What to Call Early Plant Formations on Land

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The phrase "plant formation" denotes the structure, growth habit and general appearance of vegetation, regardless of its exact taxonomic composition. Plant formations such as heath and woodland can now be recognized from the fossil records of both plants and soils. There is a problem, however, with some kinds of polar and desert vegetation and geologically early plant formations on well drained soils. These consist of thalloid plants with only rhizoids, or of plants with only slender rhizomes, runners or fibrous roots, even in non-peaty and non-waterlogged soils. The term "polsterland" has been proposed for formations of well drained soils dominated by lichens or plants lacking true roots. The term "brakeland" has been proposed for vegetation of well drained soils dominated by herbaceous plants with rhizomes and roots not so densely turf-forming as in grasslands. There is some indication from studies of fossil spores and soils that polsterlands and brakelands may have been widespread during Late Ordovician to Devonian time, before the advent of trees and other woody plants that heralded the appearance of most kinds of plant formations now found in modern vegetation.

INTRODUCTION

In geology a "formation" is a named rock unit; a kind of rock address. In botany, the term "formation" is used in another sense again, for the general structure and appearance of vegetation. Wooded grassland, for example, is a plant formation of grasses with scattered trees. The wooded grasslands of Africa are composed of different genera (grasses mainly *Themeda*, and trees, *Acacia*) from those of South America (*Trachypogon, Curatella*) or Australia (*Dichanthium, Eucalyptus*), but in each region the general appearance of this vegetation is similar (Cole, 1986). The global mapping of plant formations was one of the earliest tasks of plant geographers culminating in the monumental work of A.F.W. Schimper (1903). Ecological research at the formational level remains of interest, particularly with

respect to nutrient cycling and productivity (Webb et al., 1983; White, 1983; Barbour and Billings, 1988; Longton, 1988).

Reconstructing ancient plant formations has long been an aim of paleobotany (Krassilov, 1975), although the way in which many assemblages of fossil plants are preserved means that reconstruction can be difficult to impossible (Spicer, 1981; Ferguson, 1985). Plant formations also are of interest to soil geographers, because they have a pronounced effect on soils. The aggregate effect of ecosystem processes such as primary production are more readily discerned in soils and paleosols than are the effects of particular species or taxonomically-defined communities of plants. The realization that vegetation could be a more important determinant of soil morphology than parent material or other factors was first established by Dokuchaev's (1883) monumental monograph on Russian grassland soils, a work that founded modern soil science as a discipline separate from geological sciences. The relationship between vegetation and soils is now treated in numerous textbooks (Foth and Schafer, 1980; Trudgill, 1988; Steila and Pond, 1989).

The study of paleosols is a relatively new approach to the problem of reconstructing vegetation. Paleosols are a record of land surfaces and their vegetation under conditions both favorable and unfavorable to the preservation of plant fossils (Retallack, 1984). Fossil plants are best preserved in poorly drained soils, which are drab-colored with siderite and other gleyed minerals. Few fossil plants are preserved in well drained soils, which are red and brown with iron oxides (hematite) and hydroxides (goethite), and may contain calcareous nodules (caliche). Vegetation of the past can be interpreted from root traces and overall profile form of paleosols, once allowance has been made for common kinds of alteration after burial (Retallack, 1990, 1991a). As this work on the geological history of plant formations proceeds (Table 1, summarized largely from Retallack, 1990), some basic nomenclatural problems have arisen.

In terms of plant formations, what are we to call the earliest vegetation of well drained soils? There are few problems with vegetation of peaty or waterlogged ground. Bog is a suitable term for a peat-forming formations of

TABLE 1—Productivity, stature and geological antiquity of plant formations.

Plant formation	Stature (m)	Rooting depth (m)	Biomass (g/m^2) dry wt.	Net productivity $(g/m^2/yr)$	Geologic antiquity (Ma)	Characteristic paleosol features
aquatic stromatolites	0.5	0.001	19–159	8–112	3500	algal lamination, often with domed form, crossed by traces of cyanobacterial sheaths
sabkha stromatolites	0.5	0.001	188–250	25–357	3500	algal lamination, often with domed form, and with pseudomorphs or crystals of evaporite minerals
microbial earth	0.001	0.001	36–363	2–196	3000	red or thick and leached paleosol with microfossils, trace fossils, isotopic depth function suggestive of life
seaweed beds	18	0.1	265–8000	2000–12,881	1400	megafossils and holdfasts in subtidal sediments, characteristic associated molluscs (e.g., kelp snails)
microbial rockland	0.001	0.001	0.7–490	20–196	1200	rock with weathering rind, endolithic microbial trace fossils or biotic isotopic depth function
polsterland	0.001–0.1	0.001–0.12	51–950	21–276	450	red or brown paleosol, with burrows, lichen stromatolites or reduction spotted, erosion-resistant mounds
salt marsh	1	0.001–0.1	209–1966	295–3700	430	black or gray paleosol with small root or rhizome traces and marine body and trace fossils
brakeland	0.001–2	0.001–1	15–991	1.5–54	420	red or brown paleosol, with small root or rhizome traces of herbaceous, but not sod-forming plants
marsh	1	0.1–0.5	111–30,000	140–15,000	400	black or gray shale, coal or chert containing abundant herbaceous plants with rhizomes or roots
pondweed	20	0.1	50–2000	134–2000	414	megafossils and holdfasts in lacustrine shale, including charophyte oogonia and *Isoetes* plants
mangal	10	0.001–1	2200–46,900	680–2556	375	black or gray paleosol, with coal, large woody root traces, marine body and trace fossils, pyrite nodules
forest	10–100	1–5	10,000–45,000	650–2000	375	thick red or brown paleosol, with large woody root traces, easily-weathered minerals such as feldspar, leached (E), clay-enriched (Bt), or ferruginized (Bs) horizons
wooded shrubland	10	0.1–1	396	34–394	370	red or brown paleosol, with scattered large woody root traces, abundant small woody root traces, easily weathered minerals and subsurface calcareous nodules (Bk)
dry woodland	10	0.5–2	4000–25,000	1200–1700	365	thick red or brown paleosol with large woody root traces, easily weathered minerals, deep calcareous nodules (Bk)

TABLE 1—Continued.

