Down-to-Earth Approaches to Vertebrate Paleontology

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Vertebrate fossils are commonly found in buried soils (paleosols) of the ancient landscapes they inhabited. Study of these soils (paleopedology) can provide information important to the interpretation of vertebrate fossils, as illustrated here with a review of biostratigraphic, taphonomic, paleoecological and evolutionary studies of Oligocene fossil soils and vertebrates in Badlands National Park, South Dakota.

A significant advantage is gained from the fact that paleosols are, by definition, in place. Fossils within them are less likely to have been resorted from rocks of different age than fossils in deposits of lakes and streams. Soil formation punctuates the sedimentary accumulation of floodplain deposits, and thus provides a limit to effective biostratigraphic resolution of sequences of paleosols containing fossil vertebrates.

Paleosols also are preservational environments for fossils. Bone is best preserved in calcareous paleosols of dry climates. Assemblages from less calcareous paleosols are subject to severe bias against preservation of small bones. Because of their higher surface-to-volume ratio, these are more prone to dissolution than large bones.

Paleosols also provide records of ancient habitats of vertebrates, particularly their local vegetation and geomorphic setting. Such information is useful not only for paleoecological reconstructions, but as evidence of selection pressures effective in mammalian evolution. Temporal resolution of sequences of paleosols also can be a critical limitation on studies of the rate of evolution of mammalian fossils.

INTRODUCTION

Fables are familiar explanatory devices in popular accounts of the fossilization of large vertebrates. Many of them are something like this: "It is nearing the end of the dry season. A herd of titanotheres is crowded around a waterhole—one of the last of a chain of pools in a parched river bed. Available forage has been eaten or trampled into the cratered mud. The animals are restless when the first thunderstorms trail across the plains nearby, but they are unprepared for the wall of turbid water that follows. Their drowned bodies are piled together with other debris of the flood in slackwater eddies of the stream. As the water subsides, the bloated carcasses rot and are scavenged. Their disarticulated bones are strewn throughout the streamside swale before burial by the next flood. Ages pass before their rocky tomb is opened in the name of science." Whether the titanotheres, chevrotains, horses, or plateosaurs are overwhelmed by floods, mudflows, or volcanic ash, the moral of such fables is consistent and unsettling. Disaster could strike at any moment and consign us to an early grave. There is good evidence that such disasters occurred (Clark, 1937; Clark and Guensberg, 1970; Weishampel, 1984; Voorhies, 1969), and to them we owe the most spectacular finds of bone breccias and articulated vertebrate fossils that now grace major museums. Such fossils also have tended to dominate the scientific study of vertebrates, but they are not the subject of this review.

About as far removed as can be imagined from such dramatic scenes of vertebrate fossilization is the accumulation of remains through normal processes of predation, disease, and old age on ancient land-surfaces (Clark et al., 1967; Bown and Kraus, 1981; Retallack, 1983). These attritional pedogenic assemblages may be disarticulated, cracked, gnawed and iron-stained, and rather unimpressive compared to catastrophic sedimentary assemblages. Nevertheless, they are of particular interest for at least two reasons. Like the paleosol containing them, most of them are in place, preserved where they lived. They are neither in migration, nor transported far, nor redeposited into younger sediments. In addition, the paleosol itself yields evidence of their former habitat, age, and preservational environment. It supplies a record of conditions during life and death of the animals, rather than just their death or redeposition in catastrophic sedimentary assemblages. These two simplifying assumptions can be a significant advantage for the interpretation of fossil vertebrates, as can be seen from the following examples, drawn from studies of the spectacularly fossiliferous Oligocene paleosols of Badlands National Park, South Dakota.

BIOSTRATIGRAPHY

The rudiments of a biostratigraphy for the scenic badlands of Late Eocene and Oligocene alluvial sediments in South Dakota and Nebraska were proposed as early as 1893, when Wortman divided these deposits according to fossil content into *"Titanotherium* Beds," overlain by *"Oreodon* Beds," then "Barren Clays," and *"Protoceras* Beds." By 1909, Osborn and Matthew had modified this to recognize biozones and the distinctive nature of the fauna in channels and floodplains: successively the *"Titanotherium* Zone," *"Oreodon* Zone" with its *"Metamynodon* Channels," and *"Leptauchenia* Zone" with its *"Protoceras* Channels." All of these stratigraphic terms and some of the generic names have since fallen into disuse, but in a sense they live on in the North American Land Mammal "ages" of Chadronian, Orellan and Whitneyan (Wood et al., 1941). A separate, purely lithostratigraphic nomenclature (Fig. 1) has been proposed for this region (Harksen and MacDonald, 1969), but the chronostratigraphic units have assumed the role of a standard for North American terrestrial deposits of this age. These mammalian stages have become better defined by radiometric dating of volcanic ashes (McDowell et al., 1973; Obradovich et al., 1973) and by correlation of paleomagnetic reversals with the deep marine record (Prothero et al., 1982, 1983; Prothero, 1985a, b).

