Predictive Stratigraphic Analysis—Concept and Application

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Pennsylvanian Vegetation and Soils

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Fossil tree lycopsids of Pennsylvanian swamps were unlike modern swamp plants botanically, but how different were Pennsylvanian vegetation types as ecosystems, as soil binders, as producers of carbon, as consumers of nutrients, and as regulators of water? Were the habitats outside the swamp vegetated at all? To what extent had the evolution of forests, initiated during Devonian time, progressed to create the variety of woody vegetation found today? These questions are difficult to impossible to answer from the evidence of fossil plants, which were preserved mainly as fragments in swampy environments where aerobic decay was inhibited by anoxia. Fortunately, there is a new line of evidence that is being applied to these and related problems: the evidence from fossil soils.

Fossil soils are by definition in the place they form, unlike many fossil plants and animals. Root traces in paleosols can be evidence of vegetation in habitats not suitable for preservation of fossil plants, including climatically dry and locally well drained sites (Retallack, 1984). The stature, biomass, and economy of ecosystems can be interpreted within broad limits from such paleosol features as the size and penetration of root systems, the degree of development of soil horizons and soil structure, and the depletion of alkaline earth and other elements that are major cationic nutrients for plants (Retallack, 1990). A variety of plant formations can be recognized from the evidence of paleosols (table 1), and only in some cases is their botanical composition known. In the ensuing discussion these vegetation types are grouped into general environmental categories of waterlogged, climatically wet, climatically dry, and frigid. Evidence from paleosols indicates that all of these varied environments supported woody vegetation by the Pennsylvanian.

The best known Pennsylvanian vegetation is that of waterlogged habitats, especially swamps of tree lycopsids

Table 1. Geological antiquity of plant formations based mainly on features of paleosols.
[E, Bt, Bs, and Bk designations from U.S. Department of Agriculture, 1975].

Plant formation	Characteristic paleosol features	Age	References
Open grassland............	Red, brown, or gray paleosol with abundant fine root traces and granular soil peds, sometimes with a shallow horizon of calcareous nodules (Bk)	Eocene	Retallack (1990).
Wooded grassland	Red, brown, or gray paleosol with abundant fine root traces and granular soil peds, and scattered large woody root traces, sometimes with subsurface clayey horizon (Bt) and deeper calcareous nodules (Bk)	.........do.........	Do.
Sea grassland...............	Root traces in shallow subtidal sediments, often associated with distinctive suite of large foraminifera	Late Cretaceous	Brasier (1975).
Fireprone shrubland	Red or brown paleosol with moderate-sized woody root traces and abundant fossil charcoal	Late Triassic	Harris (1957).
Heath	Sandy, noncalcareous paleosol with moderate-sized woody root traces and shallow siderite nodules or other indicator of high water table	Early Triassic	Retallack (1977).
Desert scrub	Red or brown paleosol with sparsely scattered large woody root traces or rhizoconcretions, and calcareous nodules (Bk horizon) close to the surface	Early Permian	Loope (1988).
Taiga............................	Paleosol with large woody root traces and frost-heave structures in periglacial deposits	Latest Pennsylvanian	Retallack (1980).
Tundra	Paleosol with small root traces and frost-heave structures in periglacial deposits	.........do.........	Do.
Bog	Black or gray shale, coal, or chert with abundant fossil plants lacking true roots, such as mosses or liverworts	.........do.........	Anderson and Anderson (1985).
Shrubland	Red or brown paleosol with clumped woody root traces of moderate size, common easily weathered minerals such as feldspar and a shallow subsurface horizon of calcareous nodules (Bk)	Pennsylvanian	Loope (1988).
Rainforest.....................	Red or brown paleosol mainly of kaolinite or other deeply weathered clay, with large woody root traces and little feldspar or carbonate	.........do.........	Keller and others (1954); Retallack (1990).
Oligotrophic forest	Red or brown paleosol principally of quartz, with large woody root traces and little clay, feldspar, or carbonate	Mississippian	Percival (1986); Retallack (1990).
Dune binders	Small but deeply penetrating root traces in eolian or fluvial sand	.........do.........	Ettensohn and others (1988); Loope (1988).
Fen	Black or gray paleosol, sometimes coal bearing, with small root traces and calcareous nodules	.........do.........	Rex and Scott (1987).
Carr	Black or gray paleosol, sometimes coal bearing, with large woody root traces and calcareous nodules	.........do.........	Retallack and Dilcher (1988).
Swamp	Black or gray paleosol, sometimes coal bearing, with large woody root traces, lacking pyrite or carbonate	Late Devonian	DiMichele and others (1987).
Wooded shrubland........	Red or brown paleosol with scattered large woody root traces and stump casts and abundant smaller woody root traces, as well as easily weathered minerals such as feldspar and subsurface calcareous nodules (Bk)	.........do.........	Retallack (1985).
Dry woodland	Thick red or brown paleosol with large woody root traces and stump casts and common easily weathered minerals such as feldspar, as well as deep subsurface calcareous nodules (Bk)	.........do.........	Retallack (1985, 1990).