Plant formation	Stature (m)	Rooting depth (m)	Biomass (g/m²) dry wt.	Net productivity (g/m²/yr)	Geologic antiquity (Ma)	Characteristic paleosol features
swamp	3–100	0.1–0.5	30,000–50,000	1300–2500	365	black or gray paleosol, sometimes coal-bearing, with large woody root traces, lacking pyrite or carbonate
fen	2	0.1–0.5	360–1820	656–1400	340	black or gray paleosol, sometimes coal-bearing, with small root traces and calcareous nodules
carr	3–100	0.1–0.5	3109–9808	576–651	330	black or gray paleosol, sometimes coal-bearing, with large woody root traces and calcareous nodules
dune binders	0.1–2	0.5	100–3000	10–800	330	small but deeply penetrating root traces in eolian or fluvial sand
oligotrophic forest	10–100	1–5	994–88,200	830–3279	330	red or brown paleosol principally of quartz, with large woody root traces and little clay, feldspar or carbonate
rain forest	10–100	1–5	8000–70,000	310–3500	305	red or brown paleosol, deeply weathered (often kaolinitic), with large woody root traces, little carbonate
shrubland	0.5–2	0.1–1	93–1200	16–400	290	red or brown paleosol with clumped woody root traces of moderate size, and shallow calcareous nodules (Bk)
bog	1	0.1–0.5	2500–4000	220–2500	290	black or gray shale, coal or chert with abundant fossil plants lacking true roots, such as mosses or liverworts
tundra	0.1–1	0.1–1	100–5850	70–870	290	paleosol with small root traces and frost-heave structures in periglacial deposits
taiga	1–10	0.5–2	2550–35,000	400–1400	290	paleosol with large woody root traces and frost-heave structures in periglacial deposits
desert scrub	10	0.1–1	100–1500	50–1200	280	red or brown paleosol, with large woody root traces, or rhizoconcretions, and shallow calcareous nodules (Bk)
heath	0.1–2	0.1–1	200–2600	100–400	240	sandy, non-calcareous paleosol, with woody root traces and siderite nodules or other indicator of high water table
fire-prone shrubland	0.5–2	0.1–1	1000–10,342	600–1986	210	red or brown paleosol with moderate size woody root traces and abundant fossil charcoal
sea grass bed	0.3	0.001–0.1	40–8100	332–2285	90	root traces and fossils in shallow subtidal sediments, often associated with distinctive suite of large foraminifera
wooded grassland	0.5–10	0.1–2	1500–6000	400–1400	45	red, brown or gray paleosol, with abundant fine root traces and granular soil peds, few large

TABLE 1—Continued.

Plant formation	Stature (m)	Rooting depth (m)	Biomass (g/m²) dry wt.	Net productivity (g/m²/yr)	Geologic antiquity (Ma)	Characteristic paleosol features
open grassland	0.5–2	0.1–2	60–30,000	56–1500	45	woody root traces, clayey (Bt) horizon above calcareous nodules (Bk) red, brown or gray paleosol, with abundant fine root traces, granular peds, shallow calcareous nodules (Bk)

Note: Antiquity of formations and their paleosols is abstracted from Retallack (1990), with additions from Walter et al. (1990), and Ivaney et al. (1990). Productivity, biomass, stature and rooting depth are from modern vegetation only (Westlake, 1966, 1975; Parker and Schneider, 1975; Wielgolaski, 1975; Ikusima et al., 1975; Rodin et al., 1975; Crisp, 1975; Rutherford, 1978; Pomeroy and Wiegert, 1981; Friedmann and Kibler, 1980; Kummerow et al., 1981; Clough and Attiwill, 1982; Whitton and Potts, 1982; Webb et al., 1983; Skujins, 1984; Rai and Proctor, 1968; Ludwig, 1986; Vincent, 1988; Vestal, 1988; Longton, 1988; de Winder et al., 1989; Guerrero and Mas, 1989; Hillman et al., 1989; Schalles and Shure, 1989; Morris and Haskin, 1990; Jones and Shachak, 1990; Shaver and Chapin, 1991). Conversion factors include gC = 0.36 g dry weight (Hillman et al., 1989), annual microbial production = 1/14 summed daily production (Krumbein and Cohen, 1977), C/N ratio of cyanobacteria = 106/15 (O'Brien, 1972), chlorophyll = 1.47% dry weight of cyanobacteria (Jones and Myers, 1965).

plants lacking true roots, such as mosses. These are now found mainly at high latitudes and altitudes, such as the *Sphagnum* bogs of the British Isles and Scandinavia (Gore, 1983). The term marsh can be used for waterlogged herbaceous vegetation of various kinds, including grasses (Gramineae), cranberries (*Vaccinium*), horsetails (*Equisetum*), and ferns (particularly *Azolla*). The term marsh also can be applied to peaty accumulations of herbaceous, early land plants, such as rhyniophytes of the Early Devonian (Siegenian) Rhynie Chert because of their rhizomes and other rootlike structures (Kidston and Lang, 1921). Pondweed is another waterlogged plant formation that contains a great variety of plants, such as algae (*Chara, Nitella*), quillworts (*Isoetes*), ferns (*Salvinia, Azolla*), and angiosperms (*Lemma*), that are either floating, or permanently submerged.

