

Completeness of the rock and fossil record: some estimates using fossil soils

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Abstract.—Surprisingly, there is a relationship between rates of sediment accumulation and the time spans for which they have been calculated. This relationship can be used to estimate expected rates for specific sedimentary environments and time spans. The most probable completeness of a given sedimentary section at a given short time span can be calculated by the ratio of the measured long-term rate of sediment accumulation to the expected short-term rate. Although the measured time span is usually based on radiometric and paleomagnetic data, the cumulative time of formation estimated from fossil soils in a sequence may also be used to calculate rates and may be useful in comparing the completeness and rate of accumulation of different sequences. By both kinds of estimates, terrestrial sedimentary successions are disappointingly incomplete. Some reasons for incompleteness are illustrated with a simple model of episodic flooding, exceeding a threshold for destruction and sedimentation over a particular kind of vegetation, and thus initiating a new cycle of soil formation. In such a model, rock record is lost to erosion during cutting and filling cycles, to overprinting of weakly developed soils by later, better-developed soils, and to continued development, near steady state, of the soils preserved.

Because fossil soils are evidence of ancient environments and ecosystems independent of the fossil record, they may provide evidence of expected kinds of fossils, such as silica phytoliths, calcareous phytoliths, pollen, leaves, fruits, seeds, charcoal, land snails, coprolites, and bones. The degree to which the kinds of fossils actually found fail to meet these expectations is a crude measure of the completeness of representation of a former ecosystem in the fossil record. Some of the discrepancy between expected and actual occurrence of fossils can be related to the original Eh and pH of a fossil soil, as approximated by the oxidation state of iron in its minerals (for Eh) and by carbonate or zeolite content (for pH). Different kinds of fossils can be envisaged as having a characteristic Eh-pH stability field within which they can be expected to have been preserved if originally present. Even under ideal conditions of preservation, it takes some time for fossils to accumulate in soils to levels at which representative collections can be made. Estimates of this temporal control on preservation can be gained by comparing fossil occurrences with the degree of development of fossil soils. Neither these chemical nor temporal factors account fully for the degree of incompleteness observed because original abundance, trampling, predation and many other factors are also important determinants of fossil occurrence.

These considerations can be used as guidelines for choosing stratigraphic sections appropriate for particular paleobiological and geological problems. For example, a study of speciation of terrestrial vertebrates would best be in a sequence of weakly developed, calcareous fossil soils (Entisols and Inceptisols), of near-uniform texture and yellow to brown color, formed under an extraordinarily high long-term rate of sediment accumulation. On the other hand, a study of coevolution of vertebrates and plants would best be based on a sequence of weakly to moderately developed, calcareous fossil soils of predominantly drab (gray, green, and blue) color, with interbedded carbonaceous shales.

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Introduction

The rock and fossil record undoubtedly provides a very biased set of clues to the nature of worlds past. Is there any possibility of determining how biased? There is no direct method, nor any possibility, of assessing all that has gone unrecorded. There are, however, some methods for gaining crude estimates of the completeness of the rock and fossil record which are of value, not as deterministic estimates of completeness, but for ranking stratigraphic sequences in terms of relative completeness and for deciding which

sequences have a record with resolution adequate for specific paleobiological or geological problems (Schindel 1982). The methods outlined here are limited to sequences of terrestrial sediments containing fossil soils. In essence, these methods are based on comparison of the actual rock or fossil record with expectations derived from the interpretation of fossil soils.

Completeness of the Rock Record

In his still-influential book, Hans Jenny (1941) argued that soils are products of a num-

ber of factors, such as climate, organisms, topographic relief, parent material, and time available for formation. Distinctive features of fossil soils may have been produced by each of these factors and can be evidence for their action in the past. The degree of development of a fossil soil, by comparison with times of formation of similar modern soils of comparable development, may give an indication of the duration of breaks in deposition within a sequence of fossil soils. For long sequences, the durations of individual events of sedimentation are generally insignificant (10^{-6} – 10^0 yr; Sadler 1981) compared to the durations of intervening periods of soil formation (10^4 – 10^6 or more yr; Birkeland 1974; Harden 1982). Cumulative interpreted times of formation for successive paleosols can be used to calculate the total duration of recognizable hiatuses, as well as rates of sediment accumulation (Retallack 1977; Bown and Kraus 1981a). Estimates of sediment accumulation rate and completeness based on paleosols are useful supplements to estimates based on radiometric and paleomagnetic data.

Estimates from long-term sediment accumulation rates.—Sadler (1981) has documented a progressive decrease in the rate of sediment accumulation estimated on longer and longer time spans and has also defended Barrell's (1917) view that this phenomenon is due to increasingly long gaps in the record of sequences deposited over longer time spans. Although individual rates of sediment accumulation are highly variable, rates are lognormally distributed about a most probable rate for a given time span and sedimentary environment. The empirically determined probability distribution of rates for fluvial systems is not evenly distributed about median rates (Fig. 1) because of gaps between optimal time spans for different methods of obtaining data on rates (Sadler 1981). The ideal relationship may be a straight line with a symmetrical probability distribution, but this cannot be assumed, and the empirical curve is used as a basis for calculations. Thus for any given time span, there is an expected or most probable rate of sediment accumulation for fluvial systems. The ratio of the measured long-term rate to the short-term expected rate is a measure of "completeness," which is defined by Sadler (1981) as the

probability that each time span of interest will be represented by sediment.

Consider the hypothetical example shown in Fig. 2. Given the thickness of a sequence and the time over which it was deposited (or time span, t), a rate of accumulation (S) can be calculated by simple division. The probability that a specified time span (t_*) is represented by sediment is given by the ratio of the measured rate (S) over the most probable rate (\bar{S}_*) for that time span (t_*) as determined from the compilation for modern rivers (Fig. 1). When the specified time span (t_*) is short—say, only a few years—for sequences deposited over thousands or millions of years (long t), then the ratio of rates (S/\bar{S}_* or completeness) will be low. Only for specified time spans in excess of those usual for the measured rate of sediment accumulation can the sequence be considered "complete," that is, unlikely to have any gaps longer than the specified time span. Time spans of rock units for such calculations can be estimated from radiometric or paleomagnetic data, as they have been by Sadler (1981), Gingerich (1982), and Sadler and Dingus (1982).

Estimates from paleosol development.—An alternative estimate of time span for sequences of fossil soils is the sum of minimum times of soil formation for the paleosols, estimated by comparison with modern soils of similar development. Minimum times of soil development are chosen for two reasons. First, soil features develop quickly at first and then more slowly as they reach steady state (Birkeland 1974, p. 176). Second, it is possible that under conditions of great climatic variability, with one extreme of the variability being very cold or very arid conditions, there may be times when soil formation is active interspersed with times when it is negligible. If this is the case for Quaternary paleosols, as argued by Morrison (1978), then most estimated minimum times for soil development may actually be closer to their times of complete development.

Temporal Completeness of the Mid-Tertiary Sequence in Badlands National Park

I have used a detailed measured section of the Late Eocene to Late Oligocene, White River, and lower Arikaree groups, in the Pinnacles area

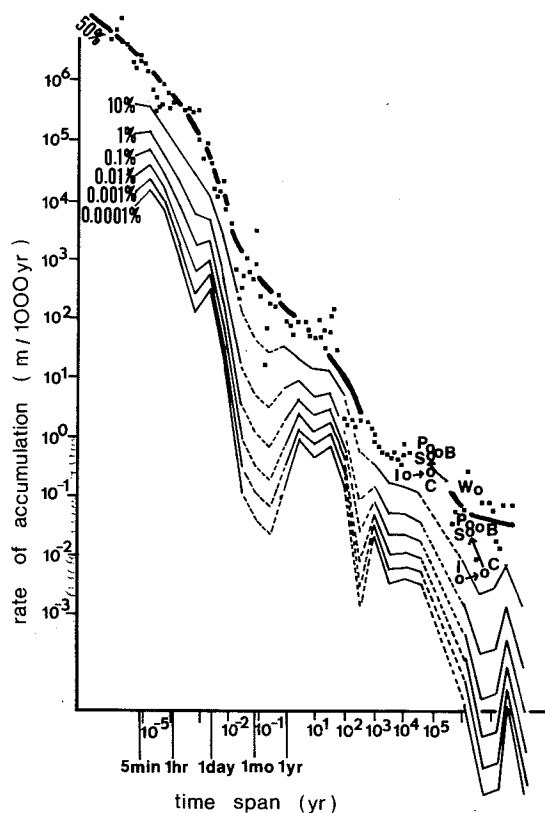


FIGURE 1. Accumulation rates of fluvial sediments from Sadler and Dingus (1982), showing median rates for a given time span (heavy line and boxes), and the distribution of rates slower than usual expressed as percentage of probability that a randomly selected rate will be slower (light lines). Labeled rates for time spans of 10^4 – 10^5 yr estimated from paleopedological data; those for time spans of 10^6 or more yr from radiometric and paleomagnetic data, for the Interior paleosol (I), Chadron Formation overlying the Interior paleosol (C), Scenic Member (S), Poleslide Member (P), and Brule Formation (B) of Badlands National Park, S.D. The rate for the Willwood Formation (W) of northwestern Wyoming is from Sadler and Dingus (1982).

of Badlands National Park, South Dakota (Retallack 1983) as an example for comparing various estimates of temporal completeness (Figs. 1, 3–6).