There are indications that a finer biostratigraphic subdivision may be feasible (Ostrander, 1985; Prothero, 1985a; Gustafson, 1986) but no comprehensive schemes have been proposed. An ill-fated scheme outlined some years ago provides an instructive cautionary tale. In his monumental work on titanothere taxonomy and evolution, Osborn (1929) followed Hatcher's field division of the Chadron Formation into three units, through which Osborn found a steady increase in body size and horn development of titanotheres with time. This superbly documented example of "Cope's Law" sometimes still appears in textbooks. The stratigraphic level of each fossil was measured from the distance above the disconformable contact of these mid-Tertiary beds with the underlying Late Cretaceous marine rocks, as would be reasonable if these were deposits of a lake or flat alluvial plain (Gregory, 1969). However, Clark (1937) found that they were laterally variable floodplain deposits on a basal disconformity with considerable topographic relief. Paleovalleys of this ancient landscape are cut well below (27 m in section of Fig. 2) a marker horizon of red, kaolinitic clay that was recognized as a strongly developed paleosol. When Osborn's data on titanothere localities were reassessed and combined with Clark's own data, the skulls no longer showed a regular evolutionary progression with geological age. As Clark (1937, p. 265) sarcastically noted, the supposed evolutionary status of the titanotheres could be used to establish their stratigraphic level. But without a prior stratigraphic basis this would be a case of circular reasoning of the type that still plagues biostratigraphic studies near major unconformities (Archibald et al., 1986).

A later discovery (Clark et al., 1967) of latest Eocene or earliest Oligocene deposits (Slim Buttes Formation) older than the deep paleovalleys and their alluvial fill (basal Chadron Formation), introduced yet another problem for finer biostratigraphic subdivision. Finds of Cretaceous marine fossils, such as baculites and inoceramid bivalves in early Oligocene alluvium (Chadron Formation), had long been recognized as evidence of resorting of older fossils into younger sediments (Loomis, 1904; Ward, 1922). But now that erosionally dissected older Tertiary sediments (Slim Buttes Formation) were recognized, the resorting of their fossils into the younger sediments (Chadron Formation) became a possibility. Similar doubts were raised by the discovery (by Harksen, 1974) of deeply incised (up to 19 m) paleochannels (Fig. 3) at a higher stratigraphic level in the sequence (near the Rockyford Ash Member of the Sharps Formation). These local channel incisions are the most obvious examples of what could be much a more pervasive problem of resorting of older fossils into younger rocks. The geological setting of Oligocene alluvial deposits around the Black Hills of South Dakota (Fig. 2) resembles that of many Tertiary alluvial deposits in the western United States that were deposited by rivers draining uplifted Precambrian crystalline mountains and an extensive overlying cover of erosionally dissected, Phanerozoic sedimentary rocks.

Some of the problems outlined involve difficulties in establishing stratigraphic levels in complex alluvial cut-and-fill sequences. Paleosols have long been used to sort out such stratigraphic problems in Quaternary alluvial and glacial deposits. As endorsed by the North American Commission on Stratigraphic Nomenclature (1982), the basic pedostratigraphic unit is a "geosol." At any particular locality a geosol is represented by a paleosol, but since geosols are meant to be laterally extensive and mappable, they effectively are buried landscapes including many individual kinds of paleosols. Geosols are recognized on the basis of such features as thickness and degree of clayeyness, which can be related to such regionally consistent paleoenvironmental conditions as paleoclimate or time available for soil formation (Birkeland, 1984). Considerable variation in density of root traces and hue of geosols is allowed, since these features can be related to local factors of soil formation such as vegetation and drainage. The thick, very strongly developed paleosols at the base of the mid-Tertiary sequence in Badlands National Park are good examples of geosols. Similar deeply weathered paleosols of about the same age have been found over large areas of the western United States (Gresens, 1981). Rather than just one paleosol, as is commonly assumed (Pettyjohn, 1961), there are at least two superimposed geosols (represented in the Pinnacles area by Yellow Mounds and Interior Series paleosols of Retallack, 1983) which enclose a thin (too much so for representation in Fig. 2) stratigraphically distinct, rock unit (Slim Buttes Formation). Further mapping of these geosols may clarify stratigraphic relationships along this complex erosional disconformity.

