ORDOVICIAN LIFE ON LAND AND EARLY PALEOZOIC GLOBAL CHANGE

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Dedicated to the memory of Professor Jane Gray (1931-2000): her ideas live on.

MANY PALEONTOLOGISTS share the opinion of McGhee (1996), who wrote "Prior to the Devonian, there was no terrestrial ecosystem to speak of. Some primitive plants precariously establishing a beachhead in protected coastal areas was about it. The interiors of the continents of the planet Earth were as barren as the rocky landscapes of Mars." Thus, it was with trepidation that I reported paleosols containing trace fossils of early land animals in the late Ordovician, Juniata Formation, of Pennsylvania (Retallack and Feakes, 1987; Retallack, 1992a, 1992b, 1993). My late colleague, Jane Gray, engendered considerable debate by reporting Ordovician and Early Silurian spores like those of liverworts (Gray and Boucot, 1977; Gray, 1985). This spore, trace fossil and paleosol evidence for life on land in the Ordovician has remained controversial (Buatois et al., 1998; Shear, 1998), but evidence for Ordovician life on land has continued to accumulate. Especially important was discovery of myriapod trackways from mid-Ordovician (Llandeilian-Caradocian) Borrowdale Volcanics of the Lake District, England (Johnson et al., 1994). Abundant arthropod burrows and tracks, and a single body fossil of an euthycarcinoid in the fluvial-eolian Tumblagooda Sandstone of Western Australia (White 1990; McNamara and Trewin, 1993; Trewin and McNamara, 1995) are now thought to be late Ordovician in age (Iaksy et al., 1998). An enigmatic assemblage of arthropods and plants from a mid-Ordovician paleokarst in Tennessee (Caster and Brooks, 1956) is now thought to have been lacustrine (Gray, 1988a). The fossil record of Ordovician land plants also has improved with the discovery of possible megafossil mosses (Snigirevskaya et al. 1992), and possible late Ordovician trilete spores (Nøhr-Hansen and Koppelhus, 1998; Richardson 1988; Strother, 1991; Strother et al., 1996). But the most abundant evidence for Ordovician life on land remains fossil soils, now exploited by increasingly thorough and sophisticated studies (Retallack, 1985, 1992a, 1992b, 1993; Feakes et al., 1989; Driese and Foreman 1991, 1992a, 1992b; Driese et al., 1992, 1997; Mora et al., 1991, 1996; Mora and Driese, 1993; Yapp and Poths, 1992, 1994, 1996; Yapp, 1993, 1996). Mounting evidence from fossils and paleosols now presents an increasingly detailed view of Ordovician ecosystems on land.

The appearance of megascopic plants and animals on land, replacing preexisting microbial ecosystems, should have had global environmental consequences, particularly on atmospheric composition. Late Ordovician atmospheric CO_2 reached the highest concentration of the entire Phanerozoic, judging from mass balance modelling (Berner, 1994, 1997) and the isotopic composition of pedogenic carbonate (Yapp and Poths, 1992; Retallack, 1993). A rise to peak atmospheric CO_2 of 16-18 PAL (present atmospheric level) from an early Ordovician low is followed by latest Ordovician decline in CO_2 and glaciation in Africa (Brenchley et al., 1994). The rise and fall of this greenhouse is not synchronous with proxies for tectonic or volcanic degassing (Bluth and Kump, 1991; Berner, 1994). Could it have been paced with key events in the evolution of life on land?

ORDOVICIAN LAND PLANTS

The direct fossil record of Ordovician land plants is poor, and their evolutionary origins remain obscure (Stebbins and Hill, 1980; Kenrick and Crane, 1997), but evidence continues to accumulate. Most convincing are abundant and widespread spores as ancient as Middle Cambrian (Gray, 1985, 1988b, 1991; Strother et al., 1996; Skilliter et al., 1998; Strother and Wood, 2000). These are permanent tetrads, often with wrinkled outer envelopes (*Tetrahedraletes grayi* Strother 1991 of Fig. 1), and with morphology and wall ultrastructure most like spores of liverworts (Gray, 1991; Taylor, 1995a, 1995b, 1996). Parent megafossil plants of these distinctive tetrads have been found in early Devonian rocks, where they are narrow, dichotomizing thalli like those of liverworts (Edwards et al., 1995). Carbonized films matching this description have been found in lacustrine shales within depressions of a paleokarst of mid-Ordovician age (Arenigian-Llanvirnian) in Tennessee (Fig. 2). These could also be impressions of algae, as was thought by Caster and Brooks (1956). Also found in the same assemblage was a folded carbonaceous ribbon with marginal fringes, called *Cestites mirabilis* (Fig. 2), and regarded as a comb of a ctenophore. Such a marine organism would have radially arranged combs, not isolated folded ones, and is unlikely in lacustrine shales (Gray, 1988a). *Cestites* is superficially similar to rhizoids and thalli of liverworts, and also deserves further attention.

Spores identified as trilete are found rarely and locally in rocks as old as late Ordovician (Ashgillian: Richardson, 1988; Nøhr-Hansen and Koppelhus, 1988; Strother, et al., 1996). Trilete spores are found in living hornworts, mosses and vascular land plants (Gray, 1985; Kenrick and Crane, 1997). Some of these microfossils show irregular folding, and it could be that what appears to be a trilete mark, is actually a taphonomic artefact of crushing (J. Gray, *pers. comm.* 1999). Crushed echinulate and rugose alete fossil spores from Cretaceous fossil mosses (Konopka et al., 1997, 1998) appear very similar to the microbaculate and microverrucate Ordovician

Besselia (Fig. 1). In addition, moss-like megafossils with cuticles and stomates (*Akdalophyton caradocki*, of Fig. 2) have been found in late Ordovician (Caradocian) shallow marine rocks with brachiopods and trilobites in southern Kazachstan. Although described as a lycopod (Snigirevskaya et al., 1992), the conducting strands of these fossils do not show the helical or annular thickening of vascular land plants (Kenrick and Crane, 1997). Other problematic carbonaceous impressions from the same deposit (*Sarituma tatjanae*) have been regarded as equisetalean (Snigirevskaya et al., 1992), but without additional anatomical details could equally be algae or other non-vascular plants.

Problematic structures cutting across bedding planes, and comparable with roots, holdfasts, stipes or stems also have been found in Ordovician rocks. Especially intriguing are tubular, complexly-ramifying structures of isotopically light ($\delta^{13}C$ of -23.4 to -25.0 percent: Argast, 1992) carbonaceous material at the disconformity on the mid-Ordovician (Caradocian) Gull River Limestone, in upper New York state. These structures show some similarities with Silurian and Devonian
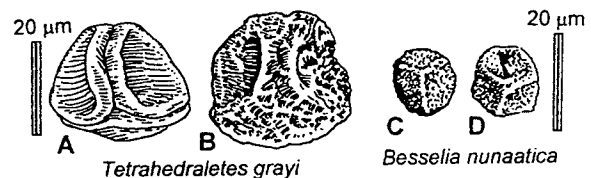

20 μm   20 μm

A   B   C   D

Tetrahedraletes grayi   *Besselia nunaatica*

FIGURE 1.— Spores of early land plants: (A), permanent tetrads without, and with, envelope of *Tetrahedralites grayi*, probably liverwort, of Late Ordovician (Ashgillian, 445 Ma) Elkhorn Formation, Ohio Brush Creek, Ohio (from Gray, 1988b): and (B), trilete spore *Besselia nunaatica*, perhaps from a mosslike plant, from the Late Ordovician (Ashgillian, 445 Ma), Troedsson Cliff Formation, in Bessels Fjord, Greenland (Nøhr-Hansen and Koppelhus, 1988). Scale bars are all 20 mm.
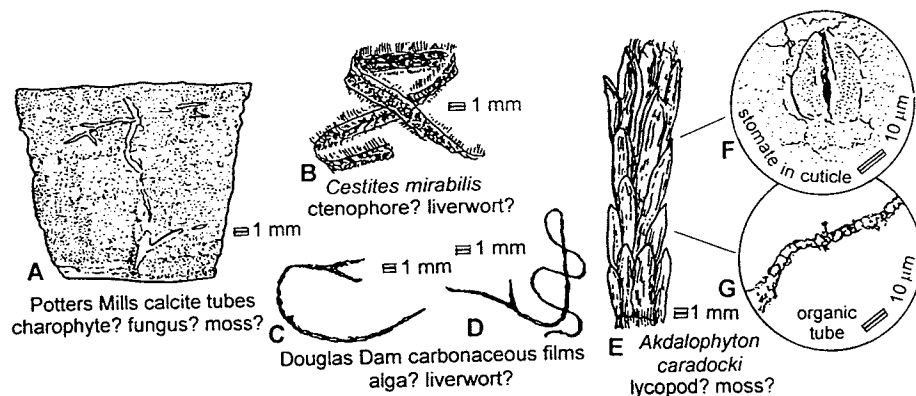
FIGURE 2.— Ordovician non-marine plant megafossils: (A), calcite cast of strata-transgressive filamentous branching structure from Late Ordovician (Ashgillian, 440 Ma) Juniata Formation near Potters Mills, Pennsylvania (Condon Museum, University of Oregon specimen F35150); (B-D), *Cestites mirabilis*, a fringed carbonaceous film, and two un-named dichotomizing, narrow, flexuous carbonaceous films from shales within paleokarst of the Early-Middle Ordovician (Arenigian-Llanvirnian, 476 Ma) unconformity near Douglas Dam, Tennessee (from Caster and Brooks, 1956); (E), *Akdalophyton caradocki*, compression of leafy stem, with enlargements of stomates and conducting tubes, from the Middle Ordovician (Caradocian) Anderkensk Suite of the Chu-Ili Mountains of southern Kazachstan (from Snigirevskaya et al., 1992). Specimens A-D are found in fluvial lacustrine facies and could be aquatic or terrestrial, but E is from marine rocks, and its cuticle and stomates mark it as terrestrial.

nematophytes, variously interpreted as lichens, fungi, or algae (Strother, 1988; Retallack, 1994a). There are also calcite-filled branching threads in red beds of the late Ordovician (Ashgillian) Juniata Formation of Pennsylvania (Fig. 2). These are found in weakly developed red paleosols, cutting across relict bedding, and have whorled monopodial primaries and dichotomously forking laterals, as in dasyclad or charophyte algae, or moss stems and rhizoids. The calcite-hematite mineralization of these casts is not promising for further resolution of their affinities (Retallack, 2000a).