Materials and methods.—The Late Eocene Yellow Mounds paleosol is developed on the unconformity with Cretaceous marine rocks at the base of the measured section (Fig. 3). The Interior paleosol is at the base of the overlying Early Oligocene Chadron Formation, which forms the lower part of the White River Group. The upper part, or Late Oligocene Brule For-

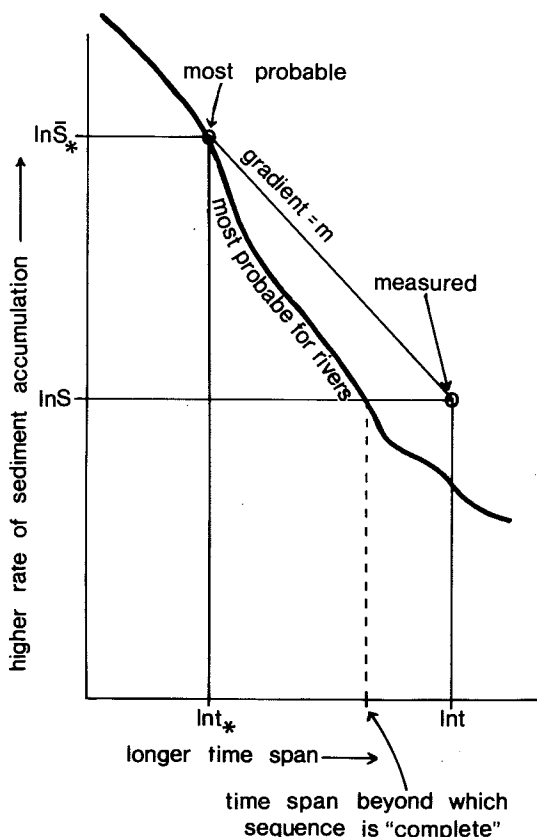


FIGURE 2. A simplified version of Fig. 1, showing the relationship of variables used to calculate the completeness of a section of known time span (t) and rate of sediment accumulation (S) by comparison with the most probable rate (S_*) at a specified time span (t_*).

mation, has been divided into lower (Scenic) and upper (Poleslide) members. The base of the Arikaree Group is marked by the base of the Rockyford Ash Member of the Sharps Formation, of later Late Oligocene age. Each of these rock units contains numerous paleosols (there are 87 in all; Retallack 1983). Magnetostratigraphic (Prothero et al. 1982) and radiometric (McDowell et al. 1973; Obradovich et al. 1973; corrected by the method of Dalrymple 1979) estimates of the age of sequences within the measured section (Fig. 3, Appendix 2) were used to calculate completeness of these units according to the method of Sadler (1981).

Rates of sediment accumulation and completeness were also estimated from the minimum time of formation of particular kinds of soils and

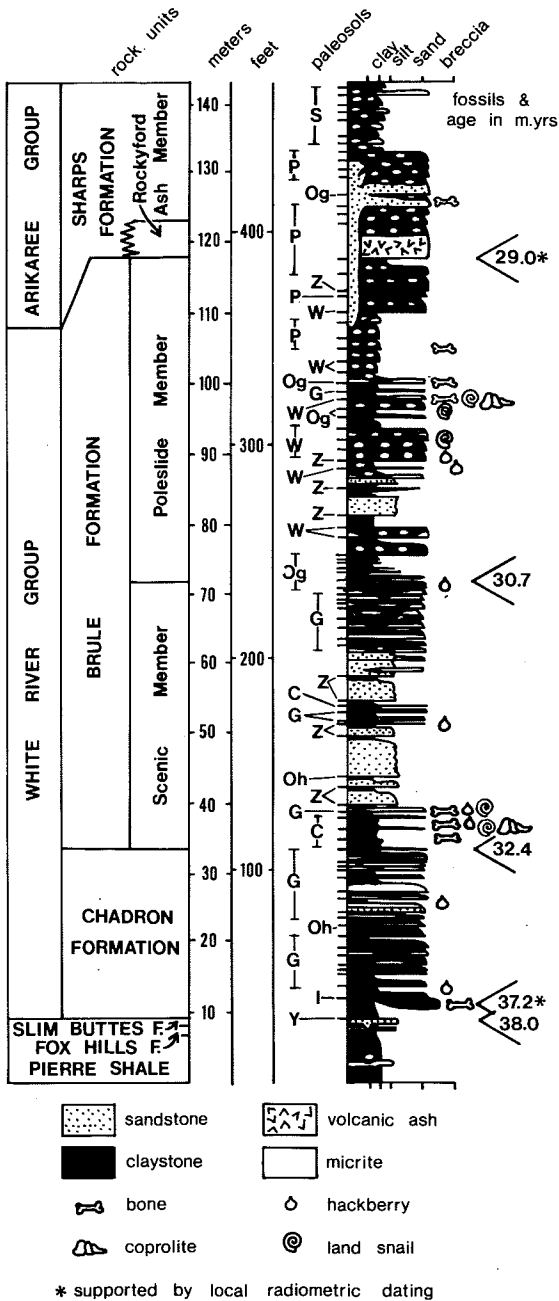


FIGURE 3. A measured section in the Pinnacles area, Badlands National Park, S.D. (modified from Retallack [1983], with absolute ages after Prothero et al. [1982], Obradovich et al. [1973], McDowell et al. [1973]).

soil features by comparison with research on Quaternary soils by Gile et al. (1966), Williams and Polach (1971), Birkeland (1974), Buol et al. (1981), and Harden (1982). The specific

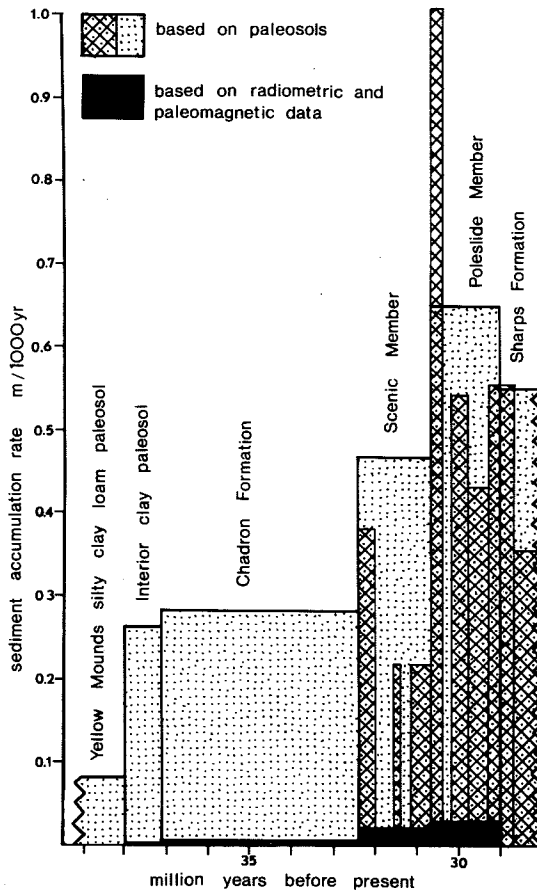


FIGURE 4. Sediment accumulation rates for different paleosols and formations of Badlands National Park, S.D., calculated from estimated time of development of fossil soils (stipple and cross-hatched) and from radiometric and paleomagnetic data (black). Cross-hatched bars are for selected sequences of paleosols.

times used were 10,000 yr for Yellow Mounds and Interior Series paleosols; 6,000 yr for Gleska Series with petrocalcic horizons; 5,000 yr for Wisangie, Pinnacles, and Samna series; 2,000 yr for Conata Series; 100 yr for Ogi Series; and 5 yr for Ohaka and Zisa series. These are all very conservative minimum estimates. Their application to particular paleosols is discussed elsewhere (Retallack 1983).