Stratigraphically overlying these prominent geosols are Oligocene alluvial sediments that are predominantly paleosols (53% of the thickness of the measured section of Retallack, 1983). Most of these can be traced laterally several miles through the badlands, but few of them are so distinctive or laterally uninterrupted by fluvial deposits that they can be used as geosols. Nevertheless, there are groups of paleosols that can be used in a way comparable to geosols. The degree of development and spacing of paleosols in the sequence shows pronounced episodicity that can be related to five separate events of erosional
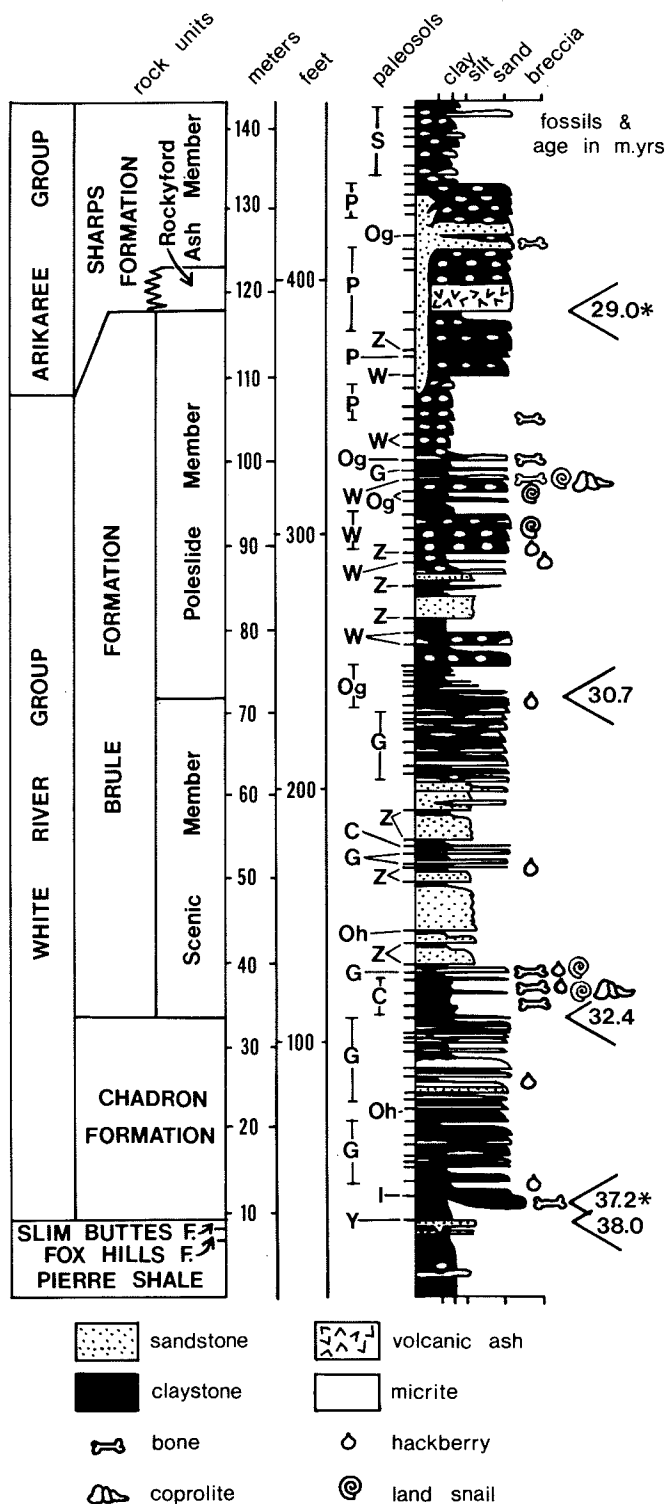
FIGURE 1—A measured section in the Pinnacles area, Badlands National Park, South Dakota (from Retallack, 1984).
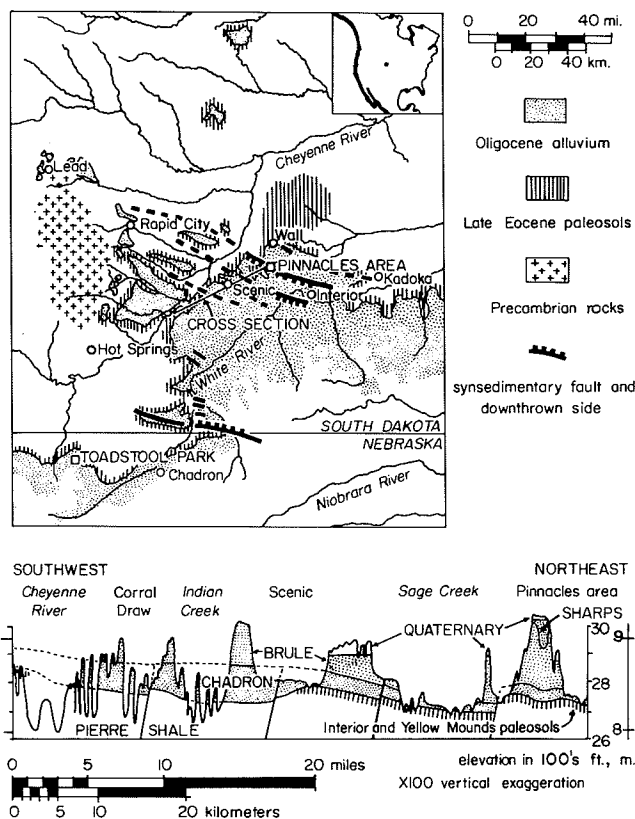

FIGURE 2—The distribution of deeply weathered late Eocene paleosols, Oligocene White River Group, and synsedimentary faults in southwestern South Dakota and northwestern Nebraska (above), with a deep valley fill of Chadron Formation revealed by a stratigraphic cross section along a northeast line through Scenic, South Dakota (below). The cross-section was reconstructed from maps by King and Raymond (1971) and Raymond and King (1976).

downcutting followed by alluvial filling (Retallack, 1986). The separate alluvial fills correspond roughly with the recognized rock units, and can be traced throughout these extensive exposures. Each cutting-and-filling cycle had a duration of about 2 million years, and it is likely that the erosional hiatus of the cutting phase occupied a considerable portion of the time. Paleosols immediately below the hiatuses are strongly developed and partly overlapping, as if formed on a stable landscape under a regime of infrequent sediment accumulation. Paleosols immediately above the hiatuses are weakly developed and well separated by intervening flood deposits, as if the landscape were rapidly regaining equilibrium after disturbance. Such subtle episodic changes in the character of paleosols have been recognized also in other fluvial sequences (Kraus and Bown, 1986; Kraus and Middleton, 1986). They offer clues to locating the big erosional gaps in sequences of paleosols that, by definition, have many small gaps.

