

DINOSAURS AND DIRT

G. J. RETALLACK

Department of Geological Sciences, University of Oregon, Eugene, 97403-1272

ABSTRACT—Many dinosaur fossils are found on and in the soils they trod in life. Bone is abundant in calcareous or smectitic paleosols that were alkaline in chemical reaction when forming, but bone dissolves in acidic soil and leaf litter. Dinosaurs from rock sequences with non-calcareous paleosols are known from footprints and bones in paleochannels (Dakota Formation, Kansas; Weald Clay, Britain; Otway Group, Australia). The best known dinosaur faunas come from sequences of red paleosols with calcareous nodules (Chinle Group, Morrison and Two Medicine Formations, western U.S.) or drab paleosols with smectite clays (Hell Creek Formation, Montana; Horseshoe Canyon and Oldman Formations, Alberta).

Red calcareous soils similar to paleosols yielding latest Triassic to Late Cretaceous saurischian dinosaurs are now found in dry climates (600–900 mm m.a.p.). This is the climate of East African game parks, but these are poor analogues for the environment of dinosaurs because they are grasslands. There were Late Cretaceous marsh grasses, but there is no evidence of sod-forming dry-land grasses or of their distinctive granular ped structures in paleosols earlier than middle Miocene. Calcareous red paleosols of the upper Chinle Group and Morrison Formation have woody root traces and subsurface horizons of clay accumulation most like soils of dry open woodland. In contrast, paleosols containing early Late Triassic therapsids and Late Cretaceous ornithischian dinosaurs are more carbonaceous yet still calcareous, indicating more effective ground cover in dry forests than during Jurassic time.

Assemblages of bones from paleosols can reveal formerly preferred habitats. Late Triassic dinosaurs of the Chinle Group were found in paleosols of dry forest, but therapsids in swampy paleosols. Late Cretaceous hadrosaurs of the Two Medicine Formation were found in well-drained paleosols, whereas associated ceratopsians were in swampy paleosols. In contrast, there is no evidence of habitat preference in red calcareous paleosols of saurischian dinosaurs within the Morrison Formation.

INTRODUCTION

MUCH OF THE WAY we see dinosaurs comes from the mind's eye of gifted artists such as Charles Knight, Eleanor Kish and Gregory Paul. Dinosaur reconstructions are not only triumphs of imagination, but hypotheses of dinosaur posture and habits testable from the evidence of bones and teeth (Czerkas and Olson, 1987). Landscapes and vegetation of dinosaur reconstructions have been thought to reflect a higher ratio of imagination to evidence, because dinosaur bones with all their glorious detail are not often preserved along with fossil plants. In this paper I aim to show that landscapes and vegetation of dinosaur reconstructions are also testable hypotheses that must satisfy the evidence of paleosols in which many dinosaurs are found. Paleosols not only preserve dinosaur fossils, but give information on preservational biases, including an explanation for the common observation that fossil bones and plants are seldom found together.

Paleosols are ancient soils. They can be recognized in sedimentary sequences from a variety of features including fossil root traces, gradational layering comparable to soil horizons and distinctive hackly structures comparable to soil peds and cutans (Figs. 1, 2; Retallack, 1990). Many paleosols are now recognized in sedimentary rocks, but unlike sedimentary structures, paleosols represent times of non-deposition and plant growth in depositional basins. Indeed, the degree of development of soil horizons in paleosols can be used to estimate the duration of the hiatus in deposition, and sequences of paleosols can be used to calculate rates of sediment accumulation (Retallack, 1986; Bown and Kraus, 1993a,b). Root traces, burrows and other trace fossils are common within paleosols, but unlike trace fossils, a paleosol is a trace of an entire ecosystem rather than of an individual. Unlike fossils, paleosols are by definition in the place they formed and not transported. Particular kinds of paleosols are characteristic of forests and woodlands, but unless there are associated fossils it may not be possible to determine whether the forest was dominated by *Eucalyptus*, *Acacia* or *Quercus* (Retallack, 1991b). Particular features of paleosols also are indicative of paleoclimate, paleotopographic setting and the parent material from which the differentiated part of the profile formed (Retallack, 1994b). There are of course problems with alteration of paleosols after burial (Retallack, 1991a), but each paleosol rep-

resents a distinct ancient environment. This outline initiates their study by naming different kinds of paleosols as pedotypes (in the sense of Retallack, 1994a) from some well known dinosaur-bearing formations in the western U.S.

FOSSIL PRESERVATION IN PALEOSOLS

Particular kinds of paleosols not only indicate the paleoenvironments of dinosaurs preserved in them, but their environment of preservation. Unlike the beautifully articulated skeletons of duckbills entombed in paleochannel sandstones of Dinosaur Provincial Park in Canada (Dodson, 1971), the preservation of dinosaurs in paleosols is not always a question of sudden and accidental death. Such catastrophically sampled dinosaurs are known from paleosols, for example the herd of small theropods from Ghost Ranch, New Mexico (Colbert, 1995). More often however, dinosaurs are found as naturally weathered fragments, stained and cracked by exposure, in the paleosols on which they died. Preservation of such an attritional assemblage of dinosaurs requires alkaline soil pH, because the calcium phosphate of bone is dissolved in acidic soils and even in unpolluted rain (pH 5.6; Retallack, 1984). Dinosaur egg and fossil snails and clams with their calcium carbonate shells are even more sensitive to acid (Carpenter et al., 1994).

Using a pH meter directly on a paleosol is not useful because groundwater during burial resets the pH of paleosols, but indications of former alkaline pH include the abundance of calcium carbonate nodules and smectite clays in paleosols (Retallack, 1990). Formerly acidic soils lack pedogenic carbonate and have more deeply weathered clay minerals like kaolinite. It is no accident that the great dinosaur-bearing formations of the world have abundant calcareous and smectitic paleosols: Triassic Chinle Group of Arizona (Kraus and Middleton, 1987), Jurassic Morrison Formation of the western U.S. (Bakker, 1986), Cretaceous Two Medicine Formation of Montana (Rogers, 1990), Cretaceous Hell Creek Formation of Montana (Retallack, 1994a). The best known dinosaur babies, eggs and nests of Montana, Mongolia, southern France and India also are in highly calcareous paleosols (Carpenter et al., 1994). Dinosaurs also are known from formations with non-calcareous and kaolinitic paleosols such as the mid-Cretaceous Dakota Formation of Kansas (Eaton, 1960; Retallack and Dilcher, 1981a,b), the early Cretaceous Otway Group of Victoria, Australia (Rich and Rich, 1993; Retal-



FIGURE 1—This outcrop shows an abruptly truncated top overlain by sandstone, and gradational horizons down from there of carbonaceous siltstone, gray claystone and mottled red claystone. all characteristic of a paleosol. It also includes large agatized stumps. It is the Late Triassic (Carnian) Nastaan pedotype in the Blue Mesa Member, Petrified Forest Member, Chinle Group, at the Giant Logs area of southern Petrified Forest National Park, Arizona.

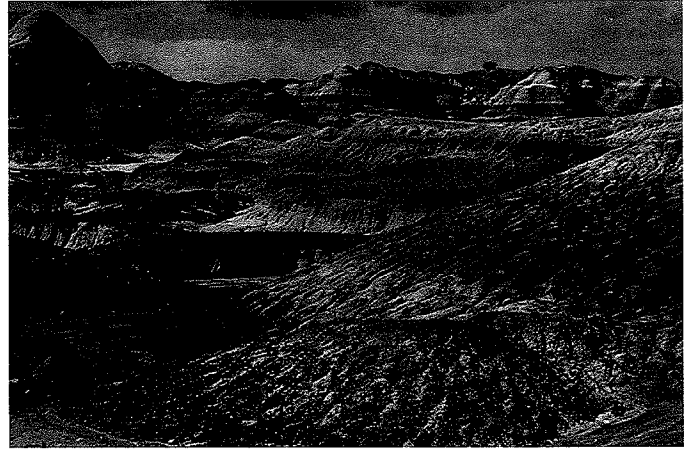


FIGURE 2—This succession of purple paleosols shows clear light gray reduction haloes around former root channels, a common early burial alteration of paleosols. These are Azid pedotypes in the type area of the Blue Mesa Member, Petrified Forest Formation, Chinle Group of Late Triassic (Carnian) age.

lack, personal observations) and the early Cretaceous Weald Clay of Britain (Kennedy, 1978; Retallack personal observations). In these formations however, bones of any kind are rare and found in lacustrine or channel facies.

Preservation of dinosaur bone and snail shells in paleosols depends upon high pH, whereas fossil skin, leaves and wood are preserved under conditions of low to negative Eh (Fig. 3). In well drained soils where most terrestrial animals live, Eh is high and positive, and such conditions are reflected in yellow, brown and red soil color from iron hydroxide minerals such as goethite and iron oxides such as hematite. Under these conditions an active community of aerobic microbes decomposes organic matter. This decomposer community must be suppressed either by waterlogging or extreme aridity for preservation of organic remains. Waterlogged conditions are reflected in paleosols by gray to green colors and coaly layers. Extreme aridity allows persistence of soluble salts such as gypsum in the soil (Retallack, 1990). Waterlogged habitats such as swamps and marshes are most common in humid climates where soils are leached of carbonate and bone by rain and organic acids from plant decay. Thus, fossil plants are best known from environments of low pH and low to negative Eh, whereas bones of land animals are best known from environments of high pH and high to positive Eh. This is why coal measure facies are so rich in fossil plants, but generally poor in fossil vertebrates (Retallack, 1984). Conditions of low pH and high to positive Eh also are common. This is the nature of soils supporting such diverse and productive communities as tropical rain forest (Retallack and Germán-Heins, 1994), but neither fossil plants or animals tend to be preserved in or around such paleosols. A fourth combination is high pH and low to negative Eh, in which both plants and bones can be preserved together. A few examples of paleosols of this kind are known, for example the Blue Forest locality and *Placerias* quarry of the Late Triassic Chinle Group of Arizona (Camp and Welles, 1956; Fiorillo and Padian, 1993) and the Stan Quarry of the Cretaceous Hell Creek Formation of South Dakota (Retallack, 1994a). These alkaline, waterlogged fen and carr environments are rare today and were also uncommon in the past.

Because of the different conditions required for preservation

of bone and organic matter it should not be assumed that fossil plants and dinosaurs from the same formation necessarily formed part of the same ecosystem. Fossil plants in the Triassic Chinle Group (Ash, 1972), Jurassic Morrison Formation (Tidwell, 1990b) and Cretaceous Hell Creek Formation (Johnson and

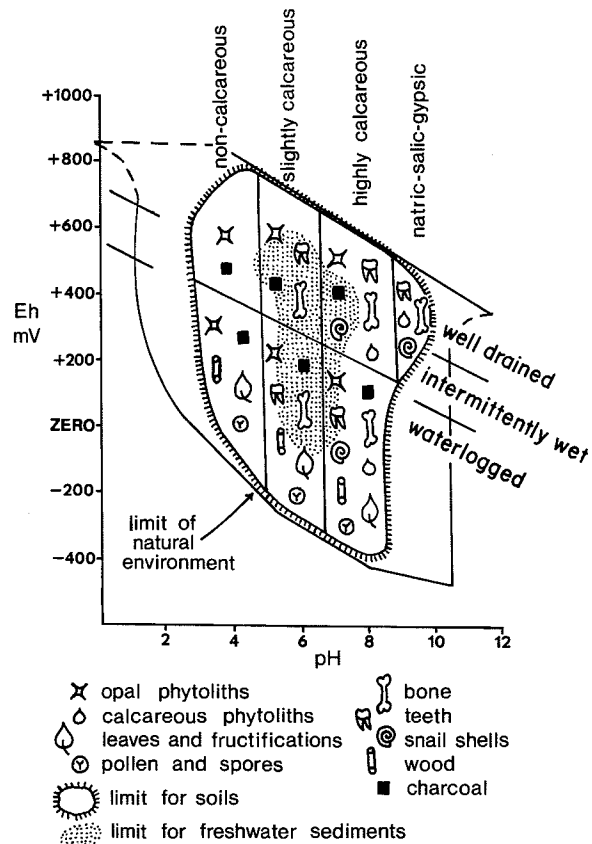


FIGURE 3—Hypothetical Eh-pH condition for preservation of a variety of different kinds of fossils (reprinted with permission from Paleobiology).

Hickey, 1990) are found in drab-colored to coaly sediments and paleosols different from the brown to red paleosols that have yielded most of the dinosaurs from these formations. In some cases the fossil plants are preserved in very weakly developed paleosols that reflect ephemeral communities early in the ecological succession to colonize ground disturbed by flooding, and in other cases in local coaly paleosols of local swamps and marshes (Retallack, 1994a). In contrast, vegetation of the red and brown dinosaur-bearing paleosols is poorly represented by plant fossils. The taxonomic composition of "upland floras" encountered by dinosaurs can be reconstructed to some extent by analysis of pollen and spores that wafted into suitable lowland habitats (Gottesfeld, 1972; Jerzykiewicz and Sweet, 1988). Such palynofloras are dominated by wind-pollinated and dispersed plants that are more common in early successional than old growth communities (Retallack and Dilcher, 1981a,b, 1988). Fortunately, the general nature of the vegetation that dinosaurs encountered over most of their habitat for most of the time can be reconstructed from paleosol data (Retallack, 1990).