Neither is there a serious problem with names for early kinds of woody plant formations. Mangal, swamp, woodland and forest each may contain very different species of plants and still are recognizable as formations. A stand of tree ferns is recognized as a woodland or forest, just as a stand of palms or pines. Ancient forests of extinct pteridophytic trees, such as progymnosperms (*Archaeopteris*: Beck, 1964), and swamps of tree horsetails (*Calamites*) and tree-lycopsids (*Lepidodendron*: DiMichele et al., 1987) also have been identified in the fossil record.

It is only with the earliest herbaceous plant communities of well drained land that suitable plant formation names do not exist. Many well drained soils now support grasslands, but this term and its regional synonyms steppe, prairie and pampas, all imply a substantial component of grasses and sedges, which are confidently known in the fossil record only as far back as early Eocene from megafossils (Crepet and Feldman, 1991) and Late Cretaceous

(Campanian) from pollen (Scott and Srivastava, 1984). The terms sward, turf, meadow, herbfield or fellfield often used for herbaceous polar and alpine plant formations, also have too strong a connotation of angiospermous vegetation that forms a sod or peat (Longton, 1988). The term shrubland can be used for vegetation of low woody plants of desert regions, such as the bluebush (*Maireana*) vegetation of central Australia (Beadle, 1981), and the term heath for low growing oligotrophic woody vegetation of coastal and alpine regions, such as the heather (*Calluna*) vegetation of the British Isles and Scandinavia (Specht, 1979). These plants are much more woody and have stouter root systems than either grasses, or the earliest herbaceous pteridophytes and bryophytes in well drained non-peaty soils. For plant formations of these ancient kinds there are no suitable terms. Here are two suggestions.

POLSTERLAND

This term has been proposed (by Retallack, 1990) for plant formations of well drained soils dominated by multicellular plants lacking roots or rhizomes. This vegetation may include mosses, lichens, or liverworts. During the geological past, it may have included also a variety of extinct land plants. Some of these organisms, such as lichens, are not technically in the Kingdom Plantae, although they are functionally plantlike in many respects. Plants of polsterlands may have leaflike organs, as in mosses, or lack them, as in liverworts. The exact nature of subaerial reproductive and vegetative organs is not an essential part of the definition of polsterland, other than their herbaceous texture and small stature. The term polsterland has been coined from the existing word polster, by analogy with grassland and woodland. Polster is a German botanical term for a

cushion of mosses or liverworts, as commonly seen on boulders or fenceposts.

Polsterlands exist today, but generally have not been recognized as a distinct formation. Polsterlands of high mountain tops are more likely to be regarded as bare rock faces or boulder fields, even when much of the rock is covered in mosses and lichens. Many tundra and alpine communities are recognized on the basis of their attractive vascular plants, such as mountain aven (*Dryas octopetala*), rather than the more abundant non-vascular plants (Bliss, 1975; Østbye et al., 1975; See and Bliss, 1980). Similarly lichens and mosses are abundant in much desert vegetation classified ecologically on the basis of more conspicuous cacti and saltbush (Friedmann and Galun, 1974; Alexander and Calvo, 1990). In other cases polsters are a minor component (synusia) of a larger vegetation association. Patches of lichens, mosses or liverworts on rocks and tree trunks of temperate forests and woodlands (Longton, 1988) cannot be regarded as forming a polsterland. Such occurrences do demonstrate that these plants with their moisture dependent reproductive systems, are not confined to waterlogged or swampy habitats.

The best examples of polsterlands known to me are in continental Antarctica. For example, on Holocene moraines near Mt Rigby, beside the Scott Glacier (elevation 610 m, latitude 85°35') is a sparse cover of the lichens *Lecanora griseomarginata, Acarospora emergens, Omphalodiscus subcerebriformis, Buellia lata* and *Alectoria congesta*. This is the closest to the poles that plantlike creatures visible to the naked eye have been found. Also found were bacteria, moulds, yeasts, algae and rotifers. The soils are thin (up to 20 cm), gravelly, and light olive gray (5Y6/2: Campbell and Claridge, 1987). In the U.S. classification they would be regarded as Pergelic Cryorthents.

Another example has been described from a flat area of Holocene till with boulders of quartz-mica-schist on Elephant Island, near the Antarctic Peninsula. This vegetation of sparse lichens (*Usnea antarctica* and *Drepanocladus uncinata*) colonizes a 5 cm surface horizon of very dark grayish brown (10YR3/2) gritty clay loam, over 8 cm of very dark gray (10YR3/1) sandy clay loam and then very dark gray (10YR3/1) clay loam with shaley schist fragments. Free calcium carbonate is available throughout the profile, but a leaching gradient and the formation of silt caps on large clastic grains has been initiated (O'Brien et al., 1979). In the U.S. taxonomy this soil is a Pergelic Cryochrept.

Productivity and biomass studies have not been reported on these examples. Phytomass (dry weight) of comparable lichens in other parts of Antarctica is some 51–950 g/m² and the productivity of bryophytes and lichens in a variety of Antarctic plant communities is some 21–250 g/m²/yr (Longton, 1988).

In warmer climates polsterlands grade into heath, such as the "lichen heath" of Hardangervidda, Norway (Østbye et al., 1975). These grow in well drained areas of persistent snow banks, where the growing season is less than 60 days. In some places the growing season is so short as to exclude all vascular plants, leaving only the lichens *Cladonia mitis* and *Cetraria islandica*. However, in most areas there are common vascular plants: *Empetrum hermaphroditicum, Vaccinium vitis-idaea* and *Festuca ovina*. The soils of these lichen heaths have a thin (10 cm) moderately organic, sandy surface (A) horizon and a subsurface spodic (Bs) horizon (Brown and Veum, 1974), and are Ferrods in the U.S. taxonomy. A surveyed plot of these lichen heaths had a total biomass of 910 g/m², of which 533 g/m² was vascular plants, 7 g/m² was mosses and 370 g/m² was lichens. Net primary production amounted to only 276 g/m²/yr. In other places however, total biomass was less than 500 g/m² and primary production also lower. Even so, these "lichen heaths" support large populations of invertebrates, including sapsucking hemipterans (161/m²), lepidopteran larvae (4/m²), chrysomelid and staphylinid beetles (4/m²), spiders (32/m²), mites (1.25 × 10⁵/m²), and collembollans (5.4 × 10⁴/m²). These mean values are all for 1971 (from Østbye et al., 1975). Nematodes also are abundant but were not surveyed. Vertebrates include lemmings and reindeer, and lichens are some 60% of reindeer diet during winter months. Vertebrates however, range through a variety of other plant formations that include a greater proportion of vascular plants.