Laterally extensive erosional landscapes within alluvial sequences, whether recognized as a distinctive geosol or by

FIGURE 3—A paleochannel (cut bank at arrow) in the Pinnacles area of Badlands National Park, incising 16 m down from the level of the Rockyford Ash Member of the Sharps Formation.

abrupt changes in paleosol character and spacing, may be as littered with resorted fossils as some modern erosional landscapes. Like paleochannels, these should be avoided for detailed biostratigraphic work. The problem of resorting can be mitigated by focusing attention on paleosols that represent minor breaks in floodplain aggradation. Degree of destruction of original bedding and degree of clayeyness of subsurface horizons are two of a number of indications in paleosols of the time over which they formed, and these can be calibrated by comparison with studies of rates of Quaternary soil formation (Retallack, 1984). Such estimates provide a useful guide to the finest temporal resolution attainable in biostratigraphic studies (Table 1).

TAPHONOMY

Compared to the beautifully preserved, articulated skeletons of some catastrophic sedimentary assemblages of fossils, those of attritional pedogenic assemblages are unimpressive for several reasons. As a carcass is torn apart by predators and scavengers, and rots away, the bones are scattered and abraded. They are trampled by hooves and gnawed by rodents. What bone remains is leached of fat and phosphate by rainwater, so that it becomes cracked and splintery. Many of these features of surficial weathering have been observed in fossil bone excavated in Badlands National Park (Clark et al., 1967) and can be compared with the condition of surficially weathered bone in comparable modern environments (Behrensmeyer, 1978, 1981).

Many bones are destroyed entirely by these surface processes, but those preserved within paleosols have survived another round of destructive processes within soils. Muscle and sinew, and leaves and pollen, are decayed by aerobic decomposers within well-drained soils in the same way as at the surface. Bone and snail shells are prone to dissolution by soil acids, including a variety of plant exudates and carbonic

acid from dissolution in soil water of carbon dioxide, which can reach high concentrations in productive soils. The degree of oxidation (Eh) or acidity (pH) of a paleosol can be interpreted from its mineralogy, and this can be used to predict what kinds of fossils should be preserved (Retallack, 1984). Such a model does not predict catastrophically incorporated elements of a fossil assemblage, but is effective for attritional pedogenic assemblages that have come into chemical equilibrium with the soil.

Almost all paleosols of Badlands National Park are yellow, brown, or red in color, and were well-drained and oxidized. Thus, the general lack of plant fossils is not surprising. Many of the paleosols were alkaline and calcareous enough to preserve bone, and some were calcareous enough to preserve snail shells. The quality of preservation varies in different paleosols, and this can be related to their degree of calcareousness. Little bone is found in the non-calcareous to weakly calcareous paleosols of the Chadron Formation. At this stratigraphic level bone is most abundant in paleochannel deposits and in calcareous streamside paleosols. In the Scenic Member of the Brule Formation, however, many floodplain paleosols are fossiliferous, and a general correlation between their degree of calcareousness and bone abundance is evident. No fossil bone was found in red, non-calcareous paleosols (Zisa Series of Retallack, 1983) of streamside swales. Bones and snails are sometimes found in strongly calcareous near-stream paleosols (Gleska Series), but both kinds of fossils are abundant in more strongly calcareous paleosols of interfluves (Conata Series). The slight difference in calcareousness of Gleska and Conata Series paleosols has resulted in a considerable difference in preservation of their mammalian assemblages. Bones of smaller mammals have a higher surface-to-volume ratio, and so are more prone to acidic dissolution than are those of large mammals. As expected, there is a much greater abundance of bones of small mammals in Conata Series than in Gleska Series paleosols, a difference which remains striking even when flattened out by plotting the logarithm of abundance versus the logarithm of body mass for each species of herbivorous mammal found (Fig. 4).

Because of ubiquitous scaling relationships between population density and turnover rate with body mass in modern mammals, the relationship between abundance and body mass should have a slope of about -1.05 (Damuth, 1982). Neither the Gleska nor Conata mammalian assemblage show this, nor any other clear relationship. The Gleska assemblage deviates from expectations more than the Conata assemblage. The observed size bias can be reversed by using a correction factor of 0.68; to calculate an increment in abundance for each species, multiply this by the difference in mass between the species in question and the heaviest species as a reference point (Damuth, 1982). This correction factor was determined empirically from studies of modern bone preservation at the surface of soils in Amboseli National Park, Kenya (Behrensmeyer et al., 1979). This value is in any case nearly identical to that for surface-to-volume scaling (0.67) that would be expected for acidic dissolution by rain or soil solutions. Rain is normally near neutral and may have a pH as low as 5.6 before being considered polluted or "acid rain." Soil solutions can be as acidic as pH 2.8 (Baas-Becking et al., 1960). Even when

TABLE 1—Temporal resolution and completeness in rock units in Badlands National Park, South Dakota

UNIT	From Paleosol Times for Formation		From Paleosol Rates of Sediment Accumulation		From Paleomagnetic and Radiometric Rates of Sediment Accumulation	
	resolution	completeness	resolution	completeness	resolution	completeness
Brule Formation	2887	35	2100	69	3,400,000	3
Poleslide Member	2364	42	1800	81	1,700,000	3
Scenic Member	3571	28	3000	59	1,700,000	3
Chadron Formation above Interior Paleosol	4706	21	6200	35	4,800,000	6