Table 1. Geological antiquity of plant formations based mainly on features of paleosols—Continued.

Plant formation	Characteristic paleosol features	Age	References
Forest	Thick red or brown paleosol with large woody root traces and stump casts, and common easily weathered minerals such as feldspar, as well as development of subsurface leached (E), clay-enriched (Bt), or ferruginized (Bs) horizons	Late Devonian	Retallack (1985).
Mangal	Black or gray paleosol, sometimes coal bearing, with large woody root traces and marine body and trace fossils, sometimes also pyrite nodules	Middle Devonian	DiMichele and others (1987); Retallack (1990).
Marsh	Black or gray shale, coal or chert containing abundant herbaceous plants with rhizomes or true roots	Early Devonian	Kidston and Lang (1921); Krassilov (1981).
Brakeland[1]	Red or brown paleosol, with small root or rhizome traces of herbaceous, but not sod-forming plants	Late Silurian	Retallack (1990).
Salt marsh	Black or gray paleosol with small root or rhizome traces and marine body and trace fossils	Early Silurian	Schopf and others (1966).
Polsterland	Red or brown paleosol, with burrows, lichen stromatolites or reduction spotted, erosion resistant mounds, as might form under plants without true roots	Late Ordovician	Retallack (1990).
Microbial rockland	Rock surface with weathering rind, endolithic microbial trace fossils or biotic isotopic depth function	Precambrian (1.2 Ga)	Beeunas and Knauth (1985).
Microbial earth	Red or thick and leached paleosol with microfossils, microbial trace fossils, soil structure, or element or isotopic depth function suggestive of life	Precambrian (3 Ga)	Grandstaff and others (1986); Retallack (1986b, 1990).
Sabkha stromatolites	Algal lamination, often with domed form, and with pseudomorphs or crystals of evaporite minerals	Precambrian (3.5 Ga)	Schopf (1983).
Aquatic stromatolites	Algal lamination, often with domed form, crossed by traces of cyanobacterial sheaths	..........do.........	Do.

[1] Brakeland denotes a formation of numerous individual plants of similar physiognomy.

(*Lepidodendron*) and marattialean tree ferns (*Psaronius*). The plants of these former peat swamps are known from fossils in coals and enclosing shales. Vegetation of swamps not so waterlogged as to encourage peat formation is found in the form of stumps and leaf litters preserved in carbonaceous shale surface horizons of gleyed soils. The plants of acidic, mineral soils ("clastic swamps" of DiMichele and others, 1987; Gastaldo and others, 1989) were similar, though more diverse, than those of peat swamps. Woody vegetation of local alkaline wetlands, or carr, also may be known from Pennsylvanian coals with calcareous nodules, or "coal balls" (Retallack, 1986a; Retallack and Dilcher, 1988). The fossil flora of these eutrophic wetlands includes a very diverse flora, but shares many species with the flora of acidic swamps (Phillips, 1980).

Marine influenced woody vegetation, or mangal, of low diversity and dominated by *Cordaites* also is known from Pennsylvanian coal-bearing paleosols having abundant pyrite and sparse marine fossils (Raymond and Phillips, 1983). Herbaceous vegetation of wetlands, such as salt marsh, marsh, and fen probably also existed during Pennsylvanian time (DiMichele and others, 1979), especially considering geologically more ancient occurrences (table 1). Indeed, many of the nonmarine limestones of the Monongahela Formation of West Virginia and Ohio (see p. 19, app. 1, locs. 1–3), which have fine root traces, abundant brecciation, and local lamination, are similar to lime muds accumulating under periphyton algal fens of the modern Florida Everglades (as described by Spackman and others, 1969). Wetland vegetation of mosses and other plants lacking true roots are well known from rocks as ancient as Early Permian (Meyen, 1982), but some moss-filled carbonaceous shales within Gondwanan glacial deposits could be as old as Late Pennsylvanian (Anderson and Anderson, 1985).

