Trace Fossil Evidence for Late Ordovician Animals on Land

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Fossil burrows within newly recognized buried soils in the Late Ordovician Juniata Formation, near Potters Mills in central Pennsylvania, represent the oldest reported nonmarine trace fossils. They are thought to have been an original part of the soil because their greater density toward the top of the paleosols corresponds with mineralogical, microstructural, and chemical changes attributed to ancient weathering and because about half the burrows are encrusted with nodular carbonate, interpreted as caliche. Associated fossil caliche, the size distribution of the burrows, and their W-shaped backfills are evidence that the burrows may have been excavated by bilaterally symmetrical organisms that grew in well-defined growth increments and were able to withstand desiccation. Among well-known soil organisms, millipedes are burrowing animals that satisfy these requirements, but have a fossil record not quite this old. This trace fossil evidence for animals on land, together with recent palynological evidence for land plants of a bryophytic grade of evolution during Late Ordovician time, are indications of terrestrial ecosystems of slightly greater antiquity and complexity than hitherto suspected.

UNDERSTANDING OF EARLY COMmunities on land has been based on the sparse fossil record of spores (1), plants (2), and arthropods (3). These kinds of fossils are preserved in reducing, waterlogged environments, either at or near where the organisms lived (4). Trace fossils, on the other hand, provide evidence of life activities in place within well-drained soil environments, where other kinds of fossils are not preserved.

Numerous (5) fossil soils (paleosols) containing abundant nonmarine trace fossils were recently recognized within the Late Ordovician (6) Juniata Formation (7) near Potters Mills, Center County, Pennsylvania. Trace fossils have been known from this sequence for some time, but because these are coastal plain deposits it had been thought that the trace fossils were indicators of estuarine or marine incursions (8). This may be the case for other trace fossils in the Juniata Formation, but not for fossil traces from red beds east of Potters Mills, for the following reasons. On paleogeographic maps for latest Ordovician time (9), Potters Mills was some 260 km east of the sea. The upper Juniata Formation here consists of

numerous channel-like sandstones, with basal scours, and trough and planar crossbedding. These sandstones form the bases of sequences fining upward, characteristic of deposition by rivers (8, 10). No marine, lagoonal, or lacustrine fossils have yet been found in these rocks (8, 11).

More convincing evidence comes from features indicating that the strata containing the trace fossils were soils. The trace fossils are most dense at the surface and truncated at the top of the paleosols. Their increased density upward parallels the development of characteristic soil structure (12, 13) and microfabric (12, 14), the abundance of clay in the profile, the degree of degradation of mica and feldspar grains, and changing chemical composition attributed to ancient weathering (12). Some of the paleosols contain numerous small dolomitic nodules that form a subsurface horizon (12, 13). These nodules ensheath about half (15) the burrows in moderately developed paleosols, but are not present around less abundant burrows in weakly developed paleosols or in burrowless associated lacustrine facies. Comparable caliche takes hundreds to thousands of years to form in modern soils (16). These are indications that the burrows were a permanent feature of the soil rather than inherited from preexisting parent material or added after soil formation had ceased.