Hyphomycete fungal hyphae appear in the Early Silurian (late Llandoverian: Pratt et al., 1978) and ascomycete spores and hyphae in the Late Silurian (Ludlovian; Sherwood-Pike and Gray, 1985), somewhat earlier than expected from molecular clock evidence of ribosomal 18S RNA (Berbee and Taylor, 1993). By later Early Silurian (late Llandoverian) ornamented trilete spores appear in abundance (Gray, 1985) and tubular microfossils have a lignin-like biochemistry (Niklas, 1982; Robinson, 1990), providing evidence for the rise to dominance of vascular land plants (Kenrick and Crane, 1997; Bateman et al., 1998). Early Silurian (late Llandoverian) megafossils of vascular land plants also have been found in China (Cai et al., 1995, 1996). Another possible Early Silurian land plant in Maine (Schopf et al., 1966) has been supported as a vascular land plant by biochemical studies of Niklas (1982), but Strother and Lenk (1983) consider it a lined burrow of a marine invertebrate. By late Silurian and into the early Devonian, there is at last a secure fossil record of charophytes (Taylor et al., 1992; Feist and Feist, 1997), lichens (Taylor et al., 1997) and liverworts (Edwards et al., 1995), all of which would have been expected much earlier from phylogenetic analyses of living plants (Fig. 3: Kenrick and Crane, 1997; Simon et al., 1993; Qiu et al., 1998).
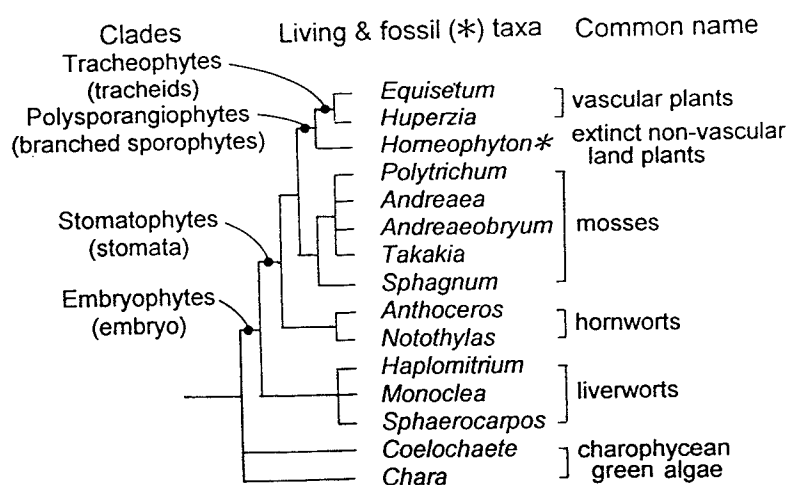
FIGURE 3.—A cladogram for major groups of early land plants using charophyte algae as an outgroup (simplified from Kenrick and Crane, 1997).

ORDOVICIAN LAND ANIMALS

The most ancient records of possible land animals are myriapod trackways (Fig. 4; *Diplichnites*, *Diplopodichnus*) from mid-late Ordovician (Llandeilian-Caradocian) Borrowdale Volcanics of the Lake District, England (Johnson et al., 1994). Some trackways were found in fine grained sandstone immediately atop a reverse-graded sandstone bed, which is unlikely to be subaqueous. Others were preserved in fine-grained parallel-bedded sandstones, which could be shallow lacustrine or fluvial in origin. The varied clarity of overlapping tracks is similar to tracks made in wet sediment as it dried. Associated mud cracks, lava flows, lapilli tuffs, and thick ash-flow tuffs indicate a terrestrial volcanic, lacustrine, and fluvial landscape.

Burrowed paleosols are found through a great thickness of the alluvial Juniata Formation of Pennsylvania (Fig. 4; Retallack, 1985, 1993; Retallack and Feakes, 1987) corresponding to much of the late Ordovician (early to middle Ashgillian: Thompson, 1970a; Dennison, 1976; Dorsch et al., 1994), and perhaps into early Silurian (Llandoverian) if one follows sequence stratigraphic correlations of Diecchio (1995). These unbranched, clay-lined, burrows with clay-silt

backfills correspond to the ichnogenus *Scoyenia* (Frey et al., 1984). Caliche nodules of the paleosols are both truncated by (Fig. 4C), and truncate the burrows (Fig. 4F), indicating that both burrows and nodules formed during soil formation (Retallack and Feakes, 1987). Their pedogenic calcite and dolomite includes isotopically light carbon, indicating soil respiration of photosynthetically produced carbon (Retallack, 1993). Features of these burrows suggestive of millipedes, in general, and polyzoniid millipedes, in particular (Retallack, 2000a), include: (1) striated, clayey wall linings (from consumed soil); (2) ellipsoidal fecal pellets with ferruginized rims (from peritrophic membranes); (3) sinusoidal backfill (from bilaterally symmetrical animal with limbs toward lower edge of body); (4) parasitic modes in size distribution of width (from 11-12 molts); and (5) lack of turnarounds, chambers, or branching (as found in burrows of creatures other than millipedes).

A great diversity of arthropod trackways and burrows (including *Diplichnites*, *Tumblagood-ichnus*, *Heimdallia*, *Protichnites*, *Siskemia*, *Didymauly ponomos* and *Didymaulichnus*) have been reported from the fluvial-eolian Tumblagooda Sandstone of Western Australia (Trewin and
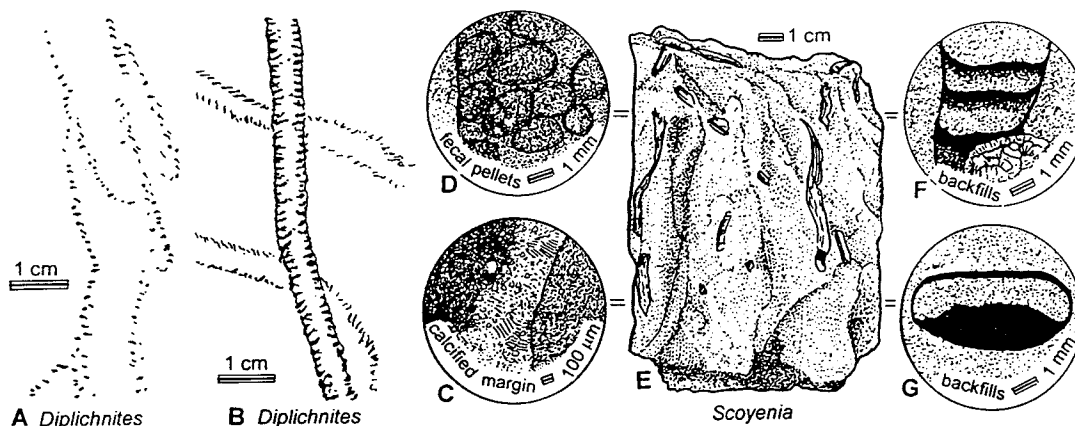
FIGURE 4.—Ordovician trace fossils attributed to non-marine arthropods: (A), *Diplichnites*, track of an arthropod like *Kalbarria* with 11 segments from the Late Ordovician (Ashgillian) Tumblagooda Sandstone of Western Australia (from Trewin and McNamara, 1995); (B), *Diplichnites*, variably impressed tracks of myriapods on a drying surface, from the Late Ordovician (Caradocian), Whorneyside Formation, Borrowdale Volcanics, in Sour Milk Gill, Lake District, England (from Johnson et al., 1994); (C-H), *Scoyenia* burrows from the late Ordovician (Caradocian, 440 Ma) Juniata Formation, near Potters Mills, Pennsylvania (from Retallack, 1993).

McNamara, 1995), now known to be late Ordovician (Caradocian-Ashgillian) in age on the basis of paleomagnetism and conodonts in overlying limestones (Iasky et al., 1998). Also found was a single body fossil of the euthycarcinoid, *Kalbarria brimmellae* (Fig. 5). This large arthropod was probably aquatic, but amphibious behavior may be indicated by trackways of appropriate gauge, with lateral slip indicating a trackmaker with 11 segments (McNamara and Trewin, 1993). There also may be marine-influenced facies of the Tumblagooda Sandstone, with trace fossil assemblages of *Skolithos* and *Diplocraterion*, but no marine body fossils have been found. The mid-late Ordovician (Caradocian), Harding Formation of Colorado contains a low-diversity, marine molluscan and fish fauna. It also preserves an estuarine assemblage of arthropod trace fossils (*Cruziana, Homopodichnus, Kouphichnium, Corpuscu-lichnus, Palaeohelcura, Caridoidichnus*) and a large aglaspid (*Beckwithia gigantea*: Fischer, 1978). Both trace and body fossil diversity of fully marine Ordovician rocks is much higher again.