Climatically humid, well-drained soils were forested well before Pennsylvanian time (table 1), but little is known botanically about this ancient vegetation. Such noncalcareous, red paleosols with large root traces and persistent weathering-susceptable minerals (Alfisols) have been reported from Pennsylvanian rocks in England (Besly and Fielding, 1989), and similar profiles exist in the Pennsylvanian and Permian Fountain Formation of Colorado, the Permian Hermit Shale of the Grand Canyon, Arizona, and the Permian Vale Formation near Lake Abilene, Texas (app. 1, locs. 4–6). All have copiously branching root traces like those of woody gymnosperms, but only in the Permian examples is there associated evidence of the plants of these humid well-drained forests, including a variety of broad-leaved seed ferns (*Supaia*, *Evolsonia*: White, 1929; Mamay, 1989). Fossil floras dominated by broad-leaved seed ferns (*Megalopteris*) also are known from sediments within ravines of an Early Pennsylvanian tropical paleokarst in northeastern Illinois (Leary, 1981). These fossil plants probably were derived from well-drained soils higher in the landscape and are further evidence of wet broad-leaved forests at that time.

There is also evidence from paleosols that forest cover extended during Pennsylvanian time onto nutrient-poor clayey soils (Ultisols) and sandy soils (quartzipsamments, dystrochepts, and perhaps also Spodosols) of humid climates. Sandy, nutrient-poor paleosols are widely known as ganisters, a Welsh mining term for these refractory quartzites in coal measures. Many of the ganister-bearing paleosols had a shallow water table as indicated by siderite nodules, but both these and thick, deeply rooted and well-drained ganisters commonly include *Stigmaria*, the root system of tree lycopsids (Percival, 1986; Retallack, 1990). Possible Pennsylvanian Ultisols have been known for some time from the diaspore clay district of the Missouri Ozark Mountains (Keller and others, 1954). The Farnberg pit (app. 1, loc. 7) contains profiles with both a horizon of clay enrichment (argillic or Bt horizon) and large woody root traces of gymnosperms. In addition to deeply penetrating root traces, one of these paleosols in the Farnberg pit also shows a surficial mat of roots. This soil is similar to those now found under Guineo-Congolian and Amazonian rainforest, but little is known about the botanical affinities of this possible Pennsylvanian rainforest, a topic long of interest to paleobotanists (Krassilov, 1975).

Dry woodland also is known earlier than Pennsylvanian time (table 1), and many slickensided, red, red-mottled, and calcareous nodular paleosols have been reported from Pennsylvanian rocks, even within major coal basins (Joeckel, 1988). The problem of calcareous, red-mottled paleosols of dry climates alternating in sequences with noncalcareous, red-mottled paleosols and thick coal beds of wet climates, has recently been attributed to Milankovitch variation in climate, and this also explains other features of Pennsylvanian cyclothemic sedimentation (Cecil, 1990). Such paleoclimatically distinct, superposed paleosols can be seen on either side of a thin and shaly margin of the Pittsburgh coal near Burnsville and Sissonville in West Virginia and also within the upper part of the Bonner Springs Shale near Holliday, Kans. (app. 1, locs. 8–10). Deeply penetrating root traces, low-angle slickensided cracks, and calcareous rhizoconcretions in these paleosols indicate that they were generally well drained, but the pattern of gray and red mottling is similar to that formed in modern soils by seasonal waterlogging ("groundwater gley" of Retallack, 1990). These paleosols, which are generally similar to those of the Indogangetic Plains of India, receive more than 1,000 mm mean annual rainfall (Hanrgram Series soils of Murthy and others, 1982) for the noncalcareous profiles and some 700 to 1,000 mm for the calcareous profiles (Sadhu Series soils). Comparable modern soils support lowland, evergreen, wet forest, and deciduous seasonally dry, monsoon forest, respectively (Champion and Seth, 1968; Retallack, 1991).

Pennsylvanian vegetation of the noncalcareous, red-mottled paleosols may have been similar to that of other gleyed paleosols ("clastic swamps" of DiMichele and others, 1987; Gastaldo and others, 1989) or to the broad-leaved wet forests of seed ferns already discussed. Vegetation of the dry-climate phase also may be known. Pith casts of calamites occur in one of these calcic-vertic-hydromorphic paleosols above the Sewickley coal near Macksburg in Ohio (app. 1, loc. 11), and casts of large gymnospermous roots and stumps in two superimposed paleosols of this kind occur below the thin Williamsburg coal in Clinton Lake Spillway, Kansas (app. 1, loc. 12). A systematic search for plant fossils in these paleosols may be quite revealing.

