A HISTORY OF SAVANNA VERTEBRATES IN THE NEW WORLD. Part I: North America

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S. David Webb

Florida State Museum, University of Florida, Gainesville, Florida 32611

INTRODUCTION

Early in the Cenozoic Era North America was covered almost entirely by forest, predominantly of a mixed mesophytic nature. During the mid-Cenozoic, however, an increasing proportion of the land opened up, forests giving way to woodland savanna, thorn forest, and thorn scrub. By the Late Cenozoic forested areas had decreased still further and much of the savanna was being replaced by grassland steppe and even desert. Today over 25% of the natural vegetation of North America consists of such nonforest biomes. Evolution of an open-country fauna naturally followed these growing opportunities, with the locus of its expansion generally near the center of the continent in the zone of prevailing westerlies.

A remarkably similar series of changes affected the fauna of temperate South America during about the same 40-million-year interval. Yet these two American faunas remained totally separated during most of the Cenozoic. Not only were the two continents physically separate, but also the centers of open-country evolution were located deep within each continent.

The dramatic climax of this history came about three million years ago, when North and South America were connected by way of the isthmian land bridge. Surprisingly, the biota that then began to interchange through the American tropics included a major component of savanna taxa.

The purpose of this review is to elucidate the evolutionary history of open-country biota, and particularly the vertebrates in that biota, in North and South America. A fundamental assumption here is that the New World record of fossil vertebrates is sufficient to reveal much of this history during successive ages of the Cenozoic. It is believed that it can indicate major adaptive tendencies, relative abundance of various adaptive types, approximate phylogenetic relationships, and even geographic patterns of distribution among Cenozoic American vertebrates.

The evolution of American savanna vertebrates provides a particularly rich historical background for studies of Recent evolution and biogeography. Although that record will never be complete, a remarkably full history has been assembled from fossil documents scattered throughout the New World. The work was well begun over a century ago by such pioneers as Leidy, Cope, and Marsh in North America and the brothers Ameghino in South America, and it has continued to grow and be refined ever since. Surely these nonforest biotopes are much better preserved than forest biotopes. Thus, a relatively complete history can be told.

A recurrent question in the study of evolution is how to distinguish the selective effects of past environments from those of the present. Likewise biogeographers attempt to partition the distributional results of past environments from those of the present. For example, Diamond (21), in his review of Haffer's book *Avian Speciation in Tropical South America* (55), asks "What is the relative importance of historical factors and of continuing processes?" Seemingly troubled by the possible importance of the past, he alleges that "Haffer tacitly assumes that present conditions either fail to provide explanations or are to be invoked only as a last resort."

In selected examples paleontology provides the best available answers to such questions by adding historic perspective. If previous distributions and previous environments can be described, then the importance of their effects relative to those of the Recent may be deduced. An instructive example is Simpson's (134) comparison of present areas of Peruvian paramo "islands" with their probable areas during the last glacial interval as an explanation for the present floral diversity on each. Her conclusion that "glacial episodes thus seem to have played a major role in determining the present diversity of high paramo plant taxa . . ." underlines the importance of history. The present is surely the key to the past, but one may assert also with good reason, that the past is the key to the present.

THE MEANING OF SAVANNA

The word *savanna* (from the West Indian *zabana*) refers to subtropical grassy or shrubby plains with scattered trees (127). It is construed here in its broadest sense to include all open-country formations with at least a few trees; only open steppe and grasslands are excluded. Thorn scrub and open deciduous forest are included. Such usage was employed by Gregory (53) in his important essay on the history of North American savanna vertebrates. It is difficult to refine the application of *savanna* to fossil vertebrate samples, unless they happen to be associated with floral samples. But it appears from Duellman's analysis (25) of faunal relationships in Central America and from Müller's studies (102) throughout the Neotropical Region that the vertebrates from all savanna formations have much closer faunal affinity among themselves than with any forest formations. Indeed, recent vertebrate faunas of the savannas have closer affinities with grassland and desert faunas, and also with nonforest highland faunas, than with forest faunas. Likewise, plant ecologists often comment upon the importance of the break between woodland (with closed canopy) and woodland savanna (with broken canopy) (16, 162). Thus, a broad construction of the term savanna seems to have a natural basis.

Two general aspects of savanna evolution seem worthy of special note. First is the rapid and innovative change that often characterizes taxa in savanna environments. Among mammals, for example, the groups that have developed hypsodont (high-crowned) dentition, clearly an adaptation to feeding in open plant formations, have experienced very rapid evolution and, in most cases, considerable diversification. Perhaps the best examples are horses and ruminants among large herbivores and voles among small herbivores. Likewise, Stebbins (138, 139) cites a number of plant families, including Gramineae, Leguminosae, and Compositae, that have risen rapidly to importance during the mid- to Late Cenozoic cycle of increasing aridity. He emphasizes the importance of savanna-like formations as a "species pump" where evolving phyla could shift first to more xeric and then back to more mesic situations. Savannas were central to an expanding complex of open-country environments that provided a major theater for rapid evolution.

A second notable feature of most savanna vertebrates is their mobility. Their locomotor systems generally show specialization of one sort or another for foraging widely, although exceptions, especially wholly fossorial groups, may be noted. Scansorial, cursorial, ambulatory, and volant modes are characteristic in open country (59). Most taxa with such locomotor styles have large home ranges and cruising ranges; many attain large size (11, 12, 69, 137). Such mobility tends to produce high genetic continuity between adjacent populations. Savanna vertebrates do not recognize barriers to their dispersal as readily as do forest dwellers (102, 105). Presumably this explains the broad continuity throughout the neotropical region between savanna faunas and other open country faunas that Müller contrasts with the more insular nature of forest centers. Sears (127) summarizes the Late Cenozoic significance of increased vagility in open country animals as follows: "Although living organisms had accomplished marvels of diffusion during the preceding multimillions of years, migration during the Late Tertiary took on new dimensions."

With these generalizations in mind, it is appropriate to examine what is known of the history of New World savanna vertebrates. In this first part we consider the North American fauna. The second part will trace the history of the South American vertebrate fauna and the great interamerican interchange.

North American Protosavanna (Paleocene–Eocene)

There are hints that an archaic open-country biota began to develop in the Rocky Mountain region early in the Tertiary. Although paleobotany documents a subtropical forest of broad-leafed angiosperms and no grasses across most of North America, there were surely many local breaks in that cover. Even if these breaks were mainly edaphic and erosional features of temporary significance, they might have formed a mobile mosaic available to a protosavanna biota.

The evidence for a possible protosavanna biota in the Early Tertiary consists of an association of red-banded sediments and certain large vertebrates that may have been open-country opportunists. In his study of Late Paleocene mammals from the Crazy Mountain Field, Simpson (135) drew attention to the vastly increased proportion of terrestrial periptychids, phenacodontids, and arctocyonids in certain localities in contrast with the more diverse samples of smaller, mainly arboreal mammals

from the principal quarry sites. Similarly, Wilson (165) found that such ferungulates constituted 91% of the floodplain facies in his Angel's Peak local fauna. Van Houten (146) further documented the two recurrent associations of large ungulates with red-banded (open-country) sediments and of small arboreal mammals with drab (forest) sediments in Late Paleocene and Early Eocene sites throughout the Rocky Mountain region. "These observations," he concluded, "strongly suggest that the grey layers accumulated in swampy woodlands, while the red layers were deposited on flood plains in savannas that displaced the wooded areas from time to time."