Polsterlands also may be found in extreme deserts, such as that near Camaná in southwestern Peru. Here there are clumps of lichens (*Teloschistes peruensis* and *Anaptychia neoleucomelana*), but apparently no phanerogamous plants (Thomson and Iltis, 1968). The lichens are scattered on sandy desert soils (map unit I-Re-c of F.A.O., 1971), which in the U.S. taxonomy (Soil Survey Staff, 1975) would be Torripsamments. In local clayey swales there are a number of minute lichens, dominated by *Buellia auriculata* and *Solenospora requieni*, but including also *Acarospora chilensis, Caloplaca cirrochroa, Collema* sp. cf. *C. tenax* and *Ramalina* sp. cf. *R. terebrata*. Similar vegetation is found near Swakopmund in Namibia, where lichens cover about 40 to 60% of the sandy soil with a biomass of 267 g/m² (Walter, 1985). The most common lichens near Swakopmund are *Ramalina maculata* and *Xanthoparmelia hyporhytida*, but *Omphalidium convolutum* also was noted. Both the extremely dry Peruvian and Namibian coastal fog deserts support "window lichens," whose thallus is buried in the soil beneath diaphanous grains so that only the discus-shaped and sand-sized apothecia emerge, and "rolling lichens" which are dispersed by wind like tumbleweeds. There is some doubt whether these lichen-dominated parts of Namibian and Peruvian fog deserts can be considered true polsterlands. Although for most of the time only scattered lichens may be visible (Thomson and Iltis, 1968, fig. 1; Walter, 1985, figs. 7.9, 7.10; Rauh, 1985, fig. 7.19), rainfall in some areas induces germination of a variety of desert ephemeral vascular plants with true roots.

Examples of polsterland grading into other plant formations are also found within deserts. Within an open dry grassland of false esparto grass (*Lygeum spartum*) in badlands of Ameria Province, southwest Spain, lichens (*Diploschistis dicapsis, Fulgensia fulgens, Squamularia lentigera, Toninia caeruleonigrescens*) and small mosses

(*Tortula* spp.) are widespread among the well spaced grasses, and cover also grassless badlands of Miocene marls and mudstones (Alexander and Calvo, 1990). These badland soils are Torriorthents in the U.S. classification. Mean annual precipitation in this area is 237 to 268 mm and mean annual temperature 22 to 23° C. The lichen rhizoids penetrate the soil to depths of up to 5 mm, and some species create a surface hummock and swale microrelief with an amplitude of 1.7 cm and wavelength of about 15 cm. The lichen cover has a marked effect in reducing erosion of these badlands. Runoff from plots with no lichens yielded 20.3 g/l of sediment, whereas runoff induced by similar conditions on lichen-stabilized slopes had only 4.9 g/l sediment.

Lichens are similarly widespread in desert shrublands and scrub of North America (MacMahon and Wagner, 1985) and the Middle East (Kappen et al., 1975). In the Negev Desert, lichen biomass varies from 73–141 g/m², and annual productivity is approximately 5–10% of that, or some 4–14 g/m²/yr.

POLSTERLANDS OF THE PAST

Ancient polsterlands could have been responsible for surficial features of paleosols reported by J.F. Dewey (in Boucot et al., 1974) from the Late Ordovician (Caradocian), Dunn Point Formation, near Arisaig, Nova Scotia. These are thick red paleosols with subsurface carbonate cement, developed on flows of andesite. Evidence for interpreting these as paleosols and for identifying them within a modern soil taxonomy has been presented elsewhere (Retallack, 1981, 1985, 1986, 1990; Feakes et al., 1989). In summary, these paleosols show considerably more profound weathering than frigid or desert soils. The Mac-Gillivray Brook and Doctors Brook profiles of Feakes et al. (1989) have relict feldspar crystals, a content of alkalis and alkaline earths, and redistribution of carbonate most like Eutrochrepts. They are similar to subhumid tropical soils that today support semi-evergreen tropical forest (Retallack, 1991b), a kind of vegetation that did not exist during Ordovician time. No root traces have been seen in these paleosols. More modest plant cover is in evidence from near-surface reduction spots and flanking scour-and-fill structures that Dewey has suggested mark the former position of clumps of land plants (Fig. 1). Other observers have noted possible burrows in these paleosols (A.N. Pearson, pers. comm., 1986).

Burrows were not discussed in a recent geochemical reevaluation of some of these paleosols (Feakes et al. 1989), but I have no reason to doubt them from experience with paleosols almost as ancient (Ashgillian part of Late Ordovician) in the Juniata Formation near Potters Mills, Pennsylvania (Retallack, 1985). These red calcareous soils on quartzose alluvium also have surficial reduction spots, presumably after remnant organic matter, but no evidence of their clumping, nor of associated erosional scouring was seen. However, these paleosols and others like them from several other sites in the Juniata Formation of Pennsylvania contain abundant burrows ranging from 1 to 21 mm
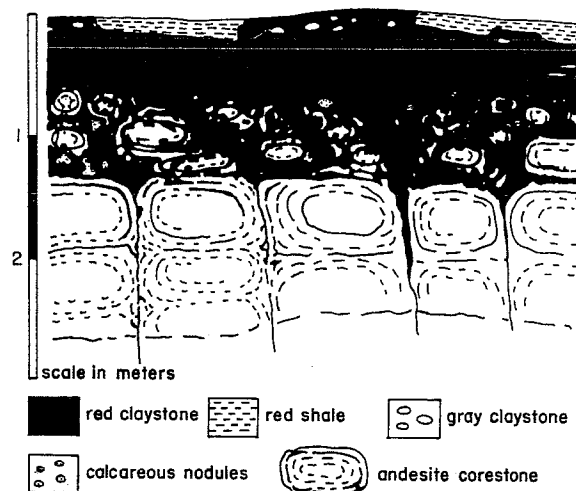