The well-known conifer (*Walchia*) and seed-fern (*Callipteris*) vegetation of fossil localities near Hamilton (Leisman and others, 1988; Rothwell and Mapes, 1988) and Garnett (Winston, 1983), both in Kansas, could also represent vegetation at the dry extreme of Milankovitch cycles. I could not find paleoclimatically instructive paleosols at either site, but both localities include evidence of channel incision and a position within their respective cyclothems that is compatible with this view. The Garnett site is south of, and at the same stratigraphic level as, a widespread calcareous paleosol to the north (Joeckel, 1988). These xeromorphic conifer-callipterid floras have in the past been taken to indicate Permian rather than Pennsylvanian time, upland rather than lowland floras, or extrabasinal rather than basinal floras (Pfefferkorn, 1980). None of these much-argued alternatives works well for the Hamilton or Garnett localities. Both sites are now known to be Pennsylvanian (Virgilian and Missourian, respectively). Both include gray to black shales with exceptional preservation of organic remains and no clear sign of red beds or well-drained paleosols. Both are also well within the boundaries of their depositional basin. Schutter and Heckel (1985) were closer to the mark in proposing Pennsylvanian "conifer savannas," but that is not a term I would use (Retallack, 1990), especially without evidence from fine root traces and granular mull humus in the paleosols for a continuous herbaceous ground cover like that provided by grasses (well demonstrated in some Miocene paleosols; Retallack, 1991). The nature of the paleosols does not exclude wooded shrubland, but the distribution of root traces in the calcareous paleosols mentioned here is more like that of open woodland or dry forest.

It could be that the conifer-callipterid dry woodland expanded at the expense of wetland vegetation of tree lycopsids and tree ferns by Milankovitch-driven climatic fluctuation the same as the more recent full glacial expansion of grassland expanded at the expense of interglacial rainforest in Africa and Amazonia. This new view of Pennsylvanian climatic variability calls for detailed reevaluation of the fossil records of both soils and plants.

A variety of woody desert vegetation types also had evolved by Pennsylvanian time, as indicated by paleosols in sequences of eolian dunes with calcareous rhizoconcretions and horizons of calcareous nodules close to the former soil surface (Loope, 1988). Pennsylvanian to Permian examples of these aridland paleosols exist in the Sangre de Cristo Formation near Howard and Coaldale in Colorado (app. 1, locs. 13–14). Their vegetation may have been structurally similar to pinyon or juniper woodlands of the North American desert Southwest. In the Permian Cutler Formation near Gateway in Colorado (app. 1, loc. 15), only small root traces were seen in thin calcareous paleosols, which may have supported vegetation structurally similar to the bluebush shrublands of central Australia. The botanical nature of Pennsylvanian woody desert vegetation remains completely unknown. There have not yet been identified any Pennsylvanian analogues of fireprone shrubland (also called chaparral, maquis, or matorral), nor desert succulent vegetation, nor any herbaceous aridland vegetation analogous to grassland.

Woody vegetation of frigid climates also may have evolved by Pennsylvanian time, judging from fossil root traces in paleosols associated with Gondwanan glacial deposits. In Carboniferous and Permian glacial deposits in the Sydney basin of southeastern Australia, there are remains of tundralike vegetation dominated by *Botrychiopsis* and taigalike vegetation dominated by *Gangamopteris* (Retallack, 1980). If woody vegetation extended to such high-latitude permafrosted soils, then it probably clothed high mountains as well.