When one scrutinizes the presumed protosavanna vertebrates for indications of savanna adaptations, he finds that they are generally quite subtle; certainly they do not include the obvious extremes of hypsodonty, cursoriality, or fossoriality that one finds later in the Tertiary. Nonetheless, the teeth of several larger-bodied taxa appear adapted for chopping coarse fodder, and a few show some modest specializations in their limbs for more efficient open-country locomotion. Perhaps the best example is *Meniscotherium* of the Late Paleocene and Early Eocene, a hare-sized animal with precociously developed molar crescents, molarized premolars, and incipiently cursorial limb elongation (46). The crescentic teeth of the pantodonts suggest a general tendency within that order toward ingesting coarse vegetation, and this seems to be corroborated in *Titanoides* of the Late Paleocene by its digging forelimbs. *Coryphodon* of the Early Eocene has generally been supposed to be an amphibious grazer, much like a *Hippopotamus*, and Simons (133) has noted striated grooves on the lingual base of the large lower canines that may indicate rooting food habits. The multihorned graviportal uintatheres of the Late Paleocene and Early Eocene have crested molars and molariform premolars that probably are adaptations to chopping moderately coarse fibers; their hornlike protuberances presumably imply herding behavior characteristic of open-country ungulates but not of forest dwellers (158). The taeniodonts developed truly hypsodont teeth, enormous canines, and large compressed claws, possibly for ant eating or root grubbing (107). While none of these are proven savanna dwellers, they do form a recurrent association of probable open-country taxa. The opportunities toward which they were groping would soon be seized by the early savanna biota.

North American Woodland Savanna

LATE EOCENE TO EARLY OLIGOCENE   North America's first true savanna regions, maintained by secular climatic conditions, emerged in the Middle and Late Eocene. Botanical and sedimentological evidence from the Rocky Mountain Province clearly indicate a marked increase in seasonal aridity during Middle Eocene time. In the geologic record of that time, the vast Lake Gosiute and the other structurally controlled Green River Lakes retreat, the organically rich Green River shales show regular seasonal varving, evaporites increase markedly (including some unique saline minerals), and deeply oxidized red-beds accumulate extensively (13). The first records of grass pollen appear, and nearly half the leaves in the Green River Flora (88) are small and compound. The families Leguminosae, Sapindaceae, and Anacardiaceae predominate and presumably represent a savanna woodland that dominated the lower slopes and was maintained there by the winter dry season.

MacGinitie called the climate of the Green River "Orizaban-subtropical" after the closely comparable woodland savanna flora now living on the slopes of snowcapped Mt. Orizaba near Veracruz, Mexico.

These same drying trends continued through the Late Eocene and Early Oligocene. The Green River Lakes had completely vanished by the Late Eocene, and the Uinta Basin sediments indicate an increasingly arid regime from the Bridgerian through the Duchesnean (latest Eocene) stages (9). Persistent volcanic activity in the Yellowstone and Absaroka centers may have contributed to further disruption of persistent forest patches. Leaf and pollen floras of the Late Eocene to Middle Oligocene, including the fabulous Florissant Flora, have been well studied. Woodland savanna, including such characteristic genera as *Ephedra, Mahonia,* and *Vauquelinia,* came to resemble that now living in the Chihuahuan region. Substantial amounts of gramineaceous pollen occurred, with a major peak of abundance in the Early Oligocene. By this time the subtropical forests had retreated "off the south toe of the Rocky Mountains" (74).

The appearance of an early savanna biota in North America produced a schism between the New and Old World. Along with tropical floras, the rich prosimian primate fauna of the Bridgerian (Middle Eocene) was the last in North America with clear Old World affinities (50, 152). By the Late Eocene, primates are notably scarce in the Rocky Mountain area. Their center of diversity presumably had shifted south into Middle America, and they were wholly cut off from their Old World cousins.

Besides decimation of arboreal species, the Late Eocene fauna of the Rocky Mountain region evinces two more positive responses to the expanding savanna flora: First, a number of native North American groups developed special adaptations to savanna living; and second, a number of new groups immigrated from Asia where they had already attained a degree of savanna adaption. In *Hyopsodus,* one of the most abundant native mammals in most Eocene deposits, Gazin (47) noted in later Eocene materials, "a distinct trend toward a more nearly lophodont [crest-toothed] condition in the molars . . . presumably in response to increasing aridity and coarser food." Among protrogomorphous rodents, several groups seem to have moved rapidly into the new adaptive zones available in the savanna. The genus *Manitsha,* which became half again as large as a modern beaver, may have been the "ground squirrel" of the Eo-Oligocene as its massive cheek teeth and heavy limbs indicate. The protoptychids were the "kangaroo rats" of that period and showed elongate hind limbs and progressive hystricomorph elaboration of their masticatory muscles (151, 173). The cylindrodontids had dentitions precociously specialized for coarse fibrous foods or sandy roots (9, 42, 173). It is noteworthy, however, that none of these native groups is thought to be closely related to later savanna-adapted taxa. Rather, they seem to have been replaced by them.

A major contingent of savanna-adapted vertebrates entered North America from Asia during the Late Eocene. The marked shift in faunal resemblance from Europe in the Early Eocene to Asia in the Late Eocene can be accounted for by final opening of the North Atlantic Ocean and reorganization of Asian plates (95, 123). The most notable immigrants are the selenodont artiodactyls, including the families Cameli-

dae, Hypertragulidae, Leptomerycidae, Agriochoeridae, and possibly also the ances-
tors of Oromerycidae, Protoceratidae, and Merycoidodontidae. The first rabbits
(*Mytonolagus*) entered during the Uintan (Late Eocene). It is noteworthy that the
tortoises had entered the New World from Europe (3) two stages earlier than the
hares, thus anticipating Aesop's account. Likewise, the first myomorph rodents
appeared: *Protadjidaumo* and *Namatomys* representing the eomyids, and *Simimys*
representing the zapodids or the cricetids or both (77, 78, 168). The hyaena-like
Hyaenodontidae and the hippo-like Amynodontidae also entered North America at
this time. The major source of early woodland savanna vertebrates thus appears to
have been Asiatic.

It may be more than coincidence that such possible protosavanna inhabitants as
the taeniodonts, uintatheres, and condylarths made their last appearances during
the Uintan (158). The Late Eocene and Early Oligocene have long been recognized
as a time of major vertebrate faunal turnover, especially in North America (9, 75).
Possibly the rapid expansion of the early savanna biota in the midcontinent had
much to do with these major faunal changes.