CHINLE GROUP

My own examination of paleosols in the Chinle Group has been limited to the Blue Mesa Member of the Petrified Forest Formation in southern and central Petrified Forest National Park, Arizona. These colorful red, purple and gray mottled claystones contain some of the most spectacular assemblages of agatized fossil wood, and have diverse assemblages of fossil leaves (Daugherty, 1941; Ash, 1970, 1972; Gottesfeld, 1972), trace fossils (Hasiotis and Dubiel, 1993, 1995) and vertebrates (Jacobs and Murry, 1980; Murry and Long, 1989; Lucas and Hunt, 1993a,b; Hunt, 1994; Parrish, 1993; Hunt and Lucas, 1994; Kaye and Padian, 1994). Largely on the basis of fossil vertebrates the beds have been dated as Late Triassic (Carnian or Adamanian local faunachron of Lucas and Hunt, 1993b). At that time northern Arizona and adjacent states were part of a broad floodplain of meandering streams draining northwest between a cordilleran volcanic arc and the ancestral Rocky Mountains into coastal lakes and the Eopacific ocean (Blakey and Gubitosa, 1983; Riggs et al., 1996).

Color mottling and banding that makes these beds so picturesque comes from a variety of paleosols (Kraus and Middleton, 1987) that are here named using the Najavo language (Young and Morgan, 1980). Nastaan (log) paleosols are thick (1–2 m) and have three distinct horizons: (1) a surface gray claystone penetrated by fossil root traces and supporting agatized stumps and logs, (2) a central gray siltstone with root traces and (3) a subsurface red claystone with scattered drab-haloed root traces. A fine example of the Nastaan pedotype is exposed in the Giant Logs area at the south end of the National Park (Fig. 1: SE $\frac{1}{4}$ SW $\frac{1}{4}$ NW $\frac{1}{4}$ S1 T16N R23E Agate House 7.5'). Other comparably thick and differentiated paleosols differ in their purple subsurface and are called the Azid (liver) pedotype. There are at least three profiles of this kind widely exposed in the lower slopes of Blue Mesa in the central part of the National Park (Fig. 2: SW $\frac{1}{4}$ NW $\frac{1}{4}$ NE $\frac{1}{4}$ S26 T18N R23E Adamana 7.5'). Azid paleosols include fossil stumps of *Araucarioxylon arizonicum* in growth position with deeply penetrating root traces in the Blue Forest area of the National Park (Gottesfeld, 1972; Ash and Creber, 1992). Also found in Azid paleosols are remains of phytosaurs (*Rutiodon crossbiensis*, including lower levels of Dying Grounds locality of Murry and Long, 1989).

Both Nastaan and Azid paleosols with their subsurface smectite-rich and weakly-calcareous, clayey horizons are similar to Alfisols, the nutrient-rich forest soils of subhumid climates receiving some 900–1200 mm rainfall per year (Soil Survey Staff, 1990). A humid-subhumid forested landscape is also indicated

by thin cuticles, slightly sunken to ununsunken stomates and stomates on both sides of fossil leaves (Ash, 1972). Locally common fossil charophytes, ostracods and bivalves are evidence of neutral to alkaline groundwater unlikely in a very humid climate (more than 1500 mm: Kietzke, 1989; Good, 1989). Seasonal variation in moisture and temperature were probably not so marked as the monsoonal climates recently proposed from climatic modelling and observations of trace fossils and growth rings in freshwater clams (Dubiel et al., 1991). The fossil wood does not show pronounced growth banding (Ash and Creber, 1992). Nor have the diffuse carbonate horizons and complexly intergrown carbonate and ferruginous concretions of known monsoonal paleosols (Retallack, 1991a, 1995) yet been reported in detailed accounts of paleosols of the Chinle Group (Blodgett, 1988; Dubiel et al., 1991). Although many of the fossil logs are preserved prone in paleochannels, the abundance of paleosols and fossil stumps is evidence that they were not transported far in this forested landscape (Fig. 4).

Early reconstructions of Petrified Forest National Park by Paul Fair emphasized a closed canopy forest of monkey-puzzle trees, but the "Colbert Murals" of 1976 and 1985 show more open forests with red clayey gullies and rock outcrops (Gillette, 1986). Neither of these versions are compatible with evidence from Nastaan and Azid paleosols. The red clay and gullies of the "Colbert Murals" are unlikely to have been exposed in these forested alluvial bottomlands, and much of the intense red color is likely to have been produced during burial dehydration (Retallack, 1991a). Nor is there compelling evidence for the distinctive monkey-puzzle tree form found in some araucarian conifers, because convincing araucarian reproductive structures have yet to be found and most of the fossil conifer foliage is scale or needle-leaved (Ash, 1972). Furthermore, living forests of *Araucaria angustifolia* in South America grow in more deeply weathered soils (map units Fh1–3a and Fh2–3h of F.A.O., 1971). Closed canopy, tall forests produce more deeply weathered soils (Ultisols) than the paleosols, and dry woodlands grow in shallower calcareous soils (Aridisols). Nastaan and Azid paleosols fall between these two extremes of degree and depth of weathering (Alfisols), and probably supported forests of medium height with a relatively open canopy. Mapping of stumps in the Blue Mesa fossil forest of the National Park shows a nearest neighbor spacing averaging 5.4 m ($n = 23$; $\sigma = 2.6$ m). The fossil logs average 91–122 cm in diameter and 18–30 m long, with the biggest some 213 cm diameter and 37 m long (Daugherty, 1941). Using regressions of diameter to height from living *Pinus rigida* (Whittaker and Woodwell, 1968) gives a forest 25–30 m tall, with some trees up to 41 m. This is neither a rain forest, nor a dry woodland, but an open forest (Smiley, 1985). Soils comparable to Nastaan and Azid paleosols are widespread in the Americas under mesic forests generally dominated by flowering plants (map units Lo8-2a, Lo19-2a of F.A.O., 1975a; Lo2-2c of F.A.O. 1971). Comparable soils in the Sierra Madre Occidentale of Mexico under oak-pine forest (map unit Lo26-2bc of F.A.O., 1975b) may be the closest modern analog to these Triassic forests.

Fossil plants are best preserved in association with Haltso (yellowish green) and Tseko (coal) pedotypes in the area around the Tepees in the central part of the National Park (SW $\frac{1}{4}$ SE $\frac{1}{4}$ NE $\frac{1}{4}$ S22 T18N R23E and SE $\frac{1}{4}$ NW $\frac{1}{4}$ NW $\frac{1}{4}$ S22 T18N R23E Adamana 7.5', respectively). Haltso profiles are simply shales with plant fossils and root traces. Their flora is dominated in some places by the large branched horsetail *Neocalamites virginianensis* and in other places by a more diverse community of cycadeoids (*Laurozamites powellii*: Weber and Zamudio-Varela, 1995) and ferns (*Phlebopteris smithii*: Daugherty, 1941; Ash, 1972; Gottesfeld, 1972). Vertebrate fossils of Haltso paleosols

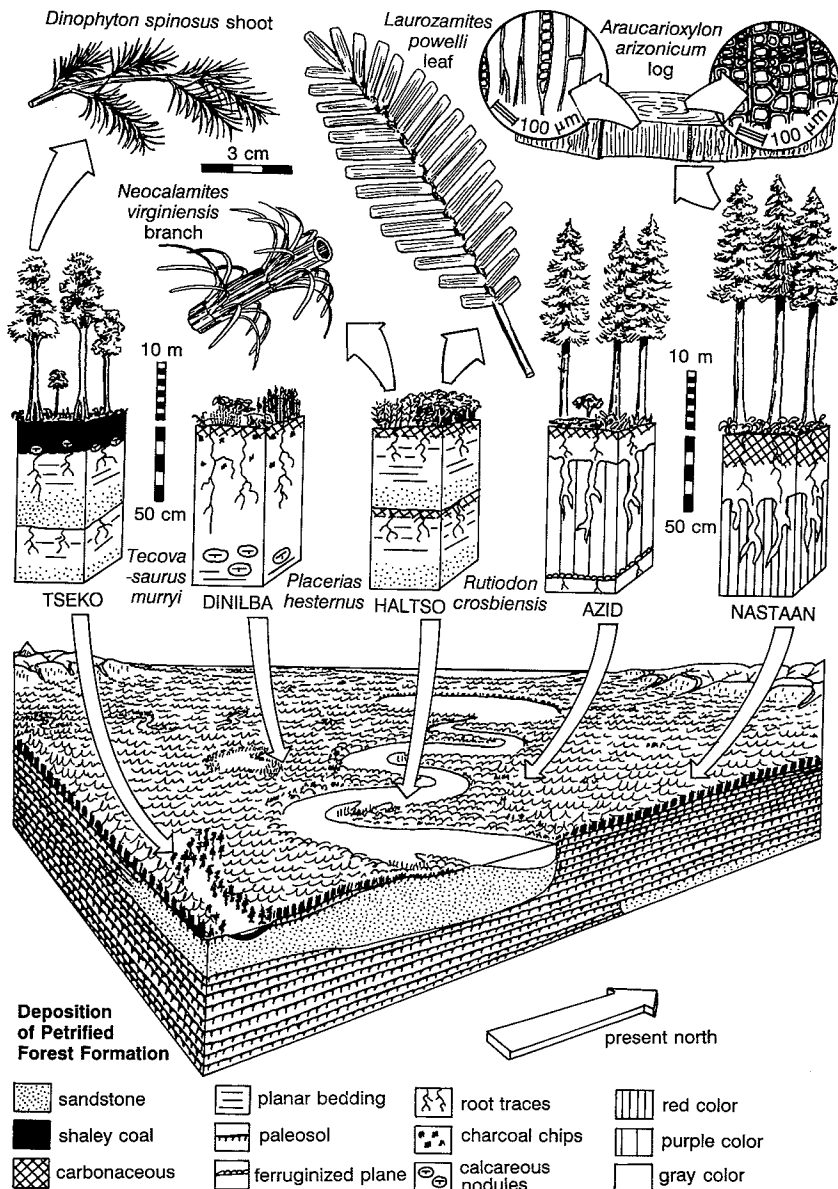


FIGURE 4—A reconstruction of soils and vegetation during the Late Triassic (Carnian) deposition of the Blue Mesa Member, Petrified Forest Formation, Chinle Group in northern Arizona.

include labyrinthodont amphibians (*Metoposaurus fraasi*) and aetosaurs (*Stagonolepis wellsi*, *Desmatosuchus haplocerus*), among others (Crocodile Hill locality of Murry and Long, 1989). Cuticle coals of the Tseko pedotype are dominated by an enigmatic, possibly gnetalean, plant (*Dinophyton spinosus*: Ash, 1970; Pigg et al., 1993), and also contain amber (Litwin and Ash, 1991). Neither Haltso nor Tseko pedotypes are common or well developed, and both represent only a few tens to hundreds of years of soil formation, unlike associated Nastaan and Azid pedotypes with their subsurface clayey horizons differentiated to an extent seen in soils tens of thousands of years old. Within the forested landscape of the Late Triassic, Haltso Entisols and Tseko Histosols represent ephemeral and local habitats. Haltso paleosols probably supported cycadeoid-fern scrub early in the ecological succession toward forest, whereas Tseko paleosols formed in local swamps.

The most prolific source of vertebrate fossils in the Blue Mesa

Member of the Petrified Forest Formation is the Dinilba (grayish) paleosol in the *Placerias* quarry near Romero Springs, southwest of St Johns (SW¼ SW¼ NW¼ S14 T12N R27E Salado 7.5'). The paleosol is a gray slickensided profile with comminuted plant debris and root traces. Its calcareous nodules are at a depth of about 1 m in the profile (Fiorillo and Padian, 1993). This kind of soil (gleyed Inceptisol) forms in seasonally dry swamps, where clay illuviation and iron oxidation (seen in Nastaan and Azid profiles) was limited by high water table and flooding for a part of the year. Such a habitat is supported by the discovery of twigs of the lycopsid *Chinlea campii* (Miller, 1968) and fish fragments (Jacobs and Murry, 1980; Kaye and Padian, 1994). However, about two thirds of the 3000 vertebrate specimens from here belong to the large (2m) dicynodont therapsid *Placerias hesternus* (this name has priority over *P. gigas* of Camp and Welles, 1956, according to Lucas and Hunt, 1993a). The association of this herbivorous therapsid with a ly-

copsid adds further support to the idea that these wetland plants were an important element of the diet of Triassic therapsids (Retallack, 1996b, 1997).