Although counterparts of many modern vegetation types can be recognized from Pennsylvanian fossil plants and soils, they were certainly distinct botanically from modern vegetation, especially in lacking angiosperms. Pennsylvanian vegetation also may have been distinctive in some ways at the functional or ecosystem level, although only subjective impressions and conjecture can currently be offered in support of this idea. For example, the abundance of coal balls in Pennsylvanian coal seams contrasts with the extreme rarity of calcareous peat today and during the Mesozoic and Cenozoic. The rarity of ferruginous zones (spodic horizons) in nutrient-poor sandy paleosols in Pennsylvanian rocks contrasts with their abundance in sandy soils today and in those as old as Eocene. Perhaps Pennsylvanian vegetation was less acidifying and iron mobilizing than modern conifers of swamps and oligotrophic forests. Many Pennsylvanian trees were less densely woody than modern conifers of these habitats, and their foliage may have yielded fewer phenolic compounds to the leaching effects of rainwater. Flying insects appear in the fossil record during Late Mississippian time, and Pennsylvanian trees may not yet have evolved such an array of acidic and mildly toxic secondary plant metabolites to deter their herbivory as have modern conifers after several hundred million years of coevolution with insects. The degree of acid leaching and of iron redistribution in Pennsylvanian compared to modern soils could bear closer examination and may be only one of a number of differences between modern and ancient ecosystems that will become apparent from the study of fossil soils.

A complex picture is emerging of Pennsylvanian vegetation and its variation with climate, drainage, substrate, and time. Even now it is possible to create maps of Pennsylvanian vegetation and to recognize changes in vegetation related to cyclothemic sedimentation. An appreciation of vegetation beyond Pennsylvanian peat swamps is growing with the examination of paleosols and their associated fossil plants often too poorly preserved to have previously commanded much attention. Nevertheless, much remains to be done, both in the gathering of primary data and the reassessment of preexisting data to accommodate new views of Milankovitch climatic variation and models of the soil-vegetation system.

REFERENCES

Anderson, J.M., and Anderson, H.M., 1985, Palaeoflora of southern Africa—Prodromus of South African megafossil floras Devonian to Lower Cretaceous: Rotterdam, A.A. Balkema, 423 p.

Beeunas, M.A., and Knauth, L.P., 1985, Preserved stable isotopic signature of subaerial diagenesis in the 1.2 b.y. Mescal Limestone, central Arizona—Implications for the timing and development of a terrestrial plant cover: Geological Society of America Bulletin, v. 96, p. 737–745.

Besly, B.M., and Fielding, C.R., 1989, Palaeosols in Westphalian coal-bearing and redbed sequences, central and northern England: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 70, p. 303–330.

Brasier, M.D., 1975, An outline of the history of seagrass communities: Palaeontology, v. 18, p. 691–702.

Cecil, C.B., 1990, Paleoclimate controls on stratigraphic repetition of chemical and siliciclastic rocks: Geology, v. 18, p. 533–536.

Champion, H.G., and Seth, S.K., 1968, A revised survey of the forest types of India: Delhi, Government of India, 404 p.

DiMichele, W.A., Mahaffy, J.F., and Phillips, T.L., 1979, Lycopods of Pennsylvanian age coals—*Polysporia*: Canadian Journal of Botany, v. 57, p. 1740–1753.

DiMichele, W.A., Phillips, T.L., and Olmstead, R.G., 1987, Opportunistic evolution—Abiotic environmental stress and the fossil record of plants: Review of Paleobotany and Palynology, v. 50, p. 151–178.

Ettensohn, F.R., Dever, G.R., and Grow, T.S., 1988, A paleosol interpretation for profiles exhibiting subaerial exposure "crusts" from the Mississippian of the Appalachian basin, *in* Reinhardt, J., and Sigleo, W.R., eds., Paleosols and weathering through geologic time—Principles and applications: Geological Society of America Special Paper, v. 216, p. 35–48.

Gastaldo, R.A., Gibson, M.A., and Gray, T.D., 1989, An Appalachian-sourced deltaic sequence, northeastern Alabama, U.S.A.—Biofacies-lithofacies relationships and interpreted community patterns: International Journal of Coal Geology, v. 12, p. 225–257.

Grandstaff, D.E., Edelman, M.J., Foster, R.W., Zbinden, E., and Kimberley, M.M., 1986, Chemistry and mineralogy of Precambrian paleosols at the base of the Dominion and Pongola Groups: Precambrian Research, v. 32, p. 97–131.

Harris, T.M., 1957, A Rhaeto-Liassic flora in South Wales: Proceedings of the Royal Society of London, v. B147, p. 289–308.

Joeckel, R.M., 1988, Geomorphology of a Pennsylvanian land surface—Pedogenesis in the Rock Lake Shale Member, southeastern Nebraska: Journal of Sedimentary Petrology, v. 59, p. 469–481.

Keller, W.D., Wescott, J.F., and Bledsoe, A.O., 1954, The origin of Missouri fire clays, *in* Swineford, A., and Plummer, N., eds., Clays and clay minerals: Publications of the National Academy of Science, v. 327, p. 7–46.