It would be of great interest to know the geographic extent of the Late Eocene
and Early Oligocene savanna in North America. The principle body of floral and
faunal evidence reviewed here accumulated in depositional basins in the Rocky
Mountain Region, but there is also a substantial record from the Pacific Coastal
Region. Floral evidence from the Pacific Northwest clearly shows that seasonal
aridity and savanna vegetation had not extended into that area (74, 171, 172). On
the other hand, the Late Eocene fauna from southern California includes several of
the same presumed savanna taxa that occur in the Rocky Mountain Region; notable
among a similar diversity of selenodont artiodactyls are the genera *Protoreodon,
Protylopus, Poebrodon,* and *Mytonolagus* (9, 14, 48, 76). During the Eo-Oligocene,
temperatures dropped and the seasonally arid *Madro-Tertiary Geoflora* began to
invade California at low latitudes and low elevations fostering southern connections
between the Rocky Mountain Region and parts of southern California (1, 4). The
Eo-Oligocene Vieja faunas in West Texas and south through Chihuahua and Puebla,
now being studied intensively by Wilson and associates (10, 35, 38, 40, 56, 57, 94,
140, 164, 174), contain a large number of the same presumed savanna vertebrates
that occur in the Rocky Mountain Region, thus strengthening the assumption of
southward continuity of savannas from the Rocky Mountain Region onto the
Mexican Plateau. The Gulf Coast and eastern North America are not affected by
these midcontinental developments and retain a moist subtropical vegetation (49).

OLIGOCENE   The scenic badlands of southwestern South Dakota and northwest-
ern Nebraska, formed predominantly from the Oligocene White River Group, are
the richest fossil vertebrate deposits in the world. It is possible to document the
progress of the savanna biota during the critical phases of the Oligocene with some
confidence. In the Orellan (Middle Oligocene) the first considerable number of taxa
had developed hypsodont (high-crowned), or at least mesodont cheek teeth (53, 141,
160; see Figure 1). At the same time, many of these same taxa underwent diversifica-
tion and adaptive radiation, suggesting that opportunities in savanna habitats were
expanding.

| |Paleo| Eo |Oligo| Mio | Plio |Pleist | Rec |

Taeniodonta
Leporidae
Castoridae
Mylagaulidae
Geomyidae
Heteromyidae
Microtinae
Elephantidae
Rhinocerotidae
Equidae
Merycoidodontidae
Camelidae
Antilocapridae
Bovidae

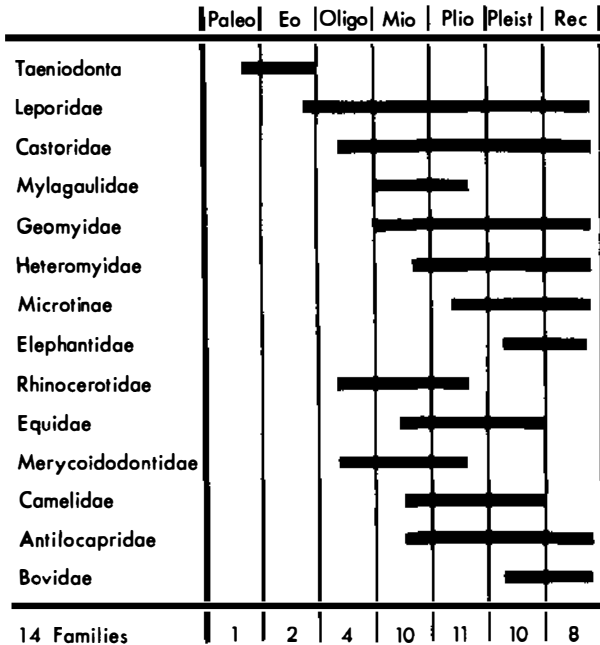14 Families   1   2   4   10   11   10   8

Figure 1   Time ranges of hypsodont mammals in North America. [After (53, 160)]

It is fortunate that in the White River Group different depositional facies can be distinguished, thus permitting an objective separation of different sets of fossil vertebrates. In the simplest model, silts and channel sandstones are taken to represent a stream-border community (the stream community itself being very limited and quite obvious), and the finer clayey sediments are taken to sample the open-country community (17, 93, 126, 136, 169). Despite the fact that the channels surely do not preserve biocenoses, and that even the clays have a biased sample (149), there is remarkable agreement among these studies as to the dominant members of the two major terrestrial communities. For example, the six commonest taxa in Wilson's (169) stream-border fauna from Whitneyan (Late Oligocene) deposits are, in order, *Protoceras* (a horned camel), *Elomeryx* (a crescent-toothed anthracothere), *Miohippus* (an early horse), *Subhydracodon* (a rhinoceros), *Agnotocastor* (the earliest beaver), and the piglike entelodonts; and these are likewise all prominent members of Matthew's (93) "forest fauna." Such facies analysis documents at least the principle taxa of the Oligocene forest and nonforest associations. *Palaeolagus* (a rabbit) and *Leptomeryx* (a ruminant) are both found to be common open-country inhabitants. There is also general agreement that the less common Leporidae (e.g. *Megalagus*) and other ruminants such as the Hypertragulidae and the Camelidae were also predominantly nonforest and nonstream-border dwellers. Clearly the little hypertragulid *Hypisodus* has all the marks of a plains grazer, including markedly hypsodont teeth, enlarged bullae, and elongate cursorial limbs. The very abundant

merycoidodonts, especially *Leptauchenia*, give ambiguous results; some workers find them more common in the open-country facies (93, 169), while others find them more frequently in the channel facies (17, 126). *Mesohippus* (a horse) and *Perchoerus* (a peccary) also occur in both. One can more easily imagine savanna taxa ranging to the stream borders than the reverse. Other possibilities are that some postmortem transport has distorted the analysis or that differently adapted sibling species have not been distinguished (148). In any event, several leporids and ruminants are determined by such independent evidence to represent an early savanna biome.

This independent evidence from facies analysis may shed light on an enigma regarding the dentitions of these early lophodont (crest-toothed) and selenodont (crescent-toothed) herbivores. As Gregory (53) observes, "the dentitions of Uintan and Orellan selenodonts are more comparable to those of browsing deer and chevrotains than to any grazers." Yet the facies analysis seems to demand that many such animals lived predominantly away from the stream border (gallery) forest. And the botanical evidence, especially from the rich contemporary Florissant Flora, makes it clear that woodland savanna was widespread, and that grasses were quite abundant within the savanna (86). A majority of ruminants living in such habitats today have hypsodont teeth and many are largely grazers. Yet in the Oligocene, a majority of the apparent inhabitants of the midcontinental savannas had teeth that must be called mesodont, or at best subhypsodont. Possibly their feeding strategies were not so narrowly specialized as in many modern savanna herbivores. More probably the absence of markedly hypsodont contemporaries may have permitted the mesodont masticators to utilize foods that at present would be preempted by more efficient feeders on coarse fiber. Thus, even though an Oligocene leptomerycid and a modern *Hyemoschus* (of equatorial African rainforests) are comparable in size and overall dental character, the leptomerycid's feeding strategy may have differed drastically because no better grazers then existed. Prairie dogs (*Cynomys*) bite off grasses and herbs close to the ground, yet their teeth are mesodont and only moderately lophate. The evidence thus suggests that feeding preferences and behavioral patterns were adapted toward open-country living first; and that dental and other morphological changes followed gradually over a period of several million years.