Results.—Completeness calculated from paleomagnetic and radiometric data was disappointingly low for time spans of less than 10^5 yr, although in all cases the Poleslide Member was more complete than the Scenic Member and the Scenic Member more complete than the

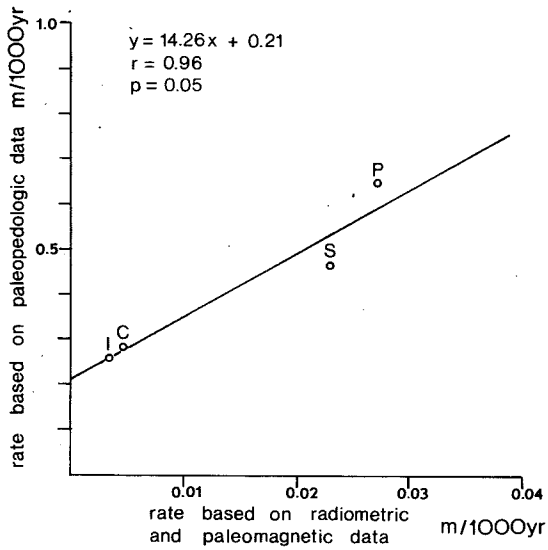


FIGURE 5. The correlation between rates of sediment accumulation based on paleopedological data and those based on radiometric and paleomagnetic data has a correlation coefficient of .96 and less than a 5% probability of being due to chance. Abbreviations are for the Interior clay paleosol (I), Chadron Formation overlying the Interior paleosol (C), Scenic Member (S), Poleslide Member (P), and Brule Formation (B) of Badlands National Park, S.D.

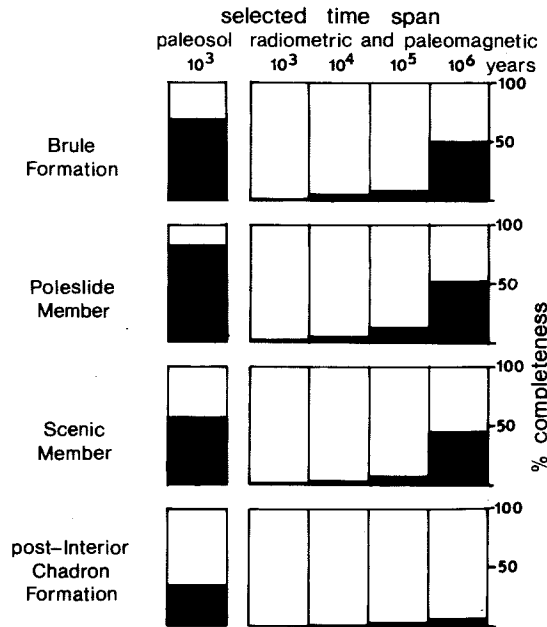


FIGURE 6. Percentage of stratigraphic completeness of different formations of Badlands National Park for different selected time spans, calculated both from paleopedological data (left column) and from radiometric and paleomagnetic data (right four columns) using formulae given by Sadler (1981).

Chadron Formation (Fig. 6). There is a probable 54% representation of 10⁶ yr intervals in the Poleslide Member, a 46% representation in the Scenic Member, but only 9% of them are likely to be represented in the Chadron Formation. From simple manipulation of the equations used (Sadler 1981, equation 3), these estimates of completeness correlate directly with the determined rate of long-term sediment accumulation. The most complete formations are those which accumulate at the fastest long-term rates (Fig. 4).

Rates of sediment accumulation based on paleosols are at least an order of magnitude faster than those based on paleomagnetic and radiometric ages (Fig. 4, Appendices 1 and 2). Although paleosol-based rates are unlikely to be accurate, they are close to median rates for fluvial systems at their time span (Fig. 1). Thus they are not improbable or unrealistic estimates. Rates of sediment accumulation based on these very different methods of estimation show comparable changes from one formation to the next. Although differing by an order of magnitude, rates for each rock unit based on each method

of estimation have a correlation coefficient of .96 and less than a 5% probability of being due to chance (Fig. 5). Rates based on paleosol development may be useful for comparing changes between sequences not amenable to paleomagnetic or radiometric dating, as has been discussed elsewhere (Retallack 1983).

Estimates of completeness based on paleosols can also be used to compare different sequences, even though the estimates are an order of magnitude greater than those based on paleomagnetic and radiometric data. The discrepancy could be lessened by recalculating with better estimates of the time of formation of the paleosols rather than the minimum estimates used here. Considering the very long chronosequences of Quaternary soils now under study (Harden 1982) and advances in dating materials older than those conventionally dated by radiocarbon, there is some promise that better estimates will soon be available.

From both geophysical and paleopedological estimates of completeness calculated here (Fig. 6, Appendix 2), the Chadron Formation, Scenic,

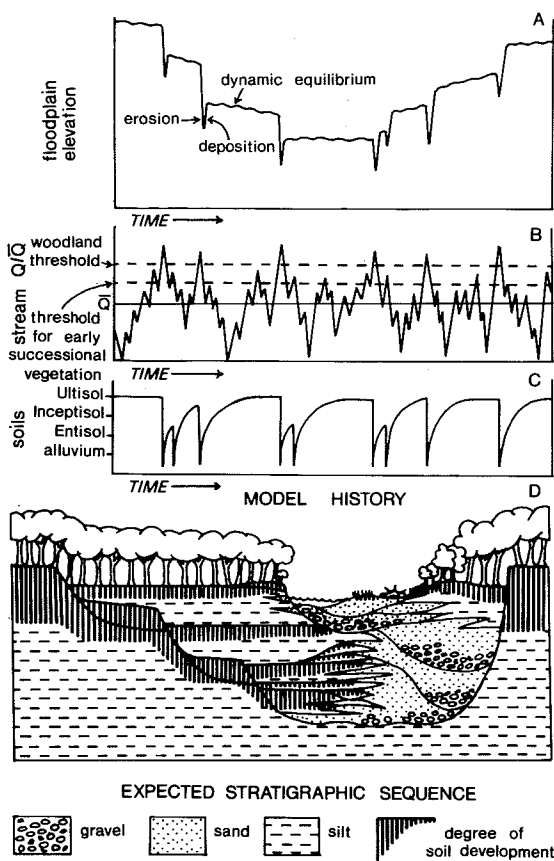


FIGURE 7. An hypothetical model illustrating sources of incompleteness in terrestrial sediments additional to visible soil development. Changes in floodplain elevation (A), produced in part by stream discharges (Q) greater than usual (\bar{Q}) and beyond thresholds for existing vegetation (B), episodically interrupt soil development (C) and produce the stratigraphic section shown (D).

then Poleslide members are progressively more complete. The least complete sequence (Chadron Formation) has abundant evidence of soil formation in the form of root traces, massive, clayey, color-differentiated soil horizons, soil structures (peds and cutans), and soil micromorphology (sepic plasmic fabrics). By contrast, the most complete sequence (Poleslide Member) has much less conspicuous evidence of soil formation. It is more uniform in color and texture and has much more abundant, little-weathered volcanic shards and more sedimentary relicts (such as bedding) than the Chadron Formation. The general appearance of a sequence of paleosols may be a crude guide to its completeness. Com-

pared to those of the Brule Formation, paleosols of the Chadron Formation are more clayey and have prominent red B horizons and associated drab A and C horizons. This clayey and "barber pole" or "candy cane" appearance is a field indication of a very incomplete sequence of paleosols.

Detailed study of fossil soils in these two units (Retallack 1983) has revealed a prominence of Petrocalcic Paleustalf (in the classification of Soil Survey Staff 1975; Buol et al. 1981) paleosols, which formerly supported woodland, in the Chadron Formation, but Andic Ustochrept and Fluvaquentic Eutrochrept paleosols, which supported savanna, in the Poleslide Member. The increasing rates of sediment accumulation between these two units are probably a reflection of decreased landscape stability and increased erosion in a progressively drier climate with sparser vegetation (Retallack 1983), a conclusion independently reached by Clark (1975).

A Model for the Formation of Sequences of Paleosols

The discrepancy between estimates of completeness from paleosols and from paleomagnetic and radiometric data are indications that sequences of paleosols are probably even more incomplete than soil development visible in preserved paleosols, for reasons best understood by considering the following simple conceptual model, based largely on the geomorphological research and models of Schumm (1977).

The model.—Consider a landscape in a humid temperate climate, in which forests and Ultisols will develop, given enough time. Assume also that the major control on deposition or erosion of streams is episodic uplift of an adjacent fault block and that the major agent of deposition and erosion of the floodplains is episodic flooding (Fig. 7A).