The *Placerias* quarry also has yielded teeth of the small ornithischian dinosaur *Tecovasaurus murreyi* (Hunt and Lucas, 1994), as well as fragmentary remains of other possible ornithischians, an anchisaurid saurischian and a theropod (Kaye and Padian, 1994). Little is known of early Late Triassic (Carnian) dinosaurs in Arizona, and it seems unlikely that Dinilba paleosols represent their preferred habitat when they are such a minor component of their vertebrate fauna.

The better known theropod dinosaurs *Eoraptor* and *Herrerasaurus* from the Ischigualasto Basin of Argentina, are of about the same age (Carnian: Sereno and Novas, 1992; Sereno et al., 1993; Rogers et al., 1993). This Argentine sequence includes red and purple mottled paleosols comparable to Nastaan and Azid pedotypes of Arizona but with more obvious calcareous nodules (Frenguelli, 1948), which can be taken as an indication of a drier climate (Retallack, 1994b). Also common in the Ischigualasto Basin are large permineralized stumps, although these belonged to the broadleaf seed fern *Dicroidium odontopteroides* (Archangelsky, 1968; Retallack and Dilcher, 1988). Thus, evidence from both Argentina and Arizona suggests an origin of dinosaurs in subhumid, open forests.

This conclusion is strengthened by observations of paleosols associated with the pack of little, articulated, theropod dinosaurs from Ghost Ranch, New Mexico (Colbert, 1995), which I will call *Coelophysis bauri* following a recent claim for conservation of this name (Colbert et al., 1992), although I see much merit also in proposals to transfer these fossils to *Syntarsus* (Paul, 1993) or *Rioarribasaurus* (Hunt and Lucas, 1993). The mass death assemblage of articulated *Coelophysis* from Ghost Ranch is from the Rock Point Formation of the Chinle Group of very late Triassic age (late Norian or Apachean local faunachron: Lucas and Hunt, 1993 b,c). The dinosaurs come from weakly developed red calcareous paleosols (Russell, 1989, p. 35; Lucas and Hunt, 1993c; Schwartz and Gillette, 1994; Colbert, 1995). Above the main fossiliferous paleosols is a thicker, red, clayey paleosol with calcareous nodules. Comparable paleosols of similar age are also known in southwestern Colorado (Blodgett, 1988; Lucas, 1993) and in the Petrified Forest of Arizona, and in the latter case have also yielded *Coelophysis* (Padian, 1986; Long and Murry, 1989). These early dinosaurs probably lived in dry woodlands, as inferred here for comparable paleosols of the Jurassic Morrison Formation.

In the early part of the Late Triassic (Carnian) woodlands and forests were taxonomically diverse and structurally complex, and may have spawned the adaptive radiation of insects (Labandiera and Sepkoski, 1993) and mammals (Lucas and Hunt, 1994). These agile new prey items may have encouraged the evolution of early predatory dinosaurs. Later in the Late Triassic (Norian) increasingly calcareous and less clayey paleosols indicate a shift to drier climate and open woodland in the western United States, as well as South America (Frenguelli, 1948) and South Africa (Kitching, 1979; Retallack, personal observations). These less productive ecosystems supported communities of large prosauropod herbivores. The faunal transition toward large dinosaurian herbivores with a gastic mill has been explained as either a competitive replacement (Bonaparte, 1982; Charig, 1984) or as an adaptive radiation following mid-Late Triassic (end-Carnian) extinction (Benton, 1983). Detailed studies of sequences of paleosols could reveal whether these communities changed abruptly or gradually.

The late Triassic decline of broadleaf seed ferns (*Dicroidium*, *Scytophyllum*, *Lepidopteris*) on humic, gleyed, eutrophic paleosols (Retallack and Dilcher, 1988) is mirrored by the Late Cre-

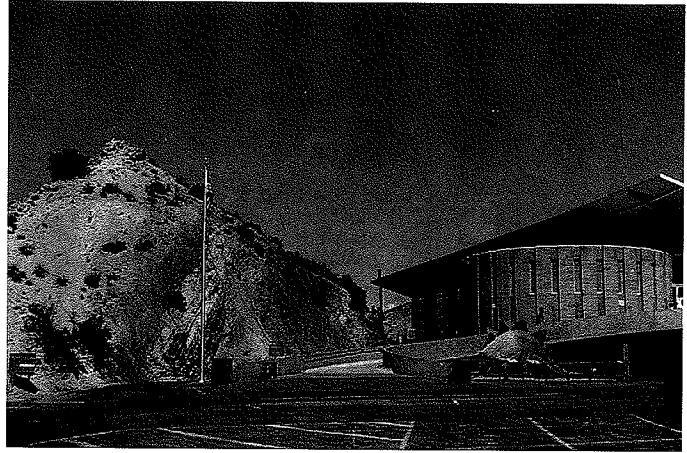


FIGURE 5—Steeply dipping paleosols of the late Jurassic (Tithonian) Morrison Formation exposed immediately to the south of the entrance to the quarry face at Dinosaur National Monument, Utah.

taceous rise of broadleaf angiosperms and ornithischian dinosaurs in comparable paleosols (Retallack and Dilcher, 1981a,b, 1986). The latest Triassic to Late Cretaceous interregnum of widespread, red, calcareous, weakly carbonaceous paleosols with saurischian dinosaurs is well exemplified by the Late Jurassic Morrison Formation of the western U.S.

MORRISON FORMATION

The Morrison Formation famous for Late Jurassic dinosaurs is widely distributed through the U.S. intermontane west in the area of the Shoshone Indian language (Miller, 1972), which I have used to name pedotypes, largely based on exposures at the entrance to the enclosed quarry at Dinosaur National Monument, Utah (Figs 5–7: SW¼ NE¼ SE¼ S26 T4S R23E Dinosaur Quarry 7.5'). This locality is in the middle part of the Brushy Basin Member of the upper Morrison Formation and probably some 149 million years old (Tithonian: Chure et al., 1994).

The Morrison Formation was deposited by streams draining east from large alluvial fans of the Rocky Mountain front, then meandering north on a low gradient floodplain into Canada (Brenner, 1983). In northeastern Utah paleochannels of the Morrison Formation were meandering with depths of 3–7 m, widths of 30–120 m and meander wavelength of 0.5 to 1.5 km (Derr, 1974).

Humid paleoclimate is indicated by fossil plants in lacustrine facies of the Morrison Formation in Colorado and coal measures in Montana, which have yielded most of the compression fossil flora of the formation (Tidwell, 1990b), but these may not be relevant to upland environments represented by red paleosols at Dinosaur National Monument. Of more relevance to environments represented by the red paleosols are permineralized remains from associated paleochannels, including stems of ferns, casts of horsetails, stems and seeds of cycadeoids, short shoots and cones of conifers, and stems of the enigmatic (possibly gnetalean) *Hermanophyton* (Tidwell, 1990a; Tidwell and Ash, 1990; Tidwell and Medlyn, 1992; West and Chure, 1994). These permineralized remains lack pronounced growth rings and indicate a subhumid to humid, warm paleoclimate without strong seasonality. This is compatible with common illitic clays in the basal Brushy Basin Member of the Morrison Formation, but not with the smectitic clays, calcretes and lacustrine cherts of the middle Brushy Basin Member that have been taken as evidence of arid to semiarid paleoclimate (Dodson et al., 1980; Petersen and Turner-Petersen, 1987; Turner and Fishman, 1991).

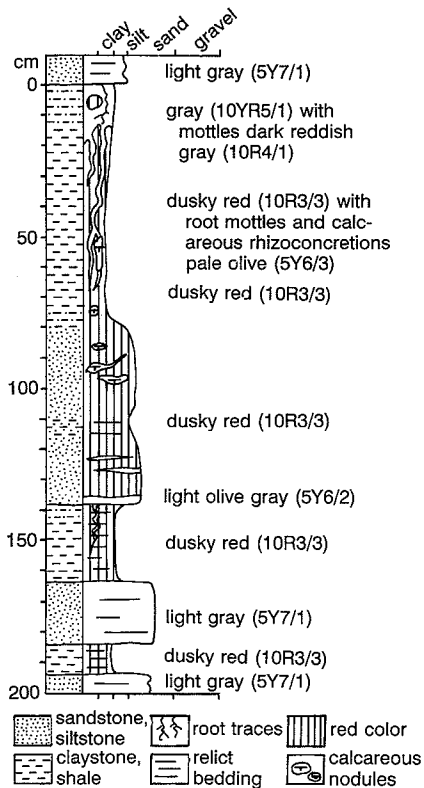


FIGURE 6—Geologic section of a red clayey calcareous paleosol (Ainka pedotype) of the late Jurassic (Tithonian) Morrison Formation exposed immediately to the south of the quarry face at Dinosaur National Monument, Utah.

Evidence from paleosols can aid in resolving these differences of opinion. The Ainka (red) pedotype was the best developed of the profiles seen, and consists of 15 cm of grey-green silty claystone grading down through an interval of drab-haloes root traces into red claystone with calcareous rhizoconcretions and nodules at a depth of 90 cm from the surface (Fig 6). The depth to the calcic horizon of soils (D) is related to mean annual rainfall (P) according to the following formula (Retallack, 1994b):

$$P = 139.6 - 6388D - 0.01303D^2$$

Considering a local burial depth of the Morrison Formation of some 2.5 km (Hintze, 1988, chart 40) and using a compaction formula of Sclater and Christie (1980), gives compaction of some 66%. Mean annual rainfall for the Ainka profile immediately above the dinosaur bearing sandstone at the Dinosaur National Monument can be estimated as 765 ± 141 mm, or roughly 600–900 mm. The depth and degree of development of the profile are compatible with a warm climate, and the weakly banded rhizoconcretions indicate a distinct dry season. This was not as marked as in monsoonal climates, as these paleosols lack the diffuse nodular horizon and intergrown carbonate and hematite of known monsoonal paleosols, such as those of the Miocene Siwalik Group of Pakistan (Retallack, 1991b, 1995).

Open forest vegetation is likely for the Ainka paleosol considering its subsurface clayey horizon, calcareous nodules, and the large woody root traces with drab haloes. The gray surface of the Ainka paleosol may reflect burial reduction of organic matter there (Retallack, 1991a), and its lateral continuity implies at least sparse ground cover. There is no indication of the granular ped structure found under grasses, nor of fossil charcoal

that would be expected from chaparral vegetation. Good possibilities for ground cover are rhizomatous lycopods such as *Lycopodium* or cormose lycopods such as *Isoetes* (suggested by Tidwell, 1990b; and Retallack, 1996b, respectively) or fern-cycadophyte undergrowth (envisaged by Miller, 1987). Such red, clayey, calcareous soils of dry climates support relatively open vegetation, such as the cypress (*Callitris*) woodlands of central New South Wales, Australia (Beadle, 1981; map unit Lk13-1/2ab and Lk10-1/2b of F.A.O., 1978b) and the pinyon-juniper woodlands of Texas, Oklahoma and New Mexico (map units Lk1-2a, and Lk2-1a of F.A.O., 1975a). Recent reconstructions compatible with this view have been offered by Paul (1987) and Hallett (1987). Comparison of the depositional environment of the Morrison Formation with the Grand Chaco of Paraguay and Argentina (by Moberly, 1960) and with the alluvial plains of the Huang-Ho and Yangtze-Kiang in China (by Mook, 1916) are not supported by the evidence of paleosols. The soils of these areas (map units Xh4-2a of F.A.O., 1971 and Gm25-2/3a of F.A.O., 1978a, respectively) are more calcareous than Morrison paleosols in the Grand Chaco and more gleyed in China. In both places soils are more influenced by grassy vegetation giving the granular soil-structure known technically as a mollic epipedon, which is unknown from the Morrison Formation. For this reason the grassy game parks of East Africa are inappropriate analogs for dinosaur communities, although such comparisons may have heuristic value (Dodson et al., 1980).

Other pedotypes of the Morrison Formation are either very weakly developed or reflect waterlogging. These were local or ephemeral parts of the landscape. Tatuhi (thin) paleosols are red with root traces and relict bedding. They probably represent vegetation colonizing stream banks after flooding. Pasiampin (sand) profiles consist of bedded sandstone with rhizomes of horsetails or other kinds of roots. These represent ephemeral streamside communities of sandbars. Kusi (gray) paleosols are gray with thick, slickensided, moderately-calcareous, subsurface horizon, and probably represent periodically waterlogged parts of the floodplain. Similar gray shales have yielded fossil horsetails in Dinosaur National Monument (Chure et al., 1994). Kusi paleosols may have supported tree ferns, horsetails, seed ferns, ginkgos and other moisture-loving elements of the fossil flora (Tidwell, 1990a,b).