NOTE: Temporal resolution is the minimum time span in years certain to be represented by some sediment in the sequence. Completeness is the percentage of a given time span (1000 years used here) represented by sediment (Sadler, 1981; Retallack, 1984).

corrected in this way the mammalian assemblages from Gleska and Conata Series paleosols do not quite conform to expectations (either of slope or variance) based on scaling relationships of modern faunas, although they are within 95% confidence limits of them (Damuth, 1982) and within the range of natural variation of scaling relationships (Peters and Raelson, 1984). Other taphonomic biases, such as local predator dens, catastrophically included components, or destruction of bone by physical shrinking and swelling of these clayey soils, are not accounted for in this analysis and could account in part for the difference. Compared to these other factors, size-related, acidic dissolution of bone is a striking taphonomic bias. In many cases it may be at fault for the complete lack of fossils of creatures that presumably existed, considering the kind of ecosystem represented by a paleosol. When size bias is not so severe it is amenable to correction on the basis of theoretical, experimental, and field observations.

PALEOECOLOGY

Two fundamental features of paleosols make them uniquely suited for paleoecological studies: they are in place and are products of paleoenvironmental conditions. Paleosols are, in a way, trace fossils of ecosystems. They cannot be resorted and still be identifiable like fossils, nor do they have a hidden agenda, like the genome of organisms, that controls their morphology. Paleosols are independent evidence of paleoenvironmental conditions in place, through which the paleoecological preferences of associated fossil vertebrates can be assessed directly.

Pioneering paleoecological studies in Badlands National Park discriminated between faunal assemblages of streamside gallery woodlands and of savanna away from streams (Clark et al., 1967). These results have been substantiated by later studies of paleosols (Retallack, 1983) that provide independent evidence for the vegetation and geomorphic setting of these large fossil collections (Fig. 4A, B). From the raw data, rabbits (*Palaeolagus haydeni*) and chevrotains (*Leptomeryx evansi*)

appear to have dominated savannas, whereas three-toed horses (*Mesohippus bairdi*) and oreodons (*Merycoidodon culbertsoni*) were more common in gallery woodlands (Fig. 4C, D). These data are pooled from attritional assemblages of isolated teeth and bone fragments collected over wide areas and in several localities, so that sheet wash, accumulation of bones around dens of predators, or other local effects, are unlikely to have biased the record. Nor are seasonal migrations likely to be recorded in these assemblages which are time-averaged over several seasons of animals living and dying in the soil. More profound are biases introduced by surface weathering and dissolution of bone in the soil, but these can be reversed by applying a theoretically and empirically reasonable correction factor (Damuth, 1982). When this is done (Fig. 4E, F) the two small taxa (rabbits and chevrotains) are more abundant than the two larger ones (horses and oreodons) in both kinds of paleosols. However, the total biomass of horses and oreodons remains greater than that of rabbits and chevrotains in the gallery woodland assemblage (Gleska Series paleosols) and the opposite relationship still holds for the savanna assemblage (Conata Series). This can be seen from the separation of the two dominant species of each assemblage by a line of equal biomass (Fig. 4E,F). In this case preliminary impressions of dominance in the fossil assemblage have been upheld after taphonomic corrections, and may reflect original abundance in these habitats.

It could be that in this early stage in the evolution of savanna ecosystems, smaller species were favored farther from streams because there, food and water were less available to mammals better adapted to browsing than to grazing. The two-taxon dominance of different habitats and the occurrence of almost all the species in each habitat, noted both for these fossil assemblages and modern mammalian communities of East Africa (Behrensmeyer, 1981), does not support the notion that communities are distinct "super-organisms." Such paleoecological hypotheses must continue to pass the increasingly stringent demands of taphonomic analysis in order to be taken seriously. But they are on firmer ground for pedogenic than for assemblages mixed and transported in
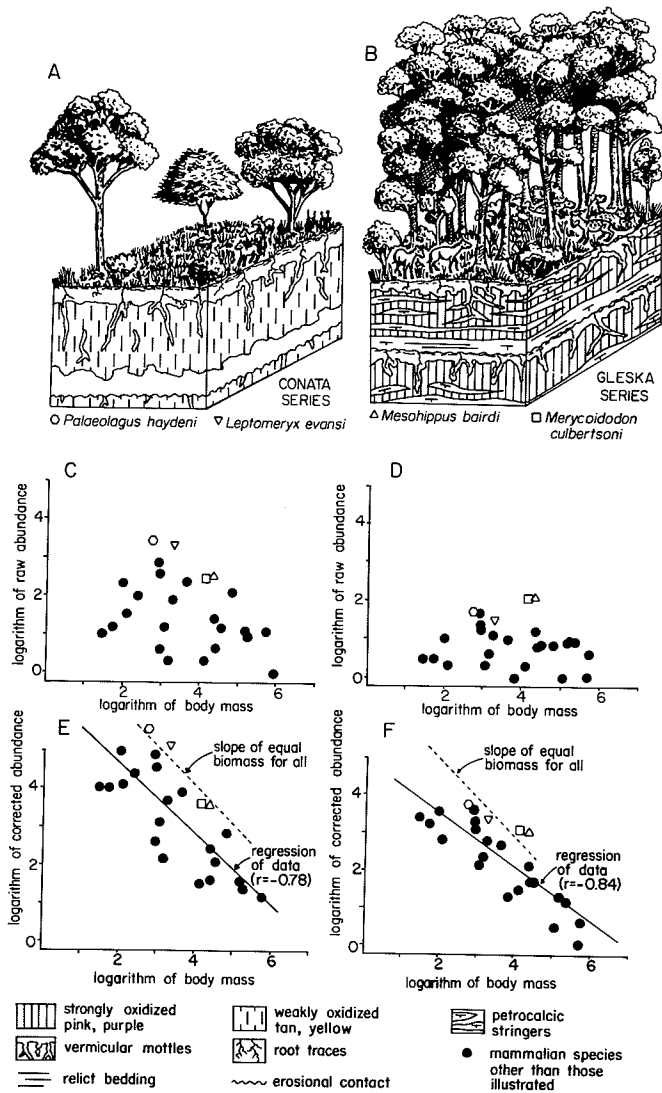
FIGURE 5—Paleochannels and moderately developed, silty, paleo-sols of the steep walls of the Brule Formation (above) in contrast to strongly developed, clayey paleosols of rounded mounds of the Chadron Formation, in the Pinnacles area, Badlands National Park, South Dakota.