Non-marine aquatic arthropods also are known from lacustrine shales of depressions in a mid-Ordovician (Arenigian-Llanvirnian) paleokarst in Tennessee (Fig. 5). Both of these aquatic arthropods, *Chasmataspis laurenci* (a xiphosure?) and *Douglasocaris collinsi* (a phyllocarid?) may be distantly related to coeval marine arthropods, but they have many unique features (Caster and Brooks, 1956). Neither form is likely to have been fully terrestrial, but the ventral shield of *Chasmataspis* is like that found in amphibious arthropods (Della Cave and Simonetta, 1991). Fossil burrows also were found (Caster and Brooks, 1956). This is not the most ancient known assemblage of lacustrine animals: the Early Cambrian Paseky Shale of the Czech Republic also contains an enigmatic assemblage of aglaspid-like arthropods and arthropod trace fossils, but nothing plausibly amphibious (Mikulas, 1995; Chlupáč, 1995).

A carbonized impression superficially similar to an earthworm (Oligochaeta) has been found in the marine, late Ordovician (Caradocian), Trenton Limestone, near Quebec, Canada (Morris et al., 1982). No burrows comparable to those of
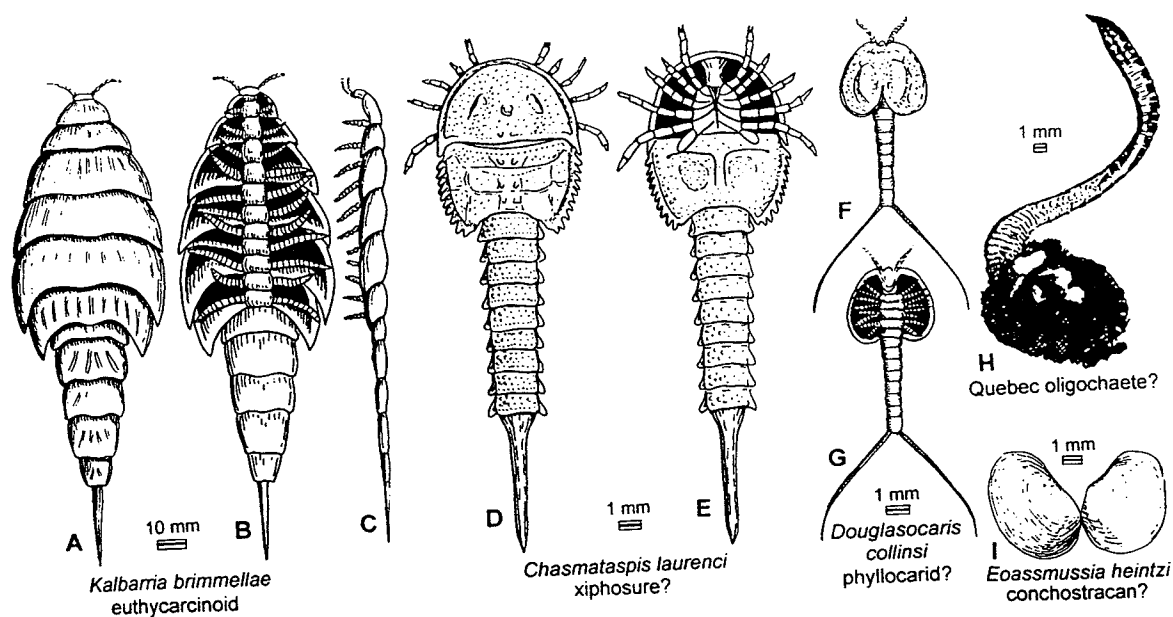
FIGURE 5.— Possible Ordovician non-marine animals: (A-C), dorsal, ventral and lateral reconstructions of the euthycarcinoid *Kalbarria brimmellae*, from the late Ordovician (Ashgillian-Hirnantian, 440 Ma) Tumblagooda Sandstone of the Murchison River, Western Australia (after McNamara and Trewin, 1993); (D-E), dorsal and ventral views of the xiphosure? *Chasmataspis laurenci* and (F-G) dorsal and ventral views of the phyllopod? *Douglasocaris collinsi*, both from shales within paleokarst of the early-mid-Ordovician (Arenigian-Llanvirnian, 476 Ma) unconformity near Douglas Dam, Tennessee (after Delle Cave and Simonetta, 1991); (H), oligochaete-like fossil from late Ordovician (Caradocian) Trenton Limestone, Quebec, Canada (from Morris et al., 1982); (I), conchostracan?, *Eoassmussia heintzi*, from the late Ordovician (Caradocian) *Chasmops* Shale of Slependen, Norway (from Soot-Ryen, 1960). Reconstructions A-C are likely to have been amphibious from associated trackways, D-F are non-marine aquatic animals, and G-H are from marine rocks, but look superficially like an earthworm and conchostracan (respectively).

earthworms have been reported from Ordovician paleosols (Retallack and Feakes, 1987; Trewin and McNamara, 1995), but these may be present in Devonian and Carboniferous paleosols (Morris et al., 1982), and are well known from Triassic and younger paleosols (Retallack, 1976; Bown, 1982). This possible oligochaete is not the only fossil of a group now entirely non-marine found in Paleozoic marine rocks. Cambrian (Robison, 1990; Della Cave and Simonetta, 1991) and Early Silurian (Mikulic et al., 1985) myriapods are found in marine rocks with trilobites (Fig. 6). Marine rocks also have yielded Cambrian onychophorans such as *Aysheaia* and Cambrian-Ordovician conchostracanlike fossils such as *Protocaris* and *Eoasmussia* (Fig. 5; Gray, 1988a; Della Cave and Simonetta, 1991). Such fossils often are regarded as marine by association and, thus, potential evidence for the marine origins of most land creatures. But these fossils are uncommon, and it is difficult to rule out chance introduction from terrestrial or non-marine habitats.

Body fossils of terrestrial millipedes and centipedes first appear in the Late Silurian
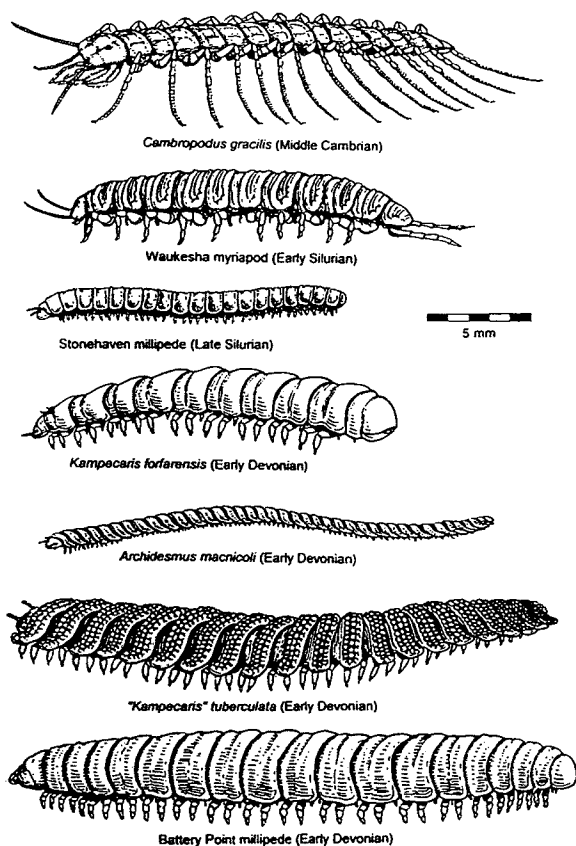
FIGURE 6.—Reconstructions of Early
Paleozoic myriapods, from top to bottom;
Cambropodus gracilis from middle
Cambrian marine rocks of Utah (Robison,
1990; Delle Cave and Simonetta, 1991),
un-named Waukesha myriapod from Early
Silurian marine rocks of Wisconsin (Mikulic
et al., 1985), un-named Stonehaven
millipede from Late Silurian Old Red
Sandstone of Scotland (Almond, 1985),
Kampecaris forfarensis from Early
Devonian lacustrine Old Red Sandstone in
Scotland (Almond, 1985), *Archidesmus
macnicoli* from Early Devonian non-marine
Old Red Sandstone in Scotland (Almond,
1985), *"Kampecaris" tuberculata* from
Early Devonian non-marine Old Red
Sandstone in Scotland (Almond, 1985),
un-named Battery Point millipede from
Early Devonian non-marine Battery Point
Formation, Quebec (Shear et al., 1996).