FIGURE 1—Sketch of the profile form and surficial erosion scours and reduction spots in a Late Ordovician paleosol developed on andesite of the Dunn Point Formation, near Arisaig, Nova Scotia (from Dewey in Boucot et al., 1974, with permission).

in diameter (Figs. 2, 3). The makers of these traces are not known, but their ability to tolerate dry soil (indicated by caliche nodules), the bilateral symmetry of their backfill structures and discrete, multiple modes in their size distribution all are suggestive of arthropods (Retallack and Feakes, 1987). There also is evidence from rounded fecal pellets in the burrows that they ate solid food. It is possible that they were entirely sustained by microbial scums and smaller animals in and on the soil, but larger vegetation is more likely considering the following additional lines of evidence. The distribution in one of the paleosols of trace elements usually complexed with organic matter (such as Li, Nb, Ni, P, Sr, Y) is a pattern of surficial depletion (Feakes and Retallack, 1988). Such a depth function is more compatible with a loose surface mat or clumps of vegetation, rather than with intimate admixture of organic matter and clay found in modern microbial earths of deserts and in grasslands of subhumid regions. In addition, analysis of the stable isotopic composition of pedogenic carbonate in these paleosols gave $\delta^{13}C_{PDB}$ values of -4.11 to $-6.93‰$ and $\delta^{18}O_{PDB}$ of -11.37 to $-12.41‰$ (Retallack and Feakes, unpubl. data from Global Geochemistry Corp.). These isotopic values reflect metamorphic alteration (oxygen values) and biological activity (carbon values) comparable to those found in Late Silurian and Mississippian red calcareous paleosols in nearby areas of the Appalachian Orogen (Mora et al., 1991). The burrowed Late Ordovician paleosols also are thoroughly weathered, and lack shallow calcareous nodules (Bk horizon) and permafrost structures of desert or frigid soils. Instead these paleosols have a profile form generally similar to Oxic Ustropepts, which now support dry monsoon forest in subhumid subtropical parts of the Indo-Gangetic Plains (Feakes and Retallack, 1988; Retallack, 1991b). Thus there is paleopedological evidence for Late Ordovician polsterlands in non-desertic and non-frigid habitats, and many more Paleozoic paleo-

FIGURE 2—Subhorizontal (above at arrows) and near vertical (below at arrows) burrows of land animals, with shiny surfaces of slickensided clay, in a loose block of paleosol from the Late Ordovician Juniata Formation, near Potters Mills, Pennsylvania. Scales in millimeters.
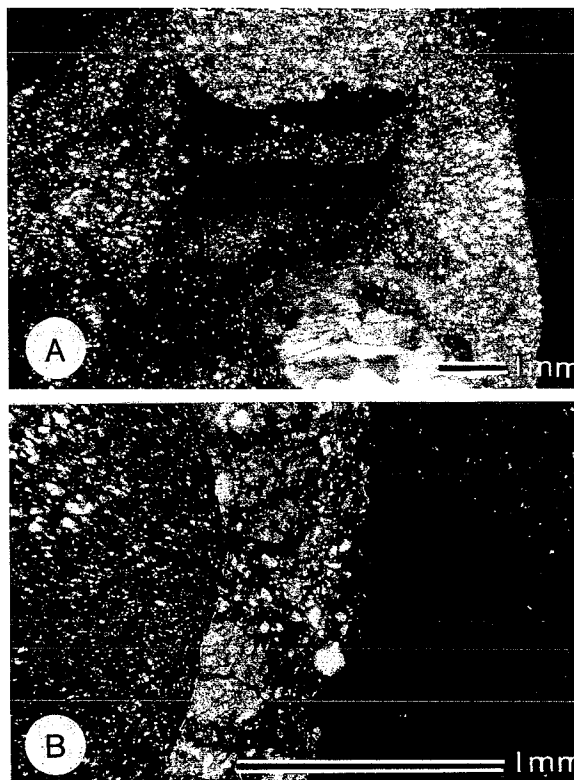

FIGURE 3—Spreiten texture of a burrow cut by a carbonate filled burrow (A) and light colored burrow-sheathing carbonate grading out into matrix to right but truncated by burrow fill with indistinct fecal pellets (B) in petrographic thin sections of Late Ordovician, type Potters Mills clay paleosol, Juniata Formation, near Potters Mills, Pennsylvania. Scale bars are 1 mm.

sols could be reexamined from this perspective (Allen, 1986).

No matter how good the evidence from paleosols becomes, it is not likely to be of much use in determining the botanical affinities of these ancient plants of well drained soils. Nor can much be expected from paleobotany, because these are environments in which megafossil plants are not preserved. Fortunately there is some evidence from paleopalynology. Land plant spores of Late Ordovician and Early Silurian age show little diversity and are mainly extinct forms with a sporopollenin envelope enclosing permanent tetrads and diads (Strother and Traverse, 1979; Gray et al., 1982; Johnson, 1985). These earliest of land plant spores are somewhat like those of living liverworts, and could represent extinct plants of a comparable grade of evolution (Gray, 1985). Nothing quite like them has been extracted from known Late Silurian and Devonian fossils of vascular land plants (Allen, 1980; Gensel, 1980), whose reproductive structures are becoming well known as a basis for their classification (Gensel and Andrews, 1984). The presumably non-vascular earliest land plants

that produced these peculiar spores are not yet known or recognized as megafossils.