In a regime of floodplain uplift, streams will begin to erode into the floodplain, although the spread of this erosion is inhibited by vegetation. Floods occur frequently, although most floods leave only a thin layer of clay on the forest floor, and this is rapidly incorporated into the developing Ultisol. On a probabilistic basis, the magnitude of floods increases with the length of time between recurrence of floods of the same magnitude. This relationship has been reported for

recurrence intervals of considerable length (300 yr by Jones [1975]) and can probably be extrapolated to thousands of years (Kochel and Baker 1982). Somewhere along this scale of increasing flood magnitude is a flood discharge capable of completely destroying the forest and initiating erosion of the floodplain to a new level of dynamic equilibrium. A flood of this magnitude has exceeded an intrinsic geomorphic threshold for a particular kind of vegetation (Fig. 7B). In the early stages of plant succession and soil development on a new floodplain, the threshold for destruction and erosion may be a flood discharge of lower magnitude and shorter recurrence interval. Weakly developed soils are unlikely to be preserved in an erosional or degradational regime, because those soils preserved are perched on terraces of the valley walls and continue to develop, while the floodplain is established at a lower level (Figs. 7C–D).

By contrast, in a regime of subsidence or floodplain aggradation, threshold or greater flood events are followed by deposition, burying the former floodplain soil and allowing renewed soil formation at a higher level. Floods above the threshold for destruction of early successional vegetation will bury and preserve Entisols or Inceptisols. However, if the flood discharges are consistently below threshold for a long period of vegetative growth, then initially weakly developed soils, as well as successive thin increments of alluvium, will be incorporated into the final, strongly developed Ultisol.

In real situations, the factors considered, as well as others such as lava flows, ash fall, landslides, fires, glaciation, or climatic change, may interact to produce local irregularities due to complex response or may produce an extraordinary deposit due to external forcing of the system. Nevertheless, the model is probably not too far from reality because the kinds of sequences generated (Fig. 7D) agree in general outline with what is observed in real sequences of paleosols, such as those of Late Eocene to Late Oligocene age in southwestern South Dakota (Retallack 1983) and of Pleistocene age in Czechoslovakia (Kukla and Kočí 1972; Morrison 1978).

Gaps in the record.—The longest gaps in the temporal record evident from this model are those associated with erosional regimes of stream

downcutting. With successive uplift and relaxation, or by a number of other causes, many cutting-and-filling sequences could, and do, follow one another (Schumm 1977). During cutting cycles, many of the previously formed paleosols may be completely eroded. In deposits of small valley systems like that depicted (Fig. 7D), the very strongly developed fossil soils of high terraces may indicate the true duration of erosive cycles. However, exceedingly strongly developed Ultisols, for example, may have sandy A horizons, more prone to sheet erosion than the original clayey alluvium (Cady and Daniels 1968). Such complications make interpretations of many, very strongly developed fossil soils difficult (Retallack 1981). In addition, the high terrace soils of originally broad floodplains may be so far distant that they cannot be effectively correlated with sequences nearer the stream. In near-stream floodplain sequences, the erosive gaps between filling cycles may appear no different than those between threshold flood deposits, even though the durations involved may differ by several orders of magnitude.

Other breaks in the record may be attributed to overprinting of weakly developed soils and thin increments of alluvium by continued soil development on the same materials. Features of prior soils which persist in later soils of a different kind are called pedorelicts (Brewer 1964) and are one indication of overprinting. If pedorelicts are not discernible, gaps due to overprinting are likely to be minor, because the undetected paleosols would be weakly developed and represent much less time than the paleosols preserved.

Finally, some of the record may be lost in the continued development of soils near steady state, in which change is not as rapid or noticeable as in the early stages of soil formation (Birkeland 1974). This is not generally an important consideration for fossil soils preserved in fluvial sediments, because these are seldom developed to the extent that sedimentary relicts are completely obliterated. Such gaps are likely to be minor, only a fraction of the time span for the formation of individual soils, and of the order of the uncertainty in determining time spans for the development of comparable Quaternary soils.

These three ways in which gaps in the rock record are formed, in addition to those visible

from fossil soil development, are only part of the reason for the temporal incompleteness of sequences of paleosols. Complex interactions of other factors introduce many temporal irregularities and were probably as common in the distant geological past as they appear to have been during the Quaternary.

Completeness of the Fossil Record

Organisms, particularly plants, are also important agents in the formation of particular kinds of soils and soil features (Jenny 1941). Thus fossil soils and soil features may be evidence of particular ecosystems, independent of other kinds of fossils, such as silica phytoliths, calcareous phytoliths, leaves, stems, fruits, seeds, pollen, spores, charcoal, land snails, coprolites, bones, and teeth. A comparison of the representation of these different kinds of fossils with the kind of ecosystem indicated by the fossil soil is a crude measure of the completeness of representation of the fossil record compared to what once lived in the soil. The differential preservation of different kinds of fossils in different kinds of fossil soils is striking (Behrensmeyer 1982b).

There are numerous processes acting to destroy potential fossils and distort the fossil record of past terrestrial life. These include predator or scavenger accumulations, trampling, surficial weathering, and microbial decay (Behrensmeyer and Hill 1980; Shipman 1981). Some mixing of fossils of different age or from different habitats is inevitable, although for assemblages of fossils in soils, this is considerably less marked than for the extremely mixed assemblages of fossils transported in stream deposits (Behrensmeyer 1982a,b).

Once an assemblage of fossils is incorporated within the soil, it is subject to a new set of destructive processes, including continued trampling by animals, bioturbation, physical compaction during swelling of wet clay, microbial decay, and chemical dissolution and encrustation. Evidence of some of these destructive processes may be preserved in fossil soils.

Paleosol chemistry.—Former Eh and pH of fossil soils may be approximated within broad classes by their mineralogy (Krumbein and Garrels 1952; Baas-Becking et al. 1960; Birkeland 1974) and micromorphology (Brewer 1964). It may be difficult in some cases to distinguish be-

tween late diagenetic and original soil mineralogy, but the petrographic relationship of minerals to original features such as root traces and soil structures often provides evidence of the original mineralogy of a fossil soil (Retallack 1983). Reduced (low or negative Eh) soils are generally permanently waterlogged, drab colored (bluish or greenish gray), carbonaceous, and usually include gley minerals such as siderite and pyrite. Leached or A2 horizons may also appear drab or light gray, but in formerly oxidized soils these are weakly carbonaceous and lack gley minerals. Their light color is due to low-density silicate minerals, especially quartz. Oxidized soils are generally well drained and are red or yellow in color, non-carbonaceous and have minerals such as ferrihydrite, goethite and hematite. Sepic plasmic fabrics in petrographic thin sections are also characteristic of well-drained soils, whereas the micromorphology of gleyed soils is more like that of ordinary sediments. Soils of low or acidic pH become depleted in carbonate as they develop. Soils are progressively more calcareous in proportion to their alkalinity and the amount of carbonate available in their parent material, wind blown dust and groundwater. Very alkaline soils (pH 9–10) may be mineralized with zeolites, gypsum, and other evaporite minerals. Clay mineralogy may also be related to soil pH, although the clays inherited from the parent material and the amount of time available for soil formation are often important overriding factors. In general, acidic soils have cation-poor clays, such as kaolinite. Alkaline soils have cation-rich clays, such as illite and smectite.

Paleosol development.—Time of formation and bioturbation may be approximated by the degree of development of soils, for which Birkeland (1974) has provided a convenient qualitative scale: weakly developed (with A-Cox and/or Cca or A-cambic B-Cox and/or Cca horizons); moderately developed (with A-B-Cox and/or Cca horizons, the latter at stage II); and strongly developed (with thick, red, clayey B horizons, prominent soil structure, or Cca at stages III or IV). To this may be added a category of very weakly developed, for soils showing little development beyond root traces. Such soils show abundant sedimentary relicts and are generally classified as Entisols (Soil Survey Staff 1975). An additional category of very strongly

developed was also used in this analysis, for soils with exceptionally thick or well-differentiated profiles and horizons (Retallack 1983). Paleosols of this kind are largely found at major geological unconformities, representing millions of years of nondeposition (Retallack 1981).

Paleosol biota.—Fossil soils may also include evidence of the kind of ecosystem (particularly vegetation) which they once supported. Summarizing from Birkeland (1974), soils of early successional vegetation may have A1-C profiles and abundant sedimentary relicts. Soils of prairie (here used broadly to include treeless grassland and desert soils) have A-C or A-C-Cca profiles with well structured (often with granular or crumb peds) and organic A horizons. Savanna soils are intermediate between these and those of woodlands, in which large root traces and both eluvial and illuvial horizons are prominent. Soils of forests (trees more than 8 m tall; Daubenmire 1968) are deeper and more strongly developed than those of woodlands. Interpretation of a fossil soil within these broad classes of vegetation implies also a particular set of soil conditions, including those other than Eh, pH, and development, and in addition a particular original biotic assemblage.

Paleontological Completeness of the Mid-Tertiary Sequence in Badlands National Park

The relationship between the nature of fossil soils and their fossil content may also be illustrated with an example from a detailed measured section of the Late Eocene to Late Oligocene White River and Arikaree groups in Badlands National Park, South Dakota (Retallack 1983).