Because of their relative scarcity, no rodents other than *Ischyromys* have been sorted out by such facies analysis. Nevertheless, the rodent fauna tends to show the same general evolutionary response as the ruminants and rabbits, with markedly increased diversification of hypsodont and otherwise savanna-adapted groups. Many of the old protrogomorph groups were apparently replaced by modern families. The first beavers, *Agnotocastor,* appear in the Early Oligocene (27). The first North American heteromyid, *Meliakrouniomys,* is recognized in the Early Oligocene (Chadronian) with progressive zygomasseteric structure and lophate, four-cusped cheek teeth; by Middle Oligocene (Orellan) the group diversifies considerably with such distinct genera as *Heliscomys, Akmaiomys,* and *Aptetomeus* (28, 57, 115). Likewise, the first Cricetidae in North America appear "at the beginning of the Oligocene" (168). This depends in part on the definition of that family and in part on what the earlier *Simimys* is. Still, the appearance of *Nonomys* (30,

77) and a new eumyine (J. H. Wahlert and E. Lindsay, unpublished data) in the Chadronian seems to indicate the modest beginning of the series of New World radiations of the Cricetidae. As Wilson (168) puts it: "The abundance of typical cricetids in the Middle Oligocene and their rarity, amounting almost to absence, in the Early Oligocene also may be a response to increasing amounts of subhumid savanna."

Wilson suggests that two fundamental structural advances triggered the revolution among modern rodent families at that time. The first, in most instances, was incisor strengthening by the change from uniserial to pauciserial enamel structure; the second, achieved by parallel evolution in many groups, was attaining greater masticatory power by shifting the several masseter muscle origins forward for greater purchase. Altogether these cranial and dental changes seem to be adaptations for securing and chopping coarser fodder. Evidently the Oligocene rodent revolution was a response to the new evolutionary opportunities in the savanna.

One of the characteristic elements of savanna and other open-country situations is a diversity of fossorial vertebrates, including both insectivores and rhizophores. In the White River one seems to find few, if any, rodents clearly specialized for a fully fossorial life, but highly specialized fossorial adaptations are evident in several insectivores. These include *Proterix* and *Cryptoryctes* among the true insectivores, and *Glyptosaurus* among amphisbaenid lizards (8, 44, 112, 113).

The commonest White River carnivore, the foxlike *Hesperocyon,* has been determined to belong to the open-plains facies by Clark, Beerbower, & Kietzke (17). *Hyaenodon* may well belong to that community also. Most other carnivores are either too rare to be assigned with certainty or else are truly eurytopic.

The possibility that faunal provinces may be distinguished within the Oligocene vertebrate samples of North America has intrigued several able paleontologists (63, 126, 159). Unfortunately many of the apparent differences between the "Plains Province" of the Big Badlands and the "Mountain Province" sampled at Canyon Ferry and Pipestone Springs in Montana have broken down either because they were based on sampling errors or because such central Wyoming sites as Bate's Hole, Flagstaff Rim, and Beaver Divide have blurred the boundaries. Furthermore, the distinctions of higher elevation and more intense volcanic activity that were thought to distinguish the "Mountain Province" in the Oligocene are removed now that the Wiggins Formation (volcanic conglomerates) has been shown to be Eocene (29, 81). Nonetheless, as Robinson (122) notes, the possibility of developing provincial concepts still seems better in the Oligocene than earlier. The work of Wilson and associates in the Big Bend of Texas now provides a number of excellent samples to compare with the northern "plains" and "mountain" samples.

MIOCENE   According to the classic story, grasslands first blanketed the Great Plains during the Miocene. The burden of this story was usually borne by the horse, in particular by the Hemingfordian transition from *Parahippus* and its browsing antecedents to *Merychippus* and its grazing descendants. While modern advances in the field of geochronology have provided improved estimates of the age and duration of these changes, and while improved sampling of the fossil faunas, espe-

cially by the Frick Laboratory, has refined and complicated the known phylogeny of Equidae (85), the well-known history of the grazing horse is still, as it were, engraved in tablets of stone.

The story becomes more interesting when additional vertebrate groups are considered. In the first place, it gains credence if more than one taxon seems to have responded to the supposed spread of grasslands. If such changes as increased crown height, enamel folding, and cement deposition on the cheek teeth were confined only to the horse, one might well argue that some *Parahippus* populations had merely crossed a genetic threshold. Instead, a large number of unrelated taxa show comparable trends accelerating during an adjacent age or two. This point has always been implicit in the best discussions of the subject. For example, in his early studies of Middle and Late Miocene faunas of the Great Basin and Mohave Desert, J. C. Merriam (97, 98) recognized the diversification and dominance not only of the merychippine, protohippine, and hipparionine horses, but also of merycodontine pronghorns and hypsodont camelids. In his great book *A History of Land Mammals of the Western Hemisphere,* Scott (125) summarized the situation as follows: "... an especially characteristic feature of later Miocene faunas was the large number of species, belonging to several different orders, which had the hypsodont, or persistently growing type of grinding teeth; many of the horses, camels, ruminants and rodents displayed this structure and as was first pointed out by Kowalevsky, the explanation is probably to be found in the spread of grasslands at the expense of the forest. . . ."

The diversity of ungulates in North America reached its apogee in the Miocene, with an array of taxa fully comparable to that in African savannas today. Besides hypsodont horses, camels, and pronghorns, one finds an extraordinary diversity of hypsodont oreodonts, diceratherine, teleoceratine and other advanced rhinos, and finally at least four kinds of gomphotheriid proboscideans. There is a notable correlation between those lineages that are most hypsodont and those that undergo the greatest diversification. For example, gomphotheriid proboscideans outstrip mammutids, protolabine camels diversify more than giraffe camels, and hypsodont horses surpass brachydont horses.

Functional studies of these Miocene ungulates usually have featured their dental and masticatory adaptations to chopping coarse fodder. For both phylogenetic and functional reasons, the postcranial skeletons deserve equal consideration, and a number of recent studies have begun to right that balance. It is impressive to find that in many ungulate groups, modifications for open-country locomotion appear at least as early, and at least as markedly, as do their masticatory modifications. Thus, Camp & Smith showed that the hypsodont lineages of horses acquired their digital springing ligaments and other progressive skeletal features about as early as they did their high-crowned teeth (15, 65). Similarly, the first hypsodont camelids also developed the pacing gait and digitigrade padded feet for efficient travel in open landscapes (155). The general coincidence of masticatory and locomotor modifications in each of these ungulate groups further implies that the underlying cause of these changes is environmental in nature.