Kidston, R., and Lang, W.H., 1921, On Old Red Sandstone plants showing structure from the Rhynie chert bed, Aberdeenshire—Part V. The Thallophyta occurring in the peat bed, the succession of plants through a vertical section of the bed, and the conditions of accumulation and preservation of the deposit: Transactions of the Royal Society of Edinburgh, v. 52, p. 855–902.

Krassilov, V.A., 1975, Paleoecology of terrestrial plants (translated by H. Hardin): New York, Wiley, 283 p.

———1981, *Orestovia* and the origin of vascular plants: Lethaia, v. 14, p. 235–250.

Leary, R.L., 1981, Early Pennsylvanian geology and paleobotany of the Rock Island County, Illinois, area—Part 1. Geology: Illinois State Museum Reports of Investigations, v. 37, 88 p.

Leisman, G.A., Gillespie, W.H., and Mapes, G., 1988, Plant megafossils from the Hartford Limestone (Virgilian-Upper Pennsylvanian) near Hamilton, Kansas, *in* Mapes, G., and Mapes, R., eds., Regional geology and paleontology of the upper Paleozoic Hamilton quarry area in southeastern Kansas: Kansas Geological Survey Guidebook, v. 6, p. 203–212.

Loope, D.B., 1988, Rhizoliths in ancient eolianites: Sedimentary Geology, v. 56, p. 301–314.

Mamay, S.H., 1989, *Evolsonia*, a new genus of Gigantopteridaceae from the Lower Permian Vale Formation, north-central Texas: American Journal of Botany, v. 76, p. 1299–1311.

Meyen, S.V., 1982, The Carboniferous and Permian floras of Angaraland (a synthesis): Lucknow, India, Biological Memoirs, v. 7, no. 1, 109 p.

Murthy, R.S., Hirekirur, L.R., Deshpande, S.B., and Veneka Rao, B.V., eds., 1982, Benchmark soils of India—Morphology, characteristics and classification for resource management: Nagpur, National Bureau of Soil Survey and Land Use Planning (ICAR), 374 p.

Percival, C.J., 1986, Paleosols containing an albic horizon—Examples from the Upper Carboniferous of northern England, *in* Wright, P.V., ed., Paleosols—Their recognition and interpretation: Oxford, Blackwells, p. 87–111.

Pfefferkorn, H.W., 1980, A note on the term "upland flora": Review of Palaeobotany and Palynology, v. 30, p. 157–158.

Phillips, T.L., 1980, Stratigraphy and geographic occurrence of permineralized coal-swamp plants—Upper Carboniferous of North America and Europe, *in* Dilcher, D.L., and Taylor, T.N., eds., Biostratigraphy of fossil plants: Stroudsburg, Pa., Dowden, Hutchinson and Ross, p. 25–92.

Raymond, A., and Phillips, T.L., 1983, Evidence for an Upper Carboniferous mangrove community, *in* Teas, H.J., ed., Tasks for vegetation science: Hague, Junk, v. 8, p. 19–30.

Retallack, G.J., 1977, Triassic palaeosols from the Narrabeen Group of New South Wales—Part 2. Classification and reconstruction: Geological Society of Australia Journal, v. 24, p. 19–36.

———1980, Late Carboniferous to Middle Triassic megafossil floras from the Sydney basin, *in* Herbert, C., and Helby, R.J., eds., A guide to the Sydney basin: Geological Survey of New South Wales Bulletin, v. 26, p. 384–430.

———1984, Completeness of the rock and fossil record—Estimates from fossil soils: Paleobiology, v. 10, p. 59–78.

———1985, Fossil soils as grounds for interpreting the advent of large plants and animals on land: Royal Society of London Philosophical Transactions, v. B309, p. 105–142.

———1986a, The Hitchcox limey peat soil as a modern analog for Pennsylvanian coals bearing coal balls [abs.]: 99th Annual Meeting of the Geological Society of America, San Antonio: Geological Society of America Abstracts, v. 18, p. 728.

———1986b, Reappraisal of a 2200-Ma-old paleosol from near Waterval Onder, South Africa: Precambrian Research, v. 32, p. 195–252.

———1990, Soils of the past—An introduction to paleopedology: London, Unwin Hyman, 520 p.

———1991, Miocene paleosols and ape habitats of Pakistan and Kenya: New York, Oxford University Press, 346 p.