Different pedotypes recognized in the Morrison Formation can be used to establish ancient communities of dinosaurs. For example, dinosaurs were collected from Ainka paleosols in the Cope Quarry near Garden Park, Colorado (Russell, 1989, p. 71) and also in the lower part of Como Ridge, Wyoming (Bakker, 1986, p. 105). A Tatuhi paleosol has yielded dinosaurs at Riggs' (1903) Fruita Quarry, Colorado (Russell, 1989, p. 73). A Kusi paleosol has yielded a diverse assemblage at the Marsh Quarry, Garden Park (Felch's YPM Quarry 1 of Ostrom and McIntosh, 1966; Russell, 1989, p. 69). Finally, parts of the paleochannel sandstone with dinosaurs at Dinosaur National Monument include Pasiampin paleosols with fossil horsetail plants (West and Chure, 1994). The dinosaurs shown on my reconstructed paleosols (Fig. 7) reflect these occurrences. The available data do not yet show clear preferences of particular taxa for particular soils. It could be that these dinosaurs ranged through a variety of habitats (Dodson et al., 1980).

The common occurrence of sauropods in well drained paleosols support the arguments made by Bakker (1971, 1986) and Coombs (1975) that large sauropods were not obligate aquatic creatures. Also pertinent to the habitats of sauropods are the comparable red calcareous paleosols with sauropod nests and bones from the Late Cretaceous of Mongolia (Jerzykiewicz and Russell, 1991), India (Sahni et al., 1994), Utah (Fouch et al., 1983; Bakker, 1986) and Texas (Lehman, 1989, 1990). Sauro-

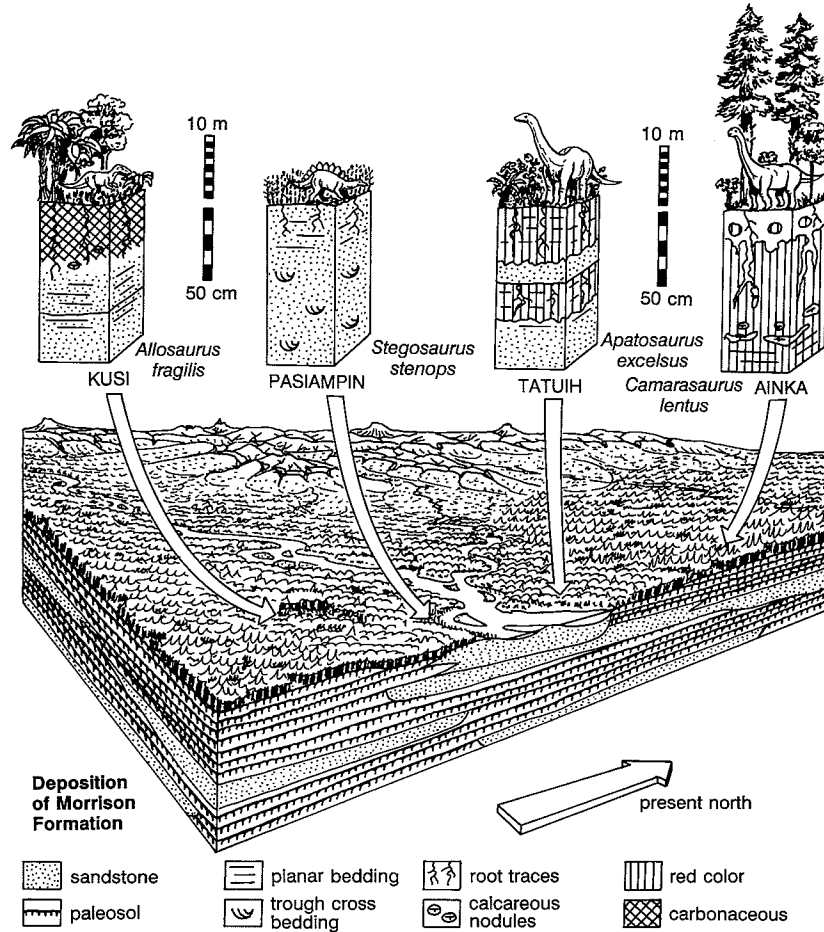


FIGURE 7—A reconstruction of soils and vegetation during the late Jurassic (Tithonian) deposition of the Morrison Formation in western Utah.

pods evidently lived in dry open woodlands of highly-oxidized, organic-lean soils.

A conundrum posed by these paleosols is how such large consumers were sustained by such low productivity aridland gymnosperm vegetation evident from fossil plants and soils. Perhaps the dinosaurs had very low population numbers, like the elephants and giraffes of Namibia (Paul and Leahy, 1994). Alternatively this imbalance between secondary and primary productivity may be redressed by postulating lower energy requirements of ectothermic mid-Mesozoic megafauna in a greenhouse climate (Russell, 1989; Farlow et al., 1995). A high ratio of secondary-primary productivity generating carbon dioxide and methane could also partly explain the Mesozoic greenhouse (Olsen, 1993). The influence of this greenhouse began to wane as more organic-rich paleosols appeared with the rise of flowering plants in the Late Cretaceous, as indicated by paleosols of the Two Medicine Formation.

TWO MEDICINE FORMATION

The upper Two Medicine Formation of late Cretaceous (Campanian) age is famous for its dinosaur eggs in nests and baby dinosaurs both in north central Montana and across the border in Alberta (Horner, 1994, 1995; Horner and Currie, 1994). My reconstruction (Fig. 8) is based on observation of paleosols at nesting sites and other dinosaur quarries in the area of Landslide Butte, north of Cut Bank, on the Blackfeet Indian Reservation (Horner, 1984a, 1989, 1992; Rogers, 1990). Their language has

been used to characterize the different pedotypes found (Frantz and Russell, 1989).

The upper Two Medicine Formation near Landslide Butte was deposited in a low gradient coastal plain flanked to the west by alluvial fans from the newly uplifted Rocky Mountain Front and the east by the waters of the Interior Seaway (Horner, 1984a). Dinosaurs are most common in this paleosol-rich clayey upper part of the formation (Rogers, 1990), whereas the angiosperm-dominated fossil flora is known from the dinosaur-poor lower part of the formation interpreted as a deltaic plain (Crabtree, 1987).

The fossil nests with eggs, much broken eggshell and bones of the baby dinosaur *Hypacrosaurus stebingeri* (Horner, 1994; Horner and Currie, 1994) are in distinctive gray-green paleosols. These Istawat (to raise a young animal) paleosols are exposed in a low knoll within a creek draining Landslide Butte (SW¼ NW¼ SW¼ S27 T37N R8W Landslide Butte 7.5') and in a nearby ridge (NW¼ NE¼ NE¼ S28 T37N R8W). They are massive profiles with few slickensided clay skins or root traces, but an horizon of calcareous nodules about 60 cm below the surface. Their drab color indicates both organic matter and perhaps seasonal waterlogging, but the carbonate nodules and root traces suggest a soil well drained for most of the year (Retallack, 1990). Nests of *Maiasaura peeblesorum* in the Two Medicine Formation near Choteau, Montana, also are green-gray in the center of the nest mound, but they have the brown color of oxidation and good drainage without any indication of an im-

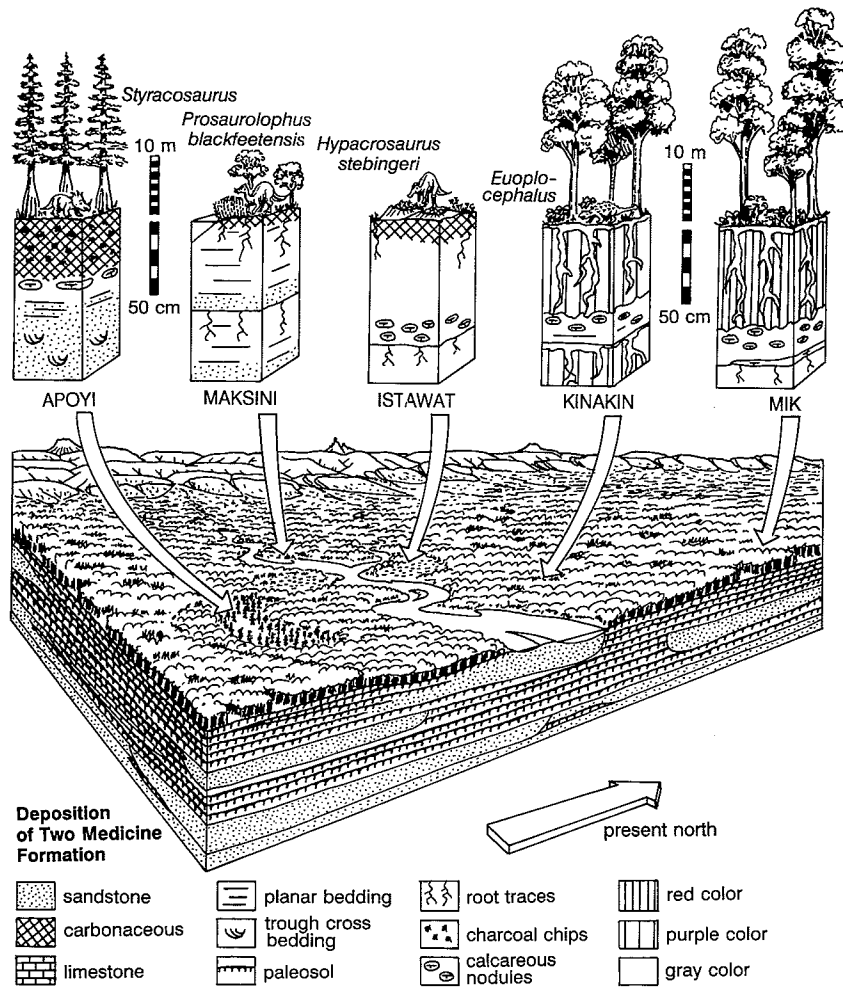


FIGURE 8—A reconstruction of soils and vegetation during late Cretaceous (Campanian) deposition of the Two Medicine Formation in northern Montana.

pervious layer that would perch the water table (Horner and Makela, 1979; Horner, 1984b). The Choteau paleosols and nests are also interdigitated with lacustrine carbonates (Horner, 1987) and have associated permineralized herbivore coprolites burrowed by dung beetles (Chin and Gill, 1996), which I have not seen at Landslide Butte. In both places nests are so abundant and closely spaced, and root traces and other plant fossils so sparse, that the nesting area was probably an extensive area of bare earth with little plant cover (Paul, 1994). The mixed indicators of gleization and good drainage may be explained if the nests like those of the living Australian mallee fowl (*Leipoa ocellata*; Firth, 1962) were covered with plant debris and soil for an incubation period while the plant debris fermented and generated heat (Horner, 1984b). Such decayed organic material would be both a source for the abundant carbonate in these paleosols and the bacterial reduction of iron oxides to maintain their gray color. Such fermentation incubation should not necessarily be extended to all dinosaur nests.

A quarry for adult *Hypacrosaurus stebingeri* low on a spur facing the Milk River north of Landslide Butte (NW¼ NE¼ NE¼ S28 T37N R8W Landslide Butte 7.5') had much bone in a Kinakin (liver) paleosol and but little in the overlying Mik (red) paleosol. A Kinakin paleosol in a creek south of the Milk River yielded remains of the ankylosaur *Euoplocephalus* (NE¼

NW¼ SW¼ S27 T37N R8W Landslide Butte 7.5'). Both Mik and Kinakin are similar paleosols with abundant drab-haloed root traces, some subsurface clay accumulation and an horizon of carbonate nodules at about 60 cm from the surface. The purple color characterizing the Kinakin paleosol may reflect an admixture of organic matter and hematite, whereas the red Mik profile was better drained and more highly oxidized. Comparable soils in Mexico today support low deciduous forest (map units Bk8-2bc and Bk7-2bc of F.A.O., 1975b). The 60 cm depth of the carbonate horizon, corrected for 64% compaction due to 3 km overburden estimated from coal ranks or 70% compaction for 2 km measured overburden (Stott et al., 1993a,b), allows calculation of former mean annual rainfall of 625 ± 141 mm or 593 ± 141 mm, or roughly 450–750 mm by either estimate. This is drier than estimated rainfall of the Ainka paleosol of the Morrison Formation, which is much less carbonaceous. These Late Cretaceous soils may have had more effective ground cover extending to drier regions than did soils of the late Jurassic.

The Maksini (carcass) pedotype is named for the articulated tail of the duckbill dinosaur *Prosaurolophus blackfeetensis* found in a quarry within the slopes of a creek draining north from Landslide Butte into the Milk River (NE¼ NW¼ SW¼ S27 T37N R8W Landslide Butte 7.5'). The Maksini paleosol is similar to, but less calcareous and green than the Haltso pedo-

type of the Petrified Forest Formation. Like it, the Maksini pedotype represents streamside communities early in ecological succession from flooding. A steep-walled scour-and-fill structure in this paleosol attests to fluvial erosion.

The Apoyi (brown) paleosol is a very dark brown carbonaceous claystone rich in coalified wood fragments, calcareous nodules and bones of the ceratopsian dinosaur *Styracosaurus* ("Dino Ridge quarry" of Rogers, 1991; SE $\frac{1}{4}$ SE $\frac{1}{4}$ NE $\frac{1}{4}$ S28 T37N R8W Landslide Butte 7.5'). This ancient soil of a swamp (Histosol) lies within a depression within a cross-bedded sandstone that forms the ridge top here. It may have developed by eutrophication of an abandoned meander of a stream. The impure clayey nature of the carbonaceous surface is similar to that in seasonally dry swamps of Louisiana today (Lytle, 1968). The bone assemblage is best explained as a drought kill, because there are very few species but many individuals, including juveniles, represented by bones that are disarticulated, scavenged and little weathered (Rogers, 1990).