FIGURE 4—Restorations of interfluve savanna on Conata Series paleosols (A) and of streamside gallery woodland on Gleska Series paleosols (B) during deposition of the Scenic Member of the Brule Formation, with plots of abundance (number of specimens) versus estimated body mass (in grams) for various species represented in collections of each (C and D, respectively) and after correction for size-related bias caused by acidic dissolution of bone (E and F, respectively). Restorations are after Retallack (1983) and abundance data from Damuth (1982).

paleochannels (Badgley, 1986) or sampled by freak catastrophes (Voorhies, 1969).

EVOLUTIONARY THEORY

As evidence for time elapsed between sedimentary events and for vegetation and other paleoenvironmental conditions

independent of associated fossils, paleosols offer information useful for assessing the tempo and mode of evolution of associated vertebrate fossils. It has been suggested, for example, that the constant morphology of fossil mammals over long stratigraphic intervals, and their abrupt appearances in the badlands of South Dakota and Nebraska, supports the model of evolutionary change known as punctuated equilibrium (Prothero, 1983, 1985a). In this view of the evolutionary process, species arise on time scales that are geologically instantaneous. This can be contrasted with phyletic gradualism—the gradual evolution of characteristics over geologically observable time spans. Distinguishing between these two kinds of speciation is fundamentally a question of temporal resolution. The time scales involved are intermediate between those of ecological time (seconds to years) and of geological time (tens of thousands to millions of years), and just the kind of time range over which soils are thought to form (Birkeland, 1984). Over time an original bedded, gray, silty deposit, for example, is converted to a massive, clayey, red soil. This process can be reconstructed by studying soils of different age whose general soil-forming conditions such as climate and vegetation are similar. These chronosequence studies of soils can be used to calibrate the ages of paleosols showing comparable degree and kind of development (Retallack, 1984).

Differences in the temporal resolution of different sequences of paleosols may be striking. The effects of soil formation are prominent in the Chadron Formation of Badlands National Park. This sequence of clayey, strongly developed paleosols has alternating pink and green paleosol horizons as gaudy as a candy cane. This contrasts with the silty, moderately developed, light brown and yellow paleosols of the Brule Formation (Fig. 5). These differences can be quantified by assigning a time of formation to each paleosol from studies of comparable Quaternary soils (Retallack, 1984). The estimates used were

conservative, in deference to the theoretical possibility that soil development reaches a steady state beyond which time it changes little. A parallel consideration is the likelihood that rates of soil formation have fluctuated markedly with climatic changes during the formation of surface soils over the past million years or so (Birkeland, 1984). These minimal values from studies of Quaternary soils can be used to calculate temporal resolution of the sequence of paleosols in Badlands National Park. The simplest way to do this is to take the average time of formation of paleosols in a sequence (Table 1). For Badlands paleosols, this gives very similar results to a more sophisticated method of analysis (of Sadler, 1981) which uses the times to calculate rates of sediment accumulation, and then compares these with expected rates for fluvial systems. Sadler's method of calculating resolution from rates of sediment accumulation is better designed for use with paleomagnetic or radiometric estimates of time spans. When these data are used to calculate resolution of the Badlands sequence (Table 1), geophysically calculated temporal resolution is orders of magnitude different from that based on paleosols. The correct answer is somewhere between these extremes. Probably it is closer to the paleopedological estimates than the geophysical ones, because of evidence from coalesced and strongly developed paleosols for large hiatuses (of the order of a million years) between the rock units on which the analysis was based (Retallack, 1986).

From these considerations the sequence in Badlands National Park does not have a temporal resolution appropriate to settle the question of whether evolution proceeded there by punctuated equilibrium or phyletic gradualism. Especially troubling is the tendency of first and last appearances of mammalian species to cluster around the major breaks between rock units (Prothero, 1985a,b). Sequences such as this may demonstrate long-term (or anagenetic) evolutionary trends, but will not resolve short-term speciation events (cladogenesis). Other sequences of paleosols of Eocene (Bown and Kraus, 1981) and of Miocene age (Behrensmeyer and Tauxe, 1982) have a temporal resolution approaching what is needed. The answers to these questions for land vertebrates are most likely to be found in Pleistocene fossiliferous paleosols that formed in rapidly accumulated sequences of tectonically active and arid regions. In most cases paleosols are more likely to impose limits than to illuminate the tempo of evolutionary change.