Fully as impressive as the open-country adaptations of Miocene ungulates are those of Miocene rodents. The outlines of their history are only now coming into sharp focus, thanks to the Hibbard Method of collecting microvertebrates and to a new generation of rodent specialists. As in the ungulates, one notices a marked tendency in many Miocene rodents to develop hypsodont dentitions presumably for masticating coarse fibers, sandy roots, or both (118). Here too one often finds simultaneous change in the locomotor system; in most hypsodont rodents the change involves adaptations for burrowing. The most spectacular Miocene adaptations for burrowing and fodder chopping occur in the now extinct mylagaulid rodents, beginning with *Mesogaulus* in the Hemingfordian and continuing with *Mylagaulus* and the horned genera *Epigaulus* and *Ceratogaulus* in the Barstovian and younger (32). Ochotonid rabbit genera multiplied rapidly (52). The greatest diversification among Miocene savanna rodents has been documented for the geomyoids (pocket gophers, etc) in a number of recent papers (45, 79, 116, 117, 119, 131, 142). *Entoptychus* in the Upper John Day Formation of Oregon exhibits the most rapid evolutionary change documented in any Tertiary land mammal lineage, with "at least eight successive stages of cheek tooth hypsodonty during its existence" of about two million years (36, 116). Heteromyidae continued to diversify through the Miocene, especially during the Barstovian and Clarendonian (79). Kangaroo rats (*Eodipodomys*), with fully specialized hind limbs, hypsodont, dentine-exposed teeth, and enlarged auditory bullae, appeared in the Late Miocene (Late Clarendonian) (150). Even among beavers, one finds root-eating burrowers, as the repeated discovery of *Palaeocastor* (of Arikareean age) in the magnificent burrows known as "Devil's Corkscrews" clearly demonstrates (109). This striking diversity of burrowing rodents in the Miocene contrasts with the limited number of known burrowing forms (few of which are rodents) in the Oligocene. Among burrowing nonmammals, rattlesnakes and owls appear to be new plains-adapted groups (62, 100).

Since its brilliant enunciation by Kowalevsky (71), paleontologists and botanists generally have accepted the view that the Miocene outburst of hypsodont mammals in north temperate regions was an adaptation to widespread grasslands or steppe vegetation. This view seemed to be confirmed by Elias's documentation (26) in the High Plains of abundant fossil hulls of *Stipidium* and *Berriochloa,* representing the needlegrass (*Stipa*) group, in the same Miocene deposits as the world's most diverse assemblage of hypsodont horses. Yet, as it now appears, this classic view was only about half true.

These supposed Miocene grasslands were considerably abridged by MacGinitie's study (87) of the Kilgore Flora from Late Miocene deposits in Nebraska. The Kilgore leaf and pollen flora represents a savanna "with mesic forests along the streams and open grassy forests on the interfluves . . . [and] no treeless prairies." It consisted of grasses, along with trees such as "small live oaks, pines, blackberry, and persimmon, with shrubs of *Mahonia,* currant, hawthorne, sagebrush, and relatively abundant species of composites."

In his excellent review of this problem, Gregory (53) points out three kinds of vertebrate evidence that convincingly corroborate the floral evidence, and permit

recognition of woodland savanna biota across much of the midcontinent. First, he notes the continued occasional presence of arboreal rodents, and one may add, the last North American primates and abundant insectivores as well (66, 83, 84). Second, among ungulates a considerable diversity of brachydont browsers and mixed feeders persist, including anchitheriine horses, chalicotheres, bunodont peccaries, moschid and dromomerycid ruminants, protoceratids, miolabine camels and, most notably, aepycameline (giraffe) camels over 12 feet tall. Third, the high total diversity of large and medium-sized herbivores in sample after sample equals that in the present African savannas and is much higher than that in treeless prairies (144). Thus Gregory's analysis of the vertebrate faunas corroborates and amplifies MacGinitie's analysis of the Kilgore Flora: Both clearly tell us that through the Late Miocene the Great Plains supported a woodland savanna with broad interdigitations of riparian forest.

The Miocene lasted nearly as long as the Eocene, spanning some 20 million years, and therefore may be expected to include major changes within its span. Thanks to a rich North American Miocene record and to a comprehensive review of its biochronology by Tedford et al (in press), patterns of faunal change can be clearly discerned within that epoch. Tedford et al recognized seven successive biostratigraphic units or subunits with durations of between two and three million years each. Fortunately, major faunal shifts occur much less frequently than these units could discriminate; thus Tedford et al recognize only three vertebrate chronofaunas. These chronofaunas maintain essentially unified generic composition while evolving through long spans of time, thus implying extended periods of ecosystem stability. The First Miocene Chronofauna in North America spans the Late Arikareean and Early Hemingfordian intervals, the second spans the Late Hemingfordian and Early Barstovian, and the third, the "Clarendonian Chronofauna" (153), spans the Late Barstovian, Clarendonian, and Early Hemphillian. The first and second of these Miocene chronofaunas each lasted about five million years, and the third endured about eight million years. By definition, each chronofauna, roughly corresponding to Early, Middle, and Late Miocene, ends with a major faunal breakdown and the next begins with a fundamental faunal reorganization. Yet in this case, these breaks do not terminate, but merely punctuate, the overall trends of adaptation and diversification in the principal savanna lineages. For example, from *Parahippus*-like stock in the First Miocene Chronofauna come diverse genera of protohippine and merychippine horses in the Second Miocene Chronofauna, and from them emerge about eight genera of pliohippine and hipparionine horses in the Third Miocene Chronofauna. Gregory's (53) usage unites these three Miocene chronofaunas along with two earlier Oligocene chronofaunas (namely the Whitneyan-Arikareean and the Orellan) in a greater North American mid-Tertiary chronofauna. This broader usage seems to exceed the original essentially generic-level definition of Olsen's and might be termed a chain of chronofaunas or a "zeugochronofauna." In any event, the overall continuity of successive autochthonous radiations in North American savanna lineages from Oligocene through Miocene included five successive chronofaunas.

The degree of continuity in North American Miocene savanna lineages can be crudely measured by asking what percentage are autochthonous products of this continent. The relatively high percentage that one indeed finds tends to corroborate Gregory's (53) emphasis on the "repeated association in successive deposits . . . of the same lineages from Orellan through Barstovian." Indeed that continuity can be followed into the Hemphillian. Horses, camels, and oreodonts are clearly native stocks, and account for most of the Miocene diversity of hypsodont ungulates (not to mention much of the diversity of brachydont ungulates). Likewise, among hypsodont rodents the heteromyids, geomyids, mylagaulids, and most of the castorids have their Oligocene ancestors in North America.

Of immigrant stock, only the merycodontine pronghorns may be counted among the first rank of savanna-adapted vertebrates. Appearing in the Early Hemingfordian, their herds diversified and spread abundantly over western North America during the Second Miocene Chronofauna. And their descendants, the antilocaprine pronghorns, were equally important members of the Third Miocene Chronofauna and thereafter (156).