(Ludlovian: Almond, 1985; Jeram et al., 1990).
By the Devonian, there was an array of millipedes
including flat-backed litter-splitting and round-
backed burrowing forms (Shear, 1998), as well
as extinct freshwater aquatic forms such as the
kampecarids (*Kampecaris forfarensis*, Fig. 6). In
recent phylogenetic analyses, onychophorans
emerge as a sister groups of tardigrades,
tardigrades a sister group of myriapods,
myriapods a sister group of euthycarcinoids, and
euthycarcinoids a sister group of insects (Fig. 7;
Friedrich and Tautz, 1995; Wills et al., 1998;
Eernisse, 1998; Wheeler, 1998). It is encouraging
to find support for these views from the fossil
record of an early Cambrian onychophoran-
tardigrade plexus (Delle Cave and Simonetta,
1991; Ramsköld and Chen, 1998), a Middle
Cambrian myriapod (Robison, 1990), a late
Ordovician euthycarcinoid (McNamara and
Trewin, 1993), and Early Devonian insects (Shear
and Kukalova-Peck, 1990).

ORDOVICIAN PALEOSOLS

Hundreds of Ordovician paleosols are found
in the Juniata Formation at dozens of localities,
but these have been studied in most detail near
Potters Mills, Pennsylvania (Figs. 8-10). Fluvial
deposition of these red beds is indicated by
stringers of intraformational breccia, trough
cross bedding, and shallow scour-and-fill
structures in the thick purple sandstones, which,
in most cases, are tabular for the extent of their
outcrop (Cotter, 1982). Cross-bedded sandstone
locally fills scours some 30-40 cm down into
underlying units (Retallack, 1993). Such
shallow, asymmetric paleochannels are similar
to those of loosely sinuous streams (Cotter
1978). Paleogeographic reconstructions show
that this locality was part of a broad coastal plain,
some 200 km inland from the sea to the west
and 120 km from the Taconic Mountains to the
east (Dennison, 1976).

Paleosols near Potters Mills can be recognized
from their red color (Munsell dark reddish brown
or 2.5YR3/4 to weak red or 2.5YR4/2), clayey
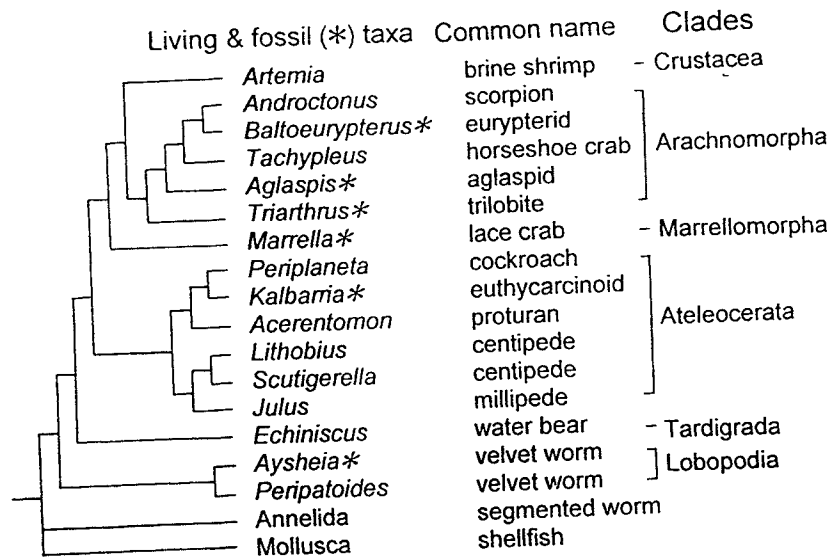texture, sharply truncated tops with alteration down

FIGURE 7.— Phylogenetic analysis of arthropods, edited from a 50% majority rule, consensus tree of recent and fossil taxa (simplified from Wills et al., 1998).

into bedded rocks, hackly appearance, and common small yellow (Munsell reddish yellow or 7.2YR7/6) carbonate nodules (Fig. 9). The hackly appearance is from clods (peds) defined by former cracks in the soil (now closed) and by clay coatings (now slickensided irregular surfaces or argillans of Brewer, 1976).

Laboratory studies (Fig. 10) have confirmed identification of these clayey red bioturbated layers as paleosols (Retallack, 1985, 1993; Feakes and Retallack, 1988). When compared with their parent alluvium in thin section, the paleosols are more clayey and ferruginized with submicroscopic hematite, and have fewer mica grains and rock fragments. There is no trace left of laminated fabric, but in its stead is the random aggregation of clay minerals characteristic of soils (microstructure called skelmosepic by Brewer, 1976). The carbonate nodules, though recrystallized, are replacive, as is usual for pedogenic carbonate (Wieder and Yaalon, 1982). The carbonate is mixed calcite and dolomite, and both minerals have the light isotopic composition of paleosol carbonate (Fig. 10), as opposed to isotopically heavy marine or lacustrine carbonate (Retallack, 1993). The Potters Mills clay

paleosol shows a regular pattern of variation in chemical composition downward toward its parent alluvium, reflecting ferruginization due to oxidation, clay formation by hydrolysis, and chemical leaching (Feakes and Retallack, 1988).

Similar field, chemical, and petrographic evidence has been used elsewhere to recognize a variety of Late Ordovician paleosols: on lateritized paleokarst (Yapp, 1993, 1996; Yapp and Poths, 1992, 1994, 1996), on andesitic flows of volcanic arcs (Boucot et al., 1974; Feakes et al., 1989), and on clayey coastal deltaic and estuarine terraces (Driese and Foreman, 1991, 1992a, 1992b). It remains to be seen how representative these are of Ordovician life and landscapes, because many Ordovician paleosols remain to be studied. Already, however, these paleosols can be interpreted as trace fossils of ecosystems and as indicators of global change.

ORDOVICIAN SOIL NUTRIENTS

The chemical composition of paleosols indicates potentially nutrients, although this must be
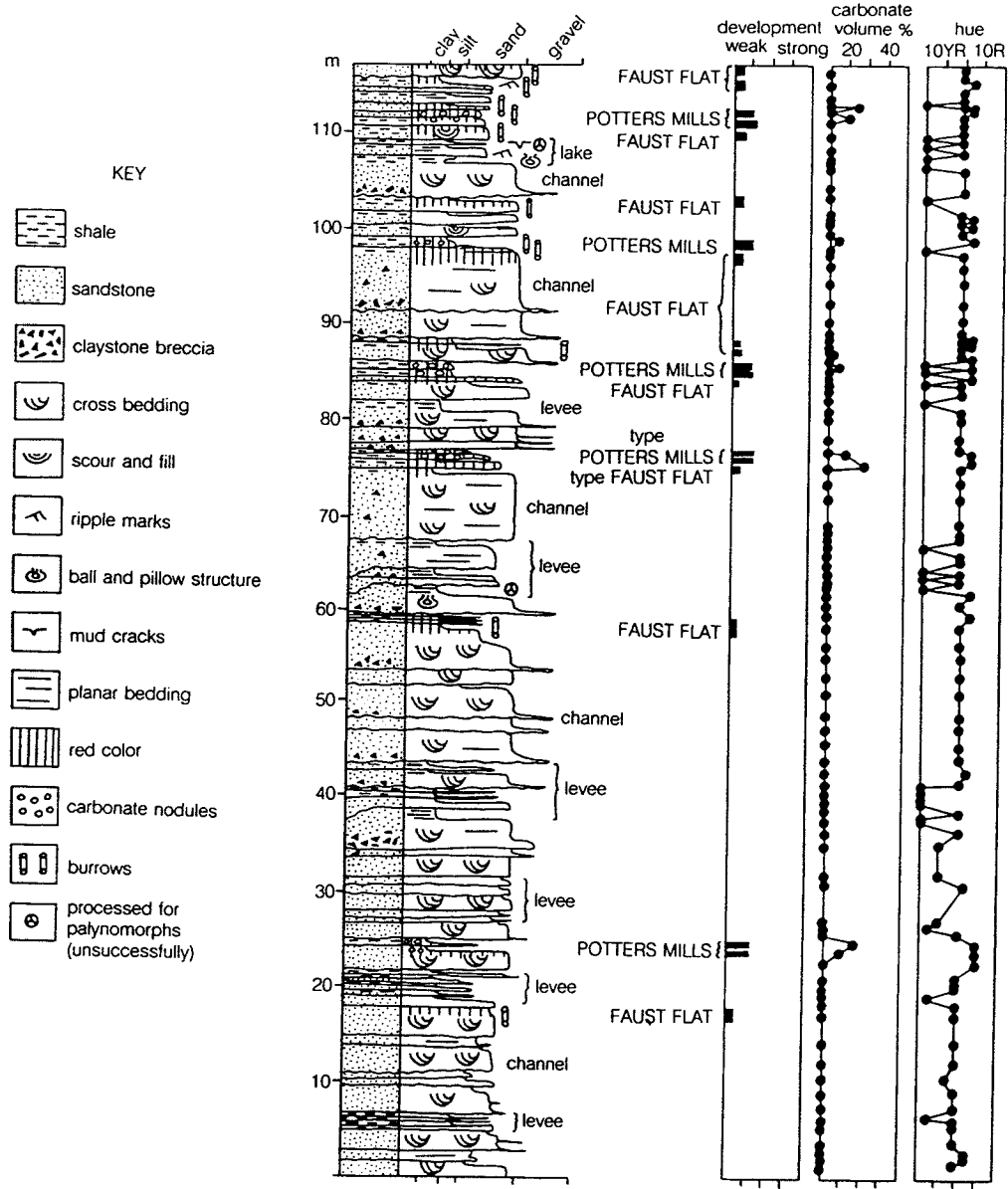
FIGURE 8.—A measured section of Late Ordovician paleosols in the Juniata Formation near Potters Mills, Centre County, Pennsylvania. Paleoenvironmental interpretations of facies and paleosol series are shown, as well as estimates of the degree of development of the paleosols, percent area of carbonate nodules and Munsell hue (following scales of Retallack, 1990).