The occurrence of duckbills in formerly well drained paleosols (Mik and Kinakin) and ceratopsians in formerly swampy paleosols (Apoyi) is surprising, because duckbills have long been regarded as water-loving creatures (*Edmontosaurus* by E. Kish for Russell, 1977; *Corythosaurus* by E. Kish for Russell, 1989) and ceratopsians compared with bison of the dry plains (*Triceratops* by R. Zallinger for the famous Peabody mural, reproduced by Czerkas and Olson, 1987). The case for aquatic duckbills was made from their occurrence as articulated skeletons in Dinosaur National Park, Alberta (Dodson, 1971), but this place of death by drowning may not have been where the animals lived. The case for dry-land ceratopsians may be traced back to skeletons of *Protoceratops* in supposed desert deposits in Mongolia (Andrews, 1932), but paleosols in the Mongolian deposits are red and clayey and have carbonate nodules at depths comparable to Mik paleosols of the Two Medicine Formation (Jerzykiewicz and Russell, 1991). The implication from paleosols that their habitat preferences were the other way around gains some force from other reconstructions of ceratopsians in swamp environments (*Styracosaurus* by Vladimir Krd reproduced by Currie, 1987; *Chasmosaurus* by G. Paul reproduced by Czerkas and Olson, 1987; *Triceratops* by E. Kish for Russell, 1977) and of duckbills in dry environments (*Edmontosaurus* by E. Kish for Russell, 1989). It will take more occurrences of dinosaur fossils in paleosols to establish statistically their environmental preferences, and it could be that there were both dry land and swamp ceratopsians and duckbills. The bone beds of Landslide Butte also confirm that ceratopsians and duckbills moved in herds (Rogers, 1990), as is apparent from bone beds and trackways elsewhere (Currie, 1987; Lockley, 1991).

The rise of ceratopsians and duckbills parallels the rise in abundance and diversity of angiosperms and decline of conifers in lowland vegetation during the Late Cretaceous (Retallack and Dilcher, 1981a,b; Bakker, 1986; Crane, 1987). The ecological separation of upland tropical saurogods and lowland subtropical to temperate duckbills and ceratopsians can be seen also from the fossil record of trackways (Lockley, 1991). The dominance of Late Cretaceous early-successional and marine-influenced paleosols by angiosperms, but continued regional dominance of palynofloras by conifer pollen, suggests that conifers dominated in upland soils (Retallack and Dilcher, 1981a,b, 1986). This line of thinking supports the contention that angiosperms with their small pollen and seeds, and abbreviated life cycle, may have been encouraged in their spread by the physical disturbance of stream and ocean margins (Retallack and Dilcher, 1981a) and by the diversification of low-browsing duckbill and ceratopsian dinosaurs (Bakker, 1978, 1986). This coevolutionary diversification of angiosperms and ornithischian dinosaurs was still in

full swing at the end of the dinosaur's time on earth, represented by paleosols of the Hell Creek Formation.

HELL CREEK FORMATION

The geologically youngest assemblages of dinosaurs are found in the sombre gray claystones and sandstones of the latest Cretaceous (Maastrichtian) Hell Creek Formation of the Dakotas and Montana (Fig. 9). My observations of its paleosols were mainly in Bug Creek south of Fort Peck and Hell Creek near Jordan, both in Montana (Retallack, 1994a). This is within the area of Blackfeet Indian language (Frantz and Russell, 1989) used to name the pedotypes found. The pedotypes were characterized with type examples from a knoll and nearby badlands cliffs in central Bug Creek, south of Fort Peck, Montana (NW $\frac{1}{4}$ NW $\frac{1}{4}$ NE $\frac{1}{4}$ S15 T22R R43E Bug Creek 7.5'), but they can be recognized widely through Montana and adjacent states.

Many paleosols in the Hell Creek Formation are weakly developed profiles associated with levee facies of streams. They probably represent early successional communities of stream-sides (Retallack, 1994a). These include massive sandstone with root traces of the Spatsiko (sand) pedotype, flaggy siltstones with root traces of the Sapakot pedotype (layer, stack) and gray shales with root traces of the Maka (short, stunted) pedotype. Spatsiko paleosols commonly contain molds and casts of horsetails (*Equisetum* sp.) and their tubers (formerly misidentified as "figs": Shoemaker, 1977). Maka paleosols include a variety of laurlean, platanoid, magnoliid and nymphaealean dicots (Shoemaker, 1966; Johnson and Hickey, 1990). Remains of both *Triceratops horridus* and *Tyrannosaurus rex* have been found in Sapakot, Maka and Spatsiko paleosols, with no clear pattern of preference.

Coal seams are rare in the Hell Creek Formation, and include seat earths and root traces indicating they were paleosols that have been designated the Sik (black, dark) pedotype. Fossil wood, leaves and pollen in these paleosols indicate swamps dominated by taxodiaceous conifers, generally similar to the cypress swamps of Georgia, Florida and Louisiana today (Retallack, 1994a).

Old growth ecosystems of interfluves away from streams and swamps are represented by thick profiles with a silty green surface and clayey gray subsurface horizon, called the Otssko (green, blue) pedotype. This and its large woody root traces are evidence that it supported woodland. A fossil plant locality in North Dakota may represent the vegetation of this pedotype, including ginkgos and sabiacean(?) and platanoid dicots (Retallack, 1994a). The smectite clays and weakly calcareous nature of Otssko paleosols are comparable to soils forming under a mean annual rainfall of 900–1200 mm. The conundrum of drab color yet deeply penetrating root traces, and the common fossil charcoal in these paleosols indicate a seasonally dry climate, like that of northern Florida today (Retallack, 1994a). Climate was even drier to the west within the rain shadow of the Rocky Mountains, as indicated by calcareous red paleosols of latest Cretaceous age in Texas (Lehman, 1989, 1990), New Mexico (Buck and Mack, 1995) and Alberta (Jerzykiewicz and Sweet, 1988).

Data from paleosols allows reassessment of prior reconstructions of the dinosaurs of the Hell Creek Formation. Widely reproduced murals by Charles Knight for the Field Museum in Chicago (Czerkas and Glut, 1982) and by Rudolph Zallinger for the Peabody Museum at Yale University (Czerkas and Olson, 1987) both depict an open landscape comparable to the wooded grasslands or "savanna" of East Africa. Such an environment would produce distinctive soils (Mollisols: paleosol examples described by Retallack, 1991b), not found in the Hell Creek Formation. Equally unlikely are reconstructions of "fern savan-

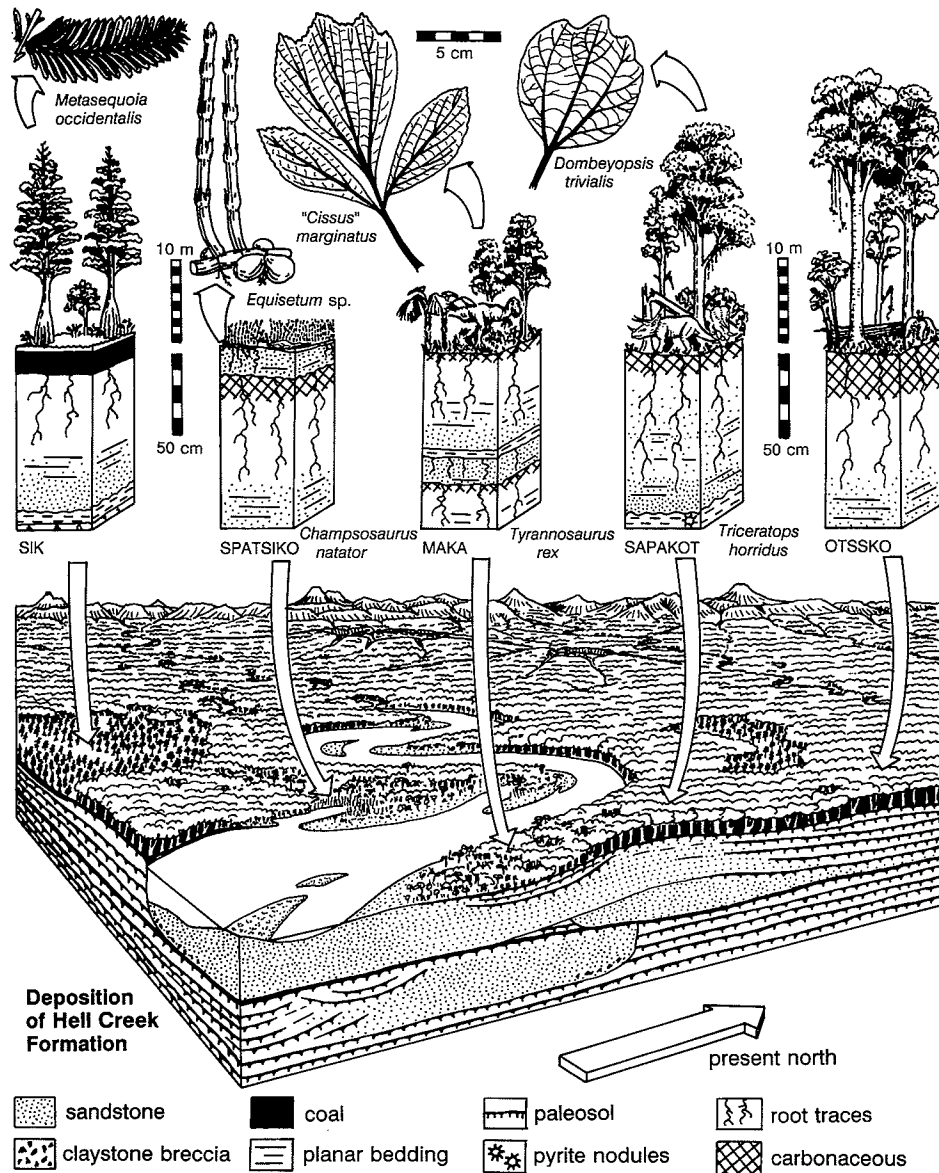


FIGURE 9—A reconstruction of soils and vegetation during Late Cretaceous (Maastrichtian) deposition of the Hell Creek Formation in eastern Montana (reprinted with permission from the Bulletin of the Geological Society of America).

nas" (Coe et al., 1987), angiosperm shrublands (Crane, 1987) or aridlands like the Kimberley region of northwestern Australia (Rigby, 1987), which would produce a suite of soils (Inceptisols and Vertisols) unlike those of the Hell Creek Formation. "Fern savannas" also have been proposed for the Late Cretaceous on the basis of a fossil plant assemblage in growth position buried by volcanic ash (Wing et al., 1993), but until the paleosol at this locality has been studied it will remain unclear whether this was an ephemeral early successional or old growth community. Also unlikely is rain forest with buttressed tree trunks like those shown by Van Valen and Sloan (1977), which grow in more deeply weathered soils (Ultisols and Oxisols) unlike those of the Hell Creek Formation (Alfisols). This latest Cretaceous landscape probably supported tropical woodlands similar to those shown by Eleanor Kish (for Russell, 1989), with local cypress swamps, also reconstructed by Eleanor Kish (for Russell, 1977).

The exceptional fossil record of dinosaurs in the Hell Creek and Lance Formations makes them the best formations in the

world to study dinosaur extinction. Massive recent collections including fossil footprints and bones have shown that dinosaurs became extinct abruptly at the top of the Hell Creek Formation (Lockley, 1991; Sheehan et al., 1991). Prior claims that they dwindled in abundance and diversity for some time before the boundary (Sloan et al., 1986), are more likely artifacts of the odds of finding such generally rare fossils near the end of their stratigraphic range (Signor and Lipps, 1982) and of the weakly calcareous nature of paleosols near the top of the Hell Creek Formation (Retallack et al., 1987). The idea that dinosaurs survived into the Paleocene (Rigby et al., 1987) reflects resorting of bone into paleochannels (Lofgren et al., 1990). This abrupt disappearance of the dinosaurs at the end of the Cretaceous is particularly striking because paleosols across the Cretaceous-Tertiary boundary confirm prior statistical estimates that this sequence in Montana does not include long breaks in sedimentation. Furthermore, paleosols below and above the boundary are not strikingly different (gleyed Alfisols, Inceptisols, Entisols and

Histosols). They reflect an unremarkable facies shift from a swamp-poor to swamp-dominated landscape, rather than a major long term environmental change that could explain such a major extinction (Retallack, 1994a).