Retallack, G.J., and Dilcher, D.L., 1988, Reconstructions of selected seed ferns: Missouri Botanical Garden Annals, v. 75, p. 1010–1057.

Rex, G.M., and Scott, A.C., 1987, The sedimentology, paleoecology, and preservation of Lower Carboniferous plant fossils at Pettycur, Fife, Scotland: Geological Magazine, v. 124, p. 43–66.

Rothwell, G.W., and Mapes, G., 1988, Vegetation of a Paleozoic conifer community, *in* Mapes, G., and Mapes, R., eds., Regional geology and paleontology of the upper Paleozoic Hamilton quarry area in southeastern Kansas: Kansas Geological Survey Guidebook, v. 6, p. 213–233.

Schopf, J.M., Mencher, E., Boucot, A.J., and Andrews, H.N., 1966, Erect plants in the Early Silurian of Maine: U.S. Geological Survey Professional Paper 550–D, p. 69–75.

Schopf, J.W., ed., 1983, Earth's earliest biosphere: Princeton, Princeton University Press, 544 p.

Schutter, S.R., and Heckel, P.H., 1985, Missourian (early Late Pennsylvanian) climate in midcontinent North America: International Journal of Coal Geology, v. 5, p. 111–140.

Spackman, W., Riegel, W.L., and Dolsen, C.P., 1969, Geological and biological interactions in the swamp-marsh complex of southern Florida, *in* Dapples, E.C., and Hopkins, M.E., eds., Environments of coal deposition: Geological Society of America Special Paper, v. 114, p. 1–35.

U.S. Department of Agriculture, 1975, Soil taxonomy, *in* U.S. Department of Agriculture Handbook 436: Washington D.C., Government Printing Office, 754 p.

White, D., 1929, Flora of the Hermit Shale, Grand Canyon, Arizona: Publications of the Carnegie Institute of Washington, v. 405, 118 p.

Winston, R.B., 1983, A Late Pennsylvanian upland flora in Kansas—Systematics and environmental implications: Review of Palaeobotany and Palynology, v. 40, p. 5–31.

Appendix 1. Mentioned localities of paleosols not studied in detail.