The paleosols and their enclosing sediments can be interpreted to reconstruct the paleoenvironmental setting of the trace fossils. Judging from the depth of the caliche horizon (17), rainfall was within the semiarid to arid range, and perhaps seasonal. The strong ferruginization of the paleosols is compatible with a warm, tropical to subtropical climate (18), although an origin of this red color by diagenetic dehydration of ferric oxyhydrate minerals cannot be ruled out (19). However, paleomagnetism (20) and marine fauna (21) of Late Ordovician rocks of this part of North America are compatible with tropical to subtropical latitudes. The paleosols formed on quartz-rich alluvial outwash of the Taconic Mountains to the east (9, 12). Within the paleosols there are no gley minerals that are suggestive of high water table, but one paleosol had what could be interpreted as a ground water calcrete a short distance (50 cm in compacted paleosol) from the top (12) and just beyond reach of the deepest fossil burrows. These generally well-drained alluvial plains included two recognizable kinds of soils (22). Clayey paleosols with caliche nodules and abundant burrows represent slightly elevated parts of the floodplain that were
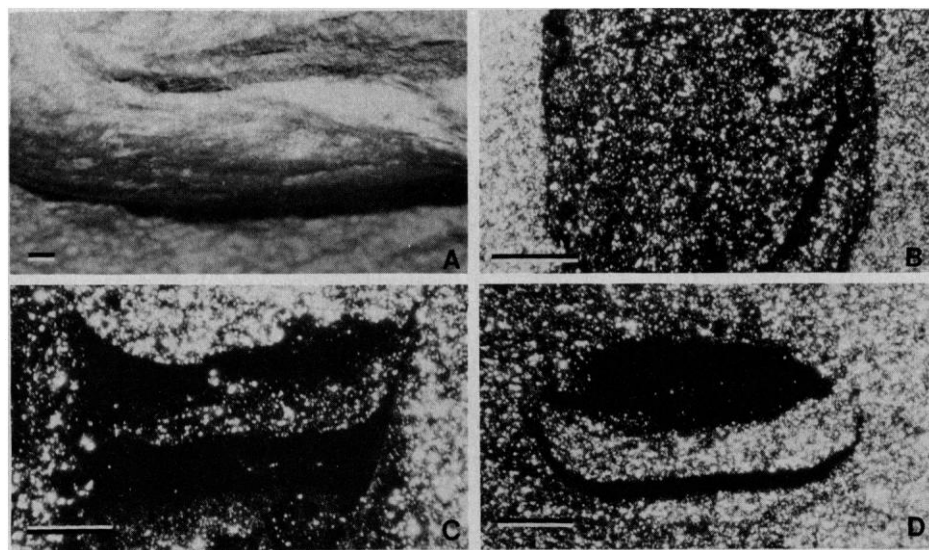

Fig. 1. Fossil burrows from Late Ordovician paleosols near Potters Mills, Pennsylvania. (**A**) In hand specimen, cracked open in bas-relief, showing surface striations and a hint of bilateral symmetry around a deep longitudinal groove. (**B**) Petrographic thin section of a burrow under crossed nicols showing ellipsoidal masses (defined by black clay skins), interpreted as fecal pellets. (**C**) Petrographic thin section under crossed nicols along axis of burrow showing W-shaped backfill structures. (**D**) Petrographic thin section under crossed nicols transverse to long axis of burrow showing bilaterally symmetrical backfill structure. (A) is from A horizon and (C) and (D) are from Bk horizon of moderately developed paleosol; (B) is from A horizon of weakly developed paleosol. Scale bars, 1 mm.

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stable for at least a few thousand years. Sandy paleosols with abundant relict bedding and burrows, but no caliche nodules, represent terraces or other streamside land surfaces which were less well drained and younger than the clayey paleosols.

Fossil burrows in the paleosols are roughly tubular and range in diameter from 2 to 21 mm. They are most obvious when filled with materials that contrast with the soil matrix, such as red clayey material from the upper parts of the paleosol which fell into sandy, lower parts of the paleosol. The filling material of the burrows is, however, quite variable. In cases where the materials inside and outside the burrow are similar, burrows can still be distinguished by a thin zone of ferruginized clay, which is strongly grooved and smeared (slickensided) by compaction of the surrounding soil (Fig. 1A). Many of the burrows are made more obvious by encrusting caliche, which is usually just outside the red clay rim of the burrow. Ferruginized ovoid masses resembling fecal pellets fill some burrows (Fig. 1B). Some burrows have alternating silty and clayey layers, transverse to the long axis of the burrow, forming a local W-shaped backfill (Fig. 1C). This backfill structure is also bilaterally symmetrical in cross sections of the burrows (Fig. 1D).

In order to gain an appreciation of the three-dimensional distribution of the burrows, large blocks of matrix containing burrows were cut into parallel slabs at approximately 1-cm intervals, and the distribution of burrows in the slabs was plotted (Fig. 2). There is some variation in the thickness of the burrows along their length. In the surface horizons of moderately developed paleosols, horizontal and vertical segments of the burrows are interconnected. In subsurface horizons of weakly developed paleosols there are more vertical burrows than horizontal burrows (23).