Materials and methods.—The entire area for several meters on either side of the trench excavated for this stratigraphic section was searched for megafossils on several occasions during three successive field seasons. The contents of the trench were examined in more detail, this being approximately 0.5 m deep and 0.5 m wide.

Fossils found generally correspond to what can be considered "background levels" of abundance rather than to unique accumulations due to bone-collecting organisms or due to catastrophic mass mortality (Clark et al. 1967). Calcareous phytoliths found in this way included

only the endocarps (pits or stones) of hackberry, *Celtis bacheri* Chaney 1925. Like those of living hackberry, *Celtis occidentalis*, these were probably once rich in calcium carbonate (up to 64.2% by dry weight of the fruit) and silica (up to 7%; Yanovsky et al. 1932; Lanning 1961). The cavity within the fossil endocarps is often filled with additional chalcedony and sparry calcite.

The only species of fossil land snail found was the large (2–3 cm diameter), globose *Pseudolisinoe leidyi* (Meek et Hall) Wenz 1923. Most of these were found as internal molds of calcareous, silty claystone on weathered surfaces of the present outcrop. Their shells may have been dissolved by modern rain, because shell was still preserved on those few specimens found within rock matrix.

The badlands of South Dakota are renowned as collecting grounds for coprolites (Abel 1926, 1935; Stovall and Strain 1936; Vogelanz 1965, 1967; Edwards and Yatkola 1974) and bones of mammals (Clark et al. 1967; Wilson 1975; Webb 1977; Bjork and MacDonald 1981). The coprolites are mainly those of carnivores and are composed of bone and calcium phosphate minerals (whitlockite, francolite, and dahllite; Edwards 1973). This is the composition of slightly dried and leached feces of modern carnivores, and some of the coprolites have longitudinal wrinkles, transverse cracks and pock-marks from gas bubbles, like modern feces of domestic dogs after a few days of drying (Vogelanz 1965). Some of the coprolites have also been impregnated with calcite (Vogelanz 1967). The bones are similar in composition (calcium phosphate) except that the hollows of the osteons have been filled with ferric oxides, calcite and calcareous clay (Greene 1853; Houston et al. 1966).

This is a very incomplete record of the presumed woodland and grassland ecosystems which once flourished here. No fossil leaves, fruits, logs, or charcoal were found. Other than isolated finds of fossil wood and fruits (Retallack 1983) and hackberry endocarps, plant fossils are surprisingly rare. No pollen and spores were found despite numerous attempts to prepare them (A. T. Cross, E. B. Leopold, and M. Zavada, pers. comm. 1981). Some preliminary preparations also failed to reveal any silica phytoliths, although the number of preparations made was insufficient to

pletteness of the fossil record, like completeness of the rock record, was always higher for the Brule Formation (including Scenic and Poleslide Members) than for the Chadron Formation. Some fossils (calcareous phytoliths) were better represented in the Scenic Member, others (land snails) in the Poleslide Member, and still others (phosphatic coprolites, bones, and teeth) were represented more or less equally in both members. The slightly greater total completeness of the fossil record of the Scenic Member compared to the Poleslide Member is the reverse of the completeness of their rock records.

The most consistently fossiliferous paleosols for bones, snails, and calcareous phytoliths are those of the Conata Series which occur at a spectacularly fossiliferous stratigraphic level (as also noted by Sinclair 1921; Wanless 1923; Clark et al. 1967). These were alkaline, Andic Ustochrept soils of interstream savanna (Retallack 1983). On the other extreme, the Interior and Yellow Mounds Series paleosols are unfossiliferous. Both (only two paleosols) were very strongly developed, well-drained, acidic, forested, and wooded soils (Retallack 1983). The very weakly developed Zisa and Ohaka Series paleosols, which probably supported early successional vegetation, are also unfossiliferous.

The role of particular soil conditions in the preservation of different kinds of fossils may be assessed from the proportion of fossiliferous paleosols with corresponding soil features (Fig. 10). Unfortunately, no dark, drab-colored (formerly reducing and waterlogged) fossil soils were seen in the Badlands of South Dakota. This is probably the reason why organic fossils, such as logs, leaves, fructifications, pollen, and spores do not occur. In the case of the single species of snail and of hackberry, it is equally conceivable that their occurrence in oxidized paleosols reflects original environmental preference as preservational bias. However, the original preference for environments of such minor differences of soil dryness is unlikely for vertebrates and their dung. Perhaps there is more opportunity for microbial and chemical destruction of bone and dung in periodically wet soils than in mainly dry ones. Since all the dry paleosols in which these fossils were preserved were also calcareous, pH may also have been a contributing factor.

The calcareous and phosphatic fossils were only

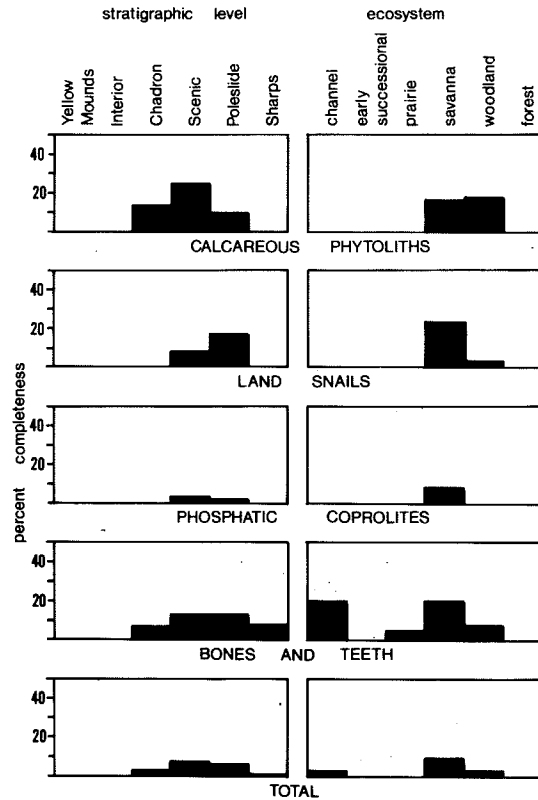


FIGURE 9. Percentage of completeness of the fossil record (or percentage of fossiliferous paleosols which would once have supported the potential fossils based on data in Fig. 8) for different interpreted original ecosystems and observed stratigraphic levels, in Badlands National Park, S.D.

found in calcareous (neutral to alkaline) paleosols, never in noncalcareous (acidic) paleosols (Fig. 10). However, they were not more frequent in proportion to the presumed alkalinity of the paleosols. This may be because of the overriding effects of other factors, such as original occurrence. Judging from fossil root traces, some of the calcareous paleosols did not support trees. If the proportion of paleosols with calcareous phytoliths of trees is recalculated without considering these paleosols of treeless vegetation, then calcareous phytoliths are more often preserved in more calcareous paleosols (Fig. 10). A similar relationship for land snails is enhanced by recalculating in a similar fashion. Neither of these species may have lived in treeless vegetation. Again this is unlikely to have been the case for mammalian bones and dung, although original mammalian populations may have been be-

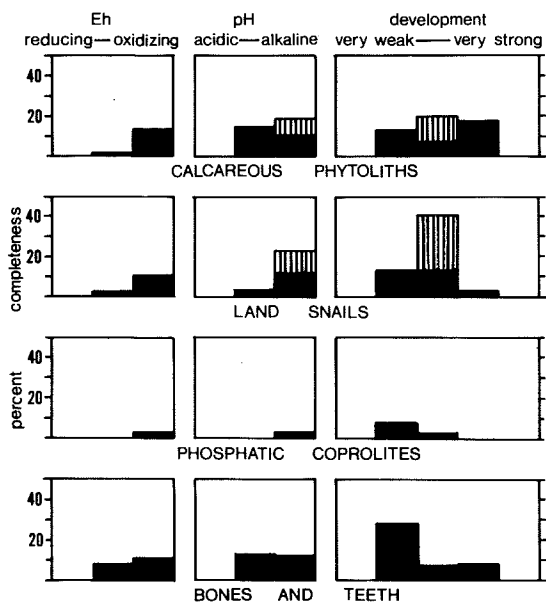


FIGURE 10. Percentage of completeness of the fossil record (or percentage of fossiliferous paleosols which would once have supported the potential fossils based on data in Fig. 8) for different interpreted Eh, pH, and degree of development of fossil soils in Badlands National Park, S.D. Ruled extensions were recalculated on the assumption that land snails and calcareous phytoliths not only were not preserved in prairie paleosols but were never present in them.

low a level at which they contributed fossils in sufficient numbers to be recognized at the coarse scale of sampling. Perhaps also there were other factors, such as the unusually long time of development of many of these paleosols of treeless vegetation, evident from their well-developed calcic horizons (stages II–III of Gile et al. 1966).