This argument becomes blurred somewhat if one considers immigrant groups that do not fully exemplify open-country adaptations (Figure 2). About a dozen of the 34 Miocene mammalian immigrant genera tabulated by Tedford et al might be regarded as forest-edge or mixed-feeding types, and thus in the broad sense savanna-adapted. These include the amphicyonids (64), the chalicotheres, the cervoid ruminants, the proboscideans, the ochotonid rabbits, the zapodid rodents, and the cricetid rodents that diversified considerably in the Barstovian. Presumably they were able to enter the more densely wooded margins of the major North American savannas and to penetrate the broader riparian forest corridors (166, 167), thus edging into the savanna fauna. This pattern further supports the view that the midcontinent supported woodland savannas, not pure grasslands.

It is interesting to note the steady increase in Old World immigrants through the Early Miocene (Gering to Marsland). Their numbers increased markedly through a period of five million years and then declined in the mid-Miocene (Figure 2). Surely this is not a stochastic pattern; rather it appears as if the doors were opening and then closing at a remarkably steady rate. Presumably, this reflects a gradual opening and reclosing of the forested habitats connecting temperate latitudes of North America and Asia. An even more marked increase in immigration rate occurred in the Late Pliocene and Pleistocene (120, 154).

The new view of woodland savanna rather than treeless prairie blanketing the interfluves during the Miocene is reasonably well documented by floral and faunal evidence in the Great Plains. One may ask whether, or to what degree, the same pattern extended to other parts of North America. The answer is that the pattern was by no means uniform, and the the Late Miocene seems to be a time of maximum regional differentiation in North America (Tedford et al, in press).

In the Pacific Northwest a sequence of rich Oligocene and Miocene floras has permitted Wolfe & Hopkins (171, 172) to document the vegetational history of this region in some detail. In the prevailing warm-temperate forest, the frequency of trees

with entire-margined leaves dropped notably in the mid-Oligocene (about 31 million years ago); several lesser fluctuations followed. The percentage then moved dramatically downward again in the Middle Miocene, about 12 million years ago. While there has been some discussion both of how well leaf margin percentages track climatic changes and of the regional significance of a local flora [with its own edaphic, orographic, and altitudinal peculiarities (6)], the large array of floras
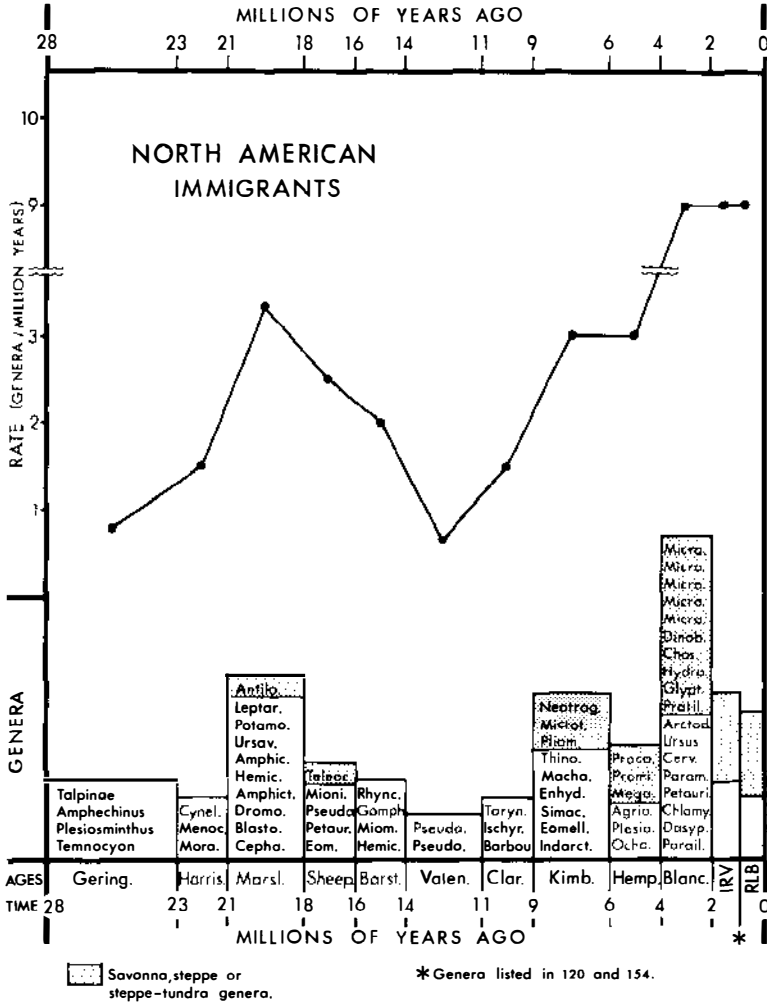

Figure 2 Immigrant mammal genera in the Middle and Late Cenozoic of North America. Note two distinct peaks, one in the mid-Miocene, one in the Plio-Pleistocene. [After (120, 154) and Tedford et al, in press]

sampled allays most serious doubts (22). Thus it seems clear that during the Middle Miocene in the Pacific Northwest mesophytic forests continued to predominate, although they moved markedly toward a cool-temperate composition. Evidence from vertebrates of coastal California gives much the same impression (67, 80).

At approximately this same time vertebrate faunas are also well represented in the Columbia Plateau. Indeed some Miocene faunas occur in direct association with floras, the most notable case being the Mascall flora and fauna (24). Shotwell (132) drew an interesting facies distinction between his Quartz Basin fauna and the contemporaneous fauna from the Red Basin and the other Oregon sites. The "Quartz Basin facies" produces diverse heteromyids, geomyids, cricetids, and zapodids, but few sciuromorph rodents; the widespread *Monosaulax* beavers and *Merychippus* horses are each represented in the Quartz Basin by a species with more complex enamel; and such probable browsers as *Hypohippus, Ticholeptus,* and *Rakomeryx* are conspicuous by their absence. This "Quartz Basin facies" is rare and suggests that within the predominant deciduous forests of the Columbia Plateau there were patches of more open (perhaps shrubby) woodland. This facies becomes more evident in Barstovian faunas as one moves southward into Nevada and the Mohave Desert; and it incorporates a greater diversity of merycodontine pronghorns and protohippine horses (130). The Tonopah local fauna of southern Nevada (58) also represents the "Quartz Basin facies."

In the Stewart Valley of west-central Nevada one finds both the "Quartz Basin facies" and the "Red Basin facies" (a deciduous forest biota) in separate but nearly correlative deposits. These local faunas are bracketed by local floras: the Fingerrock Flora below, the Stewart Valley Flora stratigraphically above. In agreement with the mammalian evidence, these floras show a marked facies shift in probable Barstovian time (5, 170): The older flora, despite its domination by live oaks, resembles the mesophytic floras of Oregon; whereas the younger flora has "few species in common with floras to the north," but has a distinctive spruce-cedar–live oak association, including some early records of uniquely Great Basin species, conspicuous pine and grass contributions, and a generally less humid character. Thus during the early part of the Late Miocene one can plot the boundary between the mesic biota of Oregon and northern California and the emerging semiarid biota of Nevada and southern California.