considering alteration after burial. For example, the degree of alteration of conodonts (CAI 4) in Ordovician limestone of central Pennsylvania indicates burial depths of 4.6-6.6 km and burial temperatures of 160-210°C (Epstein et al., 1977). Comparable estimates come from studies of fluid inclusions, organic matter maturation, clay diagenesis, and stable isotopic studies in nearby New York (Sarwar and Friedman, 1995). This is compatible with the abundance of dioctahedral illite and trioctahedral chlorite in the Juniata Formation (Thompson, 1970b) and the marked
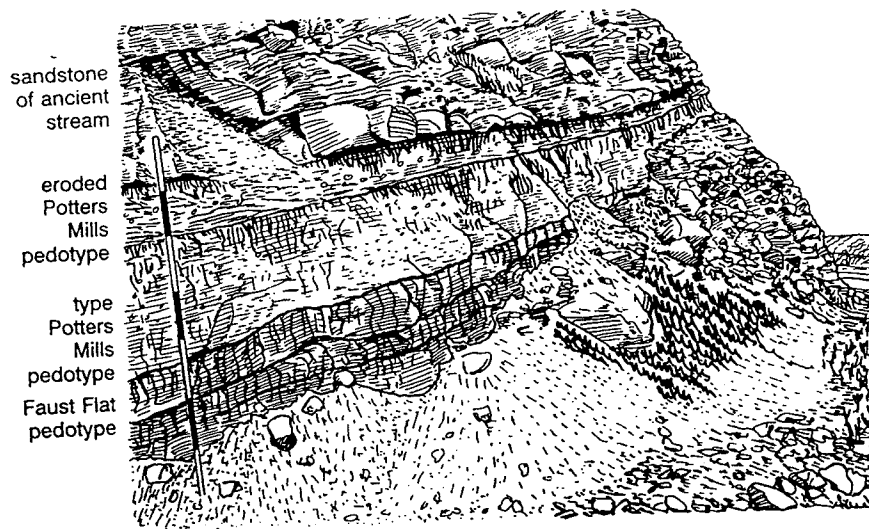
FIGURE 9.—Interpretive sketch of view toward the west of the type Potters Mills clay and Faust Flat silty clay paleosols in road cut exposures during 1982. The top of the Potters Mills clay is at the base of the upper black band on the staff, which is graduated in feet. Photographs of this view have been published elsewhere (Retallack, 1985, 1993).

illitization of the paleosols (Feakes and Retallack, 1988). Potash may have been introduced with orogenic fluids during deep burial, although this common assumption is no longer clear for paleosols (Mora et al., 1998) or sediments (Bloch et al., 1998). Even aside from potassium there was a good supply of other cationic bases (sodium, magnesium and calcium), in Ordovician paleosols of floodplains in Pennsylvania (Feakes and Retallack, 1988), coastal terraces in Tennessee (Driese and Foreman, 1991, 1992a, 1992b) and volcanic terranes of Nova Scotia (Feakes et al., 1989). Only the paleokarst ironstone paleosols of Wisconsin (Fig. 11) are likely to have been low in cationic mineral nutrients (Yapp, 1993).

Nutrient procurement in most Ordovician paleosols was not limited by induration. Ordovician paleosols of floodplains in Pennsylvania were developed in friable floodplain sediments, as indicated by their deeply reaching burrows (Retallack and Feakes, 1987). Similarly, on volcanic terranes in Nova Scotia, the paleosols have surficial erosional scour-and-fill structures as evidence of loose soil (Boucot et al., 1974). In Tennessee, Ordovician paleosols were inundated by the sea and burrowed by *Skolithos*, which lacks the morphology of hard substrate boring traces (Driese and Foreman, 1991, 1992a, 1992b). The upper part of the Wisconsin ironstone paleosols are cemented heavily by hematite, which may have formed an indurated lateritic cuirasse during the later stages of development, prior to cover by Early Silurian dolomites. These indurated soil crusts would have been the most nutritionally problematic of known Ordovician paleosols.

Abundant mineral cations in a loose soil are necessary, but still not sufficient, for large plants and animals. Some kind of microbial nutrient procurement community also is needed to mobilize these elements in forms accessible to large plants and animals (Stevenson, 1986). Such a system is likely to have operated within the floodplain paleosols of Pennsylvania in view of the declining abundance of phosphorus, together with affiliated trace elements (Li, Nb, Sr, and Y), toward the top of the Potters Mills clay paleosol (Fig. 10; Feakes and Retallack, 1988). The burrow-encrusting carbonate with its biogenically-derived light carbon isotopic composition, also could have been microbially-precipitated (Jones and Pemberton, 1987).

WATER BALANCE IN ORDOVICIAN SOILS

Many living Ordovician soils were well drained, although waterlogged profiles also are known, and burrows and other traces of life are common in both. The degree of oxidation, development, and depth of burrowing of paleosols in Pennsylvania are indications that they formed on well drained parts of the landscape (Feakes and Retallack, 1988). Presumably this would have been on an alluvial terrace, perhaps no more than a meter or so above water table. Most of the red Juniata Formation represents a facies comparable to sediments of the north Indian bhabhar, whereas the underlying and interfingering drab-colored Bald Eagle Formation can be compared with dhankar and terai sediments of the Indo-Gangetic lowlands (Retallack, 1991a). In contrast, the Juniata Formation of Tennessee probably was deposited in lowland coastal facies similar to the Rann of Kutch, because Ordovician paleosols in Tennessee were overlain by marine rocks, but even here many of the paleosols are cracked and slickensided like soils that were seasonally dry (Driese and Foreman, 1991, 1992a, 1992b). In Nova Scotia, red, oxidized paleosols formed on columnar jointed lavas, weathered to corestones at the upper end of the columns, and fragments of the paleosols were caught up in the flows (Boucot et al., 1974; Feakes et al., 1989). Not seen were pillowing of lavas in lakes, lava injection or hydrothermal lava spines from reaction with waterlogged soil. Paleokarst lateritic paleosols of Wisconsin also were oxidized pervasively with goethite and hematite, indicating a well drained soil (Yapp, 1993).

Another component of water balance is mean annual rainfall, which can be estimated for the
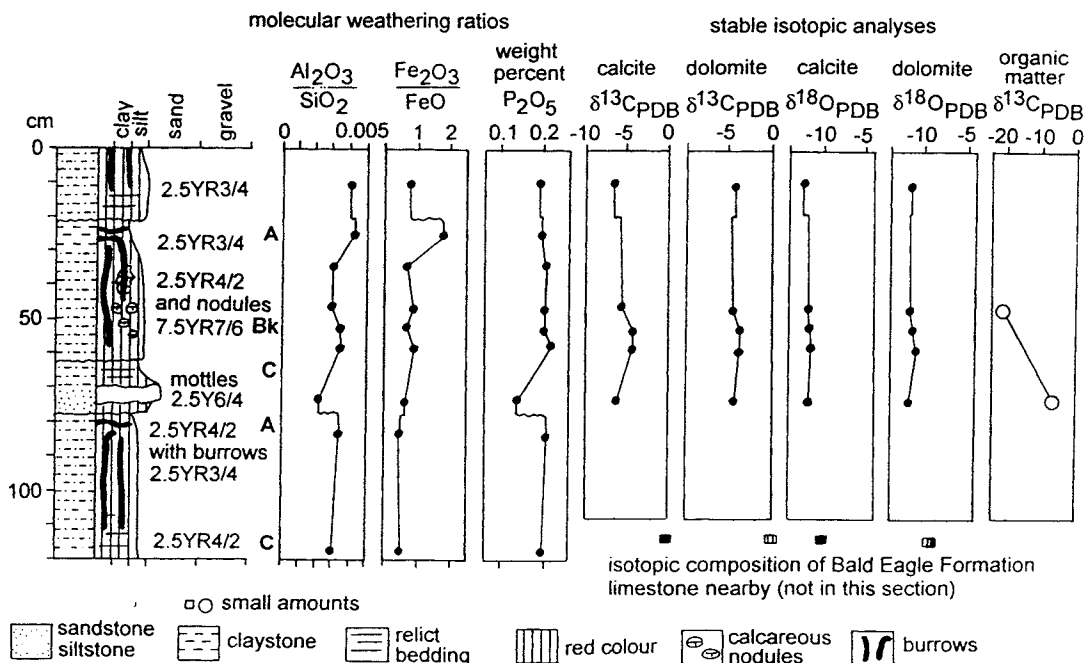