Further information on the nature and diversity of the burrowing organisms can be gleaned from the variation in size of the burrows. Diameters of numerous burrow segments from a moderately developed paleosol and from a weakly developed paleosol were measured with vernier calipers accurate to 0.1 mm (Fig. 3). The maximum diameter was measured normal to the long axis of

burrows cracked open in the field, so that they were exposed in bas-relief. These data for both paleosols, plotted at intervals of 0.5 mm or finer, show numerous modes in addition to broader peaks. Such parasitic modes are common in size distributions of arthropod fossils (24), in which they are interpreted as growth increments. The number of burrowing species is not revealed by these minor modes, but perhaps by the overall shape of the distributions. When plotted at 1-mm increments to smooth out the parasitic modes, the distribution of burrow diameters in the moderately developed paleosol is skewed but unimodal. The distribution of burrow diameters in the weakly developed paleosol, however, is irregular and has a greater total range than in the other paleosol (25). These differences could reflect a greater diversity of megascopic burrowing organisms or greater fluctuation in environmental conditions in early successional, nearstream communities, compared to communities of more stable interfluves.

The fossil record of early land animals large enough to make these burrows is sparse. Fossil annelid worms superficially similar to earthworms have been found in shallow marine rocks as old as Middle Ordovician (26) and fossil velvet worms (Onychophora) in marine rocks of Middle Cambrian age (27). Neither group of soft-bodied organisms is likely to have made the fossil burrows in Late Ordovician paleosols of the Juniata Formation because some of these were (at least seasonally) very dry soils (28). Furthermore, the W-shaped backfill structures and fully inflated outline of the burrows are unlike those made by earthworms (29). Similar objections can be raised against these being burrows of velvet worms, which today may hide in soil cracks but do not burrow (30). The backfill and striations of the burrows, together with the numerous parasitic modes of burrow diameter and caliche in the paleosol, are more compatible with an arthropod burrower, which was bilaterally symmetrical, had marked growth increments, and was resistant to desiccation. Eurypterids and aglaspids were in existence by Ordovician time, and horseshoe crabs (Xiphosurida) by Silurian, and have been found in nearshore marine and lagoonal sediments (3, 31, 32). Despite arguments that some Silurian eurypterids were amphibious (33) and that some Pennsylvanian horseshoe crabs ventured high into the tree canopy (34), these organisms are unlikely to have been permanent residents of dry soils, nor were they likely to have been especially active burrowers. The oldest spiders and centipedes are Devonian in age (3). Today these carnivores either exploit existing cracks in the soil or make simple burrows (35)
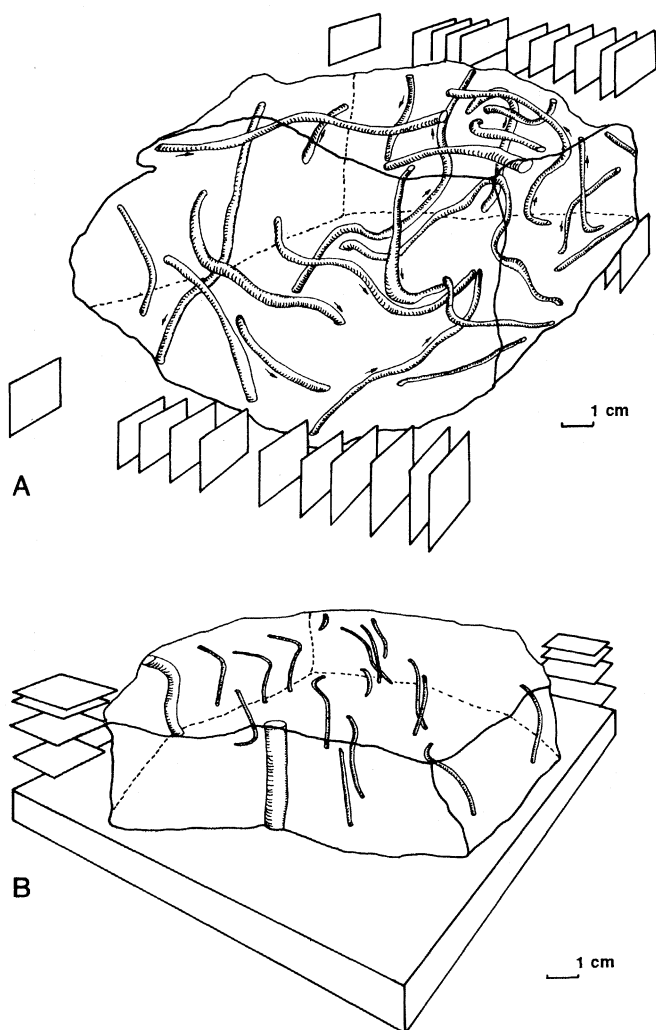