By the latest Miocene a scrub or steppe-adapted Great Basin fauna had expanded to nearly its present range. It was characterized by the appearance of abundant arvicolines (*Promimomys* and *Microtoscoptes*), endemic antilocaprines (*Ilingoceras* and *Sphenophalos*), badgers (*Pliotaxidea*), and by the spread of steppe-adapted horses (*Pliohippus*) at the expense of forest-adapted horses (*Hipparion*) (130).

It is more difficult at present to discuss the Late Miocene biota of the Colorado Plateau. Several samples, notably from the Flint Creek beds of western Montana and the Lemhi Valley in Idaho resembling the Mascall and other mesic-adapted faunas of the Columbia Plateau, have been found (68, 72, 103, 111, 122, 143). While there is clear evidence here of continuity between the plains and the far west, the mammalian faunas include predominantly mesic forest types and few, if any, species adapted to less humid conditions.

The Middle and Late Miocene record provides numerous suggestions that the evolution of less humid savanna biota was centered about the Mexican Plateau. The history of the flora has been treated under the rubric "Madro-Tertiary Geoflora." One of its earliest records is the Tehachapi Local Flora associated with the Phillips Ranch Local Fauna of Hemingfordian age in southern California, and the surviving elements now reside in the arid and semiarid southwest (6, 175). A number of savanna-adapted Miocene vertebrates seem to follow a southern distribution between the Plains and the Southwest. For example, the precociously hypsodont gazelle camels (*Stenomylus*) have been discovered in Middle Miocene sites in southern California, Arizona, and New Mexico (45, 176). And the important Zia Sand Fauna from New Mexico produces a progressive aridity-adapted fauna, including stenomylines, Cynarctoides, mylagaulids, geomyids, and heteromyids, during successive phases of the Middle Miocene (43, 45). These faunas agree with the floras of the Rio Grande Trench in indicating a downdropped southern savanna corridor connecting the Plains faunas with those of the Southwest (7).

The accepted evolutionary history of the Miocene peccaries *Cynorca* and *Dyseohyus,* revised by Woodburn (175), emphasizes the same pattern. In the earlier Miocene *Cynorca* was widely distributed in mesic situations from Oregon and California to the Texas Gulf Coast and High Plains and a little later in Florida and Maryland. The mid-Miocene range of its descendant, *Dyseohyus,* however, shows evidence of adaptation to subhumid conditions and a more southerly distribution, which appears to have its center in the Mexican Plateau, with one northern arm (*D. fricki*) reaching southern California and southern Nevada, and another (*D. stirtoni*) extending into the High Plains via the Rio Grande Trench (in Texas). Confirmation of this pattern comes from Dalquest & Mooser's (20) recognition of *D. stirtoni* in the Zoyatal Local Fauna in central Mexico.

The four known Miocene faunules of central Mexico have received special attention, partly because of their possible focal role in the history of the semiarid biota of North America. While the results are still tantalizing, these faunules do show remarkable continuity with the Great Plains savanna fauna at least in the grazing horses, camels, and oreodonts (20, 33, 34). Ferrusquia (34) suggests these samples represent both "una sabana, ambiente apropriado para *Merychippus, Oxydactylus* y probablamenta el protoceratido traguloide, y un bosque lluvioso tropical, ambiente adecuado para *Merychyus* y *Gomphotherium.* "

One notes that in the course of the Miocene an interesting shift occurred in the affinities of the vertebrate fauna around the Gulf of Mexico. During the Early Miocene the Garvin Gully Fauna of Texas and the Thomas Farm Local Fauna of Florida exhibit considerable endemism in the herpetofauna and among the browsing artiodactyls where the Florida tragulids, nothokematids, and peculiar protoceratids seem largely to supplant the moschids and dromomerycids so characteristic of the Plains (2, 39, 108, 163). The Gaillard Cut Local Fauna of Panama (161) samples virtually the same Gulf Coast Fauna that Tedford et al have appropriately distinguished as the Miocene Gulf Coast Chronofauna.

By mid-Miocene (Barstovian) time the peculiarities of the Gulf Coast Fauna have nearly disappeared and closer faunal continuity is reestablished with the Great

Plains Fauna. This is most clearly indicated by the Trinity River Local Fauna, in which the diverse sample of artiodactyls wholly resembles plains samples (37, 108; Tedford et al, in press). And the same carries up through the later Miocene Cold Spring and Lapara Creek faunas.

The faunal nexus between the Plains and the subhumid region of the Mexican Plateau, established during the Middle Miocene, persisted into Late Miocene. But evidently major barriers were beginning to separate these faunas from the Great Basin and Mohave Desert faunas to their west and northwest. The beginnings of such a separation may be perceived earlier in the specific distinction between *Dyseohyus fricki* (in the far west) and *D. stirtoni* (from Mexico to the High Plains). It is more evident, however, by the Late Miocene (Clarendonian) when a major suite of hypsodont horses, including *Calippus, Astrohippus,* and *Pseudhipparion,* and the shovel-tusked gomphothere *Amebelodon* range from the Plains and the Gulf Coast into Arizona and Chihuahua, but not into the far west (73, 153). One may speculate that the region of the present Sonoran and Mohave Deserts may already have begun to form a barrier to savanna-adapted taxa in the Great Plains and Chihuahua regions.

Presumably, the increased Late Miocene continuity between the Gulf Coast Fauna and the Plains Fauna represents an eastward expansion of the savanna corridor that earlier had been largely confined to the Rio Grande Trench. Presumably, the corresponding reduction in the area of subtropical forest enclaves led to the extinction of most of the peculiar Miocene browsing fauna of the Gulf Coast, and to the final break between the mesic forests of the southeast and those of the tropics. A probable broadening of the Gulf Coastal savanna corridor does not contradict the more general view of Graham (49) that warm-temperate forests of essentially modern aspect prevailed over most the southeastern United States. But Graham's (51) study of a Late Miocene pollen flora in Veracruz shows no tropical rainforest elements, up to 45% grass pollen, and oak and pine-oak woodland predominating, suggesting that the temperate character of the northern Gulf Coast woodland savanna extended far to the south as well.

The Late Miocene extension of woodland savanna around much of the Gulf Coast also produced a major disjunction between the mesic forests of eastern United States and those of Central America. This disjunction is very clearly documented in fossil Amphibia and Reptilia of North America (31). Until about Late Miocene time, north-temperate records of many groups of mesic herptiles are relatively abundant (2, 31, 61, 62, 70, 82, 99, 110, 145). Subsequently, as Estes' review (31) clearly shows, many of these taxa disappear from the fossil record (mainly in temperate latitudes) only to reappear as Recent members of Central American mesic faunas (124). Jaçanas (106) provided a similar example among birds. The Late Miocene establishment of a broad Gulf Coastal woodland savanna produced the final disjunction between forest biotas of Middle America and the eastern United States (90, 91).