Paleosols show special promise for assessing the role of selection pressures on evolution. Much has been made of the role of vegetation in shaping mammalian evolution. A classical example is the development of high-crowned (hypsodont) teeth, elongate limbs (cursoriality) and a reduced number of digits in horses. These are widely regarded as adaptations for fleeing predators over open ground, and for grinding coarse, gritty grasses. They are so often found in mammalian assemblages of modern savanna and steppe that such grassy conditions of the past often have been interpreted from fossil evidence of hypsodonty or cursoriality. Such inferences are tantamount to assuming that animals are optimally adapted to their environment, an assumption lampooned by Gould and Lewontin (1979) as the "Panglossian paradigm." What is needed is evidence of vegetation independent of vertebrate fossils. Since the chemical conditions (reducing) for preserva-

tion of plant fossils to a large extent exclude those for preservation of mammal bone (alkaline), fossil bones and leaves are found together infrequently (Retallack, 1984). In the absence of generally available paleobotanical evidence, root traces and paleosol horizons containing fossil bones are a guide to vegetation in which land vertebrates lived.

Oligocene mammalian faunas of Badlands National Park have been interpreted widely as savanna faunas (Clark et al., 1967; Webb, 1977). Considering that their limb proportions and tooth height are intermediate between those of forest faunas of the Eocene and prairie mammals of Miocene age in the western United States, such an interpretation is intuitively reasonable and empirically justified. Data on hypsodonty of horses (Fig. 6A) is similar to that for body size of horses (MacFadden, 1986) in showing the intermediate position of fossil horses from Badlands National Park only slightly in advance of Eocene horses and well below Miocene horses. Data on limb proportions (Fig. 6B), based on the observation that cursorial mammals have foot or hand bones (metatarsal or metacarpal) that approach in length major bones of the limbs (femur or humerus), also demonstrate the position of ungulates from Badlands National Park intermediate between older and younger faunas.

In contrast, a closer examination of a variety of features of carnivores, such as mode of locomotion, body mass, and limb proportions, in Badlands fossils and several modern assemblages has shown that these Oligocene carnivores had levels of adaptation most similar to carnivores of modern tropical forest (Van Valkenburgh, 1985). Similar results have been gained in comparable analyses of ungulate fossils from Badlands National Park (Janis, pers. comm., 1984). It could be assumed, following the "Panglossian paradigm," that these creatures lived under more wooded conditions than previously thought. However, these faunas maintained about the same adaptive grade (the "White River chronofauna" of Emry, 1981, among others) for some 10 million years (Fig. 6C, D), and there is evidence from paleosols that they lived at first in open woodlands, then in savanna with gallery forest, and ultimately in a landscape with few trees remaining along streams (Retallack, 1983). Some changes in the fauna can be attributed to what would have been increasingly hostile conditions for a forest-adapted fauna. Dwarfing is found in many lineages, and both burrows and burrowing mammals are more common toward the top of the sequence. Nevertheless, the persistence of a diverse fauna, including such high browsers as camels, is surprising in the face of these environmental changes. Not until near the Oligocene-Miocene boundary (or mid-Arikareean North American mammal "age") did a major faunal overturn signal the appearance of markedly more hypsodont and cursorial mammals (Webb, 1977).

Although these Oligocene faunas were in a way maladapted to their habitat, they persisted through several cycles of environmental deterioration. It could be argued that such adaptive imbalances are a feature of early stages in the emergence of grazing ecosystems, when communities were recruited from whatever organisms were locally available. Perhaps a mammalian community is more than just the sum of its parts, and species with a place in the ecosystem that enable viable populations to persist are able to shoulder aside the
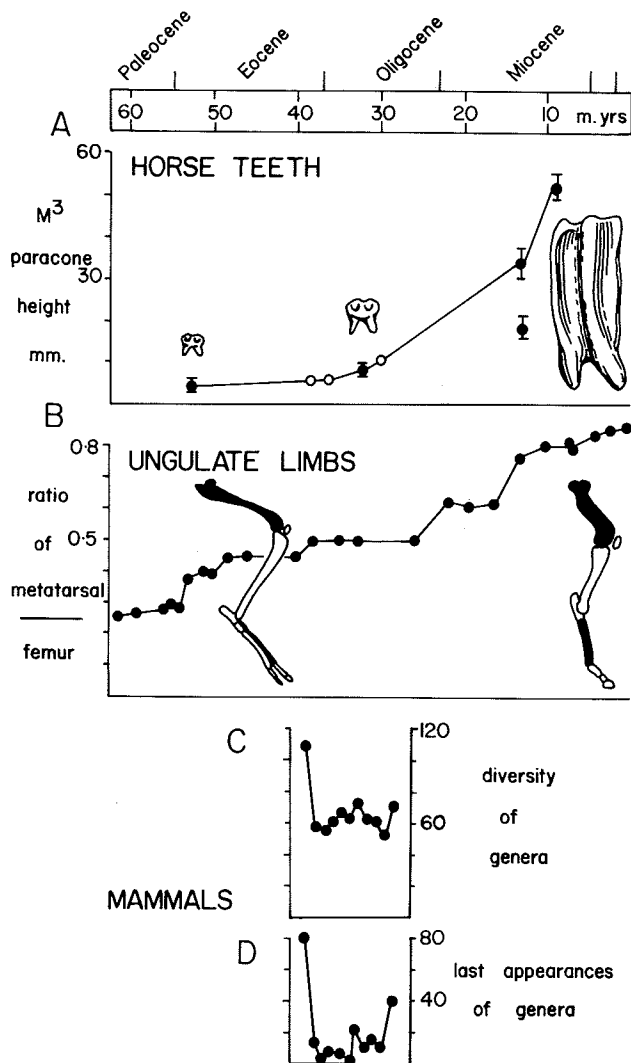
FIGURE 6—Some indices of mammalian adaptation and evolutionary turnover, based in part (Oligocene data) on fossils from Badlands National Park, South Dakota. Hypsodonty **(A)** is represented by height of upper M3 of horses (after Simpson, 1944, with geological ages corrected as recommended by Skinner and Taylor, 1967; Skinner and MacFadden, 1977; Woodburne and MacFadden, 1982). Cursoriality is revealed by the ratio of femur to metatarsal of ungulates (after Bakker, 1983). Diversity **(C)** and last appearances **(D)** of genera of fossil mammals are from a taxonomic review (of Prothero, 1985).