BRAKELAND

This is a term for formations of herbaceous plants with rhizomes, runners or fibrous roots (Retallack, 1990). Plants in such vegetation lack appreciable wood and the tap roots of shrubs. Also lacking are the densely leafy, sod-forming rhizomes found in grasses and sedges. "Fern brake" is a non-technical and somewhat archaic (Middle English) phrase for a stand of ferns. It has been used to describe early successional vegetation of bracken fern (*Pteridium aquilinum*), that flourishes after forest fires or overgrazing (Watt, 1955). The phrase fern brake also has been widely applied to stands of other ferns, such as the scrambling masses of spider fern (*Gleichenia dicarpa*) common in southeast Asia and Australia (Beadle, 1981). In some cases, fern brakes are merely vegetative extensions of individuals. The term brakeland is meant in a wider sense for a formation of numerous individual plants of similar physiognomy. Such vegetation could include many kinds of herbaceous plants, such as rhyniophytes, zosterophylls, trimerophytes, horsetails, lycopods and some herbaceous

dicots, as well as ferns. Some of these plants are pteridophytic, others are flowering plants. Some have leaves and others do not. The taxonomically significant subaerial morphology of plants is not an essential part of the definition of brakelands, other than that they are herbaceous and not of great stature. The formation term has been coined by analogy with grassland and woodland.

There are many kinds of herbaceous plants other than grass in modern vegetation that have not been regarded as distinctive formations either because they are minor parts (synusiae) of other plant associations or because they are an ephemeral stage in plant succession on disturbed ground. A variety of ferns have been found to colonize fresh volcanic ash. Especially well documented examples are the early successional vegetation on ashes of the 1883 explosion of Krakatau, Indonesia (Simkin and Fiske, 1983) and the 1982 eruption of volcano El Chichon, Mexico (Burnham and Spicer, 1985). These ferns were, and will be, supplanted by forest. Similarly, horsetails (*Equisetum arvense*) are locally conspicuous in herbaceous dune binding vegetation around the Great Lakes of North America (Cody and Britten, 1989).

Other herbaceous plants form minor parts (synusiae) of other kinds of plant formations. Examples include large patches of lycopods (*Lycopodium cernuum*) on sandstone cliff faces and of mountain lycopods (*Lycopodium deuterodensum*) on patches of sandy soil in temperate sclerophyll woodlands of central eastern New South Wales (Beadle, 1981). Large clumps of clubmoss (*Lycopodium fastigiatum*) and dwarf ferns (*Blechnum penna-marina*) are common in high alpine regions of New Zealand (Allan, 1961). Similar herbaceous plants are part of alpine fellfields in most mountains of the world. Herbaceous plants also form synusiae of desert scrub. For example, the resurrection plant (*Selaginella lepidophylla*) colonizes cliffs and talus in deserts of Mexico and the southwestern United States (Lundell, 1966). The common name of this plant refers to its amazing ability to regenerate on watering from what appears to be a completely desiccated and dead plant. Spore-bearing plants may depend on free water for the growth of gametophytes and the meeting of gametes, but water does not have to be there all the time.

Modern vegetation most like my concept of brakeland is found in the fog loma desert of coastal southwestern Peru and northern Chile, from Trujillo to Iquique. Characteristic is *Tillandsia*, a genus of rhizomatous herbs in the largely epiphytic monocot family Bromeliaceae. Especially widespread is *T. latifolia*, which forms nearly pure stands of scattered cushions covering several square kilometers (Rauh, 1985). These plants acquire water and nutrients from fog, and commonly have strongly reduced roots. Their cushionlike form up to 30 cm high is easily dislodged and can be rolled by wind in classical tumbleweed fashion. They are widespread on plains and terraces up to elevations of 1000 m. Their soils include desert sandy loams, gravels and rock outcrops (map unit I-Re-c of F.A.O., 1971), which in the U.S. taxonomy (Soil Survey Staff, 1975) are Torripsamments and Torriorthents. Desert ephemerals are also prominent in these communities after rain.

Even in these regions of only 0.6 to 0.8 mm mean annual precipitation, there may be local cacti, shrubs and grasses, which become more prominent in areas receiving more than 3 mm mean annual rainfall.

Also similar in places to my concept of brakelands is the *Dryas integrifolia* "cushion-plant-lichen" association of raised beaches in the Truelove Lowland of Devon Island, Arctic Canada (Bliss, 1975, 1977). Vegetative cover is sparse, with 37% bare ground, 20% cover mainly by dicot herbs (*Dryas integrifolia, Saxifraga oppositifolia*), with some sedges (*Carex nardina*) and dwarf shrubs (*Salix arctica*), 38% by 5 species of lichens and 5% by 10 species of mosses. The soil here has a poorly developed desert pavement (0–2 cm) over a dark brown (7.5YR3/2) alkaline very gravelly sand (2–13 cm, horizon Ahk), over an alkaline very gravelly sand to loamy sand (13–82 cm, horizon Ck) on frozen gravel and sand (horizon Cz). This soil has been identified as a Pergelic Cryorthent in the U.S. taxonomy (Walker and Peters, 1977). It is rooted only to a depth of 20 cm. The biomass of this vegetation is 498 g/m^2, of which 434 g/m^2 is vascular plants, 15 g/m^2 is mosses and 49 g/m^2 is lichens. Net plant production of a plot of this vegetation was measured at only 22.4 g/m^2/yr, but other comparable polar vegetation has biomass in the range 15 to 991 g/m^2 and productivity of 1.5 to 54 g/m^2/yr (Longton, 1988). This is sufficient to support a diverse assemblage of invertebrates on the raised beaches of Devon Island, mainly nematodes (3.8×10^6/m^2), rotifers (1×10^2/m^2), enchytraeid worms (9.7×10^3/m^2), tardigrades (2.5×10^3/m^2), mites (7.4×10^3/m^2), collembolans (18.2×10^3/m^2) and nematoceran flies (3×10^2/m^2). Total invertebrate productivity has been estimated at 1.4 g/m^2/yr (Bliss, 1975). A variety of vertebrates including lemming and muskox live in this area and range over other vegetation types as well.