Loc. no.	Locality
1	Morgantown Mall, W. Va. (grid reference 854869, Osage 7.5-minute quadrangle, Monongalia County), in 600-m-long east-west cut for new mall, 1 mile west-northwest of intersection of highways I–79 and U.S. 19, are exposed Pittsburgh, Redstone, Fishpot and Sewickley coals of the Monongahela Formation, and gray calcareous paleosols above and below the nonmarine unranked Redstone limestone (Late Pennsylvanian): examined March 1, 1991.
2	Weston, W. Va. (grid reference 195496, Weston 7.5-minute quadrangle, Lewis County), in roadcuts of ramp within northwestern quadrant of cloverleaf at intersection of highways I–79 and U.S. 33 is exposed unranked Redstone limestone and Pittsburgh coal and its underclay, all of the Monongahela Formation (Late Pennsylvanian): examined March 2, 1991.
3	Bridgeport, Ohio (SE¼NE¼SE¼NW¼ sec. 33, T. 3 N., R. 2 W., Lansing 7.5-minute quadrangle, Belmont County), in roadcuts south of eastbound highway I–70 near base of descent into Ohio Valley is exposed a sequence of nonmarine limestones disrupted by well-preserved root traces and cradle knolls at several levels above the Sewickley coal of the Monongahela Formation (Late Pennsylvanian): examined March 3, 1991.
4	Manitou Springs, Colo. (SW¼SE¼NE¼NW¼ sec. 5, T. 14 S., R. 67 W., Manitou Springs 7.5-minute quadrangle, El Paso County), in gully 100 m north and up from Alpine Trail Road near Williams Canyon, are exposed several ganister-bearing paleosols with stigmarian root systems and siderite nodules, overlain by a sequence of red paleosols with deeply penetrating, drab-haloed, woody root traces, all in the Fountain Formation (Pennsylvanian and Permian): examined July 2, 1979.
5	Grand Canyon, Ariz. (grid reference 018917, Phantom Ranch 7.5-minute quadrangle, Coconino County), in red beds west of the Kaibab Trail are a sequence of red paleosols with ferruginized woody root traces and concretions forming the entire Hermit Shale (Permian): examined March 12, 1978.
6	Lake Abilene, Tex. (grid reference 158685, View 7.5-minute quadrangle, Taylor County), roadside gully south of unsealed road climbing the hill north of the dam wall exposes two thick red paleosols with gymnospermous roots, divided by bedded siltstone and sandstones covering and containing locally abundant remains of the seed fern *Evolsonia texana* in the Vale Formation of the Clear Fork Group (Early Permian): examined October 28, 1990.
7	Drake, Mo. (NE¼NW¼SW¼ sec. 30, T. 43 N., R.5 W., Goerlisch Ridge 7.5-minute quadrangle, Gasconade County), in the southeastern corner and uppermost levels of Farnberg pit, 3 miles southwest of Drake, are exposed several red clayey paleosols with woody root traces, in the Cheltenham Clay, which lies unconformably on paleokarst into the Ordovician Jefferson City Dolomite and is overlain conformably by the Fort Scott Limestone (Middle Pennsylvanian): examined November 3, 1989.
8	Locality 8. Burnsville, W. Va. (grid reference 314025, Burnsville 7.5-minute quadrangle, Braxton County), in roadcut to east of northbound highway I–79 are exposed a thin Pittsburgh coal overlying a noncalcareous green- to red-mottled paleosol and overlain by a calcareous red-mottled paleosol with mukkara structure, all Monongahela Formation (Late Pennsylvanian): examined March 2, 1991.
9	Sissonville, W. Va. (grid reference 445662, Sissonville 7.5-minute quadrangle, Kanawha County), roadcut south of frontage road on hill in southeast quadrant of cloverleaf at intersection of highway I–77 and Haines Branch Road exposes a thin gray claystone equivalent to the Pittsburgh coal, here forming the surface horizon of a noncalcareous red-mottled paleosol and overlain by a calcareous red-mottled paleosol with large cradle knolls and root traces, also of the Monongahela Formation (Late Pennsylvanian): examined March 2, 1991.
10	Holliday, Kans. (center sec. 6, T. 12 S., R. 24 E., Edwardsville 7.5-minute quadrangle, Johnson County), roadcuts to the east of southbound highway I–435, 1 mile east of Holliday, expose a maroon-colored noncalcareous paleosol with woody root traces overlain by the lower portion of a gray calcareous paleosol all in the upper part of the Bonner Springs Shale, which is truncated by the marine Merriam Member of the Plattsburg Limestone, Lansing Group (Late Pennsylvanian, Missourian): examined June 25, 1991.
11	Macksburg, Ohio (SW¼SE¼NW¼ SE¼ sec. 18, T. 5 N., R. 8 W., Lower Salem 7.5-minute quadrangle, Washington County), roadcut 1 mile south of Macksburg on highway I–77 exposes noncalcareous underclay to the Sewickley coal, which is overlain by a red-mottled calcareous paleosol with mukkara structure, all Monongahela Formation (Late Pennsylvanian): examined March 3, 1991.
12	Clinton Lake Spillway, Kans. (NW¼NE¼ NW¼ sec. 8, T. 13 S., R. 19 E., Lawrence West 7.5-minute quadrangle, Douglas County), in northern bank of spillway is exposed the Oread Limestone of the Shawnee Group overlying the Lawrence Formation of the Douglas Group, the latter including a thin Williamsburg coal overlying two thick gray- to red-mottled calcareous paleosols with deep cracks and large casts of woody roots and stumps (Late Pennsylvanian, Virgilian): examined June 25, 1991.
13	Howard, Colo. (grid reference 248578, Howard 7.5-minute quadrangle, Fremont County), in roadcut east of highway U.S. 50 and the Arkansas River, 2 miles west of Howard, are exposed steeply dipping red paleosols with carbonate nodules in the Sangre de Cristo Formation (Pennsylvanian to Permian): examined May 13, 1979.
14	Coaldale, Colo. (grid reference 312514, Howard 7.5-minute quadrangle, Fremont County), in roadcut south of highway U.S. 50 and Arkansas River, 4 miles west of Coaldale, are steeply dipping red paleosols with carbonate nodules in the Sangre de Cristo Formation (Pennsylvanian to Permian): examined May 13, 1979.
15	Gateway, Colo. (NW¼NE¼NW¼SE¼ sec. 21, T. 51 N., R. 19 W., Gateway 7.5-minute quadrangle, Mesa County), low in cliffs above the dry wash 1 mile southwest of Gateway are thin red calcareous paleosols with abundant small root traces in the Cutler Formation (Permian): examined May 14, 1979.