mammals were? How robust are mammalian communities in the face of paleoenvironmental change? What, if not their own efforts and abilities, determines the geological persistence of species and of ecosystems? Other studies of paleosols and vertebrates will be needed before general answers emerge.

CONCLUSIONS

During the last century many of the great vertebrate-bearing formations of the western United States were regarded as lake deposits, their faunas thought to have been entombed by catastrophic events of the past. By the turn of the century, the contrast between truly lacustrine, varved, fish-bearing shales, such as the Green River Formation, and massive, variegated, tetrapod-bearing claystones became apparent. Many of the massive, variegated sequences, such as those of Badlands National Park, were reinterpreted as floodplain deposits (Gregory, 1969). It is only recently that the abundance and pervasiveness of paleosols in these formations has been appreciated (Retallack, 1981, 1983; Bown and Kraus, 1981; Kraus and Bown, 1986). This changing view of vertebrate-bearing deposits calls for a wider application of pedogenic, as opposed to sedimentary, models for understanding the fossilization of vertebrates in them. It also presents new opportunities to probe aspects of past ecosystems that were hitherto inaccessible to analysis.

These new research directions stem from two simple observations of soils. Paleosols are, by definition, in the place where they formed, and they are passive products of environmental conditions. They reflect the ravages of climate, organisms, and geomorphic processes over time, on whatever starting materials were available. These conditions can be interpreted from paleosols by comparison with features that they produce in modern soils. Such deductions can be trusted to apply to the exact location of the paleosols, since a paleosol would be destroyed beyond recognition if transported elsewhere. Fossil bones and leaves, on the other hand, have a form that only partly reflects paleoenvironmental conditions, and they can be transported considerable distances from their usual habitat. Such resorting can be a shortcoming for biostratigraphic and paleoecological studies which rely on accurate information about occurrences. For such studies, assemblages of fossils in paleosols may be a more accurate guide to the times and places when the animals lived than their remains mixed in deposits of lakes and stream channels. As indicators of time by their degree of development, paleosols provide evidence for breaks in sedimentation that are useful for assessing temporal resolution in biostratigraphic and evolutionary studies (Retallack, 1984). Paleosols also represent preservational environments for vertebrates. The composition of paleosols can be a clue to the kinds of fossils expected. Fossil bone is best preserved in calcareous alkaline soils of dry climates. Even small variations in carbonate content can be related to large biases in the preservation of small bones which are more prone to acidic dissolution than large ones (Damuth, 1982). Once these taphonomic biases have been considered, evidence for vegetation from paleosols can be used to assess mammalian habitats and selection pressures on their evolution (Retallack, 1983).

Other ways of exploiting information from paleosols for understanding fossil vertebrates are bound to be devised in the

isolated appearance of evolutionary novelty. Mammals have since become much more strikingly adapted to grasslands, but whether they ever can be considered optimally adapted seems empirically doubtful and theoretically illogical (Bakker, 1983). The view of animals and of communities "making do" in adverse conditions and with somewhat inadequate equipment takes some of the edge off the idea that evolution is a race or a game that nobody wins (Adams, 1986). Using paleosols, it is now possible to ask how well-adapted to their vegetation fossil

future. Paleopedology remains a little-explored scientific discipline, in contrast to the widespread and historic concern for more sophisticated understanding of mammalian ecology and evolution. We have, after all, evolved on the landscape like other mammals, and should be more than a little concerned about our effects on the soils that support us.

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In the physical sciences it is axiomatic that a given process or condition must be explained by a single law or theory. In the life sciences, by contrast, various forms of pluralism are frequent. . . . The response of a complex system is virtually never a strict response to a single extrinsic factor but rather the balanced response to several factors, and the end result of an evolutionary process may be a compromise between several selection forces. In the study of causations the biologist must always be aware of this potential pluralism.

—Ernst Mayr