FIGURE 10.—Chemical weathering indices, phosphorus content and stable isotopic composition of the Potters Mills clay paleosol (above) and Faust Flat silty clay paleosol (below) near Potters Mills, Pennsylvania (data from Feakes and Retallack, 1988; Retallack, 1993).
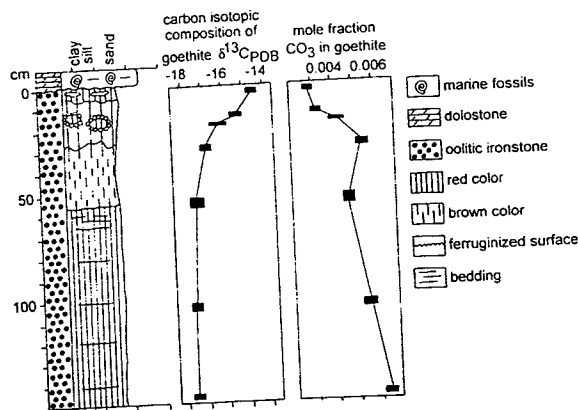
31

FIGURE 11.—Isotopic composition of carbonate and mole fraction carbonate in goethite of a Late Ordovician (Ashgillian) paleosol from the Neda Formation at Iron Knob, Wisconsin, showing surprisingly high soil respiration by adjustment of soil to atmospheric values (from Yapp and Poths, 1994: with field data by Retallack).

paleosols from depth to their calcic horizon, despite recent claims to the contrary from poorly-constrained data (Royer, 1999; Retallack, 2000b). Depth to calcic horizon should not be confused with the depth of leaching of carbonate in paleosols (Quade and Cerling, 1995), which is a function of time for formation of the soil rather than only rainfall (Ruhe, 1969). In a global compilation (Retallack, 1994b), the relationship between depth to calcic horizon (d in -cm) and mean annual precipitation (P in mm) can be fitted with reasonable accuracy (r=0.79 and 1s=141 mm), by the following binomial equation.

$$P = 139.6 - 6.388d - 0.01303d^2$$

Using this equation and a decompaction algorithm (Caudill et al., 1997) appropriate for burial depths of the Potters Mills clay paleosol, with a Bk horizon now at a depth of 19 cm, but originally more like 23-34 cm, results in mean annual rainfall estimates of 280-342 ± 141 mm. There is no indication from molecular weathering ratios for

sodium enrichment that would be expected during salinization found in soils of dry climate (less than 300 mm mean annual rainfall: Retallack, 1985). Thus, a semiarid climate of some 300-500 mm per annum is indicated by the Potters Mills clay paleosol. Comparably dry climate also is indicated by shallow calcareous nodules in Ordovician paleosols of Nova Scotia (Boucot et al., 1974). Although dry, this is not too arid for either mosses or millipedes (Crawford et al., 1987; Bailey and de Mendonca, 1990). Such water stress may have been exacerbated by high temperature and evapotranspiration, considering the low late Ordovician paleolatitude of these paleosols (Zeigler et al., 1979). Monsoonal seasonality in precipitation and a paleotemperature of 23°C was estimated from oxygen isotopic analysis of a late Ordovician lateritic ironstone paleosol in Wisconsin (Yapp, 1993).

Use of the rainfall-calcic transfer function can be compromised by different atmospheric levels of carbon dioxide in the past, by differences in soil respiration, by erosion of the surface of paleosols, and by compaction of the upper clayey part of paleosols during burial. The effects of compaction have been taken into account by using standard formulae (Caudill et al., 1997). The Potters Mills paleosol, with its relatively complete burrow system buried by siltstone rather than a paleochannel sandstone (Retallack and Feakes, 1987), was less obviously eroded than other paleosols in this sequence. One would expect that soil respiration in the Ordovician would be very different than now, but surprisingly, depth functions of isotopic variation in carbonate carbon and in carbonate abundance within goethite of a late Ordovician paleosol in Wisconsin (Fig. 11) implies soil respiration comparable to that of modern deserts and grasslands (Yapp and Poths, 1994). The depth function of isotopic data for the Potters Mills paleosol is not as complete (Fig. 10) as the Wisconsin paleosol (Fig. 11), but comparable as far as it goes. Ordovician atmospheric levels of carbon dioxide are thought to have been much elevated compared to now (Yapp and Poths, 1992; Retallack, 1993, 1997). This would have the effect of acidifying soils and creating carbonate horizons deeper in the soil (McFadden et al., 1991), all other
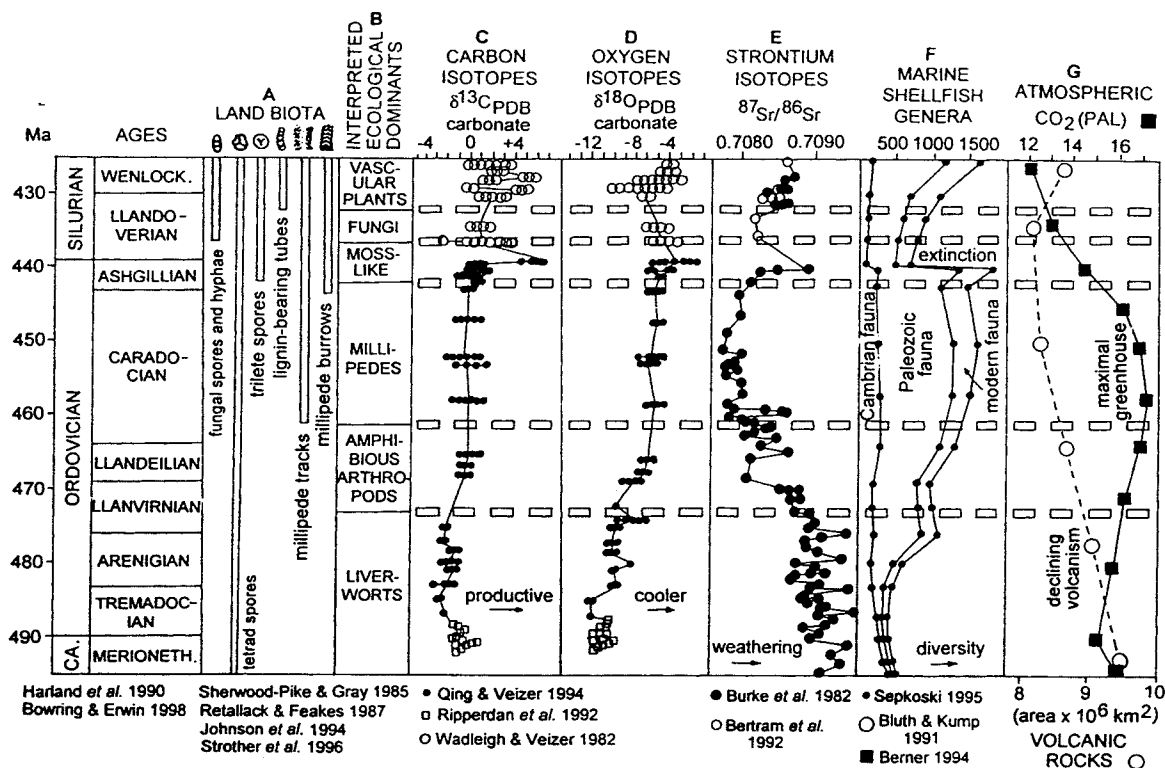
FIGURE 12.—Temporal range of selected terrestrial microfossils and trace fossils, and variation in marine isotopic indicators, faunal diversity and volcanic activity: (A), terrestrial fossil ranges; (B), interpreted ecologically dominant organimsms; (C-D), $d^{13}C$ and $\partial^{18}O$ of brachiopod shells; (E), $^{87}Sr/^{86}Sr$ of marine limestone and phosphate; (F), marine diversity; (G), modelled partial pressure of atmospheric CO_2 and observed area of volcanic rocks. The time scale is from Harland et al. (1990), modified for new data of Bowring and Erwin (1998).

factors being equal, so that the precipitation estimate is an upper limit. Thus, some Ordovician soil communities were tolerant of dry climate.

Seasonality of rainfall is also evident from the diffuse spread through the paleosols from Pennsylvania and Nova Scotia of carbonate nodules that, in some cases, show concretionary growth zones. Both diffuse spread of nodules and internal growth zones in carbonate nodules are characteristic of modern and fossil soils of the monsoonal Indo-Gangetic Plains of India and Pakistan (Retallack 1991a). A strongly seasonal climate also is indicated for Ordovician Appalachia by Vertisol-like paleosols (Driese and Foreman, 1992a, 1992b) and oxygen isotopic composition of the late Ordovician paleosol in Wisconsin (Yapp, 1993).

OXYGEN CONSUMPTION OF LATE ORDOVICIAN SOILS

Soils and their ecosystems consume oxygen in two distinct ways: chemical oxidation of minerals, and respiration by soil animals and microbes. The vivid red color and strong ferruginization of many Late Ordovician paleosols are evidence of an oxidizing atmosphere (Feakes et al., 1989; Feakes and Retallack, 1988). Ferruginized paleosols from Nova Scotia are on andesite flows mafic enough (Holland, 1984: R = 0.12) to require at least 0.04 atmospheres of partial pressure O_2 during the Late Ordovician, or about 0.2 PAL (present atmospheric level). Carbon isotopic composition of goethite in a Late Ordovician

paleosol in Wisconsin led Yapp and Poths (1996, Yapp, 1996) to propose at least 0.1 PAL O_2.

Whereas atmospheric O_2 was probably lower than now, CO_2 was much higher. Carbon isotopic composition of Late Ordovician paleosols in Wisconsin (Yapp and Poths, 1992) and Pennsylvania (Retallack, 1993) are evidence for some 4800-5800 mA (16-19 PAL) of CO_2. Late Ordovician atmospheres interacting with paleosols from Pennsylvania and Wisconsin had a markedly different ratio of O_2/CO_2 (2-14) compared with this ratio today (about 600: Holland, 1984).