No fossils were found in either very weakly or very strongly developed paleosols (Fig. 9). The latter were also noncalcareous, and probably once strongly acidic, and so unsuitable for the preservation of calcareous and phosphatic fossils. The very weakly developed paleosols probably supported sparse, early successional vegetation, may have been partly waterlogged and were unlikely to have been strongly acidic (Retallack 1983). It is likely that the accumulation of fossils like those found in other paleosols of the sequence took some time. This was presumably more than the few years, or few tens of years, during which these very weakly developed soils formed. For longer times and greater degree of development, the data at hand (Fig. 10) do not

support the idea that fossil accumulation proceeds indefinitely with time, at least not to the extent that it overrides other factors. All the paleosols in the weakly to strongly developed categories were calcareous to very calcareous and intermediate to dry, so that these were unlikely to have been overriding factors. Nor does adjustment for the likelihood that hackberries and snails did not live in treeless vegetation (Fig. 10) produce a linear increase of fossil frequency with degree of development. The overriding factors may be related to aspects of the original ecosystem or preservational environment which cannot be resolved at this level of analysis.

Fossils were most frequently found in savanna paleosols (Fig. 9), except the calcareous phytoliths of hackberries, which were equally frequent in savanna and woodland paleosols. There may be two factors equally responsible: because savanna paleosols combine all the most favorable aspects of the factors already considered, and because life was more abundant on the savanna. The quantity of bone preserved in some of these paleosols is impressive. Walking along the superimposed Conata Series paleosols at the base of the Scenic Member (the famed "Red Layer" or "Turtle-Oreodon Layer" of Sinclair [1921]), it is usual to find bone scrap every few meters.

Factors determining fossil occurrence in paleosols of Badlands National Park do not seem simple. The factors of Eh, pH, soil development, and nature of the ecosystem appear to be complexly interrelated. The low proportions of fossiliferous paleosols are an indication of the insignificance of the fossil record compared to the original biota and of the operation of factors other than those considered. Only at extremes are the discussed factors evident. No bone, teeth, phosphatic coprolites, snails, or calcareous phytoliths were found in paleosols presumed to have been acidic; no organic coprolites, pollen, spores, or plant megafossils were found in oxidized paleosols; and no fossils were found in very weakly developed paleosols.

Other Studies Relevant to Fossil Preservation in Paleosols

Although few experimental studies on the preservation of fossils in soils under different conditions of Eh and pH have been reported, much can be gleaned from the occurrence of

fossils in Quaternary paleosols, in archaeological excavations, and from their chemical solubility, as outlined in the following paragraphs.

Phytoliths and spicules.—Biogenic opal phytoliths and sponge spicules are stable in a wide range of Eh and pH, and accumulate in a variety of modern soils (Wilding and Drees 1972; Wilding et al. 1979). Their distribution is dependent on Eh only to the extent that silica phytoliths become enriched as a concentrate in soils in which associated organic matter is destroyed by oxidation. Opal phytoliths and spicules are very weakly soluble at a pH below 9, although appreciably more soluble than quartz, but both quartz and opal are dissolved at pH above 9 (Leo and Barghoorn 1976).

The occurrence of calcareous phytoliths in soils has been little studied, although they have been obtained from prehistoric human coprolites (Bryant and Williams-Dean 1975). The endocarps of hackberry, *Celtis occidentalis*, may contain 25%–64% calcium carbonate by dry weight of the whole fruit and 2%–7% silica (Yanovsky et al. 1932; Lanning 1961). This may account for the favored preservation of fossil hackberry endocarps in oxidized, calcareous paleosols of Tertiary age in the Great Plains of North America (Retallack 1983).

Land snails.—Conditions favorable for the preservation of calcareous phytoliths are probably similar to those for aragonite (rarely calcite) shells of land snails in soils, reviewed by Evans (1972). Snails are not found in acidic or neutral noncalcareous soils but are common in alkaline (pH 7.5–8.0) soils. Dissolution of shells in acidic soils proceeds rapidly once the organic periostracum decays (within about 1 yr in nonwaterlogged soils). Although the distribution of fossil land snails is to a certain extent due to differential preservation, many species have larger living populations in areas of calcareous soils.

Bones and teeth.—The preservation of bones and teeth is also controlled more by pH than Eh (Chaplin 1971), although these phosphatic fossils would be expected to persist at lower pH than calcareous phytoliths or shells (Krumbein and Garrels 1952). In seasonally dry, subtropical Zimbabwe (Rhodesia), human bones in 700-yr-old graves were well preserved under alkaline (pH 6.2–7.9) termite mounds but had been completely destroyed in adjacent acidic (pH 4.1–

5.4) soils, in which skeletons of farm animals showed noticeable corrosion and flaking after only 20 yr (Watson 1967). In cool temperate, humid, northwestern Europe, human bodies interred in acidic reducing peats for thousands of years (mostly since 100 B.C. to 500 A.D.) showed varying degrees of bone calcification, and in one case complete loss of bone within preserved skin and other soft tissues (Glob 1969). Among 95 human skeletons buried 1,200–700 yr ago near Hamburg, Illinois, Gordon and Buikstra (1981) found a significant correlation between degree of bone decomposition and the acidity of the surrounding soil. They recognized several stages of etching, pitting, and powdering, analogous to the stages of cracking and splintering noted by Behrensmeyer (1978) in surficially weathered bones. Gordon and Buikstra also found that skeletons of infants were less well preserved than those of adults. This as well as the poor preservation of skeletons of small compared to large mammals in modern soils (Behrensmeyer 1981) and of baby compared to adult dinosaurs in alluvial sequences (Carpenter 1982) can be interpreted as due to preferential dissolution of bones which are smaller and so have a higher ratio of surface area to volume.

Teeth persist in more acidic conditions and for a longer time than bones and are often found in Quaternary paleosols without associated bones (Evans 1972). This is probably because of the greater density and lesser permeability of teeth compared to bone (Shipman 1981).

Coprolites.—Feces have varied compositions, including, for example, fiber, pollen, spores, calcareous phytoliths, shells, scales, arthropod exoskeletons, bones, and teeth (Bryant and Williams-Dean 1975; Edwards and Folk 1979). As coprolites, these materials may be petrified by impregnation or replacement with calcite, siderite, or silica (Bradley 1946; Amstutz 1958; Vogeltanz 1967). Organic-rich coprolites, produced mainly by herbivores and omnivores, are preserved only in situations in which aerobic bacterial decay is limited by freezing in permafrost, by excessive acidity in peat bogs, by excessively reducing waterlogged environments, or by extreme desiccation in deserts (Heizer and Napton 1969). Coprolites of birds and carnivorous mammals also contain appreciable amounts of bone (Mellett 1974) and other materials of sim-

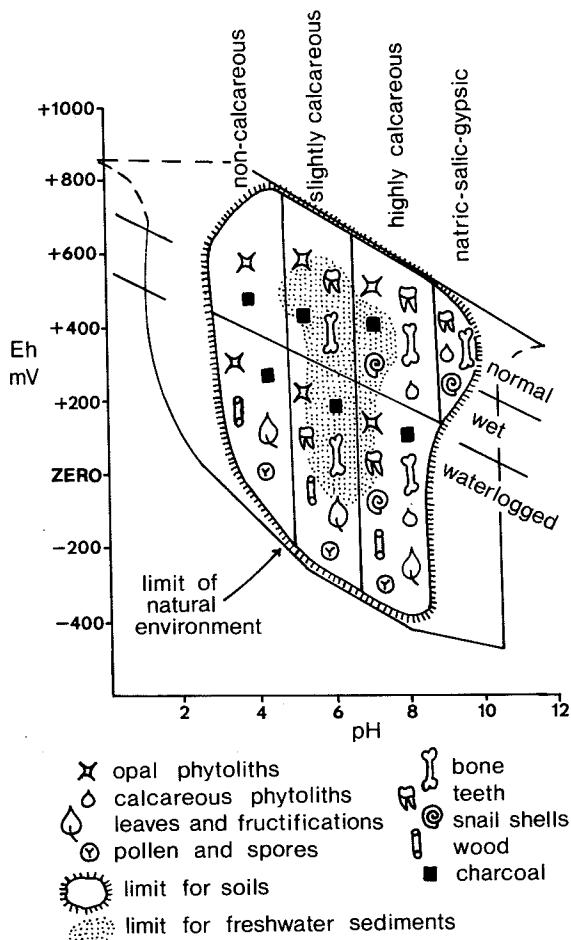


FIGURE 11. Theoretical Eh-pH stability fields for common kinds of terrestrial fossils preserved in fossil soils (modified from Baas-Becking et al. 1960, figs. 7, 8, 11).

ilar, calcium phosphate composition (Edwards and Folk 1979). Avian guano is generally not regarded as coprolitic because of its usual amorphous shape, but its composition becomes similar to that of bone as its organic matter decomposes or is leached. Fresh excrement of captive pelicans has only 4% P_2O_5 , but this has been enriched to 19% in modern Peruvian accumulations of pelican guano and 29% in old Peruvian guano (Hutchinson 1950). This process and guano itself are favored in or adjacent to biologically productive ecosystems in dry climates, in which rainfall is less (usually much less) than 1,000 mm (Hutchinson 1950). Similar conditions and processes may account for the reduc-

tion in volume, shriveling, and then (after a few weeks or months) bleaching, cracking, and powdering of the dung of domestic dogs (Vogeltanz 1965; Edwards and Yatkola 1974). Like bone, calcium phosphates are generally stable under alkaline conditions, but the degree of acidity at which they dissolve depends on their exact chemical composition (Lindsay and Vlek 1977).