Polar brakelands grade into bogs, heaths, grasslands and tundra. On Devon Island, for example, raised beaches with brakelands ("cushion plant-lichen communities" just described) are surrounded by lowland peaty soils with bog ("cushion-plant moss") and marsh ("graminoid-moss"), and granitic rock outcrops with tundra ("dwarf shrub heath-moss") formations (Bliss, 1975). On South Georgia Island, east of Tierra del Fuego, vegetation dominated by rhizomatous herbs (*Acaena tenera*) on glacial till has some similarity with brakeland, as defined here, but includes common grasses (*Dechampsia antarctica, Festuca contracta*), which dominate grasslands on better developed brown soils nearby (Smith and Walton, 1975).

BRAKELANDS OF THE PAST

Evidence for brakelands in paleosols is much more copious than that for polsterlands. Calcareous red paleosols are abundant in Late Silurian to Early Carboniferous alluvial sequences of the British Old Red Sandstone (Allen, 1986) and in the comparable North American Bloomsburg Formation and Catskill magnafacies (Retallack, 1985). Both carbonate nodule morphology and its light carbon isotopic composition in these paleosols indicate that they supported at least sparse vegetation (Mora et al., 1991). Like
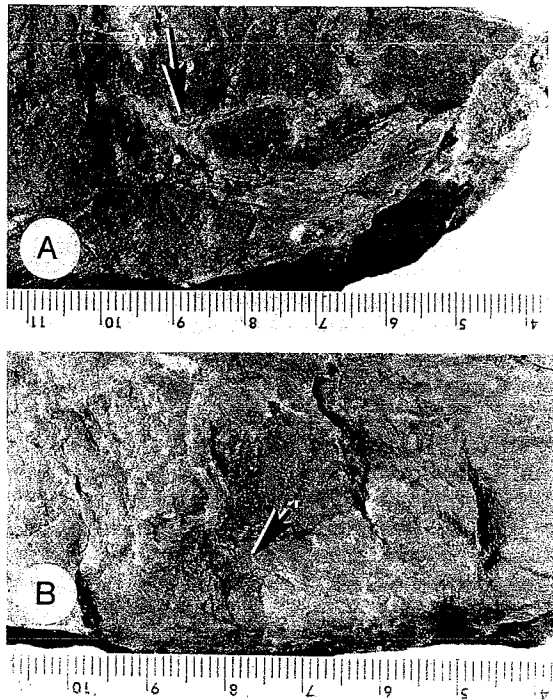
FIGURE 4—Subhorizontal, irregularly tubular structures, showing monopodial branching (at arrow in **A**) and dichotomous branching (at arrow in **B**), after plant rhizomes, in a Late Silurian paleosol (Faust Flat Series of Retallack, 1990, fig. 18.11), Bloomsburg Formation, near Palmerton, Pennsylvania.

the Ordovician paleosols already discussed, these paleosols are similar in ways other than bioturbation to modern soils of subhumid tropical parts of the Indo-Gangetic plains under monsoon forest (Retallack, 1990, 1991b). Formerly well drained paleosols as old as Late Silurian (Ludlovian) have evidence of bioturbation of their surface horizons, well before the paleobotanically documented appearance of large woody plants, but not before the appearance of a variety of extinct kinds of early vascular land plants that traditionally have been regarded as marsh plants. Some of the bioturbation in these red paleosols consists of simple tubes, similar to the animal burrows already discussed in Late Ordovician paleosols. Less distinct trace fossils also are found: silt and clay filled irregular tubules (ortho-isotubules of Brewer, 1976). Some of these show equiangular "Y" and "H" branching (Fig. 4) similar to that found in rhizomes of early land plants such as rhyniophytes and zosterophylls (Gensel and Andrews, 1984; Hao, 1989). There is no clear evidence from paleosols of the botanical affinities of these plants. Indeed, it is difficult to distinguish whether early rhizomatous land plants were vascular or non-vascular even in exquisitely preserved fossils (Edwards and Edwards, 1986). What is clear from the paleosols is that oxidized calcareous soils of a type found in subhumid tropical climates and well drained sites supported a cover of rhizomatous early land plants during Silurian time (Retallack, 1985).

Additional evidence of animals in another kind of landscape is provided by sand-filled burrows up to several millimeters wide in the surface of a mid-Silurian (Wenlockian) paleosol developed on basalt of the Clogher Head Formation of Ireland (Wright et al., 1991). The burrows are in the uppermost 80 cm of a thick (1.8 m) clayey paleosol developed on a basalt flow. Although there is some chemical evidence of impeded drainage, this paleosol represents deep weathering of basalt over a period of at least tens of thousands of years.

Remains of the earliest known vascular land plants appear in rocks of mid-Silurian (Wenlockian) age and from then on they have a continuous fossil record to the present (Edwards and Fanning, 1985; Gensel and Andrews, 1984). During the Early Silurian (mid-Llandoverian) spores similar to those isolated from early land plant fossils first appear in shallow marine, fluvial and lacustrine rocks (Gray, 1985). Indeed, the diversity of dispersed spores by Late Silurian time far exceeds that of spores isolated from megafossil early land plants. The disparity in apparent diversity between fossil spores and megafossil plant remains increases dramatically during Devonian time. These divergent diversifications of plants and spores have been attributed to mosaic evolution (Knoll et al., 1984): in other words, more rapid evolution of spore morphology than of sporangial or stem features seen in megafossils. The discovery of a variety of different kinds of spores in morphologically similar megafossils supports this view to some extent (Fanning et al., 1988). However, mosaic evolution is not a good explanation why spores appeared in the fossil record earlier than megafossils and remained more diverse than megafossils or the spores found in them at every stratigraphic level. Evidence from paleosols now demonstrates that some land plants lived in well drained soils where the parent plants were not preserved (Retallack, 1985, 1990). Thus the spore record may be a truer reflection of the early diversification of land plants, compared with the more taphonomically biased megafossil record (Gray, 1985).