These indications of catastrophic extinction on time scales of less than 10 Ka are compatible with theories relating the extinction of the dinosaurs to environmental effects attendant on impact of a large (10 km) asteroid in Yucatan, central America (Alvarez et al., 1995). Potential kill mechanisms include cooling, darkness and acid rain. There have been claims for frost damage of latest Cretaceous fossil leaves (Wolfe, 1991), but I have seen no frost heave structures in latest Cretaceous paleosols. Darkening of the sky with dust and cooling may be indicated by the preferential extinction of evergreen rather than deciduous fossil plants (Johnson and Hickey, 1990), but the paleosol record has remained mute on this subject also. Acid rain on the other hand should leave a record in paleosols because strong acids such as nitric acid from shocking of the atmosphere and sulfuric acid from vaporization of target evaporites should exaggerate the natural weathering by weak acids of alkali and alkaline earth cations from paleosols. My calculations of cation depletion of Cretaceous and Paleocene paleosols of Bug Creek revealed no outstanding acidification of paleosols, but the boundary bed at Brownie Butte is exceptionally leached, and compatible with reaction with strong acid. The thin (2 cm) kaolinitic microspherulitic boundary bed was at first interpreted as a weakly developed paleosol (Fastovsky et al., 1989), but the supposed root traces are now interpreted as plant stalks (Alvarez et al., 1995). Silicate ejecta from the Yucatan impact may have scrubbed the atmosphere of much impact-generated acid. Shocked quartz and smectitic, iridium-bearing clays of the overlying impact layer which arrived only hours later show less marked acid leaching (Retallack, 1996a). The effect of acid rain in Montana was also mitigated by smectitic and calcareous soils and groundwater (Retallack, 1994a). The survival there of fish and amphibians, but extinction of many molluscs indicates pH depression of groundwater to less than 5.5 but no less than 4 (Weil, 1994). Acid rain would also brown vegetation, leading to extinction of large dinosaur herbivores and their predators. Among mammals, insectivores and detritivores survived preferentially (Sheehan and Hansen, 1986; Sheehan and Fastovsky, 1992), as would be expected from acid induced interruption of primary productivity. In humid, carbonate-poor landscapes with less buffering capability than the subhumid floodplains of Montana, the effect of acid rain may have been completely devastating, rather than an agent of selective extinction.

CONCLUSIONS

This preliminary account of the kinds of paleosols containing dinosaurs has introduced a number of topics that could benefit from continued research of the kind outlined here.

Dawn of Dinosaurs.—The earliest known Triassic dinosaurs were small cursorial theropods living within forested landscapes represented by deeply-rooted clayey paleosols (Alfisols). These agile carnivores may have been drawn to the insects, mammals and other small animals supported by these complex forest communities.

Sauropod Soils.—Prosauropods and large sauropods such as *Camarasaurus* and *Apatosaurus* were probably not aquatic, but lived in open woodlands of dry, dusty soils now represented by red, weakly-clayey and strongly-calcareous paleosols (Aridisols, calcic Alfisols). They appeared in dry tropical uplands during the latest Triassic following the demise of therapsids and their carbonaceous humid broadleaf forested paleosols. Sauropods maintain their dominance in such paleosols of low-productivity, conifer woodland from Jurassic to Late Cretaceous. By Late

Cretaceous time, there were also faunas dominated by ceratopsian and duckbill dinosaurs within carbonaceous lowland paleosols that supported broadleaf angiosperm woodland.

Dusty Duckbills.—Duckbill dinosaurs such as *Hypacrosaurus* and *Maiasaura* nested in soils (calcic Inceptisols) of seasonally well-drained lowlands in dry climates. Thus not all duckbill dinosaurs were aquatic. The spread of angiosperms with their weedy reproductive cycle may have been encouraged by the rise of destructive herds of low browsing duckbills and dramatic sea-level changes of the Cretaceous.

Soggy Ceratopsians.—Some ceratopsians such as *Styracosaurus* lived in swamps (Histosols), rather than dry plains (Alfisols, Inceptisols). Their preservation in large numbers of single species in such paleosols supports other indications that these creatures moved in herds.

Dinosaur Demise.—The extinction of dinosaurs at the end of the Cretaceous is not associated with dramatic long-term changes of environment, thus favoring short term catastrophic events in their demise. Similar suites of paleosols (gleyed Alfisols, Inceptisols, Entisols and Histosols) are found in both latest Cretaceous and earliest Tertiary sediments of Montana. Acid rain as a consequence of impact shocking of the atmosphere and vaporization of evaporites provides a mechanism for selective extinction of these large creatures and is indicated by short-term leaching of the Cretaceous-Tertiary boundary bed. Its potentially even more catastrophic effect may have been buffered by reaction with silicate ejecta during ballistic transit and by calcareous, smectitic floodplain soils after arrival in Montana.

ACKNOWLEDGMENTS

I thank Don Wolberg and Ed stump for inviting me to participate in Dinofest. John Horner graciously showed me over his Landslide Butte localities in Montana in 1987. Bob Sloan generously provide unpublished information and allowed use of his sieves in the Bug Creek area of Montana, where research was funded in part by NSF grant EAR9103178. Gregory Paul, Guy Leahy, David Archibald and Jack Horner offered useful discussions.

REFERENCES

- ALVAREZ, W., P. CLAEYS, AND S. W. KIEFFER. 1995. Emplacement of the Cretaceous Tertiary boundary shocked quartz from Chicxulub Crater. *Science*, 269:930–935.
- ANDREWS, R. C. 1932. The new conquest of Asia. *American Museum of Natural History*, New York, 687 p.
- ARCHANGELSKY, S. 1968. Studies on Triassic fossil plants from Argentina. II The leaf genus *Dicroidium* and its possible relation to *Rhexoxylon* stems. *Palaeontology*, 11:500–512.
- ASH, S. R. 1970. *Dinophyton*, a problematical new plant genus from the Upper Triassic of southwestern United States. *Palaeontology* 13: 646–663.
- . 1972. Plant megafossils of the Chinle Formation, p. 23–41. In C. S. Breed, and W. J. Breed (eds.), *Investigations in the Triassic Chinle Formation*. *Bulletin of the Museum of Northern Arizona*, 47.
- , AND G. T. CREBER. 1992. Palaeoclimatic interpretation of the wood structures of the trees in the Chinle Formation (Upper Triassic), Petrified Forest National Park, Arizona, U.S.A. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 96:299–317.
- BAKKER, R. T. 1971. Ecology of the brontosaurus. *Nature* 229:172–174.
- . 1978. Dinosaur feeding behavior and the origin of flowering plants. *Nature*, 274:661–663.
- . 1986. *The dinosaur heresies*. William Morrow, New York, 481 p.
- BEADLE, N. C. W. 1981. *The vegetation of Australia*. Cambridge University Press, London, 690 p.
- BENTON, M. J. 1983. Dinosaur success in the Triassic: a non-competitive ecological model. *Quarterly Review of Biology*, 58:27–55.
- BLAKEY, R. C., AND R. GUBITOSA. 1983. Late Triassic paleogeography and depositional history of the Chinle Formation, southern Utah and northern Arizona, p. 57–76. In M. W. Reynolds, and E. D. Dolly

- (eds.), Mesozoic paleogeography of the west-central United States. Rocky Mountain Section, Society of Economic Paleontologists and Mineralogists, Denver.
- BLODGETT, R. H. 1988. Calcareous paleosols in the Triassic Dolores Formation, southwestern Colorado, p. 103–121. In J. Reinhardt, and W. R. Sigleo (eds.), Paleosols and weathering through geologic time: principles and applications. Special Paper of the Geological Society of America, 216.
- BONAPARTE, J. F. 1982. Faunal replacement in the Triassic of South America. *Journal of Vertebrate Paleontology*, 2:362–371.
- BOWN, T. M., AND M. J. KRAUS. 1993a. Soils, time and primate paleoenvironments. *Evolutionary Anthropology*, 2:11–21.
- , AND ———. 1993b. Time-stratigraphic reconstruction and integration of paleopedologic, sedimentologic and biotic events (Willwood Formation, Lower Eocene, northwest Wyoming, U.S.A.). *Palaios*, 8:68–80.
- BRENNER, R. L. 1983. Late Jurassic tectonic setting and paleogeography of western Interior, North America, p. 119–132. In M. W. Reynolds, and E. D. Dolly (eds.), Mesozoic paleogeography of the west-central United States. Rocky Mountain Section, Society of Economic Paleontologists and Mineralogists, Denver.
- BUCK, B. J., AND G. H. MACK. 1995. Latest Cretaceous (Maastrichtian) aridity indicated by paleosols in the McRae Formation, southcentral New Mexico. *Cretaceous Research*, 16:559–572.
- CAMP, C. L., AND S. P. WELLES. 1956. Triassic dicynodont reptiles. Part 1. The North American genus *Placerias*. *Memoir of the University of California*, 13:255–341.
- CARPENTER, K., K. F. HIRSCH, AND J. R. HORNER. 1994. Introduction, p. 1–11. In K. Carpenter, K. F. Hirsch, and J. R. Horner (eds.), *Dinosaur eggs and babies*. Cambridge University Press, New York.
- CHIN, K., AND B. D. GILL. 1996. Dinosaurs, dung beetles and conifers: participants in a Cretaceous food web. *Palaios*, 11:280–285.
- COE, M. J., D. L. DILCHER, J. O. FARLOW, D. M. JARZEN, AND D. A. RUSSELL. 1987. Dinosaurs and land plants, p. 225–258. In E. M. Friis, W. G. Chaloner, and P. R. Crane (eds.), *The origins of angiosperms and their biological consequences*. Cambridge University Press, New York.
- COLBERT, E. H. 1995. *The little dinosaurs of Ghost Ranch*. Columbia University Press, New York, 247 p.
- , A. J. CHARIG, P. DODSON, D. D. GILLETTE, AND J. H. OSTROM. 1992. Case 2840. "*Coelurus*" *bauri* (Cope 1887) (currently *Coelophys* *bauri*: Reptilia, Saurischia): proposed replacement of the lectotype by a neotype. *Bulletin of Zoological Nomenclature*, 49:276–279.
- COOMBS, W. P. 1975. Sauropod habits and habitats. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 17:1–33.
- CHARIG, A. J. 1984. Competition between therapsids and archosaurs during the Triassic period: a review and synthesis of current theories. *Symposium of the Zoological Society of London*, 52:597–628.
- CHURE, D., C. TURNER, AND F. PETERSON. 1994. An embryo of *Campitosaurus* from the Morrison Formation (Jurassic, Middle Tithonian) in Dinosaur National Monument, p. 298–311. In K. Carpenter, K. F. Hirsch, and J. R. Horner (eds.), *Dinosaur eggs and babies*. Cambridge University Press, New York.
- CRABTREE, D. R. 1987. Angiosperms of the northern Rocky Mountains: Albian to Campanian (Cretaceous) megafossil floras: *Annals of the Missouri Botanical Garden* 74:707–747.
- CRANE, P. R. 1987. Vegetational consequences of the angiosperm diversification, p. 107–144. In E. M. Friis, W. G. Chaloner, and P. R. Crane (eds.), *The origins of angiosperms and their biological consequences*. Cambridge University Press, New York.
- CURRIE, P. J. 1987. New approaches to studying dinosaurs in Dinosaur Provincial Park, p. 101–117. In S. J. Czerkas, and E. C. Olson (eds.), *Dinosaurs past and present*, v. 2. University of Washington Press, Seattle.
- CZERKAS, S. A. 1987. A reevaluation of the plate arrangement on *Stegosaurus stenops*, p. 82–99. In S. J. Czerkas, and E. C. Olson (eds.), *Dinosaurs past and present*, vol. II. University of Washington Press, Seattle.
- , AND D. F. GLUT. 1982. Dinosaurs, mammoths and cavemen: The art of Charles R. Knight. New York, E.P. Dutton, 119 p.
- , AND E. C. OLSON (EDS). 1987. *Dinosaurs past and present*, vols. I & II. University of Washington Press, Seattle, 161 and 149 p.
- DAUGHERTY, L. H. 1941. The Upper Triassic flora of Arizona. Carnegie Institution of Washington Publication, 526:108.
- DEER, M. E. 1974. Sedimentary structures and depositional environments of paleochannels in the Jurassic Morrison Formation near Green River, Utah. *Brigham Young University Geology Studies*, 21(3):3–39.
- DODSON, P. 1971. Sedimentology and taphonomy of the Oldman Formation (Campanian), Dinosaur Provincial Park, Alberta (Canada). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 10:21–74.
- DODSON, P., A. K. BEHRENSMEYER, R. T. BAKKER, AND J. S. MCINTOSH. 1980. Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation. *Paleobiology*, 6:208–232.
- DUBIEL, R. T., J. T. PARRISH, J. M. PARRISH, AND S. C. GOOD. 1991. The Pangean megamonsoon—evidence from the Upper Triassic Chinle Formation, Colorado Plateau. *Palaios*, 6:347–370.
- EATON, T. H. 1960. A new armored dinosaur from the Cretaceous of Kansas. *Contributions to Paleontology of the University of Kansas*, 8:1–24.
- FA.O. (FOOD AND AGRICULTURE ORGANIZATION). 1971. Soil map of the world. Vol. IV. South America. U.N.E.S.C.O. Paris, 193 p.
- . 1975a. Soil map of the world. Vol. II. North America. U.N.E.S.C.O. Paris, 210 p.
- . 1975b. Soil map of the world. Vol. III. Mexico and central America. U.N.E.S.C.O. Paris, 96 p.
- . 1978a. Soil map of the world. Vol. VIII. North and Central Asia. U.N.E.S.C.O. Paris, 165 p.
- . 1978b. Soil map of the world. Vol. X. Australasia. U.N.E.S.C.O. Paris, 221 p.
- FARLOW, J. O., P. DODSON, AND A. CHINSAMY. 1995. Dinosaur biology. *Annual Review of Ecology and Systematics*, 26:445–471.
- FASTOVSKY, D. E., K. MCSWEENEY, AND L. D. NORTON. 1989. Pedogenic development at the Cretaceous-Tertiary boundary, Garfield County, Montana. *Journal of Sedimentary Petrology*, 59:758–767.
- FIORILLO, A. R., AND K. PADIAN. 1993. Taphonomy of the Late Triassic *Placerias* Quarry (Petrified Forest Member, Chinle Formation) of eastern Arizona, p. 133–134. In S. G. Lucas, and M. Morales (eds.), *The non-marine Triassic*. *Bulletin of the New Mexico Museum of Natural History and Science*, 3.
- FIRTH, H. J. 1962. The mallee fowl. Angus and Robertson, Sydney, 231 p.
- FOUCH, J. D., T. F. LAWTON, D. J. NICHOLS, W. B. CASHION, AND W. A. COBBAN. 1983. Patterns and timing of synorogenic sedimentation in Upper Cretaceous rocks of central and northeast Utah, p. 305–336. In M. W. Reynolds, and E. D. Dolly (eds.), *Mesozoic paleogeography of the west central United States*. Society of Economic Paleontologists and Mineralogists, Rocky Mountain Section, Denver, v. 2.
- FRANTZ, D. G., AND N. J. RUSSELL. 1989. *Blackfoot dictionary of stems, roots and affixes*. University of Toronto Press, Toronto, 470 p.
- FRENGUELLI, J. 1948. Estratigrafia y edad del llamado retico en la Argentina. *Gaea*, 8:159–309.
- GILLETTE, D. D. 1987. The age of transition: *Coelophys* and the Late Triassic Chinle fauna, p. 132–152. In S. J. Czerkas, and E. C. Olson (eds.), *Dinosaurs past and present*, vol. 1. University of Washington Press, Seattle.
- GOOD, S. C. 1989. Non-marine mollusca in the upper Triassic Chinle Formation and related strata of the western Interior: systematics and distribution, p. 233–248. In S. G. Lucas, and A. P. Hunt (eds.), *Dawn of the age of dinosaurs in the American Southwest*. New Mexico Museum of Natural History and Science, Albuquerque.
- GOTTESFELD, A. S. 1972. Paleoecology of the lower part of the Chinle Formation in the Petrified Forest, p. 59–73. In C. S. Breed, and W. J. Breed (eds.), *Investigations in the Triassic Chinle Formation*. *Bulletin of the Museum of Northern Arizona*, 47.
- HALLETT, M. 1987. Bringing dinosaurs to life, p. 97–113. In S. J. Czerkas, and E. C. Olson (eds.), *Dinosaurs past and present*, v. 1. Washington University Press, Seattle.
- HASIOTIS, S. T., AND R. F. DUBIEL. 1993. Trace fossil assemblages in Chinle Formation alluvial deposits at the tepees, Petrified Forest National Park, Arizona, p. G42–G43. In S. G. Lucas, and M. Morales (eds.), *The non-marine Triassic*. *Bulletin of the New Mexico Museum of Natural History and Science*, 3.
- , AND ———. 1995. Termite (Insecta: Isoptera) nest ichnofos-

