of Lujanian time. These events correspond to the two highest periods of extinction in the South American land mammal record. Environmentally-induced episodes of faunal turnover correspond to changes in chronofaunas, and the change from the Pan-Araucanian to Pan-Pampean chronofauna also corresponds to the arrival of stratum 3 groups. In each case, environmentally-induced and immigration-induced episodes correspond to major periods of faunal turnover, resulting in disaster (extinction) for some taxa and opportunities (origination) for others. Disaster and opportunity are interrelated processes and resulted in multiple faunal relays, particularly during the latter half of the Age of Mammal in South America.

The familial and generic diversity of South American land mammals increased

through the Cenozoic. Several interrelated features of South American history and the fossil record account for this. First, the quality of the record increases through the Cenozoic: probability of preservation is greater in progressively younger rocks which generally have broader occurrences and less attrition from diagenetic processes. For example, two large hiatuses in the Paleocene and Eocene record account for about 12 Myr (40%) of that interval; later faunas are not separated by such large hiatuses. Second, phases of Andean orogeny increased habitat heterogeneity and, presumably, adaptive opportunities through the later Cenozoic. Third, generic richness per family increased, so that Oligocene to Recent families average 30% more genera than those in the Paleocene and Eocene (this is probably a result of the above two factors). Fourth, the land mammal fauna was apparently enriched by "insinuator" immigrants of strata 2 and 3, which presumably were able to exploit ecological vacua not occupied by native taxa. As stated eloquently by Patterson & Pascual (1972): "Continental faunas that have been evolving for millions of years are not wide open to invaders, but there will be gaps and chinks within them, portions of the environment not fully, perhaps not at all, exploited; some of their faunal elements may be less or more effective in the exploitation of niches, or even of a zone, than similarly adapted forms living elsewhere. When two such faunas become joined via a land connection, those elements of each that either are able to move into the gaps and chinks of the other, or are better adapted to exploit zones or niches, will readily be able to invade."

Our data further suggest that family diversity increase is primarily immigration-induced, while generic diversity increase is primarily environmentally-induced. Family diversity patterns show plateaus following immigration events while generic diversity patterns show continued increase related to cumulative ecological heterogeneity through time.

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