The depleted carbon isotopic composition ($\delta^{13}C$) of paleosol carbonates in Pennsylvania and Wisconsin indicates a large component of carbon from soil respiration. Particularly notable are rapid attenuation of carbonate isotopic composition and of the mole fraction of carbonate in goethite near the surface of a late Ordovician paleosol from Wisconsin (Fig. 11). At depth, soil pores are so fine that soil gases become dominated by respired CO_2, but the curve of adjustment from those isotopic values to atmospheric values reflects respired CO_2 output (Keller and Wood, 1993). Similar depth functions of isotopic composition are found in desert and grassland soils, and imply suprisingly high soil respiration rates for this late Ordovician paleosol (Yapp and Poths, 1994). Thus, Ordovician soils supported healthy populations of animals or heterotrophic microbes, and probably were impressive O_2 consumers.

CARBON DIOXIDE CONSUMPTION OF LATE ORDOVICIAN SOILS

Soils consume CO_2 in carbonic acid that weathers silicate minerals, as well as CO_2 used biologically by photosynthesis and chemosynthesis to produce organic matter. Hydrolytic weathering of silicate minerals consumes carbonic acid (H_2CO_3) and exports bicarbonate (HCO_3^-) to oceans or lakes for deposition in amounts that can affect atmospheric composition (Berner, 1994). This acid (or proton) consumption is roughly equivalent in moles to carbon consumption by chemical weathering. Thus, acid consumption of paleosols is a proxy of carbon consumption by weathering,

and can be computed from the distribution within paleosols of major oxides of base cations using a variety of formulae given by Retallack (1996a). The total acid consumption of the Late Ordovician Potters Mills clay paleosol was 428 keq.ha^{-1} (data of Feakes and Retallack, 1988). Using the same algorithms, the Late Silurian North Milton paleosol consumed 163 keq.ha^{-1}, which is probably low for Silurian paleosols because of marine diagenesis of that profile (as documented by Driese et al., 1992, whose data was used for this analysis). In contrast, the Middle Devonian Rosemary paleosol, the oldest known forested paleosol, consumed 1271 keq.ha^{-1} (Retallack, 1997). Acid consumptions of 10^3-10^4 keq.ha^{-1} are normal for moderately developed Cretaceous, Tertiary, and modern soils (Retallack, 1996a). Hence, acid and carbon consumption in Late Ordovician paleosols was modest compared with that of Devonian to modern soils.

Yet another possible carbon dioxide sink are nodules of carbonates, such as dolomite and calcite in Late Ordovician paleosols. The similar isotopic composition of pedogenic dolomite and calcite from late Ordovician paleosols in Pennsylvania may be taken as evidence for dolomitization during soil formation (Fig. 10). But even with both minerals as a carbon sink, the nodules in these paleosols are small and scattered (less than 30% by volume), and only 5 paleosols from a local sequence of 19 profiles have any significant carbonate content (Fig. 8). Other known Ordovician paleosols are mainly non-calcareous (Feakes et al., 1989; Driese and Foreman, 1991, 1992a, 1992b; Yapp, 1993). I know of no late Ordovician paleosols with large and abundant carbonate nodules like those in paleosols of Devonian and younger age (Retallack, 1991a, 1992a; Driese and Mora, 1993). Pedogenic carbonate does not appear to have been a large carbon sink in the Ordovician, and is probably not important to modern atmospheric carbon content either (Berner, 1994).

Another sink for CO_2 is organic matter, but there is very little organic carbon in known Ordovician paleosols (Retallack, 1993; Yapp, 1993), even considering order-of-magnitude losses expected on burial of well-drained paleosols

(Retallack, 1991b). Former soil humus can be indicated by gray-green discoloration of the upper part of a paleosol due to burial gleization. Late Ordovician paleosols in Wisconsin (Retallack and P. M. Sheehan, personal observations), Pennsylvania (Retallack, 1985), and Nova Scotia (Boucot et al., 1974) have small and scattered spots of burial gleization. Extensive burial gleization of Late Ordovician paleosols in Tennessee has been attributed to marine hydromorphism (Driese and Foreman, 1991, 1992a, 1992b). Thus, Ordovician soils were a meager carbon reservoir and a poor source of organic-rich sediment that could bury organic carbon away from the atmosphere.

Isotopically-light carbon in both organic matter and carbonate in Ordovician paleosols (Retallack, 1993; Yapp and Poths, 1992, 1994), as well as in paleosols of the Silurian and subsequent periods (Mora et al., 1991), is evidence for substantial isotopic fractionation of carbon by photosynthesis. The degree of fractionation between organic matter and coexisting carbonate in early Paleozoic paleosols indicates dominantly soil-derived CO_2 in soil gases (Mora et al., 1991, 1996; Retallack, 1993). Nevertheless, primary production was limited by small size, clumped distribution, and shallow rooting depth of hypothesized microbial crusts, liverworts, and mosses (Boucot et al., 1974; Feakes and Retallack, 1988). In summary, Ordovician paleosols were unimpressive carbon sinks in terms of weathering, carbonate accumulation, humification, and primary productivity.

ORDOVICIAN ECOSYSTEM PERSISTENCE

Ordovician paleosols also differ from modern soils in their duration of formation, and this would have consequences for the environmental influence of their ecosystems. In the qualitative scale of Retallack (1990), the Potters Mills clay paleosol of Pennsylvania is weakly developed, but the Faust Flat clay is very weakly developed. Faust Flat profiles probably represent less than 100 years or so of soil formation. The calcic horizon of the Potters Mills clay is differentiated only to a modest extent (Stage I of Gile et al., 1966, and of Wieder and Yaalon, 1982). Development of nodules and clay skins in the Potters Mills clay paleosol is comparable to that seen in surface soils of the Indo-Gangetic Plains after about 400 to 4500 years (Ahmad et al., 1977; Courty and Féderoff, 1985). This order of magnitude of time is represented by this degree of soil formation in many parts of the world (Birkeland, 1990).

The short time for paleosol formation, and their separation by great thicknesses of fluvial sandstone, are indications of rapid accumulation of this sequence, compared with other thick submontane alluvial fan sequences, such as the Late Silurian Bloomsburg Formation of Pennsylvania, the Late Devonian Catskill magnafacies of upper New York state, and the Siwalik Group of Pakistan (Retallack, 1990). Using an estimated soil development time of 100 years for Faust Flat and 4000 years for Potters Mills profiles, the measured sequence (Fig. 8) accumulated at a rate of 249 cm/Ka, which is appreciably faster than 34-71 cm/Ka estimated in a similar fashion from paleosols in the Miocene Siwalik Group of Pakistan (Retallack, 1991a). The increased dominance and development of paleosols in comparable molasse sequences through geological time, like long-term changes toward meandering rather than braided streams (Cotter, 1978), may reflect the evolution of a firmer grip on the landscape by increasingly bulky and complex terrestrial ecosystems.

Comparable studies of development have not yet been attempted on paleosols from Tennessee (Driese and Foreman, 1991, 1992a, 1992b), Nova Scotia (Boucot et al. 1974; Feakes et al., 1989) or Wisconsin (Yapp, 1993; Yapp and Poths, 1992, 1994, 1996). The Wisconsin profile appears strongly developed and has a complex cementation history, and may represent a long time (perhaps 10^5-10^6 years) of soil formation. Nevertheless, this kind of paleosol does not appear to have been common among known Ordovician paleosols. There are now large areas of moderately to strongly developed forest and grassland soils in alluvial basins that did not exist in the Ordovician, when weakly developed soils were more widespread. Such a different global scale distribution of Ordovician soils that were only modest carbon

sinks would have had consequences for both paleoclimate and life on land.

ORDOVICIAN LIVERWORT-MILLIPEDE POLSTERLANDS

Diplichnites tracks and *Scoyenia* burrows are only the most obvious remains of a formerly widespread late Ordovician ecosystem of alluvial and volcanic landscapes in semi-arid, seasonally dry tropical regions. These distinctive trace fossils can be attributed to millipedes (Retallack and Feakes, 1987; Johnson et al., 1994). Furthermore, an isotopic depth-function of high soil respiration indicates large populations of animals and heterotrophic microbes in late Ordovician paleosols (Retallack, 1993; Yapp and Poths, 1994). Such high soil respiration and implied high secondary productivity also calls into question the long held idea that early Paleozoic millipedes were entirely detritivorous (Shear, 1998). Millipedes today consume large amounts of both fresh and rotting mosses (Bailey and de Mendonca, 1990), rejecting only vascularized woody tissues (Crawford et al., 1987). High soil respiration of Ordovician soils probably also meant that millipedes were supported by a variety of other organisms not preserved. Erosional scour and fill structures in paleosols from Nova Scotia are evidence of clumps of low growing vegetation offering local resistance to erosion (Boucot et al., 1974). I have proposed the term polsterland for such sparse clumped vegetation of non-vascular land plants (Retallack, 1992b). Chemical traces of plants and humification in these paleosols are meager (Feakes and Retallack, 1988), and include isotopically light carbon in organic matter and carbonate of the paleosols (Retallack 1993; Yapp and Poths, 1994). Liverworts, or comparable plants, were a likely part of this community, judging from the wide distribution of their spores in Ordovician and older rocks (Gray 1985, 1991; Strother et al., 1996; Skilliter et al., 1998; Strother and Wood, 2000). These liverwort-millipede polsterlands of the Ordovician represent a distinct phase in the evolution of early land communities (Eoembryopytic of Gray, 1993; early Anatomical Phase of Bateman et al., 1998),

following lichen-microbial earths of the Cambrian-Precambrian (Retallack, 1992b, 1994a; Retallack and Mindszenty, 1994), and later supplanted by tracheophyte-spider brakelands of the Silurian-Devonian (Retallack, 1992a, 1992b; Eotracheophytic of Gray, 1993; late Anatomical Phase of Bateman et al., 1998). As in many semi-arid tropical ecosystems today (Ahn, 1970; Jones and Wild, 1975), animals and respiring microbes of Ordovician polsterlands dominated their plant resources to keep the soil clean of organic matter. Ordovician communities were distinct in their high oxygen consumption relative to low carbon consumption and primary production.