- sils from the Upper Triassic Chinle Formation, Petrified Forest National Park, Arizona. *Ichnos*, 4:119–130.
- HINTZE, L. F. 1988. Geologic history of Utah. Brigham Young University, Special Publication, 7, 202 p.
- HORNER, J. R. 1979. Nest of juveniles provide evidence of family structure among dinosaurs. *Nature*, 282:296–298.
- . 1984a. Three ecologically distinct vertebrate faunal communities from the Late Cretaceous Two Medicine Formation of Montana, with discussion of evolutionary pressures induced by Interior Seaway fluctuations. Field Conference of the Montana Geological Society, 1984:299–303.
- . 1984b. The nesting behavior of dinosaurs. *Scientific American*, 250(4):130–137.
- . 1987. Ecological and behavioral implications from a dinosaur nesting site, p. 51–83. In S. J. Czerkas, and E. C. Olson (eds.), *Dinosaurs past and present*, v. 2. University of Washington Press, Seattle.
- . 1989. The Mesozoic terrestrial ecosystems of Montana. Field Conference of the Montana Geological Society, 1989:153–162.
- . 1992. Cranial morphology of *Prosaurolophus* (Ornithischia: Hadrosauridae), with descriptions of two new hadrosaurid species and an evaluation of hadrosaurid phylogenetic relationships. *Occasional paper of the Museum of the Rockies*, 2:119.
- . 1994. Comparative taphonomy of some dinosaur and extant bird colonial nesting grounds p. 116–123. In K. Carpenter, K. F. Hirsch, and J. R. Horner (eds.), *Dinosaur eggs and babies*. Cambridge University Press, New York.
- , AND P. J. CURRIE. 1994. Embryonic and neonatal morphology and ontogeny of a new species of *Hypacrosaurus* Ornithischia, Lambeosauridae from Montana and Alberta, p. 312–336. In K. Carpenter, K. F. Hirsch, and J. R. Horner (eds.), *Dinosaur eggs and babies*. Cambridge University Press, New York.
- , AND R. MAKELA. 1979. Nest of juveniles provides evidence of family structure among dinosaurs. *Nature* 282:296–298.
- HUNT, A. P. 1993. Taxonomy of phytosaurs (Reptilia: Archosauria) from the Blue Mesa Member of the Petrified Forest Formation Petrified Forest National Park, northeastern Arizona, p. G44–G45. In S. G. Lucas, and M. Morales (eds.), *The non-marine Triassic*. Bulletin of the New Mexico Museum of Natural History and Science, 3.
- , AND S. G. LUCAS. 1993. Comments on a proposed neotype for *Coelophysis bauri* (Cope 1887) (Reptilia, Saurischia) Case 2840. *Bulletin of Zoological Nomenclature*, 50:147–150.
- , AND ———. 1994. Ornithischian dinosaurs from the upper Triassic of the United States, p. 227–241. In N. C. Fraser, and H.-D. Sues (eds.), *In the Shadow of Dinosaurs*. Cambridge University Press, Cambridge.
- JACOBS, L. L., AND P. A. MURRY. 1980. The vertebrate community of the Triassic Chinle Formation, near St. Johns, Arizona, p. 55–72. In L. L. Jacobs (ed.), *Aspects of vertebrate history: essays in honor of Edwin Harris Colbert*. Museum of Northern Arizona Press, Flagstaff.
- JERZYKIEWICZ, T., AND D. B. RUSSELL. 1991. Late Mesozoic stratigraphy and vertebrates of the Gobi Desert. *Cretaceous Research*, 12:345–377.
- , AND A. R. SWEET. 1988. Sedimentological and palynological evidence of regional climatic changes in the Campanian to Paleocene sediments of the Rocky Mountains, Canada. *Sedimentary Geology*, 59:29–76.
- JOHNSON, K. R., AND L. J. HICKEY. 1990. Megafloal change across the Cretaceous-Tertiary boundary in the northern Great Plains and Rocky Mountains, U.S.A., p. 433–444. In V. L. Sharpton, and P. D. Ward, (eds.), *Global catastrophes in earth history*. Special Publication of the Geological Society of America, 247.
- KAYE, F. T., AND K. PADIAN. 1994. Microvertebrates from the *Placerias* quarry: a window on Late Triassic vertebrate diversity in the American Southwest. In N. C. Fraser, and H.-D. Sues (eds.), *In the shadow of the dinosaurs*, p. 171–196. Cambridge University Press, Cambridge.
- KENNEDY, W. J. 1978. Cretaceous. In W. S. McKerrrow (ed.), *The ecology of fossils*, p. 280–322. M.I.T. Press, Cambridge, Massachusetts.
- KIETZKE, K. 1989. Calcareous microfossils from the Triassic of the southwestern United States, p. 223–232. In S. G. Lucas, and A. P. Hunt (eds.), *Dawn of the age of dinosaurs in the American Southwest*. New Mexico Museum of Natural History and Science, Albuquerque.
- KITCHING, J. W. 1979. Preliminary report on a clutch of six dinosaurian eggs from the Upper Triassic Elliot Formation, northern Orange Free State. *Palaeontographica africana*, 22:41–45.
- KRAUS, M. J., AND L. T. MIDDLETON. 1987. Dissected paleotopography and base-level changes in a Triassic fluvial sequence. *Geology*, 15:18–21.
- LABANDEIRA, C. C., AND J. J. SEPKOSKI. 1993. Insect diversity in the fossil record. *Science*, 261:310–315.
- LEHMAN, T. H. 1989. Upper Cretaceous (Maastrichtian) paleosols in Trans-Pecos Texas. *Bulletin of the Geological Society of America*, 101:188–203.
- . 1990. Paleosols and the Cretaceous/Tertiary transition in the Big Bend region of Texas. *Geology*, 18:362–364.
- LITWIN, R. J., AND S. R. ASH. 1991. First early Mesozoic amber in the western hemisphere. *Geology*, 19:273–276.
- LOCKLEY, M. 1991. *Tracking dinosaurs*. Cambridge University Press, Cambridge, 238 p.
- LOFGREN, D. L., C. L. HUTTON, AND A. C. RUNKEL. 1990. Reworking of Cretaceous dinosaurs into Paleocene stream deposits, upper Hell Creek Formation, Montana. *Geology*, 18:874–877.
- LUCAS, S. G. 1993. The Upper Triassic Chinle Group, western United States, p. G2–G4. In S. G. Lucas, and M. Morales (eds.), *The non-marine Triassic*. Bulletin of the New Mexico Museum of Natural History and Science, 3.
- , AND A. P. HUNT. 1993a. A dicynodont from the upper Triassic of New Mexico and its biochronologic significance, p. 321–325. In S. G. Lucas, and M. Morales (eds.), *The non-marine Triassic*. Bulletin of the New Mexico Museum of Natural History and Science, 3.
- , AND ———. 1993b. Tetrapod biochronology of the Chinle Group (Upper Triassic), western United States, p. 327–329. In S. G. Lucas, and M. Morales (eds.), *The non-marine Triassic*. Bulletin of the New Mexico Museum of Natural History and Science, 3.
- , AND ———. 1993c. Field guide to nonmarine Triassic strata of the southern Colorado Plateau, New Mexico and Arizona, p. G1–G58. In S. G. Lucas, and M. Morales (eds.), *The non-marine Triassic*. Bulletin of the New Mexico Museum of Natural History and Science, 3.
- , AND ———. 1994. The chronology and paleobiogeography of mammalian origins, p. 335–351. In N. C. Fraser, and H.-D. Sues (eds.), *In the shadow of dinosaurs*. Cambridge University Press, Cambridge.
- LYTLE, S. A. 1968. The morphological characteristics and relief relationships of representative soils in Louisiana. *Bulletin of the Louisiana Agricultural Experiment Station*, 631:31.
- MILLER, C. N. 1968. The lepidophytic affinities of the genus *Chinlea* and *Osmundites walkeri*. *American Journal of Botany*, 55:109–115.
- . 1987. Land plants of the northern Rocky Mountains before the appearance of flowering plants. *Annals of the Missouri Botanical Garden* 74:692–706.
- MILLER, W. R. 1972. *Neuwe natekwinappheh: Shoshoni stories and dictionary*. University of Utah Anthropological Papers, 94: 172.
- MOBERLY, R. 1960. Morrison, Cloverly, and Sykes Mountain formations, northern Bighorn Basin, Wyoming and Montana. *Bulletin of the Geological Society of America*, 71:1137–1176.
- MOOK, C. C. 1916. Study of the Morrison Formation. *Annals of the New York Academy of Sciences*, 27:39–191.
- MURRY, P. A., AND R. A. LONG. 1989. Geology and paleontology of the Chinle Formation, Petrified Forest National Park and vicinity, Arizona, and a discussion of vertebrate fossils of the southwestern Upper Triassic, p. 29–64. In S. G. Lucas, and A. P. Hunt (eds.), *Dawn of the age of dinosaurs in the American Southwest*. New Mexico Museum of Natural History, Albuquerque.
- OLSEN, P. E., profiled by C. ZIMMER. 1993. The war between animals and plants. *Discover*, 14:16–17.
- OSTROM, J. H., AND J. S. MCINTOSH. 1966. *Marsh's dinosaurs*. Yale University Press, New Haven, 388 p.
- PADIAN, K. 1986. On the type material of *Coelophysis* Cope (Saurischia: Theropoda), and a new specimen from the Petrified Forest of Arizona (Late Triassic: Chinle Formation), p. 45–60. In K. Padian (ed.), *The beginning of the age of dinosaurs*. Cambridge University Press, Cambridge.
- PARRISH, J. M. 1993. Distribution and taxonomic composition of fossil vertebrate accumulations in the Upper Triassic Chinle Formation, Petrified Forest National Park, p. 393–396. In S. G. Lucas, and M. Mo-