Plant fossils.—The preservation of unburnt wood, leaf cuticle, plant fructifications, spores, and pollen is controlled more by Eh than by pH (Krumbein and Garrels 1952; Baas-Becking et al. 1960). Although potential fossils of this kind accumulate as litter at the surface of well-drained and oxidized soils, they are progressively broken down to amorphous organic matter or destroyed completely. This is more because of the activity of aerobic microbial heterotrophs, such as fungi and bacteria, than to direct chemical oxidation (Elsik 1971; Havinga 1971). To a lesser extent, microbial activity also appears to be related to pH. Havinga (1971) observed greater microbial destruction of pollen and spores in the A horizon of a calcareous (3% $CaCO_3$), alkaline (pH 7.2) alluvial clay than in the A horizon of an acidic (pH 4.6), podzolized sand. Others have observed that mildly alkaline soils (pH 6.5–8.1) are often barren of recognizable pollen and spores (Dimbleby 1957), although in very alkaline soils (pH 9 or more) microbial activity may be inhibited and allow pollen preservation (Potter and Rowley 1960).

Charcoal.—Burnt wood (or fusinite, in the terminology of coal petrography) is appreciably more resistant to microbial and chemical degradation and has a longer residence time in soils than other kinds of organic matter. Fossil charcoal can be distinguished from unburnt coalified wood by its silky luster and (under the scanning electron microscope) absence of a middle lamella between adjacent cell walls (Cope and Chaloner 1980). Charcoal has been widely used for radiocarbon dating of late Quaternary paleosols, which appear to have formed under a wide range of Eh and pH (Dimbleby 1955; Vogel and Zagwijn 1967; Bowler and Polach 1971; Evans 1972; Fölster and Hetsch 1978; Csongor et al. 1980). To my knowledge, charcoal has not yet been found in paleosols which were once extremely alkaline (pH 9–10), presumably be-

cause trees seldom grew in or near such soils, rather than because charcoal would not be preserved in them.

A Model for Chemical Control of Fossil Preservation in Paleosols

Considering the foregoing discussion, each kind of fossil can be considered to be chemically stable under certain general conditions of pH and Eh (Fig. 11). Original Eh and pH are of greater significance for fossils in soils (here taken to include acidic peat bogs) than for fossils in freshwater sediments because of the longer time over which these conditions act in soils and because of the greater range of conditions found in soils (Baas-Becking et al. 1960).

This model for fossil preservation predicts only the most usual case. Potential fossils will tend to decay or dissolve under conditions outside those in which they are normally preserved, but such destruction takes time. Remains of some creatures not favored for preservation by prevailing conditions may be entombed during burial of a paleosol and could be preserved under certain circumstances, although these remains would be rare compared to accumulated, preferentially preserved fossils. In none of the data presented on the fossils and fossil soils of the Pinnacles area of Badlands National Park is there such an exceptional case. Reports of a complete skeleton of an alligator and of "titanotheres graveyards" in a sedimentary setting like that of the very weakly developed, noncalcareous Ohaka Series paleosols (Clark 1937; Clark et al. 1967) could be such exceptions.

A Model for Temporal Variation in Conditions of Preservation in Paleosols

The Eh- or pH-controlled dissolution of potential fossils in soils takes time. For example, in Zimbabwe (Rhodesia), Watson (1967) noted corrosion and flaking of 20-yr-old bones in acid (pH 4.1–5.4) soils, but no 700-yr-old skeletons remained in them. Accumulations of fossils in soils under favorable conditions also takes time. In Amboseli National Park, Kenya, Behrens-meyer (1982a, p. 43) has suggested that "it would take 10^3 – 10^4 yrs to accumulate a 'fossiliferous' paleosol with 10–1,000 bones per m^2 ,

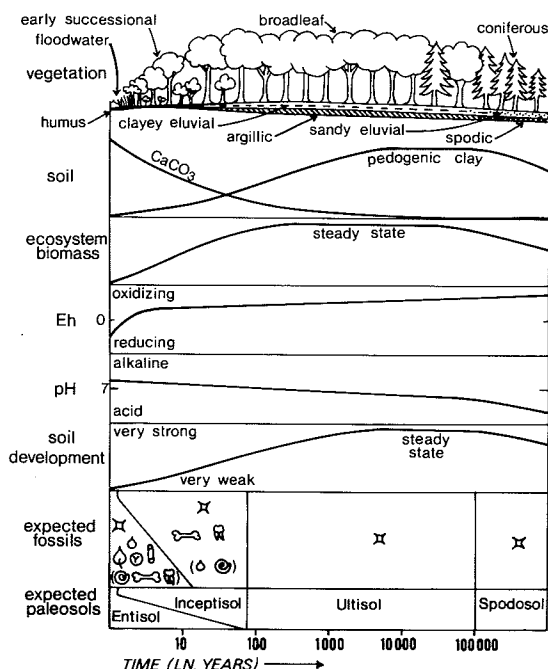


FIGURE 12. An hypothetical model illustrating the relationships of physical, chemical, and temporal factors in the development of soils and ecosystems and in the kinds of fossils and paleosols preserved.

representing the 10 major herbivores." As is apparent from the data presented from Badlands National Park, neither the accumulation nor destruction of fossils in soils with time is likely to be simple. Even without major environmental changes, a constant depletion or addition of fossils under a constant balance of contributing and destructive agents is unlikely to continue indefinitely, as can be seen from the following conceptual model, based largely on ideas developed by Jenny (1980).

Consider the results of a million years or more of undisturbed vegetative growth and soil development on flat-lying, moderately calcareous, alluvial, sandy siltstone in a humid climate (Fig. 12). Such sites are very rare because of widespread disruption of ecosystems by flooding, landslides, or other local catastrophes. Even without such disruptive events, there are pronounced changes in vegetation and soils with time. Conditions are briefly reducing and mildly alkaline within the moderately calcareous alluvium deposited by floodwaters. With retreat of

floodwaters, oxidizing conditions are encouraged by the bioturbation of early successional plants and animals forming an Entisol. With the later growth of trees and shrubs, soil development proceeds to the level found in Inceptisols, with the progressive leaching of CaCO_3 and other materials (such as Mg^{++} , Na^+ , and K^+), under increasingly acidic conditions. Easily weathered minerals, such as mica and feldspars in the original alluvium, are slowly converted to clay. This may be leached out of the upper (A) horizon and accumulate in a clayey (argillic) subsurface (B) horizon, at which point the soil is an acidic, oxidized Ultisol. Once the soil is strongly developed, there may be little discernible change for tens or hundreds of thousands of years, a condition called steady state or climax. However, the leaching of nutrient cations and loss of weatherable minerals proceeds until the productivity of the soil reaches critically low levels. This may ultimately result in an oxidizing, acidic Spodosol supporting stunted coniferous forest, on nutrient-poor, quartz-rich, sandy soils with a shallow sesquioxide-rich (spodic B) horizon.

At each phase in this hypothetical model, different communities of animals and plants may contribute to different assemblages of fossils in different fossil soils. Initial flooding may have entrained organic plant material, such as leaves and pollen, which is later destroyed within the developing Entisol. This early successional soil may preserve snails, bones, and teeth given large enough populations and enough time. With time, plant megafossils, pollen, and spores are completely destroyed, leaving bones and teeth as the most prominent fossils. With increasingly acidic pH, the amounts of calcareous phytoliths and snails preserved in the soils will be the first to decline, followed by bones and then teeth. Ultimately, only silica phytoliths will be preserved in the Ultisol or Spodosol.