This new view of Ordovician terrestrial ecosystems indicates that life on land was more widespread than marsh vegetation of waterlogged marine and lake margins, and also more ecologically versatile than simply pioneering vegetation of disturbed sedimentary environments (Bateman et al., 1998). Ordovician polsterlands occupied a variety of well drained habitats including some presenting hardship, such as nutrient-poor lateritic ironstones and climatically arid regions. Indeed, as pioneering and as tolerant plants, those of the Ordovician may have been as effective as many plants still living (Gray, 1985; Edwards and Selden, 1993). What Ordovician terrestrial communities lacked was competitive ability: for example, shade and humus production by plants, and predator size and ferocity. Even here, however, the introduction of vertically oriented mosses in a world of microbial crusts and liverworts, and occasional terrestrial excursions of large arthropods, represent initiation of coevolution toward the bulky and complex communities that followed in the Silurian and thereafter.

HYPOTHESIS LINKING ORDOVICIAN LIFE ON LAND AND GLOBAL CHANGE

Inflections in time series of a variety of global change indicators (Fig. 12) coincide with a six phase schedule of early Paleozoic evolutionary innovation: (1) Middle Cambrian advent of liverworts, (2) early-mid-Ordovician (Llanvirnian)

excursions of amphibious arthropods (horseshoe crabs and euthycarcinoids), (3) late-mid-Ordovician (Llandeilian) addition of millipedes, (4) late Ordovician (Ashgillian) appearance of mosses and other early land plants (stomatophyte clade of Kenrick and Crane, 1997), (5) Early Silurian (late Llandoverian) appearance of higher fungi (Hyphomycetes and Ascomycetes), and (6) later Early Silurian (late Llandoverian) rise to dominance of vascular plants. A plausible hypothesis for global changes at these evolutionary events is that innovations in primary productivity (liverworts, stomatophytes, vascular land plants) can have widespread consequences: (1) initiate deeper weathering of soils; (2) consume atmospheric CO_2 by weathering, by biomass building, and by redeposition of organic-rich soil; (3) cool global climate by mitigating greenhouse gases; (4) fertilize the ocean with nutrients; and (5) drive up isotopic values of $\delta^{13}C$, $\delta^{18}O$ and $^{87}Sr/^{86}Sr$ in marine rocks and fossils (Schwartzman and Volk, 1989; Retallack, 1996b; Martin, 1996). Conversely, innovations in secondary productivity on land (amphibious arthropods, millipedes, fungi) that promote carbon oxidation, reverse these trends and usher in greenhouse conditions.

Alternative hypotheses include control of global climate by changes in continental configuration, mountain uplift, or volcanic activity. Time series data on these aspects of Ordovician environments are difficult to obtain, but those available (Bluth and Kump, 1991; Berner, 1994; Kump et al., 1995; Sheehan et al., 1996), do not track well isotopic and biotic indications of Ordovician global change (Fig. 12).

The degree of weathering and primary production of Ordovician paleosols was modest compared with forested ecosystems of the Middle Devonian and later (Retallack, 1992a, 1992b, 1993, 1997), but was a considerable advance over microbial earths of the Precambrian (Retallack and Mindszenty, 1994). Already in the early Ordovician, effective chemical weathering is indicated by relatively high values of $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ in marine carbonate. Both isotopic values increased substantially to an Early Ordovician high from a low in the Middle Cambrian (*Glossopleura*

zone; Ripperdan et al., 1992; Montañez et al., 2000). The organisms on land responsible for this high level of weathering may have included liverwortlike plants, represented by spore tetrads as ancient as Middle Cambrian (Skilliter et al., 1998; Strother and Wood, 2000). Such effective weathering is critical to the release of nutrients such as phosphorus and bicarbonate into the ocean (Schwartzman and Volk, 1989). Oceanic fertilization from the land may be an explanation for observed dramatic late Cambrian to early Ordovician diversification of phytoplankton (Tappan and Loeblich, 1973), and of fleshy, shelled invertebrates (Jablonski et al., 1983; Bambach, 1993; Sepkoski, 1995; Martin 1996), and increased depths of burrowing into the sea floor and heights of filter-feeding above the sea floor (Bottjer et al., 1996).

The advent of likely amphibious horseshoe crabs and other arthropods in the mid-Ordovician (Arenigian-Llanvirnian: Caster and Brooks, 1956; Gray, 1988a) coincides with inflexions in several global change geochemical indicators (Fig. 12). Slightly increased global primary productivity may be indicated by very slightly rising values of $\delta^{18}O$ in marine carbonate, and $\delta^{13}C$ in marine carbonate and organic matter (Qing and Veizer, 1994). However, less overall chemical weathering is indicated by a decline in $^{87}Sr/^{86}Sr$ of marine carbonate (Burke et al., 1982). Large amphibious arthropods were presumably only part of a largely microscopic fauna that cropped terrestrial vegetation, limiting its productivity and role in soil formation.

Late Ordovician (Caradocian) advent of millipedes predated the peak of atmospheric CO_2 greenhouse, as modelled from sedimentary mass balance (Berner, 1994) and confirmed from isotopic composition of paleosols (Mora et al., 1991, 1996; Retallack, 1993, 1997). While isotopic values of $\delta^{18}O$ and $\delta^{13}C$ reached a plateau at this time, $^{87}Sr/^{86}Sr$ values plummeted to low values, reflecting declining terrestrial weathering (Burke et al., 1982). Millipede and other animal consumption of plants on land could explain both the atmospheric greenhouse and declining chemical weathering.

During the latest Ordovician (Ashgillian), mosses and other early land plants began to displace liverworts. Marine isotopic systems were perturbed strongly, with peaks in $\delta^{18}O$ and $\delta^{13}C$, and pronounced elevation of $^{87}Sr/^{86}Sr$ (Wang et al., 1993; Brenchley et al., 1994). The latest Ordovician (Hirnantian) also was a time of mass extinction, especially of deep water trilobites, graptolites and conodonts, concomitant with glaciation (not bolide impact of Overbeck et al., 1993) in Saharan Africa and global marine regression (Brenchley et al., 1994; Sheehan et al., 1996; Finney et al., 1999). Although atmospheric CO_2 was on its way down, CO_2 partial pressures were remarkably high for a time of glaciation (Berner, 1994). This modelling problem is not alleviated by a computed 4.5% reduction in solar luminosity during the Late Ordovician (Gibbs et al., 1997). Moss-like early land plants, with their deeper rhizoids and vertical growth, could have created more organic soil which, when eroded and deposited, provided the substantial carbon sink needed (Kump et al., 1995) to explain severe perturbation of marine carbon isotopic composition (Wang et al., 1993; Brenchley et al., 1994). Marine productivity and carbon sequestration also would have been stimulated by increased supply of nutrients from weathering on land (Martin, 1996).

Appearance of fungal hyphae in the Early Silurian (Llandoverian: Pratt et al., 1978; Sherwood-Pike and Gray, 1985) coincided with cessation of glaciation and recovery from marine excursions of $\delta^{13}C$, $\delta^{18}O$, and $^{87}Sr/^{86}Sr$. Enhanced consumption of plant material could have resulted in a minor resurgence of greenhouse conditions.

The rise to abundance of vascular land plants in the Early to Late Silurian (late Llandoverian and thereafter; Cai et al., 1995, 1996) coincides in time with globally rising values of $\delta^{18}O$ in marine carbonate, $\delta^{13}C$ in marine carbonate and organic matter, and $^{87}Sr/^{86}Sr$ of marine carbonate (Wadleigh and Veizer, 1982; Bertram et al., 1992). During the Early Silurian, atmospheric CO_2 partial pressure began its long fall to a late Devonian-early Permian low (Berner, 1994; Mora et al., 1996; Retallack, 1997). This long-term trend has been attributed widely to the role of increasingly bulky land plants and more thoroughly weathered soils as atmospheric CO_2 sinks (Berner, 1994, 1997; Algeo et al., 1995; Retallack, 1997).

Although compatible with a variety of evidence, this hypothesis of biotic control of atmospheric composition and temperature during the Ordovician is clearly in need of further detailed testing. Cambrian and early Ordovician soil ecosystems remain a mystery. Ordovician paleosols are the most abundant underexploited source of evidence in the short term, but more aggressive fossil hunting unhindered by negative expectations could lead to great discoveries.

ACKNOWLEDGMENTS

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