DISCUSSION

The concepts of polsterland and brakeland involve more than just labels for marginal kinds of modern vegetation and for early land vegetation. These concepts have implications for the ecology, taphonomy and evolution of early land plants.

Polsterlands and brakelands can be envisaged as evolutionary intermediates between microbial earths and rocklands of Precambrian time and shrublands, woodlands and forests of Devonian and younger times. Evidence for the antiquity of different kinds of plant formations comes both from the study of fossil plants and soils, and has been reviewed at length elsewhere (Retallack, 1990). From this perspective (Table 1), well drained soils, as well as other parts of the landscape, were prepared for woody plants by prior herbaceous and microbial communities in a way that mimics the ecological succession of vegetation in disturbed ground (Kimmins, 1987), but on a geological time scale.

This geological phenomenon has been called "quasi-succession" (by Wolfe and Upchurch, 1986), but may better be termed simply "evolutionary succession" (Van Couvering, 1980). In both these ecological and evolutionary successions, the process is initiated by establishment of microbial nutrient procurement systems and then nutrient reserves sufficient to support the growth of large plants. The role of nutrients in evolutionary succession of vegetation on land is also apparent from the later afforestation of nutrient-poor soils, such as Ultisols and Spodosols, compared to nutrient-rich soils, such as Alfisols (Table 1). Why evolutionary succession takes so long is uncertain. Effective arguments have been advanced for the idea that the evolution of early land ecosystems was controlled by environmental inhibition (Chapman, 1985) or by the tempo of co-evolution between microbes, plants and animals (Beerbower, 1985). This debate will become increasingly testable as more is learned from palynological and paleopedological evidence of polsterlands and brakelands.

A critical component of the arguments presented here for polsterlands and brakelands as distinctive vegetation types of the past is that taphonomic processes in well drained soils of the early Paleozoic were qualitatively, if not quantitatively, similar to those of the Tertiary and Quaternary (Retallack, 1984). Organisms left burrows and rhizome traces in highly oxidized calcareous paleosols, yet organic matter was not preserved, presumably due to decay by decomposer microbes. In this respect, Ordovician and Silurian paleosols are no different from Devonian and geologically younger, red, calcareous paleosols with burrows and root traces, but little organic matter (Retallack, 1985, 1986; Allen, 1986; Bown and Kraus, 1987). How far back in geological time this taphonomic regime operated in well drained soils is an open question that depends on how the various lines of evidence for life in Precambrian paleosols are assessed (Retallack, 1990). Nevertheless, this great taphonomic bias limits the usefulness of paleobotanical data for studying ancient polsterlands and brakelands.

Conventional wisdom has it that Silurian and Devonian land plants were confined to seashores, swamps and streamsides by their pteridophytic reproductive system (Knoll et al., 1984; Edwards and Davies, 1990). Because these are just the places where fossil plants are most readily fossilized, this view encourages optimism about the completeness of this supposed record of the "invasion of the land" by plants. An alternative view of Stebbins and Hill (1980), is that land plants evolved from unicellular soil algae, completely independent of multicellular aquatic algae. Testing of these conflicting ideas has just begun using the evidence of paleosols for the antiquity and geographic distribution of Paleozoic microbial earths, polsterlands and brakelands.

The marginal distribution of modern polsterlands and brakelands compared to their likely distribution in the distant geological past, is similar to the restricted habitat of modern versus ancient microbial earths (Wright, 1985), microbial rocklands (Friedman and Weed, 1987) and stromatolites (Awramik, 1971). The case for a wide distribution of microbial earths and rocklands during Precambrian time is only beginning to be assembled (Wright, 1985; Retallack, 1990). The case for stromatolites however has been much discussed. Formerly widespread in many Precambrian nearshore marine, lacustrine (Schopf, 1983) and fluvial environments (Elmore, 1983), they are now restricted to hypersaline or otherwise chemically unusual lagoons or lakes (Walter, 1976), rock varnish of deserts (Perry and Adams, 1976) and crevices in rock outcrops (Reams, 1990). The decline of stromatolites in chemically milder, better watered and nutrient-rich habitats has been attributed to the advent of herbivorous invertebrates, especially snails (Garrett, 1969; Awramik, 1971; Monty, 1973; Stinchcomb, 1975, 1986; Runnegar et al., 1979). Another view is that the preservation of stromatolites has become much less likely because of changes in the composition of sea water since Precambrian time (Grotzinger, 1990). Others again argue that microbial mats were inhibited by the growth of seaweeds (Farmer, 1989). Seaweeds underwent a great evolutionary radiation during the Late Precambrian decline of stromatolites (Walter et al., 1990).

Similar arguments can be made for polsterlands and brakelands of the past. They may have been mercilessly cropped by increasingly diverse herbivores, less favored by declining atmospheric carbon dioxide and less acid rainfall, or outcompeted and shaded out by shrublands and woodlands beginning in the Middle Devonian. These are other questions for which documenting the stratigraphic and geographic distribution of polsterlands and brakelands of the past may be useful.

Many biotic elements of polsterlands, brakelands, microbial rocklands and microbial earths remain as early successional stages to geologically younger and more complex shrublands and woodlands. The various levels of structure in modern vegetation may thus be considered not only as functional components, but as historical artifacts. Terrestrial vegetation appears to have evolved by degrees, and important intermediate steps in its evolution were structurally and energetically distinctive, but currently rare kinds of vegetation, here called polsterlands and brakelands.

ACKNOWLEDGMENTS

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