Fig. 2. Three-dimensional arrangement of burrows within paleosols reconstructed from large rock specimens, slabbed along planes indicated, of (**A**) upper horizon of moderately developed paleosol and (**B**) lower horizon of weakly developed paleosol.
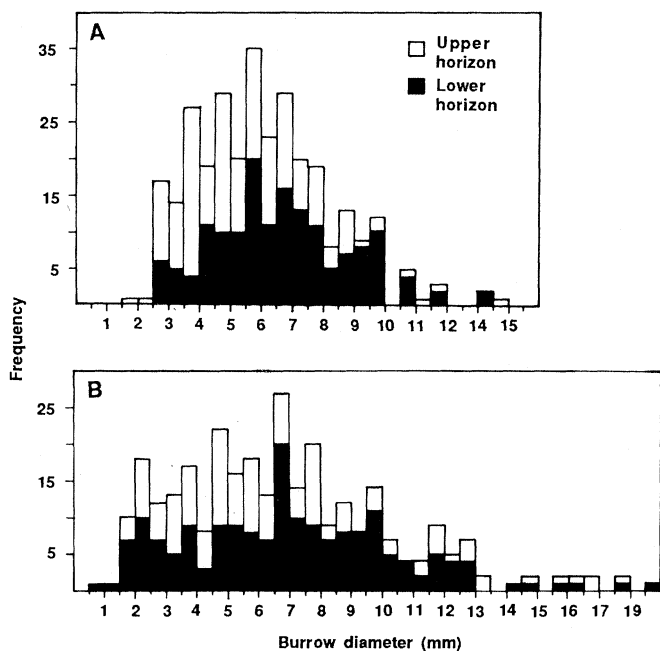
unlike the fossils. Scorpions have been thought to be among the earliest of land animals and now excavate simple shallow burrows (35). Careful reexamination of Silurian to Pennsylvanian scorpions, however, has shown that they were probably aquatic (3). Millipedes first appear in marine rocks of Early Silurian age (36, 37), and some millipedes now are active burrowers (38). Although they appear in the fossil record slightly later than the trace fossils under consideration, these are the most likely of known fossil or modern animals to have excavated them. There remains a possibility that the burrows were made by organisms completely extinct and unknown, or by organisms which by virtue of their functional morphology and modern behavior seem to us to be inadequate burrowers.

The existence of sizable burrowing organisms, such as millipedes, on dry land during Late Ordovician time also implies the existence of some kind of terrestrial fodder at this early time. This is unlikely to have been large plants with roots, because there are no structures in these paleosols that could be construed as rhizome or root traces. The burrowers conceivably could have fed on soil algae, now thought to have been widespread well back into Precambrian time (39). However, spores of land plants in permanent tetrahedral clusters have recently been reported from rocks as old as Late Ordovician (40). The interpretation of these spores has been controversial. They are like those of some modern liverworts and mosses and appear to represent extinct early land plants of a comparable grade of evolution (1). Such low-growing, leafy vegetation could have supported large populations of

burrowing arthropod herbivores and detritivores, as well as a variety of litter organisms. These trace fossils in paleosols are additional evidence for Late Ordovician terrestrial ecosystems of rather greater complexity and biomass than has hitherto been suspected.

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6. The Juniata Formation is latest Ordovician in age; Ashgillian in the British scale or Richmondian in the North American one [R. J. Ross, *Publ. Int. Union Geol. Sci.* **12** (1982)].
7. The outcrops under consideration, 4.2 km east of Potters Mills, have been mapped in the uppermost Juniata Formation by D. M. Hoskins [in *Atlas of Preliminary Geologic Quadrangle Maps of Pennsylvania*, T. M. Berg and C. M. Dodge, Eds. (Geologic Survey of Pennsylvania, Harrisburg, 1981), p. 533].
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13. These are platy peds of Soil Survey Staff [*Handbk. U.S. Dep. Agric.* **436** (1975)].
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