North American Steppe (Pliocene and Pleistocene)

The last step in dismantling the once continuous forests of North America came in the Pliocene, about five million years ago. Woodland savanna changed to steppe in

the High Plains and over major parts of the arid southwest. The evidence, as Gregory (53) clearly analyzed it, consists of four points: absence of arboreal species, absence of browsing (especially giraffoid) species, restricted diversity even of grazing species, and (as a composite of these) lower overall faunal diversity. Gregory went on to show that in the Great Plains these features only partly characterize the Early Hemphillian (Latest Miocene), but are fully applicable to the Late Hemphillian and Blancan (Late Pliocene) faunas. The final shift from woodland savanna to treeless prairie (except narrow belts of riparian forest) accounts for the final demise of the Third Miocene Chronofauna of Tedford et al in the Late Hemphillian. Thus the midcontinental steppe came into existence no more than five or six million years ago.

The change from woodland savanna to steppe had a dramatic effect on the vertebrate fauna. In the High Plains, the browsing horses, the tapirs, most of the peccaries, most of the proboscideans, and all of the moschid and dromomerycid ruminants disappeared—presumably in response to the nearly total disappearance of their browse. What might seem more surprising is the loss (without apparent replacement) of predominantly grazing types, including four genera of hypsodont horses, two genera of hypsodont camels, and three genera of antilocaprines. Furthermore, at the end of the Hemphillian less than two million years later, another chronofaunal breakdown occurred with the further loss from the former savanna fauna of three more genera of hypsodont horses, the last mylagaulid rodents, the last New World rhinocerotids, and three more genera of antilocaprines. Among rodents, the cricetids experienced an important radiation, especially the more hypsodont groups such as sigmodontines and phyllotines (Baskin, in press). Wilson (166) observed that "there is an increase in hypsodonty in Middle Pliocene forms ... in response to the increasing aridity ... a response which culminated in the upper Pliocene appearance of many of our Recent genera with long-crowned teeth."

The spread of steppe and desert conditions in the Pliocene has long been suggested by students of paleobotany. In the Great Plains grass hulls are common (26, 41), as are caliche deposits, suggesting increased evaporation, but no major flora directly confirms the current view of forests narrowly restricted to riparian sites. The most direct Pliocene evidence of steppe vegetation comes from southern California where the Mt. Eden Flora produces desert border chaparral (4).

The relative recency (five million years) of steppe conditions in the Great Plains is reflected in the relative paucity of endemic steppe-adapted ("pure grassland") taxa in the modern biota. Most of the grasses themselves range more widely and more diversely into surrounding woodland biomes, particularly to the southeast; the grasshoppers also have greater diversity outside the Central Plains with major centers of diversity to the west and southwest. Similar patterns are evident within the mammals (23). And to most birds that range through the region, as Mengel (96) puts it, the steppe per se represents "a hostile Sea."

During the Pliocene the expanding steppe of central North America did not connect broadly with the central Asiatic steppe. Instead the two steppes were at first separated in Beringia and in boreal latitudes by broad bands of forest, mesophytic during most of the Pliocene and earliest Pleistocene and coniferous taiga during much of the Pleistocene, which continued to filter the steppe elements. Not until the

Late Pleistocene did continuous tundra and steppe-tundra corridors connect the Old and New World steppe biota (54, 60, 128). Instead, forest-adapted vertebrate immigrants, such as *Petaurista*, a flying squirrel, *Parailurus*, a panda, and *Ursus*, bears enter during Hemphillian and Blancan time (121, 144a). Nonetheless, Hemphillian deposits of North America yield an increasingly important contingent of Old World steppe elements that filtered through the northern forests. Most notable are the arvicoline rodents, which began to enter North America in increasing numbers and with characteristically explosive diversification upon arrival (89). Zapodine jumping mice may have come from the same source at this time, or they may actually have gone in the opposite direction. *Neotragocerus* of Hemphillian deposits is the first of a number of Old World bovids to disperse to the New World; and *Procoileus* is the first of a number of progressive Cervidae adapted to some degree of open-country living. The rate of immigration from the Old World continued to accelerate through the Blancan and younger stages (120). Even so, a majority of the surviving plains and desert vertebrates of North America have North American ancestors from the Miocene or older; the dominance of native stock merely became less clear in the Late Cenozoic than it had been in the Miocene.

A renewed pattern of provincialism developed within temperate North America during the Pliocene, principally because certain forest enclaves were not greatly affected by the onset of drier climatic conditions. In the Pacific Northwest and northern California many elements of the older mesic biota persisted. The aplodontids were represented then by *Liodontia*, as they are now by *Aplodontia* (129); their poor urine concentration (104) partly explains their consistent history of restriction to mesic forest.

The biota around the Gulf of Mexico was not so deeply affected by the Pliocene onset of drier conditions. There presumably the prevailing tendency toward desiccation was countered by the effects of summer rains from the Gulf, and these same effects seem to have extended west onto the Mexican Plateau into Chihuahua. The evidence for this is the remarkable resemblance between the savanna vertebrates of the Yepomera Local Fauna in Chihuahua and the Bone Valley Fauna in Florida (73, 157). Furthermore, the El Ocote Local Fauna near Aguascalientes samples much the same fauna in southern Mexico (101). Thus, although the Late Miocene savannas gave way to Pliocene grasslands in the Great Plains, they persisted on through the Pliocene in a broad belt southward from about latitude 30 degrees north.

This subtropical savanna biota that persisted around the Gulf of Mexico and into Central America played an extremely important role in the interamerican faunal interchange which began in the latest Pliocene. We shall take up this subject in Part II of this review.

Extinctions

As much of North America's savanna vegetation gave way to steppe, the diversity of the savanna biota declined markedly (18, 19, 53). A majority of the large ungulates disappeared (53, 154), whereas most of the surviving steppe- and desert-adapted taxa were small to medium-sized.

The resemblances between the Late Pliocene (Hemphillian and Blancan) extinctions and the Late Pleistocene (Rancholabrean) extinctions in North America are striking. While there are differences between the two sets of circumstances (notably the presence of man in the Late Pleistocene), the similarities should not be dismissed lightly. In both instances, a cumulative set of large mammal extinctions coincided with climatic deterioration, and a corresponding increase in small mammal taxa. The Late Pliocene extinctions involved about 30 mammalian genera in North America, while the Late Pleistocene extinctions involved about 20 genera (92, 147, 154). Thus, even though the former extinctions may have been spread over a longer period of time (up to three million years), the changes seem to have been more devastating. Furthermore, several of the large vertebrates that are counted as Late Pleistocene extinctions are still living in Central America and/or South America; these include giant tortoises, capybaras, jaguars, spectacled bears, tapirs, and llamas. The fact that the same genera (if not species) survived in subtropical savannas but became extinct in north temperate steppes suggests that environmental deterioration had something to do with their north temperate demise. Reed (114) notes a similar pattern of reduced extinction in subtropical latitudes in the Old World (e.g. elephants and rhinoceroses became extinct in northern Eurasia, but live on at lower latitudes). Thus, the reduction in savanna area may be causally related to the loss of large vertebrates in the Late Cenozoic of North America.

ACKNOWLEDGMENTS

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