This particular model was chosen because the differences are striking, and because soil and ecosystem development in humid temperate climates are well understood (Jenny 1980). A similar model would account for many aspects of the geological setting of fossil plants and vertebrates in the Early Eocene, Willwood Formation of northwestern Wyoming (Wing 1980; Winkler 1980; Bown and Kraus 1981a,b; Gingerich 1982; personal observations). Comparable

successional development, followed by steady state and then by declining productivity and desertification, with the development of desert pavements or calcrete or silcrete horizons, could also be proposed for arid land ecosystems and soils (Goudie 1973; Dregne 1976). Such a model may be more closely analogous to formation of the upper portion of the sequence in Badlands National Park, South Dakota (Retallack 1983). The important general feature of such models is that the optimal conditions for preservation of a particular kind of fossil are a trade-off between a number of different environmental factors which vary in time, even within undisturbed systems. Fossil soils may be important clues to the nature of these particular paleoenvironmental and temporal factors.

Conclusions

As estimates of the actual completeness of the rock and fossil record, those presented here are clearly unrealistic. Nor can the evidence of preservational biases presented here be used to reconstruct original communities in any detail. A great deal of additional information would need to be integrated with these findings in order to achieve that aim. The value of these estimates is in their use for comparing different sedimentary sequences and assessing the appropriateness of their temporal or paleontological resolution for particular paleobiological problems.

Making up for lost time.—Sequences with the highest temporal resolution are those with the highest long-term sediment accumulation rates. In terrestrial floodplain deposits, these are sequences of Entisols and Inceptisols, with limited pedogenic alteration, abundant sedimentary relicts, and more or less uniform color and texture. Floodplain deposits of low temporal resolution have low long-term sediment accumulation rates and numerous strongly developed paleosols, each with well-differentiated and distinctly colored and textured soil horizons.

These criteria, and completeness estimates, can be used to compare sedimentary sequences, such as the Late Eocene and Oligocene White River and lower Arikaree Groups of southwestern South Dakota (discussed here) and the Early Eocene Willwood Formation of northwestern Wyoming (Bown 1980; Bown and Kraus 1981a,b). From this latter sequence, Gingerich (1976, 1977,

1980, 1982) has gathered a great deal of impressive evidence for rates of evolution of archaic mammals. The Willwood Formation was a better choice for such studies than any sequence in the Badlands of South Dakota because it has a higher sediment accumulation rate and completeness for any given time span (as estimated by Gingerich 1982; Sadler and Dingus 1982). Nevertheless, the best sequences are only likely to be complete at a resolution of 100,000 yr (Gingerich 1982), and this is too coarse a resolution to provide evidence for the tempo and mode of speciation of mammals. These data thus appear more informative in understanding anagenetic rather than cladogenetic evolutionary change.

Fortunately, the Willwood Formation is unlikely to be the best possible sequence for such studies for two reasons. First, its rate of sediment accumulation is not unusual for fluvial systems, that is, not appreciably higher than median long-term rates at its time span (Fig. 1). Second, fossil soils in the Willwood Formation are numerous and well developed. In general appearance, it is a "barber pole" or "candy cane" formation, like the Chadron Formation and Scenic Member in Badlands National Park (personal field observation).

In addition, Gingerich (1976) did not originally attain the maximum temporal resolution possible for the sequence because of his broad sampling interval. Most samples were from stratigraphic intervals of 5 m. This would correspond to at least four successive paleosols in the areas studied by Bown and Kraus (1981a) and Winkler (1980). A small part of the sequence has recently been sampled paleosol by paleosol (Winkler 1980; Gingerich 1982). This is the finest theoretically worthwhile level of sampling in sequences of paleosols.

Making up for lost fossils.—The most complete fossil record for a variety of kinds of fossils, should be in calcareous, gleyed paleosols. Examples include the Pennsylvanian locality for edaphosaurs near Garnett, Kansas (Riesz et al. 1982) and the Late Jurassic "dirt beds" of the Dorset coast, England (Seward 1898, 1917; West 1975). Sequences of such paleosols are likely to provide the best fossil record of coevolution of organisms preserved in different ways. It is unfortunate that such lithologies are gen-

erally formed in seasonally dry, swampy habitats, when many spectacular examples of coevolution, such as that of Tertiary mammals and grasses (Stebbins 1981), took place in very different settings.

The models discussed also provide guidelines for the kinds of paleosol sequences in which particular fossils are best preserved. These are gleyed fossil soils of coal measures for fossil plants, and oxidized, strongly calcareous fossil soils of variegated and red beds for bones and land snails. Sequences of strongly calcareous paleosols seem best for studies of vertebrate paleoecology and evolution. Unfortunately, this limits investigation to faunas of open vegetation and semiarid to arid climates.

These criteria can also be used to compare different sedimentary sequences. Conditions for preservation of vertebrate fossils in the Willwood Formation of Wyoming were very good but not the best possible. I have been able to dig out and examine carefully the measured sections made by Bown and Kraus (1981a, figs. 2, 3) and Winkler (1980, sec. 1). All these Willwood paleosols appeared to have been Alfisols (of at least three main kinds), together with some Inceptisols and Entisols of kinds which could reasonably be expected to have developed into Alfisols, given enough time for development. The Inceptisols and Alfisols seen were all at least weakly calcareous, as established by field application of dilute hydrochloric acid. Many have numerous calcareous nodules. They are also comparable to paleosols of Badlands National Park in being clayey and composed largely of smectitic clays; additional indications that the well developed profiles were Alfisols. Studies of fossil occurrence in Willwood paleosols comparable to those reported here have not yet been undertaken. From my own observations, I predict that this sequence is intermediate in paleontological completeness between the Chadron and Brule Formations.

Looking for the best sequence.—For any particular group of terrestrial fossils and kind of paleoecological, coevolutionary, or evolutionary investigation, some sequences will provide more appropriate stratigraphic and paleontological resolution than others. Selection of a field area on the basis of such considerations as convenience, fossil abundance, and length of exposed sections

may not necessarily result in the best choice. Information from sediments and paleosols in a sequence may be used to choose a field area with appropriate resolution for a particular problem as well as to assess the resolution of studies already completed.

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APPENDIX 1. Rates of sediment accumulation based on estimates of paleosol development for selected subdivisions of the formal stratigraphic units of Late Eocene and Oligocene sedimentary rocks in the Pinnacles area, Badlands National Park, S.D. Rates for formal units are given in Appendix 2.

Sequence	Thickness (m)	Time span from paleosols (yr)	Sedimentation rate from paleosols (m/1,000 yr)
Upper Sharps Fm. (Samna Series only)	9.91	28,000	0.354
Lower Sharps Fm. & upper Poleslide Mbr (ashy breccia interval)	22.28	40,105	0.556
Interstream Poleslide Mbr (base of Ogi Series to top of highest Wisangie Series)	13.1	30,100	0.435
Nearstream Poleslide Mbr (top of sandstone to base of Ogi Series)	10.97	20,205	0.543
Upper Poleslide Mbr (above sandstones)	31.09	62,310	0.499
Lower Poleslide Mbr (below sandstones)	9.14	8,605	1.063
Upper Scenic Mbr (above sandstones)	10.21	47,100	0.217
Middle Scenic Mbr (between sandstones)	3.90	18,010	0.217
Lower Scenic Mbr (below sandstones)	6.40	17,005	0.376
Interior paleosol	2.62	10,000	0.262
Yellow Mounds paleosol above Fox Hills Fm.	0.82	10,000	0.082

APPENDIX 2. Estimates of sediment accumulation rate and of completeness based on paleosol development and on paleomagnetic and radiometric data for Late Eocene and Oligocene sedimentary rocks in the Pinnacles area, Badlands National Park, S.D. The expected rates of sediment accumulation used to calculate completeness (from Sadler 1981) were 0.80 m/1,000 yr (for 10³ yr), 0.45 (for 10⁴), 0.26 (for 10⁵), and 0.05 (for 10⁶).

Sequence	From paleosols				From paleomagnetic and radiometric data					
	Thickness (m)	Time span × 1,000 yr	Rate m/1,000 yr	Completeness 10 ³ yr	Time span × 1,000 yr	Rate m/1,000 yr	Completeness			
							10 ³ yr	10 ⁴ yr	10 ⁵ yr	10 ⁶ yr
Brule Fm.	84.59	153.055	0.553	0.69	3,400	0.025	0.031	0.056	0.096	0.500
Poleslide Mbr	46.18	70.920	0.651	0.81	1,700	0.027	0.034	0.060	0.104	0.540
Scenic Mbr	38.41	82.135	0.468	0.59	1,700	0.023	0.029	0.051	0.088	0.460
Chadron Fm. above Interior paleosol	22.56	80.005	0.282	0.35	4,800	0.0047	0.0059	0.010	0.018	0.094