- rales (eds.), The non-marine Triassic. Bulletin of the New Mexico Museum of Natural History and Science, 3.
- PAUL, G. S. 1987. The science and art of restoring the life appearance of dinosaurs and their relatives: a rigorous how-to guide, p. 4–49. In S. J. Czerkas, and E. C. Olson (eds.), Dinosaurs past and present, v. 2. University of Washington Press, Seattle.
- . 1993. Are *Syntarsus* and the Whitaker Quarry theropod the same genus?, p. 397–402. In S. G. Lucas, and M. Morales (eds.), The non-marine Triassic. Bulletin of the New Mexico Museum of Natural History and Science, 3.
- . 1994. Thermal environments of dinosaur nestlings: implications for endothermy and insulation, p. 279–287. In K. Carpenter, K. F. Hirsch, and J. R. Horner (eds.), Dinosaur eggs and babies. Cambridge University Press, New York.
- , AND G. D. LEAHY. 1994. Terramegathery in the time of the dinosaurs: restoring the metabolics of colossal dinosaurs, p. 177–198. In G. D. Rosenburg, and D. L. Wolberg (eds.), Dinofest. Special Publications of the Paleontological Society, 7.
- PETERSEN, F. AND C. TURNER-PETERSEN. 1987. The Morrison Formation of the Colorado Plateau: recent advances in sedimentology, stratigraphy, and paleotectonics. *Hunteria*, 2(1):1–18.
- PIGG, K. B., W. C. DAVIS, AND S. ASH. 1993. A new permineralized Upper Triassic flora from Petrified Forest National Park, Arizona: a preliminary report, p. 411–413. In S. G. Lucas, and M. Morales (eds.), The non-marine Triassic. Bulletin of the New Mexico Museum of Natural History and Science, 3.
- RETALLACK, G. J. 1984. Completeness of the rock and fossil record: estimates using fossil soils. *Paleobiology*, 10:59–78.
- . 1986. Fossil soils as grounds for interpreting long term controls on ancient rivers. *Journal of Sedimentary Petrology*, 56:1–18.
- . 1990. Soils of the past. Unwin-Hyman, London, 520 p.
- . 1991a. Untangling the effects of burial alteration and ancient soil formation. *Annual Review of Earth and Planetary Sciences*, 19: 183–206.
- . 1991b. Miocene paleosols and ape habitats of Pakistan and Kenya. Oxford University Press, Oxford, 346 p.
- . 1994a. A pedotype approach to latest Cretaceous and earliest Tertiary paleosols in eastern Montana. *Bulletin of the Geological Society of America*, 106:1377–1397.
- . 1994b. The environmental factor approach to the interpretation of paleosols, p. 31–64. In R. Amundson, J. Harden, and M. Singer (eds.), Factors of soil formation: a fiftieth anniversary perspective. Special Publication of the Soil Science Society of America, 33.
- . 1995. Paleosols of the Siwalik Group as a 15 Ma record of South Asian paleoclimate, p. 36–51. In S. Wadia, R. Korisettar, and V. S. Kale (eds.), Quaternary environments and geoarchaeology of India: essays in honour of S.N. Rajaguru. Memoir of the Geological Society of India, 32.
- . 1996a. Acid trauma at the Cretaceous-Tertiary boundary in eastern Montana. *GSA Today*, 6(5):1–7.
- . 1996b. Early Triassic therapsid foot prints from the Sydney Basin, Australia. *Alcheringa*, 20:301–314.
- . 1997. Earliest Triassic origin of *Isoetes* and quillwort adaptive radiation. *Journal of Paleontology* (in press).
- , AND D. L. DILCHER. 1981a. A coastal hypothesis for the dispersal and rise to dominance of flowering plants, v. 2, p. 27–77. In K. J. Niklas (ed.), Paleobotany, paleoecology and evolution. Praeger, New York.
- , AND ———. 1981b. Early angiosperm reproduction: *Prisca reynoldsii* gen. et sp. nov. from mid-Cretaceous coastal deposits in Kansas, U.S.A. *Palaeontographica*, B179:103–137.
- , AND ———. 1986. Cretaceous angiosperm invasion of North America. *Cretaceous Research*, 7:227–252.
- , AND ———. 1988. Reconstructions of selected seed ferns. *Annals of the Missouri Botanical Garden*, 75:1010–1057.
- , AND J. GERMÁN-HEINS. 1994. Evidence from paleosols for the geological antiquity of rain forest. *Science*, 265:499–502.
- , G. D. LEAHY, AND M. D. SPOON. 1987. Evidence from paleosols for ecosystem changes across the Cretaceous-Tertiary boundary in eastern Montana. *Geology*, 15:1090–1093.
- RICH, P. V., AND T. H. RICH. 1993. Wildlife of Gondwana. Reed, Chatsworth (Australia), 276 p.
- RIGBY, J. K. 1987. The last of the North American dinosaurs, p. 118–135. In S. J. Czerkas, and E. C. Olson (eds.), Dinosaurs past and present, vol. II. University of Washington Press, Seattle.
- RIGBY, J. K. JR., K. R. NEWMAN, J. SMIT, S. VAN DER KAARS, R. E. SLOAN, AND J. K. RIGBY, SR. 1987. Dinosaurs from the Paleocene part of the Hell Creek Formation, McCone County, Montana. *Palaios*, 2:296–302.
- RIGGS, E. S. 1903. Structure and relationships of opisthocoelian dinosaurs. Part I. *Apatosaurus*. *Field Columbian Museum Geology*, 2: 165–196.
- RIGGS, N. R., T. R. LEHMAN, G. E. GEHRELS, AND W. R. DICKINSON. 1996. Detrital zircon link between headwaters and terminus of the Upper Triassic Chinle-Dockum paleoriver system. *Science*, 273:97–100.
- ROGERS, R. R. 1990. Taphonomy of three dinosaur bone beds in the Upper Cretaceous Two Medicine Formation of northwestern Montana: evidence for drought-related mortality. *Palaios*, 5:394–413.
- , C. C. SWISHER, P. C. SERENO, A. M. MONETTA, C. A. FORSLER, AND R. C. MARTINEZ. 1993. The Ischigualasto tetrapod assemblage (Late Triassic, Argentina) and ⁴⁰Ar/³⁹Ar dating of dinosaur origins. *Science*, 260:794–797.
- RUSSELL, D. A. 1977. A vanished world: the dinosaurs of western Canada. National Museum of Natural Sciences, Ottawa, 142 p.
- . 1989. The dinosaurs of North America. University of Toronto Press, Toronto, 240 p.
- SCCLATER, J. G., AND P. A. F. CHRISTIE. 1980. Continental stretching: an explanation for the post-mid-Cretaceous subsidence of the North Sea Basin. *Journal of Geophysical Research*, 85:3711–3739.
- SCHWARTZ, H. L., AND D. GILLETTE. 1994. Geology and taphonomy of the *Coelophysis* quarry, Upper Triassic Chinle Formation. *Journal of Paleontology* 68:1118–30.
- SERENO, P. C., C. A. FORSTER, R. R. ROGERS, AND A. M. MONETTA. 1993. Primitive dinosaur skeleton from Argentina and the early evolution of dinosaurs. *Nature*, 361:64–66.
- , AND F. E. NOVAS. 1992. The complete skull and skeleton of an early dinosaur. *Science* 258:1137–1140.
- SHEEHAN, P. M., AND D. E. FASTOVSKY. 1992. Major extinctions of land-dwelling vertebrates at the Cretaceous-Tertiary boundary, eastern Montana. *Geology*, 20:556–560.
- , AND T. A. HANSEN. 1986. Detritus feeding as a buffer to extinction at the end of the Cretaceous. *Geology*, 14:868–870.
- , D. E. FASTOVSKY, R. G. HOFFMAN, C. B. BERGHAUS, AND D. L. GABRIEL. 1991. Sudden extinction of the dinosaurs, latest Cretaceous, upper Great Plains, U.S.A. *Science*, 254:835–839.
- SHOEMAKER, R. E. 1966. Fossil leaves of the Hell Creek and Tullock Formations of eastern Montana. *Palaeontographica*, B119:54–75.
- . 1977. Fossil fig-like objects from the Upper Cretaceous sediments of the Western Interior of North America. *Palaeontographica*, B161:165–175.
- SIGNOR, P. W., AND J. P. LIPPS. 1982. Sampling bias, gradual extinction and catastrophes in the fossil record. In L. T. Silver (ed.), Geological implications of impacts and large asteroids on the Earth, p. 291–296. Special Publications of the Geological Society of America, 190.
- SLOAN, R. E., J. K. RIGBY, L. VAN VALEN, AND D. GABRIEL. 1986. Gradual dinosaur extinction and simultaneous ungulate radiation in the Hell Creek Formation. *Science*, 234:1173–1175.
- SMILEY, T. L. 1985. The geology and climate of the indigenous forest, Petrified Forest National Park, Arizona, p. 9–16. In E. H. Colbert, and R. R. Johnson (eds.), The Petrified forest through the ages. Museum of Northern Arizona Bulletin, 54.
- SOIL SURVEY STAFF. 1990. Keys to soil taxonomy. Monograph Soil Management Support Services, Blacksburg, Virginia, 19: 422.
- STOTT, D. F., W. G. E. CALDWELL, D. J. CANT, J. E. CHRISTOPHER, J. DIXON, E. H. KOSTER, D. H. MCNEIL, AND F. SIMPSON. 1993a. Cretaceous, p. 358–438. In D. F. Stott, and J. D. Aitken (eds.), Sedimentary cover of the craton of Canada. Geological Survey of Canada, Geology of Canada, v. 5, and Geological Society of America, Geology of North America, v. D-1.
- , J. DIXON, J. R. DIETRICH, D. H. MCNEIL, L. S. RUSSELL, AND A. R. SWEET. 1993b. Tertiary, p. 439–465. In D. F. Stott, and J. D. Aitken (eds.), Sedimentary cover of the craton of Canada. Geological Survey of Canada, Geology of Canada, v. 5, and Geological Society of America, Geology of North America, v. D-1.
- TIDWELL, W. D. 1990a. A new osmundaceous species (*Osmundacaulis*

- lemoni* n.sp.) from the Upper Jurassic Morrison Formation, Utah. *Hunteria*, 2(7):1-11.
- . 1990b. Preliminary report on the megafossil flora of the Upper Jurassic Morrison Formation. *Hunteria* 2(8):1-12.
- , AND S. R. ASH. 1990. On the Upper Jurassic stem *Hermanophyton* and its species from Colorado and Utah, U.S.A. *Palaeontographica*, B218:77-92.
- , AND D. A. MEDLYN. 1992. Short shoots of the Upper Jurassic Morrison Formation, Utah, Wyoming and Colorado, U.S.A. *Review of Palaeobotany and Palynology*, 71:219-238.
- TUCKER, M. E., AND M. J. BENTON. 1982. Triassic environments, climates and reptile evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 40:381-379.
- TURNER, C. E., AND N. S. FISHMAN. 1991. Jurassic Lake T'oo'dichi: a large saline lake, Morrison Formation, eastern Colorado Plateau: *Bulletin of the Geological Society of America*, 103:538-558.
- VAN VALEN, L., AND R. E. SLOAN. 1977. Ecology and extinction of the dinosaurs. *Evolutionary Theory*, 2:37-64.
- YOUNG, R. W., AND W. MORGAN. 1980. *The Navajo language*. University of New Mexico Press, Albuquerque, 1069 p.
- WEBER, R., AND G. ZAMUDIO-VARELA. 1995. *Laurozamites*, a new genus and new species of bennettitalean leaves from the Late Triassic of North America. *Revista Mexicana de Ciencias Geológicas*, 12:68-93.
- WEIL, A. 1994. K/T survivorship as a test of the acid rain hypothesis. *Abstracts of the Annual Meeting of the Geological Society of America*, 26:A335.
- WEST, L., AND D. CHURE. 1994. *Dinosaur: the Dinosaur National Monument Quarry*. Dinosaur Nature Association, Vernal, Utah, 40 p.
- WHITTAKER, R. H., AND G. M. WOODWELL. 1968. Dimensions and production relations of trees and shrubs in the Brookhaven forest, New York. *Journal of Ecology*, 56:1-25.
- WING, S. L., L. J. HICKEY, AND C. C. SWISHER. 1993. Implications of an exceptional fossil flora for Late Cretaceous vegetation. *Nature*, 363:342-344.
- WOLFE, J. A. 1991. Palaeobotanical evidence for a June "impact winter" at the Cretaceous/Tertiary boundary. *Nature*, 352:148-152.

